Ecological Functions of Spatial Pattern in Dry Forests
Implications for Forest Restoration

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Spatial variability in dry forest stands increases ecological resilience, function, and process

The spatial arrangement of trees within a stand is an important component of forest structure and function in forests dominated by dry pine species where the occurrence of low to moderate severity wildfire was historically frequent (Fig. 1). Spatial pattern (Box 1) both influences and is influenced by forest processes such as fire behavior, insect mortality, pathogen spread, stand development (e.g., regeneration and crown development), and forest hydrology. A clearer understanding of the role that pattern plays in maintaining processes and functions of dynamic forest ecosystems can further improve forest restoration outcomes and effectiveness.

Reference conditions have been reconstructed at numerous sites with active fire regimes across the western United States, and these reference conditions are often used to guide restoration treatments. However, greater understanding of the relationships between pattern, process, and function is needed to help managers make more informed decisions regarding tree spatial arrangement in restoration treatments.

In recent years, a large number of studies have investigated how spatial patterns of trees affect ecological processes and functions in dry forests. In this brief, we summarize our findings of a literature review evaluating these studies. Management that incorporates spatial variability and seeks to realign forest patterns with underlying biophysical conditions may increase stand resilience, ecosystem function, and the capacity of treated stands to adapt to future disturbances, drought, and climate change.

A CLEARER UNDERSTANDING OF ROLE THAT PATTERN PLAYS IN MAINTAINING PROCESSES AND FUNCTIONS OF DYNAMIC FOREST ECOSYSTEMS CAN FURTHER IMPROVE FOREST RESTORATION OUTCOMES AND EFFECTIVENESS.

Research Highlights

• Canopy density and species composition are primary drivers of ecological function and processes. Spatial pattern acts as a secondary driver. Reducing density, increasing mean tree size, and favoring early seral species in restoration treatments will increase resistance to high severity fire, insect, and drought.
• Treatments that result in uniform and variable stand spatial patterns confer similar resistance to fire, insects, and drought.
• Variable spatial patterns are generally more beneficial than uniform patterns for wildlife and understory vegetation abundance and diversity.
• Openings can retain snow longer and can limit spread of pathogens and parasites.
• More variable spatial patterns lead to more variable disturbance effects, which reinforce these patterns over time.
• Variable overstory spatial patterns also drive greater variability in tree regeneration and growth, reinforcing multi-aged stand structure over time.

{ Box 1 } TREE SPATIAL PATTERN DEFINITION

In this brief, we refer to spatial pattern as the spatial arrangement of the types, species, numbers and sizes of individual structural elements within a stand or patch (e.g., trees, logs, snags), as well as the amount and configuration of open areas unoccupied by trees. Tree spatial pattern is inherently linked to density (e.g., number and size of trees; trees acre⁻¹ or basal area in ft² acre⁻¹), and the horizontal and vertical arrangement of trees, which is constrained by density.

Pattern can vary across productivity gradients in a given forest type. Pattern at larger spatial scales (e.g. watersheds) is also an important driver of ecosystem processes and functions, but is beyond the scope of this brief.

Figure 1. Frequent fire forests in the western United States are often dominated by dry pine species like ponderosa pine (Pinus ponderosa), Jeffrey pine (Pinus jeffreyi), and sugar pine (Pinus lambertiana). Other fire-resistant species, such as Douglas-fir (Pseudotsuga menziesii) or western larch (Larix occidentalis), are also common. Mean fire return intervals in these forests historically averaged less than 35 years and fires were generally low severity with some moderate severity events. Note that these species can occur in moist, historically mixed-severity forest types as a minor component. Data adapted from: Wilson et al. 2013.
Elements of Spatial Pattern

Dry forests with active, frequent fire regimes are composed of an uneven-aged, shifting mosaic of irregularly spaced individual trees, tree clumps, and openings (Fig. 2). All sizes of trees are present, though large (e.g., >21” DBH), and old, fire-resistant species (e.g., ponderosa pine, Jeffery pine, sugar pine, western larch) dominate the low to moderate density canopy.

Early seral trees regenerate in small openings (0.25 to 2 acres), forming dense clumps that are thinned out over time by frequent fire, insects, and competitive mortality. Thinning of these clumps slows as trees mature and reach older age classes. Bark beetles, pathogens, and torching events during wildfires cause partial or complete mortality of clumps of trees, creating new openings for regeneration. Isolated individual trees originate over time as a result of these disturbance processes or occasionally from isolated regeneration events.

Within stands, disturbances cause some elements of spatial pattern to shift over time and space, while other elements, such as openings, may persist more permanently as a function of edaphic (e.g., soil) conditions or below-ground interactions.

A clear envelope of stand density and spatial pattern emerges from dry forest reference sites (Fig. 3, Fig. 4). Widely spaced individual trees, clumps, regeneration patches, and openings often occur in a range of proportions, sizes, and spatial configurations (Fig. 3). As tree density increases, the range of pattern increases and clumping becomes more common (Fig. 4).

Figure 2. Dry forest spatial patterns consist of multiple elements including widely spaced individual trees, overstory tree clumps that can range in size from 2-4 trees to 15 or more trees, denser patches of mid- or overstory trees from 0.25 to 1 acre in size, regeneration patches of seedlings and saplings, and linear or sinuous openings from 0.25 to 2 acres in size. Other patch types, such as rock outcrops, riparian areas, and aspen stands provide important habitat variety.

Figure 3. Examples of different spatial configurations of overstory trees found in dry forest reconstruction sites. Spatial configurations can vary between (A) low density with low clumping (TPA >6” DBH: 15-30 TPA), (B) moderate density (30-50 TPA) with moderate clumping, to (C) higher density (50-80 TPA) with high clumping (Churchill et al. 2017).
Spatial Pattern Processes & Functions

Spatial variability in dry forest stands is an important component of forest structure that governs different ecological processes and functions from the micro- to meso-scale (e.g., 0.1 to 10+ acres). Table 1 lists seven key ecological parameters affected by the spatial patterning of trees in dry forests, and the associated implications that restoring the density and/or spatial arrangement might have on those processes and functions.

<table>
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| FIRE BEHAVIOR          | Density   | • Canopy density and connectivity, as well as surface and ladder fuel loading, are the primary drivers of crown fire potential.  
|                        | Spatial Arrangement | • Variable tree patterns result in patchy surface fuel loadings, in turn creating more variable fire behavior and burn patterns. Similar reductions in crown fire potential occur within variable density and uniform treatments.  
• Localized torching may occur within clumps that have ladder fuels.  
• Openings can act as mini fire breaks to stop crown fire, but also act to increase surface fire intensity due to higher wind speeds and increased understory fuels levels. | Miller and Urban 2000, Knapp et al. 2006, Symons et al. 2008, Bigelow & North 2012, Linn et al. 2013, Kennedy & Johnson 2014, Lydersen et al. 2015, Ziegler et al. 2017, Parsons et al. 2017 |
| DROUGHT RESISTANCE     | Density   | • Significant reductions in overstory tree density (> 20% BA) can increase site water availability over the short-term.  
• Thinning increases water usage by residual trees. | Skov et al. 2004, Troendle et al. 2010 |
| INSECTS & PATHOGENS    | Density   | • Lower basal area and stem densities increase tree vigor, increase resilience to bark beetle attacks, and reduce susceptibility to pathogen spread.  
• Trees in thinned treatments have greater foliar nitrogen content, needle toughness, and basal area increment, likely due to increased moisture availability. | Larsson et al. 1983, Schmid and Mata 1992, Negron and Pop 2004, Fettig et al. 2007, Wallin et al. 2008, Negron et al. 2017 |
|                        | Spatial Arrangement | • Root diseases spread through contact with infected roots, and may remain isolated and have limited spread where spatial patterns contain clumps and openings.  
• Mistletoe seed dispersal ranges from 3-52 ft (1-16m), with most seeds intercepted by nearby (6-12 ft) trees. Spread may be limited where openings are present.  
• Variable and uniform treatments have similar resistance to insect-related mortality, and both treatment types have lower mortality rates than untreated stands. | Williams et al. 1986, Ferguson et al. 2003, Geils et al. 2002, Conklin & Geils 2008, Fettig & McKelvey 2014 |
| SNOW RETENTION         | Spatial Arrangement | • Compared to uniform treatments, variable density treatments increase duration of snow cover as well as snow water equivalent. Canopy openings shaded by surrounding trees retain snow longer in the melt season.  
• The area directly under clumps has reduced snow accumulation because radiation from tree boles melts snow and canopy cover intercepts snowfall. | Kittredge 1953, Lundquist et al. 2013, Schneider et al. 2015, Picard 2015, Stevens 2017 |

Table 1. Modifying spatial pattern and tree density through restoration treatments can influence dry forest processes and functions.
Management Implications

Treatments designed to restore a range of processes and functions in dry forests are most likely to succeed when they 1) reduce stand density, 2) retain large trees and drought- and fire-tolerant species, and 3) create variable tree patterns. Reducing stand density and managing for drought- and fire-tolerant species composition promote resistance and resilience to crown fires, insects, and drought. Restoring spatial heterogeneity has the added potential to create higher quality wildlife habitat, increase understory plant diversity and abundance, inhibit parasite and pathogen spread, and increase snow retention. Importantly, variable tree patterns and the ecosystem functions they promote do not appear to sacrifice resistance to crown fire, insects, or drought, and may increase some aspects of resilience.

Managers can use the natural range of variability found in reference sites (Fig. 4) to develop desired conditions and treatments that are aligned with the current and future biophysical environment and meet multiple management objectives (Fig. 5). For example, managers may choose treatment prescriptions aimed at creating low, moderate, or high density and clumping pattern (Fig. 3) for a stand based on desired short and long-term functional objectives (Table 1). How patterns within individual stands scale across a project area to create landscape level conditions will have a major effect on functional outcomes.

Figure 4. Dry forest historical spatial pattern reference plots (green dots) display a clear envelope (black outline) of pattern with a general increase in clumping as tree density increases. This envelope gives managers treatment options to maintain their desired functions in a dry forest stands. Note: Figure includes a subset of reference plots primarily from Pacific Northwest dry forests. © Derek Churchill

Table 1 (continued). Modifying spatial pattern and tree density through restoration treatments can influence dry forest processes and functions.

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| TREE REGENERATION & GROWTH | Spatial Arrangement | • Variable overstory spatial patterns result in more variable regeneration patterns and growth.  
• Regeneration generally establishes in groups or patches after disturbances. Soil disturbance, moisture, and competition from understory vegetation appear to the main factors driving regeneration.  
• Shade-tolerant species regenerate better in thinned areas or clumps while shade-intolerant species regenerate best in small to large openings.  
| WILDLIFE HABITAT | Spatial Arrangement | • Ungulates prefer treated areas (e.g., thinned, burned) with abundant graminoid or shrub forage.  
• Small dense patches create visual barriers and hiding cover from humans along roads.  
• Habitat heterogeneity is extremely important for small mammals. Herbaceous plants provide foraging habitat and small (0.5-1 acre) dense patches of undergrowth and coarse woody debris provide refuge.  
• Different bird species have specific structural needs for nesting and roosting habitat. Spatial variability also creates diverse habitat for prey when foraging.  
• Northern Spotted owl (NSO) and Northern Goshawk (NG) nest and roost in moderate to large clumps and forage in open (NG) to closed canopy stands (NSO) and in small (NSO) to large (NG) openings.  
• White-headed woodpeckers prefer isolated or small clumps of large, old trees or snags for nesting and dense clumps of small diameter trees for foraging.  
| UNDERSTORY DIVERSITY | Spatial Arrangement | • Variable overstory patterns, such as canopy openings, increase fine scale heterogeneity in light, water, and nutrients which subsequently affect the diversity and abundance of understory species.  
• Openings >27 ft (9 m) from the nearest overstory tree can result in increases in native understory plant cover and species richness.  


References


Schneider, E., A. J. Larson, and K. Jencso. 2015. Small scale variability in snow accumulation and ablation under a heterogeneous mixed-conifer canopy. Oral Presentation at the University of Montana Graduate Students Research Conference.


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