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

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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. We 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. We 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: we 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. We 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 our analyses revealed that whitebark pine growth at our sites was more temperature limited than water limited. While some management goals were achieved, many were not, and there were some unintended consequences. Our 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, 1982; 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.

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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, 2001; Keane and Arno, 1993; 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). Our 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 (Nyland, 1996; O'Hara, 1988). 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 (Abella et al., 2007; Barth et al., 2015; Keeling et al., 2006). 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 (Maloney et al., 2008; Waring and Six, 2005). 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 (Perkins, 2015; Tomback et al., 1993). 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