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GLOBAL CHANGE AND WHITEBARK PINE: RESTORATION, REFUGIA, AND ALPINE TREELINES

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GLOBAL CHANGE AND WHITEBARK PINE: RESTORATION, REFUGIA, AND ALPINE TREELINES

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Global change and whitebark pine: restoration, refugia, and alpine treelines

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Abstract:

Whitebark pine is a major component of subalpine forests in western North America. The species occupies harsh high-mountain sites up to treeline, where it is often the dominant species. The species is ecologically important but is also a valuable species for studying the dynamics of alpine treelines. However, whitebark pine has experienced significant mortality in recent decades from mountain pine beetle outbreaks and white pine blister rust. This kind of rapid environmental change presents significant challenges to our understanding and management of the dynamics of ecological communities. On one hand, the effects of climate change on forest ecosystems could provide unique opportunities to study how species, populations, communities, and ecosystems respond to large-scale disturbance. On the other, prediction of future ecosystem behaviors and associated management decisions are complicated by a current lack of understanding of long-term dynamics. Managers are responding to indirect effects of climate change by expanding restoration activities into previously unmanaged, and often poorly understood, forest ecosystems. In this dissertation I investigated three aspects of whitebark pine ecology and conservation: 1) the ecological responses of whitebark pine stands to restoration treatment, 2) the potential of treeline habitats as refugia from mountain pine beetle attack, 3) and the climate-related processes that control growth form at treeline.

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Introduction

In this dissertation I investigated three aspects of whitebark pine ecology and conservation: 1) the ecological responses of whitebark pine forests to restoration treatment, 2) the potential of treeline habitats as refugia from mountain pine beetle outbreaks, 3) and the climate-related processes that control the krummholz growth form above alpine treelines.

Rapid environmental change presents significant challenges to our understanding and management of the dynamics of ecological communities. On one hand, the effects of climate change on forest ecosystems could provide unique opportunities to study how species, populations, communities, and ecosystems respond to large-scale disturbance. On the other, prediction of future ecosystem behaviors and associated management decisions are complicated by a current lack of understanding of long-term dynamics. Managers are responding to indirect effects of climate change by expanding restoration activities into previously unmanaged, and often poorly understood, forest ecosystems.

Whitebark pine is a major component of subalpine forests in western North America. The species occupies harsh high-mountain sites up to treeline, where it is often the dominant species (Arno and Hoff 1989). Some authors consider the species to be foundational to subalpine ecosystems (e.g., Ellison et al. 2005) due to its role facilitating the establishment of other conifers (Callaway 1998, Tomback et al. 2014) and use of its seeds by numerous animal species, including the endangered grizzly bear (*Ursos arctos horriblis*; Kendall and Arno 1990). It was once thought to be a member of the *Pinus* subsection *Cembrae*, the stone pines, whose chief unifying characteristic are large, wingless seeds housed in indehiscent cones (Lanner 1990). However, phylogenetic studies have revealed that this taxonomic grouping in not monophyletic – in fact the closest relative of whitebark pine is the giant-coned sugar pine (*Pinus lambertiana*) (Gernandt et al. 2005). Still, the “stone pines” share an ecological kinship; birds in the genus *Nucifraga*, the nutcrackers, are dispersal agents of all these pines. Nutcrackers are scatter-hoarders, each making 32,000-98,000 small caches (< 15 seeds) in a single season (Hutchins and Lanner 1982a, Tomback 1982). Dispersal by the Clark’s nutcracker (*Nucifraga columbiana*) has important implications for the recruitment dynamics of whitebark pine. Many nutcracker caches are not in locations favorable for germination (i.e., in tree branches), although the birds do make a proportion of caches below ground (Hutchins and Lanner 1982a, Tomback 1982, Lorenz et al.

2011). The unrecovered, below-ground caches are in improved positions to germinate relative to wind-dispersed seeds that land on the ground surface. Thus, granted unrecovered caches are present in sufficient quantity, whitebark has the potential to establish on bare or recently disturbed sites before wind-dispersed species establish. However, the majority of cache site locations are associated with some sort of cover (Tomback 1982, Lorenz et al. 2011), On productive sites, whitebark pine is thought to be maintained by this dispersal ability following fire, where over time the species is hypothesized to be displaced by its more shade tolerant associates (Arno and Hoff 1989), although there is little empirical support for this stand trajectory (e.g., Campbell and Antos 2003). Whitebark pine can form nearly monotypic stands throughout its range, though it often initiates mixed-species forest islands on open sites through facilitation (Franklin and Dyrness 1973, Callaway 1998, Tomback et al. 2014).

Whitebark pine has a range that is more extensive than that of any other North American five-needle white pine (Tomback and Achuff 2010). As a result, it exists in a wide range of ecological contexts, with varying disturbance regimes and community dynamics (Larson and Kipfmueller 2012). There are conflicting perspectives in the literature on the successional role of whitebark pine. Whitebark pine has most often been termed a pioneer species in the literature, because it can regenerate in abundance after fire (Arno 1986). Succession models based on this role predict that whitebark pine will be replaced by more shade tolerant species in the absence of fire (Keane et al. 1990, Keane 2001). However, stand reconstructions using dendrochronological methods have found considerable variation in successional pathways in whitebark pine (Campbell and Antos 2003, Larson et al. 2009). In their study stands, Campbell and Antos (2003) report that successional replacement only occurs after 500 years or more. The authors further make distinctions between the ecology of lodgepole pine (*Pinus contorta*), a shade-intolerant, fast-growing species clearly adapted to frequent and severe disturbance, and the ecology of whitebark pine. By contrast, whitebark pine can establish at all seral stages and can release after 150 years or more of suppression in the understory, in addition to establishment after fire (Campbell and Antos 2003).

The exotic fungal pathogen, *Cronartium ribicola* (the cause of white pine blister rust), and climate-change-driven outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have caused drastic whitebark declines in recent decades, generating concern for the future of the species and subalpine ecosystems. Both mountain pine beetle and blister rust could make whitebark pine populations more vulnerable to fire disturbance, through different mechanisms and on different scales. Predators are known to increase the likelihood that disturbance will cause prey population extinction (Schoener et al. 2001). Mountain pine beetle tends to kill the largest trees in a stand, increasing the population percentage of smaller, more fire-susceptible trees while also increasing fuel loads. Conversely, stands with partial mortality are effectively thinned by beetles, which may ultimately increase resilience to fire. Partial mortality by beetles may also be an important natural selection process leaving the trees most adapted to future climates (Millar et al. 2007b, 2012, Six et al. 2018). Blister rust affects individuals of all ages and sizes; the distribution and impact of blister rust on whitebark pine varies by region. The disease often kills the top branches of trees first, effectively eliminating the trees' reproductive contributions (Maloney et al. 2012). This affects whitebark pine populations across a landscape. Diminishing cone crops reduces the efficacy of Clark's nutcrackers as a dispersal agent (more caches are recovered when seeds are sparse), thereby reducing the ability of whitebark pine to colonize newly disturbed sites. Both mountain pine beetle and blister rust have impacted whitebark pine though a majority of the species' range. Fire, once a force that maintained the species on more productive sites, may now put many whitebark pine populations at risk of extinction. Climate conditions in the Greater Yellowstone Ecosystem are projected to support a much higher frequency of large and severe fires by the mid-21st century (Westerling et al. 2011). Based on our knowledge of these combined factors, many whitebark pine populations will clearly be challenged with climate change.

In response to whitebark decline, ecologists and managers are advocating and implementing extensive conservation and restoration activities in an attempt to mitigate further mortality in the short-term and to aid future population recovery. We lack perspective, however, in the long-term responses of whitebark pine to mountain pine beetle-caused mortality throughout the variety of habitats that contain whitebark pine. Treeline environments, the marginal upper-elevation habitats where stunted whitebark are often the dominant species, may play an important role in whitebark pine populations. The treeline habitat is a potential refuge from mountain pine beetle (Logan et al. 2010, Macfarlane et al. 2013). If the long-lived individuals at treeline can evade beetles and reproduce, they may be an important source of seed for otherwise dwindling whitebark pine populations. Furthermore, treeline whitebark may change in growth form with climate change. Low lying krummholz may grow to form new forests with even greater reproductive capacity.

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Chapter 1: Ecological effects and effectiveness of silvicultural restoration treatments in whitebark pine forests

Abstract

Silvicultural thinning treatments to restore whitebark pine (*Pinus albicaulis*) are widely used in subalpine forests throughout the western United States (US) and Canada. The objectives of these treatments are to (1) improve the condition of whitebark pine at all ages, (2) to improve seedling recruitment processes, and (3) mitigate the damage caused by mountain pine beetle (MPB; *Dendroctonus ponderosae*) and white pine blister rust (WPBR; caused by the fungus *Cronartium ribicola*). However, there is some disagreement about the ecological basis of restoration and a paucity of information on the effects these activities – few treatments have been monitored to assess their success. I investigated the ecological effects of silvicultural restoration treatments in whitebark pine forests and evaluated their success by retrospectively sampling five treatment sites in the western US 6-10 years after implementation. I found strong evidence of growth release at a site previously characterized by closed-canopy stands. Growth responses in more open, park-like stands, however, were variable: I found weak growth increases at one site, weak growth decreases at another and no response at two other sites. At the site with strong growth increases, trees with previous damage from WPBR infection had growth increases similar to uninfected trees. I found low rates of whitebark pine seedling recruitment overall, and no increase in whitebark pine recruitment associated with treatments at any site. However, at one site, treated stands had higher regeneration of non-target species than did untreated stands. Post-treatment mortality (mostly from the late 2000s MPB outbreak) was significantly lower in the treated stand at the closed-canopy site; at the other sites, there was no difference in mortality between treated and untreated stands. The treatments had little detectable effect on short-term

growth-climate relationships, although my analyses revealed that whitebark pine growth at my sites was more temperature limited than water limited. While some management goals were achieved, many were not, and there were some unintended consequences. My results call for a closer examination of the ecological basis of silvicultural restoration treatments in whitebark pine and an expanded use of adaptive management.

1. Introduction

Whitebark pine (*Pinus albicaulis*) is a major component of upper subalpine forests in western North America. The species occupies high-mountain sites up to the alpine treeline, where it is often the dominant species (Arno and Hoff 1989). Some consider the species to be foundational to subalpine ecosystems (e.g., Ellison et al., 2005) due to its role facilitating the establishment of other conifers (Callaway 1998, Tomback et al. 2014) and use of its seeds by numerous animal species, including the endangered grizzly bear (*Ursos arctos horriblis*; Kendall and Arno 1990). The Clark's Nutcracker (*Nucifraga columbiana*) acts as the primary dispersal agent for whitebark pine by making thousands of seed caches in a season, a portion of which are buried 1-2 cm in the ground (Hutchins and Lanner 1982b, Tomback 1982). Germination of unclaimed ground caches is the primary mechanism of whitebark pine establishment (Tomback 2001). Much of the ecology of whitebark pine remains unknown, however – intensive study only began in the 1980s, unlike other western conifers of commercial value.

Whitebark pine populations are declining in many parts of the species' range, presenting major conservation concerns for these subalpine forest ecosystems. A warming climate has caused whitebark pine declines from MPB outbreaks (*Dendroctonus ponderosae*; Logan and Powell 2001, Macfarlane et al. 2013). The invasive fungal pathogen *Cronartium ribicola* (the cause of WPBR) has also caused high mortality in some areas, as well as potential decreases in fecundity where whitebark pine survives (Arno and Hoff 1989, Keane and Arno 1993, Shepherd et al. 2018). A century of fire exclusion has also been proposed as a contributor to whitebark pine decline by allowing shifts in forest composition to species that may have historically been removed by fire (Arno 1986, Keane and Arno 1993, Keane 2001, Kendall and Keane 2001). These rapid declines have led to the species' listing as Endangered under the Canadian Species at Risk Act (COSEWIC 2010), its consideration for listing under the U.S. Endangered Species Act (NRDC 2008), and inspired extensive interest in the restoration of whitebark pine forests (Keane et al. 2012). The most common restoration activities are planting of blister rust-resistant seedlings, prescribed fire treatments, and silvicultural thinning, intended to promote survival of whitebark pines and to encourage regeneration (Keane et al., 2017a; Keane et al., 2012). However, research over the last 15 years has added both nuance to and uncertainty about the ecological basis of some restoration activities, suggesting that the outcomes of restoration are also uncertain. Furthermore, there is only one study reporting the effectiveness of silvicultural restoration treatments in whitebark pine forests (Keane and Parsons 2010). My objective was to assess the ecological effects and success of silvicultural restoration treatments in whitebark pine forests to provide information needed to improve these activities.

The goals of silviculture in restoration of forest ecosystems are quite different than production-oriented silviculture, although aspects of both approaches employ the same underlying biological mechanisms and tactics. Foresters have traditionally used silvicultural thinning to modify stand development processes to promote greater growth and economic value of target tree species and individuals (O'Hara 1988, Nyland 1996). Improved growth from reduced competition may also improve survival rates of residual trees; long-term declines in radial growth – possibly due to increasing competition – often precedes mortality in conifers (Cailleret et al. 2016). Silvicultural restoration is used in southwestern US ponderosa pine (*Pinus* *ponderosa*) forests as a fire surrogate and in some cases can be an effective strategy to restore historical structure and decrease tree mortality from wildfire (Covington et al. 1997, Fulé et al. 2001). The structure and composition of many forest types in western North America have been affected by altered management regimes – a century of fire exclusion has allowed species compositional and structural changes in forests with historical frequent low- or mixed-severity fire regimes (Keeling et al. 2006, Abella et al. 2007, Barth et al. 2015). Silviculture is chosen for restoration treatments because it allows direct manipulation of stand composition and structure.

Scientists have long suspected that fire exclusion has allowed species composition changes in 'seral' whitebark pine stands, where whitebark pine is assumed to be replaced over time by subalpine fir (*Abies lasiocarpa*; Arno, 1986; Keane, 2001). However, empirical studies in the last two decades have found that frequent fire has lesser impact on subalpine fir and that species composition changes in whitebark pine forests take place over longer time periods than once thought. Species composition change in subalpine forests proceeds over centuries and may never lead to complete replacement of whitebark pine (Campbell and Antos 2003, Larson and Kipfmueller 2012) and fire regimes in many whitebark pine communities are still within their historical intervals (Larson 2009, Larson et al. 2009). Larson et al. (2009) also found that frequent low-severity fires didn't reduce subalpine fir abundance, and that subalpine fir began establishing before fire exclusion began. These findings suggest that current abundances of subalpine fir may not represent a fire exclusion-induced change in species composition for these types of whitebark pine communities, in contrast with simulation modelling of developmental changes in whitebark pine stands (Keane et al., 1990; Keane et al., 2017). Furthermore, 'seral' whitebark pine communities are not represented throughout the range of whitebark pine, and subalpine fir is absent from some regions (Larson and Kipfmueller 2012). The ideas of compositional change in whitebark pine stands from fire exclusion stem from deterministic concepts of forest successional change, a framework that may limit understanding of the complexities of vegetation change (Binkley et al. 2015).

Although there is little evidence for successional replacement of whitebark pine (Amberson et al., *in press*), there is evidence that thinning subalpine fir and other tree species can increase rates of radial growth in whitebark pine of all sizes (Keane et al. 2007, Retzlaff et al. 2018). Reducing competition for individual trees may have additional benefits in promoting the growth and survival of dwindling whitebark pine populations. Trees that are not limited by competition may have increased cone production (González-Ochoa et al. 2004). Faster-growing whitebark pines are expected to exhibit greater resistance to disease and insect attack and removing species like subalpine fir and lodgepole pine should decrease the risk of whitebark pine mortality from crown fires (Keane et al. 2012). Furthermore, it is unknown if trees that have damage from WPBR exhibit growth response to treatment.

Restoration in whitebark pine forests is not necessarily designed to reverse potential replacement of whitebark pine. However, many of the common goals of these treatments – for example, reducing competition, reducing mortality, promoting regeneration, and promoting resistance and resilience to disease and disturbance – are thought to increase growth and survival of otherwise threatened whitebark pines. On one hand, thinning treatments have long been employed to reduce stand risk to bark beetle attacks by reducing host density and to decrease competitive effects on residual trees, which may in turn enhance tree defense (Amman et al. 1988). On the other, there is some evidence that thinning may increase incidence of WPBR over time by promoting *Ribes*, an alternate host for *Cronartium ribicola* (Hungerford et al. 1982, Maloney et al. 2008). Moreover, thinning without branch pruning increases incidence and severity of blister rust cankers in western white pine (*Pinus monticola*; Schwandt et al. 1994). MPB attack rates could also increase due to damage to remnant trees (Waring and Six 2005, Maloney et al. 2008). But, Hood et al., (2016) found that MPB-caused mortality in ponderosa pine was greatly reduced by the removal of Douglas-fir (*Pseudotsuga menziesii*). Aniballi et al. (2015) and Sturdevant et al., (2015) reported that thinning around and pruning individual whitebark pines decreased attack and mortality from MPB.

Whether restoration treatments enhance whitebark pine recruitment is also unclear. Whitebark pine seeds can potentially reach recently disturbed sites before other tree species via long-distance dispersal by Clark's nutcrackers and may establish in abundance after fire because open areas created by burns offer relatively competition-free environments (Tomback et al. 1993, Perkins 2015). However, the importance of natural open areas and those created by silvicultural treatments for regeneration is still unclear. Research to date has shown limited recruitment in response to thinning and burning, though nutcrackers are active in treated areas (Keane and Parsons 2010). In natural stands, Amberson et al. (*in press)* found higher rates of recruitment in microsites with vegetative cover than in open areas, potentially due to facilitative effects (shading) by vegetation in general or by specific plants (Perkins et al. 2015). Lorenz et al. (2011) also found that nutcrackers make more ground caches in microsites with vegetative cover, rather than in burns. Successful dispersal and establishment of whitebark pine is further limited by the condition of local mature whitebark pines that are the seed source, many of which have been killed or damaged by MPB or WPBR (Leirfallom et al. 2015).

Climate-growth relationships have not been explicitly considered in restoration plans for whitebark pine to date but are an important consideration for the management of the species in a changing climate. Growth-climate relationships have been observed to shift over decadal time scales in a number of conifer species, including whitebark pine. Youngblut and Luckman (2013) observed a reduction in whitebark pine growth after the 1950s despite a strong positive correlation with summer temperature. They attributed this decline to increases in summer cloud cover, WPBR-caused mortality, and increased potential for moisture stress. Decreasing the potential for negative effects on forests due to climate change is an important goal of silvicultural intervention in western forests (Millar et al. 2007a).

Given the current threats to whitebark pine forests and the paucity of data on restoration effects (Keane and Parsons 2010), there is a clear need for increased information about the ecological effects and effectiveness of silvicultural treatments to restore whitebark pine. My objective was to assess the short-term ecological impacts of silvicultural treatments to restore whitebark pine at five study sites in the northern Rocky Mountains and Inland Northwest, USA. Specifically, I asked whether treatments: 1) released whitebark pine trees from competition – measured as an increase in radial growth – and whether such response was limited by WPBR damage, 2) increased recruitment rates in whitebark pine or in other conifer species, 3) decreased mortality rates of mature whitebark pine trees, and 4) decreased the strength of growth-climate relationships in whitebark pine trees. I also asked whether treatments achieved the goals stated by managers.

2. Methods

2.1. Site descriptions and sampling design

I retrospectively sampled five whitebark pine silvicultural restoration sites located in Montana, Idaho, and Oregon on US Forest Service lands during summer 2012 (Figures 1 & 2, Table 1). Sites were selected from the results of a survey sent to land managers about restoration activities in high-elevation pines in the western United States (C. Nelson, unpublished data). I selected silvicultural restoration treatments in whitebark pine stands that would be at least five years old at the time of sampling (2012). The Granite Butte (GB; implemented 2002) restoration treatment in Montana was located on the continental divide in a closed-canopy stand dominated by lodgepole pine (*Pinus contorta*) and subalpine fir. Stands at Snowbank Mountain (S4 and SM; implemented 2004 and 2006) and Whitehawk Mountain (WH; implemented 2005) sites in Idaho and the Vinegar Hill (VH; implemented 2002) site in Oregon were characterized by a patchy structure, with some large park-like openings (Figure 2). Subalpine fir and lodgepole pine were present at all sites, with Douglas-fir and Engelmann spruce (*Picea engelmannii*) as minor components at S4 and VH. Silvicultural prescriptions for the restoration treatment at each site varied, although each involved removing subalpine fir and other competing species (Table 1). A widespread MPB outbreak that occurred from approximately 2001-2009 throughout the region affected all five sites, with peak mortality occurring after most treatments had been implemented (Creeden et al. 2014).

I obtained stated goals of restoration treatments from decision memos and other documents provided by US Forest Service managers. The goals of the GB restoration were to create open areas where whitebark pine and lodgepole pine could successfully regenerate, allow for dominance of existing overstory whitebark pine (which would serve as seed trees), and to reduce the probability of lethal crown fires in the treatment stand. Lodgepole pine was expected to be the majority of the regeneration, but the treatment was to be considered a success if 25 % of the post-treatment regeneration cohort is whitebark pine. Managers intended the S4 and SM restoration treatments to release immature whitebark pine trees (presumably small non-cone producing individuals; size not specified) from competition with other species, encourage natural regeneration around cone-producing whitebark pine, and reduce the susceptibility of mature whitebark pine trees to MPB. The primary goal of the treatment at VH was to reduce MPB-caused mortality risk by increasing whitebark pine tree growth via removal of subalpine fir and other species that compete with whitebark pine. At WH, the goals were to reduce competition and fire hazard from around mature whitebark pine and to create openings for regeneration.

At each site, I identified treated areas using GIS polygon layers provided by US Forest Service managers. None of the restoration treatments I studied were implemented with paired, randomized controls. Thus, I selected nearby analogous untreated stands to serve as comparisons. Untreated stands were selected that had no obvious signs of differing stand history from treated stands (but treated areas at S4 and SM were directly adjacent roads and there were no suitable untreated stands that were also near roads), were clearly outside of treatment polygons, and had similar aspect, elevation, and species composition to the treated stands. All untreated stands were within ~2 km of the treated stands.

I used a systematic sampling design based on the FIREMON fire effects monitoring protocol (Lutes et al. 2006). Ten circular 11.3 m radius plots (400 m^2; whitebark pine trees and saplings only) and twenty 2.1 m radius plots (125 m^2; seedlings of all species) were located using a 40 m grid within each of the paired stands at each site. I placed 400 m^2 plots at alternate points on the grid to ensure a minimum of 56.6 m (diagonal distance) between plot centers and 125 m^2 seedling plots at every grid point. Half of the 125 m^2 plots were nested within 400 m^2 plots. I continued to establish plots until I reached the edges of treated areas. Mature whitebark pine trees were present in approximately half of the treated area at the GB site, so I confined the grid to that portion of the treated stand. I sampled all sites in July & August 2012.

2.2. Data collection

I counted all live and dead whitebark pine trees and saplings within each 400 m^2 plot. I defined trees as individuals ≥ 11.4 cm diameter at breast height (dbh) and saplings as individuals < 11.4 cm dbh and > 1.37 m tall. Fused stems were considered separate if their junction occurred below 1.37 m. I measured dbh on all live and dead whitebark pine > 1.37 m tall. I counted seedlings (individuals < 1.37 m tall) of all tree species in the 125 m^2 plots. I estimated the age of seedlings by counting as many primary stem internodes as we could perceive, representing the youngest possible age for a seedling. I dealt with the imprecision of this method by placing seedling establishment dates into equal size before and after bins (bins sizes were 6-10 years, varying by site due to differing treatment dates).

In each 400 m^2 plot, I collected increment cores for radial growth measurements from the two largest living whitebark pine trees within the two largest size classes available (> 25 cm dbh, 10 to 25 cm dbh, or 5 to 10 cm dbh; $n = 20$ trees for each treated and untreated stand). If a plot did not contain two live whitebark pine in two size classes, I selected whitebark pine trees from outside the plot area to a maximum of 27 m from plot center to keep sampling within respective stand boundaries. For the purpose of selecting trees for coring, multi-stemmed whitebark pine were considered individuals; I considered the dbh class of the largest stem only. I cored each live tree stem at two opposite radii at ~ 1.37 m to account for possible unequal distribution of growth around the stem. I preferentially selected radii perpendicular to slope direction (along the contour) and perpendicular to tree lean direction. Increment cores were returned to the laboratory in paper straws where they were later processed and visually cross-dated against each other using standard dendrochronological techniques (Stokes and Smiley 1968). Cores were then digitally scanned and measured using CooRecorder software (Larsson and Larsson 2013). Visual cross-dating was verified using COFECHA and CDendro software (Holmes 1983, Larsson and Larsson 2013). Ring measurements were made using CooRecorder (0.01 mm precision) or using a Velmex measuring system when greater viewing resolution was required. Trees that had one or both cores that were not datable were removed from analyses, resulting in 16-20 trees per stand at each site. I calculated a single mean ring width series from the two cross-dated cores from each tree. These raw tree series were detrended and standardized into a ring width index (RWI) in subsequent analyses, described below. Many trees at GB had partial growth rings for 2012 (no late wood) at the time of sampling, thus I removed 2012 growth at this site.

I characterized the competitive environment around trees cored for growth analyses by measuring dbh, species, and distance (tree center to tree center at ~ 1.37 m) of each neighbor tree within 11 m of the cored tree. Eleven meters is roughly 3.5 x an assumed crown radius of 3.14 m, as specified by Lorimer (1983). I used these data to compute Hegyi's competition index (Hegyi 1974, Contreras et al. 2011).

I assigned WPBR and MPB ratings to all live whitebark pine using the USDA Forest Service Region One Common Stand Exam protocols (USDA Forest Service 2016). WPBR infection was rated on a scale of 0 to 4. Zero means no visible infection, 1: branch infections greater than 60 cm from the main bole, 2: branch infections between 15 cm and 60 cm from the bole, 3: a bole infection or a branch infection closer than 15 cm from the bole, and 4: top kill, with a portion of the bole girdled by the infection, killing the branches above. I also visually estimated the percentage of the crown that had been killed by WPBR infections. MPB infestation was rated on a scale of 0 to 6. Zero means no evidence of MPB, 1: unsuccessful bole attack (all pitch tubes containing dead beetles), 2: strip attack, 3: successful bole attack, 4: top kill only, 5: successful attack last year (dead tree with red needles or dying tree), 6: older dead.

All dead whitebark pine with bark still attached were counted in each 400 m^2 plot. Single increment cores were extracted from all dead stems qualifying as trees ($\geq$ 11.4 cm dbh). I identified cause of death in the field by examining main stems for evidence of cankers, rodent chewing, and previous top kill (WPBR), or by the presence of pitch tubes, boring dust, j-shaped galleries on stem wood, or blue stain fungus on increment cores (MPB). Because MPB attacks live trees only (Six and Wingfield 2011), I considered MPB as the cause of death if there was any evidence of MPB attack.

2.3. Analyses

I treated each site individually in my analyses because stand characteristics, treatment prescriptions, restoration goals, and years since treatment varied among sites. Treated stands, and subsequently the untreated stands, were not randomly selected. Managers may have chosen stands for restoration based on unique characteristics (e.g., dense competition, severity of WPBR infection, etc.). I attempted to handle these limitations by using a Before-After-Control-Impact (BACI) framework (Stewart-Oaten et al. 1986). The after period was defined as the year after treatment until sampling in 2012 (GB: 10 years, S4: 8 years, SM: 6 years, VH: 10 years, WH: 7 years). Many trees at GB had partial growth rings for 2012 (no late wood) at the time of sampling in early July 2012, thus I defined the after period as 2003-2011 (9 years) for growth analyses only. I defined the before period as the equal amount of time directly proceeding the after period, including the treatment year. I assessed effects on each variable by testing the significance of the following before/ after and treated/ untreated differences: Treated After - Treated Before (T_A-T_B), Untreated After - Untreated Before (U_A-U_B), Treated Before - Untreated Before (T_B-U_B), and Treated After - Untreated After (T_A-U_A). I defined statistical significance as P-values less than or equal to 0.05 for all tests described below. All analyses were performed in the R environment (R Core Team 2018).

I assessed tree radial growth response to treatment using two analysis techniques with data derived from increment core measurements. First, I used a time series approach called intervention detection to identify significant growth outliers – release or suppression events that might be caused by sudden changes in surrounding stand structure or by disease – in each tree's growth series (Druckenbrod et al. 2013, Rydval et al. 2015, 2016a, 2017). My objective with this approach was to determine if the number of growth outliers differed between treated and untreated stands, and if outlier frequency changed between before and after treatment time periods. The process involves initial detrending to remove long-term age/size related growth trends (Cook and Peters 1997), then identifies growth release and suppression events through the entire length of a tree ring series via departures in moving averages of autoregressive residuals. These growth outliers are labelled with a start year and then iteratively removed from a tree ring series by fitting and subtracting trend curves from the outlier period so that the next largest growth outlier can be identified. The end result is a "disturbance-free" series. The signal of growth outliers (the "disturbance index") contained within the ring-width series is estimated as the difference between the disturbance-free series and the original series. I provide a complete description of the intervention detection method in appendix A of the supplementary material. An R script and required data to run this analysis is available through Mendeley Data.

After I had obtained a list of release and suppression growth outliers for each tree at each site, I defined the response variable as the difference in percentage of trees recording outliers for each before/ after and treated/untreated combination described above (*n* = 16-20 trees per stand at each site). I tested the significance of the observed differences in percent trees recording outliers using permutation tests in which I randomly permuted both stand (treated/untreated) and period (before/after) labels 100,000 times. Two-sided P-values were computed by dividing the number of times the permuted differences were as least as large as the observed differences by 100,000 (Roff 2006). I repeated these tests for both growth release outliers and growth suppression outliers.

Because intervention detection is less sensitive to subtle or slow changes in growth rates (Druckenbrod et al. 2013), I performed a complementary analysis on cumulative RWI as a response variable using the same BACI framework described above. RWI was preferred over basal area increment (BAI) because of the prevalence of multi-stemmed trees with fused trunks at S4 and SM. These trees had large dbh values, but ring-width series from these stems represented growth in a smaller stem than what I was able to measure, producing inflated BAI values. I computed RWI by first power transforming tree mean ring width series to approximate homoscedasticity (Cook and Peters 1997), then fitting a negative exponential curve or a straight line with negative slope to model age-related trends (Fritts 1976). These trend lines were then subtracted from the transformed series to create a detrended, standardized residual series that has no units (Cook and Peters 1997). Cumulative RWI was calculated for each tree as the sum of annual RWI values for each before and after period. I defined the response variable as the difference in mean (among all trees in each stand) cumulative RWI for each before/after and treated/untreated combination described above (n = 16-20 trees per stand at each site). I used Tukey's biweight robust mean of cumulative RWI to reduce the effect that outlier trees might have on results (Mosteller and Tukey 1977). I used permutation tests to test the significant of observed changes in mean cumulative RWI between stands. I permuted both stand and period labels 100,000 times and computed two-sided P-values by dividing the number of times the permuted differences were as least as large as the observed differences by 100,000.

To determine what effect WPBR had on changes in growth between time periods, I compared before-after change in cumulative RWI between stands (treated or untreated) and trees with three damage levels from WPBR: trees with WPBR rating of 0 (none), trees with WBPR rating 1-4 and 10 % or less crown kill (low), and trees with WBPR rating 3-4 and more than 10 % crown kill (high). My experimental unit for this analysis was the tree (n = 16-20 trees per stand at each site). I tested for differences in RWI change using factorial (stand x WPBR damage level) type-3 sum of squares ANOVA to account for unbalanced numbers of trees between groups.

I compared the effect of treatment on whitebark tree mortality rates as the difference in average proportion of whitebark pine trees that died in each plot between treated and untreated stands after treatments were implemented, with plot as the experimental unit (*n* = 10 plots per stand at each site). I tested significance of my results using permutation tests where I randomly permuted stand labels among plots 100,000 times. I excluded the period before treatment in mortality analyses because peak mortality from the MPB outbreak occurred after treatment implementation at my sites.

Seedlings were split into two age bins: minimum establishment age within the before period or within the after period. I tested for differences in seedling recruitment rates (count of seedlings$\cdot$plot$^{-1}\cdot$period^{-1}; *n* = 20 plots per stand at each site) between the BACI levels described above along with seedling species using negative binomial generalized linear models using a log link. The models used seedling count as the dependent variable, with period, stand, and species as predictors. I allowed for all possible crosses between predictors to account for interactive effects. I used analyses of deviance to determine the significance of effects.

I computed annual potential evapotranspiration (PET), a water balance metric of available energy in the environment (Stephenson 1990), for each study site using Thornthwaite-type water balance equations, based on the methods of Lutz et al. (2010) and using R code written by Dilts et al. (2015). Data inputs included monthly 0.00833° gridded TopoWx temperature (Oyler et al. 2014), monthly 0.0416° gridded PRISM precipitation (Daly et al. 2008), local slope and aspect (collected in the field and computed as an average of all plots within each site), and latitude. Soil water holding capacity data was not available for most of the sites. Instead, I assumed a soil available water capacity of 100 mm for all sites (Dilts et al. 2015).

I examined statistical relationships between RWI series from individual whitebark pine trees and PET series for each before/after and treated/untreated combination to determine if treatments caused changes in the strength of growth-climate relationships. I examined growth-climate relationships in two ways. First, I tested for relationships in interannual sensitivity by calculating first differences of individual RWI series and PET series. First differences are a way to remove all other sources of variation except interannual variation, and thus represent sensitivity (Youngblut and Luckman 2013). I also examined relationships between 3-year mean RWI series and PET series to determine how growth trends related to climate trends. Pearson correlation coefficients were calculated between PET series and RWI series for each tree, for both treated and untreated stands in both the before- and after-treatment periods. I tested for effects of stand and period on mean correlation coefficients using factorial type-3 ANOVA (n = 16-20 trees per stand at each site). I then used Tukey honestly significant difference tests to determine differences in levels.

3. Results

At the time of measurement, 6-10 years after treatments were implemented, 32.9 % of whitebark pine trees were dead in treated and untreated stands combined across all sites (102 dead trees of 310 trees total sampled; Table 2). These trees died between 1970 and 2012. The majority were killed by MPB (86.1 %; 87 trees), although 37.9 % (33 trees) of these also had signs of WPBR infection. Only 14 trees (13.9 %) were killed by WPBR alone. I could not identify cause of death in one tree. Nearly half (48.1 %; 100 trees) of the 208 living trees I sampled were infected with WPBR.

Ninety-nine of 562 (17.6 %) sampled whitebark pine saplings in both treated and untreated stands were dead across all sites (Table 3). Of these dead saplings, 3 % (three saplings) were killed by MPB, 62.6 % (62 saplings) by either WPBR or *Ips* beetles (star galleries were present on many saplings). I couldn't identify cause of death in 34.3 % (34 saplings) of saplings. The majority of dead saplings occurred at GB, where overall stem density was high (342.5 –

422.5 saplings ha^{-1}). Of the 463 living saplings I sampled, 39.1 % (181) were infected with WPBR.

3.1. Tree growth release from competition and effect of white pine blister rust

Many more trees recorded growth releases after treatment in the treated stand than the untreated stand at GB (T_A-T_B: +55 %, $P < 0.001$; T_A-U_A: +60 %, $P < 0.001$) and there were several fewer trees recording growth suppressions in the treated stand after the treatment compared to before (T_A-T_B: -30 %, $P = 0.004$; Table 4). I found no other significant differences in growth outliers at the other sites (Table 4).

I also found increases in cumulative RWI (unitless – positive values are relatively higher growth, negative values relatively lower) in the treated stand at GB (T_A-T_B: +1.07, $P = 0.008$; T_A-U_A: +1.29, $P = 0.029$; Table 4, Figure 3). Growth also increased from before treatment in the treated stand at VH (T_A-T_B: +1.47, $P = 0.012$), but there was no significant difference between treated and untreated stands after treatment. I detected no further differences in mean cumulative RWI (Table 4, Figure 3).

The effect of WPBR damage on growth response varied among sites. Damage from WPBR did not affect growth response in whitebark pine trees – change in cumulative RWI from before to after treatments – at GB in either stand. (WPBR damage: $F = 0.22$, $df = 2$, $P = 0.28$; WPBR damage x stand: $F = 0.83$, $df = 2$, $P = 0.44$; stand: $F = 8.17$, $df = 1$, $P = 0.007$; $n = 20$ trees per stand; Figure B.1). Trees with up to 80 % crown kill from WPBR still recorded releases at GB. Trees with high damage from WPBR showed declining growth at VH in the treated stand only, although there were only two trees in this category. There was a growth increase after treatment in the treated stand for whitebark pine trees in low and none WPBR damage levels and a growth decrease in the high level (WPBR damage: $F = 1.33$, $df = 2$, $P = 0.28$; WPBR damage x stand: *F* = 6.89, *df* = 2, *P* = 0.003; stand: *F* = 8.28, *df* = 1, *P* = 0.007; *n* = 18-20 trees per stand). I found a significant, though modest, decline in cumulative RWI in all WPBR damage levels in the untreated stand at WH, but not in the treated stand (WPBR damage: *F* = 1.31, *df* = 2, *P* = 0.28, WPBR damage x stand: *F* = 1.90, *df* = 2, *P* = 0.17; stand: *F* = 4.67, *df* = 1, *P* = 0.04; *n* = 20 trees per stand, Figure B.1). Growth response at SM and S4 between trees in WPBR damage categories and between stands was not distinguishable (*n* = 16-20 trees per stand; Figure B.1).

3.2. Recruitment

With the exception of GB, all sites had mean recruitment rates below 1 seedling per plot per period for all species (*n* = 20 plots per stand at each site). I found no seedlings of any species in plots at SM, and thus did not perform analyses for that site. At GB there was a clear increase in subalpine fir recruitment in the treated stand after treatment implementation (T_A-T_B difference), with an apparent decline in the untreated stand (U_A-U_B difference; Figure 5). There was also an increase in lodgepole pine recruitment in the treated stand after implementation, with no change in the untreated stand. Both subalpine fir and lodgepole pine recruitment rates were indistinguishable between treated and untreated stands in the before period (T_B-U_B), but clearly different after treatment (T_A-U_A). There was no apparent effect of treatment implementation on the whitebark pine recruitment rate (Figure 4). These differences resulted in significant stand x period, stand x species, and period x species interactions on seedling count (seedlings plot^{-1} period^{-1}), but no significant stand by period by species interaction (Table 5). At VH, I found a significant stand by species interaction, but no stand by period, period by species, or stand by period by species interactions (Table 5). The stand by species interaction was driven by a slightly higher subalpine fir recruitment rate in the untreated stand relative to the treated stand in the after period (T_A-U_A), although overall subalpine fir recruitment rates were very low. I found no differences – and very low recruitment rates – at both S4 and WH, with no significant stand by period, stand by species, period by species, or stand by period by species interactions (Table 5).

3.3. Mortality of whitebark pine trees

Mortality was significantly reduced between treated and untreated stands (T_A-U_A difference) at only one of the five sites (GB; *Diff* = -0.37, *P* = 0.019, *n* = 10 plots per stand). The untreated stand at GB experienced 37% mortality after the treatment; in contrast, there was no mortality in the treated stand during the same period. Mortality rates between stands were indistinguishable before treatment at GB (Figure 5). I found no evidence that treatments prevented mortality at the other sites (S4, *Diff* = 0.11, *P* = 0.99; SM, *Diff* = 0.13, *P* = 0.47; VH, *Diff* = 0.083, *P* = 0.88; WH, *Diff* = -0.05, *P* = 0.62; *n* = 10 plots per stand at each site).

3.4. Growth-climate relationships

The periods after treatment at all sites was drier on average than the 1981-2010 normal. climatic water deficit (CWD; calculated as PET-AET) was 18.12 – 40.6 mm above normal and AET (water availability) was 4.8 - 21.7 mm below normal. I initially examined relationships CWD between RWI series and found mostly positive correlations, indicating that trees at my sites were more energy limited than water limited (Ford et al. 2017). Instead I used PET. Overall correlations between RWI and PET series were stronger than those with CWD.

Mean correlations between first differenced RWI and PET were generally positive across sites, stands, and periods (range: 0.042 - 0.433; Figure 6, Figure B.2). I observed changes in short-term climate sensitivity of whitebark pines at SM, represented by a significant T_A-T_B decrease in climate sensitivity - mean correlation changed from 0.43 in the before period to 0.04

in the after period (period: $F = 6.2$, $df = 1$, $P = 0.02$; stand x period: $F = 6.85$, $df = 1$, $P = 0.011$; Table B.1, Figure B.2). I found no further differences in climate sensitivity at the other sites.

Relationships between growth and climate trends changed from negative relationships to positive for both treated and untreated stands at S4 and WH, as indicated by significant main effects of period on correlations between climate and growth trends at S4 ($F = 37.4$, $df = 1$, $P < 0.001$; Table B.2) and WH ($F = 51.2$, $df = 1$, $P < 0.001$) driven by significant changes in both stands from negative to positive correlations (Table 4; Figure B.3). Growth had an upward trend in the treated stand at VH after treatment, while PET showed little trend during this period; there was a significant stand by period interaction at VH ($F = 5.58$, $df = 1$, $P = 0.021$; Figure 6, Figure B.3).

3.5. Success of whitebark pine restoration treatments

The primary goals for restoring whitebark pine at GB were to encourage regeneration (at least 25 % whitebark pine), allow for dominance of existing overstory whitebark pine, and reduce probability of lethal crown fires. The first goal of encouraging new regeneration in whitebark pine was not accomplished, though some of the anticipated new lodgepole pine regeneration did occur (Figure 4). Even considering advance regeneration (older seedlings that were present before treatment), the percentage of seedlings by species in the treated stand was far from the target (values are means with 95 % M.o.Es; subalpine fir: 70.5 ± 13 %, whitebark pine: 6.2 ± 3.6 %, lodgepole pine: 23.3 ± 13.1 %). This is an overall decrease in subalpine fir relative abundance and increase in lodgepole pine but no change in whitebark pine relative to the untreated stand (subalpine fir: 95.5 ± 2.4 %, whitebark pine: 4.1 ± 2.4 %, lodgepole pine: 1.4 ± 1.4 %). However, new regeneration of subalpine fir was stimulated by the treatment (Figure 4). Existing overstory whitebark pines were nearly the only trees left standing and were certainly the dominant trees on the site after treatment. No fires moved through the treated area before the time of sampling, so there was no way to assess if the treatment reduced mortality risk from fire. However, the treatment did effectively reduce mortality during a mountain pine beetle outbreak.

The two treatments at Snowbank Mountain (S4 and SM) intended to release immature whitebark pine from competition, encourage natural regeneration of whitebark pine, and reduce mortality risk from MPB in mature whitebark pine. I did not take increment cores from small diameter whitebark pine to avoid causing damage, so I cannot assess the first goal of these treatments. I found no evidence of growth release in mature whitebark pine at these sites. Treatments did not significantly increase whitebark pine regeneration at S4 and SM and did not appear to prevent mortality from MPB (Figure 5).

Managers designed the restoration at VH to reduce MPB-caused mortality in whitebark pine via increased tree growth rates. I did find evidence of an increase in whitebark pine growth at VH (Figures 3 and 6), suggesting a reduction in competition, but no reduction in MPB-caused mortality (Figure 5).

The treatment at WH was designed to reduce competition on whitebark pine, reduce fire hazard, and create openings for regeneration. I found no evidence for a reduction in competition (Figures 3 and 6). No fires occurred at the site before sampling, so I have no assessment of fire hazard reduction. The treatment had no apparent effect in reducing MPB-caused mortality. Finally, I also found no increase in whitebark pine regeneration.

4. Discussion

Restoration efforts in whitebark pine forests continue to be a management priority in many parts of the species' range. Yet, treatments are rarely assessed for their effects or success. I addressed this gap with my study and found that treatments had varying effects and in the short-term (6-10 years) had often not achieved stated goals.

4.1. Tree growth release from competition and effect of white pine blister rust

The positive growth response at GB suggests that growth of whitebark pines in this closed-canopy stand was most likely limited by competition. Average growth response was delayed until approximately 3 years after treatment (Figure 6), likely due to allocation of resources to primary growth in crown and roots (Vincent et al. 2009). The growth increase after this initial delay was rapid for 2-3 years and had flattened before the time of sampling. I found some evidence for growth release across the treatment stand at VH, though this was manifested in changes in cumulative RWI in the treated stand only. RWI was not different from the untreated stand in the after period and there were no changes in growth interventions. Average tree growth appears to gradually increase during the after period in the treatment stand (Figure 6).

There are several potential explanations for the growth response at some sites and lack of response at others. In forest stands with multiple canopy layers, growth release in mid-canopy and smaller trees is common after thinning, while little or no response in observed in the largest, canopy emergent trees (Willis et al. 2018). At my sites, the average relative dominance of whitebark pine in park-like stands was likely higher than the closed-canopy stands – canopy dominant trees are less likely to be affected by competition from neighbors than mid- or lower-canopy trees (D'Amato and Puettman 2004). Thinning around canopy-dominant whitebark pine may not increase their growth. However, it is also possible that the treatments at some of the park-like sites did not remove enough neighbors to release whitebark pines. For example, at S4, the prescription called for leaving the largest (> 20.3 cm dbh) subalpine firs. Additionally, I did not examine growth response in whitebark pines with diameter < 11.4 cm, and I preferentially selected trees that were in larger size classes. Smaller trees may well have responded to the treatments. Finally, it is also possible that whitebark pines at some sites were not limited by competition and did not need to be treated.

I found that trees at GB with severe damage from blister rust respond to silvicultural treatment by increasing radial growth - with no significant difference in magnitude of growth release compared to undamaged trees (Figure B.1). At VH, the other site with evidence of growth release, I saw the opposite effect – high damage trees showed declining growth after being treated. I am not sure what could have caused these diverging effects at my sites, but there are reports in the literature of WPBR cankers becoming inactive over time in western white pine (*Pinus monticola*; Hungerford, 1977). It is possible that my two sites had different proportions of whitebark pine with inactive cankers. However, it is unclear whether inactive cankers represent trees that had overcome infections. Additionally, my results may be an artifact of small sample sizes within WPBR damage levels. Generally, damage from WPBR had surprisingly little effect on growth response.

4.2. Recruitment

I found no evidence that any of the restoration treatments altered whitebark pine recruitment rates. This suggests that either restoration treatments do not lead to increased recruitment (e.g., through increased nutcracker caching or improved competitive environment), that seed sources were not plentiful enough at any of the sites for a recruitment response to have occurred, or that climatic conditions were not suitable for regeneration during the study period. I found very low whitebark pine recruitment rates at all sites, in all periods and stands. This could indicate chronically low cone-crops due to tree mortality and damage from blister rust. Despite the potential of long-distance dispersal by nutcrackers, nearby seed-source density is important for whitebark pine recruitment in disturbed areas (Leirfallom et al. 2015). Nutcrackers recover and consume higher proportions of their caches when cone crops are smaller, leading to less germination potential (Siepielski and Benkman 2007). Although I do not have cone production data specific to my sites, other researchers observed masting events throughout the study region in the periods after many treatments were implemented. Crone et al., (2011) observed notable cone crops in 2003 and 2005 at their Montana and Idaho field sites, and Sala et al. (2012) observed a large mast event during 2005 in whitebark pine at their western Montana field site. Thus, it is likely that cone crops occurred after treatment, at least at some sites and that additional factors contributed to the recruitment failure.

For example, Lorenz et al. (2011) found that nutcrackers make a small proportion (~ 15 %) of caches in the ground in high-elevation whitebark pine habitat, and the probability of cache site selection for ground caches decreased with distance from trees and increased with increasing understory cover. This nutcracker avoidance of openings may explain the lack of recruitment response that I observed. Besides seed limitation, climatic conditions are known to be important drivers of recruitment in stressful environments (Holmgren et al. 2006). All study sites were drier than 1981-2010 normals on average in the years after treatment. Whitebark pine seedling survival and photosynthetic performance is known to be improved with herb and tree cover under low water conditions near treeline (Maher et al. 2005) – perhaps some cover would benefit natural regeneration (Perkins et al. 2015).

It is notable that all sites except for GB had such low recruitment of all species for all periods. These sites were relatively open, park-like stands compared to the dense subalpine forest at GB, suggesting very different natural recruitment dynamics. The large gap created by the treatment at GB created an opportunity for establishment where competition for light was likely the most limiting factor. In contrast, light is generally not limiting in the open park-like stands, suggesting climatic or microsite limitations. Seed sources for lodgepole pine and subalpine fir appear to be adequate for positive recruitment response to disturbance.

It is also possible that human land use influences recruitment dynamics; I observed cattle grazing at VH, WH, and SM. Grazing by sheep and cattle is generally associated with fire-suppression and increased recruitment of conifers in the lower-elevation montane forests of the western U.S. regionally (Belsky and Blumenthal 1997). However, cattle grazing in subalpine and alpine environments in the European Alps is linked to inhibited recruitment in high-elevation swiss stone pine (*Pinus cembra*), a pine with similar recruitment ecology to whitebark pine (Vittoz et al. 2008). Given the considerable resources allocated to restoring whitebark pine and current threats to whitebark pine populations, investigations to understand the impact of grazing on whitebark pine recruitment are clearly needed.

4.3. Whitebark pine tree mortality

I found strong evidence that the treatment at GB reduced whitebark pine tree mortality within the treatment stand. The 2000s MPB outbreak killed an estimated ~40% of trees in the untreated stand, while I found no dead trees in treatment stand plots. This may have been due to a dramatic reduction in beetle host density at this site – the treated area had many lodgepole pines, another common MPB host species, removed. Although I cannot rule out the potential effects of heightened tree defenses on beetle deterrence, individual tree defense becomes unimportant relative to host density during an outbreak (Boone et al. 2011). The untreated stand was continuous with the treated stand at GB – plots in the two stands were ~ 100 m apart, so it is unlikely that the difference in MPB-caused mortality was due to random patchiness in MPB distribution.

I found no effect of treatment on mortality at any of the other sites – mortality occurred at indistinguishable rates in treated and untreated stands. Lodgepole pine was present at all sites, but in much lower abundances than GB. Also, many of the whitebark pine trees at the other sites existed in multi-stemmed clusters – which was comparatively rare in the dense stands at GB. Because of lower lodgepole densities and perhaps higher proportion of clustered whitebark pine stems, the treatments at VH, WH, S4 and SM did not substantially alter MPB host density, and likely had little effect on whitebark pine vulnerability to beetle attack during the outbreak. Whitebark pine trees may continue to be killed by MPB despite silvicultural intervention – active application of carbaryl insecticide and verbenone anti-aggregate pheromone may help reduce mortality (Keane et al. 2012).

4.4. Growth-climate relationships

Overall, I found no compelling evidence that treatments altered interannual growth sensitivity to climate or that treatments changed relationships between growth trends and climate trends over the periods that I examined. Climate sensitivity decreased over time for trees in the treated stand at one site: SM. This might indicate a decreasing influence of climate variation on whitebark pine growth, but more likely is the result of low annual variability in PET after treatment (Figure 6). Furthermore, there were no differences in sensitivity between treated and untreated stands. The period I examined may not be long enough to assess whether sensitivity to climate was altered by reduction in competition. The shifts from negative relationships to positive ones between growth and climate trends for both treated and untreated stands at S4 and WH may indicate a shifting role of climate in whitebark pine growth and perhaps the limited role of competition in mediating growth-climate relationships at those sites. However, an upward growth trend in the treated stand at VH, possibly due to release from competition as discussed above, led to a decoupling from the climate trend. This decoupling effect would likely continue only as long as growth was increasing, however.

My analyses revealed interesting relationships between whitebark pine growth and climatic water balance variables. In my initial analyses, I examined correlations between growth and climatic water deficit (CWD), the difference between PET and available water (actual evapotranspiration minus AET; Stephenson 1990) – a representation of cumulative drought stress through a year. Higher CWD values should then lead to lower growth. However, I found that CWD was positively related to whitebark pine growth at my sites, as was PET, despite recent years being drier than 1981-2010 normals. I interpret this result to indicate that whitebark pines at my study sites are more limited by growing season temperatures than by moisture availability and that deficits are probably not high enough at these sites to induce water stress in this species. Ford et al. (2017) found that tree growth in montane forests in Mt. Rainier National Park (Washington State, USA) were likely temperature limited, also indicated by positive correlations between growth and CWD. In contrast, Millar et al. (2012) found the expected negative correlations between CWD and whitebark pine growth in the Sierra Nevada, California, USA. It is also possible that water balance models do not adequately describe environments at my sites – instrumentation is sparse in high mountains creating increased potential for errors in interpolation (Oyler et al. 2014). These differences highlight the need for increased understanding of growth-climate relationships over the range of whitebark pine and should serve as a caution against assuming relationships are similar in different regions.

4.5. Success of whitebark pine restoration treatments

Many of the goals of restoration treatments were not achieved in the time period I examined. Radial growth increased dramatically at GB and somewhat at VH, suggesting that large whitebark pines at these sites were previously limited by competition. At the other sites, competition may have been less important. The only reduction in mortality occurred at GB – where the strongest growth release occurred, indicating a possible link between tree growth rates and resistance to MPB. But, this treatment also dramatically reduced density of the alternate MPB host, lodgepole pine – it is also plausible that the decrease in density was a direct cause of reduction in MPB hazard. None of the treatments appeared to increase whitebark pine regeneration during the time periods I examined, indicating that thinning treatments are not an effective strategy to stimulate whitebark pine regeneration.

Although the stated goals of the restoration treatments I studied did not directly concern WPBR, reducing the deleterious effects of this introduced disease is a general goal of whitebark pine restoration range-wide (Keane et al. 2012). I found that silvicultural restoration – in areas where competition limits growth – may have equal growth release benefits for uninfected whitebark pine trees as for those damaged by WPBR.

The success of restoration treatments is difficult to evaluate without the inclusion of control stands or trees simultaneous with treatments. I selected untreated comparison stands that were as similar as possible to the treated stands, but I still cannot rule out differences due to random distributions of insects or disease, or that managers may have selected stands specifically because of these impacts.

5. Conclusions and management implications

The success of silvicultural treatments in whitebark pine seems to heavily depend on site conditions and treatment prescription. Treatments implemented in closed-canopy stands, like GB, may have greater potential for positive growth responses in whitebark pine and may help trees avoid mortality during MPB outbreaks. However, I found no evidence that treatments helped natural recruitment in whitebark pine, though I found strong evidence that treatments can increase recruitment in other competing conifer species. I also found that trees with damage from WPBR – possibly with inactive cankers – can release in response to reduction in competition. These trees will likely continue to grow and represent a complementary and faster route to restoring seed production on site to growing trees from seedlings. Care must be taken in selecting sites for restoration – silvicultural strategies that are effective in reducing competition in more productive forests may not be appropriate for high-elevation whitebark pine forests where competition is not as limiting. However, competition does limit growth in some proportion of whitebark pine forests, exemplified by the GB site.

I found that restoration treatments often did not have their intended effects, and sometimes had negative or unintended consequences. These results indicate that I do not fully understand some crucial aspects of the ecology of whitebark pine forests and how ecological responses might differ across the species' range. Additionally, I expect mortality, growth, and recruitment ecology of whitebark pine to be altered by climate change (Hansen et al., 2016; Keane et al., 2017). Active adaptive management is a strategy that accepts such uncertainty as an operational principle by applying concepts from experimental design; for example by establishing a BACI (before-after-control-impact) design (Elzinga et al. 2001, Larson et al. 2013). Many of the limitations of this study would be reduced, if not eliminated, by proper experimental design (Platt 1964, Elner and Vadas 1990). The key element of experimental design is the use of controls that are exposed to the same range of conditions as the treatments, minus the treatment itself. Managers or researchers could identify all potentially treatable trees within an area, then randomly or systematically (e.g., every other tree) select half of those trees for treatment, leaving the other half untreated – the key being that control and treatment trees are equally likely to occur in any given location within a stand. Harrington's (2013) study of the mortality risks of large duff mound burning during prescribed fire treatments in western larch (*Larix occidentalis*) is an excellent example of this type of experimental design used in an adaptive management context.

Additionally, the manager could collect data on initial WPBR and competitive status and other tree attributes before treatment. A BACI design is an effective design for restoration treatments because it includes a baseline data along with controls and replication – required elements to make confident inferences about the effects of a treatment (Elzinga et al., 2001). A further advantage to using the principles of experimental design is that it would allow managers to test varying levels of treatment to learn which is the most effective in a given context. With subsequent monitoring and data collection, the manager will then have a powerful basis to adjust restoration techniques for greater success and will be providing essential information to other managers interested in restoring whitebark pine forests. Continuing use of adaptive management will allow for the most informed decision-making and allow for detection of changes in the effects of treatments as forests change.

My most important recommendations for future restoration treatments in whitebark pine forests are:

- Do not discount trees with WPBR damage; these trees can experience growth release if limited by competition.
- Silvicultural treatments may not always result in reduced MPB-caused mortality. Anticipate losses and actively protect trees from MPB attack using carbaryl and/or verbenone applications.
- Silvicultural treatments probably will not enhance whitebark pine regeneration. Planting blister rust resistant whitebark pine seedlings is likely required to achieve

desired whitebark pine regeneration. Consider protection of planted seedlings in areas where grazing permits are issued.

- Implement and monitor treatments using appropriate experimental designs for active adaptive management. This will allow trials of new strategies and strong inference about the effects of treatment – this is the most efficient way of selecting strategies that have positive outcomes and eliminating those that have negative outcomes. Foster relationships with scientists to facilitate this process.

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Tables

Table 1. Descriptions (year implemented, location, elevation, climate normals, treatment prescription, and competition index) for each of whitebark pine restoration treatments examined. All sites were sampled July and August 2012. Competition indices are expressed as means and margins of error (M.o.E. for 95% confidence intervals) based on Hegyi's competition index (Hegyi, 1974) calculated for 19-37 trees in each stand at each study site.

Site	Year	Location	Elevation	Climate normals 1981-2010* (mean ± M.o.E.)		Treatment prescription†	Competition index (mean ± M.o.E.)	
				CWD	*AET*		*Treated*	*Untreated*
Granite Butte (GB)	2002	Lincoln RD, Helena NF, Montana	2180-2250 m	36±12 mm	191±8 mm	Remove all other species	0.3±0.1	5.1±1.3
Snowbank Mountain '04 (S4)	2004	Cascade RD, Boise NF, Idaho	2100-2300 m	92±18 mm	197±12 mm	Remove ABLA < 8in. (20.3cm) DBH within 30ft (9.1m) of PIAL	0.9±0.8	0.7±0.6
Snowbank Mountain '06 (SM)	2006	Cascade RD, Boise NF, Idaho	2400-2530 m	50±12 mm	160±8 mm	Remove ABLA < 8in. (20.3cm) and girdle ABLA 8-18in. (20.3cm-45.7cm) DBH within 15ft (4.6m) of all PIAL Remove/girdle all ABLA within 8ft (2.4m) of PIAL > 5in. (12.7 cm) DBH	0.9±0.5	1.3±0.7
Vinegar Hill (VH)	2002	North Fork John Day RD, Umatilla NF, Oregon	2150-2480 m	111±20 mm	184±14 mm	Remove/girdle all other species within 50ft (15.2m) of PIAL > 15ft (4.6m) tall or 20ft (6.1m) of PIAL < 15ft (4.6m) tall	0.4±0.2	0.7±0.2
Whitehawk Mountain (WH)	2005	Lowman RD, Boise NF, Idaho	2400-2560 m	79±17 mm	188±10 mm	Remove all other species	0.3±0.2	1.9±0.7

* CWD = Annual climatic water deficit. AET = Annual actual evapotranspiration. † Species codes are as follows: ABLA = subalpine fir, PIAL = whitebark pine. M.o.E.= Margin of error from 95% confidence interval.

Table 2. Whitebark pine tree (stems ≥ 11.4 cm diameter at breast height) population characteristics and condition at each restoration site in treatment and untreated stands. QMD: quadratic mean diameter. WPBR: white pine blister rust. All values except for QMDs are arithmetic means accompanied by margins of error for 95% confidence intervals. All statistics are plot-level (*n* = 10 plots per stand at each site) summaries as measured 6-10 years post-treatment.

Site	Live QMD (cm)	Dead QMD (cm)	Live Stem Density (stems·ha^{-1})	Dead Stem Density (stems·ha^{-1})	Live Basal Area (m^2·ha^{-1})	Dead Basal Area (m^2·ha^{-1})	Live WPBR Infected (%)
GB							
Untreated	14.6	16.4	40.0 ± 22.6	77.5 ± 56.2	0.7 ± 0.39	1.6 ± 1.1	64.6 ± 29.3
Treated	23.0	21.5	45.0 ± 23.6	15.0 ± 15.1	1.9 ± 1.64	0.5 ± 0.7	79.6 ± 27.0
S4							
Untreated	56.3	41.7	20.0 ± 16.4	0	5.0 ± 5.0	0	30.0 ± 55.5
Treated	35.0	0.0	32.5 ± 14.7	5.0 ± 7.5	3.1 ± 2.5	0.7 ± 1.2	75.0 ± 31.6
SM							
Untreated	45.9	47.0	52.5 ± 24.5	7.5 ± 12.1	8.7 ± 4.7	1.3 ± 2.0	31.5 ± 26.8
Treated	39.3	47.7	72.5 ± 33.1	50.0 ± 61.4	8.8 ± 6.4	8.9 ± 10.3	48.5 ± 19.0
VH							
Untreated	37.4	46.8	77.5 ± 45.0	20.0 ± 18.5	8.5 ± 5.0	3.4 ± 3.2	34.1 ± 28.7
Treated	35.0	46.5	47.5 ± 25.9	12.5 ± 15.2	4.6 ± 3.5	2.1 ± 2.5	7.3 ± 11.4
WH							
Untreated	30.7	29.6	42.5 ± 41.3	42.5 ± 73.0	3.1 ± 3.9	2.9 ± 5.1	62.5 ± 51.8
Treated	30.3	31.3	90.0 ± 38.8	25.0 ± 41.3	6.5 ± 4.0	1.9 ± 3.5	65.9 ± 24.1

Table 3. Whitebark pine sapling (stems < 11.4 cm diameter at breast height) population characteristics and condition at each restoration site in treatment and untreated stands. QMD: quadratic mean diameter. WPBR: white pine blister rust. All values except for QMDs are arithmetic means of plot survey data accompanied by margins of error for 95% confidence intervals. All statistics are plot-level (*n* = 10 plots per stand at each site) summaries as measured 6-10 years post-treatment.

Site		Live QMD (cm)	Dead QMD (cm)	Live Stem Density (stems·ha^{-1})	Dead Stem Density (stems·ha^{-1})	Live Basal Area (m^2·ha^{-1})	Dead Basal Area (m^2·ha^{-1})	Live WPBR Infected (%)
GB								
	Untreated	5.7	7.0	422.5 ± 226.9	215.0 ± 87.7	1.1 ± 0.4	0.8 ± 0.4	48.2 ± 15.8
	Treated	4.6	6.5	342.5 ± 213.3	25.0 ± 18.9	0.6 ± 0.4	0.1 ± 0.1	68.3 ± 12.5
S4								
	Untreated	3.1	0.0	5 ± 7.5	0	0.004 ± 0.01	0	0
	Treated	0.0	0.0	0	0	0	0	-
SM								
	Untreated	6.5	0.0	17.5 ± 12.1	0	0.1 ± 0.1	0	0
	Treated	4.8	0.0	72.5 ± 78.4	0	0.1 ± 0.2	0	29.5 ± 29.5
VH								
	Untreated	4.2	4.8	97.5 ± 129.9	2.5 ± 5.7	0.1 ± 0.2	0.005 ± 0.01	7.6 ± 9.9
	Treated	6.1	0.0	72.5 ± 57.5	0	0.2 ± 0.2	0	1.1 ± 2.6
WH								
	Untreated	6.4	6.7	52.5 ± 45.0	2.5 ± 5.7	0.2 ± 0.1	0.01 ± 0.02	18.4 ± 34.7
	Treated	5.6	2.0	75.0 ± 75.9	2.5 ± 5.7	0.2 ± 0.2	0.001 ± 0.002	4.5 ± 10.6

Table 4. Results from permutation tests on differences between treated and untreated stands (*n* = 10 plots per stand at each site) and between before and after periods at the stand-level (% trees w/ releases and w/ suppressions) or mean responses at the tree-level (cumulative RWI). Significant results are shown in bold with an asterisk. Percentages and means were calculated from 16-20 trees per stand at each site. Time periods span 6-10 years between sites. The after periods begin the year following treatment implementation. The before periods span an equal number of years before the treatment, including the year treatments were implemented.

Site*	% Trees w/ Releases		% Trees w/ Suppressions		Cumulative RWI	
	Difference	P-Value	Difference	P-Value	Difference	P-Value
GB						
U_A-U_B	0	1.0	0	1.0	-0.4	0.4
T_A-T_B	**55.0**	**< 0.001 ***	**-30.0**	**0.004 ***	**1.1**	**0.008 ***
T_A-U_A	**60.0**	**< 0.001 ***	-10.0	0.4	**1.3**	**0.03 ***
T_B-U_B	5.0	0.7	20.0	0.06	-0.2	0.7
S4						
U_A-U_B	-6.3	0.5	-6.3	0.6	-0.3	0.7
T_A-T_B	0	1.0	-5.3	0.6	-0.7	0.2
T_A-U_A	5.3	0.5	10.5	0.3	-0.9	0.4
T_B-U_B	-1.0	0.8	9.5	0.3	-0.5	0.4
SM						
U_A-U_B	0	1.0	0	1.0	0.0	0.8
T_A-T_B	0	1.0	10.0	0.06	0.0	1.0
T_A-U_A	0	1.0	10.0	0.07	-0.1	0.8
T_B-U_B	0	1.0	0	1.0	-0.1	0.9
VH						
U_A-U_B	5	0.6	5.0	0.4	0.4	0.5
T_A-T_B	0	1.0	-5.6	0.4	**1.5**	**0.01 ***
T_A-U_A	6.1	0.5	-5.0	0.5	1.4	0.2
T_B-U_B	11.1	0.2	5.6	0.3	0.4	0.6
WH						
U_A-U_B	0	1.0	-5.0	0.6	-0.3	0.1
T_A-T_B	0	1.0	0	1.0	0.1	0.7
T_A-U_A	0	1.0	10.0	0.2	0.1	0.6
T_B-U_B	0	1.0	5.0	0.6	-0.1	0.7

* U = untreated, T = treated. Subscripts A and B denote after and before time periods, respectively.

Table 5. Analysis of deviance table of results from negative binomial generalized linear models

(log link) on seedling counts per plot (*n* = 20 plots per stand at each site) per time period (7-10 years) for all possible stand (treated/ untreated), period (before/ after), and species (subalpine fir, whitebark pine, and lodgepole pine) interactions. Recruitment period was established using seedling age estimates.

Site:		**GB**		**S4**		**VH**		**WH**	
Predictors	*df*	$\chi 2$	P-Value	$\chi 2$	P-Value	$\chi 2$	P-Value	$\chi 2$	P-Value
Stand	1	**28.1**	**< 0.001***	**13.9**	**< 0.001***	1.1	0.3	**8.3**	**0.004***
Period	1	0.8	0.4	0.4	0.5	0.0	0.8	0.8	0.4
Species	2	**266.0**	**< 0.001***	**8.5**	**0.01***	**22.4**	**< 0.001***	**10.9**	**0.004***
Stand:Period	1	**13.3**	**< 0.001***	0.0	1.0	0.0	0.8	1.9	0.2
Stand:Species	2	**16.4**	**< 0.001***	0.0	1.0	**6.1**	**0.048***	1.4	0.5
Period:Species	2	**60.8**	**< 0.001***	5.8	0.054	2.5	0.3	0.9	0.6
Stand:Period:Species	2	1.6	0.4	0.0	1.0	0.0	1.0	0.0	1.0

Figure captions

Figure 1. Locations of the five whitebark pine restoration treatments used in this study. The Snowbank Mountain site contained two restoration treatments; one implemented in 2004 and the other in 2006.

Figure 2. The whitebark pine stands that were treated at each of the restoration sites I examined in this study (Table 1). a) Granite Butte (GB). There was a strong impact of treatment on stand structure. Note small whitebark pine trees and abundant lodgepole pine regeneration in the foreground. The closed-canopy untreated stand is visible in the background. b) Snowbank Mountain '04 (S4) and c) Snowbank Mountain '06 (SM). There was little impact of treatment on stand structure – stands were open and not all competitors were removed. d) Vinegar Hill (VH). The stand had an open stand structure. Girdled subalpine fir and lodgepole pine are visible at left and in the background. e). Whitehawk Mountain (WH). The stand had an open stand structure. Girdled subalpine fir visible throughout. Photo credits C. Maher.

Figure 3. Radial growth response to treatments, expressed as Tukey's biweight robust mean tree-level cumulative ring-width index (RWI) during before and after periods for both treated and untreated stands at each site (*n* = 16-20 trees per stand at each site). Vertical lines represent ±1 standard error of the median to more accurately reflect variance associated with Tukey's biweight robust mean. Different letters denote statistically significant differences.

Figure 4. Change in mean seedling recruitment per hectare (*n* = 20 plots per stand) from the before period to the after period (10 years each) at the GB whitebark pine restoration site,

Montana. ABLA: *Abies lasciocarpa* (subalpine fir), PIAL: *Pinus albicaulis* (whitebark pine), PICO: *Pinus contorta* (lodgepole pine). Vertical bars represent ± 1 s.e.

Figure 5. Mean proportion of whitebark pine trees (≥ 11.4 cm dbh) dying per year in sample plots (*n* = 10 plots per stand at each site) through 2011 at each restoration site. Vertical bars represent ± 1 s.e. Dashed vertical lines mark the years treatments were implemented. An MPB outbreak occurred across the region from ~2001-2009.

Figure 6. Ring-width index (RWI) chronologies in treated and untreated stands (*n* = 16-20 trees per stand at each site) and potential evapotranspiration (PET) series for each site. Actual values are displayed along with first differences (interannual sensitivity) and 3-year means (trends). Vertical dashed lines mark the years of treatment implementations. X-axes show the before and after periods unique to each site. I computed chronologies using Tukey's bi-weight robust mean (Mosteller and Tukey 1977) for each treated and untreated stand for each site.

Figure 1.

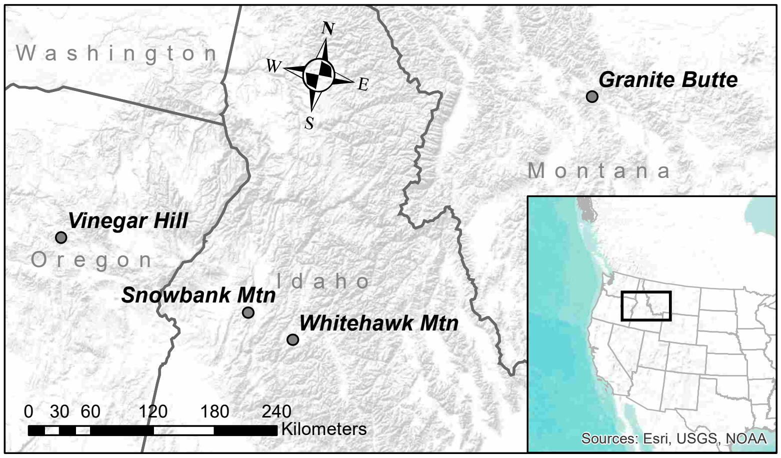

Washington
N
W
E
S
Granite Butte
Montana
Vinegar Hill
Oregon
Idaho
Snowbank Mtn
Whitehawk Mtn
0 30 60 120 180 240
Kilometers
Sources: Esri, USGS, NOAA

Figure 2.

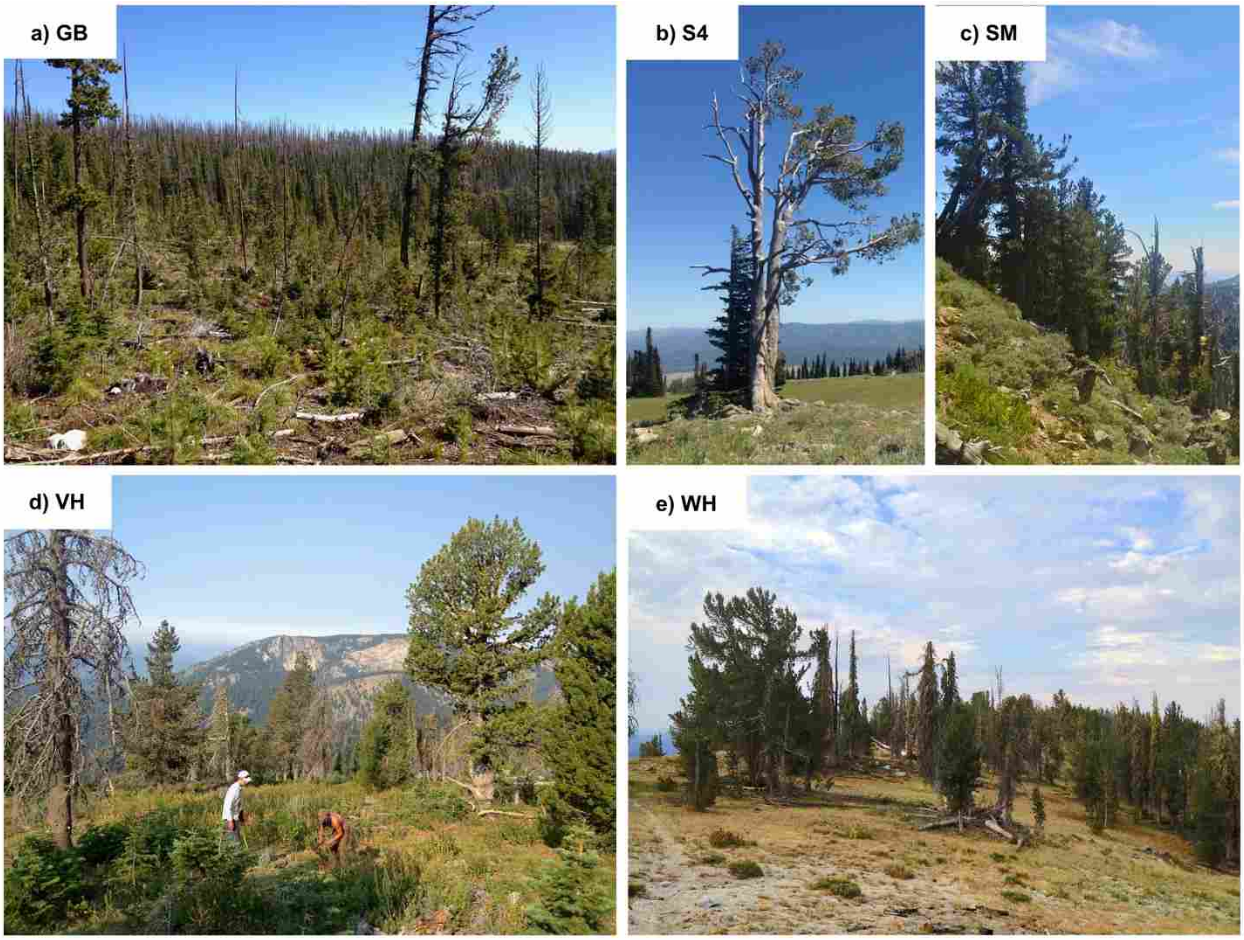


Figure 3.

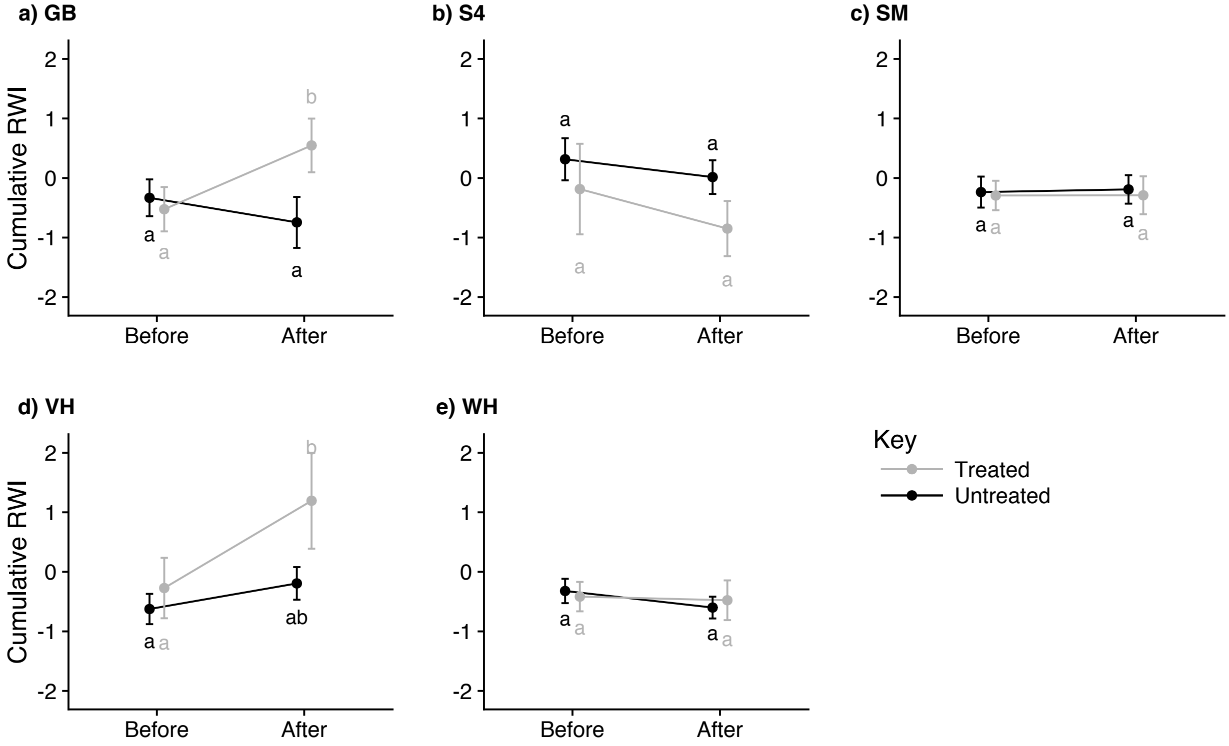

a) GB
b) S4
c) SM
d) VH
e) WH
Cumulative RWI
2
1
0
-1
-2
Before
After
a
b
ab
Key
Treated
Untreated

Figure 4.

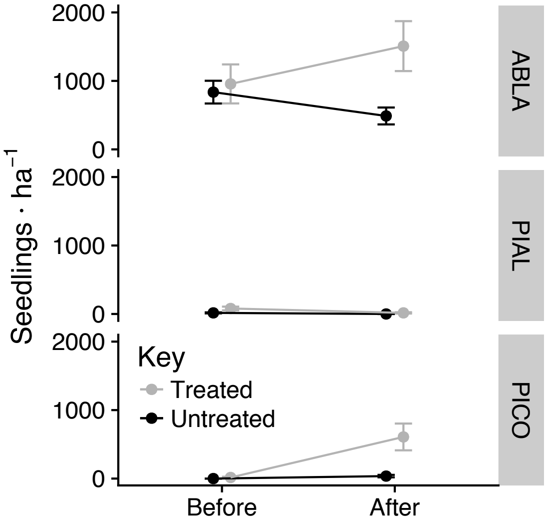

Seedlings · ha^{-1}
2000
1000
0
ABLA
PIAL
PICO
Key
Treated
Untreated
Before
After

Figure 5.

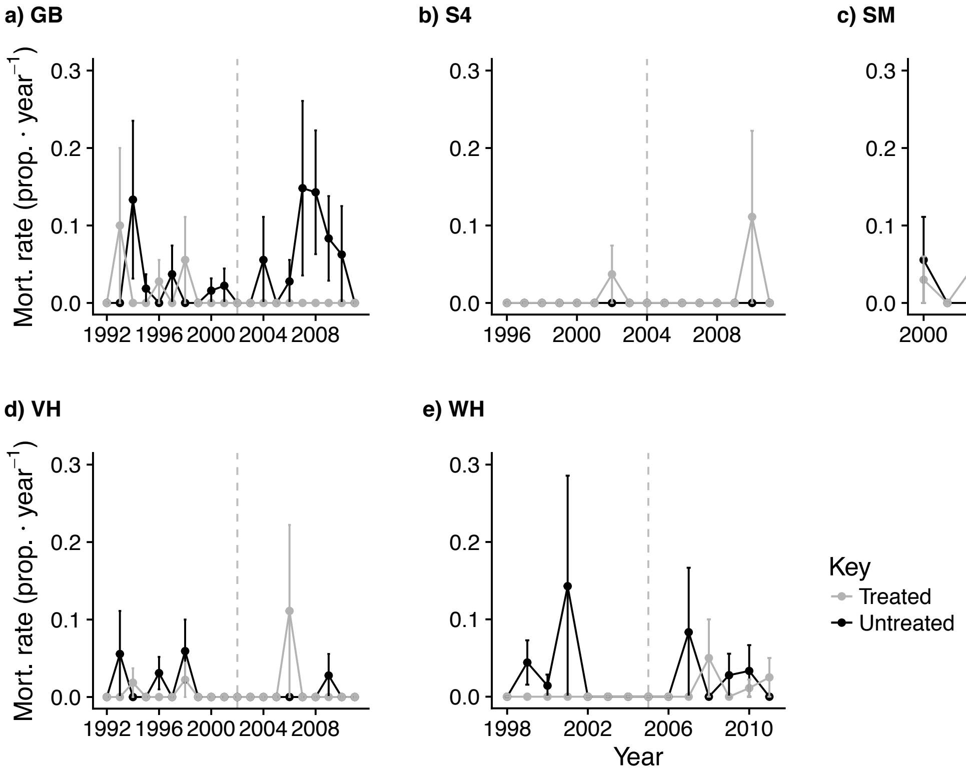
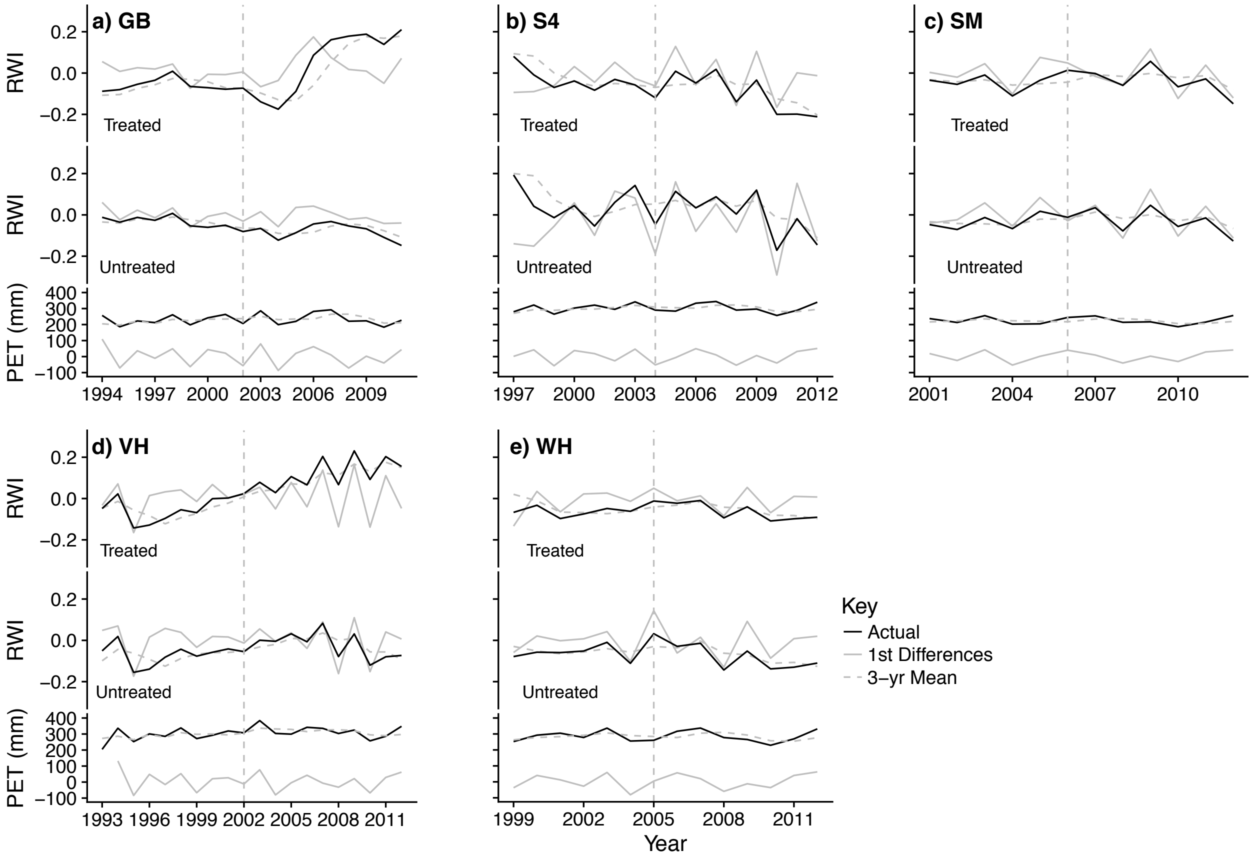

a) GB
b) S4
c) SM
d) VH
e) WH
Mort. rate (prop. · year^{-1})
0.3
0.2
0.1
0.0
1992
1996
2000
2004
2008
1998
2002
2006
2010
Year
Key
Treated
Untreated

Figure 6.



a) GB
b) S4
c) SM
d) VH
e) WH
RWI
PET (mm)
Treated
Untreated
0.2
0.0
−0.2
400
300
200
100
0
−100
1994 1997 2000 2003 2006 2009
1997 2000 2003 2006 2009 2012
2001 2004 2007 2010
1993 1996 1999 2002 2005 2008 2011
1999 2002 2005 2008 2011
Year
Key
Actual
1st Differences
3−yr Mean

Chapter 2: High survival of whitebark pine in the treeline ecotone after mountain pine beetle outbreaks suggests a role for krummholz zones as disturbance refugia

Abstract

Mountain pine beetles (*Dendroctonus ponderosae*; MPB) have caused extensive mortality of whitebark pine (*Pinus albicaulis*) throughout the species' range. In the highest mountains where these trees occur, they grow across alpine treeline ecotones – the vegetation gradients where growth forms transition from trees to shrub-like krummholz. Although treeline whitebark pine exist within a broader landscape of widespread MPB-caused mortality, some of these krummholz-form populations appear to have survived the most recent outbreaks. This observation motivated the hypothesis that stunted growth forms in the upper treeline ecotone escape MPB attack and that these habitats serve as disturbance refugia for whitebark pine. In order to assess whether treeline ecotone populations, and in particular the krummholz growth form, could serve as refugia for whitebark pine from the most recent MPB outbreaks in the US Northern Rocky Mountains and to distinguish between mechanisms unique to alpine treeline ecotone edges and mechanisms that might cause morality gradients at other forest edges, I surveyed whitebark pine mortality along 500 m transects at alpine treeline and other forest edges at 10 randomly selected sites in the US Northern Rocky Mountains. Mortality was nearly absent near alpine treeline edges (mean of 0.03 % dead within 100 m from the edge), but not at other forest edges (mean of 19.8 % dead within 100 m from the edge). This supports the hypothesis that upper treeline ecotone habitats are refugia, and that treeline whitebark pine may avoid MPBs because of transitions in growth form. Although reproductive output was limited near alpine treelines edges (means of 16 cones per ha and 12.9 viable seeds per cone within 100 m from the edge) compared to in the subalpine forest (means of 317.1 cones per ha and 32.5 viable seeds per

cone 100-500 m from the edge), the fact that there were trees producing viable seed suggests that treeline habitats may still serve as population refugia over long time periods. However, surviving whitebark pine existed at all elevations at greater density than dead ones (by ~236 per ha) across the study region, indicating a strong potential for these forests to recover from the recent MPB outbreaks in the short-term without treeline refugia.

Introduction

Widespread tree mortality is occurring globally as forests react to the impacts of climate change (van Mantgem et al. 2009, Allen et al. 2010, Anderegg et al. 2015). Increasing drought stress and warmer temperatures have precipitated outbreaks of phytophagous insects (Anderegg et al. 2015, Stephens et al. 2018). For instance, in western North America, mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks have been a leading cause of mortality of whitebark pine (*Pinus albicaulis*; Macfarlane et al. 2013, Jules et al. 2016, Meyer et al. 2016), a high-elevation species categorized as warranting listing as an endangered species in the U.S. (NRDC 2008) and listed as endangered in Canada (COSEWIC 2010). Because temperature directly affects MPB population and outbreak dynamics, high-elevation habitats have become more suitable for MPB as climates warm (Bentz et al. 1991, Logan and Powell 2001, Hicke et al. 2006). Increasing temperatures and recent MPB outbreaks have led to projections of a shrinking bioclimatic niche of whitebark pine (e.g., Chang et al. 2014). However, much remains unknown about how whitebark pine populations will respond to these impacts. In this study, I investigate one potential mode of resilience in tree populations to severe climate-related disturbances: the potential of alpine treeline ecotone habitats to serve as refugia for whitebark pine from MPB outbreak.

Whitebark pine is a common, and often dominant, species forming alpine treelines throughout its range in western North America (Arno 1984). Whitebark pine alpine treeline ecotones are gradients from forest or woodland with tall trees – the timberline – to dispersed shorter stature trees – the treeline, *sensu stricto* – and finally to patchy shrub-like krummholz growth forms that extend into the alpine zone and form the tree species limit and the upper edge of the ecotone (Körner and Paulsen 2004). In whitebark pine populations impacted by MPB outbreaks, these alpine treeline ecotone habitats are hypothesized to serve as refugia. In their extensive aerial survey of MPB-caused whitebark pine mortality in the Greater Yellowstone Ecosystem, Logan et al. (2010) and Macfarlane et al. (2013) observed that mortality gradients often corresponded with growth-form gradients at treeline – live whitebark pine krummholz in the treeline ecotone persisted above forests with extensive mortality. Macfarlane et al. (2013) hypothesize that "long-term survival of the species likely resides in the [krummholz] growth form found throughout the ecosystem near treeline, because it is too small for beetles to attack..." Thus far, no fine-scale data exist to evaluate this hypothesis, although survivors at treeline are visible in some locations (Fig. 1).

Refugia are one mechanism by which populations or ecosystems may be resilient to the impacts of disturbance, climate change, or predators over various time scales. The term refugia originally referred to *glacial* refugia – contracted areas that maintained temperate plant populations in the otherwise unfavorable climate of glacial cycles during the Pleistocene (Bennett and Provan 2008), but has since become a more inclusive term used to describe subsets of populations or ecosystems that are relatively buffered from impacts or changes occurring elsewhere (e.g., Morelli et al. 2016, Meddens et al. 2018). As commonly used, refugia are not defined by their size, although this may be a critical aspect of their existence, depending on the species involved. For example, dispersed 'microrefugia' are proposed as a mechanism of rapid recolonization of expanding habitats after the Last Glacial Maximum (Rull 2009). Refugia in predator-prey dynamics can be spatial (e.g., sites where predators are restricted or less abundant) or they can be related to prey size, typically where prey above a certain size threshold become less vulnerable to predators (Bechara et al. 1993). These refugia maintain prey populations and buffer top-down control because new populations are able to expand out from the refugial populations (Costamagna and Landis 2011). A treeline refugium for whitebark pine, if present, would be unique among refugia because it would represent a disturbance refugium, but also because treeline habitats harbor atypical populations of stunted individuals. However, the unique characteristics of these treeline populations may be intrinsic to their survival.

The small stems and contorted shapes of krummholz and other treeline growth forms may underpin the mechanisms of whitebark pine survival in treeline ecotone habitats. MPBs have long been known to prefer larger diameter trees (Cole and Amman 1969). The ultimate causes for this preference are thought to be driven by improved brood success in trees with thicker phloem, which tend to be of larger diameter (Amman 1972). Proximally, however, the causes of MPB preference for large trees appear to be related to dispersal and detection. Beetles may use visual cues to select hosts (Strom et al. 1999, Campbell and Borden 2006a, 2006b) or they may land randomly and initiate galleries based on chemical cues after landing (Hynum and Berryman 1980, Raffa and Berryman 1982). Either mechanism can explain the observation that smaller-diameter pines are attacked that are close to emergence trees, perhaps because they present a larger target than distant small trees (Mitchell and Preisler 1991, Perkins and Roberts 2003). The characteristic decrease in size and stature along alpine treeline ecotones creates ever more distance from likely emergence trees. The vertical orientation of most tree stems may also influence beetle attraction (Shepherd 1966). The krummholz growth form may interfere with these typical visual cues even if it can possess large stems, since main stems are at a low angle to the ground and are often covered by foliage. Foliage cover may also physically shield krummholz stems by blocking beetles from landing on the bark surface. On the other hand, alpine treeline edges may share attributes with other forest edges that affect MPB spread and impacts; edges are known to enhance and diminish the effects of herbivores, depending on the behavior of the herbivore (Cadenasso and Pickett 2000). There is some evidence that forest edges enhance MPB impacts via reduced dispersal rates, particularly when the edge borders an area of low host density (Powell and Bentz 2014, Chen et al. 2014, Powell et al. 2018). Because temperature is a central factor in beetle development and the synchrony of emergence – both are crucial to MPB success in killing host trees (Bentz et al. 1991), low temperatures in the upper treeline ecotone due to the adiabatic lapse rate typically observed as one ascends mountain slopes (Barry 2008) is another characteristic of alpine treelines that could influence MPB-caused mortality.

Viable refugial habitats must also contain individuals capable of reproduction for persistence and to allow expansion into other environments. Treeline growth-forms of subalpine trees, however, have generally been observed to have reduced reproductive output due to severe growing conditions (Tranquillini 1979, Körner 2012). Although treeline populations of whitebark pine may act more as population sinks than sources, there is some evidence that reproduction does occur within these marginal habitats (Rogers et al. 1999) although rates of cone production and seed viability have not been previously examined. Additionally, though treeline reproductive output may be small, seeds from these regions may reach far away locations due to the long distance dispersal ability of Clark’s nutcrackers, the primary dispersal agent for whitebark pine (Tomback 1982, Lorenz et al. 2011).

Given the expected reproductive limitations of treeline whitebark pine, *in situ* forest survivors are also likely to contribute to future populatons. Indeed, treeline habitats may not be crucial refugia if there are sufficient survivors in forest interiors. The MPB preference for larger diameter trees should result in surviving seedlings, saplings, and small trees within attacked stands. In fact, there is some evidence that MPB-impacted forests may provide ideal seedling establishment sites; Larson and Kipfmueller (2010) observed a pattern of higher regeneration of whitebark pine in forests that had heavy MPB-caused mortality. If small diameter whitebark pines are abundant, these survivors might allow for population recovery between outbreaks without refugia. An understanding of the patterns of whitebark pine survivors of widespread MPB outbreaks is crucial for predicting the future status of these ecologically important trees.

The purpose of this research is to determine if treeline ecotone populations could serve as refugia for whitebark pine from MPB outbreaks in the US northern Rocky Mountains and whether these populations represent the greatest potential for future whitebark pine population recovery. I addressed these goals in three ways. First, I surveyed live and dead whitebark pine across treeline ecotones downslope into subalpine forests to determine if survival near the treeline is a common pattern. Second, I distinguished between possible mechanisms for this pattern by comparing results from alpine treeline ecotone edges with results from other forest edges. Third, I characterized reproductive output in surviving whitebark pine across the treeline ecotone downslope into subalpine forests. Four research questions guide this study:

(1) Do krummholz whitebark pines in the treeline ecotone have higher rates of survival of mountain pine beetle outbreaks than do upright trees in the forest zones in the US Northern Rocky Mountains?

(2) Does whitebark pine survival differ between populations along alpine treeline ecotones and other forest to non-forest ecotones?

(3) What is the current reproductive output (number of cones and viable seed) of krummholz whitebark pine in treeline habitats relative to subalpine forests?

Materials & Methods

Field site selection

Upper subalpine forests in the US northern Rocky Mountains typically consist of mixed-species stands of subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea englemannii*), occasionally limber pine (*Pinus flexilis*), and whitebark pine, which often forms nearly pure stands at the highest elevations near treeline (Pfister et al. 1977, Arno and Hoff 1989). I used GIS layers of MPB-caused forest mortality, alpine vegetation type, and whitebark pine occurrence to create a sampling frame of possible field site locations using ArcMap (ESRI 2010). Maps of MPB-caused mortality in the US states of Idaho, Montana, and Wyoming were obtained from the USDA Forest Service's Forest Health Protection aerial detection surveys (ADS; Forest Health Protection 2014). ADS data tend to underestimate the magnitude of beetle-caused mortality because surveys are not flown everywhere in every year and surveys are biased toward recording very recent mortality (1-2 years post-outbreak), as only trees with red needles are detected (Meddens et al. 2012, Macfarlane et al. 2013). I used a detailed 2008 aerial survey focused specifically on MPB-caused mortality of whitebark pine in the Greater Yellowstone Ecosystem that addressed many limitations of ADS data in that region (Macfarlane et al. 2013). I then filtered all mortality data to include only polygons where MPB-caused mortality was observed in whitebark pine and where these areas overlapped with or were adjacent to alpine vegetation recorded in USGS GAP land cover layers (US Geological Survey Gap Analysis Program (GAP) 2011). Additionally, I noticed gaps in ADS coverage within the range of whitebark pine (range map from Whitebark Pine Ecosystem Foundation 2014), but where MPB-caused mortality and treelines were were apparent from stock ESRI World Imagery satellite photographs. These areas included parts of the Selway-Bitterroot, Anaconda-Pintler and

Scapegoat wilderness areas, and the Flint Creek Range, East Pioneer Mountains, and Highland Mountains in Montana. I included these areas in the sampling area by visually identifying the elevation of the upper edge of the treeline ecotone in ArcMap using satellite imagery and digital elevation models. I then defined contour lines that were ~200-300m in elevation below these edges. All land area above these contours was added to the sampling area.

After all potential sampling area had been identified, I used stock ESRI World Imagery satellite photos to manually verify that the resulting polygons are in alpine treeline habitats (high mountain areas with apparent growth form changes or forest density gradients typical of treeline), contain some whitebark pine (distinctive crown shape is visible), and contain some evidence of recent MPB-caused mortality in the subalpine forests (red or grey standing trees). The final sampling frame is the collection of polygons shown in blue in figure 2.

I selected field sampling locations within the sampling frame by randomly placing 10 sampling points using the random point tool in ArcGIS (n = 10; Fig. 2). Field sampling locations were determined independent of accessibility. All sampling points landed within US National Forests. Three of the 10 landed in federally designated wilderness areas. At each sampling point, I initiated two transects: one at the nearest alpine treeline ecotone edge (TL) and one at the nearest other forest edge (OE) (Fig. 3). I defined TL edges as the highest elevation 'outpost' krummholz (i.e., the local whitebark pine species limit, *sensu* Körner and Paulsen 2004) that was visible from satellite imagery. OE edges were defined as whitebark pine forest boundaries that were at least 150 m from the nearest contiguous forest and could be formed by avalanche paths, forest-meadow interfaces, geologic and topographic edges, or other forest margins that are not associated with elevation-related boundaries. TL transects were oriented downslope using contour lines to capture the transition from krummholz into subalpine forest. OE transects were oriented perpendicular to the edge extending into the forest. All transects were 50 m wide and

500 m long (map distances). Transects were divided into twenty 50 m by 25 m sections (the unit of analysis). After transects were positioned on the landscape, transect section outlines were ported to a GPS device to guide sampling in the field.

Field sampling

Within each transect section, I tallied all dead and live whitebark pine krummholz and upright trees. Krummholz were defined as whitebark pine with ‘crowns’ that were 1 m or more across and at least as wide in any horizontal dimension as they were tall, but were less than 3 m tall. Trees were defined as any whitebark pine stems that were at least 3 m tall. Fused stems were considered separate if their junction was below 1.4 m from the ground. Smaller krummholz-type and shorter upright stems were considered saplings or seedlings and were not counted in mortality surveys. I made this distinction to avoid assigning the krummholz growth form to young individuals that might become trees. I later used these classifications to calculate the proportion of tree-form whitebark pine in each transect section.

I recorded cause of death for dead whitebark pines that retained some bark – I assumed that krummholz and trees without bark died long before the most recent MPB outbreaks. MPB was determined as the cause of death by peeling away bark and identifying of one or more of the following: j-shaped galleries, pitchout, or frass (according to USDA Forest Service Common Stand Exam criteria; USDA Forest Service 2012). The cause of death in whitebark pine that had evidence of both white pine blister rust (swollen stems, rodent chewing, and excessive pitch bleeding) and MPB attack was assumed to be MPB. Although WPBR infection may increase the likelihood of MPB attack in some cases (Bockino and Tinker 2012), the larvae of tree-killing beetles like MPB feed on living phloem. Thus, a tree with signs of MPB attack was most likely killed by the attack, not by WPBR before the attack. Cause of death was recorded as ‘other’ if

MPB evidence was absent. Mortality field sampling was completed in July-October 2015 and July-August 2016. I estimated pre-outbreak density of whitebark pine as the sum of both live and dead individuals (krummholz and trees) in each transect section. I was not able to sample 3 sections along the OE transect at the Lemhi site that were located on a small cliff.

To characterize changes in size distributions along alpine treeline ecotone edges, I tallied all living and dead whitebark pine by height (individuals < 3 m tall) or diameter at breast height (> 3 m tall) classes along an additional, separate TL transect at one of my sites.

I characterized the reproductive contributions of whitebark pine populations along treeline ecotone edges at a subset of 3 sites that were nearest to roads (table 1). At these sites, I established 1-2 extra (peripheral to original mortality transects) TL transects (all 50 m x 500 m) by choosing the next nearest treelines from the original sampling points (2 – 3 cone count transects at each of 3 sites; *n* = 7 transects total). Transects were oriented downslope using the same methods described above and divided into ten 50 m x 50 m sections. In each section of each transect, on all cone-bearing whitebark pines I counted the number of cones visible from the ground using binoculars. I also collected cones to estimate viable seed production on all cone-bearing whitebark pines that were safe to climb or had cone-bearing branches that were accessible from the ground (1-7 cones per whitebark pine). I caged cones along 4 of the 7 cone-count transects (all 3 sites represented; table 1) in July 2016 to protect them from seed predators and then collected the cones in September-October 2016. Not all transect sections containing cone-bearing whitebark pine had trees that were safe to climb, but all 50 m x 50 m transect sections were represented with at least one cone-bearing whitebark pine across all transects and sites. The number of cones collected varied both within and across sites. Viability of seeds from each cone was estimated using x-ray images (Berdeen et al. 2007). A seed was considered viable if an embryo was visible. X-rays were performed at the USDA Forest Service Nursery in Coeur d'Alene, Idaho.

Analyses

To determine if survival of whitebark pine was higher near the edge along alpine treeline ecotones than it was at lower points on the transect, and if this pattern was stronger along alpine treeline ecotone edges compared to other forest edges, I constructed a negative binomial generalized linear model predicting the number of MPB-killed whitebark pine in each transect section (25 x 50 m) as a function of 1st and 2nd- order orthogonal polynomials of distance from edge (the centroid distance of each transect section from the edge), edge type, and the interactions between each polynomial term with edge type (distance x edge type, distance^2 x edge type). Site was included as fixed block effect to account for between-site variability in MPB-caused mortality (e.g., due to differences in MPB attack pressure and pre-outbreak stand density). I expected that MPB-caused mortality would have a curvilinear relationship with distance from edge and that this relationship may vary depending on edge type. I then tested the null hypotheses that the number of MPB-killed whitebark pine was equivalent for different values or levels of each predictor term in the model using a Chi-squared analysis of deviance test. Transect sections that contained no whitebark pine trees or krummholz (live or dead) were removed from the dataset (30 of 397 total sections across all sites) prior to analyses to avoid the influence of these false zeros in the interpretation of effects.

To test for overall differences in density of post-outbreak living and MPB-killed whitebark pine across whole transects, I performed a two-way factorial ANOVA (site as the unit of analysis) with density type (live vs. MPB-killed) and transect (TL vs. OE) as factors. I then performed a Tukey HSD post-hoc analysis to determine differences between means.

Patterns in cone density in each large transect section (50 x 50 m) were assessed with a negative binomial generalized linear model, with distance from edge and site (as a blocking factor) as predictors. I tested the null hypothesis that cone density was equivalent between distances using an analysis of deviance test. Sample sizes of seed counts were too low in some transect sections across sites (two different sections were represented at just one site each) to fit meaningful models predicting seed attributes as a function of distance. I give a descriptive interpretation of this data instead.

All analyses were performed in the R environment (R Core Team 2018).

Results

Whitebark pine mortality was significantly lower within the alpine treeline ecotone populations, which had nearly zero MPB-killed whitebark pine until ~125 m map distance below the highest outpost krummholz (I observed 1 krummholz that had been killed by MPB), than near other forest edges or in forest interiors (Fig. 4). This pattern was reflected by a significant interactive effect on total MPB-killed whitebark pine between distance from edge and edge type ($\chi^2 = 76.99$, df = 2, $P < 0.0001$, table 2), but no significant main effect of distance ($\chi^2 = 5.47$, df = 2, $P = 0.065$). There was a significant blocking effect of site, reflecting substantial among-site differences in overall mortality rates (2-24% mortality for TL transects, 1-85% for OE transects; $\chi^2 = 156.18$, df = 9, $P < 0.0001$; tables 2 and 3).

I found that density of living whitebark pine was greater, by 236 whitebark pines per ha on average, than the density of MPB-killed whitebark pine along both ecotone types ($F_{1,\,736} = 115.7$, $P < 0.0001$; Fig. 5). Edge type was not important for this pattern: live density was higher on average than MPB-killed density over the study region. There were no statistically significant differences in densities overall between OE transects than TL transects ($F_{1,\,736} = 2.65$, $P = 0.1$), and there was no interaction between status (live vs. dead) and edge type on whitebark pine density ($F_{1,\,736}$ = 0.06, P = 0.8).

There was a clear pattern of mortality with distance from the edge along the one TL transect where I surveyed size distributions (Fig. 6). But the mortality pattern was only apparent in larger diameter (> 10 cm DBH) whitebark pine, with a sharp increase in density at ~ 200 m from the edge. Most of these larger diameter trees were dead, and they represented the majority of the mortality. Most smaller diameter (≤ 10 cm DBH) whitebark pine were surviving – these included some trees (> 3 m tall) and seedlings of any size. Consistent with the observed pattern of high densities at the lower treeline ecotone along mortality transects, the highest density observed was of small whitebark pines in this position (Fig. 6).

Upper treeline habitats had less reproductive output than did the lower subalpine forests (in 2016; Fig. 7). Lower elevations typically had higher cone density (range 0 – 2404 cones·ha^{-1}) than did higher elevations near the treeline edge, although overall cone density varied among sites (site means between 85 – 502 cones·ha^{-1}). I found a statistically significant effect of distance from edge on cone density (χ^2 = 21.3, df = 1, P < 0.0001) and a significant effect of site on overall cone density (χ^2 = 11.9, df = 2, P = 0.003). Cone production per cone-bearing whitebark pine varied greatly at all elevatons. Although sample sizes were low at high elevations, these observations were within the range of observations at lower elevations. However, cones at high elevations did appear to contain fewer viable seeds than those at lower elevations (Fig. 7).

Discussion

Identification of refugia, and an understanding of the mechanisms that maintain them, will be an important aspect of conserving future distributions and abundance of forest species in an era of rapid climate change (Millar et al. 2007a, Dobrowski 2011, Morelli et al. 2016). My findings suggest that populations of the krumholtz growth form may serve as a refugia for whitebark pine in areas with high pressure from MPB. Whitebark pines in the alpine treeline ecotone persisted through the most recent MPB outbreaks, despite mortality in the forests below. This pattern was unique to treeline edges – which also have unique growth form transitions not found at other edges. These results support the hypothesis that krummholz whitebark pines evade MPB because of characteristics of their shrub-like growth form, and that treeline habitats may be long-term refugia from this disturbance. However, I also found that there are many more surviving whitebark pine trees in subalpine forests of the US northern Rocky Mountains than were killed in the most recent MPB outbreaks. This finding indicates that some whitebark populations remain intact and that treeline refugia may not be necessary for heavily impacted populations to recover in the short-term. It further suggests that there may not be a need for management intervention in some locations, and that some management actions may be harmful, e.g., the use of prescibed fire where survivors are smaller trees, saplings, and seedlings.

The effects of ecotones on MPB-caused mortality in whitebark pine appears to be strongest at alpine treeline edges, suggesting that the unique growth-form transition of these ecotones is implicated in mechanisms moderating MPB-caused mortality. Stems in some treeline whitebark pines are smaller diameter (Clausen 1965) and krummholz are often covered in a mat of foliage in addition to being prostrate in stature, all of which may make these individuals less likely to be attacked by MPB because of disruption of visual cues or physical blockage. Another mechanism by which some krummholz may evade MPB attack is through strip-bark stems – a common feature of krummholz (King and Graumlich 1998) where partial cambium death on the wind-exposed face of stems results in bark retained only on the sheltered ground-facing portion. The interpretation that unique attributes of alpine treeline edges disrupt of beetle spread or attack is also supported by recent research suggesting that MPBs may cause relatively higher mortality at forest edges (Powell and Bentz 2014, Chen et al. 2014, Powell et al. 2018). Thus, the decline in MPB-caused mortality at treeline edges likely indicates a decline in the density of suitable hosts. This is in contrast with the mortality pattern observed near other forest edges, where the decrease in mortality was less dramatic or there was an increase.

Lower temperature in the treeline ecotone is another plausible explanation for the observed survival near alpine treeline edges. I do not have fine scale temperature data along my treeline transects during the outbreaks (~2001-2009; Creeden et al. 2014) and cannot directly evaluate this possibility. Still, it is well known that temperatures decrease with increasing elevation (due to adiabatic lapse rates; Barry 2008) and that MPB population dynamics are sensitive to temperature (Logan and Powell 2001, Hicke et al. 2006), as is the case for most insects. For example, Piper and Fajardo (2014) reported a sharp elevation boundary in defoliation of *Nothofagus pumilio* in Chilean Patagonia caused by caterpillars of *Ormiscodes amphimone*, which they attributed to an elevation-related thermal threshold of the caterpillar. Low temperatures, however, would likely influence beetle brood success more than attack density (Dooley et al. 2014). Thus, if temperature were the driving factor, I would expect to observe more mortality in treeline whitebark pine from MPB attacks – if not from the action of larvae then by associated fungi introduced during attack (Six and Wingfield 2011). Instead, this was exceedingly rare – I found only one dead krummholz with signs of MPB attack across the 10 field sites (834 total krummholz counted). Another potential mechanism is interruption of pheromone signals (or of beetle flight) by wind – pheromone plumes are diluted by circulation in more open stands (Thistle et al. 2004). Although all forest edges are likely windier than forest interiors, alpine treeline edges are likely windier places than their lower elevation counterparts. However, upslope winds might facilitate transport of beetles to habitats above treeline.

Surviving trees at lower elevations will likely have an immediate impact on whitebark pine populations, given their abundance and greater reproductive potential, than treeline refugia. My findings of higher densities of surviving whitebark pine than dead are consistent with what Goeking and Izlar (2018) found in smaller size classes of whitebark pine, although I reach a different conclusion than these authors did about the future of whitebark pine populations. Goeking and Izlar (2018) focused on the loss of larger trees (> 12.7 cm diameter at breast height; DBH) and used declining basal area of living whitebark pine as primary indicator of population decline. Basal area is a potenitally misleading indicator of population status because larger dead trees contribute disproporionately to basal area. This focus on large trees ignores crucial demographic processes. For example, Jules et al. (2016) found that whitebark pine population growth was most sensitive to the status of whitebark pines in the 0.01-10 cm DBH size class, which had the highest survivorship. The whitebark pine trees surveyed in this study included some – but not all – of these smaller diameter trees (I counted as trees all whitebark pines > 3 m tall, regardless of diameter). However, because smaller lower elevation survivors will grow into larger trees that are suitable hosts for MPB, they may be vulnerable in future outbreaks (Perkins and Roberts 2003). On the other hand, Millar et al. (2007b) found that limber pine (*Pinus flexilis*) in the Sierra Nevada mountains, California, USA killed by MPBs during a drought were more sensitive to climatic fluctuations than were surviving trees, which had higher relative survival during a subsequent drought. Millar et al. (2012) found a similar pattern in whitebark pine killed by MPBs – trees that survived had higher growth during the relatively warm and dry 20th century than did dead trees, though the opposite was true during the cooler and wetter 19th century. The authors of both of these studies conclude that MPBs may have selected out the trees that were least adapted to current climate conditions. Indeed, recent genetic work in the Pioneer Mountains, Montana, USA revealed that whitebark and lodgepole pines that survived recent

MPB outbreaks are genetically distinct from MPB-killed trees, further suggesting the possiblility of heritable resistance (Six et al. 2018). Thus the high numbers of surviving trees exposed to MPB observed in this study may represent whitebark pine that are more resilient to MPB outbreaks than the previous populations as whole.

A continuting risk to survivors at all elevations is white pine blister rust (WPBR; caused by the exotic fugus *Cronartium ribicola*), which infects whitebark pine of all sizes and ages, and has been documented in krummholz (Resler and Tomback 2008). While this disease may kill trees very slowly, it kills branches and tops of trees where female cone production occurs, causing a decline in fecundity (Maloney et al. 2012). Trees with severe WPBR infections may also have greater risk of attack from MPB (Bockino and Tinker 2012). However, a 12-year demographic analysis of whitebark pine populations in Crater Lake National Park, Oregon, USA, found that MPBs – not WPBR – were responsible for population declines, despite a nearly 45% infection rate by the end of the study period (Jules et al. 2016). Maloney et al. (2012) similarly found that whitebark pine populations in the Lake Tahoe Basin, California, USA were stable due to high survivorship despite a mean WPBR infection rate of 35% (range 1 to 65%). Although these results likely cannot be extrapolated to regions with much higher infection rates like the Crown of the Continent ecosystem (northwest Montana, USA into the Canadian provinces of British Colombia and Alberta) where infection rates of ~80% have been observed (Smith et al. 2013), they indicate that MPB outbreaks present a more acute danger to whitebark pine populations than WPBR. Additonally, these studies documented continuing increases in infection rates over time – WPBR may become a more important factor affecting whitebark pine populations in more areas throughout the species's range and may currently represent the greatest threat to krummholz populations.

Treeline ecotone habitats are also not immune to fire and are tracking the wildfire trends of lower elevation forests (Cansler et al. 2016). As climates warm, fire risk to treeline whitebark pine may also increase. Interactions between ameliorating condiditons for establishment above current tree species limits and morality from fire are expected to result in complex changes in the structure of alpine treeline ecotones (Cansler et al. 2018). However, some of these scenarios may result in more area covered by krummholz in the treeline ecotone, with higher species limits and lower timberlines. If possible, whitebark pine krummholz zones and beetle impacted forests should be protected from wildfire – smaller-diameter surviving whitebark are especially vulnerable to mortality from fire (e.g., Keane and Parsons 2010). The use of prescribed fire should thus be avoided in these forests.

Although there is some uncertainty for the future of forest survivors of the most recent MPB outbreak, treeline populations may represent stable refugia that are resilient to disturbances far into the future. For example, krummholz whitebark pine in the Sierra Nevada mountains, CA can live over 1000 years expanding downwind via branch-layering, persisting despite multiple losses of the older stems. (King and Graumlich 1998). Populations of long-lived species can have low apparent fecundity yet still maintain positive growth rates due to low mortality rates (Barber 2013). In the year that I sampled, cone and viable seed production was lower in treeline habitats than in the subalpine forest. This may be an accurate reflection of the relative reproductive contribution of whitebark pine in these stressful environments given the resource costs of masting (Sala et al. 2012). Nonetheless, my results indicate that viable seed production does occur in these habitats. The periodic nature of mast-seeding in whitebark pine (e.g., Crone et al. 2011) and the longevity of some krummholz suggests further suggests that occassional mast seeding events may allow reproductive contributions from treeline habitats over long time spans. For example, I observed an abundant cone crop in August 2018 at a treeline site in the Pioneer

Mountains, Montana, USA (Fig. 8). Furthermore, there is genetic evidence of establishment in krummholz mats from seed produced by whitebark pine krummholz (Rogers et al. 1999).

For montane species, complex mountainous terrain can allow for the persistence of suitable microclimates in a changing climate (Dobrowski 2011, Morelli et al. 2016, Millar et al. 2018). Insects may cause species extirpations despite availability of suitable refugia if refugial environments are also suitable for insects. However, many insect outbreaks are episodic – i.e., mortality pressure on tree populations might not be constant into the future, possibly allowing for some population recovery between outbreaks. Indeed, I found that there are many surviving whitebark pine in MPB-impacted subalpine forests. While there is some uncertainty about the future of survivors in subalpine forests, krummholz whitebark pines in treeline ecotones represent refugia from current and future MPB outbreaks that will at least allow for population persistence and may eventually contribute to population establishment in other habitats.

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Tables

Table 1. Site coverage of sampling actions performed in this study. The mortality and survivor tallies include two transects at each randomly-selected field site – one along an alpine treeline ecotone edge (TL) and one along another forest edge. Whitebark pines were classified as krummholz or trees and live or dead. I conducted cone counts and collection along TL edges at the three most accessible sites. A detailed survey of diameter and height size classes of each live and dead whitebark pine was conducted at 1 TL transect. All transects were 50 m wide by 500 m long (horizontal map distance), length oriented perpendicular to the edge.

Site	Mort./survivor tally	Cone counts	Cone collection	Size distribution
Beartooth	✓	✓ (2 TL transects)	✓ (1 TL transect)	-
Cedar	✓	-	-	-
Gravelly	✓	✓ (2 TL transects)	✓ (2 TL transects)	✓ (1 TL transect)
Hoback	✓	-	-	-
Lemhi	✓	✓ (3 TL transects)	✓ (1 TL transect)	-
Pioneer	✓	-	-	-
Snowcrest	✓	-	-	-
Targhee	✓	-	-	-
Wind River	✓	-	-	-
Woodward	✓	-	-	-

Table 2. Analysis of deviance table of predictors of the proportion of MPB-killed whitebark pine in transect sections from a polynomial negative binomial generalized linear model. Poly(dist,2): 1st and 2nd order orthogonal polynomial terms of distance from edge along transects. Edge type: alpine treeline ecotone or other forest edge. Site: the 10 field sampling sites (Fig. 2). The last term is an interaction term between distance and edge type.

Predictor	χ^2	df	P-value
poly(dist,2)	5.47	2	0.065
edge type	31.27	1	< 0.001
site	156.18	9	< 0.001
poly(dist,2) x edge type	76.99	2	< 0.001

Table 3. Summary of results across whole transects at each site sampled in this study. Whitebark pine edge types are alpine treeline ecotones (TL) or other forest edges (OE). Proportion tree-form is relative to krummholz growth forms. Values are means of all transect sections (*n* = 20) ± 1 standard error of the mean. PIAL: *Pinus albicaulis* (whitebark pine).

Site	Edge type	MPB-killed PIAL (proportion)	Tree-form PIAL (proportion)	Pre-outbreak PIAL density (no.·ha^{-1})
Beartooth	TL	0.04 ± 0.02	0.43 ± 0.11	319 ± 67.7
	OE	0.05 ± 0.02	1.00 ± 0.00	453 ± 51.2
Cedar	TL	0.16 ± 0.04	0.71 ± 0.10	365 ± 89.1
	OE	0.27 ± 0.07	1.00 ± 0.00	139 ± 21.6
Gravelly	TL	0.14 ± 0.05	0.66 ± 0.10	344 ± 75.9
	OE	0.85 ± 0.04	1.00 ± 0.00	368 ± 78.9
Hoback	TL	0.17 ± 0.06	0.71 ± 0.12	143 ± 53.2
	OE	0.74 ± 0.06	1.00 ± 0.00	148 ± 24.5
Lemhi	TL	0.02 ± 0.02	0.64 ± 0.09	242 ± 37.5
	OE	0.03 ± 0.02	1.00 ± 0.00	285 ± 54.8
Pioneer	TL	0.03 ± 0.02	0.83 ± 0.08	949 ± 156.6
	OE	0.01 ± 0.01	1.00 ± 0.00	1411 ± 105.4
Snowcrest	TL	0.24 ± 0.06	0.67 ± 0.10	168 ± 31.5
	OE	0.46 ± 0.04	1.00 ± 0.00	362 ± 38.3
Targhee	TL	0.08 ± 0.04	0.93 ± 0.03	149 ± 18.5
	OE	0.21 ± 0.05	1.00 ± 0.00	309 ± 36.3
Wind River	TL	0.11 ± 0.05	0.80 ± 0.11	298 ± 58.4
	OE	0.20 ± 0.04	1.00 ± 0.00	406 ± 38.1
Woodward	TL	0.17 ± 0.05	0.80 ± 0.08	284 ± 41.8
	OE	0.34 ± 0.08	1.00 ± 0.00	109 ± 28.6

Figure captions

Figure 1. Surviving whitebark individuals at treeline (green band) with extensive mortality (grey trees) in the subalpine forest below. Tobacco Root Mountains, Montana, USA.

Figure 2. Map of the study area in western North America and location of the sampling frame where there is mountain pine beetle-killed whitebark pine near alpine treeline; blue polygons) and field location of beetle-caused mortality transects sites (yellow circles) in the US Northern Rocky Mountains. At each of 10 sites, I surveyed one alpine treeline edge and one other forest edge at each site to compare mortality gradients. Orange circles represent sites where I conducted additional sampling to characterize cone and seed production along alpine treelines.

Figure 3. Design of alpine treeline and other forest edge transect sampling. Edges are represented with thick white lines. Yellow grids represent transects, with twenty 50 m by 25 m sections. All transects were 50 m wide by 500 m long (map distances). Alpine treeline transects were initiated downslope from the local highest elevation ‘outpost’ krummholz whitebark pine. Transects at other forest edges extended into the forest perpendicular to the edge. Other forest edges could be meadows, cliffs, talus slopes, avalanche paths, lakes, etc.

Figure 4. Number of mountain pine beetle-killed whitebark pine (PIAL) along alpine treeline (black dots) and other forest edges (grey dots; *n* = 10 sites). Lines are predictions from a negative binomial model. Grey bands represent 95% confidence intervals around model predictions.

Figure 5. Mean density of living (dashed grey lines) and mountain pine beetle-killed (solid black lines) whitebark pine (PIAL) along alpine treeline and other forest edges (*n* = 10 sites). The

mean percentage of tree-form whitebark pine (in contrast with krummholz growth forms) at each transect position is represented as colored points. White represents 100 % tree-form (0 % krummholz) and red 0 % tree-form (100% krummholz). Grey bands represent ± 1 standard error of the mean.

Figure 6. A.) Patterns of live (dashed grey lines) and dead (solid black lines) whitebark pine (PIAL) in two inclusive size classes along a single intensively sampled alpine treeline transect (*n* = 1). B.) Diameter distribution of live and dead whitebark pine along the same transect. The smallest size class, < 10 cm diameter at breast height (DBH), included trees, saplings, and seedlings of all sizes.

Figure 7. Mean reproductive attributes of whitebark pine (PIAL) along alpine treeline edges at 3 sites in the US northern Rocky Mountains in 2016. Vertical bars represent ± 1 standard error of the mean. A.) Cone density along 7 alpine treeline transects. B.) Cone production expressed as the number of cones produced by each cone-bearing whitebark pine. Numbers in boxes indicate the sample size (number of transects sections containing cone-bearing trees) for each transect position. Points show estimates for all sections containing cone-bearing whitebark pine. C.) Viable seed production expressed as the number of viable seeds in each cone. Numbers in boxes indicate the sample size (number of transect sections where cones were sampled for seed viability analysis). Points show estimates for all sections where cones were sampled. Error bars are absent when there was only 1 sample.

Figure 8. Cone-bearing whitebark pines at treeline in the Pioneer Mountains, Montana, USA.

Figure 1.

Figure 2.

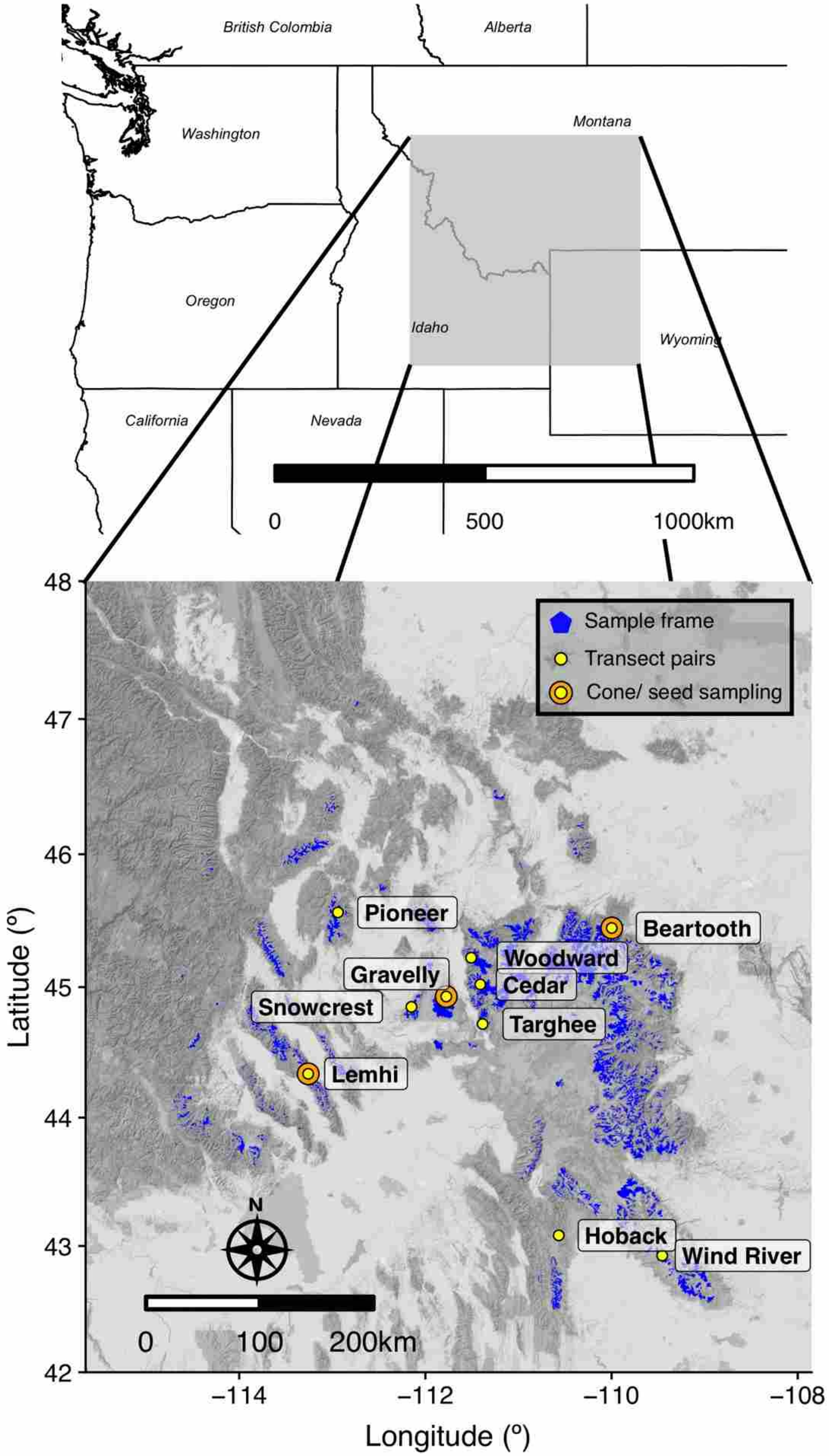

British Colombia
Alberta
Washington
Montana
Oregon
Idaho
Wyoming
California
Nevada
0
500
1000km
Sample frame
Transect pairs
Cone/ seed sampling
Pioneer
Beartooth
Woodward
Gravelly
Cedar
Snowcrest
Targhee
Lemhi
N
Hoback
Wind River
0
100
200km
48
47
46
45
44
43
42
Latitude (°)
−114
−112
−110
−108
Longitude (°)

Figure 3.

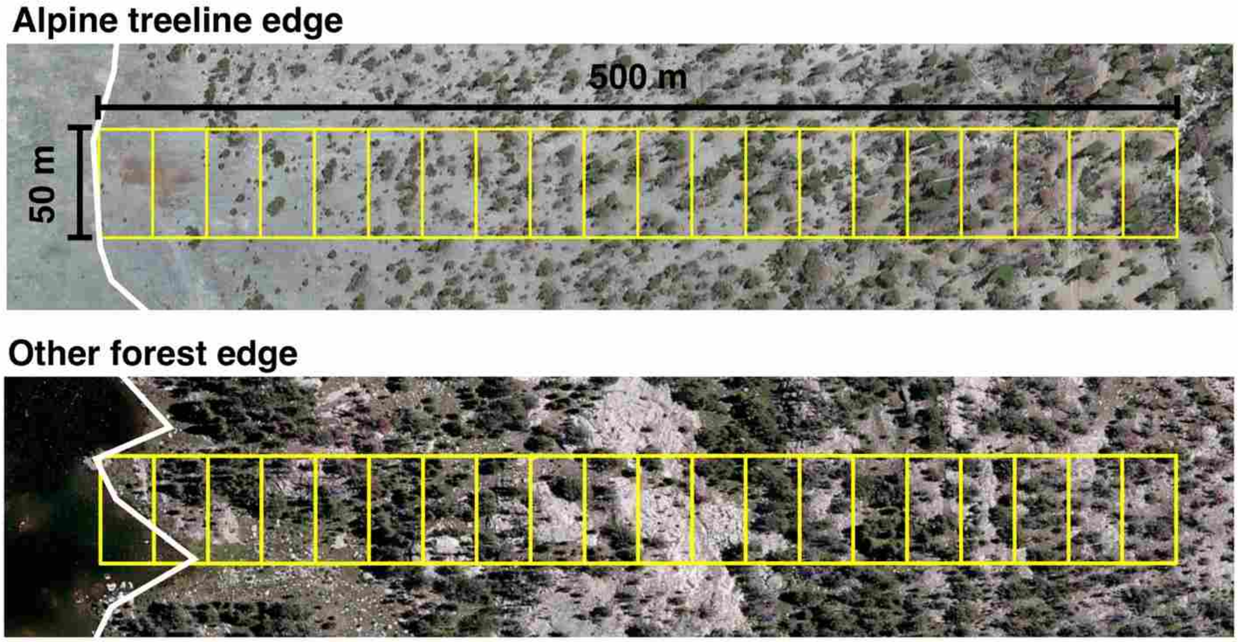


Figure 4.

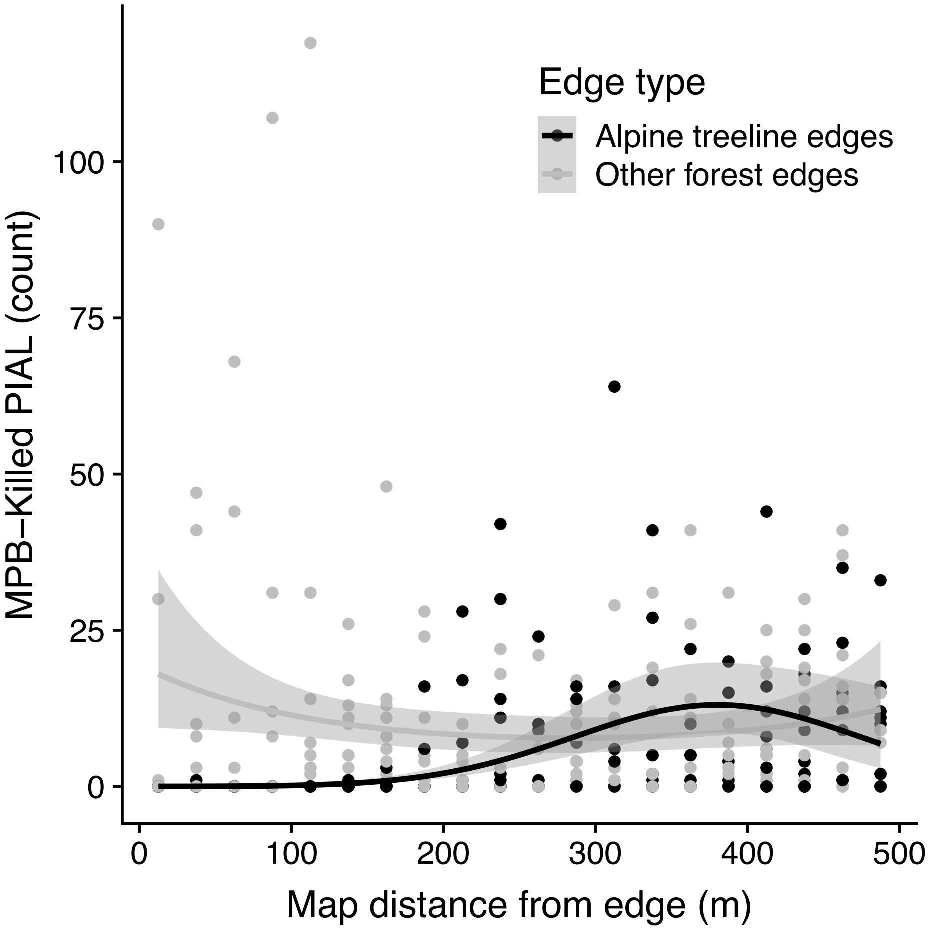

Edge type
Alpine treeline edges
Other forest edges
MPB–Killed PIAL (count)
0
25
50
75
100
0
100
200
300
400
500
Map distance from edge (m)

Figure 5.

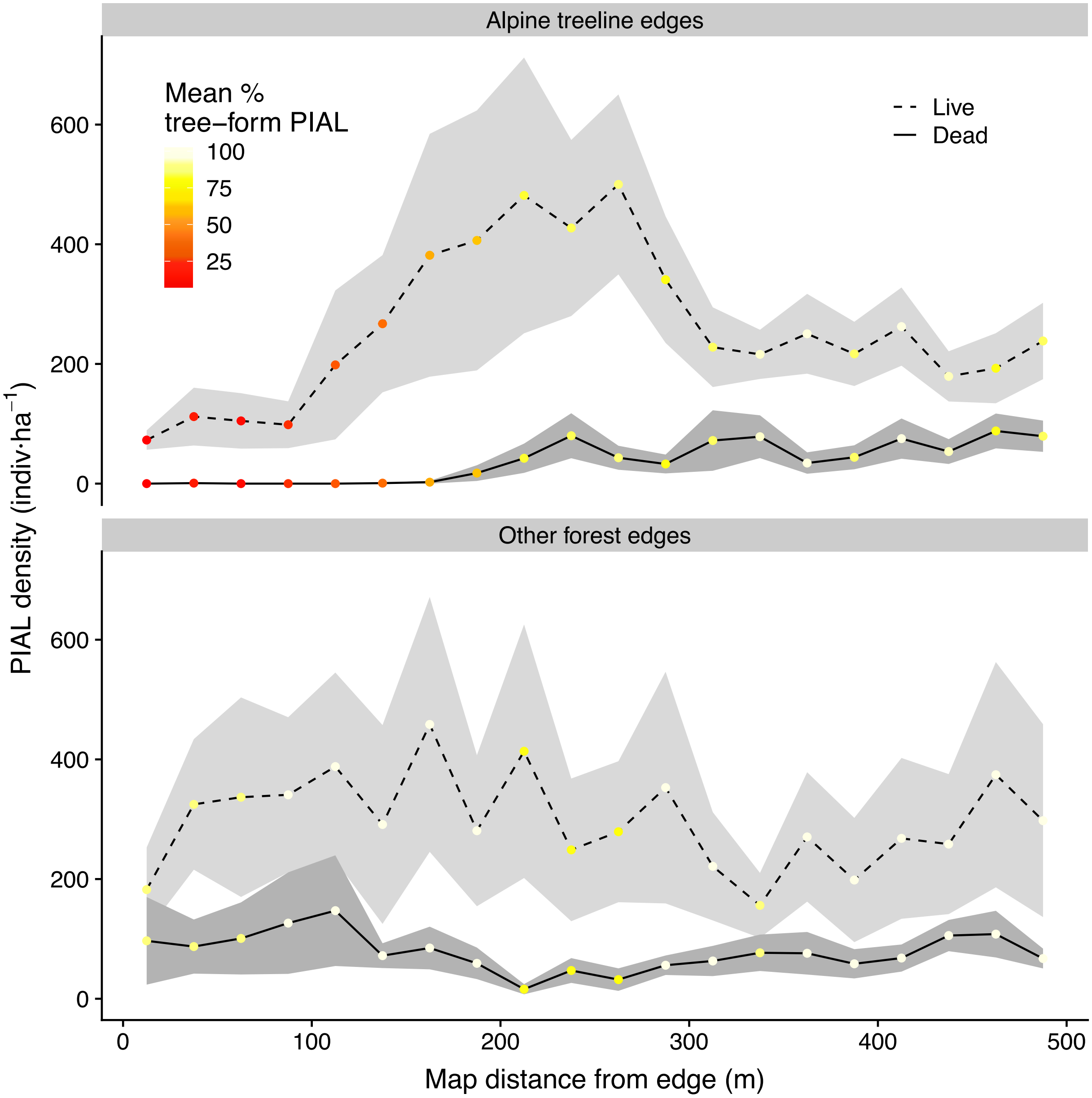
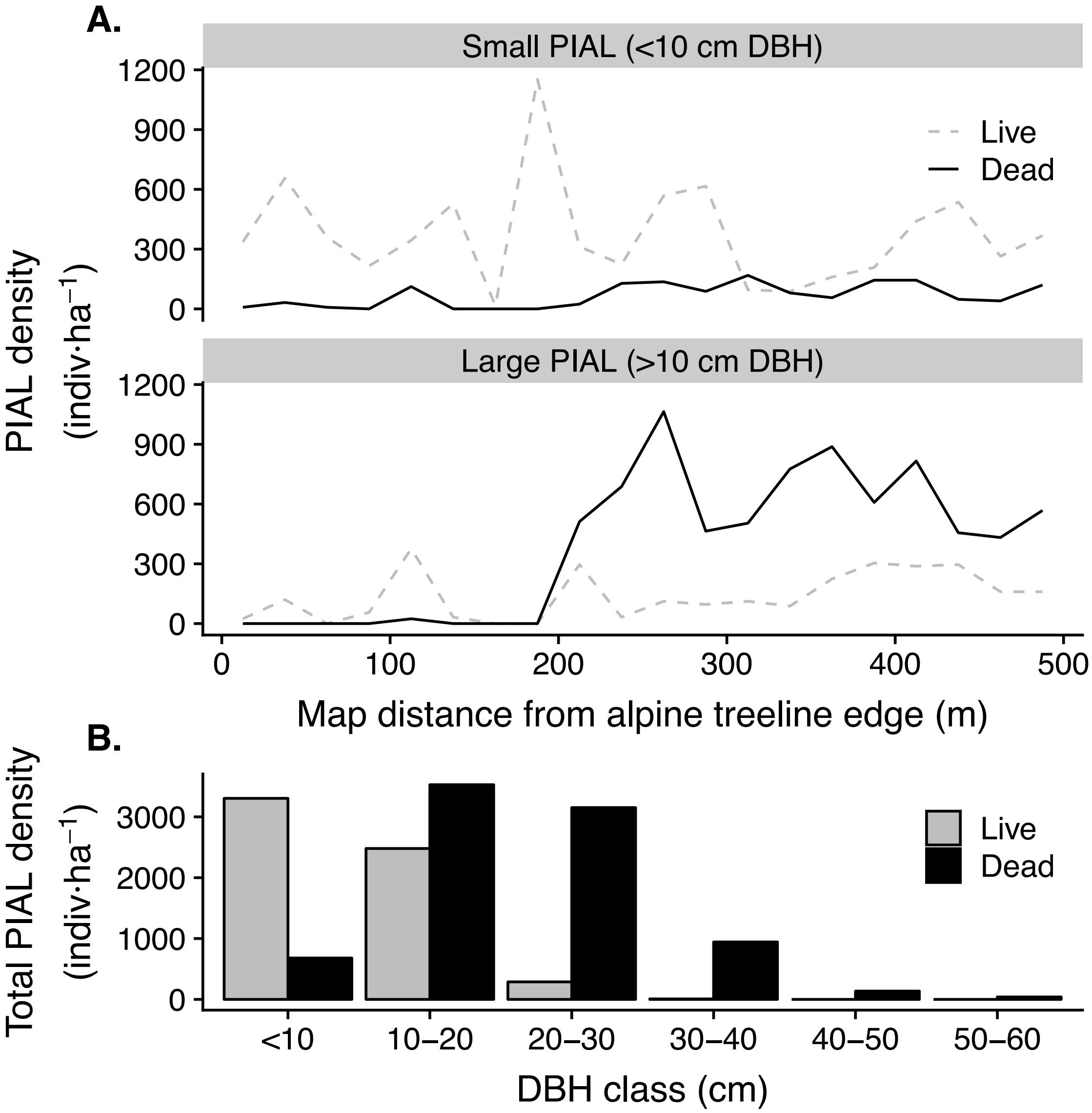

Alpine treeline edges
Mean %
tree–form PIAL
100
75
50
25
Live
Dead
600
400
200
0
Other forest edges
600
400
200
0
PIAL density (indiv·ha^{-1})
0
100
200
300
400
500
Map distance from edge (m)

Figure 6.



A.
Small PIAL (<10 cm DBH)
Large PIAL (>10 cm DBH)
Live
Dead
PIAL density (indiv·ha⁻¹)
1200
900
600
300
0
0
100
200
300
400
500
Map distance from alpine treeline edge (m)
B.
Total PIAL density (indiv·ha⁻¹)
3000
2000
1000
0
<10
10–20
20–30
30–40
40–50
50–60
DBH class (cm)
Live
Dead

Figure 7.

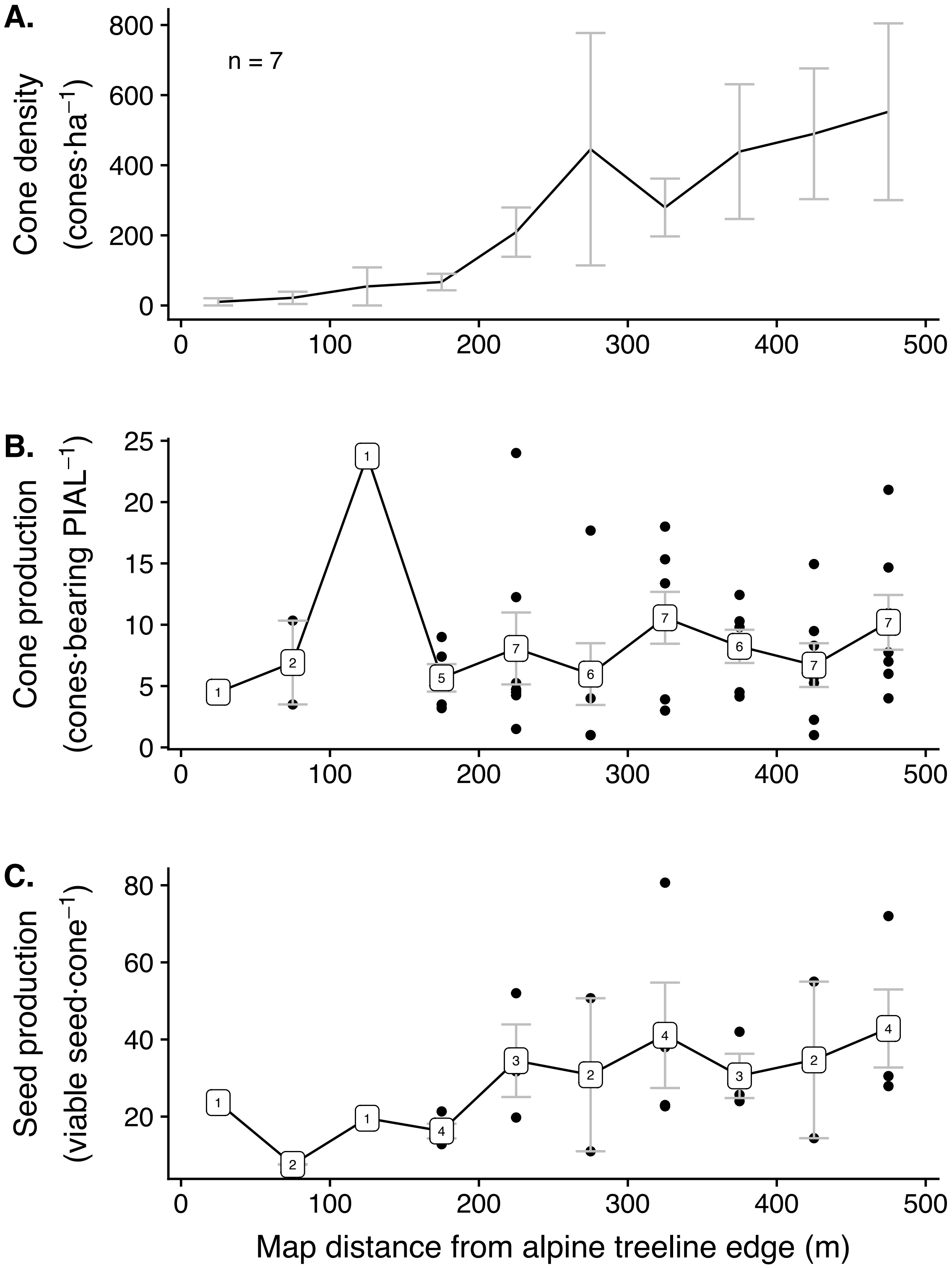

A.
Cone density
(cones·ha^{-1})
n = 7
0
200
400
600
800
0
100
200
300
400
500
B.
Cone production
(cones·bearing PIAL^{-1})
0
5
10
15
20
25
1
2
1
5
7
6
7
6
7
7
C.
Seed production
(viable seed·cone^{-1})
20
40
60
80
1
2
1
4
3
2
4
3
2
4
Map distance from alpine treeline edge (m)

Figure 8.

Chapter 3: Winter damage is a more important factor than summer temperature for maintaining the krummholz growth form above alpine treelines

Abstract

Understanding the processes that control alpine treelines has been a central question in ecology and is growing in importance with concern over climate change. Cold growing seasons are generally thought to be the ultimate cause of alpine treelines globally. However, winter winds have been recognized as a locally important force shaping growth forms near alpine treelines through desiccation and damage from wind-transported snow and may, therefore, play a primary role in maintaining shrub-like krummholz growth forms. To distinguish between the effects of growing season temperature, winter damage and their interaction on preventing upright tree growth, I conducted a field experiment on krummholz growth forms of *Pinus albicaulis* over the summer and winter of 2015-2016 at 10 mountain top sites in the Tobacco Root Mountains, MT, USA. I experimentally manipulated four factors using a fully crossed design: shoot position (natural position in the krummholz mat vs. propped up above the krummholz mat), summer warming (warming chamber vs. ambient), winter exposure (shelter cage vs. exposed), and elevation position (local high vs. low krummholz). I also conducted an observational study of the climatic conditions that have allowed recent natural upright stem emergence from krummholz. Propped shoots that were exposed to winter damage experienced the highest mortality (10-50%), while propped shoots in shelter cages and shoots located within the krummholz mat, whether caged or not, had low mortality (0-10%). Mat shoots had higher growth rates than did surviving propped shoots during the early growing season after experimental treatments were established. Natural upright stem establishment was associated with a period of warmer than average summer temperatures, but also of warmer winter temperatures, lower winter wind speeds, and lower

snowpack. Our experimental results support the hypothesis that wind maintains the krummholz form. Although warmer growing season temperatures may increase the opportunities for emergent shoot establishment, alterations in the conditions that cause winter damage will also be necessary for the survival of these shoots.

Introduction

Alpine treeline ecotones, the vegetation boundaries encompassing the elevational limits of the tree growth form, are a common feature of mountain ecosystems around the world. Understanding the mechanisms that regulate these ecotones – the interface between forest and alpine vegetation – can yield insight into the processes that govern the distribution of species and biomes (Risser 1995) and their response to changing climate. For at least 150 years, scientists have sought to explain the causes of alpine treelines (Holtmeier 2009). Continuing debate about the mechanisms causing and maintaining treelines is testament to their complexity.

One recent approach to extract concrete understanding of the universal causes of alpine treelines has been a focus on temperature-related physiological limitations on the tree growth form, specifically related to the upright stature of trees (Körner 1998). Körner (1998, 2012a, 2012b) hypothesizes that upright growth is constrained upslope of treeline because the free atmosphere above the ground during the growing season is too cool to allow growth, while temperatures in the protective boundary layer near the ground reach higher daytime temperatures, suggesting a functional difference between upright trees and shrubs. At some treeline ecotones, there are tree species that bridge this functional difference by transitioning from the upright tree form to the shrub-like krummholz growth form (Fig. 1), which allows individuals to grow above the treeline (*sensu stricto*; Körner and Paulsen 2004). Although temperature has been implicated as a regulator of the upright tree growth form, winter exposure has also been recognized as an important force shaping growth forms in alpine treeline ecotones through desiccation and damage from wind-transported snow (e.g., Hadley and Smith 1983). Our objective in this study was to determine the relative importance of these factors in maintaining the krummholz growth form.

The striking similarity of growing season temperatures and the physiology of trees at diverse alpine treelines around the world suggests that temperature limitation of growth may be the ultimate cause of alpine treeline (the growth-limitation hypothesis; Körner 1998, Hoch and Körner 2003). Other factors are known to interact at local scales to determine exact treeline elevation, including slope, aspect, geomorphic processes, edaphic limitations, snowpack, winds, and disturbances such as snow avalanches and fire (Arno 1984, Holtmeier 2009, Körner 2012a, Cansler et al. 2018), though these factors are thought to complicate understanding of the 'ultimate' causes (Körner 2012a). However, wind and its interactions with snow have long been hypothesized as important limiters of upright tree growth at treelines (Griggs 1946, Wilson 1959). Indeed, given their prominence in the atmosphere, mountain tops and ridges are very windy places due to the Bernoulli effect – where air is compressed against a mountain's windward flank causing it to rush over the mountain (Lemelin et al. 1988, Barry 2008). Adiabatic cooling, a universal process in mountains globally, also results in higher proportions of precipitation falling as snow in mountains. Wind and snow should thus be common at alpine treelines, although their relative importance in determining growth form above treeline is debatable.

A simple prediction that follows from the growth limitation hypothesis is that alpine treelines will advance in a warming climate. Temperature-correlated positional change at arctic and alpine treelines is well documented (LaMarche and Mooney 1972, Luckman and Kavanagh 1998, Camarero and Gutiérrez 2004, Gamache and Payette 2004, Wang et al. 2006). Indeed, increased recruitment of seedlings above current treeline has been observed at some treelines sites with recent warming, but no response has been observed at others (Harsch et al. 2009). The distinction appears to be related to the structure and pattern of tree species populations and individuals in the treeline ecotone, i.e., the treeline form (Harsch and Bader 2011). Diffuse treelines, where single-stemmed and upright trees become shorter and less dense, are showing greater recruitment response to warming than abrupt treelines (contiguous forest with trees >3 m tall directly bordering alpine vegetation) or krummholz treelines (characterized by a growth form transition from upright tree to shrub), where recruitment appears to be more limited by winter conditions (Harsch et al. 2009). However, while seedling establishment above the current treeline is a requisite condition for treeline advance, these seedlings have no guarantee of growing as upright trees. Because alpine treeline is fundamentally a growth-form boundary (or 'life-form' boundary, *sensu* Körner 2012a), analyses of recruitment processes alone are missing a crucial aspect of change at treelines.

Elevational shifts in growth form have been observed at many alpine treelines. Some krummholz individuals are extremely long-lived (King and Graumlich 1998), and there are descriptions and examples of upright leader establishment in krummholz (Lavoie and Payette 1992, Earle 1993, Hessl and Baker 1997, Devi et al. 2008, Kharuk et al. 2010), although pulses of establishment may be episodic, rather than directional (Millar et al. 2004). There is also at least one example of the opposite transition: the formation of a krummholz zone from a forest of upright trees (LaMarche and Mooney 1972). Several authors (e.g., Smith et al. 2003, Holtmeier 2009) have described processes that allow "flagged" trees to form during favorable years when apical shoots can escape the snow-abrasion layer immediately above the average snow surface (often assumed to be coincident with the current height of the krummholz mat). Needle and shoot dieback due to strong, snow-laden winter winds has been inferred to be the major sculptor of the krummholz growth form (Griggs 1946, Daly 1984), and the degree of wind deformation in conifers has been used to estimate prevailing wind speed and direction at high-elevation sites (Robertson 1986, Wooldridge et al. 1996). Indeed, needle desiccation and mortality are higher for windward than leeward branches and minimal for branches buried in snow (Hadley and Smith 1983). The rate of needle cuticle wax erosion due to abrasion from wind-transported snow is worst between about 0 and 1 m above the snow surface, corresponding with the overlap between high concentrations of windborne snow particles and increasing windspeeds with height above the snow surface – and this effect increases with increasing elevation (Hadley and Smith 1987, 1989). In this harsh environment, consecutive years of suitable conditions likely must occur to enable vertical leader establishment above the abrasion zone. A prediction that follows from this hypothesis is that vertical growth can only occur during conditions when winter damage is ameliorated. This may allow for some upright stem establishment in krummholz populations, but long-term survival of these shoots is less likely (as in Millar et al. 2004).

While growing season temperatures and winter damage may each have direct effects on growth form, these factors are also likely to interact. Specifically, growing season temperature may interact with winter damage in two important ways. First, incomplete needle and cuticle development due to effectively shorter growing seasons above treeline may enhance the effects of winter wind desiccation (Tranquillini 1979, Hadley and Smith 1986). Second, low ambient growing season temperatures in the free atmosphere above krummholz mats may constrain vertical growth rates such that escape from the abrasion zone is uncommon before shoots die. However, Millar et al. (2004) found increased rates of krummholz branch growth was associated with warmer minimum temperatures in the latter half of 20th century. The erosive effects of winter wind are known to be highest near the snow surface, and are higher overall at higher elevations (Hadley and Smith 1989). Because this erosive effect may occur independently of growing season temperature gradients above the ground – it is possible that the relative importance of growing season temperature and winter damage varies within a few meters from the ground, and that this relationship is different at different elevations.

Although alpine treelines have been studied extensively, to our knowledge there are no experimental studies that directly test the interactive effects of growing season temperature and winter damage on limiting upright shoot emergence from krummholz. Our objective was to identify the processes that maintain the krummholz growth form by describing patterns of natural upright stem establishment from krummholz and their relation to temperature, snowpack and wind and by experimentally manipulating live krummholz shoots to alter their position with respect to the krummholz mat and their summer and winter environments at two elevations. Specifically, I asked: 1) What climatic conditions were associated with the establishment of naturally occurring emergent stems above krummholz mats? 2) How do growing season temperature and winter damage affect survival and growth of shoots within and above krummholz mats, and do effects vary with elevation?

Methods

Site description

This study was conducted at 10 sites in the Tobacco Root Mountains, a sub-range of the northern Rocky Mountains located in southwestern Montana, USA (Fig. 2). Species composition of the subalpine forests and treeline ecotone is similar to that of much of the northern US Rockies and Inland Northwest, with *Pinus contorta*, *Picea englemannii*, *Abies lasiocarpa*, and *Pinus albicaulis* existing in mixed-species stands (Arno 1984). Near the alpine treeline, *P. albicaulis* becomes dominant and is the most common krummholz-forming species beyond the treeline, though *A. lasiocarpa* and *P. englemannii* can also occur as krummholz.

I used *P. albicaulis* krummholz as a study system. *P. albicaulis* commonly forms krummholz above alpine treelines throughout its range, which covers central western North America. Genetic analysis indicates that growth form differences in the species represent phenotypic plasticity, not local adaptation or differentiation (Rogers et al. 1999). This relatively undifferentiated genetic structure is due to dispersal by Clark's nutcracker (*Nucifraga colombiana*; Bruederle et al. 1998), a scatter-hoarding bird that caches seeds, primarily from tree-form *P. albicaulis*, throughout forest stands and across treeline ecotones. Thus, krummholz *P. albicaulis* represent 'potential trees' currently enduring an unfavorable environment, rather than ecotypic variation, making this species an appropriate subject for studies of environmental influences along treeline ecotones.

Establishment of natural upright stems

To determine rates of establishment of natural upright stems from krummholz in the Tobacco Root Mountains, I sampled 45 upright stems at nine sites (sites 1-3 and 5-10 in Fig. 2). At each site, 5 stems were selected for sampling by standing at the highest accessible point above the local krummholz limit and randomly choosing a downslope compass direction. I sampled the first upright shoot I encountered in that direction that met the 25 cm criterion and its 4 nearest neighbors that also met that criterion. I limited sampling to uprights stems with shoot tips at least ~25 cm above the surrounding krummholz mat. By limiting selection to stems 25 cm and above, I aimed to capture the population of stems that have survived the abrasion zone immediately above the krummholz mat. For each sampled stem, I measured vertical height above the krummholz mat, marked the point on each stem where it intersected the current krummholz mat height, cut the stem at this point and later took a cross-section to determine the year the stem reached mat height. I estimated the pith year on each stem cross-section by visually crossdating (Stokes and Smiley 1968) using a regular pattern of frost-damaged rings.

Environmental conditions

I obtained interpolated monthly gridded temperature and 10 m surface wind time series data for all pixels covering the Tobacco Root mountains from the TopoWx model (800 m resolution; Oyler et al. 2014) and from the TerraClimate dataset (4 km resolution; Abatzoglou et al. 2018), respectively. I then extracted point estimates from the gridded datasets at each of the 10 study sites and used the average of these point estimates in subsequent analyses. Peak snow depth timeseries were obtained from annual (measured in March, April, and May) National Resource Conservation Service snow course data at Branham Lakes (marker 11D14; Fig. 2).

I compared conditions in the summer of 2015 and winter 2015-2016 in relation to climate normals using average monthly temperatures from TopoWx temperature data (1981-2010), average monthly wind speed from TerraClimate (1981-2010), and peak annual snowpack from the Branham Lakes snow course data (1981-2010). Climatic conditions in the summer of 2015 and winter of 2015-2016 were near 1981-2010 normals for most variables: July mean temperature (10.51°C, 95.0% of normal), December mean temperature (-9.34°C, 98.2% of normal), mean August wind (3.67 $m \cdot s^{-1}$, 99.8% of normal), mean December wind (4.47 $m \cdot s^{-1}$, 101.8% of normal), and peak snow depth (212.7 cm, 101.8% of normal).

I installed temperature loggers (HOBO Pendant brand) at a random subset of 5 of the experiment sites. Loggers were placed on wooden stakes within krummholz mats and at ~0.5 m above the mat to characterize air temperature differences between krummholz mat interiors and ambient conditions just above the mat experienced by propped shoots. Loggers recorded temperature at 10 min. intervals and were housed within durable ventilated radiation shields. Loggers were in place from 1 Aug. 2015 until 23 June 2016.

I further characterized environmental conditions through the experiment using daily instrumental records of snow depth and modelled wind speed. I used snow depth data from the two SNOTEL meteorological stations (Serreze et al. 1997) in the Tobacco Root Mountains, Albro Lake (Station ID 916; 45.6º N, -111.6º W) and Lower Twin (Station ID 603; 45.51º N, -111.92º W). These stations are located at 2530 m, and 2408 m elevation, respectively. I extracted 700 mb (roughly equivalent to 3,050 m elevation) daily mean wind speed data from ERSL NCEP/NCAR Reanalysis 1 (Kistler et al. 2001).

To estimate the effect of wind abrasion at experimental sites, I installed 1.5 m tall PVC pipes coated with erodible wax within krummholz mats to characterize the relative abrasive action of winter wind. Pipes were mounted on rebar extended from the ground through krummholz mats into the air above the mats. This method is a simplified version of that used by Hadley and Smith (1989). Abrasion was measured as differences between pre- and post-winter circumference at 20 cm increments along the pipe. Circumference was measured by wrapping a string around each increment, then measuring the length of the string. Two pipes each were placed in each krummholz mat that also contained the temperature loggers.

Krummholz shoot experiment

To test the primary environmental influences on treeline, I used a replicated (*n* = 10) factorial design with shoot position (upright vs. mat), late summer warming (warmed vs. ambient), shelter from winter damage (sheltered vs. exposed), and elevation position (lowest local krummholz vs. highest local krummholz) as main effects and shoot mortality and shoot growth as response variables (Fig. 3). To simulate upright shoot growth, I secured naturally prostrate krummholz shoots to wooden stakes to place them roughly 0.5 m above the top of the krummholz mats. I paired these propped shoots with shoots within the same krummholz mat that I also secured to short wooden stakes, but for which the stakes were located entirely within the mat. All shoots were secured to wooden stakes using plastic zip-ties covered with vinyl tubing to protect stems. Stakes were fitted with threaded bolts to allow installation and removal of clear polycarbonate warming chambers and sturdy fine mesh cages (made with aluminum window screen and ¼ inch (6.35 mm) galvanized hardware cloth, reinforced with aluminum flashing), for summer warming and winter shelter, respectively. Both warming chambers and shelter cages were wrapped around shoots, creating cylindrical enclosures that were open on the top and bottom (Fig. 3). At each site, I installed treatments at both local high- and low-elevation limits of the krummholz growth form, defined as matted, shrub-like *P. albicaulis* that are wider than they are tall with stems < ~1 m from the ground. This included some krummholz with natural emergent stems. Each factor was crossed such that propped/mat shoot pairs were either warmed in the summer and protected in the winter, only warmed in the summer, only protected in the winter, or neither warmed nor protected (Fig. 3).

The experiment was replicated at 10 treeline sites (sites are blocks; $n = 10$). Individual krummholz were selected at each low- and high-elevation portion of each site by first identifying 5-10 *P.albicaulis* that classify as krummholz. In most cases, the low-elevation replicates were directly downslope from the higher ones (mean 86 m, range 30-270 m below). Treatments were then randomly assigned to four krummholz at each low- and high-elevation location. Warming chambers were installed between 17 July to 10 August 2015. These were exchanged for shelter cages between 9 October and 15 October 2015. The experiment was recovered between 23 June and 4 July 2016.

I recorded shoots as dead (when the experiment was recovered in 2016) if the shoot tip was broken off or if all needles were stripped off and the apical bud was desiccated. I cut all surviving experimental shoots and transported them to the laboratory where I measured height increment growth as internode length (2013-2015) and partial growth in 2016 as the length of the new shoot from the internode to the shoot tip.

I tested the temperature and wind effects of warming chambers and shelter cages in two separate experiments. First, to determine the effect of warming chambers on temperature, I repeated the warming and shoot position factors (four possible levels) of the shoot experiment with temperature loggers in small PVC radiation shields at a separate treeline research site in the Pioneer Mountains, Montana, USA. Krummholz shoots were propped up and attached to wooden stakes alongside the loggers to accurately simulate the conditions in the main experiment. I replicated this experiment four times across 16 krummholz individuals ($n = 4$) for the month of August 2018. Second, to determine the effect of shelter cages on wind speed, I attached two pole-mounted cup anemometers to the roof rack of a vehicle with one sheltered and the other exposed, one each on the driver's side and passenger's side, and then drove at town and highway speeds to capture a range of wind speeds. The cage materials used were identical to those used in the shoot experiment. I repeated this with the anemometer position switched to account for bias in either instrument.

Analyses

Establishment of natural upright stems

I examined relationships between the number of natural emergent stems establishing each year and climate variables using Pearson correlations. Climate variables included monthly mean temperatures for each month of a water year (October-September), monthly mean wind speeds for each water year, and peak annual snow depth (taken as the maximum of March, April or May measurements) and were computed as 11-year running means (i.e., the 5 years before and after each year in the analysis) to account for lag effects and imprecision in the stem age estimates.

Krummholz shoot experiment

I tested for differences in temperatures (daily maximum, mean, and minimum) during the shoot experiment between the within-mat and above-mat environments and between elevation positions (high vs. low) and seasons (1 Aug. - 15 Oct. 2015, 15 Oct. 2015 - 1 Mar. 2016, and 1 Apr. - 23 Jun. 2016) using factorial ANOVAs. I allowed for main effects for each factor and for interaction between the two. I also tested for a block (site) effect.

I estimated wax loss as differences between the pre-winter mean circumference of all height positions on each cylinder and the measured post-winter circumference at each height position – thus the pre-winter circumference was standardized for each wax cylinder. This partially controls for bias generated by small pre-winter circumferences with little wax coating. These positions showed little difference pre- and post- winter, but this was not representative of actual erosion. I tested for differences in wax loss by elevation and by height position above the ground using a two-way factorial ANOVA.

I analyzed shoot survival/ mortality using a binomial logistic generalized linear model with shoot position, warming, shelter, and elevation as factor predictor variables. However, shoot mortality was a rarer event than anticipated, to the extent that many factor combinations (10 of 16 possible combinations) had complete shoot survival after the duration of the experiment. This precluded valid modelling of mortality with this dataset – estimates of coefficients were inflated because of fitted probabilities of 0 or 1 (Venables and Ripley 2003). However, I interpret this result as meaningful in the context of the experimental design, despite the inability of models to describe the effects. Many classic ecological experiments relied upon experimental design alone, rather than statistical models, to infer effects of treatments (e.g., Connell 1961). Still, I verified our inferences by running a binomial logistic model of an altered dataset in which one mortality event was added to each of the 10 factor combinations that had complete survival. This simulated dataset represents weaker effects than what I actually observed but allowed a statistically valid model to be built. I compared the results from a Chi-square analysis of deviance test on this model with our inferences from the actual experimental results.

I analyzed height growth in surviving shoots by first standardizing the growth series of each shoot from 2013. This was necessary because of observed variation in previous shoot growth that was unrelated to the experimental manipulations (2013-2014). Standardization allows correct evaluation of the treatment effects without bias introduced by absolute differences in growth rates among shoots. The partial 2016 growth (stems were measured before elongation had completed) of each surviving shoot was expressed as z-scores of the 2013-2016 series. I then tested for the effects of experimental treatments on relative shoot growth using Gaussian generalized linear models with shoot position, shelter, warming and elevation as predictors. I allowed for direct effects and all possible interactive effects. I used a Chi-square analysis of deviance test to determine the effects of each factor and their interactions on growth.

I assessed the effects of the warming chambers on temperature (mean daily maximum, mean, and minimum) using ANOVA models, with separate models for each temperature response variable and with shoot position and warming as experimental factors. To test the effects of shelter cages on wind speed, I regressed exposed anemometer wind speed against sheltered wind speed using linear regression and interpreted the slope of the regression as the magnitude of difference in wind speed.

Results

Establishment of natural upright stems

The majority of natural upright stems established from 2000-2008 (Fig. 4), with higher rates of stem establishment in recent years. Only four stems had establishment dates before 1990. The oldest stem established in 1978, and the youngest in 2010. Stem height seemed to be limited between ~ 0.75 - 1 m above krummholz mats, with the exception of one fast-growing stem that established in 1998. Establishment was associated with a period of warmer than average July temperatures and December temperatures, but this warming occurred within a period of relatively lower winter winds and lower snowpack, though summer winds were higher during this period (Fig. 4). The number of stems establishing was significantly positively correlated with 11-year moving average monthly temperatures in November, December, January, March, April, May, and July through September (Table 1). February and June mean temperatures were not associated with stem establishment. The 11-year moving averages of monthly wind speed in December through February and in June were significantly negatively correlated with stem establishment (Table 1). There were significant positive relationships between 11-year moving average wind speeds in August and September. Trends in November, March through May, and July wind speeds were unrelated to stem establishment. The 11-year moving average of peak annual snow depth was significantly negatively correlated with stem establishment (Table 1).

Krummholz shoot experiment

Daily maximum temperatures through the shoot experiment were warmer within krummholz mats than above mats during the summer/fall (~1.5 °C) and winter (~0.5 °C), but there were on average higher daily maximums above mats in the spring (~0.5 °C) – this pattern held at both elevations, indicating that krummholz mats were likely buried in snow for much of the winter and spring (Table 2, Fig. 5). Daily means were scarcely warmer within krummholz mats in nearly every season – by ~0.2 °C on average. Above mats, daily minimums were slightly warmer in the summer/fall (~0.2 °C), slightly cooler in winter (~0.2 °C), and ~0.75 °C cooler in spring compared to within mats (Table 2, Fig. 5). I found significant block (site) effects – the higher elevations at two sites had much higher maximum temperatures above mats than within mats in spring and much lower minimums above mats in spring than other sites.

Snow accumulation in early November coincided with an equalization in temperatures between the within- and above-mat environments. Temperatures in the two environments remained similar until mid-March, when five large snowfall events (3-day snow accumulation > 15 cm) appeared to have important effects on temperature differences. The subsequent melt and re-accumulation cycles corresponded with large differences between within- and above-mat environments – maximum temperatures were higher above the krummholz mats after storms, but minimums were cooler (Fig. 5). The highest wind speeds occurred between October and April. There was also measurable snow available for transport during much of this time.

I found clear evidence for the overall abrasive effects of winds at our study sites. There was an apparent trend of higher wax loss between 30 and 90 cm above the ground, particularly at low elevations, but this pattern was not statistically distinguishable. There was nearly complete wax loss from cylinders at all heights (within krummholz mats and above) across treatments (~2.7 – 3.5 cm loss in circumference on average) – but I found no significant differences in wax loss with height from ground ($F_{7, 304} = 0.81$, P = 0.58), elevation position ($F_{1, 304} = 1.6$, P = 0.21), or their interaction ($F_{7, 304} = 0.27$, P = 0.97).

Exposed, propped shoots – whether they were warmed or not and across both elevations – experienced higher mortality (10-50%) than did sheltered propped shoots and mat shoots (Fig. 6). I observed no mortality in sheltered shoots (propped or mat locations) at high elevation and only one (10%) mat shoot (which was in a shelter cage) died at low elevation. Shelter from winter winds and shoot position were clearly the most important factors determining shoot mortality overall. However, at low elevation there did appear to be a possible reduction of shoot mortality in exposed, propped shoots that were warmed in the previous summer. The analysis of the simulated high-mortality dataset corroborated these results (Table 3).

Shoot position was the only significant factor predicting new growth in 2016. Growth in surviving shoots after winter was greater overall in mat shoots than in propped shoots (shoot position $\chi^2 = 3.8$, df = 1, P = 0.009). This difference was most noticeable in exposed shoots (Fig. 7), although I found no significant effect of shelter ($\chi^2 = 1.7$, df = 1, P = 0.09) and no interaction between shelter and shoot position ($\chi^2 = 0.62$, df = 1, P = 0.30). There were no direct or interactive effects of warming treatments or elevation on 2016 relative growth. Two sites had significantly higher overall 2016 relative growth than the other eight, reflected in a significant block effect ($\chi^2 = 10.7$, df = 9, P = 0.03).

Warming chambers did increase daily maximum and mean temperatures above ambient conditions, but daily minimums were slightly cooler or indistinguishable from ambient, for both mat and propped shoots (25.7°C vs. 20.6°C in daily maximums: $F_{1, 12} = 88.0$, P < 0.001; 13.4°C vs. 11.7°C in daily means: $F_{1, 12} = 66.3$, P < 0.001; 5.0°C vs. 5.4°C in daily minimums: $F_{1, 12} = 18.6$, P = 0.001; Fig. 8). Mat shoots overall experienced higher daily maximum temperatures (24.7°C vs. 21.6°C; $F_{1, 12} = 32.3$, P < 0.001), and cooler daily minimum temperatures than did propped shoots (4.7°C vs. 5.7°C; $F_{1, 12} = 99.6$, P < 0.001). There were no differences between shoot positions in daily mean temperatures (12.6°C vs. 12.5°C; $F_{1, 12} = 0.14$, P = 0.71). I found no significant interactive effects between warming and shoot position for daily maximum and daily means, but there was a significant interaction between these factors on daily minimum temperatures ($F_{1, 12} = 9.4$, P = 0.01). This interaction was driven by lower minimum temperatures in the warming chambers for the propped shoots only (Fig. 8).

Winter shelter cages reduced wind speeds by ~17% – the regression model of sheltered wind speed to exposed wind speed produced a line with a slope of 1.168 that explained the majority of the observed variance ($R^2 = 0.99$, P < 0.001; Fig. 8).

Discussion

Our experimental and observational results help resolve questions about the mechanisms that limit the elevation position of alpine treelines, which have intrigued scientists for over a century. This study demonstrates that physical mechanisms related to wind and snow that cause shoot mortality and damage during winter are important constraints on emergent growth in krummholz near the upper edges of alpine treeline ecotones. Physical damage inflicted to shoots that grow above the protective boundary layer or snowpack may thus be an important functional difference between a tree and a shrub (Körner 2012b).

Recent research has focused on temperature-related physiological limits that prevent upright growth above treelines as a singular and primary cause for the growth form boundary at treeline. Growing season temperatures are similar at many alpine treelines globally (Körner and Paulsen 2004) and upright stems are exposed to low growing season temperatures, which may limit growth rates by constraining carbon sink processes (e.g., cell expansion; Körner 2012a, 2012b). However, low temperatures are one of many important stressors on tree growth along alpine treeline ecotones (e.g., nutrient limitations; Sullivan et al. 2015). Upright stems have also been known previously to be at greater risk of physical damage during winter (Hadley and Smith 1986). Mountains globally are cooler than their surroundings, but – in contrast with Körner's (2012a) statement that “treelines are not especially windy places…” – are often the windiest places relative to their surroundings due to their physical prominence (e.g., see the global topographic wind speed map in the Global Wind Atlas 2.0, https://globalwindatlas.info). Additionally, the same processes that result in cooler temperatures in mountains also make snow common in most of Earth's high mountains (NASA Earth Observatory, https://earthobservatory.nasa.gov).

Because testing for the effects of growth limitation was outside the scope of our experiment, I cannot rule out the role of growing season temperature in controlling upright stem growth. I did find that natural emergent shoots largely established during a period of warmer July temperatures. However, this period was also characterized by relatively low winter winds, low snowpack, and warmer winter temperatures; the latter two are also expected with climate change (e.g., Pederson et al. 2013). Warmer snow has a higher threshold wind speed for transport than colder snow and lower snowpack would lead to less snow transport overall. Wind speeds as low as 4-11 and 7-16 $m \cdot s^{-1}$ can transport dry, cold snow, and wet, warm snow, respectively (Li and Pomeroy 1997), corresponding well to the mean winter wind speeds observed by Hadley and Smith (1983) to be associated with needle death. There is some evidence that winter westerly winds have decreased in recent decades in the US Pacific Northwest, but it is unclear if this trend will continue (Luce et al. 2013). This combination of conditions may interact to reduce the likelihood of winter damage and allow some growth form change to occur.

The observed relationships between natural emergent stem establishment and trends in climate variables, paired with the experimental result that shoots exposed in winter have higher mortality rates than protected shoots, suggest that a combination of interacting factors – rather than temperature alone – are responsible for the conditions that maintain the krummholz growth form. This finding has important implications for change at krummholz treelines. For example, the association of natural emergent stem establishment and lower snow years may indicate that upright stems may become more common if snowpack continues its decreasing trend (Pederson et al. 2011, Millar et al. 2004). Interestingly, natural stem establishment occurred during a period of relatively higher August wind speeds. Very high summer wind speeds should have a negative effect on upright growing shoots from increased transpirative water loss. In an experimental manipulation similar to that used in this study, Wilson (1959) propped up naturally prostrate *Salix arctica* branches using guy lines and monitored their status over a growing season to understand the effects of summer wind, finding that greater exposure was detrimental to growth and survival. Mild wind speeds can have a positive effect on growth, however, because increased mixing of air facilitates gas exchange by decreasing the boundary layer around photosynthetic tissues (Telewski 2012).

There were some limitations of the experimental implementation that limit inferences. First, while warming chambers clearly did increase temperatures, chambers were installed relatively late in the growing season and may not have strongly affected growth or development. For example, Rossi et al. (2009) found that *Pinus cembra* below treeline initiated shoot elongation in mid-June. Still, at low elevations there seems to have been a reduction in mortality in the exposed propped shoots that were also warmed. This could reflect greater cuticle development from warmer temperatures and thus greater resistance to winter damage (Tranquillini 1979). On the other hand, many shoots died as a result of physical breakage to stem tips, which no amount of cuticle development or height growth would prevent. Dead shoots that were not broken appeared desiccated – a well-documented cause of death in conifer needles due to winter wind exposure (Hadley and Smith 1986, 1989). Thus winter damage near the tree species limit may be a first-level mechanism limiting upright growth in some environments, *sensu* Harsch and Bader (2011). Also, the winter shelter cages were designed to reduce abrasion to shoots from wind-transported snow, but I did not directly measure wind or snow particle movement during the shoot experiment. However, I was able to demonstrate in a separate experiment that the winter shelter cages altered the wind environment by reducing wind speeds by ~17%. The effects of abrasion over winter were also apparent from the loss of wax from the PVC pipes.

Temperature differences between shoot positions through the experiment were complex. Growing season maximum temperatures were warmer within mats than above mats, but minimums were cooler within mats. Winter temperatures were always slightly cooler above mats, perhaps reflecting a greater exposure to harsh winter conditions. In spring, temperatures above mats reached higher daily maximums than within mats – perhaps because mats were buried in snow after spring snow storms, keeping them from above-freezing day time temperatures of spring. Conversely, the cost of being free of the snow in spring was being exposed to below-freezing temperatures at night. These temperature swings could be one mechanism that reduced surviving propped shoot growth, although desiccation damage was also likely important. The damage inflicted to exposed shoots, and their low growth, suggests that repairing winter damage is a possible important use for the high non-structural carbon concentrations observed in treeline trees and krummholz (Hoch and Körner 2012).

Many exposed upright shoots in our experiment survived, suggesting that some emergent shoot survival is possible even under normal climatic conditions. However, repeated damage through multiple winters could effectively prevent permanent establishment of upright stems. Natural shoots that do survive in a given year contribute to a population of emergent stems that successfully establish above krummholz mats. However, these stems appear short-lived at our study sites, and their establishment may be episodic in general (Millar et al. 2004). Pereg and Payette (1998) describe the establishment and eventual degradation of stems above the winter snowpack in *Picea mariana* at arctic treelines with chronic exposure to wind-transported snow.

The existence of these emergent stems further indicates that current krummholz mats do not represent a thermal limit to growth. However, the apparent 1 m height threshold that I observed could indicate a thermal limit. If meristem growth at 1 m decreases such that height growth stagnates in the cool air at this height, this would make eventual attrition from winter damage more likely.

Wind and wind-related damage can cause deformation of trees in a variety of environments (see Telewski (2012) for a comprehensive review of potential causes of wind-deformation) and is not unique to mountainous terrain. For example, Wells and Shunk (1937) summarized studies that found damage from salt spray (likely caused by desiccation from osmotic water loss) as a major factor producing shrub-like growth forms of tree species in coastal environments. The processes that form krummholz-type growth forms at arctic treelines, however, may be nearly identical to those discussed here at alpine treelines. Pereg and Payette (1998) use stem analysis to describe the formation of progressively stunted black spruce (*Picea mariana*) growth forms at arctic treeline as related to wind exposure and snow depth, with the matted, krummholz forms occurring in the most wind-exposed sites. In the southern hemisphere, Daniels and Veblen (2003) also describe several krummholz-like growth forms of *Nothofagus pumilio* at treeline in the southern Andes mountains. Some species appear to be more susceptible to assuming krummholz growth forms than others. First, the formation of prostrate stems may be in part due to the mechanical properties of their wood – denser, stiffer wood is more sensitive to permanent deformation than softer, more flexible woods (e.g., *Pinus ponderosa* is more susceptible to crown deformation than *Abies balsamea*; Telewski 2012). Second, dense hedge-like growth in krummholz can result from the loss of apical dominance through shoot death (Holtmeier 2009). Species that are less susceptible to shoot death, e.g., winter deciduous species such as *Larix spp.*, may thus also be less likely to form krummholz.

Alpine treeline ecotones are complex ecological boundaries that are unlikely to be explained by a single factor alone (Holtmeier 2009, Harsch et al. 2009, Sullivan et al. 2015, Piper et al. 2016, Cansler et al. 2018). With the consideration of an additional factor, winter damage in this case, the usefulness of alpine treelines as bellwethers for the effects of temperature increases is diminished. Crabtree and Ellis (2010) reached a similar conclusion with their finding that shrub height would continue to be restricted in alpine lichen-heath at windy sites, despite increases in temperature. A filter approach, with multiple factors that have shifting relative importance, would be a better framework for understanding treeline positions at different sites around the world, rather than a singular focus on temperature. At treelines where abrasion by wind-driven snow is possible, a warming climate may not directly result in treeline advance, unless warming temperatures also cause changes in precipitation and wind that reduce the risk of damage.

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Tables

Table 1. Pearson correlation coefficients (*r*) for relationships between natural stem establishment and 11-year moving averages of monthly mean temperatures (tavg), monthly mean wind speed (ws), and peak annual snow depth. Years were expressed as water years (Oct.-Sept) in this analysis. Significant correlations ($P \leq 0.05$) are displayed in bold face font.

Variable	***r***	**P-value**
Oct_tavg	0.01	0.448
Nov_tavg	**0.64**	**<0.001**
Dec_tavg	**0.66**	**<0.001**
Jan_tavg	**0.46**	**<0.001**
Feb_tavg	0.17	0.079
Mar_tavg	**0.34**	**<0.001**
Apr_tavg	**0.18**	**0.009**
May_tavg	**0.17**	**0.004**
Jun_tavg	-0.22	0.244
Jul_tavg	**0.60**	**<0.001**
Aug_tavg	**0.53**	**<0.001**
Sep_tavg	**0.39**	**<0.001**
Oct_ws	**0.50**	**<0.001**
Nov_ws	-0.11	0.084
Dec_ws	**-0.32**	**<0.001**
Jan_ws	**-0.27**	**<0.001**
Feb_ws	**-0.20**	**0.005**
Mar_ws	0.22	0.809
Apr_ws	0.07	0.986
May_ws	0.33	0.647
Jun_ws	**-0.43**	**<0.001**
Jul_ws	0.16	0.847
Aug_ws	**0.68**	**<0.001**
Sep_ws	**0.35**	**<0.001**
Snow_depth	**-0.58**	**<0.001**

Table 2. Effects of elevation, season, site (block), and elevation x season interaction on difference in temperature (daily maximum, daily mean, and daily minimum) between shoots located within krumholtz mats and those propped above mats, tested using ANOVA models. Seasons were defined as summer/fall (1 Aug. – 15 Oct. 2015), winter (16 Oct. 2015 – 30 Feb. 2016), and spring (1 Mar. – 23 Jun. 2016). Significant results (P ≤ 0.05) are highlighted with bold font.

		Difference in daily max.		**Difference in daily mean**		**Difference in daily min.**	
	df	F-value	P-value	F-value	P-value	F-value	P-value
Variable							
Elevation	1, 3270	1.1	0.304	0.0	0.871	2.7	0.101
Season	2, 3720	**190.2**	**< 0.001**	**3.5**	**0.030**	**76.2**	**< 0.001**
Site	4, 3720	**34.5**	**< 0.001**	**7.1**	**< 0.001**	**14.3**	**< 0.001**
Elevation x Season	2, 3720	**11.1**	**< 0.001**	2.8	0.061	1.3	0.265

Table 3. Effect of experimental factors (shelter, shoot position, elevation, and warming) on shoot survival/mortality, based on Chi-squared analysis of deviance test on altered shoot survival/ mortality data. Mortality events were added to perfectly separated factor combinations – i.e., that showed complete survival in the original dataset – to allow fitting of a binomial logistic model. These results thus represent weaker effects than those observed.

Predictor	***df***	χ^2	**P-value**
Shelter	1	4.21	0.040
Shoot position	1	4.05	0.044
Shelter x Shoot position	1	2.43	0.119
Elevation	1	1.11	0.292
Shoot position x Elevation	1	0.67	0.414
Warming x Elevation	1	0.66	0.416

Figure captions

Figure 1. Diagrammatic representation of the growth-form transitions that occur along krummholz treeline ecotones.

Figure 2. Location of the study area in the Tobacco Root Mountains in the western US (inset map) and the sites (circles with numbers; $n = 10$) for the krummholz shoot experiment. The terrain of the Tobacco Root Mountains is represented with a digital elevation model, with shades corresponding to elevation. The two squares represent the SNOTEL stations used in this study (Albro Lake and Lower Twin). The triangle indicates the location of the snow course marker at Branham Lakes.

Figure 3. Design of krummholz shoot experiment showing four factors: shoot position (propped vs. mat), late summer warming (warmed vs. ambient), winter shelter (sheltered vs. exposed), and elevation position (lowest local krummholz vs. highest local krummholz). Grey shoots represent experimentally manipulated shoots that were supported by wooden stakes.

Figure 4. Number of naturally occurring emergent stems in the treeline ecotone in the Tobacco Root Mountains establishing each year and associated climatic conditions during the period 1967-2016. Establishment represents when stem heights reached the current krummholz mat. Climate variables are displayed as 11-year moving-window averages centered on each year (5 years before and after; thick black lines), and as annual values (thin grey lines).

Figure 5. Daily time series of environmental conditions during the krummholz shoot experiment from 1 Aug. 2015 – 23 Jun. 2016. Top: daily maximum, mean, and minimum differences

between within and above krummholz mats (differences are averaged across high- and low-elevation positions). Positive values indicate warmer conditions for mat shoots relative to propped shoots. Middle: mean snowpack depth measured at two SNOTEL monitoring stations in the Tobacco Root Mountains. Vertical bars represent 3-day snow events when more than 15 cm of snow accumulated. Bottom: daily mean modelled 700mb windspeed (~ 3,050 m) derived from the ERSL NCEP/NCAR Reanalysis 1.

Figure 6. A) Post-winter survival (proportion living of all shoots; light grey) and mortality (proportion dead of all shoots; dark grey) of experimentally manipulated krummholz shoots in June/July 2016 (*n* = 10 sites). B) Photographs of a sheltered pair of krummholz shoots that survived the winter (top) and an exposed pair in which the propped shoot died, but the mat shoot survived (bottom). Note the damage to the needle tips in the propped shoot in the top panel, and the damage throughout the entire krummholz mat in the bottom panel.

Figure 7. Relative partial shoot growth in 2016 in experimentally manipulated shoots that survived the winter, expressed as z-scores; i.e., number of standard deviations from the 2013-2016 mean shoot length for each shoot. Z-scores were calculated to standardize across different intrinsic growth rates of krummholz branches – 2016 shoot length minus the mean shoot length of each branch (2013-2016) divided by its standard deviation. Negative numbers indicate that the partial growth measured in June 2016 was typically smaller than the mean length of all years. The baseline of y-axis was placed at -2 to facilitate interpretation. Vertical lines represent ± 1 standard error of the mean.

Figure 8. Effects of warming chambers (A) and shelter cages (B) on temperatures and wind speed, respectively. Different letters in panel A indicate significant differences within temperature categories. Vertical bars represent ± 1 standard error of the mean.

Figure 1.

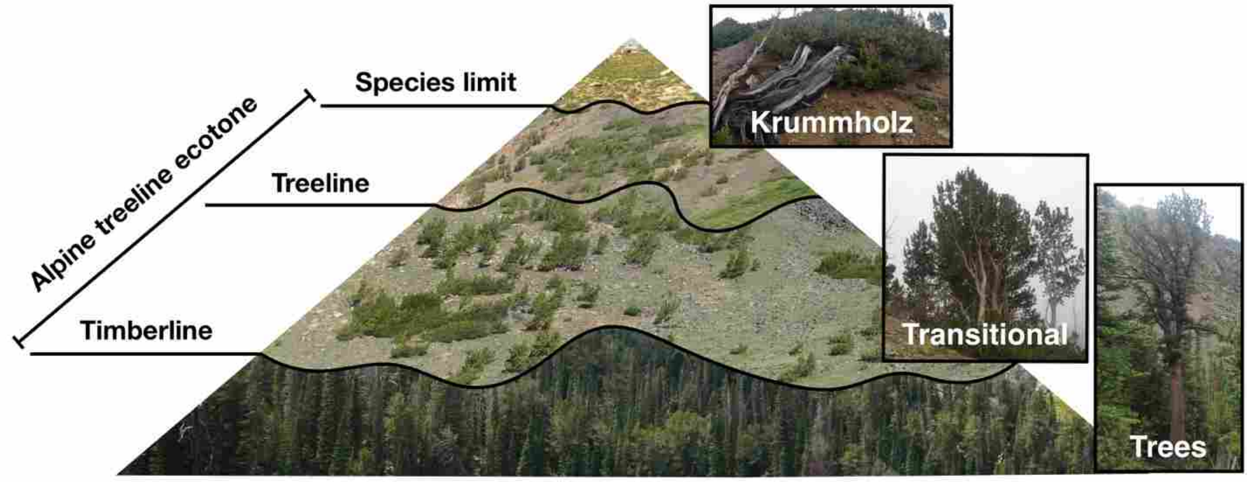
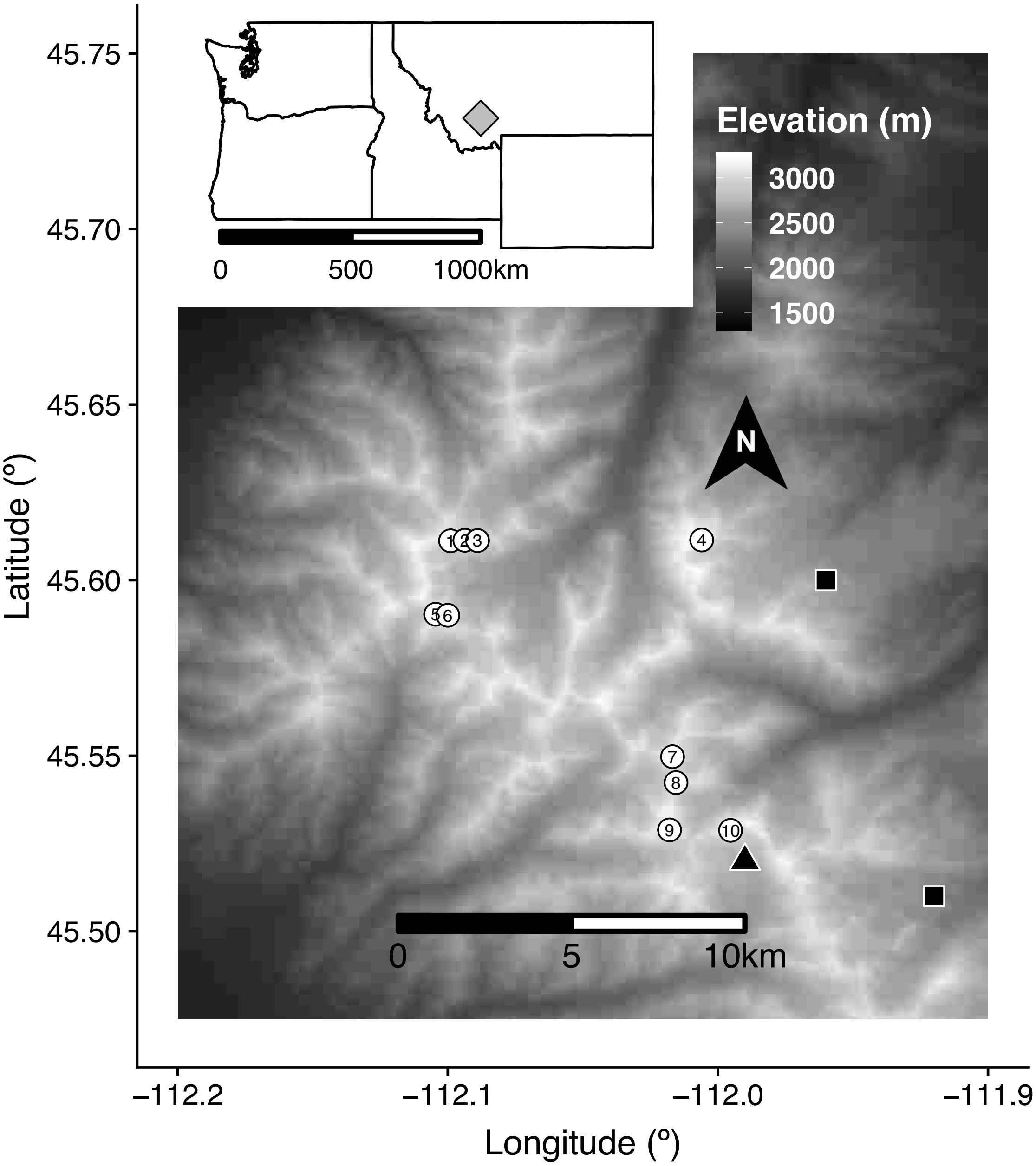
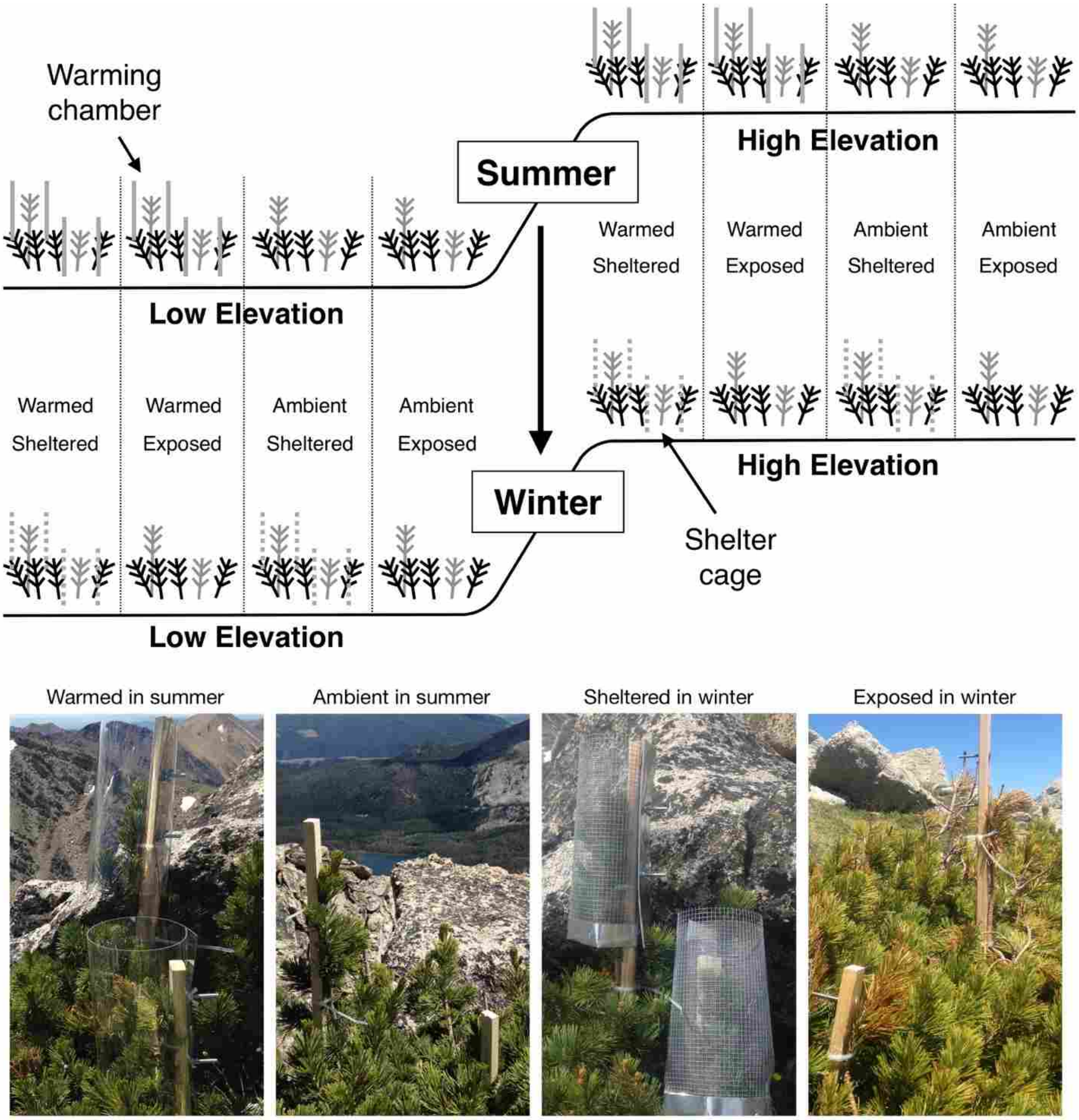

Species limit
Alpine treeline ecotone
Treeline
Timberline
Krummholz
Transitional
Trees

Figure 2.



45.75
45.70
45.65
45.60
45.55
45.50
Latitude (°)
−112.2
−112.1
−112.0
−111.9
Longitude (°)
0
500
1000km
Elevation (m)
3000
2500
2000
1500
N
1
2
3
4
5
6
7
8
9
10
0
5
10km

Figure 3.



Warmed in summer

Ambient in summer

Sheltered in winter

Exposed in winter

Figure 4.

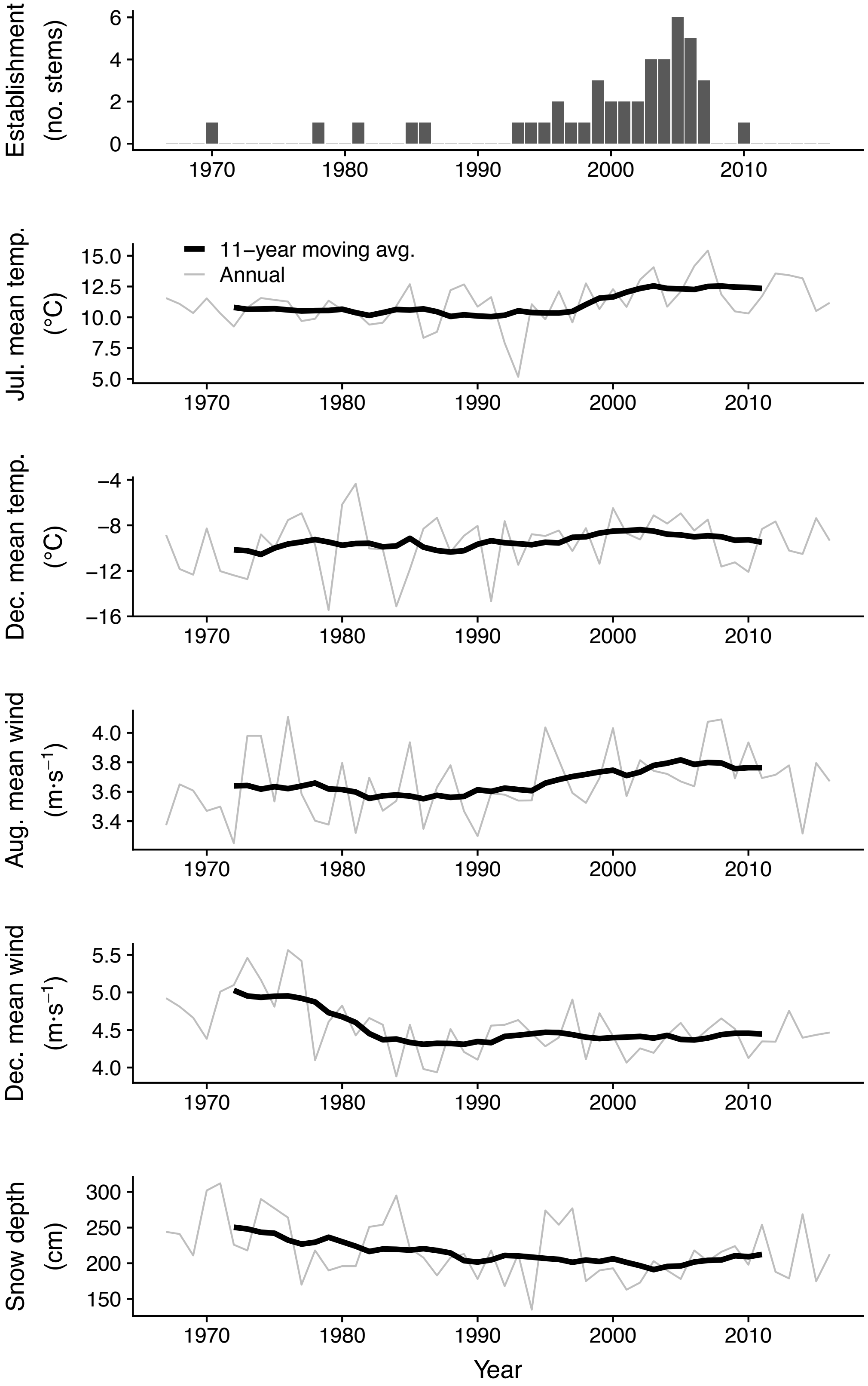
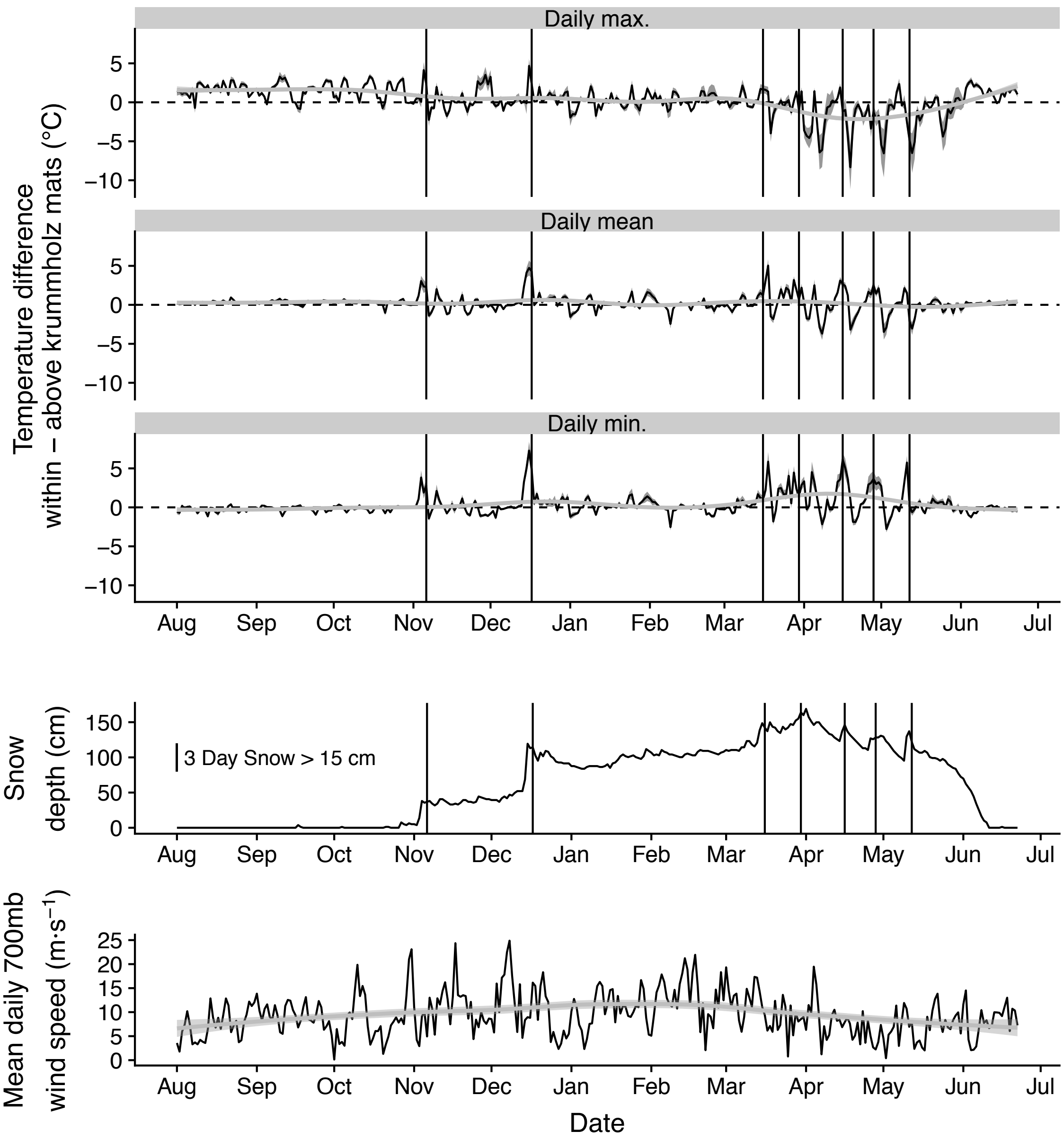

Establishment
(no. stems)
0
2
4
6
1970
1980
1990
2000
2010
11−year moving avg.
Annual
Jul. mean temp.
(°C)
5.0
7.5
10.0
12.5
15.0
Dec. mean temp.
(°C)
−16
−12
−8
−4
Aug. mean wind
(m·s⁻¹)
3.4
3.6
3.8
4.0
Dec. mean wind
(m·s⁻¹)
4.0
4.5
5.0
5.5
Snow depth
(cm)
150
200
250
300
Year

Figure 5.



Daily max.
Daily mean
Daily min.
Temperature difference
within – above krummholz mats (°C)
5
0
−5
−10
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Snow
depth (cm)
150
100
50
0
3 Day Snow > 15 cm
Mean daily 700mb
wind speed (m·s⁻¹)
25
20
15
10
5
0
Date

Figure 6.

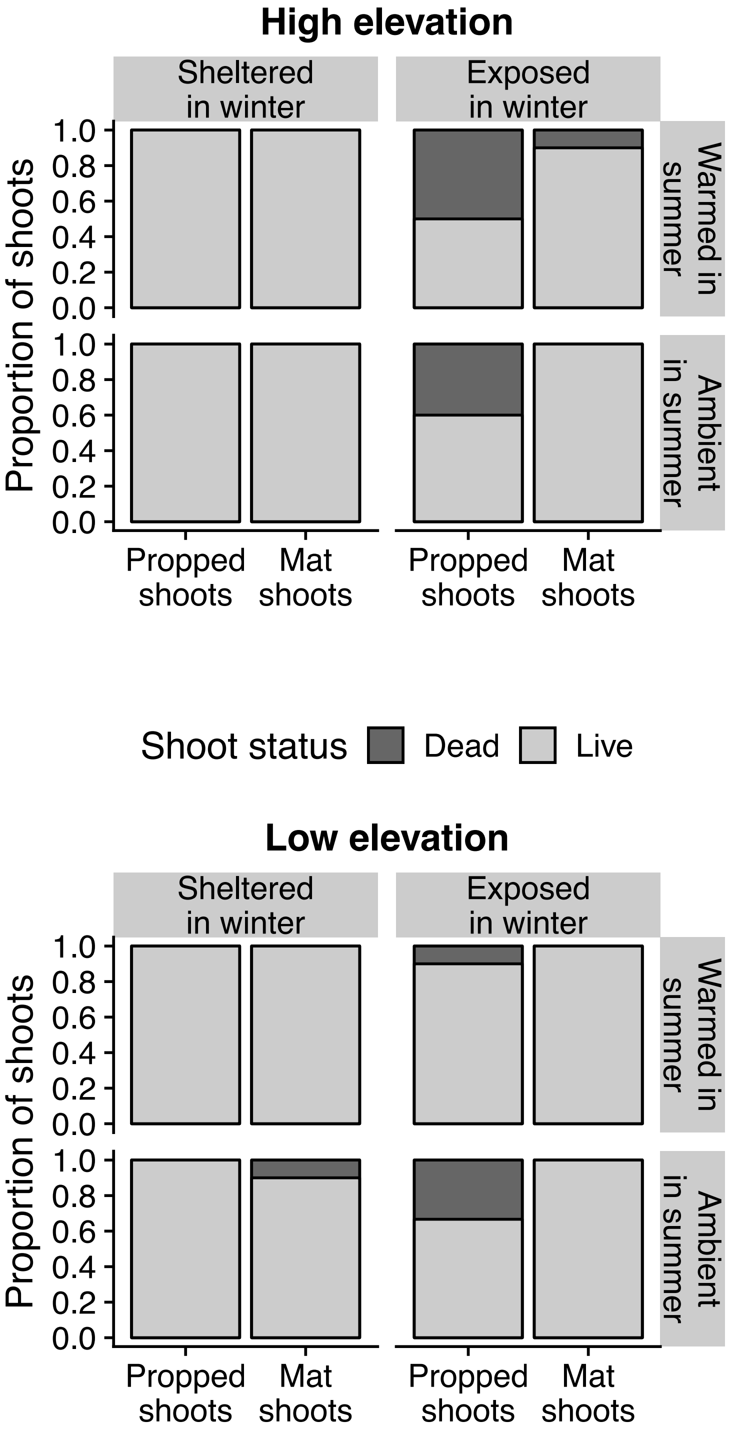

High elevation
Sheltered in winter
Exposed in winter
Warmed in summer
Ambient in summer
Proportion of shoots
1.0
0.8
0.6
0.4
0.2
0.0
Propped shoots
Mat shoots
Shoot status
Dead
Live
Low elevation

Figure 7.

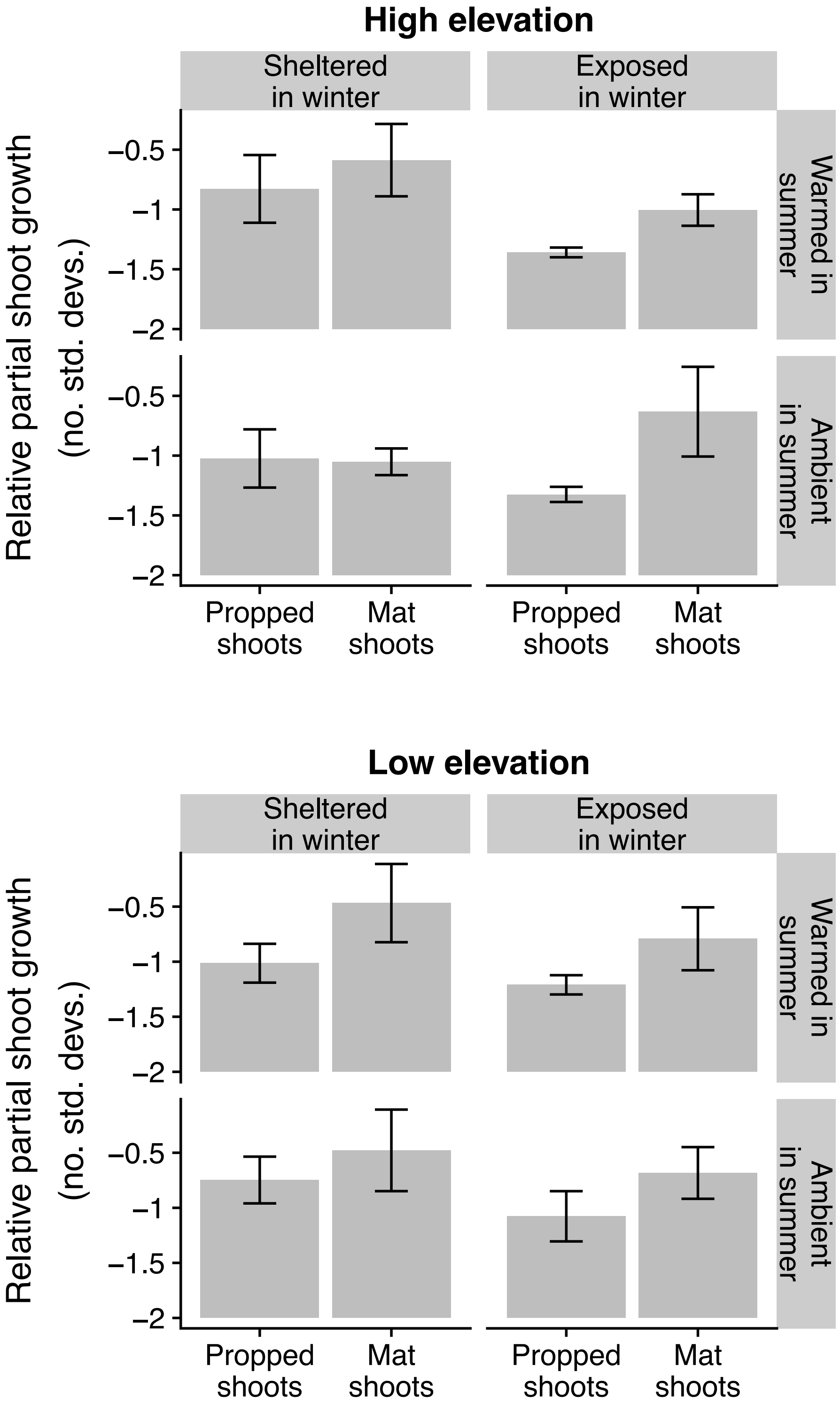
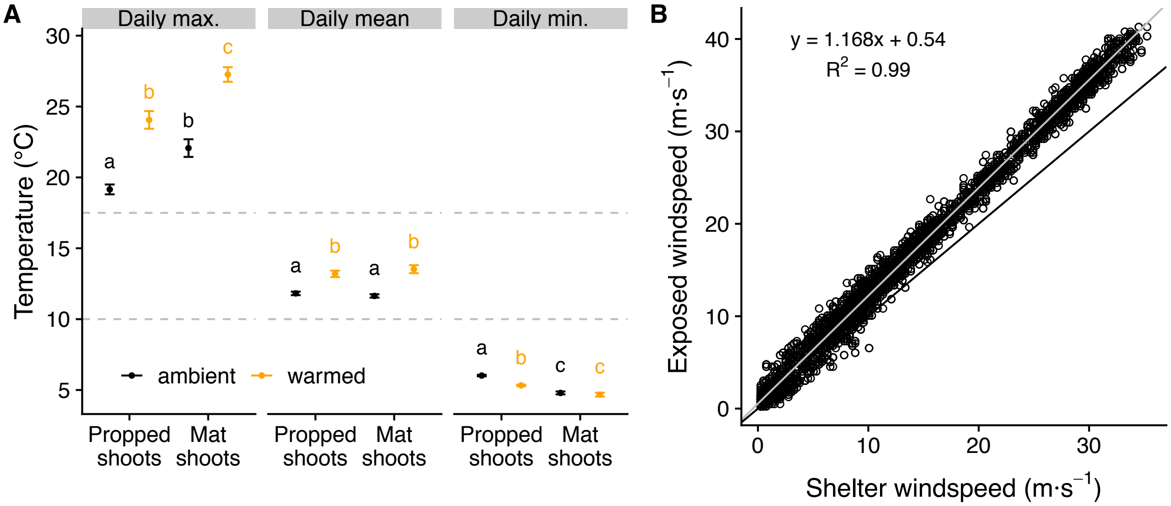

High elevation
Sheltered in winter
Exposed in winter
Warmed in summer
Ambient in summer
Relative partial shoot growth (no. std. devs.)
−0.5
−1
−1.5
−2
Propped shoots
Mat shoots
Low elevation
Sheltered in winter
Exposed in winter
Warmed in summer
Ambient in summer
Relative partial shoot growth (no. std. devs.)
−0.5
−1
−1.5
−2
Propped shoots
Mat shoots

Figure 8.


A
Daily max.
Daily mean
Daily min.
Temperature (°C)
30
25
20
15
10
5
a
b
b
c
a
b
a
b
a
b
c
c
ambient
warmed
Propped shoots
Mat shoots
Propped shoots
Mat shoots
Propped shoots
Mat shoots
B
y = 1.168x + 0.54
R2 = 0.99
Exposed windspeed (m·s−1)
Shelter windspeed (m·s−1)
0
10
20
30
40

Supplementary material for chapter 1: Description of the intervention detection method as implemented in the R environment and additional results figures.

Contents

Appendix A: Description of the intervention detection method for idenitifying growth outliers in tree ring series. (Page 1)

Appendix B: Additional results figures and tables to accompany the manuscript. (Page 14)

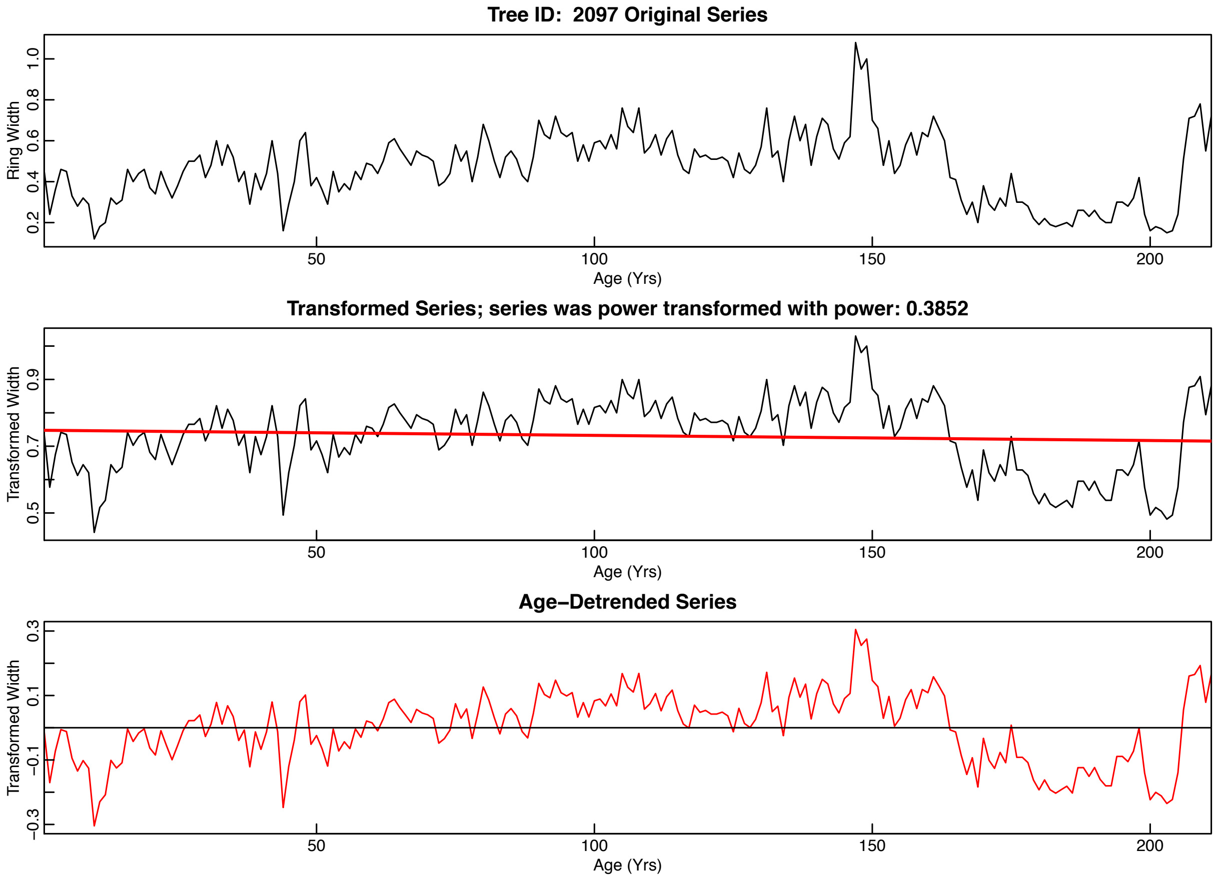
Appendix A

Intervention detection

We used an analysis method called intervention detection to identify abrupt changes in growth caused by silvicultural treatments or by natural disturbances. The method is derived from work by Druckenbrod et al. (2013), and later modified by Rydval et al. (2015, 2016, 2017). The conceptual foundation of this statistical approach to identifying growth departures of biological origin derives from earlier work by Warren (1980), Cook (1985), Warren and LeBlanc (1990), and Druckenbrod (2005). Cook's (1985) model of aggregate tree growth posits that tree ring width series are composites of meaningful ecological signals at distinct relative frequencies. These signals include a low-frequency size-related trend (ring width decreases as a tree adds wood to an ever-increasing surface area), high- to middle- frequency signals from interannual to decadal climate fluctuation, and disturbance signals at multiple scales. It is assumed that rapid changes in growth are due to tree or stand-level disturbance rather than shifts in climate. Originally coded in MatLab (Mathworks 2011), we adapted the method for use in the R environment (R Core Team 2018) using pseudocode provided by Druckenbrod et al. (2013) and through personal communication with D. Druckenbrod.

The analysis begins by power or natural log transforming raw tree ring width series to approach constant variance throughout the series. The optimal power of transformation is estimated using the methods of Cook and Peters (1997). If the estimated optimal power ≤ 0.1, the series is log transformed. We then apply modified negative exponential or linear detrending to the series with the goal of removing size-related decreases in ring width over the length of the entire series (Fritts 1976, Cook 1985). A decrease in ring width with increasing tree age is often observed as secondary growth occurs over an increasingly large surface as the tree grows larger, and doesn't necessarily indicate a decrease in growth, per se. Because the early rapid ring-width decline described by a modified negative exponential curve is best suited to complete series (i.e., including pith) from open-grown trees, characteristics that did not apply to many whitebark pines in our study, negative exponential fits often failed. In these cases, a linear regression was used to remove long-term growth trends. Series with positive trends or no detectable trends were standardized using the mean of the series. Trends or means were removed by subtracting the transformed series by the fitted values, resulting in residual series with a mean of 0 (Cook and Peters 1997). In cases with no decreasing trend, or with an increasing trend, no detrending was performed, and the series mean was subtracted instead (Figure A.1). We performed this step using a modified version of the detrend.series() function from the dplR package (Bunn 2010) to compute residual ring width indices instead of ratio indices.

The transformed, detrended series are then fit with an autoregressive (AR) model. The order of the best fitting AR model is determined using the Burg method (Burg 1978). We then used the residuals of the best fit AR model to identify departures from the growth trend as described by the AR model. We sequentially calculated moving window averages along the residual series starting with the first year in the series and ending with the last possible value for all possible window widths from 5 years to one third of the series length. For each possible window width, we calculated Tukey's biweight robust mean and scale, robust estimators of central tendency and spread (Mosteller and Tukey 1977). The sequential arithmetic means are considered to significantly deviate if they lie outside 3.29 scales from the biweight mean in either


Tree ID: 2097 Original Series

Transformed Series; series was power transformed with power: 0.3852

Age–Detrended Series

Figure A.1. Graphical output of the initial transformation and age-detrending process. The top panel shows the original ring-width series, in original units. The middle panel shows the ring-width series after power transformation, with the trend line in red. The bottom panel displays the transformed after the long-term trend has been subtracted. The age-detrended series is then used in subsequent processes of intervention detection.

direction (releases or suppressions), corresponding approximately to a 99% significance level. A list of significant outliers is generated and the largest deviation from the biweight mean is selected in the current iteration. This step allows identification of growth outliers, their direction, and estimation of their start year and duration.

After the largest outlier is identified, it is then removed by fitting a Warren or Hugershoff curve to the series data from the start year of the outlier period through the end of the series (Warren 1980, Warren and MacWilliam 1981, Fang et al. 2010). The Hugershoff curve takes the following form:

(1) $$y = ax^b e^{(-cx)} + d$$

Where *y* represents the transformed ring width, and *x* the age relative to the start of the series. The parameters *a*, *b*, *c*, and *d* are first approximated by assuming a general shape of all outlier trends. The Warren curve follows the same exponential form as equation 1, only without the intercept parameter, *d*. The final parameters are obtained through via maximum likelihood estimation using optimization techniques. We used the optimx package in R to minimize the loss function using a variety of optimization algorithms (Nash and Varadhan 2011). The best fitting set of parameters, for both Warren or Hugershoff curves, is selected by minimizing the deviance for the period including the outlier and the remainder of the series. Once the outlier trend has been modeled, the model predictions are subtracted from the series. The series mean for the 5 years before the beginning of the outlier series is then added to the differences. If there are less than 5 years in the series before the outlier period (e.g., when an outlier is detected at the beginning of a series), the 5 years after the end of the outlier period are added instead. This last step is done to maintain local continuity in the ring width series, and to avoid generating step artefacts due to a sudden change to values centered around 0. The result is a modified version of the original ring width series with the outlier removed (Figures A.2 and A.3).

This outlier identification and removal process is iterated until no further outliers are detected. Once the iterations are complete, the age-detrending and power transformation performed on the original series are reversed, returning a disturbance-free series (outliers removed) expressed in the original units (mm). A disturbance index is then calculated as the difference in ring width between the original series and the disturbance-free series.

We created an addition wrapper function that performs intervention detection on multiple series in a collection of ring width series. Key outputs from this function are a list containing all outliers with their associated statistics, start date, duration, and direction (release or suppression) for each series, along with a plot displaying this data for each series included in the collection.

Figures A.4 – A.8 show the result plots for all trees at each of our whitebark pine restoration sites.

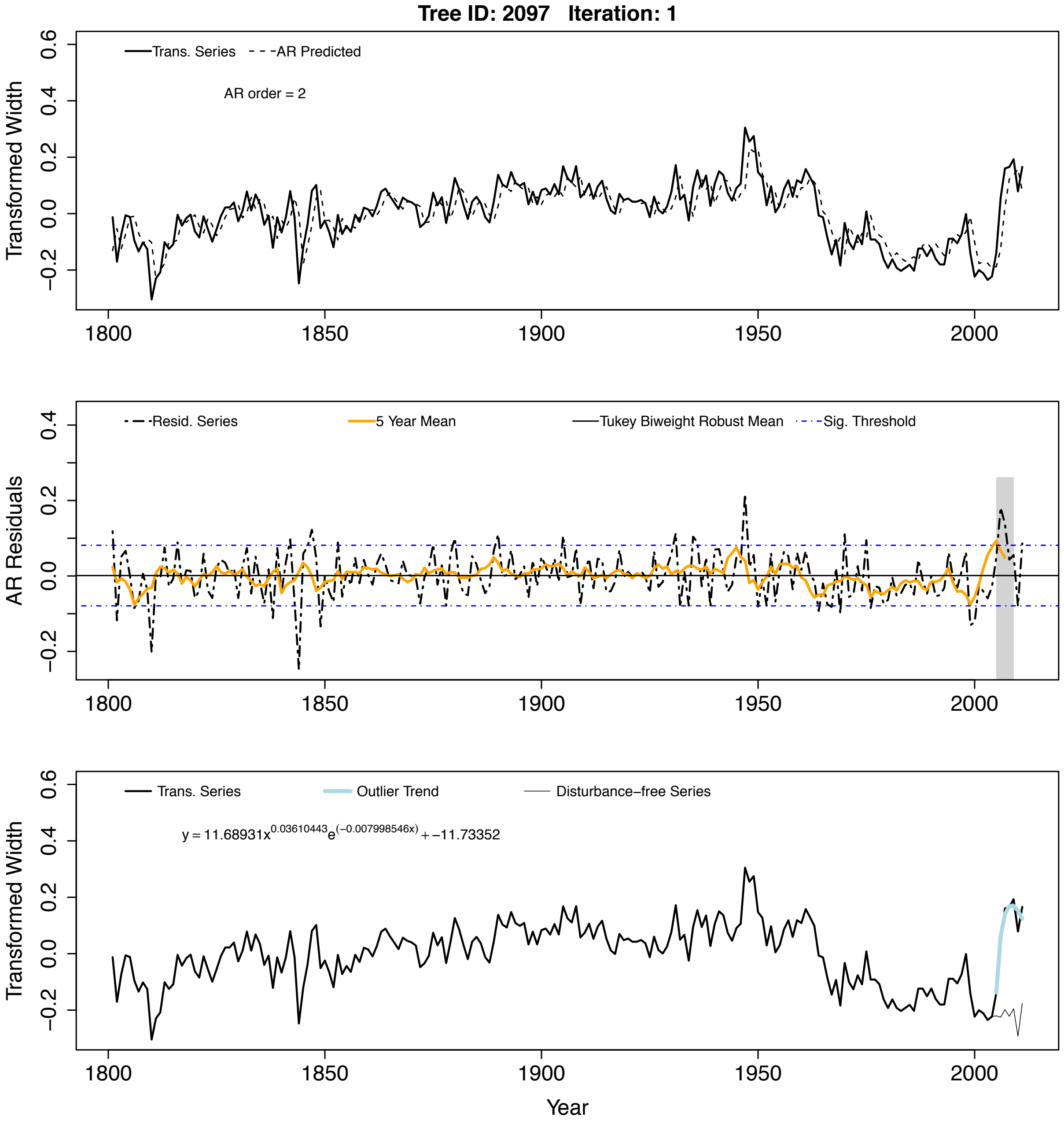


Figure A.2. Example intervention detection output of a mean ring-width series from a single whitebark pine tree. This tree experienced a growth release after treatment (implemented in 2002). Panel A) displays the transformed tree-ring series after it has been age-detrended, along with the predictions from the best fitting autoregressive model (AR order = 2). A large growth release is visible ~ 2005. Panel B) summarizes the process of identifying growth outliers through running means of AR residuals. The 5-year running mean reaches its max value in 2005. This running mean is also clearly outside of the significance threshold of 3.29 robust scales from the Tukey biweight robust mean (TBRM). Panel C) displays the outlier removal process. A trend curve is fit to the series starting from the outlier period (the Outlier Trend). The disturbance-free series is calculated as the difference between the trend curve and the transformed series plus the series mean from before the outlier period. The process is reiterated until no further outlier periods are detected. Two subsequent outliers were detected in this series.

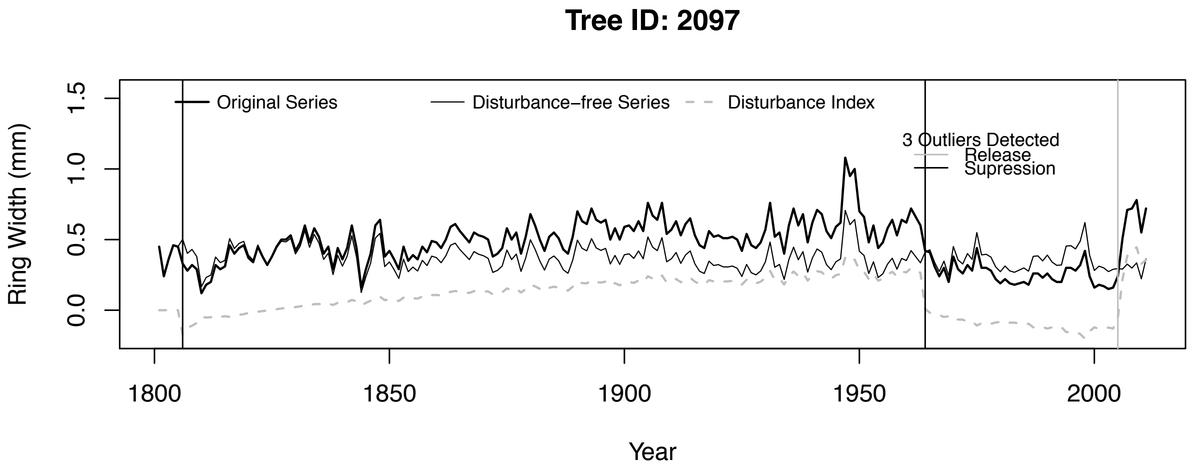


Figure A.3. Example final output of the intervention detection analysis. The original tree ring series is displayed along with the final disturbance-free series and the disturbance index in original units (mm). The start years of growth outliers are indicated with vertical lines: grey lines are release events and black lines are suppression events. Two more growth outliers (both suppression events) were detected after the initial iteration shown in figure 2.

Figures A.4-A.8. Complete records of growth outliers detected by intervention detection for all trees at each of the five whitebark pine restoration sites. Horizontal lines represent individual tree growth series.

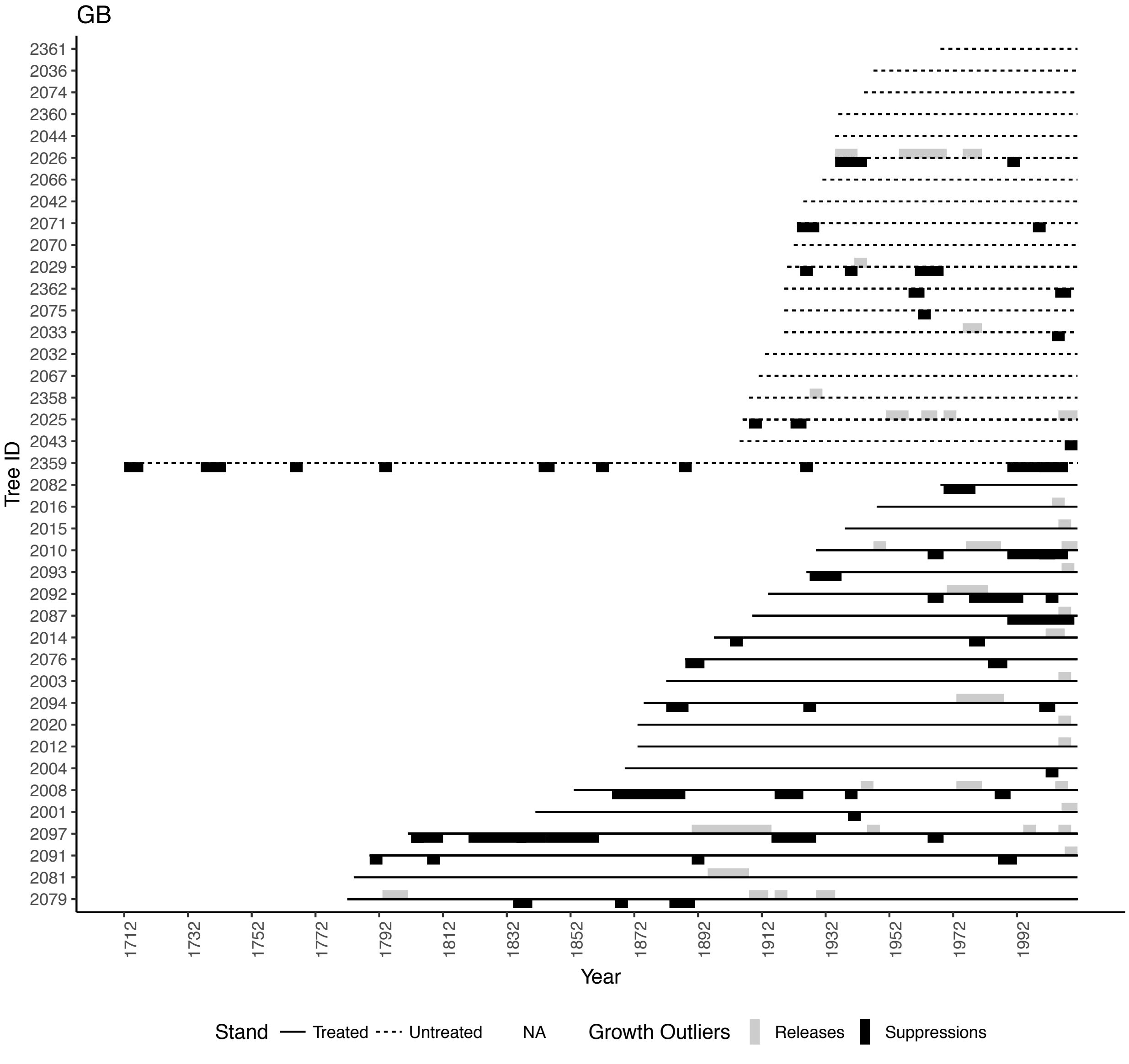


Figure A.4. Granite Butte.

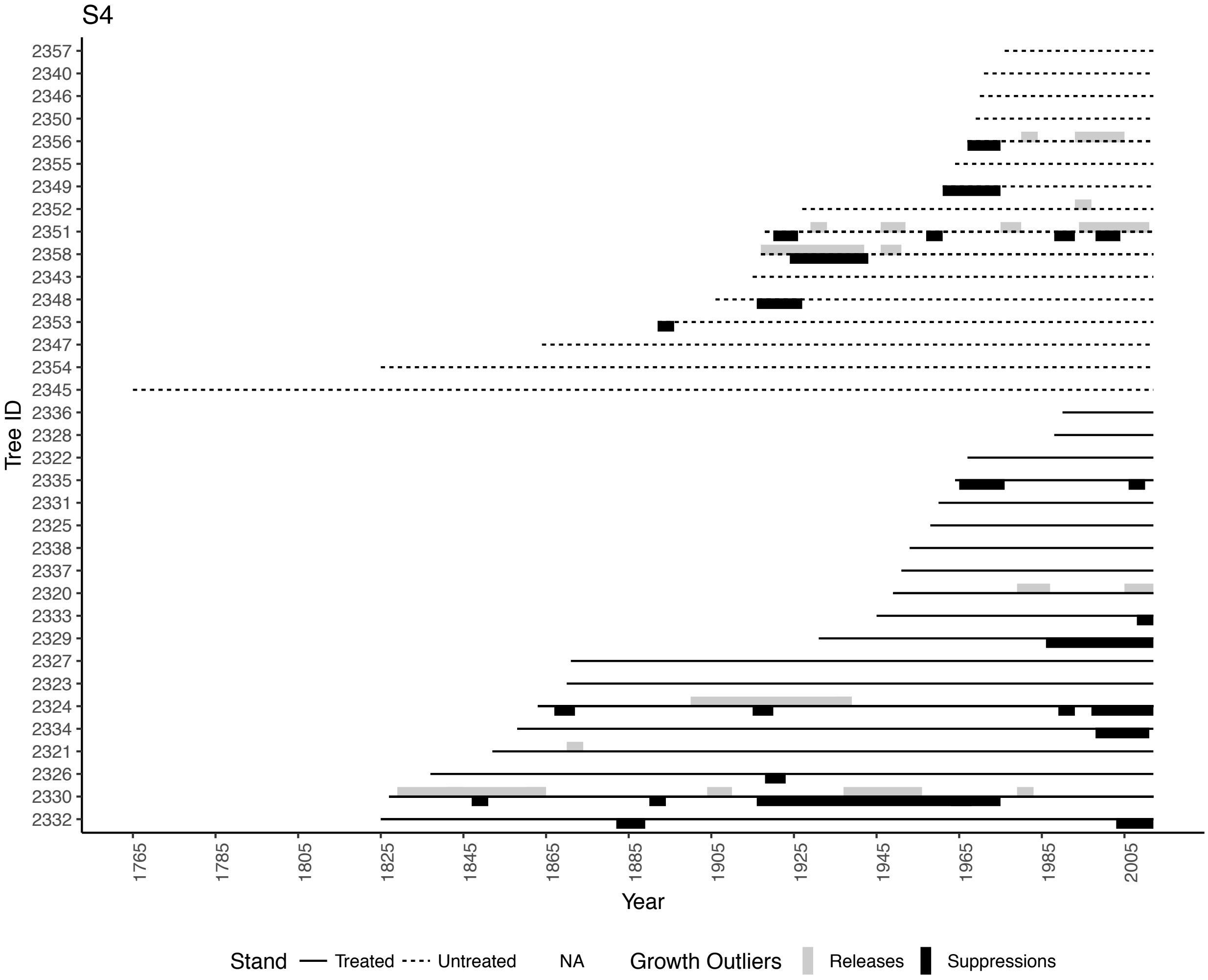


Figure A.5. Snowbank Mountain ’04.

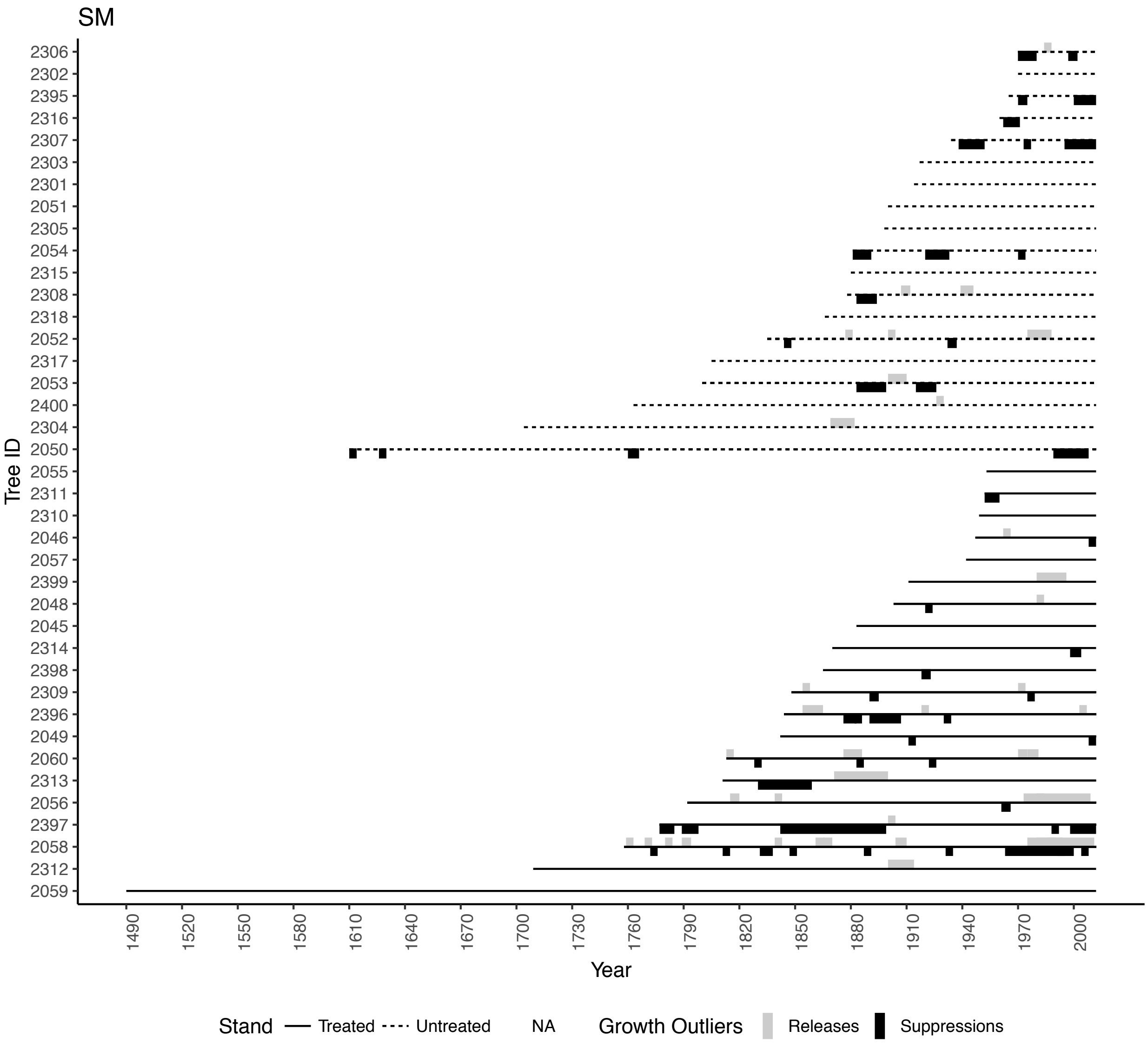


Figure A.6. Snowbank Mountain ’06.

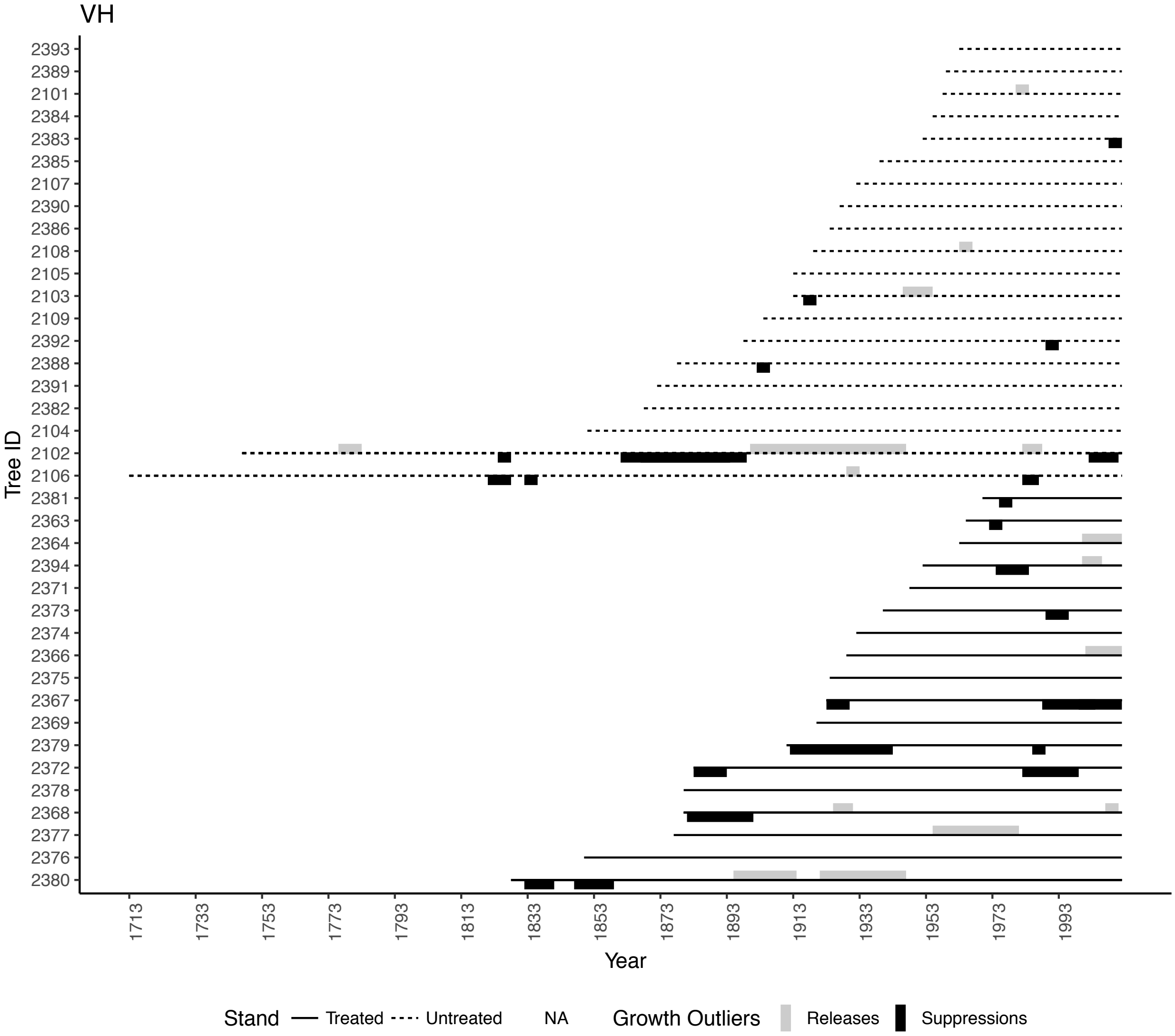


Figure A.7. Vinegar Hill.

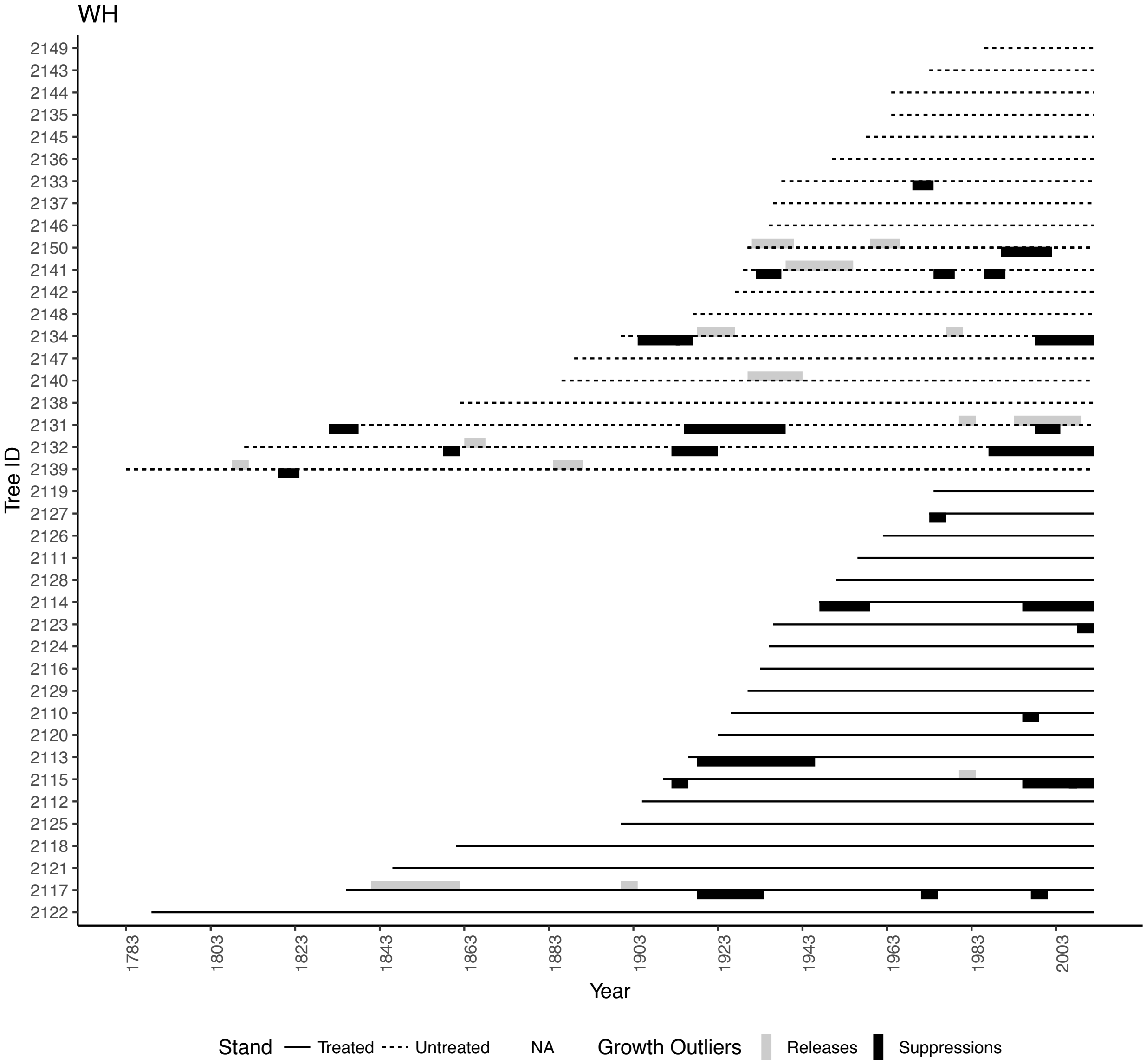


Figure A.8. Whitehawk Mountain.

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Appendix B

Supplementary figures

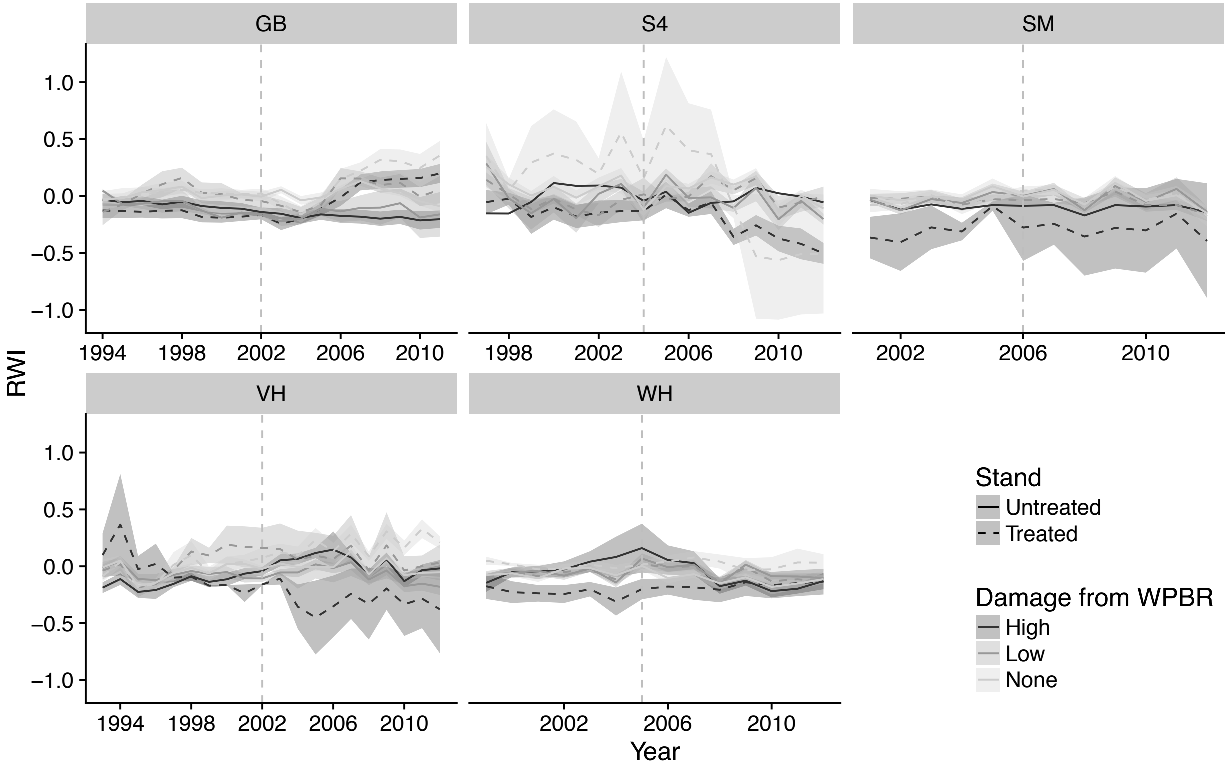

Figure B.1. Mean ring-width index series of treated and untreated stand whitebark pine with three levels of white pine blister rust damage after treatment implementation (*n* = 16-20 trees per stand at each site). Bands around lines represent ± 1 standard error. Vertical dashed lines represent years of treatment implementation.

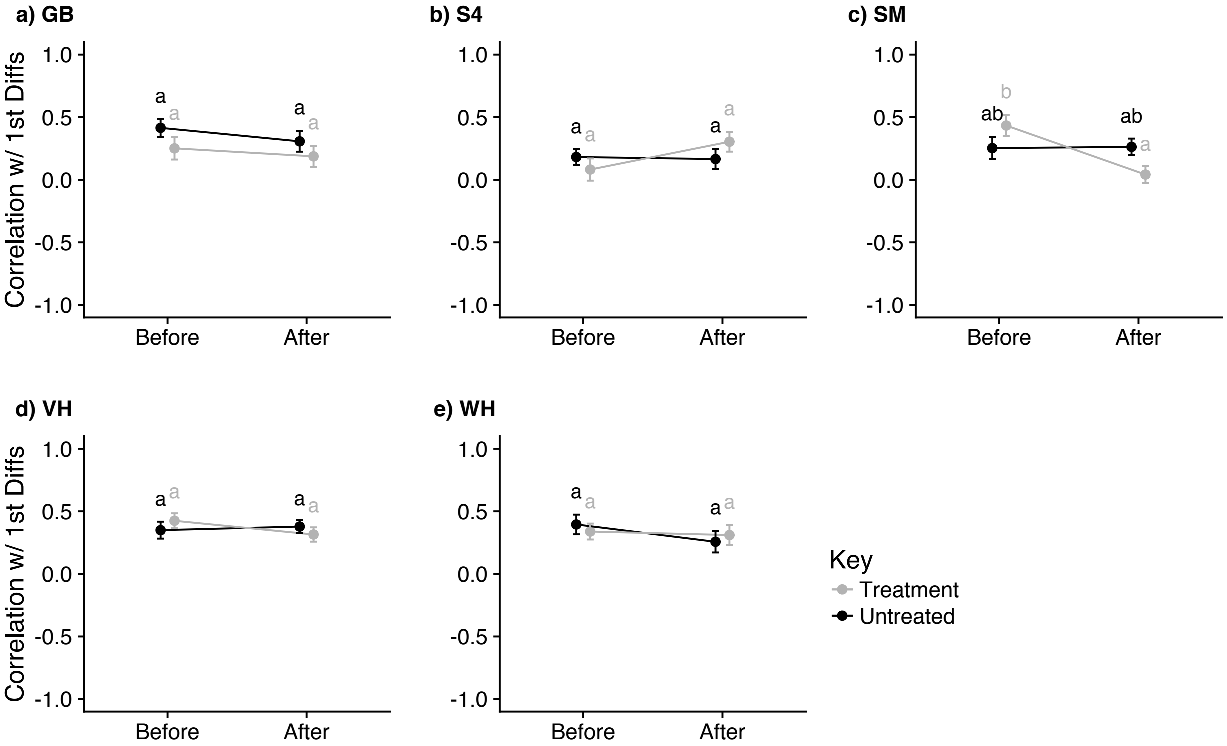

Figure B.2. Changes in interannual growth sensitivity to potential evapotranspiration (PET) between treated and untreated stands and between periods (before and after treatment implementation). Sensitivity is expressed as Pearson correlation coefficients between first differenced RWI and first differenced PET (*n* = 16-20 trees per stand at each site). Distinct letters represent statistically significant differences. Vertical bars represent ± 1 s.e.

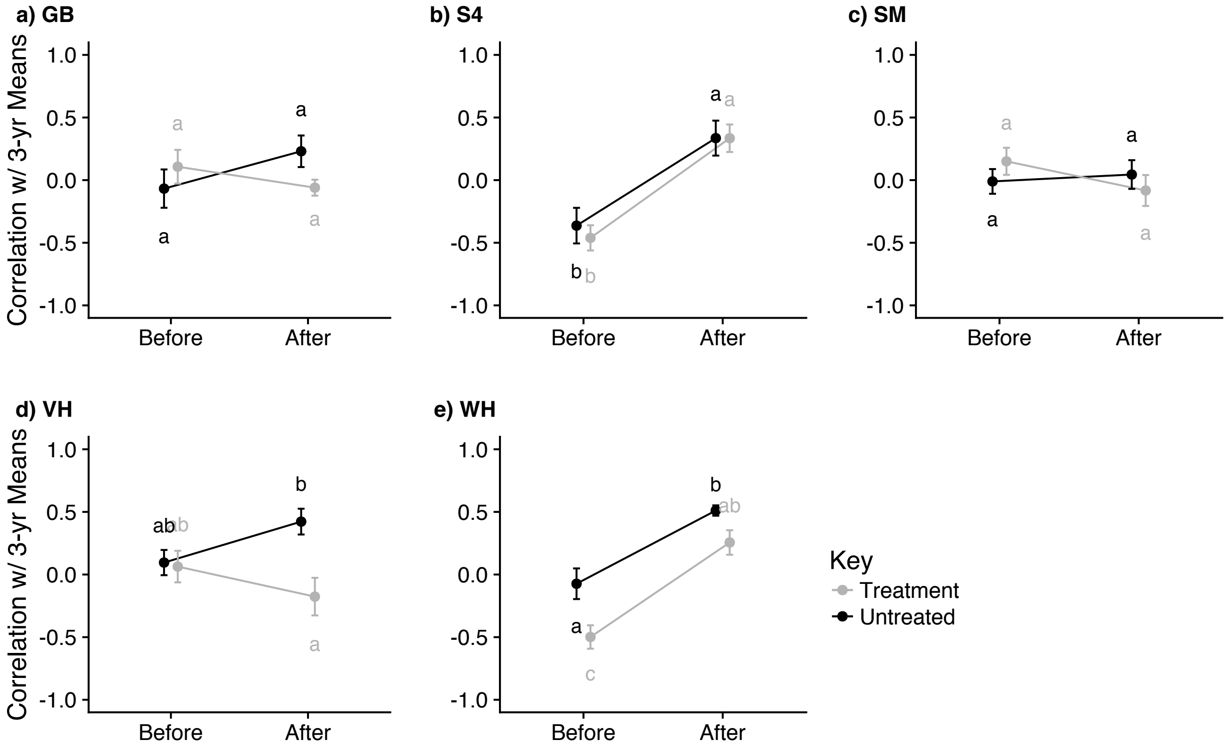

Figure B.3. Changes in relationships of growth trends to trends in potential evapotranspiration (PET) between treatment and untreated stands and between periods (before and after treatment implementation). Relationships between trends are expressed as Pearson correlation coefficients between 3-year mean RWI and 3-year mean PET (*n* = 16-20 trees per stand at each site). Distinct letters represent statistically significant differences. Vertical bars represent ± 1 s.e.

Table B.1. Type III ANOVA table showing effects of stand and period on correlations between first differenced ring-width index (RWI) series and first differenced potential evapotranspiration (PET). *n* = 16-20 trees per stand at each site. Significant results are shown in bold with an asterisk. Marginally non-significant results are shown in bold only.

Site		**GB**		**S4**		**SM**		**VH**		**WH**	
	df	F	P-Value	F	P-Value	F	P-Value	F	P-Value	F	P-Value
Stand	1	2.96	0.09	0.06	0.81	0.07	0.79	0.01	0.92	0.00	0.99
Period	1	1.09	0.30	1.65	0.20	**6.20**	**0.02***	0.46	0.50	1.17	0.28
Stand:Period	1	0.07	0.79	2.21	0.14	**6.85**	**0.01***	1.35	0.25	0.52	0.47

Table B.2. Type III ANOVA table showing effects of stand and period on correlations between 3-year mean ring-width index (RWI) series and 3-year mean potential evapotranspiration (PET). *n* = 16-20 trees per stand at each site. Significant results are shown in bold with an asterisk. Marginally non-significant results are shown in bold only.

Site		**GB**		**S4**		**SM**		**VH**		**WH**	
	df	F	P-Value	F	P-Value	F	P-Value	F	P-Value	F	P-Value
Stand	1	0.22	0.64	0.16	0.69	0.02	0.88	**6.91**	**0.01***	**13.21**	**< 0.01***
Period	1	0.28	0.60	**37.41**	**< 0.01***	0.63	0.43	0.13	0.72	**51.20**	**< 0.01***
Stand:Period	1	3.52	0.06	0.16	0.69	1.66	0.20	**5.58**	**0.02***	0.82	0.37