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Historical dominance of low-severity fire in dry and wet mixed-conifer forest habitats of the endangered terrestrial Jemez Mountains salamander (*Plethodon neomexicanus*)

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ABSTRACT

Anthropogenic alteration of ecosystem processes confounds forest management and conservation of rare, declining species. Restoration of forest structure and fire hazard reduction are central goals of forest management policy in the western United States, but restoration priorities and treatments have become increasingly contentious. Numerous studies have documented changes in fire regimes, forest stand structure and species composition following a century of fire exclusion in dry, frequent-fire forests of the western U.S. (e.g., ponderosa pine and dry mixed-conifer). In contrast, wet mixed-conifer forests are thought to have historically burned infrequently with mixed- or high-severity fire—resulting in reduced impacts from fire exclusion and low restoration need—but data are limited. In this study we quantified the current forest habitat of the federally endangered, terrestrial Jemez Mountains salamander (*Plethodon neomexicanus*) and compared it to dendroecological reconstructions of historical habitat (e.g., stand structure and composition), and fire regime parameters along a gradient from upper ponderosa pine to wet mixed-conifer forests. We found that current fire-free intervals in Jemez Mountains salamander habitat (116–165 years) are significantly longer than historical intervals, even in wet mixed-conifer forests. Historical mean fire intervals ranged from 10 to 42 years along the forest gradient. Low-severity fires were historically dominant across all forest types (92 of 102 fires). Although some mixed- or high-severity fire historically occurred at 67% of the plots over the last four centuries, complete mortality within 1.0 ha plots was rare, and asynchronous within and among sites. Climate was an important driver of temporal variability in fire severity, such that mixed- and high-severity fires were associated with more extreme drought than low-severity fires. Tree density in dry conifer forests historically ranged from open (90 trees ha^{-1}) to moderately dense (400 trees ha^{-1}), but has doubled on average since fire exclusion. Infill of fire-sensitive tree species has contributed to the conversion of historically dry mixed-conifer to wet mixed-conifer forest. We conclude that low-severity fire, which has been absent for over a century, was a critical ecosystem process across the forest gradient in Jemez Mountains salamander habitat, and thus is an important element of ecosystem restoration, resilience, and rare species recovery.

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1. Introduction

Mixed-conifer forests of western North America are diverse and geographically variable, due to a wide range of bio-climatic conditions and disturbance regimes that span a large geographic distribution (Agee, 1993; Romme et al., 2009; Vankat, 2013). This variability offers great opportunities to study interactions between disturbance regimes, bio-climatic conditions, species composition, and forest structure (e.g., Merschel et al., 2014). However, the variability also poses challenges for management of these forests and rare, declining species that depend on them, particularly as we face climate change and increasing fire occurrence and severity (Westerling et al., 2006; Miller et al., 2009; Allen, 2015). In the southwestern United States (broadly defined as Arizona, New Mexico and adjacent areas), mixed-conifer forests are associated with bio-physical settings that are wetter and cooler than ponderosa pine forests, but drier and warmer than spruce-fir forests. General sub-classifications of a complex continuum of mixed-conifer forests include dry mixed-conifer (where ponderosa pine is present) and wet mixed-conifer (where ponderosa pine is rare or absent; Romme et al., 2009). More complex classifications that incorporate

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successional stage illustrate the importance of bio-climatic setting and disturbance regimes on current composition and structure (Merschel et al., 2014).

Wet mixed-conifer forests are commonly considered to have low or uncertain restoration need (Schoennagel and Nelson, 2011). Naturally long fire intervals, shade-tolerant tree species, and high tree densities that historically fueled high-severity fire support the hypothesis that many wet mixed-conifer and upper montane forests have been minimally affected by fire exclusion (Schoennagel et al., 2004; Hessburg et al., 2007). However, high variability and limited data across the large geographic range of mixed-conifer forests have resulted in an incomplete understanding, and uncertainty in restoration needs, over large areas of wet mixed-conifer or upper montane forests (Schoennagel and Nelson, 2011). In contrast, dry mixed-conifer forests in many regions of the West have increased in density and high-severity fire risk following anthropogenic fire exclusion, and consequently have high restoration needs (e.g., Fulé et al., 2009; Hagmann et al., 2013, 2014). These dry forests have been the focus of recent challenges to prevalent ecological history paradigms and restoration practices (e.g., Odion et al., 2014).

Fire was historically the primary disturbance in western mixed-conifer forests (Agee, 1993), although other disturbances, such as insect outbreaks, played an important role (Swetnam and Lynch, 1993). Historical fire regimes across mixed-conifer forests were variable, due to differing local physiographic, bio-climatic, and fuel conditions (Taylor and Skinner, 2003). In the southwestern U.S., there is a general trend of increasing fire interval and fire severity with increasing elevation and moisture, but patterns have been difficult to quantify and likely cannot be explained with simple linear models (e.g., Swetnam and Baisan, 1996; Brown et al., 2001; Margolis and Balmat, 2009; Tepley and Veblen, 2015). Historical fires in dry mixed-conifer forests of the southwestern U.S. were frequent (4–30 year intervals on average), and low to mixed-severity with relatively small (<100 ha) high-severity patch sizes (Dieterich, 1983; Swetnam and Baisan, 1996; Grissino-Mayer et al., 2004; Fulé et al., 2009; Margolis and Balmat, 2009; Tepley and Veblen, 2015). Similar fire regimes dominated by low-severity fires were historically present in dry mixed-conifer forests throughout western North America (Heyerdahl et al., 2001; Stephens et al., 2003; Taylor and Skinner, 2003; Scholl and Taylor, 2010), although this paradigm has been recently challenged using indirect evidence of historical fire severity from General Land Office surveys (see Williams and Baker, 2012 and response by Fulé et al., 2014).

Fire regimes in wet mixed-conifer forests are less studied, due in part to challenges posed by high-severity fire that leaves less direct evidence (i.e., lack of fire scars; Johnson and Gutsell, 1994), and dominant species that do not consistently record and preserve external fire scars (e.g., *Pseudotsuga menziesii* [Douglas-fir] and *Abies* spp.; Tepley and Veblen, 2015). Fire history methods that combine multiple lines of evidence (e.g., tree ages, tree-ring growth changes, traumatic resin ducts, and fire scars) are often necessary in these forests (Margolis et al., 2007; Heyerdahl et al., 2012; Tepley and Veblen, 2015). Limited data from the southwestern U.S. suggest that historical fire regimes in wet mixed-conifer/aspen forests had longer intervals than dry mixed-conifer with some mixed- or high-severity fire, but also exhibited a high degree of variability that included: multi-decadal or longer intervals (Abolt, 1997; Tepley and Veblen, 2015), shorter intervals when adjacent to grasslands or dry conifer forest (Touchan et al., 1996), mixed-severity fire (Tepley and Veblen, 2015), and large patches (>1000 ha) of high-severity fire at their upper ecotone with spruce-fir forests (Margolis et al., 2007). Fire histories from cool or wet mixed-conifer forests in other regions (e.g., including *Abies magnifica* [red fir] or *Picea engelmannii* [Engelmann spruce]) suggest similar variability, and an overall trend of longer intervals with mixed- and high-severity fire in some topographic settings (Taylor and Skinner, 1998; Beaty and Taylor, 2008; Marcoux et al., 2013). Given the variability of mixed-conifer ecosystems and related fire regimes (Korb et al., 2013), their importance as habitat for rare species (e.g., Mexican spotted owls [*Strix occidentalis lucida*]; U.S. Fish and Wildlife Service, 2011), and uncertainty around their restoration needs across the West, there are insufficient data describing historical fire regimes and associated stand structures, as well as drivers of variability among mixed-conifer ecosystems (Schoennagel and Nelson, 2011).

Fire-climate relationships are important for understanding the drivers of spatio-temporal variability in historical, modern, and future fire regimes (Swetnam and Betancourt, 1990; Westerling et al., 2006; Littell et al., 2009; Williams et al., 2015). Dry mixed-conifer forests historically burned under moderate to severe drought conditions sufficient to desiccate fuels, and depending on surface fuel structure or adjacent forest types, required wet conditions in prior years to increase fuels that sustained spreading fire (Touchan et al., 1996; Swetnam and Baisan, 1996; Margolis and Balmat, 2009; Korb et al., 2013). Wetter mixed-conifer/aspen or upper montane forests generally require drier conditions during the fire year to desiccate fuels, but do not require prior year moisture, due to generally higher productivity and fuel loads (Swetnam and Baisan, 1996; Schoennagel et al., 2011). Typically, fire-climate relationships are analyzed for a single forest type or fire regime (e.g., only low-severity fire regimes), but direct comparisons between forest types and fire regimes within a particular landscape or region are useful for understanding how they may respond differently to climate change. For example, comparisons between ponderosa pine and mixed-conifer forests in the Jemez Mountains (Touchan et al., 1996) and across the southwestern U.S. (Swetnam and Baisan, 1996) both revealed that fire occurrence in ponderosa pine was historically more dependent on prior wet years than in mixed-conifer forests. Additionally, climate has been identified as a driver of temporal variability in fire severity in recent decades (Dillon et al., 2011). This suggests that increasingly severe drought- and temperature-driven moisture stress alone may lead to increasingly severe fire (e.g., Williams et al., 2013). However, many forests and fire regimes have been highly altered by over a century of human land use (e.g., Fulé et al., 1997), and thus may not accurately reflect natural fire-climate dynamics. Centuries-long tree-ring reconstructions containing temporal variability in fire severity are rare, and offer unique opportunities to test for relationships between climate and temporal variability in fire severity.

The Jemez Mountains salamander (*Plethodon neomexicanus*; hereafter "salamander") is a rare terrestrial salamander endemic to the Jemez Mountains of New Mexico (Degenhardt et al., 1996). This lungless fossorial salamander has limited dispersal capabilities, spends most of its life in belowground void spaces, and requires moist surface conditions to access forest floor arthropods, its primary food source (U.S. Fish and Wildlife Service, 2013). Site-level declines in salamander population numbers have been associated with recent extreme droughts and large, severe fires, which prompted it to be listed as a federally endangered species (U.S. Fish and Wildlife Service, 2013). Critical habitat for the salamander is primarily mixed-conifer forests, ranging from dry mixed-conifer to wet mixed-conifer (U.S. Fish and Wildlife Service, 2013). The salamanders generally move very little horizontally, with an average home range of 8.0 m^2 (Ramotnik, 1988). This suggests that current salamander habitat in mixed-conifer forests, or nearby habitat, was likely inhabited by the salamander in the late 19th century prior to extensive human land use changes. Reduced fire frequency and increased forest density associated with anthropogenic fire exclusion in some dry mixed-conifer forests in the