Forest change over 155 years along biophysical gradients of forest composition, environment, and anthropogenic disturbance

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ABSTRACT

Understanding temporal forest change across spatial biophysical gradients is fundamental to managing dynamic forests across variable landscapes. This is especially true for identifying how biophysical variation mediates forest development through multi-century changes in climate and eras of forest manipulation by humans. We examined 155 years of forest change across a 13,000-ha mixed conifer landscape in the Spring Mountains, Nevada, USA. We reconstructed forest composition at 31 sites in 1855 (pre-Euro-American settlement, and near the end of the Little Ice Age), 1881 (logging era), 1900 (before establishment of government forest reserve), 1950 (mid-century fire exclusion), and 2009 (present forest). Differing from many other western conifer landscapes, density of large trees (>50 cm in diameter) increased through time. Aside from large trees and one measure of species compositional change, five other measures of forest change (e.g., percent difference in tree density) were spatially variable across the landscape and not well represented by 'average' change in the study area. Forest composition in 1855 minimally influenced the next 155 years of forest change. In contrast, the amount, timing, and direction of forest change were linked with topographic gradients. Forests on warm slope aspects incurred the least amount of change, which also was delayed in time, whereas forests on cooler aspects already appreciably changed by 1900. Warm aspects were the only ones to lose trees during the most recent 60-year period (1950–2009), with a decline in median tree density of 13%, compared to continued gains on moister sites. Management applications of this spatio-temporal variation include anchoring fuel treatments around areas of open, little-changed forest to increase effective size of treatments.

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1. Introduction

Knowledge of trajectories of forest change, and how they differ in different parts of the landscape, is fundamental to forest conservation and management. Trajectory to lose forest diversity or features valued by managers, for example, could spur management intervention to conserve desired features of forests (Strom and Fulé, 2007; Lydersen et al., 2013; Verstraeten et al., 2013). Recent examples include: trajectories to lose moderately shade tolerant tree species in deciduous forest, triggering group-selection cutting to create openings for tree recruitment (Klingsporn Poznanovic et al., 2013); loss of species-rich meadows in *Larix decidua* (European larch) forest following tree encroachment, identifying necessity of tree cutting or reintroducing fire if open forests are to be maintained (Garbarino et al., 2013); and reversing declining

understory plant diversity by conducting prescribed burning in mixed conifer forest (Webster and Halpern, 2010).

Feedbacks (via biotic interactions reinforcing trajectories), environmental filters, and disturbance history are three main factors influencing spatio-temporal variability in forest vegetation across landscapes and through time. Negative feedbacks can promote resistance to change, whereby species initially present on a site reinforce their own dominance (Halpern and Lutz, 2013). Examples of this include: tree species modifying the soil environment, through litter deposition, conducive to recruitment of their seedlings; localized seed dispersal or sprouting, enabling recruitment of new individuals among adults or following death of adults; and adaptation to fire, allowing one species to usurp growing space from another in fire-prone environments, to which both species are adapted in the absence of fire (Binkley and Giardina, 1998; Maloney, 2014). Environmental site conditions can filter spatio-temporal change by interacting with species traits including tolerances for temperature, moisture, and soil rooting depth (Lydersen and North, 2012). Disturbance history can affect forest trajectories

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via different eras of anthropogenic disturbance persistently influencing forest development (Östlund et al., 1997). For example, selectively cutting a certain tree species could remove the seed source, potentially shaping forest development for a long time. Studies that examine forest change both through time and across spatial biophysical gradients are rare, yet valuable for understanding interacting suites of factors related to forest development (e.g., Lydersen and North, 2012; Hagmann et al., 2013; Halpern and Lutz, 2013).

Semi-arid coniferous forests of *Pinus ponderosa* (ponderosa pine) and mixed conifers occupy over 23 million ha in western North America and offer unique opportunity for ecological insights to forest change on a management-priority landscape (Schoennagel and Nelson, 2011). Major anthropogenic influences on these forests during and after Euro-American settlement in the 1800s to the present have corresponded with particular time periods (e.g., Cocke et al., 2005; Kitchen, 2012; Kilpatrick et al., 2013). Tree cutting began in the late 1800s or early 1900s in most areas, and the most valuable tree species – *P. ponderosa* – was often selectively cut. Introduction of livestock, generally at higher stocking levels than today, also corresponded with the early logging era. The 1900s was a period of 'forest protection', including establishment of government-owned forest reserves and suppression of fire from lightning and human ignitions. In contemporary forests, management priorities include reducing hazardous fuels in now long-unburned forest, enhancing plant and wildlife habitat diversity, and recreation or balancing cutting and grazing at levels generally lower than historically (Covington et al., 1994; North et al., 2012; Abella and Springer, 2015).

A semi-arid climate preserving dead wood, combined with long life spans of tree species, has enabled detailed dendroecological reconstruction of past forest tree density and composition in several study areas across this forest type (Brown et al., 2008; Fulé et al., 2009; Taylor et al., 2014). Based on remeasurement of century-old forest inventory plots, the dendroecological reconstructions can be accurate to within 10% of actual tree density (Moore et al., 2004). Reconstruction estimates are not necessarily sensitive to wood decomposition rate, owing to wood persistence (Taylor et al., 2014). These dendroecological studies, combined with analysis of historical photos (e.g., Zier and Baker, 2006) and long-term timber inventory plots (e.g., Hagmann et al., 2013), have reported three main forest changes from the late 1800s (before pervasive Euro-American settlement) to the present. First, tree density has increased dramatically, mainly in small- to medium-sized stems (Fulé et al., 2009; Larson and Churchill, 2012; Lydersen et al., 2013). Second, forest composition has shifted from dominance by fire-tolerant (and generally shade intolerant) tree species, such as *P. ponderosa*, toward *Abies concolor* (white fir) and other species of lower fire tolerance (Minnich et al., 1995; Barbour et al., 2002; Abella et al., 2012). Third, density and proportion of large-diameter trees have declined (Brown et al., 2008; Lutz et al., 2009; Hagmann et al., 2013).

However, have these changes largely been uniform across landscapes, or have trajectory, magnitude, and timing of change varied across biophysical gradients of landscapes? Here, we examined 155 years of forest change across different anthropogenic disturbance eras and biophysical gradients of pre-Euro-American forest condition and environment. We asked: (1) What is the range of change in total tree density, large-tree density, and species composition across the landscape?, (2) Does pre-Euro-American settlement forest condition influence subsequent change?, (3) Are topography and soil related to forest change?, and (4) Have different eras of human disturbance, including logging and fire exclusion, displayed different trajectories of forest change? We further place results in a long-term climatic context, as the beginning of Euro-American manipulation of these forests corresponds with

near the end of the Little Ice Age (late 1800s), which followed the much warmer Medieval Warm Period (Williams et al., 2013).

2. Methods

2.1. Study area and land-use history

Our study area was the 5500-km² Spring Mountains, in the northern Mojave Desert in Nevada, USA (Fig. 1, Fig. S1). These mountains rise to a maximum elevation of 3632 (Charleston Peak) over surrounding desert shrubland 750 m in elevation (Niles and Leary, 2007). Major forest communities include: woodlands of *Pinus monophylla-Juniperus osteosperma* (single-leaf pinyon pine-Utah juniper) at low elevations (ca. 1800–2400 m), *P. ponderosa* and mixed conifer forest occupying middle elevations (ca. 2400–2800 m), and monotypic *Pinus longaeva* (Great Basin bristlecone pine) at the highest elevations exceeding 2800 m (Abella et al., 2012). Ground-layer vegetation is usually sparse and dominated by shrubs and perennial forbs (Abella and Springer, 2012). Soils, derived from limestone, dolomite, sandstone, and quartzite, represent several orders including Mollisols and Alfisols (Lato, 2006). Topography is highly dissected and includes canyons, steep hillslopes bisected by small drainages, and nose slopes and ridgetops. A weather station in *P. ponderosa* forest at an elevation of 2415 m has recorded the following 2009–2013 climatic means: 68 cm yr⁻¹ of precipitation, −2 °C January daily minimum, and 24 °C July daily maximum (Rainbow Canyon SNOTEL station, Natural Resources Conservation Service, National Water and Climate Center, Portland, Oregon).

Major historical events in land use have included logging, grazing, establishment of the area as a federal reserve, and initiation of a policy of fire exclusion (U.S. Forest Service, Spring Mountains National Recreation Area, Las Vegas, Nevada). European settlement beginning in the mid-1800s brought different land-use practices than those of primarily hunting and gathering of Native American groups. The first large Euro-American settlement occurred in Las Vegas in adjacent desert to the Spring Mountains in 1855. After that time, sawmills were established in several locations in the mountains to harvest primarily *P. ponderosa*, coupled with cutting of woodland trees for charcoal. The federal government established the Mt. Charleston Forest Preserve in 1906 (managed by the U.S. Forest Service), and along with it, the area was managed under a policy of fire suppression beginning in 1910. This was similar to most federal lands in the western USA (Falk et al., 2011). Ranching began in the mid-1800s, and some livestock were kept in the area until 1988 when grazing allotments were decommissioned.

We collected data within 13,000 ha of the eastern and northern Spring Mountains (encompassing Lee and Kyle Canyons) containing mid-elevation forest of *P. ponderosa* and mixed conifers (Fig. 1). These lands, administered by the U.S. Forest Service, are within Spring Mountains National Recreation Area of the Humboldt-Toiyabe National Forest.

2.2. Data collection

We sampled 31 sites across the landscape: 10 at Terrestrial Ecological Unit Inventory (TEUI) sites and 21 by generating random geographic coordinates with the criterion that sampling points be outside roadways and developed areas (e.g., campgrounds). The TEUI sites were stratified by soil parent material and were established by the U.S. Forest Service for purposes of soil classification and climate monitoring (Winthers et al., 2005). Sites spanned a representative gradient of topographic position and slope aspect (Fig. 1).