TREEREGENERATION FOLLOWING LARGE WILDFIRES IN SOUTHWESTERN
PONDEROSA PINE FORESTS

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ABSTRACT

TREE REGENERATION FOLLOWING LARGE WILDFIRES IN SOUTHWESTERN PONDEROSA PINE FORESTS

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Wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have recently increased in size and severity, leaving large, contiguous patches of tree mortality, and raising concerns about post-fire recovery. Ponderosa pines are a dominant species in the Southwest and they evolved with low- to moderate-severity fire regimes. They are poorly adapted to regenerate after large, high-severity fires because they do not have serotinous cones, re-sprouting capabilities, or long-lived seed banks. Additionally, high-severity fires can favor competing understory plants or induce long-term changes to soil nutrient dynamics and surface fuel loads, potentially altering ponderosa pine regeneration niches. Furthermore, high-severity wildfires and the loss of ponderosa pines may alter fungal community composition, including pine-symbiotic ectomycorrhizal (EM) fungi and saprotrophic fungi, which are important for forest recovery and productivity. My research objectives were to understand the effects of fire severity > 10 years post-fire on: (1) the spatial patterns, and interactions of regenerating ponderosa pine and sprouting tree species, (2) ponderosa pine regeneration niches and seedling growth, and (3) fungal sporocarp and root tip EM community composition and colonization. My study sites for the first objective included large, 4-ha plots located in two types of high-severity (100% tree mortality) burn, either adjacent to residual live forest edges (edge plots) or > 200 m from any residual live trees (interior plots) in two Arizona wildfires, the 2000 Pumpkin and 2002 Rodeo-Chediski Fires. Study sites for the last objectives included both high-severity edge and interior plots, as well as moderate-severity, and unburned plots on the Pumpkin fire. I found that ponderosa pine regeneration densities were
lower in the interior compared to the edge of large high-severity burn patches, and regeneration was spatially heterogeneous on both wildfires. However, I did not find evidence that regenerating ponderosa pines were negatively impacted by the presence of re-sprouting trees. More time could eventually lead to higher ponderosa pine densities, but given the predictions for warming climates and increased fire severity, this heterogeneous stage of forest development, that includes native sprouting species could be more resilient to drought and high-severity fires than dense pine stands. I also found that high-severity burns altered understory vegetation and surface fuel loads, but soil properties were similar compared to moderate-severity and unburned areas. I discovered certain niche characteristics that favored ponderosa pine growth, and found that growth was consistently greater in the high-severity edge plots compared to other treatments. Niche characteristics such as overstory tree canopy (-), course woody debris (CWD; +), forb cover (+), Muhlenbergia montana (+) cover, and soil phosphate (+) were important explanatory variables favoring ponderosa pine growth. Surrounding exotic plant cover did not negatively affect ponderosa pine growth. These results suggest that if ponderosa pines can survive the first few critical years after germination, proximity to some forbs and CWD may help increase their growth rates. However, the fact that greater fine fuel biomass and CWD were adjacent to pine seedlings might put them at increased risk from surface fires until they are taller and more fire resistant. My data also revealed that high-severity burn patches had long-term consequences for EM sporocarp communities, and EM inoculum species pools. High-severity burn plots had a unique sporocarp community composition, and a shift in dominant sporocarp functional groups, with 5-13 times lower EM sporocarp densities, and 4-7 times lower EM sporocarp species richness compared to unburned and moderate-severity plots. In contrast, saprotrophic sporocarp densities and richness were similar among treatments, even with the large amount of woody debris in the high-severity burn patches. These results suggest
that large patches of high-severity fire have long-term consequences for EM sporocarp communities, which may reduce reproduction of some species or influence recovery. Managers may want to prioritize the protection of surviving trees within or surrounding large burn patches, as well as naturally regenerating ponderosa pines, to conserve local adaptations, future ponderosa pine seed and EM sources. Also, planted pines may have improved growth near some CWD or forb cover, but they may be at risk for future fires until they are tall enough to survive higher flame lengths. By understanding how above- and belowground communities recover after disturbances, we can improve management plans aiming for forest health and resiliency.
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PREFACE

The following manuscript chapters have been written to appear in peer-reviewed journals. The first dissertation chapter is a general introduction to the work that I completed for my dissertation. The second chapter, “Spatial patterns of ponderosa pine regeneration in high-severity burn patches” was accepted for publication in Forest Ecology and Management in September 2017, and published in November 2017. The third chapter, “Persistent effect of fire severity on ponderosa pine regeneration niches and growth” is a manuscript that I plan to submit to a peer-reviewed journal, and it is formatted for Forest Ecology and Management. The fourth chapter, “Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest” was submitted for publication to Soil Biology and Biochemistry in February 2019, and is currently still under review. The fifth chapter presents general conclusions and management implications for the data presented throughout my dissertation.
Wildfire severity and area burned are expected to increase in many conifer forests due to warmer climates and increased fuel loads (Westerling et al., 2006; Jolly et al., 2015; Abatzoglou and Williams, 2016; Kitzberger et al., 2017), raising concerns for post-fire recovery. Larger, more severe wildfires, along with warmer climates can cause widespread conifer mortality (McDowell et al., 2016; Abatzoglou and Williams, 2016), and limit conifer regeneration for extended periods of time (Stevens-Rumann et al., 2018). Ponderosa pine (Pinus ponderosa) forests are one of the dominant forest types in the semi-arid western US currently at risk from increased fire severity. Large high-severity burn patches are in stark contrast to the low- to moderate-severity wildfires that dominated their historical fire regime (Covington and Moore, 1994; Swetnam and Baisan, 2003). Ponderosa pines are poorly adapted to regenerate after large-high-severity fires because they do not have serotinous cones, sprouting capabilities, or long-lived seed banks. 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; He et al., 2012; Chambers et al., 2016).

Previous studies have 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). However, 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). 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). 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). 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). 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).

In addition to regeneration spatial patterns, it is not well understood how fire severity can impact post-fire regeneration niche characteristics or growth over time. The “regeneration niche” includes suitable environmental factors for different stages of seed production, germination, and growth into mature trees (Grubb, 1977; Clark et al., 1999). Previous research demonstrates variable effects of severe fire on understory plant communities and soils, but it is unclear if large patches (> 200 ha) of high-severity fire will have persistent effects on ponderosa pine niche characteristics or growth. Pine seedling growth can be affected by competition for light, water, and nutrients with other regenerating species (Pearson, 1942; Schwinning and Kelly, 2013). Severe fires open canopy gaps and can create favorable habitat for understory exotic (e.g. Alba et al., 2015) or native (e.g. Abella and Fornwalt, 2015) plant communities, that could each
potentially compete with regenerating conifers. Severe fires can also induce changes to soil nutrients and properties (Covington and Sackett, 1992; Neary et al., 2012; Ross et al., 2012) and increase surface fuel loads which could increase future fuel hazards for a period of years to decades (Roccaforte et al., 2012; Coppoletta et al., 2016). The presence of logs, stumps or scattered slash can protect soil surfaces from erosion, temperature extremes, and evaporation, and may create favorable microsites for post-fire seedling growth because of increased moisture and wind protection (Pearson, 1950; Fajardo et al., 2006; Castro et al., 2011; Flathers et al., 2016). If seedlings survive the high-mortality stage of the first few years after germination, it is unclear if niche components including surrounding plant communities, soil, and litter conditions will differ among different fire severities or continue to influence seedling growth over a decade after the fire.

Finally, high-severity fires and the loss of dominant ponderosa pines across large patches of the landscape may alter fungal community composition, including pine-symbiotic ectomycorrhizal (EM) fungi and saprotrophic fungi. Soil fungi are important components of the soil microbial community that may influence ecosystem resilience and stability after disturbances because of their diverse functions as plant mutualists and decomposers (Buscardo et al., 2015; Gehring et al., 2017; Yang et al., 2018). Previous studies have found that fire can have both direct (e.g., heat-induced mortality) and indirect (e.g., altering soil and litter chemistry, increasing host-mortality and fuel cover) effects on both EM and saprotrophic fungal communities (Kipfer et al., 2010; Buscardo et al., 2011; Bhatnagar et al.; 2018; Awad et al., 2019). The limited studies on the effects of high-severity wildfires on fungal communities in ponderosa pine forests have yielded contrasting results, including either a reduced (Glassman et al., 2016) or similar (Cowan et al., 2016) EM richness, density, and community composition.
compared to pre-fire or unburned areas. There is still much to learn about whether or not increased fire severity, especially resulting in large patches of 100% mortality, often > 200 m from live trees, will have long-term effects on both EM and saprotrophic fungal communities.

To address the knowledge gaps described above, I investigated ponderosa pine regeneration spatial patterns, niche characteristics, growth, and surrounding fungal communities > 10 years after wildfires that had extensive high-severity burn patches. This dissertation research investigates decadal effects of fire severity on: (1) the density, spatial patterns, and interactions of regenerating ponderosa pine and sprouting tree species, (2) ponderosa pine regeneration niches and seedling growth, and (3) fungal sporocarp and root tip EM community composition and colonization. I also discuss management implications for the major results of my research. My study sites for the first objective included large, 4-ha plots located in two types of high-severity (100% tree mortality) burn, either adjacent to residual live forest edges (edge plots), or > 200 m from any residual live trees (interior plots) in two Arizona wildfires, the 2000 Pumpkin and 2002 Rodeo-Chediski Fires. Study sites for the last objectives included both high-severity edge and interior plots, as well as moderate-severity, and unburned plots on the Pumpkin fire.

**Literature Cited**


Chapter 2: 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.

**Highlights:**

- We measured tree regeneration patterns in high-severity burn patches
- Ponderosa pine regeneration densities were lower farther from forest edges
- Ponderosa pine spatial patterns were similar between edge and interior plots
- Intraspecific facilitation may be important for ponderosa pine regeneration

**Keywords:** *Pinus ponderosa*; fire severity; forest resilience; spatial heterogeneity; Gambel oak (*Quercus gambelii*); Arizona
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 meters 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 11-26 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: H₁: 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; H₂: Ponderosa pine and sprouting species will display a spatial pattern of repulsion; H₃: Height of ponderosa pine regeneration will be greater near residual live trees and with less inter- and intra-specific competition.

Methods:

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 10-15 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 6,500 ha, including 1,400 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 2,350 to 2,600 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 2,000 to 2,350 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; Rodman et al., in review). Other common species included grasses such as Arizona fescue (*Festuca arizonica* Vasey) and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.), forbs, and shrubs such as Fendler's ceanothus (*Ceanothus fendleri* A.) on the Pumpkin Fire, and Fendler's ceanothus, Gambel oak
We used Monitoring Trends in Burn Severity (MTBS, 2014) maps with field validation to identify all high-severity burn patches $> 10$ ha in the Pumpkin and Rodeo-Chediski Fires. We used ArcGIS 10.1 (ESRI, 2012) to randomly select three high-severity burn patches per wildfire, within which we established one 4-ha (200 x 200 m) “edge” plot and one 4-ha “interior” plot, for a total of six 4-ha plots per wildfire. Edge plots were established in high-severity burn patches adjacent to residual live trees, and interior plots were established where no surviving trees were found within at least 200 m from the plot boundaries (Fig. 1). From observation, most residual tree edges had high densities, e.g., 250-1000 trees/ha with very little understory vegetation. Plots were at least 30 m away from any roads and from another plot. Edge plot perimeters ranged from 2 – 220 m from residual live trees, and interior plot perimeters ranging from 203 – 455 m from residual live trees. This design allowed us to measure large areas, but does not capture regeneration in between plots, and the partial overlap of distance from residual live trees may limit a true separation between plot types.

*Determining regeneration density and spatial patterns*

To test the hypothesis that ponderosa pine regeneration densities and aggregation will be higher in edge than interior plots, we recorded the spatial location of all regenerating trees ($\geq 10$ cm in height). We established reference points with a GPS (Trimble GeoXH with Terrasync, accurate to $\pm 20$ cm) within each plot and used a rangefinder (Laser Technologies Inc. TruePulse 360-B, accurate to $\pm 38$ cm distance and $\pm 1^\circ$ azimuth) to mark the geographic location of regenerating trees from each reference point. We verified that regeneration establishment dates were post-fire by whorl-counting and determining pith age on a subset of 46 regenerating
ponderosa pines from both wildfires. Regenerating ponderosa pines were from multiple cohorts ranging from 2-9 years post-fire on the Pumpkin Fire and 5-13 years post-fire on the Rodeo-Chediski Fire. The two wildfires were treated as separate case-studies because of differences in soil types and pre-fire understory vegetation, and because post-fire regeneration in the Rodeo-Chediski Fire was dominated by sprouting species.

We tested for differences in ponderosa pine regeneration density between edge and interior plots on each fire with a measure of “intensity” that accounts for spatially explicit patterns, using mppm (model fitted to multiple point patterns) with the spatstat package in R v.3.4.1 (R development Core Team, 2016), as described by Baddeley et al. (2015). Intensity is measured as stems per m² and can vary across each plot with a inhomogeneous process; therefore density is intensity integrated over a larger area. We assumed a Poisson spatial point distribution because we were interested in evaluating overall location-dependent density for this analysis and not patterns of inhomogeneity within plots. We considered the three plots within each edge or interior location as replicates. The model results were interpreted similarly to a typical Analysis of Variance (ANOVA) that evaluates the null hypothesis that the treatment level effects of location are simultaneously zero by generating t-statistics and associated p-values (Bell and Grunwald, 2004). Juniper species on the Pumpkin Fire were excluded from this model because some plots did not contain juniper regeneration. We also tested for differences in stem density in each individual plot with distance from forest edge by using a Thomas process (kppm: cluster process model) model that evaluates Poisson-distributed parent clusters with offspring distributed as bivariate normal (Baddeley et al., 2015). The null hypothesis tests the conditional slope being equal to zero where the response is the log-intensity, and significance is determined by a Z-statistic and associated p-value (Baddeley et al., 2015). For these plot-level assessments,
we accounted for other covariates such as Beer’s aspect (Beers et al., 1966), elevation, percent slope, and topographic position index (TPI) (Jenness, 2006), each measured at 10-m resolution. We did not find any consistent patterns for these covariates across edge and interior plots on either fire.

To compare regeneration spatial patterns between edge and interior plots, we used the *spatstat* package (Baddeley et al., 2015) in R v.3.4.1. We first used a Monte Carlo method to test the hypothesis that the points exhibited Complete Spatial Randomness (CSR) on each plot. We used the inhomogeneous Ripley’s K(r) function (Baddeley et al., 2015) for all plots, unless they exhibited homogeneous patterns within the plot, where we used the traditional form of the Ripley’s K(r) function (Ripley, 1976, 1977, 1979). To determine whether regeneration was distributed in a uniform, random or aggregated fashion, we used Ripley’s K(r) function or the inhomogeneous Ripley’s K(r) function for all plots. These tests compare the distances of all pairs of points, the null hypothesis being that all points are randomly distributed (Ripley, 1976). The variance was stabilized to simplify visual interpretations by using the L(r)-r transformation (Besag, 1977). Interpretation of point pattern analysis results were limited to lag distances of 0-100 meters (half the shortest plot dimension; *sensu* Dixon, 2002) to minimize the influence of unobserved points near observed points close to the plot edge (Boots and Getis, 1988). Significant aggregation or uniformity was determined by comparing observed L(r)-r transformation values to a 95% confidence envelope based on 999 permutations of simulated complete spatial randomness (Upton and Fingleton, 1985). We quantified patch sizes from the lag distance and value of L(r) at the highest point of separation from CSR (Boyden et al., 2005; Sánchez Meador et al., 2009).
Determining species interactions and predictors of regeneration height

To test the hypothesis that pine and sprouting species will display a spatial pattern of repulsion, we performed Ripley’s bivariate K_{12}(r)-r analysis (Lotwick and Silverman, 1982) on each plot, also using the spatstat package in R v.3.4.1. For this analysis, we pooled spatial locations of the sprouting species, Gambel oak and alligator juniper, as “sprouters” on the Rodeo-Chediski Fire, and we also tested individual effects of each sprouter species on ponderosa pine spatial patterns. We analyzed ponderosa pine regeneration as an event occurring a posteriori populations of sprouting species (holding the location of sprouting species constant) instead of randomizing the location of all species, assuming that most sprouting species established soon after the wildfires, whereas ponderosa pine establishment likely occurred later (Harrington, 1989; Haire and McGarigal, 2010). We used the Ripley’s K_{12}(r) bivariate function transformed form, L_{12}(r)-r, proposed by Besag (1977) to calculate the distances between points from different populations and formed confidence envelopes by holding the locations of the sprouting species constant while simulating ponderosa pine locations. Interpretation of analysis results were limited to lag distances of 0-50 meters (one-quarter the shortest plot dimension) to describe relationships between two or more point patterns (e.g., pine regeneration and established oak), to minimize the influence of unobserved points near observed points close to the plot edge, and to maximize comparisons to similar studies reporting bivariate patterns in pine regeneration (e.g., Sánchez Meador and Moore, 2010). A 95% confidence envelope was created by 999 Monte Carlo simulations of the independent point processes null hypothesis (Goreaud and Pélissier, 2003), to evaluate deviations from the null hypothesis. In our case, the null hypothesis was that the location of ponderosa pine and sprouting species was produced from two independent spatial point processes. The alternative hypothesis was that the position of ponderosa pine seedlings was
dependent on the location of sprouting species; \( L_{12}(r) \)-r values > 0 indicate a positive dependence between species, and \( L_{12}(r) \)-r values < 0 indicate repulsion between species (Goreaud and Pélissier, 2003).

To test the hypothesis that ponderosa pine regeneration height will be greater near residual live trees and with less interspecific competition, we measured the heights of all stem-mapped regeneration, and we derived the distance from each regenerating ponderosa pine to the nearest residual live ponderosa pine tree and the density of regeneration within 1 m of each regenerating pine. We determined the distance from each regenerating ponderosa pine to the nearest residual live ponderosa pine tree using imagery (Google Earth©, 2016) and field validation, including trees found along the forest edge, as well as single trees within the interior of the burned patches. We used the Proximity-Near tool in ArcGIS to determine the closest mature trees from all regeneration. We defined amount of competition as the density of neighbors within a fixed radius of 1 m around each regenerating ponderosa pine. Density and height of neighboring ponderosa pines (intraspecific competition) and sprouting species (interspecific competition) was determined within the 1-m buffer around each regenerating ponderosa pine. We used a generalized linear mixed model (GLMM) with a log-link function and Gaussian distribution to test the effects of closest residual ponderosa pine tree and the density and height of intra- and interspecific neighbors on ponderosa pine height, and we included plot as a random effect in the model. All GLMM analyses were done using SAS 9.4 (SAS PROC GLIMMIX© 2017). We tested the effect of Gambel oak and alligator juniper density on ponderosa pine height separately to understand the influence of each species.
Results:

Regeneration density and spatial patterns

Regenerating ponderosa pine densities were lower in the interior plots than edge plots on the Pumpkin Fire ($t = -8.6; p < 0.01$; Fig. 2A), supporting part of our first hypothesis. All plots exhibited inhomogeneous point processes, except one interior plot (interior 2) on the Pumpkin Fire (Appendix A). At a plot level, pine density significantly decreased with distance from forest edge in two out of the three edge plots (three edge plots: $p = 0.01, 0.05, 1.0$), and density did not differ with distance in any of the interior plots ($p = 1.0$ in all three interior plots; Appendix B). Ponderosa pine densities were highly variable on both edge and interior plots (edge plots: 13, 51.3, 153.8 stems ha$^{-1}$; interior plots: 15.2, 31.2, 12 stems ha$^{-1}$) (Fig. 2A). Other tree species made up a small portion of the total regeneration. We documented an average of 15.2 quaking aspen ($\text{Populus tremuloides}$ Michx.) stems ha$^{-1}$ in the interior plots and 9.1 stems ha$^{-1}$ in the edge plots. We found an average of 6 juniper stems ha$^{-1}$ in the edge plots and 4.8 juniper stems ha$^{-1}$ in the interior plots. These were likely alligator juniper or Rocky Mountain juniper ($\text{Juniperus scopulorum}$ Sarg.), but we could not identify juveniles to species. We found an average of < 1 Douglas-fir ($\text{Pseudotsuga menziesii}$ (Mirb.) Franco) stem ha$^{-1}$ in the interior plots, and Douglas-fir was not observed in the edge plots. Both edge and interior plots on the Pumpkin fire were dominated by understory herbaceous plants.

On the Rodeo-Chediski Fire, ponderosa pine regeneration densities were also lower in the interior plots than the edge plots ($t = -3.5; p < 0.01$; Fig. 2B). All plots exhibited inhomogeneous point processes (Appendix A). At a plot level, ponderosa pine densities decreased significantly with distance from forest edge in two out of the three edge plots (three edge plots: $p = 0.01, < 0.01, 1.0$), and one interior plot ($p = 0.05$). Ponderosa pine densities were not correlated with
distance from forest edge in one interior plot (p = 1.0), and density actually increased (p = 0.01) with distance in one interior plot (Appendix B). Ponderosa pine density was highly variable on edge and interior plots (edge plots: 148.5, 86.3, 45.8 stems ha⁻¹; interior plots: 44.5, 27.3, 124.0 stems ha⁻¹). One interior plot located 220-420 m from any residual live trees unexpectedly had almost 3 times higher regeneration densities than a nearby edge plot (interior and edge plots 3). Both edge and interior plots on the Rodeo-Chediski Fire were dominated by sprouting species. We documented an average of 969 Gambel oak stems ha⁻¹ (58, 415.8, and 2,433.8 stems ha⁻¹) on the edge plots and 453 Gambel oak stems ha⁻¹ (246, 8.3, and 1,104.5 stems ha⁻¹) on the interior plots. We found an average of 330 alligator juniper stems ha⁻¹ (14.3, 519, 457.5 stems ha⁻¹) on the edge plots and 464 alligator juniper stems ha⁻¹ (77, 291.8, 94.8 stems ha⁻¹) on the interior plots. The relationship between ponderosa pine vs. sprouter density was not consistent. The edge plot with the highest density of sprouting species had the least ponderosa pine regeneration. However, the interior plot with the highest density of sprouting species, had the most ponderosa pine regeneration.

Contrary to our hypothesis, we did not observe differences in ponderosa pine spatial patterns between edge and interior plots on the Pumpkin Fire (Fig. 3, Table 1, Appendix C). Ponderosa pine regeneration exhibited significant small-scale aggregation in two edge and two interior plots from approximately 1-22 m lag distance, and had uniform and/or random spatial patterns at larger scales (Fig. 3, Table 1, Appendix C). Ponderosa pine regeneration did not fall outside complete spatial randomness in one edge and in one interior plot (Fig. 3, Table 1, Appendix C). Regeneration that displayed aggregation had patch sizes ranging from 0.001 – 0.045 ha on one edge and one interior plot (edge 2, interior 1) (Table 1, Appendix C). Aspen regeneration was significantly aggregated on 5 of the 6 plots at varying lag distances (from 1-10
m up to 1-75 m) and displayed spatial randomness at other distances (from 59-100 up to 1-100 m) on the Pumpkin Fire (Appendix D and E).

We also did not observe differences in ponderosa pine spatial patterns between edge and interior plots on the Rodeo-Chediski Fire (Fig. 3, Table 1, appendix C). Pine regeneration exhibited significant small-scale aggregation from 1 – 35 m lag distances, and had uniform and/or random spatial patterns at larger scales on all plots (Fig. 3, table 1, Appendix C). Average patch sizes ranged from 0.001-0.031 ha, with the highest density on 2 interior plots (Table 1, Appendix C). Furthermore, Gambel oak and alligator juniper were also significantly aggregated in all edge and interior plots at varying distances, except Gambel oak displayed a random distribution in one interior plot (Fig. 4, Appendix F). Gambel oak and alligator juniper also had varying patch sizes, and on some plots the patch is almost as large as the 4-ha plot due to such high densities (Fig. 4, Appendix E).

**Ponderosa pine species interactions and regeneration height**

Populations of ponderosa pine and sprouting species were spatially independent, contrary to our second hypothesis (Fig. 5). Ponderosa pine and quaking aspen populations were spatially independent on all edge and interior plots on the Pumpkin Fire. Ponderosa pine and pooled sprouting species (alligator juniper and Gambel oak) were spatially independent on all edge and interior plots on the Rodeo-Chediski Fire (Fig. 5), and when sprouting species were analyzed separately, ponderosa pine and individual populations of alligator juniper and Gambel oak were spatially independent on all plots (Appendix F). There was a trend for more repulsion between pine and alligator juniper on plots when juniper regeneration was dense, and attraction with Gambel oak, but there were no statistically significant patterns (Appendix F).
Contrary to our third hypothesis, regenerating pine height was not greater near residual live trees or with less interspecific competition, and model differences were driven by density and similar heights of intraspecific neighbors. Distance from residual live trees did not explain variation in regenerating ponderosa pine heights on either wildfire (Pumpkin Fire: $F = 1.40, p = 0.24$; Rodeo-Chediski Fire: $F = 0.22, p = 0.64$; Appendix G). The Pumpkin Fire had too few sprouting neighbors within 1-m radius of regenerating ponderosa pines for the model; therefore only intraspecific neighbors were included for neighborhood density and height variables. Neighborhood intraspecific density ($F = 4.73, p = 0.03$) and height ($F = 9.21, p < 0.01$) were both positively correlated with ponderosa pine height on the Pumpkin Fire (Fig. 6A, Appendix H). Neighborhood intraspecific density ($F = 45.47, p < 0.01$) and height ($F = 171.13, p < 0.01$) were also both positively correlated with ponderosa pine height on the Rodeo-Chediski Fire, but the heights of neighboring sprouting species were not significant predictors of ponderosa pine height (Fig. 6B, Appendix H). Neighboring Gambel oak ($F = 1.90, p = 0.17$) and alligator juniper density ($F = 3.33, p = 0.07$) were also not significant predictors of ponderosa pine height (Appendix H).

**Discussion:**

Our study found that pine densities were lower in the interiors of high-severity burn patches than near forest edges, consistent with previous studies (Haire and McGarigal, 2010; Chambers et al., 2016). Seed dispersal from forest edges, protection from wind and sun, and favorable soil conditions near forest edges likely led to higher ponderosa pine densities than in the interior plots (Teste et al., 2009; Haire and McGarigal, 2010; Reynolds et al., 2013; Chambers et al., 2016; Kemp et al., 2016). It may take longer for regeneration to occur within the interiors than the edges of burn patches due to dispersal by wind or birds vs. high seed pressure...
from nearby residual trees. Low ponderosa pine regeneration densities in both plot types, and a
dominance of either understory herbaceous plants or sprouting trees, could be due to a lack of
adequate ponderosa pine seed-sources, slow recovery, or unfavorable post-fire habitat or climate
conditions for ponderosa pine regeneration (Pearson, 1950; Larson and Schubert, 1970; Haire
and McGarigal, 2010). These results could also be from superior regeneration strategies from
herbaceous or sprouting species that allowed them to quickly recover in these large, treeless
patches (Bond and Midgley, 2001; Battaglia et al., 2002). We investigated potential differences
in regeneration densities from topography and aspect and found no consistent patterns, although
two Colorado studies found reduced pine regeneration on lower elevations and more southerly
aspects (Chambers et al., 2016, Rother and Veblen, 2016).

Even though pine densities were lower in interior than edge plots, regenerating ponderosa
pines were nonetheless found over 300 m from any residual live tree in all interior plots,
suggesting long-distance dispersal may be an important mechanism for regeneration in the
interior of burn patches (Haire and McGarigal, 2010; Lesser and Jackson, 2013). Similar to our
findings, post-fire ponderosa pine regeneration has been found > 200 m from residual live trees
(Bonnet et al., 2005; Haire and McGarigal, 2010), and even up to > 10 km away from parent
trees, likely from scatter-hoarding by corvids and other birds (Lesser and Jackson, 2013;
Pesendorfer et al., 2016). Long-distance dispersal of seeds can have a critical effect on species
survival and increase genetic diversity in patchy landscapes (Ozawa et al., 2013). Long-distance
dispersal likely contributed to the heterogeneous spatial patterns of regenerating ponderosa pine
in the interior plots as well.

We did not observe differences in the spatial patterns of regenerating ponderosa pine
between plot types as expected, suggesting factors other than proximity to forest edges, such as
animal seed dispersal or favorable microhabitat contributed to small-scale ponderosa pine aggregation in both edge and interior plots (Oliver and Ryker, 1990; Lesser and Jackson, 2013; Pesendorfer et al., 2016). Ponderosa pine regeneration was spatially aggregated at scales similar to those found in managed ponderosa pine stands in Arizona and Montana (Fajardo et al., 2006; Sánchez Meador and Moore, 2010). Small-scale spatial aggregation in the edge plots may have been from rodents because they usually cache ponderosa pine seeds within 30 m of seed-source trees (Vander Wall, 2003); whereas birds may have contributed to seedling aggregation in the interior plots because they can cache seeds > 10 km away from parent trees (Lesser and Jackson, 2013). Aggregated ponderosa pine regeneration could occur in pockets of preferred microhabitat, such as favorable soil conditions or near logs or stumps that provide extra moisture or wind protection (Oliver and Ryker, 1990; Teste et al., 2009; Sánchez Meador and Moore, 2010; Castro et al., 2011). Southwest prevailing winds can also influence the spatial location of seed dispersal, but we did not observe regeneration aggregating along this direction. Post-fire ponderosa pine can regenerate in clumps, as well as by remotely dispersed individuals, depending on seed sources and competition with sprouting species (Haire and McGarigal, 2010).

We expected a spatial pattern of repulsion between ponderosa pine and sprouting species because competition with sprouters influenced seedling regeneration in other studies (Fulé and Covington, 1998; Higgins et al., 2008). We observed a dominance of sprouting tree species on the Rodeo-Chediski Fire, a pattern similarly found by other studies (Barton, 2005; Savage and Mast, 2005; Strom and Fulé, 2007; Coppoletta et al., 2016). Even though sprouting species were found at high densities, we found spatial independence between ponderosa pine and sprouting species on all of our plots, suggesting that sprouting species did not repulse nor attract pine regeneration. Regenerating ponderosa pine had a random association with the locations of
Gambel oak trees in northern Arizona under different harvesting regimes (Sánchez Meador and Moore, 2010). Perhaps interspecific competition or facilitation is not always a strong driver of pine regeneration and survival. There is evidence that ponderosa pine can establish beneath oaks and eventually overtop them as they mature, which can sometimes lead to decreases in sprouting species (McDonald, 1990; Vankat, 2013).

Interspecific competition and distance from forest edges did not influence ponderosa pine growth as expected. Ponderosa pine regeneration height in large high-severity burn patches could be the result of seedling age, microsite conditions, herbivory or facilitation (Fajardo and McIntire, 2011; Waring and Goodrich, 2012; Smith et al., 2016), rather than distance from forest edge or competition. A limitation of this study was not knowing the age of each pine seedling. We attributed differences in regenerating ponderosa heights between the two wildfires (2-3X taller on the Rodeo-Chediski Fire) to differences in temperature, moisture, soil nutrients, or herbivore or insect damage (Puhlick et al., 2012, 2013). The positive correlation between ponderosa pine height and neighboring ponderosa pine heights and densities, suggests that similar ages established together or similar environmental conditions influenced establishment and growth (Oliver and Ryker, 1990). It is also possible that facilitation could be a stronger process than intraspecific competition, a pattern observed by Fajardo and McIntire (2011), and led to greater height and ultimately survival. Rapid height growth may also allow regenerating ponderosa pines to survive a subsequent fire (Bailey and Covington, 2002; Battaglia et al., 2009). Approximately half of the ponderosa pine regeneration on the Rodeo-Chediski Fire and a fourth on the Pumpkin Fire had heights > 1.4 m, with a measurable diameter at breast height (DBH). Ponderosa pine seedlings can be more fire-resistant at 3 m height (Bailey and Covington, 2002),
and those ~2 m tall are predicted to require > 2 m tall flame length to cause mortality (Battaglia et al., 2009).

If established post-fire ponderosa pines survive and regeneration continues to occur on these high-severity burn patches, some tree cover will be regained, even if below historical densities. Historical ponderosa pine densities ranged from 49-115 trees ha\(^{-1}\) in areas near the Pumpkin and Rodeo-Chediski Fires, determined by dendrochronological reconstructions of forest structure in 1879 (Rodman et al., 2016; Rodman et al., in review). Four out of our twelve plots fell within this range, and others were just below based on a projected 44% survival rate of seedlings to mature trees from the 5th to 50th year after planting in northern Arizona (DeWald and Mahalovich, 2008; Ouzts et al., 2015). Pine regeneration is potentially faced with additional challenges such as fire, drought, herbivory, disease, and further competition with neighboring species that could reduce survival rates (Huffman et al., 2012; Waring and Goodrich, 2012; Savage et al., 2013; Rother and Veblen, 2016). However, most regenerating pines have already made it through the high-mortality stage, within the first few years of germination (Pearson, 1950), and new seedlings on our study sites are still establishing. The small subset of aged post-fire ponderosa pines (data not shown) revealed an age range of 2-13 years-old, suggesting that regeneration is episodic in this area and not necessarily concentrated in the first few years after the fires, similar to findings by Haire and McGarigal (2010). We did not observe any pine seedlings or saplings that were producing cones on our plots; in the future, such reproduction may become a localized seed-source and serve to fill in treeless gaps, assuming seedlings survive and reproduce.

Historical ponderosa pine forests also had patterns of structural heterogeneity at multiple spatial scales (Mast and Wolf, 2004; Reynolds et al., 2013; Rodman et al., 2016), including trees
of different size and age classes and an open structure over large portions of the landscape (Sànchez Meador et al., 2011). Regenerating ponderosa pines on our study sites already exhibit some patterns of spatial and structural (variable seedling ages and heights) heterogeneity, but with reduced average patch sizes. Regenerating ponderosa pine patch sizes from our plots averaged ≥ 3 X smaller than reported historical regeneration patch sizes (averaging 0.01 ha) across northern Arizona (reviewed in Stephens and Fry, 2005). Ponderosa pine regeneration patch sizes varied across the burned landscape, and the stem-maps revealed openings, widely-spaced single seedlings, and seedling aggregation, similar to the mosaic of fire-frequent forests described by Larson and Churchill (2012). However, it is unclear if regeneration on our study sites will emulate historical spatial patterns because drier conditions, increased wildfire activity and widespread conifer loss are forecasted to increase in the coming decades (McDowell et al., 2016; Abatzoglou and Williams, 2016).

Conclusions and management implications:

Both spatial and non-spatial information on post-fire regeneration are vital for future management plans. By contrasting the edge and interiors of burn patches, we found that 12+ years post-fire, in high-severity burn patches, ponderosa pine regeneration had similar heterogeneous spatial patterns and interactions with neighboring species, yet lower densities in the interior patches. Intraspecific facilitation and more time could eventually lead to higher ponderosa pine densities. However, given the predictions for warming climates and increased wildfires (McDowell et al., 2016; Abatzoglou and Williams, 2016), this heterogeneous stage of forest development, that includes native sprouting species could be more resilient to drought and high-severity fires than dense pine stands. Forest managers may need to adopt new objectives such as accepting forest types that could be more adapted to climate change and high-severity
fires (including more drought-tolerant sprouting species). High-severity wildfires and climate change are predicted to favor sprouting species over ponderosa pine on the Rodeo-Chediski Fire (Strom and Fulé, 2007; Azpeleta et al., 2014). New vegetation types may be a future reality, especially since a combination of adequate moisture and fire-free periods are needed for the initiation of ponderosa pine regeneration and maintenance of pine-dominant forests (Iniguez et al., 2016). Future climate change is predicted to result in large-scale vegetation displacement and reorganization for some elevation zones in Arizona (Flatley and Fulé, 2016). Post-wildfire non-forested patches or alternative vegetation types can also be areas of resilience to climate variability and resistance to subsequent fire within portions of the pine-dominant landscape (Coop et al., 2016; Schoennagel et al., 2017).

We recommend that managers use an experimental/adaptive approach to reach goals of resilient landscapes and fire-adapted communities in light of the prediction of potential vegetation shifts and increased risk of high-severity wildfires in the future. Biotic and abiotic conditions vary greatly across western US ponderosa pine forests (Oliver and Ryker, 1990), and management treatments should adapt accordingly. There is value in experimenting with a variety of treatments by incorporating a before–after–control–impact (BACI) design; this approach is useful in controlling confounding factors, so that observed changes are likely due to management treatments (Underwood, 1994). Potential post-fire management strategies could include introducing fire (with seasonal variabilities), while regeneration is small if overly dense, or waiting for trees to reach greater heights to become more fire-resistant (Bailey and Covington, 2002; Battaglia et al., 2009). If management goals are to restore ponderosa forests, planting pine seedlings in the interiors of high-severity burn patches could be an option (Ouzts et al., 2015). However, plantings should reflect the goal of spatial heterogeneity instead of uniformity, and
should not be overly dense so that they increase future fire severity (Thompson et al., 2007). There are also advantages for a natural recovery processes, such as increased plant diversity and more resilient vegetation types (Haire and McGarigal, 2010; Fornwalt and Kaufman 2014; Coop et al., 2016).

Other management options revolve around reducing the potential for large high severity fires by increasing thinning and managed fire to maintain recently treated stands that resemble historical forests or thinning high density stands (Fulé et al., 2012; Stevens-Rumann et al., 2012; Stephens et al., 2016; Huffman et al., 2017). Pre-wildfire thinning and prescribed fire treatments on the Rodeo-Chediski Fire reduced fire severity and significantly increased ponderosa pine regeneration, compared to untreated areas (Shive et al., 2013). Restoration efforts to reduce the risk of stand-replacing wildfires should include the goal of spatial heterogeneity to increase resilience to future climate and wildfire conditions, as recommended by Larson and Churchill (2012), and long-term, permanent plots are essential for quantifying treatment success or ecosystem changes over time (Sánchez Meador and Moore, 2010).

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Appendix H: Ponderosa pine seedling height and density of intraspecific neighbors within 1 m radius from both wildfires.

Literature Cited


Upton, G., Fingleton, B., 1985. Spatial data analysis by example: Point pattern and quantitative data. Wiley and Sons, NY, US.


Table 1. Lag distances and average patch sizes (determined by the lag distance and maximum deviation from complete spatial randomness (CSR)) for ponderosa pine regeneration with spatial aggregation, uniform, or CSR distributions from univariate Ripley’s K, corresponding to the stem maps shown in Fig. 3. Individual Ripley’s K outputs are shown in Appendix D.

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</table>
**Figure 1.** Location of 4-ha research plots within the high-severity burned area of the 2000 Pumpkin Fire and the 2002 Rodeo-Chediski Fire in Arizona, USA. Study plots are not to scale.
Figure 2. Ponderosa pine regeneration densities (stems ha\(^{-1}\)) were lower in interior plots than edge plots in large high-severity burn patches for both (A) the 2000 Pumpkin Fire and (B) the 2002 Rodeo-Chediski Fire. The central boxes span the first to the third quartile, a center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.
Figure 3. Stem maps of ponderosa pine regeneration 13 years after the Pumpkin Fire and 12-13 years after the Rodeo-Chediski Fire in 3 edge plots along residual live ponderosa pine trees and 3 plots >200 m from any residual live ponderosa pine trees (interior). Plots are rotated for this figure (north arrows are correct) to line up forest edges for ease of interpretation, but actual plot locations occur at varying distances from residual live forest edges and other plots.
Figure 4. Stem maps of Gambel oak (blue squares) and alligator juniper (brown triangles) regeneration 12-13 years after the Rodeo-Chediski Fire in 3 plots along the forest edges (edge), and 3 plots >200 m from any live residual ponderosa pine tree (interior).
Figure 5. Ripley’s K_{12}(t) bivariate statistic is shown for the comparison of ponderosa pine regeneration to sprouting species locations (quaking aspen (POTR) in the Pumpkin Fire and alligator juniper and Gambel oak (sprouters) in the Rodeo-Chediski Fire) in three edge plots and three interior plots. The x-axis (r) is the lag distance, and the y-axis is the square root, variance-stabilizing transformation of Ripley’s K. The red line (values = 0) is the expectation under complete spatial randomness and the shaded areas are the 95% confidence limits. Values that fall outside of the confidence interval are significant; values > 0 indicate attraction and values < 0 indicate repulsion between ponderosa pine and sprouting species.
Figure 6. Regenerating ponderosa pine height was significantly correlated with the average height of neighboring intraspecific ponderosa pine regeneration in both the A) Pumpkin Fire and B) Rodeo-Chediski Fire.
Appendix A: Results from Monte Carlo method to test for Complete Spatial Randomness (CSR) on each plot, indicating all plots exhibited inhomogeneous point processes, except for one plot on the Pumpkin Fire (Interior 2).

<table>
<thead>
<tr>
<th>Pumpkin Fire</th>
<th>X²</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge 1</td>
<td>36.3</td>
<td>0.05*</td>
</tr>
<tr>
<td>Edge 2</td>
<td>180.96</td>
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</tr>
<tr>
<td>Edge 3</td>
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<tr>
<td>Interior 1</td>
<td>56.51</td>
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</tr>
<tr>
<td>Interior 2</td>
<td>27.22</td>
<td>0.28</td>
</tr>
<tr>
<td>Interior 3</td>
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<td>0.001*</td>
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<table>
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<th>p</th>
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<tr>
<td>Edge 1</td>
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<tr>
<td>Edge 2</td>
<td>1977</td>
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<tr>
<td>Edge 3</td>
<td>561.14</td>
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<tr>
<td>Interior 1</td>
<td>129.09</td>
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<tr>
<td>Interior 2</td>
<td>88.67</td>
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</tr>
<tr>
<td>Interior 3</td>
<td>148.21</td>
<td>0.001*</td>
</tr>
</tbody>
</table>
Appendix B: Results of the kppm model testing for differences in ponderosa pine stem intensity with distance from residual live trees. The x-axis illustrates distance from residual live trees (m), and the y-axis and the black lines near the x-axis indicate regenerating ponderosa pine intensity per m². The scale differences between panels are due to differences in seedling locations along varying distances from residual live trees.
Appendix C: Results of the univariate Ripley’s K statistic (transformed as L(r) as lag distance) for ponderosa pine in each plot, corresponding to the stem maps shown in fig 3. The shaded area is the expectation under complete spatial randomness; values that fall outside of this are statistically significant; values > 0 (red line) indicate aggregation and values < 0 indicate uniform spatial distribution.
Appendix D: Stem maps of aspen regeneration 13 years after the Pumpkin Fire in 3 plots along the forest edges, and 3 plots >200 m from any live tree (Interior plots).
Appendix E: The lag distance for aspen stems on the Pumpkin Fire and Gambel oak and alligator juniper stems on the Rodeo-Chediski Fire with spatial aggregation, complete spatial randomness, or uniform spatial distribution from the univariate Ripley’s K, corresponding to the stem maps shown in Appendix A and Fig. 4. Values that fall outside the 95% confidence limits > 0 indicate aggregation and values < 0 indicate uniform spatial patterns, and values within the confidence limit are expected under complete spatial randomness.

<table>
<thead>
<tr>
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<tr>
<td>Aspen</td>
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</tr>
<tr>
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<td>1 - 60</td>
</tr>
<tr>
<td>Edge 2</td>
<td>1 - 75</td>
</tr>
<tr>
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<td>1</td>
</tr>
<tr>
<td>Interior 1</td>
<td>1 - 58</td>
</tr>
<tr>
<td>Interior 2</td>
<td>1 - 15</td>
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<td>Edge 3</td>
<td>1</td>
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<tr>
<td>Interior 1</td>
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</tr>
<tr>
<td>Interior 2</td>
<td>1 - 100</td>
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<tr>
<td>Interior 3</td>
<td>1 - 100</td>
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<table>
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<td>1 - 100</td>
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<td>Interior 3</td>
<td>1 - 80</td>
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Appendix F: Ripley’s $K_{12}(t)$ bivariate statistic is shown for the comparison of ponderosa pine regeneration to location of Gambel oak and alligator juniper in the Rodeo-Chediski Fire. The red line is the expectation under complete spatial randomness and the shaded areas are the 95% confidence limits. Values that fall outside of the confidence interval are significant; values > 0 indicate attraction and values < 0 indicate repulsion between ponderosa pine and sprouting species.
Appendix G: Distance from residual live ponderosa pine trees (or potential seed sources) is not significantly correlated with regenerating ponderosa pine height on either wildfire.
Appendix H: Ponderosa pine seedling height is positively correlated with the density of intraspecific neighbors within 1 m radius in the A) Pumpkin Fire and the B) Rodeo-Chediski Fire, but density of Gambel oak and alligator juniper are not significant predictors of ponderosa pine height in the Rodeo-Chediski Fire. Model fit with 95% confidence limits.
Chapter 3: Persistent effect of fire severity on ponderosa pine regeneration niches and growth

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This chapter is formatted for Forest Ecology and Management
Abstract

Several recent studies have documented low pine regeneration after large patches of high severity fire in US ponderosa pine forests. Regeneration niche characteristics such as plant community composition, woody debris, and soil attributes influence post-fire conifer establishment. What is less known is if fire severity can cause long-term differences in regeneration niche attributes or influence ponderosa pine seedling growth in subsequent decades. We quantified regeneration niche attributes of 360 naturally regenerating ponderosa pine seedlings and measured their influence on seedling growth within the Pumpkin Fire that burned in 2000 in Arizona, USA. Plots were located in unburned, moderate-severity, and two types of high-severity (100% tree mortality) burns, either adjacent to residual live forest edges (edge plots), or > 200 m from any residual live trees (interior plots). We found that all burn plots had greater exotic plant and coarse woody debris (CWD) cover, and a different plant community composition compared to unburned plots. High-severity burn plots had the greatest fine fuel biomass. Soil properties were similar among treatments. Ponderosa pine growth (stem diameter at root collar (DRC), and length of terminal leader) was lower in the unburned compared to burned plots. High-severity burn plots had larger DRCs compared to unburned plots, and ponderosa pine terminal leader growth was consistently greater in the high-severity edge plots compared to other treatments. Finally, niche characteristics such as overstory tree canopy (-), CWD (+), forb cover (+), Muhlenbergia montana (+) cover, and soil phosphate (+) were important explanatory variables favoring ponderosa pine growth. Surrounding exotic plant cover did not negatively affect ponderosa pine growth. These results suggest that if ponderosa pines can survive the first few critical years after germination, proximity to some forbs and CWD may help increase their growth rates. However, the fact that greater fine fuel biomass and CWD were
adjacent to pine seedlings might put them at increased risk from surface fires until they are taller and more fire resistant.

Key words: Arizona, Pinus ponderosa, Forest resilience, Soils, Surface fuels, Understory plant communities

1. Introduction

Contemporary wildfires in US ponderosa pine (Pinus ponderosa Lawson &C. Lawson) forests have increased in size, leaving a mosaic of burn severity including larger, contiguous patches of tree mortality (Dillon et al., 2011; Singleton, 2019), which often limit post-fire regeneration (Savage and Mast, 2005; Ouzts et al., 2015; Chambers et al., 2016; Owen et al., 2017; Stoddard et al., 2018). Ponderosa pine is a dominant forest type in the semi-arid western US. The historical fire regime in SW ponderosa pine forests mainly consisted of low- to moderate-severity fire, which left heterogeneous spatial patterns of surviving trees, in contrast to the recent large, high-severity (100% tree mortality) burn patches (Covington and Moore, 1994; Swetnam and Baisan, 2003; Rodman et al., 2016). Ponderosa pines are poorly adapted to regenerate in large patches of high-severity fire because they do not re-sprout or have serotinous cones, and do not maintain long-lived soil seedbanks (Oliver and Ryker, 1990; He et al., 2012). Studies conducted 10+ years after high severity fires found reduced ponderosa pine regeneration at distances farther (50 – 200 m) from seed sources (Chambers et al., 2016; Owen et al., 2017; Ziegler et al., 2017). Although regeneration densities were low, some spatially heterogeneous, natural regeneration occurred after high-severity fires, even >200 m from residual seed sources (Owen et al., 2017; Ziegler et al., 2017). To conserve and protect naturally recovering ponderosa
pines that can survive > 10 years post high-severity fire, or improve restoration success, it is important to understand post-fire regeneration niches and whether or not they influence seedling growth and survival.

The “regeneration niche” includes suitable environmental factors for different stages of seed production, germination, and growth into mature trees (Grubb, 1977; Clark et al., 1999). Ponderosa pines require several conditions to coincide for successful germination and establishment. Some components of the ponderosa pine regeneration niche include favorable climate, high mast years that produce a large seed supply, a well-prepared seedbed, lack of competing vegetation, sufficient soil moisture, and protection from fire, browsing animals or other pests (Pearson, 1950; Larson and Schubert, 1969; Schubert, 1974; Savage et al., 1996; Feddema et al., 2013; Iniguez et al., 2016). If seedlings survive the high-mortality stage of the first few years after germination, niche components including surrounding plant communities, soil, and litter conditions may continue to influence growth and survival of established seedlings (Pearson, 1950; Stein and Kimberling, 2003; reviewed in Dey et al., 2019).

Previous research demonstrates variable effects of severe fire on understory plant communities and soils, but it is unclear if large patches (> 200 ha) of high-severity fire will have persistent effects on ponderosa pine niche characteristics or growth. Pine seedling growth can be affected by competition for light, water and nutrients with other regenerating species (Pearson, 1942; Schwinning and Kelly, 2013). Severe fires open canopy gaps and can create favorable habitat for understory exotic (e.g. Alba et al., 2015) or native (e.g. Abella and Fornwalt, 2015) plant communities, that could each potentially compete with regenerating conifers. For example, tall, dense bunchgrasses, like Arizona fescue (Festuca arizonica) can negatively affect ponderosa pine establishment and growth (Pearson, 1942; Schubert, 1974; Puhlick et al., 2012). However,
certain shrubs or other seedlings may act as nurse plants for some regenerating pines under stressful site conditions (Fajardo et al., 2006; Stultz et al., 2007). Severe fires can also induce short-term increases in available soil nutrients (Covington et al., 1991; Covington and Sackett, 1992), and either long-term reductions (Smith et al., 2017; Ross et al., 2012), or long-term increases in total soil nutrients (Johnson and Curtis, 2001), depending on the amount of combustion, mineralization, and regeneration dynamics. Additionally, severe fire can alter soil structure and increase soil temperature and pH, but effects are often short-lived (Ulery et al., 1993; Robichaud, 2000; Huffman et al., 2001; Neary et al., 2012). Ponderosa pine tends to grow well on slightly acidic and loam soils (Schubert 1974). Puhlick et al. (2012) also found that post-fire ponderosa pine regeneration densities were highest where soil clay content and pH were lowest. In addition, severe fire increases surface fuel loads which could increase future fire risk for a period of years to decades (Roccaforte et al., 2012; Coppoletta et al., 2016). Furthermore, regenerating ponderosa pines could grow better near unburned forest edges than the far interior of burn patches because of protection from wind and sun (Oliver and Ryker, 1990; Li and Wilson, 1998), and proximity to available microbial symbionts (Nara, 2006; Grove et al., 2019; Owen et al., in review). Finally, several studies show severe fires increase CWD cover, but have variable effects on fine fuels in the first two decades post-fire (Passovoy and Fulé, 2006; Keyser et al., 2008; Sabo et al., 2009; Roccaforte et al., 2012). The presence of logs, stumps or scattered slash can protect soil surfaces from erosion, temperature extremes, and evaporation, and may create favorable microsites for post-fire seedling growth because of increased moisture and wind protection (Pearson, 1950; Fajardo et al., 2006; Castro et al., 2011; Flathers et al., 2016).

The goal of this study was to understand post-fire environmental influences on the growth of naturally regenerating ponderosa pine seedlings. We examined: 1) understory plant,
soil and fuel characteristics surrounding regenerating ponderosa pines 13 and 14 years post-fire, and 2) regenerating ponderosa pine growth rates (11 – 15 years post-fire) across different fire severities and unburned areas, after the 2000 Pumpkin Fire near Flagstaff, AZ. The Pumpkin Fire was selected because it had extensive patches of high-severity fire, moderate-severity fire, and nearby unburned areas. We tested the following hypotheses about niche characteristics in high-severity burn plots compared to both moderate-severity and unburned plots: H₁: high-severity burn plots will have the greatest shrub, herbaceous, and exotic species cover, and a different understory plant community composition due to opening of the tree canopy. However, moderate-severity burn plots will have the greatest understory plant richness and diversity, supporting the intermediate disturbance hypothesis (Connell, 1978). H₂: High-severity burn plots will have the greatest CWD cover and fine fuel biomass, but similar soil properties because of the length of time since fire. Additionally, we tested the hypotheses that regenerating ponderosa pine growth rates will be: H₃: highest in the moderate-severity plots because they are intermediate in terms of canopy cover or potentially less harsh site conditions compared to severely burned areas; and H₄: negatively correlated with surrounding understory plant cover, but positively correlated with CWD and available soil nutrients.

2. Materials and methods

2.1 Study sites and plot design

We investigated ponderosa pine regeneration niches 13 and 14 years post-fire, and ponderosa pine growth 11 – 16 years after the Pumpkin Fire that burned in 2000 in northern Arizona. The Pumpkin Fire burned approximately 6,500 ha, including 1,400 ha of high-severity fire on the Kaibab and Coconino National Forests (http://www.mtbs.gov/; Fig. 1). Our plots ranged from 2,350 to 2,600 m elevation, with 3 – 20% slope at mostly SW aspects. The mean 16
year (2000-2016) post-fire annual water year (Oct.-Sept.) precipitation was 49.12 cm (Western Regional Climate Center (WRCC): https://wrcc.dri.edu, Accessed 2/15/19) and the mean temperature was 7.2°C (Prism Climate Group: http://prism.oregonstate.edu/. Accessed 10/7/16). This region receives most of its annual moisture from late-summer rains that typically occur July – August and from winter precipitation. We conducted our field sampling August – September, 2013 – 2016. Late-summer moisture was highest in 2013 compared to the 16 year average post-fire (Fig. S1). The soils were derived from basalt and additional site characteristics are described in Owen et al. (in review).

We used Monitoring Trends in Burn Severity (MTBS, 2013) maps with field validation to identify different burn severities and unburned sites for plot selection. We used ArcGIS 10.1 (ESRI, 2012) to randomly select three sites within each burn-severity or unburned area. We established 4-ha (200 x 200 m) plots on each site, including “unburned” (UB), “moderate-severity” (M), “high-severity edge” (HE) and “high-severity interior” (HI) plots, for a total of twelve 4-ha plots (Fig. 1). Unburned plots were not thinned or burned for the past 20 years. Unburned areas had high tree densities, ranging from 560-1160 trees/ha. Moderate-severity plots had a spatial heterogeneity of post-fire surviving trees ranging from 120-490 trees/ha, including small patches of high-severity fire < 1 ha in size. Both high-severity edge and interior plots had 100% tree mortality from the wildfire, but high-severity edge plots were established adjacent to forest edges or residual live trees whereas high-severity interior plots were established where no surviving trees were found within at least 200 m from the plot boundaries (see Fig. S2 for plot photographs).
2.2 Understory plant communities

To characterize the plant community composition of regeneration niches, we measured plant cover variables within 1- X 1-m quadrats surrounding 30 naturally regenerating ponderosa pines in each 4-ha plot, totaling 360 quadrats. Each seedling was randomly selected from all seedlings (using a random number generator) that were spatially mapped in each 4-ha plot from a previous study (Owen et al., 2017). In each quadrat we estimated percent overstory tree canopy cover (averaging 5 readings/plot) using a GRS vertical densitometer (Geographic Resource Solutions, Arcata, California, USA). Understory plant, and bare ground cover were measured in August – September 2013 and 2014. Total plant, life form (herbaceous plants, graminoids, and shrubs), exotic plant, and individual plant species cover were estimated by eight coverage classes. We used the following coverage classes: 0 = 0%; trace = <1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, and 6 = 95–100% in each 1- X 1-m frame, a method modified from Daubenmire (1959). We calculated coverage estimates for each treatment by determining midpoints of each cover class. Plants were identified to species in the field or collected, identified and stored at the USDA Rocky Mountain Research Station (RMRS) herbarium in Flagstaff, Arizona. Scientific nomenclature followed the USDA PLANTS Database (http://plants.usda.gov), and plant nativity followed the Flora of North America (http://beta.floranorthamerica.org). We also determined plant species richness, Shannon’s diversity and evenness (Shannon’s diversity index / ln richness) in each quadrat. We examined plant cover variables, richness, diversity and evenness using repeated measures analysis of variance and tested for treatment, year and treatment X year interactions in SAS 9.4 (SAS PROC GLIMMIX©, 2017). Fire-severity was a fixed effect and replicated plots were a random effect. We included beta distributions for percent cover values and evenness, a negative binomial
distribution for species richness and gamma distributions for diversity. Beta distributions that included many zero values were transformed similar to Smithson and Verkuilen (2006). If significant differences were found, we used the post hoc Tukey–Kramer HSD test on least-squares means for subsequent pair-wise comparisons (Kramer, 1956).

To test the first hypothesis that understory plant community composition will differ among treatments, we used the program PC-ORD 6.0 to examine species composition (McCune and Mefford, 1999). We created a non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis distance to examine community-level differences (McCune and Mefford, 1999). We used permutational multivariate analysis of variance (PERMANOVA), and subsequent pair-wise comparisons to test for differences in plant communities among treatments and sampling years. Cover and soil variables from a second matrix (percent overstory tree canopy, CWD, exotic species, and forb cover; and soil variables: moisture, pH, NO$_3^-$, NH$_4^+$, PO$_4^{3-}$) were overlaid on this ordination by creating a joint biplot. We rotated the ordination based on the unburned sites, and observed overlays from the second matrix to understand if they were correlated with any community differences. Rotation can help find the axis best related to any observed community differences and potential correlation of cover and soil variables (McCune and Grace, 2002; Bowker et al., 2011). If PERMANOVA results were significant, we then calculated dispersion (a measure of beta diversity) as measured by individual dissimilarity from the treatment group centroid in multivariate space, described by Anderson et al. (2006), and used indicator species analysis (indicator value = frequency X relative abundance) to determine if particular species were driving community differences (McCune and Grace, 2002).
2.3 Surface fuel and soil characteristics

To test the second hypothesis that high-severity burns will have the greatest fine fuel biomass, we destructively measured herbaceous plant biomass in July 2016 near each quadrat. We measured fine fuel biomass by clipping all herbaceous plants at ground level in 0.25-m² circular frames, 1 m east of each seedling quadrat, and we tried to represent the conditions at the seedling. The biomass samples were dried in an oven at 70°C for 3 days and weighed to the nearest 0.1 g (Moore et al., 2006). We analyzed plant biomass using GLMMs with a gamma distribution and used pair-wise comparisons in SAS 9.4 (SAS PROC GLIMMIX©, 2017).

We characterized surface fuel cover near regenerating ponderosa pines by fuel types. We measured total fine woody fuels (surface litter), coarse woody debris (CWD; dead woody materials, including logs and branches ≥ 7.62 cm diameter), tree bole/stump, rock, and bare ground cover similar to plant cover variables above. We separated CWD from total fine woody fuels cover by using a go/no-go gauge (Brown, 1974). We analyzed percent fuel cover variables using GLMMs with beta distributions, including pair-wise comparisons, as described above, in SAS 9.4 (SAS PROC GLIMMIX©, 2017).

To explore difference in regeneration niche soil properties among treatments, we measured the physical and chemical properties of soil from each quadrat in September 2013. Three mineral soil (0–15 cm) samples were collected with a soil core (3 cm diameter X 15 cm length) within the 1 X 1-m frame from each seedling plot and composited. We measured gravimetric soil moisture by weighing samples before and after drying in an oven at 105 °C (Carter, 1993). We measured soil temperature in the field (between 10:00 am and 2:00 pm) with a soil thermometer (Spectrum model 6300; ± 2° accuracy). Soil pH was measured following the method of Carter (1993) with an Orion 550A pH meter (Thermo Electron Corporation, Beverly,
MA). Percent silt, sand, and clay were determined by particle size analysis with a hydrometer, similar to Bouyoucos (1962), and percent gravel was determined by sieving and weighing the > 2 mm portion of the sample. Soil aggregate stability (a measure of erodibility) was determined in the field for 5-cm subsurface soils using a soil stability kit (Synergy Resource Solutions, Inc., Bozeman, MT). Soil aggregates were ranked on an ordinal scale of 0 (least stable) to 6 (most stable) (‘slake scores’) (Herrick, 2000). Percent total soil carbon and nitrogen were measured on a C/N analyzer (ThermoQuest EA Flash 1112, Milan, Italy). Finally, the concentrations of nitrate, ammonium and phosphate (NO$_3^-$, NH$_4^+$, PO$_4^{3-}$) were measured on a Lachat AE Flow Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA) using methods described in Lachat Instruments, Inc. (1990; 2003; 2007). We analyzed percent soil moisture, silt, sand, clay, gravel, and nutrient concentrations using GLMMs with beta distributions, and soil temperature and pH using GLMMs with gamma distributions. We analyzed soil aggregate stability (categorical data 0 – 6) using an ordered logit model, similar to Agresti (2013). We tested pair-wise comparisons, as described above in SAS 9.4 (SAS PROC GLIMMIX®, 2017).

2.4 Regenerating ponderosa pine

We estimated regenerating ponderosa pine age by counting branch whorls on each trunk, similar to Shatford et al. (2007). To verify accuracy in the whorl count estimates, we destructively sampled 26 seedlings of various ages outside of our plots and determined pith age by counting growth rings. We compared whorl-counts to pith age using multi-response permutation procedures similar to Haire and McGarigal (2010). Unlike Haire and McGarigal (2010), we found a significant difference between whorl counts and pith age (F = 9.68; p = 0.03),
and our whorl counts were on average 1.5 years younger. Therefore, we added 1.5 years to our whorl counts to make them similar to pith age.

To test the third hypothesis that regenerating ponderosa pines will have the highest growth rates in moderate-severity burn plots compared to unburned and high-severity burn plots, we measured seedling growth in each quadrat. In September 2016, we measured diameter at root collar (DRC), total height, and annual growth (the length of annual growth of the terminal leader from 2011-2015) on all regenerating ponderosa pines. We measured DRC at ground level, similar to McPherson et al. (2016). We tested for differences in total height and DRC among treatments using GLMMs with gamma distributions, and seedling age as a covariate. We tested for differences in seedling growth and age among treatments, years and treatment-year-age interactions by using repeated measures GLMM analysis with a gamma distribution. Tree or seedling age can influence growth rates (Weiner and Thomas, 2001; Johnson and Abrams, 2009), so we included age as a continuous variable.

To test the fourth hypothesis that regenerating ponderosa pine growth is influenced by particular abiotic and biotic variables, we used GLMM to determine the relationship between niche characteristics that we considered to be important for seedling growth and ponderosa pine DRC and growth rates. Predictor variables included percent overstory canopy cover, soil nutrients (NO₃⁻, NH₄⁺, PO₄³⁻), pH and percent clay content, and CWD, forb, graminoid, shrub, exotic and major species cover (> 10% cover). Response variables included DRC and 4-year growth rates, and we used age as a covariate. We used GLMM with gamma distributions and determined 95% confidence intervals in SAS 9.4 (SAS PROC GLIMMIX©, 2017).
3. Results

3.1 Post-fire plant communities

We found a total of 86 understory plant species within the two sampling years and they were predominantly native and perennial (Table S1). Many plant species were only found in burned plots, including *Populus tremuloides* Michx. (quaking aspen), which was only found in the high-severity burn plots. We found a total of 30 plant species in the unburned plots, 58 species in moderate-severity plots, 60 species in high-severity edge plots, and 41 species in high-severity interior plots (Table S1). Three species were only found in unburned plots, nine were unique to moderate-severity plots, five were unique to high-severity edge plots, and eight were only found in high-severity interior plots. We found 11 exotic species, mostly in the burned plots. The most common exotic species found in the burned plots were *Bromus tectorum* L. (cheatgrass), *Taraxacum officinale* F.H. Wigg. (common dandelion), and *Tragopogon dubius* Scop. (yellow salsify) (Table S1).

Regeneration niches differed among treatment types due to differences in overstory tree canopy cover as well as differences in cover of dominant understory species. Overstory tree canopy cover was absent in the high-severity burn plots, and higher in the unburned (mean and SE: 16.11 (4.60)) compared to the moderate-severity plots (mean and SE: 8.61 (2.58); F = 6.42; p = 0.01). In general, regeneration niches in burned plots were characterized by higher exotic species cover, a tendency of higher species richness, and differences in some dominant species cover compared to unburned plots (Table S2, and 1). All burn types differed from unburned areas in terms of dominant species cover that included a native shrub, *Ceanothus fendleri*, native forbs, *Bahia dissecta* and *Oxytropis lambertii*, and a native grass, *Elymus elymoides* (Table 1). *Mahonia repens* (a native shrub) cover was greatest in the high-severity interior plots and
intermediate in the high-severity edge compared to the moderate-severity and unburned plots. Finally, higher exotic species cover on burned plots was dominated by *Bromus tectorum*, which was absent from unburned plots. *B. tectorum* cover was highest in the high-severity interior plots in 2013, but lower and more similar to the other burn types in 2014 (Table 1).

All treatments had different plant community composition, (PERMANOVA $F = 39.62; p < 0.01; 2013$ results in Fig. 2). The percent cover of forbs and exotic species were more highly correlated with community differences between the unburned and burned plots for both years (2013 results shown in Fig. 2), and they explained more of the variance than overstory and CWD cover, or soil variables (all $r^2 < 0.05$). Species dispersion differed among treatments ($F = 80.29, p < 0.01$; average distance to centroid: unburned = 0.70 moderate-severity = 0.85, high-severity edge = 0.84, high-severity interior = 0.85). Pairwise PERMANOVA comparisons show plant dispersion on unburned plots was lower than on all burned plots ($p < 0.01$), and all burned types were similar ($p > 0.01$). Plant community composition also differed between sampling years (PERMANOVA $F = 4.15; p < 0.01$; ordination not shown). We did not find any significant indicator species for each treatment ($IV > 25$).

3.2 *Surface fuel and soil characteristics*

Herbaceous fine fuel biomass near ponderosa pine regeneration niches was lowest in the unburned plots, intermediate in moderate-severity, and greatest in high-severity burn plots, supporting our second hypothesis (Fig. 3A). Herbaceous fine fuel biomass was nearly four times higher in the high-severity plots, and twice as high in the moderate-severity plots compared to the unburned plots (Fig. 3A).

Coarse woody debris (CWD) cover was similar between both high- and moderate-severity burn plots, but higher in all burned plots compared to the unburned plots, partially
supporting our second hypothesis (Fig. 3B). Litter (all size classes), and rock cover were similar among treatments, but stump cover was higher in all burned compared to unburned plots (Table S3).

All treatments had similar soil pH, nutrient concentrations, temperature, and stability in support of our first hypothesis, but we found treatment differences for soil texture (Table S4). Percent soil N, C, NO$_3^-$, NH$_4^+$, PO$_4^{3-}$, and soil temperature were all similar among treatments (see Appendix 7 for mean values/treatment). Percent soil clay content was highest in the unburned compared to the burned plots and percent silt content was similar among treatments (Table S4). Sand content was greatest in the high-severity interior plots, intermediate in high-severity edge and moderate plots, and lowest in the unburned plots. Percent gravel content was highest in the moderate-severity and high-severity interior plots intermediate in high-severity edge, and lowest in the unburned plots (Table S4). Finally, soil stability was variable within each treatment, with most scores falling within an intermediate stability range, and stability was similar among treatments (Fig. S3).

3.3 Regenerating ponderosa pine

Regenerating ponderosa pines had high survival rates throughout the course of our study: only 4 of the 360 seedlings in our study died between 2013 and 2016 (two in high-severity interior, one in high-severity edge, and one in moderate-severity burn plots). The estimated year of establishment ranged from 2001-2008 with the most establishing in 2005, the wettest water year of the study (Fig. 4).

Ponderosa pine growth varied among treatments and years but was highest in the high-severity edge plots, contrary to our second hypothesis (Figs. 5A, B, and C). Ponderosa pine DRC was higher in high-severity burned than unburned plots, but DRC in the moderate-severity plots
was similar to both high-severity and unburned plots (Fig. 5A). Ponderosa pine seedlings were taller in the high-severity edge plots compared to other treatments, even though seedlings were older in unburned plots (Fig. 5B). We found significant treatment X age (F = 3.64; p = 0.01), and treatment X year interactions (F = 2.40; p < 0.01) for terminal leader growth, therefore we analyzed groups separately. Ponderosa pine regeneration was on average 3.5 years older in the unburned plots compared to all burned plots (data not shown; F = 205.39; p < 0.01). Seedlings on unburned plots were older but had less leader growth than on burned plots (Fig. 5C). Ponderosa pine terminal leader growth in 2011 (F = 9.06; p < 0.01) and 2015 (F = 6.68; p < 0.01), were higher in all burned compared to unburned plots (Fig. 5C). Ponderosa pine terminal leader growth in 2012 (F = 12.87; p < 0.01), 2013 (F = 13.41; p < 0.01), and 2014 (F = 17.96; p < 0.01), was greatest in high-severity edge plots, intermediate in both moderate- and high-severity interior plots, and lowest in the unburned plots (Fig. 5C).

Some niche characteristics had unexpected correlations with pine seedling growth. There was a strong trend for a negative relationship between ponderosa pine DRC and overstory tree canopy cover, but there was a positive correlation with surrounding *M. montana*, forb, and CWD cover (Fig. S4). We found that most regenerating ponderosa pines in high-severity burned areas (~85%) were growing near CWD or stumps, compared to moderate-severity plots (62%) or unburned (6%) plots (data not shown). Ponderosa pine growth rates over 4 years from 2011 – 2015 were partially explained by a negative correlation with overstory tree canopy cover, and positive correlations with surrounding *M. montana*, forb cover, and soil PO$_4^{3-}$ (Fig. 6). We also found a positive correlation between ponderosa pine growth rates and CWD cover (Fig. 6). Ponderosa pine DRC and growth rates were not correlated with soil pH, clay content, NH$_4^+$, or NO$_3^-$, or other dominant understory species cover, contrary to our hypothesis (all p > 0.1).
4. Discussion

Our study found that a wildfire with large, high-severity burn patches had decadal-scale impacts on understory plant communities surrounding naturally regenerating ponderosa pines. Both moderate- and high-severity fire had mostly native, diverse and productive understory plant communities compared to unburned areas, similar to other long-term studies after large, mixed-severity wildfires (Abella and Fornwalt, 2015; Gibson et al., 2016). The trend of greater average forb and shrub cover on our high-severity burn plots was also similar to findings in previous studies (Barton, 2005; Shive et al., 2013; Abella and Fornwalt, 2015). Evidence suggests that severe burning could either lead to a dominance in shrub communities (Savage and Mast, 2005; González-De Vega et al., 2016), or regenerating pine can establish beneath or near shrubs and eventually overtop them (McDonald, 1990; Vankat, 2013). We did not find evidence that shrub cover influenced regenerating pine growth on our plots, but forb cover was positively correlated with ponderosa pine growth, discussed further below. Previous studies have shown that understory species richness, diversity, and productivity can increase with moderate-severity burns (Abella and Fornwalt, 2015; Burkle et al., 2015). Richness can either increase (Kuenzi et al., 2008; Shive et al., 2013) with high-severity burns, or remain similar between different burn severities (Crawford et al., 2001), in mainly ponderosa pine-dominated forests. However, exotic plants can also increase (typically with low abundances) compared to unburned areas, and others have found this to be especially evident after high-severity fires (Kuenzi et al., 2008; Shive et al., 2013; Abella and Fornwalt, 2015). Our results from the high-severity interior patches support these findings.

Most of the exotic plant species found on our plots are not considered long-term threats to native communities or ecological function, except for *B. tectorum* (Sieg et al., 2003; Keane et
al., 2008; McGlone and Eagan, 2009). *B. tectorum* is a highly invasive annual grass that can outcompete native plant species and increase fire frequencies (Young et al., 1987; Keane et al., 2008). However, we only found an average of 11 – 23% *B. tectorum* cover in 2013 (higher spring precipitation), and 6 – 9% *B. tectorum* cover in 2014. Plots were measured in summer, so we could have underestimated cool-season annuals. Even though exotic plant cover was higher on the burned than unburned plots, we did not find evidence that ponderosa pine growth was impacted by their presence. Both exotic plant and forb cover helped to explain understory community composition differences among burned and unburned plots, and surprisingly ponderosa pine growth was positively correlated with forb cover.

Both forb and *M. montana* cover were important positively correlated variables for regenerating pine growth, providing evidence for facilitation, or similar habitat preferences. *M. montana* along with Arizona fescue were the most dominant grasses in both moderate-severity and unburned plots, but *M. montana* only had approximately 1-4% cover in the high-severity burn plots. *M. montana* is a more shade-tolerant and less-aggressive competitor than Arizona fescue and there could be a positive interspecific interaction between *M. montana* and regenerating ponderosa pines on sites with some tree canopy (Pearson, 1942). *Muhlenbergia* spp. and forb cover in other studies had positive effects on ponderosa pine seedling densities and survival (Pearson, 1942; Puhlck et al., 2012; Ouzts et al., 2015). Similarly, forb cover may have a positive interspecific interaction with regenerating ponderosa pines in the high-severity burns, providing some protection from wind, sun and frost. This interaction is consistent with the “stress gradient hypothesis (SGH),” which predicts that with increasing abiotic stresses, facilitative interactions among plants are stronger than competitive interactions, and some species can mitigate stressors to create more favorable habitat by providing some protection from
wind and sun (Bertness and Callaway, 1994). Alternatively, the co-occurrence of seedlings with forbs and *M. montana* may simply be due to better conditions for all understory plants in places with low overstory tree canopy cover. Even in the unburned plots, regenerating ponderosa pines were mainly found under small canopy openings.

Severe fire led to increases in CWD, consistent with other studies (Passovoy and Fulé, 2006; Roccaforte et al., 2012; Bassett et al., 2015), and ponderosa pine growth was positively correlated with CWD. We expected CWD to have a positive effect on regenerating ponderosa pines growth because debris may provide extra moisture or wind and sun protection (Sánchez Meador and Moore, 2010; Castro et al., 2011). Flathers et al. (2016) also found that young (1 – 2 years old) ponderosa pine seedling density and diameter were positively associated with litter cover. However, increased CWD and fine fuel biomass adjacent to regenerating pine seedlings might put them at increased risk from surface fires in the burned plots until they are taller and more fire resistant. Ponderosa pine seedlings become more fire-resistant at 3+ m height (Bailey and Covington, 2002). Seedlings were on average < 2 m tall on all treatments from our study, but the increased growth rates of seedlings on the high-severity plots could help them survive a subsequent fire (Bailey and Covington, 2002; Battaglia et al., 2009).

We expected similar soil properties among treatments because we sampled 13 years post-fire, and others found similar nutrient content 1 – 5 years post severe-fire (from pile burning) (Covington et al., 1991; Covington and Sackett, 1992), but we anticipated more soil variables, such as available N, to correlate with ponderosa pine growth. Although we found similar soil pH, temperature and nutrients among treatments over ten years post-fire, similar to findings from Certini (2005), and Turner et al. (2007), others have found long-term reductions (DeLuca et al.,
2002), or increases (Brais et al., 1995) in available nutrients after severe fires in boreal forests. Additionally, severe fire can either increase nitrogen mineralization rates (Grady and Hart, 2006), or nitrification rates decades after fires (Kurth et al., 2014) in different ponderosa pine forests. There is evidence of N limitation in some ponderosa pine forests (Menge et al., 2012), but on our sites soil $\text{PO}_4^{3-}$ was more correlated with plant growth. Previous studies have shown that southwestern ponderosa pines that were fertilized with both N and P had greater diameter growth, but not height (Wagle and Beasley, 1968; Heidmann, 1985). Weathering of mineral P is a slow process, and fine root turnover and the role of symbiotic mycorrhizal fungi in P-uptake are likely contributing to the correlation between $\text{PO}_4^{3-}$ and regenerating pine growth (Schlesinger, 1991; Allen, 1991; Delucia et al., 1997), but future studies could examine this further. The soils on our plots were mostly loam or clay-loam and the differences in percent gravel, sand and clay are likely not from fire (reviewed in Certini, 2005), but from site selections. Puhlick et al. (2012) found reduced ponderosa pine regeneration densities where clay content was high, but we did not find evidence that soil texture influenced seedling growth. We did expect higher soil temperatures on the high-severity burn plots from lack of canopy cover, and soil temperature to influence growth rates (Pearson, 1950; Schubert, 1974), but our data lacked a thorough account of temporal soil temperatures, from only once/year sampling. Future studies could use data loggers similar to Oakley and Blanken (2004) to understand fire severity effects on soil temperature and moisture, and seedling growth.

We expected regenerating ponderosa pine to have the highest growth rates in moderate-severity plots compared to the other treatments, but surprisingly our results suggest that if seedlings can establish in the high-severity burns, their growth may not be inhibited by site conditions. Younger (1 – 2 years old) ponderosa pine seedling height can be positively
associated with overstory basal area (Flathers et al., 2016), but older seedlings and saplings require more sunlight to grow and survive (Pearson, 1910), and our results support this. The regenerating pines had already survived the high-mortality stage, within the first few years of germination (Pearson, 1950). The estimated age of post-fire ponderosa pines was 4-11 years-old in 2013, suggesting that regeneration was episodic, similar to findings by Haire and McGarigal (2010). We did not observe any cone-producing ponderosa pine seedlings or saplings on our plots, but if the current regeneration survives and is able to reproduce, their reproduction will help to fill in treeless gaps. Since 2013, only four out of the 360 seedlings we measured died, but they may be faced with additional challenges such as fire, drought, herbivory, or disease that could reduce their survival rates (Huffman et al., 2012; Waring and Goodrich, 2012; Savage et al., 2013; Iniguez et al., 2016; Rother and Veblen, 2016).

5. Conclusions and management implications

Large, high-severity wildfires in ponderosa pine forest are expected to become more common in the future (Jolly et al., 2015; Abatzoglou and Williams, 2016; Kitzberger et al., 2017), furthering the challenge for natural ponderosa regeneration, which may already be constrained by climate (McDowell et al., 2016; Petrie et al., 2016; Stevens-Rumann et al., 2018). Our results indicate long-term changes to understory plant communities and fuel loads from severe fire, and highlight certain post-fire niche characteristics important for pine growth. However, our results also indicate that naturally regenerating seedlings may be at risk from future fires, due to surrounding fuels. Managers may want to prioritize protecting natural regeneration that can establish and survive after high-severity fires, and residual trees surrounding large, high-severity patches. Local adaptations and future seed sources may be critical for their survival in future climates (Lucas-Borja et al., 2017; Gehring et al., 2017;
When high-severity fires occur, managers could consider postponing fuel reduction treatments or prescribed fire around regenerating seedlings until they are tall enough to survive such treatments. Managers may want to retain some large branches and logs in high-severity burn patches until seedlings are taller, because our results indicate they may be important for growth, and others have shown they encourage conifer regeneration and beneficial microbial populations (Sánchez Meador and Moore, 2010; Castro et al., 2011). Managers may also want to protect surviving trees or “legacy trees” within or surrounding large burn patches to conserve future pine seed (Kemp et al., 2016; Stephens et al., 2018). Thinning treatments could be focused on dense stands near high-severity burn patches to protect ponderosa pine seed sources. Finally, we suggest monitoring post-fire areas for exotic species to evaluate any future threats.

It is becoming increasingly apparent that predictions of warmer climates and increased occurrences of large, high-severity wildfires should be factored (McDowell et al., 2016; Abatzoglou and Williams, 2016; Kitzberger et al., 2017) into post-fire treatment plans. Climate change is predicted to result in large-scale vegetation shifts in southwestern forests (Flatley and Fulé, 2016). Non-forested high-severity burn patches or alternative vegetation types can be areas of resilience to climate variability and to subsequent fire within portions of the pine-dominant landscape (Coop et al., 2016; Schoennagel et al., 2017, Parks et al., 2018). However, if management goals are to restore ponderosa forests that are not regenerating naturally, planting pine seedlings in the edge or interiors of high-severity burn patches could be an option (Ouzts et al., 2015). Planting in spatial heterogeneous patterns and not overly densely would avoid increasing future fire severity (Thompson et al., 2007; North et al., 2019). Our results suggest planted pines may have improved growth near some CWD or forb cover, but they may be at risk
for future fires until they are tall enough to survive higher flame lengths (Bailey and Covington, 2002; Battaglia et al., 2009). Other management options revolve around reducing the potential for large high severity fires by increasing thinning dense stands and using managed fire to lower tree densities, more in line with historical forest conditions (Fulé et al., 2012; Stephens et al., 2016; Huffman et al., 2017).

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Figure S4: Relationship between niche attributes and ponderosa pine diameter at root collar (DRC).

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Table 1
Mean (1 SE) dominant understory plant species cover (> 10% cover in one treatment/year) among treatments. F and p values are shown for treatment (TRT), sampling year (YR), and TRT X YR interactions. Different letters indicate significant differences among treatments, and superscript numbers indicate differences within a treatment type between years. *Indicates non-native, exotic species.

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Fig. 1. Location of 4-ha study areas within different burn-severity and unburned areas of the 2000 Pumpkin Fire, Arizona, USA. Study areas are to scale, and UB = unburned, M = moderate-severity, HE = high-severity edge (near residual live trees), and HI = high-severity interior (at least 200 m from any live tree). We placed 1-m² quadrats around randomly selected ponderosa pine seedlings for quantifying abiotic and biotic conditions within each of these study areas.
Fig. 2. NMDS ordination biplot showing differences in understory plant communities surrounding regenerating ponderosa pines among different fire severities and unburned plots. The axes represent the position of communities relative to each other. Each point represents the understory community for each quadrat (360 total), and the closer the points are, the more similar they are. All treatments are different; the vectors for percent forb and exotic plant cover are represented by red lines, and the length of each and associated $R^2$ represent the strengths of the correlation.
Fig. 3. A) Herbaceous fine fuel biomass near regenerating ponderosa pines was lowest in the unburned plots, intermediate in moderate-severity, and greatest in both high-severity edge and interior plots. B) Percent coarse woody debris (CWD) cover was lowest in the unburned compared to all burned plots. Boxplots represent the variation between sites, and span the first to the third quartile. A center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.
**Fig. 4.** The number of randomly selected ponderosa pines from each post-fire treatment (moderate-severity = white, high-severity edge = gray, and high-severity interior = black), from each estimated year of establishment (x-axis), for a total of 270 seedlings (90/burn treatment). This figure includes seedlings from burn plots only, the 90 unburned seedlings are not included. The red dots and line represent total precipitation for each water year (in cm) from (Western Regional Climate Center (WRCC): https://wrcc.dri.edu, Accessed 2/15/19).
Fig. 5. A) Ponderosa pine diameter at root collar (DRC) was higher in all burned compared to unburned plots. B) Ponderosa pine total height was higher high-severity edge plots compared to other treatments. C) Ponderosa pine growth (the length of annual growth of the terminal leader) varied among treatments and year, but was mostly highest in the high-severity edge plots. Ponderosa pine DRC and total height were measured 2016. Boxplots in A and B represent the variation between sites, and span the first to the third quartile. A center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.
Fig. 6. Ponderosa pine growth rates over 4 years from 2011 – 2015 were partially explained by overstory tree canopy cover, surrounding forb and *M. montana* cover, and soil phosphate. There was a strong trend for a positive correlation between growth rates and CWD cover. GLMM fit is shown with 95% confidence limits.
Supplementary Material

**Figure S1**: Annual water year (Oct-Sept) precipitation (cm) for 2000 – 2016, the amount of precipitation from September – December is shown in blue, January – March in orange, April – May in grey, and June – August in yellow.
Figure S2: Photographs of study sites on the 2000 Pumpkin Fire. We established three 4-ha plots on each site, including unburned (560-1160 trees/ha), moderate-severity (120-490 trees/ha), high-severity edge (0 trees/ha) and high-severity interior (0 trees/ha) plots, for a total of twelve 4-ha plots. High-severity edge plots were established adjacent to forest edges, and high-severity interior plots were established at least 200 m from any live tree.
Table S1: Plant species list, including life form (forb, graminoid, shrub, tree; separated by horizontal lines), family, scientific and common names, duration (annual (A), perennial (P), biennial (B)), year in which species were found (B indicates both years), Treatment (TRT) in which species were found (unburned (UB), moderate-severity (M), high-severity edge (HE), and high-severity interior (HI), and frequencies (FR) per treatment (maximum = 360). *Exotic species

<table>
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<th>Life form</th>
<th>family</th>
<th>Species</th>
<th>common name</th>
<th>Duration</th>
<th>Year</th>
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<th>TRT 2014</th>
<th>FR 2013</th>
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<td>prostrate</td>
<td>A P</td>
<td>2013</td>
<td>M</td>
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<tr>
<td>Polygonaee forb</td>
<td><em>Eriogonum alatum</em> Torr.</td>
<td>winged</td>
<td>P</td>
<td>2013</td>
<td>UB; M</td>
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<tr>
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<td>P B</td>
<td>HE</td>
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<td>buckwheat</td>
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<td>B</td>
<td>M; HE</td>
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<tr>
<td>Polygonaee forb</td>
<td><em>Potentilla subviscosa</em> Greene</td>
<td>buckwheat</td>
<td>P B</td>
<td>M; HE</td>
<td>HE</td>
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<td>2013</td>
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<tr>
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<td>redroot</td>
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<td>2013</td>
<td>UB; M</td>
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<td>M; HE</td>
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<td>Wyoming</td>
<td>P</td>
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<td><em>Linaria dalmatica</em> (L.) Mill.*</td>
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<td></td>
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<td>HI</td>
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<td>2013</td>
<td>M</td>
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<td>M</td>
<td>M</td>
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<td>M; HE; HI</td>
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<td>B</td>
<td>M; HE; HI</td>
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<td>2013</td>
<td>M</td>
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<td>UB; M; HE; HI</td>
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<td>Poaceae</td>
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<td>creeping barberry</td>
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<td>HI</td>
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<td><em>Ribes cereum</em> Douglas</td>
<td>wax currant</td>
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<td><em>Ceanothus fendleri</em> A. Gray</td>
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<td>B</td>
<td>M; HE; HI</td>
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<td>shrub</td>
<td>Rosaceae</td>
<td><em>Cercocarpus ledifolius</em> Nutt.</td>
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<td>P</td>
<td>B</td>
<td>HE</td>
<td>HE</td>
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<td>shrub</td>
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<td><em>Juniperus</em> sp. (likely <em>osteosperma</em>)</td>
<td>juniper sp. (small seedling)</td>
<td>P</td>
<td>B</td>
<td>M; HE</td>
<td>HE</td>
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<td>Cupressaceae</td>
<td><em>Pinus ponderosa</em> Lawson &amp; C. Lawson</td>
<td>ponderosa pine</td>
<td>P</td>
<td>B</td>
<td>M; HE; HI</td>
<td>M; HE; HI</td>
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<td><em>Populus tremuloides</em> Michx.</td>
<td>quaking aspen</td>
<td>P</td>
<td>B</td>
<td>HE; HI</td>
<td>HE</td>
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<td>tree</td>
<td>Salicaceae</td>
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<td>B</td>
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Table S2: Mean (SE) percent canopy cover for total plant and bare ground, different life forms (tree, shrub, forb, graminoid), exotic plants, and species richness, Shannon’s diversity, and evenness in each treatment and averaged between years, or shown separate if there was a significant interaction between treatment and year. F and p values are shown for treatment (TRT) and sampling year (YR) interactions, and separately for year and treatment. Different letters indicate significant differences among treatments, and superscript numbers indicate differences within a treatment type between years.

<table>
<thead>
<tr>
<th>Cover variables (%)</th>
<th>Unburned</th>
<th>Moderate-severity</th>
<th>High-severity edge</th>
<th>High-severity interior</th>
<th>( F_{TRT\times YR} )</th>
<th>( p_{TRT\times YR} )</th>
<th>( F_{YR} )</th>
<th>( p_{YR} )</th>
<th>( F_{TRT} )</th>
<th>( p_{TRT} )</th>
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<tbody>
<tr>
<td>Total plant 2013</td>
<td>80.56 (2.98)</td>
<td>84.86 (2.68)</td>
<td>89.03 (1.84)</td>
<td>90.38 (2.12)</td>
<td>5.61</td>
<td>&lt;0.01*</td>
<td>0.37</td>
<td>0.55</td>
<td>2.33</td>
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<td>Total plant 2014</td>
<td>84.53 (2.57)</td>
<td>82.36 (2.94)</td>
<td>90.86 (1.42)</td>
<td>89.19 (1.66)</td>
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<tr>
<td>Bare ground 2013</td>
<td>3.08 (1.83)</td>
<td>2.62 (1.17)</td>
<td>1.36 (0.55)</td>
<td>1.32 (0.53)</td>
<td>3.17</td>
<td>0.02*</td>
<td>0.18</td>
<td>0.67</td>
<td>4.19</td>
<td>0.05*</td>
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<td>Bare ground 2014</td>
<td>2.93 (1.08)</td>
<td>3.56 (1.29)</td>
<td>1.47 (0.71)</td>
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<td>Tree 2013</td>
<td>37.97 (4.73)</td>
<td>40.78 (4.61)</td>
<td>56.36 (4.43)</td>
<td>46.19 (5.03)</td>
<td>1.29</td>
<td>0.29</td>
<td>6.43</td>
<td>0.01*</td>
<td>1.06</td>
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<td>Tree 2014</td>
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<td>42.25 (4.54)</td>
<td>64.69 (4.80)</td>
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<td>Shrub</td>
<td>0.03 (0.03)</td>
<td>7.62 (2.29)</td>
<td>22.38 (4.02)</td>
<td>27.62 (4.43)</td>
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<td>0.01</td>
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<td>11.70</td>
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<td>Forb 2013</td>
<td>30.61 (4.14)</td>
<td>51.05 (4.87)</td>
<td>56.23 (4.38)</td>
<td>53.76 (4.45)</td>
<td>8.17</td>
<td>&lt;0.01*</td>
<td>24.83</td>
<td>&lt;0.01*</td>
<td>0.88</td>
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<td>Graminiod 2013</td>
<td>69.41 (4.73)</td>
<td>65.69 (4.61)</td>
<td>57.29 (4.73)</td>
<td>65.24 (5.03)</td>
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<td>12.74</td>
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<td>Graminiod 2014</td>
<td>69.33 (5.01)</td>
<td>59.49 (5.15)</td>
<td>54.32 (4.75)</td>
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<td>Exotic</td>
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<tr>
<td>2013</td>
<td>4.98 (0.32)</td>
<td>8.02 (0.45)</td>
<td>8.60 (0.49)</td>
<td>9.13 (0.57)</td>
<td>0.33</td>
<td>0.81</td>
<td>40.26</td>
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<td>4.38 (0.29)</td>
<td>6.54 (0.40)</td>
<td>7.30 (0.51)</td>
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<td>1.57</td>
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<td>1.04 (0.07)</td>
<td>1.49 (0.08)</td>
<td>1.57 (0.07)</td>
<td>1.63 (0.07)</td>
<td>0.69</td>
<td>0.77</td>
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</tr>
<tr>
<td></td>
<td>0.69 (0.03)</td>
<td>0.77 (0.03)</td>
<td>0.76 (0.03)</td>
<td>0.78 (0.03)</td>
<td>0.78</td>
<td>0.70</td>
<td>2.16</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Table S3:** Mean (SE) percent cover of litter (all size classes), stump and rock in each treatment. Different letters indicate significant differences among treatments.

<table>
<thead>
<tr>
<th>Cover variables (%)</th>
<th>Unburned</th>
<th>Moderate-severity</th>
<th>High-severity edge</th>
<th>High-severity interior</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter</td>
<td>88.89 (2.42)</td>
<td>90.39 (2.59)</td>
<td>91.42 (1.85)</td>
<td>91.42 (2.08)</td>
<td>1.84</td>
<td>0.14</td>
</tr>
<tr>
<td>Stump</td>
<td>0.74 (0.71)a</td>
<td>3.36 (1.77)b</td>
<td>4.53 (1.48)b</td>
<td>4.96 (1.57)b</td>
<td>2.75</td>
<td>0.04*</td>
</tr>
<tr>
<td>Rock</td>
<td>10.17 (3.25)</td>
<td>12.94 (3.64)</td>
<td>11.58 (3.30)</td>
<td>11.45 (3.33)</td>
<td>0.40</td>
<td>0.75</td>
</tr>
</tbody>
</table>
Table S4: Mean (SE) properties of 0-15 cm mineral soil. Different letters indicate significant differences among treatments.

<table>
<thead>
<tr>
<th>Soil property</th>
<th>Fire severity</th>
<th></th>
<th></th>
<th></th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Unburned</td>
<td>Moderate</td>
<td>High-edge</td>
<td>High interior</td>
<td></td>
</tr>
<tr>
<td>Total N (%)</td>
<td></td>
<td>0.26 (0.01)</td>
<td>0.27 (0.01)</td>
<td>0.26 (0.01)</td>
<td>0.30 (0.02)</td>
<td>0.15</td>
</tr>
<tr>
<td>Total C (%)</td>
<td></td>
<td>3.10 (0.22)</td>
<td>2.92 (0.24)</td>
<td>3.35 (0.23)</td>
<td>4.50 (0.34)</td>
<td>13.18</td>
</tr>
<tr>
<td>NH$_4^+$ (ppm)</td>
<td></td>
<td>0.62 (0.14)</td>
<td>0.51 (0.09)</td>
<td>0.77 (0.09)</td>
<td>0.66 (0.08)</td>
<td>1.64</td>
</tr>
<tr>
<td>NO$_3^-$ (ppm)</td>
<td></td>
<td>0.04 (0.01)</td>
<td>0.11 (0.04)</td>
<td>0.12 (0.03)</td>
<td>0.12 (0.04)</td>
<td>1.1</td>
</tr>
<tr>
<td>PO$_4^{3-}$ (ppm)</td>
<td></td>
<td>1.08 (0.05)</td>
<td>1.09 (0.07)</td>
<td>1.15 (0.08)</td>
<td>1.15 (0.07)</td>
<td>0.83</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td></td>
<td>14.54 (0.17)</td>
<td>14.85 (0.16)</td>
<td>15.44 (0.18)</td>
<td>15.63 (0.18)</td>
<td>1.53</td>
</tr>
<tr>
<td>pH</td>
<td></td>
<td>5.42 (0.05)</td>
<td>5.59 (0.07)</td>
<td>5.70 (0.01)</td>
<td>5.72 (0.07)</td>
<td>0.31</td>
</tr>
<tr>
<td>Gravel (% &gt; 2 mm)</td>
<td></td>
<td>19.37 (1.12)$^a$</td>
<td>27.45 (1.33)$^c$</td>
<td>24.30 (1.30)$^b$</td>
<td>28.94 (1.20)$^c$</td>
<td>23.16</td>
</tr>
<tr>
<td>Sand (% &lt; 2 mm)</td>
<td></td>
<td>27.79 (1.70)$^a$</td>
<td>31.20 (1.48)$^b$</td>
<td>31.37 (1.74)$^b$</td>
<td>34.31 (1.45)$^c$</td>
<td>7.32</td>
</tr>
<tr>
<td>Clay (% &lt; 2 mm)</td>
<td></td>
<td>28.48 (1.17)$^a$</td>
<td>26.30 (1.39)$^b$</td>
<td>26.85 (0.97)$^b$</td>
<td>23.37 (1.29)$^b$</td>
<td>7.13</td>
</tr>
<tr>
<td>Silt (% &lt; 2 mm)</td>
<td></td>
<td>43.72 (1.89)</td>
<td>41.84 (1.98)</td>
<td>41.78 (1.88)</td>
<td>42.33 (2.05)</td>
<td>0.61</td>
</tr>
</tbody>
</table>
Figure S3: Frequency of stability scores ranging from 1 (low stability; white) to 6 (high stability, black) were similar among treatments ($F = 0.21; p = 0.89$); there is a total of 90 scores/treatment.
**Figure S4:** There was a strong trend for a negative relationship between ponderosa pine DRC and overstory tree canopy cover. DRC was partially explained by a positive correlation with surrounding *M. montana*, forb, and CWD cover. GLMM fit is shown with 95% confidence limits.
Chapter 4: Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest

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This chapter is in review with Soil Biology and Biochemistry
Abstract:

Over the past three decades, wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity. These wildfires can remove large, contiguous patches of mature forests, alter dominant plant communities and increase woody debris, potentially altering fungal community composition. Additionally, post-fire conditions may shift dominant fungal functional groups from plant-symbiotic ectomycorrhizal (EM) fungi to more saprotrophic fungi. We investigated the long-term (13 years post-wildfire) effect of fire severity on 1) fungal sporocarp density, functional groups and community composition and 2) EM colonization and community composition from naturally regenerating ponderosa pine seedlings on the Pumpkin Fire that burned in 2000 in Arizona, USA. Plots were located in unburned areas, moderate-severity burned areas, and two high-severity (defined as 100% tree mortality) burned areas, either adjacent to residual live forest edges (edge plots), or >200 m from any residual live trees (interior plots). We found that high-severity burn plots had a unique sporocarp community composition, and a shift in dominant sporocarp functional groups, with 5-13 times lower EM sporocarp densities, and 4-7 times lower EM sporocarp species richness compared to unburned and moderate-severity burn plots. In contrast, saprotrophic sporocarp densities and richness were similar among treatments, even with the large amount of woody debris in the high-severity burn patches. Regenerating ponderosa pine seedlings had similar EM colonization and richness among treatments, yet high-severity interior plots had a different community composition and a lower relative abundance of EM species compared to moderate-severity burn plots. These results suggest that large patches of high-severity fire have long-term consequences for EM sporocarp communities, which may reduce reproduction of some species. Further, available EM inoculum in high-severity burn patches is
resilient, but the total species pool remains small in the interior burn patches, even 13 years post-fire.

**Highlights:**

- Fungal communities were assessed across different fire severities in a pine forest.
- High-severity burns had long-term consequences for EM sporocarp communities.
- Saprotrophic sporocarp density did not increase following burning despite increased woody debris.
- Total EM inoculum species pool was low in interior high-severity burn patches.

**Key words:** forest resilience; ectomycorrhizal fungi, saprotrophic fungi, wildfire

1. **Introduction**

   Fire is a natural and beneficial process in most forest ecosystems, releasing nutrients into the soil and reducing accumulated fuels, but the severity and length of fire seasons across the globe are predicted to increase with rising temperatures and altered fuel conditions, leading to increased tree mortality (Jolly et al., 2015; Abatzoglou and Williams, 2016; Kitzberger et al., 2017; Krofcheck et al., 2018). Large-scale changes in fire behavior are driven by climate changes, such as increased temperature and droughts, particularly in areas with high fuel loads (Shive et al., 2013; Sieg et al., 2017; Yocom Kent et al., 2017). Wildfire frequency and area burned in many forest types are predicted to increase with warmer climates and increased fuel densities (Westerling et al., 2006, 2016; Flannigan et al., 2013). Wildfires with large patches of high-severity fire, along with warmer climates are forecasted to cause widespread conifer...
mortality and extensive shifts in plant species distributions in the coming decades (Rehfeldt et al., 2006; McDowell et al., 2016; Abatzoglou and Williams, 2016; Flatley and Fulé, 2016; Stevens-Rumann et al., 2018). These studies predict long-term consequences for aboveground communities, but knowledge of the effects of increased fire severity on soil biota, such as fungi, are limited and somewhat contradictory (e.g. Holden et al., 2013; Cowan et al., 2016; Glassman et al., 2016).

Soil fungi, including ectomycorrhizal (EM) fungi and saprotrophic fungi, are important components of the soil microbial community that may influence ecosystem resilience and stability after disturbances because of their diverse functions as plant mutualists and decomposers (Buscardo et al., 2015; Gehring et al., 2017; Yang et al., 2018). Ectomycorrhizal fungi increase water and nutrient uptake for their plant hosts in return for carbon, and evidence suggests some may also decompose soil organic matter (SOM) (Smith and Read, 2008; Shah et al., 2016). Saprotrophic fungi play an important role in nutrient cycling and are responsible for decomposing wood, plant litter, and SOM (Cairney and Meharg, 2002). Saprotrophic and EM fungi coexist in the soil, and competition, facilitation (e.g. sharing P through leaky hyphae or hyphal senescence), or avoidance (extending mycelium in the opposite direction) can occur, as well as a partitioning of different functional groups driven by available carbon sources (Lindahl et al., 1999; Boddy 2000; Cairney and Meharg, 2002; Clemmensen et al., 2013). It is critical to understand how fire can influence both functional groups because they may influence ecosystem resilience though forest regeneration and nutrient cycling.

Fire can have direct and indirect effects on fungal communities. A direct consequence of fire is heat-induced mortality from high soil temperatures, however some fungal species are more resilient to heat, especially in the form of spores (Peay et al., 2009; Kipfer et al., 2010; Carlsson
et al., 2014). Fire can select for heat-tolerant EM and saprotrophic species that have likely evolved within historically fire-prone ecosystems (Carlsson et al., 2012, 2014; Kipfer et al., 2010; Glassman et al., 2016). Fire can indirectly influence saprotrophic community composition or decomposition rates by changing the structure and chemistry of soil and litter (Ficken and Wright, 2017; Bhatnagar et al., 2018). For example, increased log cover could increase white and brown rot decomposers, capable of degrading lignin or cellulose and hemicellulose; alternatively, increased herbaceous plant C inputs could favor different guilds of saprotrophic fungi (Zhou and Hyde 2002, Ficken and Wright, 2017; Bhatnagar et al., 2018). Nutrient availability and soil conditions can drive EM and saprotrophic biomass found in forest soils (Awad et al., 2019). Fire can also indirectly alter fungal communities and reduce available inoculum by causing host mortality or shifting dominant plant communities (Buscardo et al., 2011, Peay et al., 2012; reviewed in Karst et al., 2014). For example, competing shrub species or arbuscular mycorrhizal (AM) plant hosts can influence the amount and distribution of EM fungi in previously pine-dominated communities (McHugh and Gehring, 2006; Buscardo et al., 2011). Shifts in EM and saprotrophic community composition and reduced species richness were also found after extensive lodgepole pine (Pinus contorta) mortality in western Canada (Pec et al., 2017). While fire may directly and indirectly influence fungal communities, there is still much to learn about whether or not increased fire severity will have long-term effects on both EM and saprotrophic fungal communities.

Previous studies have shown variable effects of high-severity fire on fungal communities. Fungal recovery after high-severity wildfires may be influenced by forest type, time since fire, and distance from available plant hosts (Visser, 1995; Treseder et al., 2004; Kipfer et al., 2011; Holden et al., 2013). For example, EM and saprotrophic species richness were low 6 years post-
fire, but recovered 41 years after stand-replacing wildfire from a chronosequence study in a Jack pine (*Pinus banksiana* Lamb.) forest (Visser, 1995). Additionally, after high-severity wildfires in boreal forests of Alaska, the proportion of ascomycetes increased and basidiomycetes decreased in the first few years post-fire, and required at least 24 years to return to pre-fire levels (Holden et al., 2013). Recovery of EM inoculum after high-severity fires may be dependent on the proximity of surviving hosts, and nearby inoculum sources such as hyphae and spores may contribute to post-fire seedling colonization (Nara, 2006; Teste et al., 2009; Peay et al., 2012; Peay and Bruns, 2014). Areas farther from surviving trees had lower EM richness and diversity five years after a high-severity wildfire in a maritime pine (*Pinus pinaster*) forest (Buscardo et al., 2011). Given the increasing size and severity of fires in some forest types in recent years, a better understanding is needed of how large patches of high-severity fire, far from surviving plant hosts, influence the recovery of fungal communities.

Wildfires in southwestern US ponderosa pine (*Pinus ponderosa*) forests have increased in size and severity, leaving large, contiguous patches of tree mortality (often ≥ 100 ha) (Dillon et al., 2011; Singleton, 2019). Ponderosa pine forests are one of the dominant forest types in the semi-arid western US, and large high-severity burn patches 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). Increases in fire size and severity in ponderosa pine forests are attributed to warmer and drier climate conditions, longer fire seasons (Dillon et al., 2011; Reilly et al., 2017), and the accumulation of canopy and surface fuel loads from over 100 years of fire exclusion (Fulé et al., 1997, 2009; Moore et al., 2004). High-severity fires in ponderosa pine forest alter dominant plant communities and increase log cover for extended periods of time (Roccaforte et al., 2012; Chambers et al., 2016; Owen et al.,
It is important to assess post-fire fungal communities because of their roles as decomposers and symbionts, and the potential for EM fungi to assist in post-fire ponderosa pine recovery. EM fungi form an obligate association with ponderosa pines, and there is evidence from greenhouse studies that ponderosa pine is dependent on EM fungi for growth and survival (Riffle and Tinus, 1982; Steinfeld et al., 2003; Barroetaveña et al., 2016).

The limited studies on the effects of high-severity wildfires on fungal communities in ponderosa pine forests have yielded contrasting results. Previous studies have found short-term effects of high-severity fire or repeated burning on fungal biomass, richness and/or community composition in ponderosa pine forests (Stendell et al., 1999; Hart et al., 2005; Reazin et al., 2016; Glassman et al., 2016). For example, a high-severity wildfire in a ponderosa pine forest reduced both EM richness and density and favored a *Rhizopogon* species 1 month post-fire, compared to pre-fire (Glassman et al., 2016). In contrast, EM richness, diversity and community composition were similar across different fire severities and unburned areas within one year post-fire in a different ponderosa pine forest (Cowan et al., 2016). In this latter study, EM fungi quickly recovered and colonized planted ponderosa pine seedlings after high-severity fire, but study sites were approximately 10-20 m from nearby live host-trees (Cowan et al., 2016). It is unclear how fungal communities will recover in large high-severity burn patches, often > 200 m from live trees.

To understand the long-term effect of fire severity on fungal communities, we assessed both aboveground sporocarps (fruiting EM and saprotrophic fungi) and EM fungi colonizing naturally regenerating ponderosa pines, 13 years after the 2000 Pumpkin Fire near Flagstaff, AZ. The Pumpkin Fire was chosen because it had extensive patches of high-severity fire, as well as moderate-severity fire, and nearby unburned areas. We hypothesized that compared to moderate-
severity and unburned areas, high-severity burn patches will have: H$_1$) greater saprotrophic and lower mycorrhizal sporocarp density; H$_2$) lower sporocarp species richness and diversity and a unique sporocarp community composition; and H$_3$) regenerating ponderosa pine seedlings with similar EM colonization rates, but lower EM richness and diversity, and a unique EM community composition. Because of the large size of the high-severity patches and the distance from live forest, we expected seedlings in these patches to have a community dominated by species with resistant propagules (e.g. *Wilcoxina* or *Rhizopogon*), but lacking some species capable of long-distance hyphal exploration associated with hyphal networks, compared to those from moderate-severity or unburned areas (Agerer, 2001; Peay and Bruns, 2014; Glassman et al., 2016).

2. Materials and methods

2.1. Study sites and plot design

We investigated the long-term effect of fire severity on fungal communities 13 years after the 2000 Pumpkin Fire in northern Arizona. The Pumpkin Fire burned approximately 6,500 ha, including 1,400 ha of high-severity fire on the Kaibab and Coconino National Forests (http://www.mtbs.gov/; Appendix S1). We define high-severity as 100% tree mortality. Our plots ranged from 2,350 to 2,600 m elevation. The mean 15 year (2001-2015) post-fire annual precipitation was 57.7 cm and the mean temperature was 7.2°C (Prism Climate Group: http://prism.oregonstate.edu/. Accessed 10/7/16). This region receives most of its annual moisture from late-summer rains that typically occur July – August and from winter precipitation. During the time of our field sampling in August – September, 2013, late-summer moisture was higher than average (mean precipitation for July: 173.3 mm, August: 103.1 mm,
and September: 105.9 mm) compared to the 15 year post-fire average (July: 75.5 mm, August: 95.0 mm, and September: 51.5 mm; Prism Climate Group). The soils were derived from basalt and ranged from shallow gravelly sandy loam to moderately deep cobbly clay loam on our study plots (WebSoil Survey: http://websoilsurvey.nrcs.usda.gov. Accessed 10/5/16). The unburned and pre-fire overstory vegetation was dominated by ponderosa pine. Common understory species included the bunch grasses, Arizona fescue (*Festuca arizonica* Vasey) and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.); forbs, such as spreading fleabane (*Erigeron divergens* Torr. & A. Gray) and silvery lupine (*Lupinus argenteus* Pursh); and shrubs including Woods’ rose (*Rosa woodsii* Lindl. var. *ultramontana* (S. Watson) Jeps.) and Fendler’s ceanothus (*Ceanothus fendleri* A.).

We used Monitoring Trends in Burn Severity (MTBS, 2013) maps with field validation to identify different burn severities and unburned sites for plot selection. We used ArcGIS 10.1 (ESRI, 2012) to randomly select three sites within each burn-severity or unburned area. We established 4-ha (200 x 200 m) plots on each site, including “unburned” (UB), “moderate-severity” (M), “high-severity edge” (HE) and “high-severity interior” (HI) plots, for a total of twelve 4-ha plots (Appendix S1). Unburned plots were selected near the other plots and they were not burned in a wildfire or managed fire for the past 20 years. Unburned areas had high tree densities, ranging from 560-1160 trees/ha. Moderate-severity plots were chosen from areas that resulted in a spatial heterogeneity of post-fire surviving trees ranging from 120-490 trees/ha, including some patches of high-severity fire < 1 ha in size. Both high-severity edge and interior plots had 100% tree mortality from the wildfire, but high-severity edge plots were established adjacent to forest edges or residual live trees, and high-severity interior plots were established where no surviving trees were found within at least 200 m from the plot boundaries. High
severity plots had a dominant understory herbaceous plant community, groundcover that consisted of woody debris and fallen snags, an average of 20 ponderosa pine seedlings/ha (interior burn patch) to 73 seedlings/ha (near forest edges), with spatially heterogeneous regeneration (Owen et al., 2017; see Figure 1). We set up plots at least 30 m away from any roads and from another plot and selected plots that had no post-fire logging, planting, or subsequent fires. To understand the effects of fire severity on fungal communities, we surveyed aboveground sporocarps within smaller quadrats located in each 4-ha plot, and we destructively sampled ponderosa pine seedlings outside each 4-ha plot, described in more detail below.

2.2. Measuring post-fire sporocarp communities

To test the first hypothesis that high-severity burn patches will have greater saprotrophic and lower EM density compared to moderate-severity or unburned areas, we surveyed post-fire sporocarps and determined their functional status. We surveyed aboveground sporocarps within 2 X 2-m quadrats surrounding 30 regenerating ponderosa pine seedlings (ranging from 4-11 years old) across different fire severities and unburned areas, for a total of 360 quadrats. The quadrats were set up around randomly selected ponderosa pine seedlings (using a random number generator) from all spatially mapped seedlings in each 4-ha plot (Owen et al., 2017). We counted all individual sporocarps within each quadrat, collected multiple reference specimens of each morphotype, and dried specimens at room temperature in the laboratory at the Rocky Mountain Research Station, Flagstaff, AZ until identification as described below.

To test the second hypothesis that sporocarp richness and diversity would be lower in the high-severity burn patches compared to moderate-severity or unburned areas, we identified sporocarps to the species level based on their morphology using a mushroom key (Arora, 1986),
and used molecular techniques when species could not be keyed out and to test some specimens for keying accuracy. To identify sporocarps using molecular techniques, we extracted DNA from each sporocarp using a Thermo MagJET Plant gDNA Kit (Thermo Fisher Scientific Baltics UAB, Vilnius, Lithuania) according to the manufacturer’s instructions. We amplified extracted DNA by polymerase chain reaction (PCR) using a fungal specific ITS-1F and ITS4 primer pair as in White et al. (1990). This primer pair, which targets the internal transcribed spacer (ITS) region of rDNA, is located between the 18S and 28S rRNA in the fungal genome (Horton and Bruns, 2001). We sequenced DNA on an ABI 3730xl Genetic Analyzer (Applied Biosystems, Foster City, California) from each sporocarp in the Environmental Genetics and Genomics (EnGGen) laboratory at Northern Arizona University, Flagstaff, AZ. The resulting sequences were assembled in BioEdit version 7.0.5.3 (Hall, 1999) and in Pregap4 of the Staden Package (Staden et al., 1998). The consensus sequences from Pregap4 were used in Genbank BLAST® searches on the NCBI website (Altschul et al., 1990) and UNITE database (Kõljalg et al., 2013). We used percentage query coverage, percentage maximum identity, and bit score data to identify the closest match to references in GenBank. Sequence similarity of ≥ 98% was used for species level identity and 95–97% for genus level identity (Kõljalg et al., 2013). We aligned sequences from a similar genus against one another using MEGA version 7.0 (Kumar et al., 2016) and considered them different species if they had ≥ 2% base pair dissimilarity. We determined species richness and evenness (Shannon’s diversity index / ln richness) for the sporocarps from each quadrat.

To test whether functional groups of sporocarps will differ in the high-severity burn patches compared to moderate-severity or unburned areas, we separated species into different functional groups (either EM or saprotrophic) based on common consensus from past studies.
(e.g. Tedersoo et al., 2006; Tedersoo and Smith, 2013) or by isotopic analysis. Most species were determined from the literature; however, eleven species were analyzed for stable isotope content. Each sporocarp was ground in a 2000 Geno/Grinder (SPEX SamplePrep, Metuchen, NJ, USA) to a fine powder, and analyzed for $\delta^{13}$C and $\delta^{15}$N on a Finnigan Delta-Plus isotope ratio mass spectrometer linked to a Carlo Erba NC2500 elemental analyzer (Finnigan MAT GmbH, Bremen, Germany). Mycorrhizal fungi were separated from saprotrophic fungi by isotopic values similar to Hobbie et al. (2001) and Hart et al. (2006).

To analyze sporocarp density, richness and evenness data, we used generalized linear mixed models (GLMM) in SAS 9.4 (SAS PROC GLIMMIX ©, 2017), with fire-severity as a fixed effect and site location as a random effect. Total, EM, and saprotrophic density and richness of sporocarps were analyzed with GLMMs with a negative binomial distribution and log-link function. Ectomycorrhizal and saprotrophic sporocarp evenness were analyzed with GLMMs with a gamma distribution. If significant differences were found, the post hoc Tukey–Kramer HSD test was used on least-squares means for subsequent pair-wise comparisons (Kramer, 1956).

To test the latter part of the second hypothesis, that high-severity burn patches have unique sporocarp communities compared to moderate-severity or unburned areas, we used permutational multivariate analysis of variance (PERMANOVA); and to visualize differences in communities among treatments, we used a redundancy analysis (RDA) in R v.3.4.1, library vegan, function rda (R development Core Team, 2018) (Ter Braak, 1994). The ordination axes represent distances showing how similar or dissimilar each community is by proximity of the data points in environmental space. All PERMANOVA analyses, including pairwise comparisons, used original counts with a Hellinger distance, which is insensitive to double zeros.
because the metric does not place importance on the mutual absence of a species (Legendre and Legendre, 2012). If PERMANOVA results were significant, we then calculated dispersion (a measure of beta diversity) as measured by individual dissimilarity from the treatment group centroid in multivariate space, described by Anderson et al. (2006), and used indicator species analysis (indicator value = frequency X relative abundance) to determine if particular species were driving community differences (McCune and Grace, 2002).

Finally, to understand if log or tree canopy cover could be driving any community differences in sporocarp community composition within each quadrat, we measured percent cover of coarse woody debris (CWD) (dead woody materials, including logs and branches ≥ 7.62 cm diameter) using a go/no-go gauge (Brown, 1974), and overstory tree canopy cover using a GRS vertical densitometer (Geographic Resource Solutions, Arcata, California, USA), averaging 5 readings/plot. We overlaid vectors on our ordination from a second matrix, consisting of CWD and overstory cover variables, and used Hellinger distance as an assessment of these environmental gradients to determine any correlation with observed differences in sporocarp communities.

2.3. Measuring EM fungi colonizing regenerating ponderosa pine seedlings

To test the third hypothesis, that regenerating ponderosa pine seedlings have similar EM colonization rates among different fire severities and unburned areas, we destructively sampled three seedlings outside each 4-ha plot (for a total of 36 seedlings) to measure EM colonization. We removed an average of 20 cm of randomly selected roots from each seedling to measure fungal propagule density by using a dissecting microscope, examined roots at 40X magnification, and quantified the percentage of live and dead EM root tips, as well as live and dead non-colonized root tips (Gehring and Whitham, 1994). We surveyed approximately 60-200
root tips per sample. To test for differences in percent EM colonization among ponderosa pine seedlings, we divided the percentage data by 100 and used a GLMM with a log-link function and a beta distribution in SAS 9.4 (SAS PROC GLIMMIX®, 2017).

To test the hypothesis that regenerating ponderosa pine seedlings from high-severity burn patches have lower EM richness and unique EM community composition compared to those from moderate-severity or unburned areas, we identified EM fungi both morphologically and with molecular techniques. We recorded different morphotypes based on different colors, shapes, and hyphal arrangements (Horton and Bruns, 2001) and froze them at -20 ºC for future molecular analysis. DNA was extracted from 2-3 representatives of each morphotype from each seedling using similar methods as described above for sporocarps. We tested for differences in richness, evenness, community composition and dispersion among treatments using the same statistical methods described for the sporocarps. Also, to understand if seedling growth and age is correlated with EM colonization and richness, we measured seedling diameter at the root collar (drc), estimated seedling pith age (by counting growth rings from a cross-section of the stem). We used partial correlation analysis to determine any association between % colonization and richness and seedling growth, while adjusting for the effect of age, in SAS 9.4 (SAS PROC GLIMMIX®, 2017). Lastly, to understand if regenerating seedlings were associated with EM fungi with different hyphal exploration types, we categorized EM genera into short, medium or long exploration types according to Agerer (2001, 2006), and Tedersoo and Smith (2013).

3. Results

3.1 Fire severity and fungal sporocarps
Total and EM sporocarp densities were lower in the high-severity burn plots compared to the unburned and moderate severity plots, partially supporting our first hypothesis. However, contrary to our first hypothesis, no differences were found in saprotrophic sporocarp densities among treatments (total density: $F = 11.11, p < 0.01$; EM density: $F = 12.01, p < 0.01$; Fig. 2A, saprotrophic density: $F = 1.43, p = 0.19$; Fig. 2A). Ectomycorrhizal sporocarp densities were approximately 5-13 times lower in the high-severity burn plots compared to the unburned and moderate-severity plots (mean EM sporocarps densities: 8.3/m$^2$ in unburned plots, 4.5/m$^2$ in moderate-severity burn plots, 1.4/m$^2$ in high-severity edge plots, and 0.6/m$^2$ in high-severity interior plots). Mean saprotrophic densities ranged from 1.5-2.3 sporocarps/m$^2$ among all treatments. The proportion of EM to saprotrophic sporocarps was much lower in the high-severity burn plots compared to the unburned and moderate-severity plots. Ectomycorrhizal sporocarp densities were 3-4 times greater than saprotrophic densities in both the unburned and moderate-severity burn plots (Fig. 2A), whereas EM densities were 0.5-0.9 times lower than saprotrophic densities in high-severity burn plots (Fig. 2A). We did not find any sporocarps in 133 of the total 360 quadrats (26-39% of the unburned and moderate-severity plots, and 44-49% of the high-severity plots had no visual aboveground sporocarps).

Similar to sporocarp densities, total and EM sporocarp richness were both lower in the high-severity burn plots compared to the unburned and moderate severity plots, partially supporting our second hypothesis. Yet, in contrast to our second hypothesis, no differences were found in saprotrophic sporocarp richness among treatments (total richness: $F = 13.69, p < 0.01$; EM richness: $F = 17.20, p < 0.01$; saprotrophic richness: $F = 1.53, p = 0.21$; Fig. 2B). Average EM sporocarp richness was 4-7 times lower in the high-severity burn plots, compared to the unburned and moderate-severity plots (mean EM richness: 1.7/m$^2$ in unburned plots, 1.3/m$^2$ in
moderate-severity burn plots, 0.4/m² in high-severity edge, and 0.2/m² in high-severity interior plots). Mean saprotrophic richness ranged from 0.2-0.5/m² across all treatments. Similar to sporocarp densities, the proportion of EM to saprotrophic sporocarp richness was much lower in the high-severity burn plots compared to the unburned and moderate-severity burn plots. EM sporocarp species richness was 4-7 times greater than saprotrophic species richness in both the unburned and moderate-severity burn plots, but EM and saprotrophic sporocarp richness were similar in both high-severity burn plots (Fig. 2B). Additionally, total and EM sporocarp evenness was lower and there was a trend for saprotrophic sporocarp evenness to be higher in the high-severity burn plots compared to the unburned and moderate severity plots (Total evenness: F = 17.67, p < 0.01; EM evenness: F = 27.84, p < 0.01; saprotrophic evenness: F = 2.60, p = 0.06; Fig. 2C).

We found a total of 65 sporocarp species, dominated by the phylum Basidiomycota (Appendix S2). Some of the more common families included *Inocybaceae*, *Agaricaceae*, *Cortinariaceae*, and *Hygrophoraceae*. We found 12 sporocarp species unique to the unburned plots and most of them were either EM or associated with litter decomposition (Appendix S2). There were two species (EM and saprotrophic) unique to the moderate severity plots, and three species (all saprotrophic) unique to the high-severity edge plots. Additionally, five species were unique to the high-severity interior plots, including two saprotrophic species associated with litter decomposition, two EM species, and *Armillaria ostoyae*, a saprotrophic species that is also parasitic to some tree species (Appendix S2).

We also found some interesting trends within different sporocarp functional groups. The most abundant mycorrhizal species was *Hygrophorus speciosus*, found in 30 quadrats, but absent from the high-severity quadrats. Other common mycorrhizal species included *Russula brevipes* +
*Hypomyces lactifluorum* (from here on referred to by common name “lobster mushroom”), *Inocybe geophylla* var. *lilacina*, and *Clavulina cristata* (all missing from high-severity burn plots; Appendix S2). Some mycorrhizal genera found in the unburned and moderate-severity plots, such as *Suillus*, *Amanita*, and most *Russulas*, were not found in the high-severity plots, except *Russula xerampelina*, which was found in one high-severity edge quadrat (Appendix S2). Common saprotrophic species included *Vasceullum curtisii* (found in 20 quadrats, in all treatments), a *Psathyrella* sp. (only found in high-severity burn plots), and *Gloeophyllum sepiarium* (common in high-severity plots and found in one unburned plot; Appendix S2). Most of the saprotrophic species known to decompose forest litter were found in the unburned plots, whereas the high-severity edge and interior plots had more white-rot and brown-rot species, associated with logs (Appendix S2).

High-severity plots had a different sporocarp community composition compared to unburned and moderate-severity plots, supporting our second hypothesis (PERMANOVA: F = 3.92, P < 0.01; Fig. 3). Pairwise PERMANOVA comparisons show high-severity plots had a different sporocarp community composition compared to unburned and moderate-severity plots (p < 0.01 for both), and there was a trend for different community composition between high-severity edge and interior plots, as well as unburned and moderate-severity plots (p = 0.06 for both). Both % overstory tree canopy cover and CWD vectors were significantly correlated with axis dbRDA1 (p < 0.01 for both), but explained very little of the variance in community composition between the two high-severity burn plots and moderate-severity and unburned plots (see low R² values; Fig. 3). Species dispersion differed among treatments (F = 6.53, p < 0.01; average distance to centroid: unburned = 0.77 moderate-severity = 0.74, high-severity edge = 0.61, high-severity interior = 0.57). Pairwise PERMANOVA comparisons show sporocarp
dispersion on high-severity edge and interior plots were similar to one another (p = 0.91), as well as unburned and moderate-severity plots (p = 0.96). There was a trend for similar dispersion between high-severity edge and moderate-severity plots (p = 0.06), and high-severity edge plots had lower dispersion than unburned (P = 0.02). Finally, high-severity interior plots had lower dispersion than both unburned and moderate-severity plots (p = 0.01 for both). There were no significant indicator species when analyzing all 360 quadrats, including many zero-inflated plots, but when collapsing data into the large plot level (n=3), there were significant indicator species from different functional groups. Two indicator species for the unburned areas were *Suillus kaibabensis* (I = 64.5, p = 0.04) and a lobster mushroom (I = 59.5, p = 0.05), and for moderate-severity burn areas, they were *Russula sanguinea* (I = 60.0, p = 0.02) and *Clavulina cristata* (I = 78.6, p = 0.04). An indicator species for the high-severity edges was *Gloeophyllum sepiarium* (I = 78.6, p = 0.04), and there were no indicator species for the high-severity interior areas.

3.2 Fire severity and EM fungi colonizing ponderosa pine seedlings

Percent live EM fungal colonization in regenerating ponderosa pine seedlings was similar among treatments (F = 1.48, p = 0.24; Fig. 4A), supporting our third hypothesis. The percentage of live EM root tips from regenerating ponderosa pine roots ranged from 23-32% colonization (Fig. 4A). The percentage of total (live + dead) EM colonization (F = 1.89; p = 0.15), and total non-colonized root tips (F = 1.28; p = 0.30) were also similar among treatments (data not shown).

Ectomycorrhizal root tip species richness (F = 1.42, p = 0.26; Fig. 4B) and evenness (F = 1.96, p = 0.15; Fig. 4C), were similar among treatments, contrary to our third hypothesis.
Although the average species richness/seedling was similar among treatments (ranging from 2-3.4/seedling; Fig. 4B), the total number of EM species colonizing regenerating ponderosa pine seedlings on the plot-level was much lower in the high-severity interior plots compared to the other treatments, especially the moderate-severity plots (Fig. 5). The total number of root-tip EM species at the plot level were: unburned = 13, moderate-severity = 15, high-severity edge = 9, and high-severity interior = 7 (Fig. 5).

We expected both high-severity plots to have different ponderosa pine EM root tip communities compared to moderate-severity and unburned plots; however, only the high-severity interior and moderate-severity EM community composition differed (p = 0.02), but all other treatments were similar (p > 0.10; PERMANOVA pairwise comparisons; Fig. 6). There were trends for EM dispersion differences among treatments (F = 2.95, p = 0.05), and for lower EM dispersion on high-severity interior compared to moderate-severity plots (p = 0.07). An indicator species for moderate-severity plots was a *Sebacina* sp. (IV = 33.3, p = 0.04), and there was a trend for indicator species for the high-severity interior plots (*Cenococcum geophilum*: IV = 37.6, p = 0.08, and *Inocybe nitidiuscula*: IV = 25, p = 0.09).

We identified 24 different EM species colonizing ponderosa pine roots (Table 1). The unburned plots had five unique species (*Boletales* sp., *Inocybe chelanensis*, *Russula integriformis* *Russula sanguinea*, and a *Tricholoma* sp.) the moderate-severity plots had seven unique species, and the high-severity interior had one unique species, *Inocybe niveivelata* (Table 1). Also, a *Wilcoxina* sp. was only found in both of the high-severity burn plot types, but absent from the unburned and moderate-severity plots. Similar to the sporocarp results, species from the genus *Russula* were mostly found in the unburned and moderate-severity plots, and absent from high-severity interior plots, but *R. brevipes* was found on one high-severity edge seedling. We found a
large discrepancy between species that were found colonizing ponderosa pine roots and those found as fruiting sporocarps. Only six out of the 24 species found colonizing ponderosa pine roots were also found as fruiting sporocarps in the same treatment type (Table 1).

The amount of EM ascomycetes \( (F = 0.39, p = 0.79) \) and basidiomycetes \( (F = 0.36, p = 0.81) \) colonizing seedlings did not differ among treatments, however, the total number of ascomycetes compared to basidiomycetes was higher within the high-severity interior sites (Table 1, Appendix S3). The EM communities in all treatment groups were dominated by taxa with short hyphal exploration types, and the relative abundance of short, medium and long hyphal exploration types was similar among treatments (Table 1, Appendix S4), contrary to our hypothesis.

Finally, regenerating ponderosa pine seedling age was correlated with growth measured by diameter at root collar (DCR) \( (F = 83.6; p < 0.001, \text{ Appendix S5 A}) \), therefore age was used as a covariate in our correlation analyses. Ponderosa pine seedling age \( (p = 0.65) \) and DCR \( (p = 0.58) \) did not differ among treatment groups (Appendix S5 B). There were no significant relationships between % EM colonization \( (p = 0.47) \), or EM richness \( (p = 0.24) \) and ponderosa pine seedling growth (Appendix S5 C, D).

4. Discussion

4.1 Sporocarp density and richness

Our study found reduced sporocarp densities and richness in large patches of high-severity fire compared to unburned and moderate-severity plots in a ponderosa pine forest, even 13 years after fire. Long-term studies on the effect of high-severity fire on sporocarp communities are limited, but similar to our findings, lower sporocarp density and richness has
been found 10 and 12 years after high-severity fire compared to unburned sites, in a *Pinus sylvestris* and a dry Afromontane forest (Dejene et al., 2017; Salo and Kouki, 2018). However, contrary to our findings, sporocarps quickly recovered 5 years post-fire in a *Pinus nigra* forest (Mediavilla et al., 2014). Also, Visser (1995) found lower sporocarp richness 6 years after high-severity fire, but similar levels 41 years post-fire in a *P. banksiana* forest. Several short-term studies on the effect of high-severity fire in a variety of forest types found a reduction in sporocarp density or richness (Martín-Pinto et al., 2006; Motiejūnaitė et al., 2014; Adamonytė et al., 2016), but Robinson et al. (2008) found no change in sporocarp richness five years post-fire in a *Eucalyptus diversicolor* forest.

Our results may be attributed to different resources and site conditions on the high-severity burn sites (Bhatnagar et al., 2018), as well as a lack of EM hosts and different fungal successional stages discussed further below (Visser, 1995; Castillo et al., 2018). Lower sporocarp density and richness on high-severity burn plots do not necessarily indicate an absence of certain species, but may be attributed to inadequate conditions for sporocarp production. Sporocarp production is highly dependent on sufficient carbohydrate sources and moisture, and sporocarp production is sensitive to air and soil temperatures (Lange, 1978; Luoma et al., 1991; O’Dell et al., 1999; Smith and Read, 2008). Our sporocarp survey was conducted during a very wet year, and low numbers of fruiting sporocarps in severely burned areas could mean conditions are rarely good 13 years after high-severity fire. Also, some species of pyrophilous “fire-loving” fungi are known to produce sporocarps only in the first 1-2 years after fire, but sporocarp production decreases with time since fire (Petersen, 1970; Robinson et al., 2008; Claridge et al., 2009). The harsh site conditions in the high-severity burn sites, characterized by a lack of overstory canopy cover (exposure to intense sunlight, and very little wind protection), and
spatially variable vegetation and downed logs could have contributed to the lack of sporocarps compared to unburned and moderate-severity sites. Others have found that a change in the structure, chemical composition and spatial variability of hosts and woody debris alters the presence of some fungi (Zhou and Hyde, 2002; Dove and Keeton, 2015; Ficken and Wright, 2017; Bhatnagar et al., 2018). For example, Bhatnagar et al. (2018) found that fungi were profiled into different functional guilds after experimentally altering the quality of available litter resources, e.g., amount of lignin, cellulose, and nitrogen. Contrary to our hypothesis, saprotrophic species density and richness were similar among treatments, but interesting trends were observed that may be explained by a change in dominant substrates among treatments (Ficken and Wright, 2017; Bhatnagar et al., 2018).

4.2 Fungal community composition

Unburned sites (characterized by high tree densities and a thick forest floor) had more litter-decomposing saprotrophic sporocarps, and high-severity burn sites (characterized by stumps and downed logs) had more sporocarps capable of brown- and white-rot decomposition. Two of the most abundant saprotrophic species were *Vascellum curtisii*, a puffball found in all treatments and associated with litter and areas of disturbance (Terashima et al., 2004), and a *Psathyrella* sp., only found on the high-severity burn plots; some members of this genus are brown-rot fungi, associated with logs (Padamsee et al., 2008). A *Crassisporium* sp. was mostly found in the high-severity burned plots and some species in this genus have a preference for fruiting on burned ground (Matheny et al., 2015). Over the larger site level, *Gloeophyllum sepiarium* was an indicator species for the high-severity edge plots, and it is a brown-rot species shown to have a high heat-tolerance, and colonize burnt wood more than non-fire-associated
saprotrophic species (Carlsson et al., 2012; 2014). Other species unique to the high-severity edge plots include an *Agrocybe* sp., a *Cystoderma* sp., and *Entoloma iodiolens*, and evidence suggests they are white-rot species (Singer, 1977; Noordeloos, 1981; Berg, 1998). Saprotrophic species unique to the high-severity interior plots included *Armillaria ostoyae* (saprotrophic white-rot species and parasitic to some trees), *Cyathus striatus*, and a *Lycoperdon* sp. (both saprotrophic and associated with litter decomposition (Reinbothe, 1964; Osono et al., 2003; Garbelotto, 2004). *A. ostoyae* was the only tree pathogen we found on our plots, and others have found that logs or stumps can be habitats for potential fungal tree pathogens (Garbelotto, 2004; van der Wal et al., 2017). Finally, there were no live trees on the high-severity burn plots and they also had a much lower proportion of EM to saprotrophic fungi than unburned and moderate-severity plots (both comprised of mature, live trees). Similarly, Sun et al. (2015) found more EM species in mature forests, and a higher relative abundance of saprotrophic species in younger forests across a boreal forest fire chronosequence study. Distance from mature EM hosts or differences in EM successional species can both influence species composition (Visser 1995; Dickie and Reich, 2005; Peay et al., 2012; Dickie et al., 2013).

The difference in both EM sporocarp and root tip communities among treatments in our study may be partially explained by distance from mature EM hosts in the high-severity plots (Dickie and Reich, 2005; Buscardo et al., 2011; Peay et al., 2012). Numerous studies show EM fungi are sensitive to high-severity fires, similar to our findings (Treseder et al., 2004; Kipfer et al., 2011; Holden et al., 2013; Glassman et al., 2016; Reazin et al., 2016). High-severity fires in ponderosa pine forests often result in large patches of tree mortality (Dillon et al., 2011; Chambers et al., 2016) and evidence suggests that EM inoculum can become limited, and community composition can differ farther from live forest edges (Dickie and Reich, 2005; Peay
et al., 2012). For example, Peay et al. (2012) manipulated the isolation of *Pinus muricata* seedlings across a natural environment and found that seedling EM colonization, EM species richness and biomass were all highest at the forest edge, but continually decreased as seedlings became more isolated from EM sources. Additionally, Dickie and Reich (2005) found lower EM colonization of *Quercus macrocarpa* seedlings at greater distances from mature forest edges (>16 m), and did not find any *Russula* species past 12 m from the forest edge, yet *Cenococcum geophilum* was the most common species found at all distances. Although we did not find a difference in EM inoculum among treatments, members of the genus *Russula* were absent from the high-severity interior burn patches, *C. geophilum* was found colonizing ponderosa pine roots in all treatments, and the high-severity interior patches had a lower species pool and community dispersion compared to the moderate-severity burn plots.

In addition to distance from EM-hosts, the successional stage of fungi may help explain differences in EM communities in high-severity burn plots. There is evidence that early-, multi- (persisting throughout the lifetime of forest stands) and late-successional EM species persist at different stages of forest development (Visser, 1995; Nara et al., 2003). Some early-successional species (e.g. *Thelephora, Cenococcum*) typically colonize seedlings and their C demand is lower than older successional species (Visser, 1995; Agerer, 2001). We found that *C. geophilum* was most abundant on root tips from high-severity interior plots. Some late successional fungi (e.g. some *Russula* and *Amanita* species) are associated with developed soil organic layers and with older and larger trees that provide more carbon, and they do not germinate well in early-successional conditions, even if host roots are present (Visser, 1995; Nara et al., 2003; Dickie et al., 2013). Species from the genera *Amanita* and *Russula* were not found as sporocarps or on root tips in the high-severity interior burn plots from our study. Additionally, two *Russula* species
were indicator species for the unburned and moderate-severity sites. Also, *H. speciosus* was a common EM sporocarp in both moderate-severity and unburned plots, but missing from the high-severity burn plots, and this species is typically found in needle litter and associated with ponderosa pine (Cripps et al., 2016). Species found in later-successional stands can colonize multiple hosts with established common mycorrhizal networks (CMNs) (Nara, 2006; Beiler et al., 2010). Long distance EM exploration types can connect with other mycelia to form CMNs for nutrient transfer, yet they require more carbon than short distance types (Agerer, 2001; 2006, Tedersoo and Smith, 2013). Evidence suggests that short-distance EM exploration types dominate in dry-forest pine seedlings, because we found a much higher relative abundance of this type in all ponderosa pine seedlings compared to medium- or long-distance exploration types, similar to the findings of Patterson et al. (2019) for *Pinus edulis* seedlings.

Ectomycorrhizal heat-tolerance and spore longevity could also play a role in post-fire recovery and may help explain the low species pool and community dispersion found colonizing seedlings from the high-severity burn plots (Kipfer et al., 2010; Glassman et al., 2015, 2016). Recent research suggests that fire could be acting as a selective agent for certain EM species (Rincón and Pueyo, 2010; Kipfer et al., 2010; Rincón et al., 2014; Glassman et al., 2016). Common EM fungi found colonizing seedlings from the high-severity plots on our study were from genera (*Rhizopogon*, *Cenococcum* and *Wilcoxina*) that others have shown can survive high heat (Peay et al., 2009; Kipfer et al., 2010). Some EM species produce sexual spores (*Rhizopogon*) or asexual chlamydospores (*Wilcoxina*) and sclerotia (*Cenococcum*) that can stay dormant for some time, or are prolific producers and contribute to early successional EM-host establishment (Glassman et al., 2015). Glassman et al. (2016) found an increase in *Rhizopogon* sp. spore abundance after a high-severity fire and proposed that EM spore banks are similar to
plant seed banks because specific species can take advantage of open niche space after fires. EM spore banks dominated by *Rhizopogon, Wilcoxina, Cenococcum* and others could be important for recovery after large-scale disturbances (like wildfires), but represent a minor subset of the mature forest soil fungal community (Glassman et al., 2015). Seedling colonization in the high-severity burn plots, far from inoculum sources, may be dependent on EM species that survive the fire. Certain species of *Wilcoxina* and *Rhizopogon* are viable for at least 6 years and some may be viable for decades (Bruns et al., 2009; Nguyen et al., 2012).

We found similar EM colonization rates among treatments, but high-severity fires may limit the distribution of certain EM species and/or their ability to find a plant host. Ponderosa pine seedlings in the high-severity burn plots from our study were colonized by a larger overall proportion of Ascomycota than Basidiomycota, and the species pool was low farthest from forest edges, potentially limited by inoculum distribution. Recent work on aerial spore dispersal gives some insight on how far spores can travel. Both *Ascomycota* and *Basidiomycota* can produce spores that are transported by wind, but a high concentration of spores fall near fruiting mushrooms (Galante et al., 2011), and some EM fungi can be dispersal-limited within distances of < 1 km (Peay et al., 2012). In a *P. muricata* forest, aerial spore communities consisted mostly of saprotrophic species (EM spores only made up 6%) and the composition of *Basidiomycota* spores was partially explained by proximity to other vegetation, and number of spores decreased farther from forest edges (Peay and Bruns, 2014). Spores can also be distributed by rodents and larger mammals (Theimer and Gehring, 2007; Ashkannejhad and Horton, 2006). However, even if some EM spores are distributed long distances under optimal conditions, low concentrations of EM spores and timing of spore dormancy could limit successful seedling colonization (Bruns et al., 2009; Peay and Clemmensen, 2018).
Finally, although high-severity fire had lasting effects on fungal communities, moderate-severity fire had comparable fungal composition as unburned areas, consistent with previous studies (Jonsson et al., 1999; Korb et al., 2003; Curlevski et al., 2011; Southworth et al., 2011). These results suggest that EM fungi are mostly resilient after low-moderate severity fire. The natural fire regime for SW ponderosa pine forests is characterized by mostly frequent, low-moderate-severity fires (Covington and Moore, 1994; Fulé et al., 1997), and fungal communities have likely evolved within this fire-prone forest (Carlsson et al., 2012, 2014; Glassman et al., 2016). Moderate-severity plots had a different sporocarp and EM community composition, higher dispersion, and a large EM species pool colonizing ponderosa pine seedlings compared to the interior high-severity burn plots. These results partially support the intermediate disturbance hypothesis, which states that an intermediate level of disturbance may increase species diversity (Connell, 1978). Ectomycorrhizal diversity was also highest after low-moderate-severity burns compared to high-severity burns and unburned sites, 12-years post-fire in a P. sylvestris forest (Salo and Kouki, 2018). We also found that ponderosa pine seedling growth was similar among treatments and there were no significant relationships between EM colonization or richness and seedling growth. Other factors such as soil or light conditions may have influenced ponderosa pine seedling growth on our study sites (Pearson, 1950; Larson and Schubert, 1969; Flathers et al., 2016). Our findings stress that fungal communities may be resilient after moderate-severity fire, but large patches of high-severity fire may limit fungal recovery, even 13 years post-fire.

4.3 Conclusions

High-severity wildfires in ponderosa pine forest may become more common in the future due to a warmer, drier climate and accumulated fuels (Jolly et al., 2015; Abatzoglou and
Williams, 2016; Kitzberger et al., 2017), and our results suggest they could have long-term consequences for fungal communities. These long-term shifts in functional groups may influence ecosystem resiliency and forest productivity. In contrast, the moderate-severity burn sites from our study had fungal communities comparable to the unburned areas, which is promising for management that includes thinning and prescribed burning with the goal of reducing the potential for high-severity fires (Hart et al., 2018). Also, managers may want to retain some large branches and logs in high-severity burn patches because others have shown they encourage regeneration and beneficial microbial populations (Sánchez Meador and Moore, 2010; Castro et al., 2011). Similarly, we observed most post-fire pine regeneration and fruiting sporocarps near logs in the high-severity burn areas in our study. Finally, managers may want to prioritize the protection of surviving trees within or surrounding large burn patches to conserve future pine seed and EM sources (Peay et al., 2010; Stephens et al., 2018).

Our study gives important insights on both above- and below-ground fungal communities in large high-severity burn patches, including those > 200 m from surviving EM-host trees, but it also had some limitations. Limitations to our study include the exclusion of some early spring and belowground fruiting species from our assessment and limited temporal and spatial sampling to a single fire. More research is needed to fully understand the long-term effects of severe-fire on fungal communities and their role in post-fire recovery.

There are some gaps in our understanding of the effects of fire on fungal communities and the relationship between EM fungi and ponderosa pines. First, more studies are needed on how fire affects saprotrophic fungi because they are an understudied functional group in most forest ecosystems (reviewed in McMullan-Fisher et al., 2011). Future studies could include approaches other than sporocarp surveys to determine if saprotrophs are present after high-
severity fires (e.g. culturing, see Kurth et al., 2013). Second, more research is needed on whether a change in EM community composition matters for regenerating pine seedlings. Most evidence on the benefits of EM to ponderosa pine comes from early greenhouse experiments and planting seedlings with and without inoculum in its non-native range (Riffle and Tinus, 1982; Steinfeld et al., 2003; Barroetaveña et al., 2016), but there is still uncertainty about the relative benefits or costs of EM fungi for regenerating seedlings (Smith and Read 2008, Smith et al., 2009).

Ectomycorrhizal fungi differ in their morphology, propagation, exploration types, water and nutrient uptake, and carbon costs (Agerer, 2001, Pena and Polle, 2014). Additionally, pine genotype and drought-tolerant EM species may play a role in recovery in future climates (Gehring et al., 2017; Patterson et al., 2019). We need a better understanding of “fire-adapted” EM species and if they are functionally similar to other EM species.

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Table 1. EM species identified from regenerating ponderosa pine seedlings from the 2000 Pumpkin Fire, and their presence in each treatment (UB = unburned, M = moderate-severity, HE = high-severity edge, and HI = high-severity interior). Species were identified from the best BLAST match to ITS sequences (% is percentage similarity of query to published reference sequence, and score is an evaluation of query and reference sequence alignment based on their length and number of gaps); phylum: A = Ascomycete or B = Basidiomycete. Hyphal exploration type based on our observation and Agerer (2001, 2006).

<table>
<thead>
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<th>Accession number</th>
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<td><em>Tricholoma myomyces</em></td>
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<td><em>Tuber separans</em> isolate</td>
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*Species were also found fruiting in these treatments.*
Fig. 1. Photographs of study sites on the 2000 Pumpkin Fire. We established three 4-ha plots on each site, including unburned (560-1160 trees/ha), moderate-severity (120-490 trees/ha), high-severity edge (0 trees/ha) and high-severity interior (0 trees/ha) plots, for a total of twelve 4-ha plots. High-severity edge plots were established adjacent to forest edges, and high-severity interior plots were established at least 200 m from any live tree.
Fig. 2. Total and ectomycorrhizal sporocarp A) density, B) richness, and C) evenness were all lower in the high-severity burn plots compared to the unburned and moderate severity plots. No differences were found in saprotrophic sporocarp density or richness among treatments, but there was a trend for higher evenness in the high-severity plots. White boxes = unburned, gray boxes = moderate-severity, patterned boxes = high-severity edge, and black boxes = high-severity interior plots. Boxplots represent the variation between sites, and span the first to the third quartile. A center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.
Fig. 3. A redundancy analysis (RDA) and PERMANOVA results show high-severity edge and interior plots have a different sporocarp community composition compared to unburned and moderate-severity plots. The closer two symbols are together, the more similar the communities are. Both % overstory tree canopy cover and course woody debris (CWD) vectors (arrows) were significant, however they explained very little of the variance in community composition. White triangles = unburned, black triangles = moderate-severity, white circles = high-severity edge, and black circles = high-severity interior.
Fig. 4. No significant differences were found among different fire severities and unburned areas for ectomycorrhizal root tip A) colonization, B) richness, or C) evenness. Boxplots represent the variation between sites, and span the first to the third quartile. A center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.
Fig. 5. Mean relative abundance (proportion) of EM species colonizing regenerating ponderosa pine seedlings in unburned, moderate-severity, high-severity edge and high-severity interior plots. Some taxonomy groups are separated by color, e.g. Ascomycetes are shown in shades of blue, **Russulaceae** in shades of orange, **Inocybaceae** in shades of green and **Thelephorales** in yellow.

Unburned Moderate-severity High-severity edge High-severity interior

- **Amphiphiema sp.**
- **Culvulina rugosa**
- **Inocybe chelansis**
- **Lactarius sp.**
- **Rhizopogon talebrosus**
- **Russula sanguinea**
- **Tuber pressa**

- **Boletales sp.**
- **Geopora sp.**
- **Inocybe nitidiceps**
- **Peziza sp.**
- **Russula brevipes**
- **Sebactina sp.**
- **Tulasiella sp.**

- **Conococum geophilum**
- **Inocybe breviceramata**
- **Inocybe niveolata**
- **Piloderma sp.**
- **Russula integriformis**
- **Tarzeita sp.**
- **Tricholoma myomyces**
- **Wilcoxina sp.**
Fig. 6. A redundancy analysis (RDA) PERMANOVA results show a difference in ponderosa pine root tip EM community composition between the high-severity interior and moderate-severity plots. The closer two symbols are together, the more similar the communities are. White triangles = unburned, black triangles = moderate-severity, white circles = high-severity edge, and black circles = high-severity interior.

PERMANOVA: $F = 1.44$, $p = 0.04$
Appendix S1: Location of 4-ha study areas within different burn-severity and unburned areas of the 2000 Pumpkin Fire, Arizona, USA. Study areas are to scale, and UB = unburned, M = moderate-severity, HE = high-severity edge (near residual live trees), and HI = high-severity interior (at least 200 m from any live tree). Smaller quadrats for quantifying fungal communities were randomly selected within each of these study areas.
**Appendix S2:** Sporocarp species identified across different burn severities from the 2000 Pumpkin Fire, their ecology (S= saprotrophic, M = mycorrhizal, P = parasitic), presence in each treatment (UB = unburned, M = moderate-severity, HE = high-severity edge, and HI = high-severity interior), and phylum (A = Ascomycete or B = Basidiomycete). Species were either identified morphologically or based on the best BLAST match to ITS sequences (score is an evaluation of query and reference sequence alignment based on their length and number of gaps, % is percentage similarity of query to published reference sequence).

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<th>Sporocarp ID or best BLAST match</th>
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<td>S</td>
<td>HI</td>
<td>litter</td>
<td>B</td>
<td>99%</td>
<td>98%</td>
<td>GU234151.1</td>
</tr>
<tr>
<td><strong>Cystoderma</strong> sp.</td>
<td>S</td>
<td>HE</td>
<td>litter</td>
<td>B</td>
<td>99%</td>
<td>98%</td>
<td>GU234151.1</td>
</tr>
<tr>
<td><strong>Entoloma brunneosericeum</strong></td>
<td>S</td>
<td>HE, HI</td>
<td>logs; white-rot</td>
<td>B</td>
<td>99%</td>
<td>99%</td>
<td>KY820057.1</td>
</tr>
<tr>
<td><strong>Entoloma iodiolens</strong></td>
<td>S</td>
<td>HE</td>
<td>logs; white-rot</td>
<td>B</td>
<td>93%</td>
<td>99%</td>
<td>KY820057.1</td>
</tr>
<tr>
<td><strong>Gloeophyllum gloeophyllum sepiarium</strong></td>
<td>S</td>
<td>UB, HE</td>
<td>logs; white-rot</td>
<td>B</td>
<td>93%</td>
<td>99%</td>
<td>KY820057.1</td>
</tr>
<tr>
<td><strong>Gymnopilus sapineus</strong></td>
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<td>HE, HI</td>
<td>logs; brown-rot</td>
<td>B</td>
<td>99%</td>
<td>99%</td>
<td>KJ001429.1</td>
</tr>
<tr>
<td>Genus</td>
<td>Identification</td>
<td>Growth Form</td>
<td>Headquarters</td>
<td>Presence</td>
<td>Presence</td>
<td>Accession Number</td>
<td></td>
</tr>
<tr>
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<td>----------------</td>
<td>-------------</td>
<td>--------------</td>
<td>----------</td>
<td>----------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td>Gymnopilus spectabilis</td>
<td>S</td>
<td>HE logs; white-rot</td>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gyromitra perlata</td>
<td>S</td>
<td>HE, HI logs; white-rot</td>
<td>B</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Hygrophoropsis aurantiaca*</td>
<td>S</td>
<td>UB logs; brown-rot</td>
<td>B</td>
<td>100%</td>
<td>91%</td>
<td>KT875014.1</td>
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<tr>
<td>Leucopaxillus gentianeus</td>
<td>S</td>
<td>UB logs; white-rot</td>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lycoperdon sp.</td>
<td>S</td>
<td>HI litter</td>
<td>B</td>
<td>86%</td>
<td>95%</td>
<td>EU833664.1</td>
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<td>HI litter</td>
<td>B</td>
<td>99%</td>
<td>100%</td>
<td>FM999653.1</td>
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<tr>
<td>Lyophyllum fumosum</td>
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<td>UB litter</td>
<td>B</td>
<td>99%</td>
<td>98%</td>
<td>KT875066.1</td>
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<tr>
<td>Mycenoides sp.</td>
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<td>UB litter</td>
<td>B</td>
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<td>99%</td>
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<tr>
<td>Panaeolus sp.</td>
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<td>M, HI litter and dung</td>
<td>B</td>
<td>98%</td>
<td>99%</td>
<td>HG936444.1</td>
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<tr>
<td>Pluteus sp.*</td>
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<td>UB, HE, HI logs; white-rot</td>
<td>B</td>
<td>99%</td>
<td>95%</td>
<td>JX136310.1</td>
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<tr>
<td>Psathyrella sp.</td>
<td>S</td>
<td>HE, HI logs; brown-rot</td>
<td>B</td>
<td>99%</td>
<td>98%</td>
<td>KC992877.1</td>
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</tr>
<tr>
<td>Rhodocollybia sp.</td>
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<td>UB litter</td>
<td>B</td>
<td>99%</td>
<td>99%</td>
<td>GU328571.1</td>
<td></td>
</tr>
<tr>
<td>Trametes versicolor</td>
<td>S</td>
<td>UB, HI logs; white-rot</td>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tricholomopsis rutilans</td>
<td>S</td>
<td>M, HI logs; white-rot</td>
<td>B</td>
<td>99%</td>
<td>97%</td>
<td>HE649946.1</td>
<td></td>
</tr>
<tr>
<td>Vascellum curtisii</td>
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<td>UB, M, HE, HI litter</td>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeromphalina sp.</td>
<td>S</td>
<td>HE, HI logs; white-rot</td>
<td>B</td>
<td>99%</td>
<td>99%</td>
<td>AB711999.1</td>
<td></td>
</tr>
</tbody>
</table>

*Both NCBI and UNITE databases list the same species, but we are somewhat uncertain about species based % query/identity results.

†May prefer post-fire condition, associated with burnt plant matter.
Appendix S3: Mean relative abundance (proportion) of ascomycetes and basidiomycetes colonizing regenerating ponderosa pine seedlings in unburned, moderate-severity, high-severity edge and high-severity interior plots.
Appendix S4: Mean relative abundance (proportion) of short, medium and long distance hyphal exploration types colonizing regenerating ponderosa pine seedlings in unburned, moderate-severity, high-severity edge, and high-severity interior plots.
Appendix S5: Regenerating ponderosa pine seedling age was correlated with growth, measured by diameter at root collar (DCR) (A); Mean ponderosa pine seedling age and DCR were similar among treatments (white bars = mean seedling age; gray bars = mean seedling DRC) (B). There were no significant relationships between % EM colonization and seedling growth (C), or EM richness and seedling growth (D).
Chapter 5: Management implications

Suzanne Owen

The results I have presented in this dissertation contribute to our understanding of ponderosa pine regeneration and fungal recovery after large, high-severity wildfires, and provide important management implications. This research is especially imperative given the predictions of increased severity and length of fire seasons (Flannigan et al., 2013; Kitzberger et al., 2017). Wildfires with large patches of high-severity fire, along with warmer climates are forecasted to cause widespread conifer mortality and extensive shifts in plant species distributions in the coming decades (McDowell et al., 2016; Abatzoglou and Williams, 2016; Flatley and Fulé, 2016; Stevens-Rumann et al., 2018). This research helps to fill some knowledge gaps over a decade after large wildfires on: 1) the spatial patterns and interactions of naturally regeneration ponderosa pines; 2) the effect of fire-severity on ponderosa pine niche attributes and seedling growth; and 3) the effect of fire-severity on soil fungal communities. Management implications for each of these are discussed below.

Both spatial and non-spatial information on post-fire regeneration are vital for future management plans, and 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; North et al., 2019). By contrasting edge and interior high-severity burn patches, I found that 12+ years post-fire, ponderosa pine regeneration had similar heterogeneous spatial patterns and interactions with neighboring species, yet lower densities in the interior patches. More time could eventually lead to higher ponderosa pine densities, but given the predictions for warming
climates and increased fire severity (McDowell et al., 2016; Abatzoglou and Williams, 2016), this heterogeneous stage of forest development, that includes native sprouting species could be more resilient to drought and high-severity fires than dense pine stands. Additionally, future climate change is predicted to result in large-scale vegetation displacement and reorganization for some elevation zones in Arizona (Flatley and Fulé, 2016). Forest managers may need to adopt new objectives such as supporting forest types that could be more adapted to climate change and high-severity fires (including more drought-tolerant sprouting species). Post-wildfire non-forested patches or alternative vegetation types can also be areas of resilience to climate variability and resistance to subsequent fire within portions of the pine-dominant landscape (Coop et al., 2016; Parks et al., 2018). Other potential post-fire management strategies could include introducing fire (with seasonal variabilities), while pine seedlings are small if overly dense, or waiting for trees to reach greater heights to become more fire-resistant if regeneration is not overly dense (Bailey and Covington, 2002; Battaglia et al., 2009). If management goals are to restore ponderosa forests, planting pine seedlings in high-severity burn patches could be an option (Ouzts et al., 2015). However, plantings should reflect the goal of spatial heterogeneity instead of uniformity, and should not be overly dense so that they increase future fire severity (Thompson et al., 2007; North et al., 2019).

In addition to information on regeneration spatial patterns, my results provide managers with a better understanding of how fire severity can impact post-fire regeneration niche characteristics and regenerating ponderosa pine growth over time. My results indicate long-term changes to understory plant communities and fuel loads from severe fire, and highlight certain post-fire niche characteristics important for pine growth. However, my results also indicate that
naturally regenerating seedlings could be at risk from future fires, due to surrounding fuels. Managers may want to prioritize protecting natural regeneration that can establish and survive after high-severity fires, and residual trees surrounding large, high-severity patches. Local adaptations and future seed sources may be critical for their survival in future climates (Lucas-Borja et al., 2017; Gehring et al., 2017). When high-severity fires occur, managers could postpone fuel reduction treatments or prescribed fire around regenerating seedlings until they are tall enough to survive such treatments. Managers could also retain some large branches and logs in high-severity burn patches until seedlings are taller, because our results indicate they may be important for growth, and others have shown they encourage conifer regeneration and beneficial microbial populations (Sánchez Meador and Moore, 2010; Castro et al., 2011). Managers may want to protect surviving trees within or surrounding large burn patches to conserve future ponderosa pine seed (Kemp et al., 2016; Stephens et al., 2018). Lastly, my results suggest that planted pines may have improved growth near some coarse woody debris (CWD) or forb cover, but they may be at risk for future fires until they are tall enough to survive higher flame lengths (Bailey and Covington, 2002; Battaglia et al., 2009). My results increase our understanding of not only post-fire regenerating ponderosa pines, but also associated and surrounding fungal communities.

My results indicate long-term consequences to EM sporocarps and total EM inoculum pools from high-severity fire, which may influence ecosystem resiliency and forest productivity. In contrast, the moderate-severity burn sites had fungal communities comparable to the unburned areas, which is promising for management that includes thinning and prescribed burning with the goal of reducing the potential for high-severity fires (Hart et al., 2018). Similar to the
implications above, managers may want to retain some large branches and logs in high-severity burn patches because others have shown they encourage regeneration and beneficial microbial populations (Sánchez Meador and Moore, 2010; Castro et al., 2011). Also, managers may want to prioritize the protection of surviving trees within or surrounding large burn patches to conserve future ponderosa pine seed and EM sources (Peay et al., 2010; Stephens et al., 2018).

Other management options revolve around reducing the potential for large high severity fires by increasing thinning dense stands and using managed fire to lower tree densities more in line with historical forests (Fulé et al., 2012; Stephens et al., 2016; Huffman et al., 2017). Pre-wildfire thinning and prescribed fire treatments on the Rodeo-Chediski Fire reduced fire severity and significantly increased ponderosa pine regeneration, compared to untreated areas (Shive et al., 2013). Additionally, our results, along with previous studies indicate that fungal communities are resilient after moderate-severity fire (Korb et al., 2003; Curlevski et al., 2011; Southworth et al., 2011). Restoration efforts to reduce the risk of stand-replacing wildfires should include the goal of spatial heterogeneity to increase resilience to future climate and wildfire conditions, as recommended by Larson and Churchill (2012) and North et al. (2019), and long-term, permanent plots are essential for quantifying treatment success or ecosystem changes over time (Sánchez Meador and Moore, 2010).

**Literature Cited**


