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Topography and overstory mortality interact to control tree regeneration in spruce-fir forests of the southern Rocky Mountains

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ABSTRACT

Climate change is driving rapid and dramatic changes in forests across the globe, as highlighted by recent widespread drought-induced tree mortality events. Long-term changes in these forest ecosystems will be dependent upon the ability of trees to regenerate following overstory mortality under a warmer and drier climate. The goal of this study was to assess how tree mortality, and environmental gradients imposed by topographic and edaphic conditions, interact to influence tree regeneration in subalpine spruce-fir forests in a region experiencing rapid climate warming. We evaluated regeneration of two widely distributed subalpine forest species of the Rocky Mountains, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), across gradients of elevation, aspect, soil type, and overstory subalpine fir mortality. In both species regeneration was strongly associated with local topography and appeared to not be adversely affected by subalpine fir overstory mortality. We found that subalpine fir seedling (height < 1.4 m) density was strongly and positively related to subalpine fir basal area prior to mortality. We also found that in areas with overstory mortality, subalpine fir regeneration was negatively associated with high morning heat load (i.e. south and east facing aspects), likely due to water stress associated with less canopy shade and greater morning insolation. In contrast, Engelmann spruce juvenile density was strongly negatively associated with elevation and did not appear vulnerable to projected warming temperatures. Taken together, our results suggest that regeneration contributes to resilience of these forests by compensating for some overstory mortality, but continued warming may adversely affect subalpine fir regeneration, particularly on south and east facing aspects.

1. Introduction

Forests globally are experiencing increasing rates of background mortality (Smith et al., 2015; van Mantgem et al., 2009) and pulses of forest die-off (Allen et al., 2010; Allen and Breshears, 1998) associated with warming climate. Among high elevation forests there are species-specific trends of decline such as sudden aspen decline (Worrall et al., 2013, 2010) and subalpine fir decline (Reich et al., 2016) that are recognized but not yet fully understood. These species-specific trends of decline can rapidly transform forest ecosystems by changing forest structure and composition (Allen et al., 2010), altering forest water budgets (Guardiola-Claramonte et al., 2011), carbon cycling (Kurz et al., 2008), and ecosystem services (Anderegg et al., 2012). In the face of this large-scale driver of forest change, future forest dynamics and structure in these ecosystems will be determined by the capacity of trees to regenerate following tree mortality under warmer and drier climate conditions.

Regeneration is strongly driven by local temperature and moisture conditions experienced by juvenile trees during germination and early survival (Alexander, 1987; Steijlen and Zackrisson, 1987), and therefore changing climatic conditions will likely be a critical factor in understanding how forests recover from disturbance. In subalpine forests, warming climate may have both positive and negative effects on regeneration. Germination and early survival of many subalpine species improves when spring temperatures are warm and snowmelt is early, providing seedlings with a longer growing season in which to establish root systems and aboveground tissue (Alexander, 1987; Little and Peterson, 1993), and limiting the risk of damage from late frosts. In contrast, unusually warm temperature in the mid-summer can damage seedlings both through temperature stress and through moisture stress due to high evaporative demand, particularly when coupled with drought (Andrus et al., 2018; Urza and Sibold, 2017). Thus, the effects of climate on regeneration following disturbance in subalpine regions are complex, and it is critical to understand the factors that contribute

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to the local temperature and moisture regime experienced by juveniles to anticipate their response.

Local temperature and moisture regimes are driven not only by large-scale climatic factors, but also by topographic and edaphic factors such as elevation, aspect and soil type that alter local water and energy balance. Lower elevation regions, where growing seasons are longer, have a greater risk of high mid-summer temperatures that limit regeneration either through heat or drought. At higher elevation juvenile development can be limited by the length of the growing season, but there is increasing evidence that heat induced moisture stress can limit establishment of conifers at high elevations as well (Kueppers et al., 2017; Moyes et al., 2015). Aspect can also influence local water balance through controls on insolation. Equator-facing aspects (southern aspects in the northern hemisphere) generally have higher temperatures and greater evaporative demand than opposing aspects (Desta et al., 2004; Elliott and Kipfmueller, 2011; Zapata-Rios et al., 2015). However, water balance across aspects is also influenced by the interaction of daily maximum insolation and daily temperature fluctuations (Young and Smith, 1983) that can manifest in contrasts between east versus west-facing aspects in addition to north versus south. Finally, soil type can affect regeneration through the effects of soil texture and depth on soil water availability to juveniles during germination and early survival (Alexander, 1984). In the topographically complex landscapes that characterize subalpine regions, these interactions may be an important component of anticipating regeneration following disturbance, particularly in light of increasing temperatures.

Subalpine forests of the southern Rocky Mountains, USA appear to be sensitive to recent climate warming. The region has undergone substantial warming over the past several decades, largely driven by an increase in annual summer maximum temperatures (Rangwala and Miller, 2010). Subalpine fir (*Abies lasiocarpa*), a co-dominant species of the Rocky Mountains subalpine forests, appears to be particularly sensitive to this warming, and is experiencing declines and mortality commonly referred to as Subalpine Fir Decline (SFD) (Colorado State Forest Service, 2013; Reich et al., 2016). The proximate mortality agent for SFD is not fully understood, but SFD is often also associated with western balsam bark beetle (*Dryocoetes confusus*) and fungal pathogens (Negrón and Popp, 2009), which may be particularly severe in regions where host trees are also undergoing increased abiotic stress related to warming climate and drought (Reich et al., 2016).

The complex topography of subalpine regions and the mediating effects of topography on local climate have resulted in non-uniform response to warming among subalpine fir in this region. Subalpine fir is experiencing trends of declining growth and mortality from SFD on warmer and drier landscape positions, but not in cooler and wetter regions (Kelsey et al., 2017; Reich et al., 2016). However, regeneration in regions of SFD has not been studied to our knowledge, and it is unclear if regeneration of subalpine species is also influenced by topographic gradients. Both subalpine fir and the co-occurring species Engelmann spruce (*Picea engelmannii*) are highly shade tolerant with low seed viability (Alexander, 1984), suggesting that regeneration in regions of SFD will predominately occur through advanced regeneration (Veblen et al., 1991). However, new seedling establishment has been observed among both species following blowdown (Kulakowski and Veblen, 2003), and subalpine fir in particular has abundant regeneration following canopy disturbances that leave the forest floor intact (Kulakowski and Veblen, 2003) likely due to its high degree of shade tolerance (Ninemets and Valladares, 2006). Importantly, regeneration levels immediately following disturbance in subalpine forests is highly predictive of longer-term (5 to 10 year) regeneration patterns following disturbances that do not disturb the forest floor (Gill et al., 2017), and thus initial regeneration in regions of subalpine fir mortality is likely predictive of future forest structure. Therefore, understanding how topography mediates climate effects on initial regeneration following mortality in subalpine forests is an important outstanding question.

The goal of this study was to assess how environmental gradients imposed by local topographic and edaphic factors and subalpine fir mortality interact to influence tree regeneration in subalpine spruce-fir forests of the San Juan Mountains, in the southern Rocky Mountains. This region has experienced rapid warming and accelerated tree mortality over the past two decades (Rangwala et al., 2012; Reich et al., 2016; Smith et al., 2015). The specific questions we addressed were as follows: 1. How does subalpine fir and Engelmann spruce regeneration vary across topographic and edaphic gradients of environmental stress?, and 2. How does overstory mortality affect tree regeneration dynamics and do these effects vary across topographic and edaphic gradients? We hypothesized that regeneration would be jointly driven by overstory stand characteristics and topographic position due to the influence of these factors on the local temperature and hydrologic regime that supports regeneration of these shade tolerant species. To address these questions, we performed a field survey to quantify tree regeneration, vegetation structure, and topographic and edaphic conditions at 15 sites in the subalpine spruce-fir forests of the San Juan National Forest in southwestern Colorado, USA. Our field survey was designed to capture a wide range of variation in environmental characteristics (elevation, aspect and soil type) that affect local temperature and moisture conditions, and to span a gradient of adult subalpine fir mortality. This work will help us anticipate how regeneration following disturbances may affect future structure and distribution of subalpine forests in the San Juan Mountains.

2. Materials and methods

2.1. Study area

This study was focused in the subalpine region of San Juan National Forest in southwest Colorado, USA (~38 °N, 108 °W; Fig. 1). The topography of this region ranges from 2000 m to 4200 m, with subalpine forests occurring between 2700 m and treeline which is located at approximately 3600 m. This highly mountainous region experiences low temperature and high snowfall in the winter, and monsoonal rainfall in the late summer (Blair, 1996), for a total of approximately one meter of precipitation annually. Maximum temperatures (~19.5 °C) usually occur in the late summer, and minimum temperatures (~ −13.9 °C) generally occur in the mid-winter. The soils of this region are principally cobbly sand clay loam (NRCS, 2005), overlaying interbedded sandstone, limestone and shale of Pennsylvanian and Mississippian age, with some Tertiary volcanics (Yager and Bove, 2002). This region has experienced rapid warming (Kelsey et al., 2017; Rangwala and Miller, 2010) with average annual temperatures having increased by ~1° C over the past three decades (Kelsey et al., 2017). Subalpine fir mortality

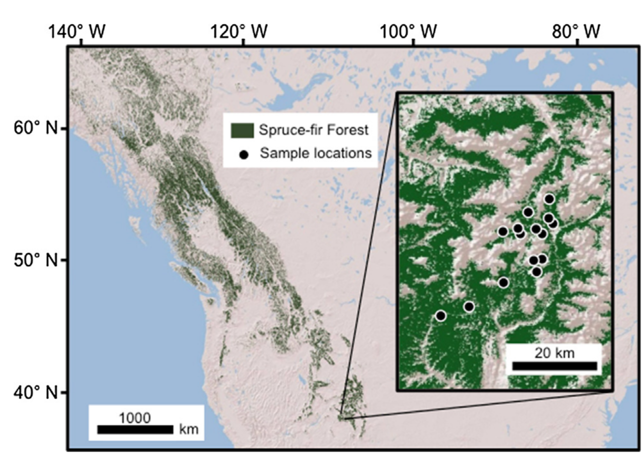

Fig. 1. Map showing the distribution of spruce-fir subalpine forest type throughout North America, and the location of study plots within southwestern Colorado, USA in the inset.