Forest Ecology and Management 411 (2018) 120–131

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Not just about the trees: Key role of mosaic-meadows in restoration of ponderosa pine ecosystems

Megan Shanahan Matonis[a,*], Dan Binkley[b]

[a] Colorado State Forest Service, Colorado State University, 5060 Campus Delivery, Fort Collins, CO 80523, USA
[b] School of Forestry, Northern Arizona University, 200 East Pine Knoll Drive, Flagstaff, AZ 86011, USA

A R T I C L E   I N F O

Keywords:
Ponderosa pine
Ecological restoration
Understory plants
Spatial patterns
Meadows

A B S T R A C T

Historical pre-settlement conditions in ponderosa pine ecosystems ranged from savannas (< 30% canopy cover) with contiguous grasslands and scattered tree groups, to forests with isolated mosaic-meadows surrounded by trees. We use the term mosaic-meadows for non-treed areas that weave around individual trees and tree groups, supporting diverse understory plant communities in ponderosa pine ecosystems. The long-term sustainability of ponderosa pine ecosystems may depend on mosaic-meadows that provide fine fuels and support frequent, low-severity fires. Increasing tree densities over the past century have eliminated mosaic-meadows and contiguous grasslands from many ponderosa pine landscapes. The link between restored ecosystem structure and function is often assumed but not empirically demonstrated, so we assessed the impact of mosaic-meadows (areas > 6 m from overstory trees) on understory vegetation in five recently thinned ponderosa pine stands and one long-undisturbed stand in Colorado. We also compared historical spatial patterns in mosaic-meadows to current conditions in ponderosa pine stands and determined whether thinning treatments are recreating historical conditions. Mosaic-meadows in ponderosa pine ecosystems declined substantially from a mean of 55% of stand area in 1860–1875 to 7% in 2010–2013 prior to tree thinning. The loss of mosaic-meadows has ecological consequences for the function of ponderosa pine ecosystems because spatial patterns of mosaic-meadows strongly influenced understory vegetation. At our sites, understory cover increased by 3%/m with distance from overstory trees, and understory richness increased from 6 species/m^2 within 1 m of overstory trees to 9 species/m^2 at 10 m away from overstory trees. Cover and richness of understory vegetation (especially native forbs) responded rapidly to creation of mosaic-meadows within 1 to 4 years after treatment. Thinning treatments at two stands brought the coverage of mosaic-meadows within the historical range of variation, but there was a noticeable lack of mosaic-meadows > 12 m from overstory trees at all treated stands. Restoration of the fundamental ecological characteristics of ponderosa pine ecosystems should intentionally include variably sized mosaic-meadows.

1. Introduction

Ponderosa pine (*Pinus ponderosa* var. *scopulorum*) ecosystems varied substantially in historical pre-settlement structure, ranging from savannas (< 30% tree cover; *sensu* McPherson, 1997) to woodlands (30–80% tree cover) and dense forests (> 80% tree cover). Ponderosa pine savannas were characterized by open, spatially contiguous grasslands with scattered tree groups. Such ecosystems were common in Arizona, New Mexico, and parts of Colorado prior to Euro-American settlement, especially on dry, south-facing slopes and in areas adjacent to grasslands where surface fires occurred frequently (every 1–25 years) (Veblen et al., 2000, Gartner et al., 2012, Reynolds et al., 2013, Brown et al., 2015). Ponderosa pine woodlands and forests occurred at higher elevation and in mesic locations, especially where fires were less frequent (> 25 year return intervals) and of mixed- to high-severity (Brown et al., 1999, Veblen et al., 2000, Baker, 2017). Woodlands and forests contained mosaic-meadows ranging from < 0.1 ha to 20 ha that supported grass, forbs, and shrubs (Kaufmann et al., 2000, Moore and Huffman, 2004, Zier and Baker, 2006). Mosaic-meadows in ponderosa pine woodlands and forests varied in shape from discrete patches to sinuous, interconnected areas weaving among tree groups (Lydersen et al., 2013, Clyatt et al., 2016).

We use the term “mosaic-meadows” to connote the variably sized and interconnected areas outside the crowns of trees. The simpler term “meadow” is often used to denote larger, stable vegetation communities, such as wet meadows, dry meadows, montane grasslands, or

* Corresponding author.
E-mail addresses: megan.matonis@colostate.edu (M.S. Matonis), dan.binkley@nau.edu (D. Binkley).

https://doi.org/10.1016/j.foreco.2018.01.019
Received 8 October 2017; Received in revised form 11 January 2018; Accepted 11 January 2018

fens. The distinct use of mosaic-meadows connotes areas > 6 m from overstory tree stems, which is the inter-tree distance commonly used for delineating tree groups and non-treed patches in ponderosa pine ecosystems (Sánchez Meador et al., 2011, Larson and Churchill, 2012, Lydersen et al., 2013). We intentionally avoid terms for mosaic-meadows that insinuate a tree-focused perspective, such as gaps, openings, non-stocked areas, under-stocked areas, and interspaces. These descriptors call to mind treeless voids, and perhaps imply a missed opportunity for increasing tree stocking. A positive focus on mosaic-meadows centers attention on the ecological importance of these features that dominated many ponderosa pine ecosystems. Some mosaic-meadows in ponderosa pine ecosystems were stable over time due to soil conditions or micro-topography, but many were transient features on the landscape created when fire, wind, or insects killed groups of trees (Kerns et al., 2001, Abella et al., 2013, Reynolds et al., 2013).

The juxtaposition of mosaic-meadows and scattered tree groups made environmental conditions highly variable in ponderosa pine ecosystems, with implications for understory vegetation, nutrient cycling, wildlife habitat, and fire behavior. Mosaic-meadows could support 5–6 times more understory cover or biomass than areas under pine canopies (Arnold, 1950, Laughlin et al., 2006, Moore et al., 2006, Abella and Springer, 2008) with 2.5–5 times greater understory richness (Abella and Springer, 2008, Laughlin et al., 2008). Mosaic-meadows had higher soil temperatures and soil moistures, and the decomposition of grass increased soil nitrogen relative to treed portions of ponderosa pine ecosystems (Hart et al., 2005). Gradients in resource conditions created environmental niches for a wide array of plant and animal species that thrived in grasslands, forests, and the ecotone between (Naumburg and Dewald, 1999, Kalies et al., 2012). Graminoids, forbs, and shrubs in mosaic-meadows provided fine fuels that carried frequent, low-severity surface fires in ponderosa pine ecosystems (Belsky and Blumenthal, 1997, Keith et al., 2010, Gartner et al., 2012). The relationship between understory fine fuels, forest density, and fire behavior is still apparent today; stands with higher understory production tend to experience lower-severity fires than adjacent, dense forests (Schoennagel et al., 2004).

Mosaic-meadows in ponderosa pine ecosystems have disappeared across large landscapes, and remaining understory vegetation is functionally different from historical conditions. Grazing and fire suppression during the 1900s, and possibly weather conditions favorable to tree regeneration, resulted in higher stand densities and fragmentation of mosaic-meadows (Belsky and Blumenthal, 1997, Kaufmann et al., 2000, Reynolds et al., 2013). Tree encroachment across grassland-forest ecotones was substantial in some areas, including mixed-conifer forests on the North Rim of the Grand Canyon National Park (Moore and Huffman, 2004) and ponderosa pine forests in the San Juan Mountains of southeastern Colorado (Zier and Baker, 2006). Mosaic-meadows in ponderosa pine and mixed-conifer forests have shrunk or disappeared as trees established between historical tree groups (Sánchez Meador et al., 2009). Mosaic-meadows completely disappeared from a dry-mixed conifer forest in California from 1929 to 2008 (Lydersen et al., 2013), and ponderosa pine ecosystems along the Front Range of Colorado were 3.7 times more likely to have trees than mosaic-meadows in 2013 relative to the mid-19th century (Dickinson, 2014). Increasing tree densities over the past century have caused substantial declines in understory richness and composition, especially for C_4 grasses (Laughlin et al., 2011).

Changes to ponderosa pine landscapes spurred considerable research on historical variability in tree density, basal area, and the size, density, and distribution of tree groups (reviewed by Larson and Churchill, 2012, Reynolds et al., 2013). The size and spatial patterns of mosaic-meadows have received less attention, even though mosaic-meadows are crucial for restoring key ecosystem structure and function in ponderosa pine ecosystems (Larson and Churchill, 2012, Lydersen et al., 2013). Restoration treatments generally focus on targets for density and spatial patterns of trees, without direct consideration of the extent and diversity of mosaic-meadows. Reduction in tree density alone does not guarantee the restoration of mosaic-meadows and diverse conditions for understory plants (Naumburg and Dewald, 1999, Churchill et al., 2013).

The link between restoring ecosystem structure and function is often assumed but not empirically demonstrated (Cortina et al., 2006), so we explored both the structural and functional role of mosaic-meadows in ponderosa pine ecosystems. We sampled understory vegetation across the gradient from trees to mosaic-meadows in six ponderosa pine stands—five that were recently harvested—and we compared meadow spatial patterns in these stands to historical pre-settlement conditions reconstructed for nearby sites. The purpose of our study was to determine (1) how spatial patterns in mosaic-meadows have changed from pre-settlement conditions (1860–1875) to the present, (2) the relationship between spatial patterns of mosaic-meadows and understory plant communities, and (3) how thinning treatments influence spatial patterns of mosaic-meadows. We studied changes in spatial patterns along with the impact of mosaic-meadows on understory vegetation to inform managers and researchers seeking to restore both structure and function in ponderosa pine ecosystems.

2. Methods

2.1. Study sites

Our research occurred in Colorado along the northern and central Front Range and the Uncompahgre Plateau in ecosystems where ponderosa pine constituted > 40% of overstory basal area (Fig. 1; Table 1). We selected our study sites to leverage existing stem maps of current conditions and reconstructed pre-settlement conditions. Five of our research sites were thinned between 2010 and 2013 with goals of reducing the potential for stand-replacing fire behavior and increasing structural complexity (Ziegler et al., 2017). The sixth site, located on the Manitou Experimental Forest in the central Front Range, had not been treated since heavy logging of large-diameter ponderosa pine between 1880 and 1886 (Boyden et al., 2005).

2.2. Northern Front Range

We sampled understory vegetation at a harvested stand in Heil Valley Ranch, which is managed by Boulder County Parks and Open Space, and we utilized data of reconstructed pre-settlement conditions from 14 nearby ponderosa pine sites (Brown et al., 2015). Ponderosa pine dominated the overstories, with trace occurrence of Douglas-fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (*Juniperus scopulorum*). Prior to Euro-American settlement, ponderosa pine savannas and woodlands were common in this area, and fire return intervals averaged about 15 to 25 years (Veblen and Donnegan, 2005, Brown et al., 2015). Infrequent, high severity fires also occurred across portions of this landscape (Veblen et al., 2000).

2.3. Central Front Range

We sampled understory vegetation at three treated stands (Long John, Messenger Gulch, and Phantom Creek) on the Pike National Forest and at one long-undisturbed, permanent plot on the Manitou Experimental Forest. We utilized stem maps of reconstructed pre-settlement conditions for six ponderosa pine sites on the Manitou Experimental Forest (M. Battaglia et al. [unpublished data]). The permanent plot on the Manitou Experimental Forest has not been harvested since the late 1880s, but we did not consider it a reference site for historical ponderosa pine conditions along the central Front Range. The stand has substantially higher tree density and basal area than historical pre-settlement conditions, and it has not experienced fire since 1846 (Boyden et al., 2005). We sampled this long-undisturbed stand to provide a perspective on the longevity of understory spatial