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Spatial patterns of ponderosa pine regeneration in high-severity burn patches

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ABSTRACT

Contemporary wildfires in southwestern US ponderosa pine forests can leave uncharacteristically large patches of tree mortality, raising concerns about the lack of seed-producing trees, which can prevent or significantly delay ponderosa pine regeneration. We established 4-ha plots in high-severity burn patches in two Arizona wildfires, the 2000 Pumpkin and 2002 Rodeo-Chediski Fires, to determine if: (1) distance from forest edge influences the density and spatial patterns of regenerating ponderosa pine and sprouting tree species, (2) interactions with re-sprouting trees affect spatial patterns of ponderosa pine regeneration, and (3) distance from forest edge and species competition affect regenerating ponderosa pine height. Plots were located in high-severity burn patches (defined as 100% tree mortality) and either adjacent to residual live forest edges (edge plots), or > 200 m from any residual live trees (interior plots). We found higher ponderosa pine regeneration densities in the edge plots (13–154 (median = 69) stems ha^{-1}) than the interior plots (12–124 (median = 29) stems ha^{-1}) on both wildfires, but no differences in spatial patterns between edge and interior plots. Ponderosa pine regeneration displayed patterns of small-scale spatial aggregation in all plots, except one edge and one interior plot on the Pumpkin Fire, which displayed random distributions. These patterns suggest both short- and long-distance dispersal play important roles in ponderosa pine regeneration in high-severity burn patches. Sprouting trees dominated tree regeneration on the Rodeo-Chediski Fire, but they were spatially independent of ponderosa pine and did not influence ponderosa pine height. Regenerating ponderosa pine height was positively correlated with neighboring ponderosa pine densities and height, suggesting that intraspecific facilitation or similar habitat preferences occur in high-severity burn patches. Collectively, these results indicate that ponderosa pines are re-establishing with heterogeneous spatial patterns in large high-severity burn patches, but often with low densities. Also, ponderosa pine regeneration could be more strongly influenced by intraspecific facilitation than interspecific competition from dense sprouting species. Future forest spatial patterns and composition are still unclear, but at this stage of development, these heterogeneous patches, characterized by drought-tolerant sprouting species or low pine densities, could be more resilient to climate change and severe wildfires than the overly-dense ponderosa pine forests that were present before the wildfires.

1. Introduction

Over the past three decades, wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity, leaving large, contiguous patches of tree mortality (often ≥ 100 ha) (Dillon et al., 2011; Poling, 2016). Increases in fire size and severity are attributed to the accumulation of abnormally high canopy and surface fuel loads from over 100 years of fire exclusion

(Fulé et al., 1997, 2009; Moore et al., 2004), warmer and drier climate conditions, and longer fire seasons (Dillon et al., 2011; Jolly et al., 2015; Reilly et al., 2017). High-severity wildfires are in stark contrast to the low- to moderate-severity wildfires that dominated the historical fire regime in ponderosa pine forests (Covington and Moore, 1994; Fulé et al., 1997; Moore et al., 2004). Consequently, there is concern for the future sustainability of ponderosa pine forests in large burn patches that kill seed-producing trees, which can prevent or significantly delay post-

fire pine regeneration (Stephens et al., 2013).

Because ponderosa pines evolved under fire regimes dominated by low- to moderate-severity wildfires, they are poorly adapted to regenerate in large patches of high-severity fire (He et al., 2012). Ponderosa pines do not sprout or have serotinous cones, and do not maintain long-lived soil seedbanks; therefore regeneration is dispersal-limited in large patches of high-severity fire and is dependent on surviving seed-sources or residual live trees (Oliver and Ryker, 1990; Chambers et al., 2016; Kemp et al., 2016). Ponderosa pine seeds are morphologically adapted for wind dispersal but their relatively large seeds rarely travel farther than 30 m from seed sources (Oliver and Ryker, 1990), which limits regeneration in the center of large, high-severity burn patches, often > 200 m from seed sources (Chambers et al., 2016). Ponderosa pine seed can also be animal dispersed, and long-distance dispersal by birds may be important for regeneration in the interiors of high-severity burn patches (Li and Wilson, 1998; Lesser and Jackson, 2013; Pesendorfer et al., 2016). However, poor ponderosa pine seed crops, seed predation, and drought can all limit tree regeneration (Pearson, 1950; Larson and Schubert, 1970).

Consistent with the above limitations, a body of research documented low ponderosa pine regeneration densities in large high-severity burn patches (Lentile et al., 2005; Savage and Mast, 2005; Roccaforte et al., 2012; Savage et al., 2013), and declining regeneration with increasing distance from residual live trees (Haire and McGarigal, 2010; Chambers et al., 2016; Rother and Veblen, 2016). For example, regeneration in Arizona and New Mexico ranged from 11 to 26 stems ha^{-1} > 200 m from forest edges in large patches of high-severity fire (Haire and McGarigal, 2010). The strongest predictor of conifer regeneration in high-severity burn patches in the Colorado Front Range was distance from surviving forest, but regeneration also declined with elevation and on more xeric sites (Chambers et al., 2016; Rother and Veblen, 2016). Less is known about how the spatial arrangement of regenerating ponderosa pines in large high-severity burn patches will differ near forest edges compared to the interior of burn patches (e.g. if there are aggregated, random or uniform spatial arrangements). Regeneration spatial patterns should be considered when planning restoration treatments, or to better predict the spatial structure of forest development (Larson and Churchill, 2012; Donato et al., 2012). Ponderosa pine regeneration could be aggregated near the edges of high-severity burn patches due to a clustering of dense pine seeds that fall relatively close to parent trees, better growing conditions, or from rodent seed caches (Oliver and Ryker, 1990; Li and Wilson, 1998; Vander Wall, 2003). Regeneration spatial patterns could also be influenced by competition with sprouting trees to capture new post-fire growing spaces (Fulé and Covington, 1998).

A potential trajectory in large high-severity burn patches in ponderosa pine-dominated forests is a dominance by sprouting tree species (Fulé and Covington, 1998; Barton, 2005; Savage and Mast, 2005; Strom and Fulé, 2007; Coppoletta et al., 2016). Following high-severity fires, sprouting species have regeneration strategies that allow them to quickly recover (Bond and Midgley, 2001; Keeley et al., 2011). High-severity burn patches could potentially exclude tree species establishing from seed and favor a dominance of sprouting species for decades to centuries after high-severity fires (Iniguez et al., 2009). This pattern has been observed in some southwestern ponderosa pine forests (Savage and Mast, 2005; Strom and Fulé, 2007) and in forests that are taxonomically related to ponderosa pine with similar adaptations to frequent fire (*P. arizonica*, *P. durangensis*, *P. engelmannii* and *P. nigra*) (McCune, 1988; Fulé and Covington, 1998; Martín-Alcón and Coll, 2016). However, it is unclear whether or not regenerating ponderosa pines in large, high-severity burn patches will exhibit random associations, attraction (implying facilitation or similar habitat preferences) or repulsion (implying a negative interaction like competition, or different habitat preferences) with sprouting tree species (Luo et al., 2012).

Competition with other species and proximity to forest edges can also affect regenerating ponderosa pine height (Li and Wilson, 1998;

Comeau et al., 1993; Nelson and Bragg, 2016), which could play an important role in site dominance and survival after subsequent fires (Bailey and Covington, 2002; Battaglia et al., 2009; Schwinning and Kelly, 2013). Variation in regeneration height across recovering high-severity burn patches could be driven by variability in seedling age, or proximity to forest edges and/or competition with sprouting species. Hypothetically, regenerating ponderosa pines may grow faster and establish sooner near unburned forest edges than the far interior of burn patches because of protection from wind and shade (Oliver and Ryker, 1990; Li and Wilson, 1998), available microbial symbionts (Nara, 2006; Teste et al., 2009), and nearby seed sources (Bonnet et al., 2005). Post-wildfire tree regeneration height can also be driven by competition for light, water and nutrients with other regenerating species (Comeau et al., 1993; Schwinning and Kelly, 2013).

The goal of this study was to better understand spatial patterns of ponderosa pine regeneration, as well as interactions with sprouting species and regeneration height in contiguous, high-severity burn patches. In order to develop spatially explicit data on post-wildfire tree regeneration, we selected high severity burn patches in two wildfires (the 2000 Pumpkin and 2002 Rodeo-Chediski Fires) and recorded the spatial location of regenerating trees in 4-ha plots located either adjacent to the forest edge (edge plots) or > 200 m from residual live trees (interior plots). We tested the following hypotheses: H$_1$: Higher ponderosa pine regeneration densities and aggregated spatial patterns will be found near forest edges; whereas lower densities and random spatial patterns will be found farther from residual live trees; H$_2$: Ponderosa pine and sprouting species will display a spatial pattern of repulsion; and H$_3$: Height of ponderosa pine regeneration will be greater near residual live trees and with less inter- and intra-specific competition.

2. Methods

2.1. Study sites and plots

We investigated the patterns of ponderosa pine regeneration in large high-severity burn patches in two large Arizona wildfires: the 2000 Pumpkin and 2002 Rodeo-Chediski Fires (Fig. 1). These fires were chosen from all 10 to 15 year old Arizona wildfires because they had extensive patches of high-severity fire (we define high-severity as 100% tree mortality) with no post-fire logging, planting, or subsequent fires. We collected data in 2013 on the Pumpkin Fire (13 years post-fire) and in 2014 and 2015 (12–13 years post-fire) on the Rodeo-Chediski Fire.

The Pumpkin Fire burned approximately 6500 ha, including 1400 ha of high-severity burned area, on the Kaibab and Coconino National Forests (http://www.mtbs.gov/). The average 15 year post-fire annual precipitation was 57.7 cm and the average temperature was 7.2 °C (Prism Climate Group: http://prism.oregonstate.edu/). The elevation ranged from 2350 to 2600 m on our plots. The soils are derived from basalt and study plots are located on soil conditions ranging from moderately deep cobbly clay loam to shallow gravelly sandy loam (Web Soil Survey: http://websoilsurvey.nrcs.usda.gov. Accessed 10/5/16).

The Rodeo-Chediski Fire burned 189,651 ha, including 68,409 ha of high-severity burn area, on the White Mountain Apache lands and the Apache-Sitgreaves National Forest (http://www.mtbs.gov/). Our plots were on the Apache-Sitgreaves National Forest, from 2000 to 2350 m elevation. The average 12-year post-fire annual precipitation was 54.5 cm and the average yearly temperature was 10.7 °C (Prism Climate Group: http://prism.oregonstate.edu/). The soils are derived from sandstone and limestone and are deeper than those at the Pumpkin Fire.

The pre-fire vegetation was dominated by ponderosa pine on both fires, as evidenced by extensive ponderosa pine snags and downed logs burned in the severely-burned areas of the fire, nearby unburned ponderosa pine forest, and dendrochronological reconstructions of forest structure in 1879 near both wildfires (Rodman et al., 2016, 2017). Other common species included grasses such as Arizona fescue (*Festuca*