



Review

Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments

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ABSTRACT

Restoring characteristic fire regimes and forest structures are central objectives of many restoration and fuel reduction projects. Within-stand spatial pattern is a fundamental attribute of forest structure and influences many ecological processes and ecosystem functions. In this review we synthesize the available spatial reference information for fire-frequent pine and mixed-conifer forests in western North America; interpret this information in the context of restoration and fuel reduction treatment design; and identify areas for future research, including recommended approaches for quantifying within-stand tree spatial patterns.

We identified 50 studies of tree spatial patterns in fire-frequent pine and mixed conifer forests, 25 of which documented spatial reference conditions. The characteristic structure of fire-frequent forests is a mosaic of three elements: openings, single trees, and clumps of trees with adjacent or interlocking crowns. This mosaic structure typically manifests at scales <0.4 ha, but sometimes extends to scales as large as 4 ha, particularly on sites with fire regimes that include both low- and moderate-severity fires. We documented preferential use of global pattern analysis techniques (90% of analyses) relative to local analysis techniques (10% of analyses). Ripley's *K* statistic, an example of global spatial pattern analysis, was the most frequently used analytic technique (38% of analyses). These findings are important because global pattern analysis does not explicitly quantify spatial heterogeneity within a pattern, the very thing spatial reference studies seek to characterize and one of the core structural attributes treatments aim to restore.

Based on these findings, we encourage managers to consciously adopt a view of forest structure that accommodates spatial heterogeneity within forest stands, and to use this conceptualization of forest structure to guide prescription development. Restoration prescriptions and marking guidelines that explicitly incorporate within-stand spatial heterogeneity—such as by specifying the numbers and sizes of openings and tree clumps, and the number of widely-spaced single trees to retain per unit area—will improve the likelihood of restoring characteristic forest structures and the ecological processes such structures support. We infer that the near-exclusive use of global pattern analysis has limited the quantity and usability of spatial reference information available to managers, has also likely limited the development and testing of novel ecological hypotheses about pattern-generating mechanisms. Consequently, we recommend that forest scientists change how they quantify tree spatial patterns by complimenting the traditional global analysis methods with local pattern analysis techniques, which quantify spatial heterogeneity within a study area.

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1. Introduction

Ongoing restoration of fire-frequent pine and mixed-conifer forests throughout the western United States is one of the most extensive and expensive forest restoration programs ever undertaken. Hundreds of thousands of hectares of public lands are being treated with prescribed fire and mechanical thinning each year at significant cost; 1.1 million ha of public forestlands were treated in the western United States in the period 2004–2008 alone (Schoennagel and Nelson, 2010). These programs are being undertaken to increase the resilience of forests that have been impacted by combination of past timber harvest, livestock grazing and fire suppression. These land uses altered the structure and composition of fire-frequent (i.e., with fire return intervals generally <35 years) pine and mixed-conifer forests—referred to hereafter as fire-frequent forests—leading to impaired ecosystem function and increased risk of high-severity wildfire (Covington and Moore, 1994; Hessburg et al., 2005). Rising fire suppression costs and potential threats to ecological and human values posed by large and severe wildfires have created a sense of urgency (Spies et al., 2006) and provided the motivation for federal legislation to facilitate fuel reduction and forest restoration activities, including the Healthy Forest Restoration Act of 2003 and Title IV of the Omnibus Public Land Management Act of 2009, which established the Collaborative Forest Landscape Restoration Program.

Restoring characteristic fire regimes and forest structures are central objectives of most restoration and fuel reduction projects in fire-frequent forests throughout western North America (e.g., Gaines et al., 2010; Roccaforte et al., 2010). The scientific basis for manipulating forest structure in fire-frequent forests is the documented shift away from historic (pre-Euro-American settlement) forest structure and composition, which has increased susceptibility

to high-severity fire (Allen et al., 2002; Agee and Skinner, 2005; Peterson et al., 2005; Noss et al., 2006). Pre-settlement forests embodied structural and compositional conditions resistant and resilient to fire (Fulé, 2008; Stephens et al., 2008); these forests persisted through numerous past disturbance events and through multiple centuries of climatic fluctuation (Agee, 1993; Allen et al., 2002). Forests with continuing frequent fire regimes and spatially heterogeneous structures exhibit this resilience to modern fires as well (Taylor, 2010), even in the face of severe drought (Stephens et al., 2008). The use of historic reference conditions to set restoration targets is sometimes debated because of climate change and increasing human influences in the landscape (Franklin and Agee, 2003; Millar et al., 2007; Reinhardt et al., 2008). However, both historic and contemporary forests with functionally intact fire regimes are characterized by more resilient forest structures than those associated with long histories of fire exclusion. Restoring characteristic forest structure, as opposed to the alternatives of (1) leaving fire-frequent forests in their current uncharacteristic fire-suppressed conditions or (2) creating fire-resistant but unnatural stand structures (such as uniform plantation-like areas of widely spaced trees) reduces short-term risk of loss to uncharacteristic wildfire while simultaneously preserving options for future generations. Such a strategy provides a foundation on which to implement climate adaptation strategies as new understanding accumulates (Fulé, 2008; Keane et al., 2009; Diggins et al., 2010; Spies et al., 2010).

Forest structure has two principal dimensions (Franklin et al., 2002): the types, number and sizes of individual structural elements (e.g., trees, logs, snags); and the arrangement of these structural elements in space. There is broad scientific consensus that restoration treatments in fire-frequent forests should address both spatial and non-spatial aspects of forest structure (e.g., Harrod et al., 1999; Moore et al., 1999; Allen et al., 2002; Taylor, 2004;

Graham and Jain, 2005; Stephens et al., 2008; North et al., 2009; Sánchez Meador et al., 2009). Despite this consensus many current fuel reduction and forest restoration prescriptions do not incorporate spatial goals but, rather, are directed toward achieving uniform, stand-level tree spacing, crown bulk density and basal area targets (e.g., Johnson, 2008; Powell, 2010; Evans et al., 2011). The spatially homogenous structural conditions that result from such prescriptions appear to fall outside of the range of known reference conditions (North et al., 2007, 2009; Stephens et al., 2008) and may fail to restore the full array of desired ecological functions, including habitat for biological diversity (Franklin and Van Pelt, 2004).

1.1. Scope and objectives

We examine spatial aspects of forest structure in fire-frequent pine and mixed-conifer forests of the western United States, including mechanisms of pattern formation and implications for the design of silvicultural treatments. Fuel reduction and restoration treatments have a clear ecological justification where forests historically experienced frequent, low- and moderate-severity fires (Schoennagel et al., 2004; Kaufmann et al., 2007; Reinhardt et al., 2008; Evans et al., 2011). We consider several fire-frequent forest types found in western North America (Kaufmann et al., 2007), and emphasize stands containing one or more of the recognized fire-tolerant conifer species—ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), western larch (*Larix occidentalis*), incense-cedar (*Calocedrus decurrens*), giant sequoia (*Sequoiadendron giganteum*), or interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Some western larch and Douglas-fir forests did experience a regime of primarily moderate- and high-severity fire events (e.g., Barrett et al., 1991; Baker, 2009); such forests are beyond the scope of this review.

Restoration and fuel reduction treatments alter tree patterns within forest stands (North et al., 2007). Changes in spatial pattern are especially apparent at tree neighborhood scale (*sensu* Frelich

et al., 1998), intertree distances of up to about 20 m, and to the within-stand patch mosaic (Fig. 1), which typically manifests at scales less than about 4 ha (Agee, 1998; Kaufmann et al., 2007). Thus, we emphasize spatial patterns of live trees at these scales and focus largely, although not exclusively, on studies presenting data for spatial locations of individual trees (i.e., stem map data). A comprehensive strategy for restoration of fire-frequent forest landscapes also requires attention to patterns at spatial scales larger than the forest stand or treatment unit (Hessburg et al., 2005; Ager et al., 2010), but a review of patterns at such scales is beyond scope of this paper.

We address three objectives: (1) Review and synthesis of the available spatial reference information for fire-frequent pine and mixed-conifer forests, including mechanisms of spatial pattern formation; (2) Interpretation of the available spatial reference information in the context of restoration treatment design and identification of current barriers to implementation; and (3) Identification of strategies to reduce barriers to implementation, including alternative spatial analysis techniques and priority areas for future research based on the literature review.

1.2. Relationship of tree spatial patterns to ecological processes

Tree spatial patterns exemplify the reciprocal dialogue between pattern and process in ecological systems. This coupling of pattern and process (*sensu* Turner, 1989) underpins the theoretical basis for incorporating spatial information in the design of forest restoration treatments.

Tree patterns at multiple scales are shaped by species interactions such as competition (Moeur, 1997) and facilitation (Baumeister and Callaway, 2006) and demographic processes, such as recruitment and mortality (Kenkel, 1988; Taylor, 2010). In turn, tree spatial patterns influence subsequent forest dynamics through neighborhood effects (Frelich et al., 1998): tree establishment (Boyden et al., 2005; Sánchez Meador et al., 2009), growth (Biondi et al., 1994;

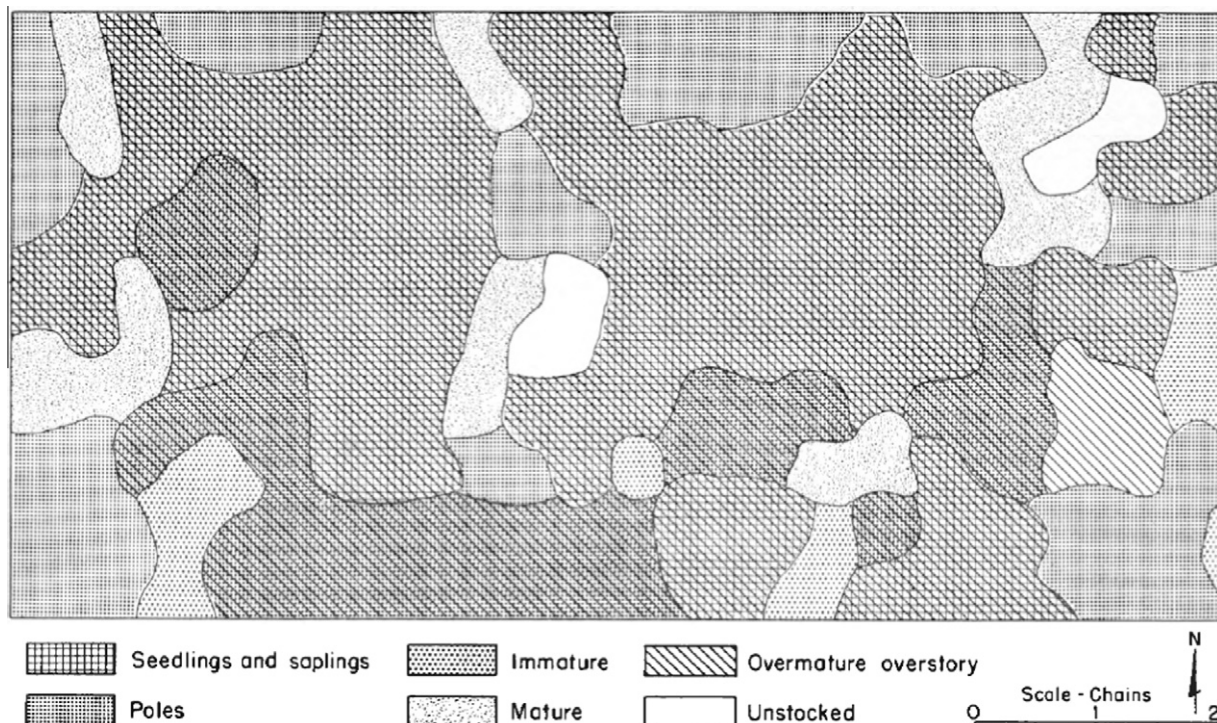


Fig. 1. The mosaic structure of an 8.1 ha (20 ac) area within an old-growth ponderosa pine forest at Blacks Mountain Experimental Forest, California, USA. Individual patches as small as 0.1 ha were mapped in this example. Note the unstocked openings within the forest matrix. 1 chain equals 20.12 meters. Map reproduced from Hallin (1959).

Van Pelt and Franklin, 1999; Palik et al., 2003), crown development (Stiell, 1978, 1982) and mortality (Olsen et al., 1996; Das et al., 2008) vary within forest stands in response to spatially heterogeneous tree patterns.

Many forest ecosystem functions and processes are sensitive to tree patterns. Tree spatial patterns induce variation in physical phenomena including the canopy light environment (Battaglia et al., 2002; North et al., 2004; Sprugel et al., 2009), snow accumulation and melt (Woods et al., 2006), soil chemistry (Bruckner et al., 1999; Kearns et al., 2003) and wind exposure (Scott and Mitchell, 2005; Pimont et al., 2011). Similarly, biological phenomena such as wildlife habitat selection and use (Long and Smith, 2000; Dodd et al., 2006), understory plant abundance, composition, and diversity (Turner and Franz, 1986; Laughlin et al., 2006), litter deposition (Hirabuki, 1991), and soil microbial communities (Turner and Franz, 1985) respond to variation in tree spatial patterns within forest stands. Tree spatial patterns also influence the spread of parasites (Shaw et al., 2005) and insects (Olsen et al., 1996) that disperse from tree to tree.

Next generation fire models capable of small scale (1–10 m) spatially explicit representations of fuels, winds and fire behavior reveal effects of heterogeneous tree patterns—canopy openings and tree clumps—on fire behavior (Parsons, 2007; Pimont et al., 2011). Relatively few empirical studies have examined the effects of spatially heterogeneous tree patterns and fuel loads on fire behavior, but recent studies indicate that tree spatial patterns influence the complex feedbacks among fine fuels (understory vegetation and tree litter) and fire behavior, which in turn influence future vegetation growth and fuel accumulation (Thaxton and Platt, 2006; Hiers et al., 2009; Mitchell et al., 2009).

1.3. Definition and application of spatial reference conditions

Spatial reference conditions are defined here as tree spatial patterns in ecosystems where pattern – process linkages are intact. For the purposes of fire-frequent forests in western North America this amounts to tree spatial patterns in forests with intact or minimally altered fire regimes; such sites are often considered old-growth forests (Kaufmann et al., 2007). Four types of studies were included when compiling information on spatial reference conditions for this review. Reconstructions based on dendrochronological methods (e.g., Arno et al., 1995) are the most common source of reference information; we embraced a liberal view of reconstruction studies and included relatively low-precision reconstructions based on tree size-age relationships (e.g., Youngblood et al., 2004), studies that only considered live trees that established prior to the estimated date of effective local fire suppression (e.g., Mast and Veblen, 1999), and reconnaissance studies (e.g., Binkley et al., 2008). Historical data sets from the early twentieth century are second source of reference condition data (e.g., Sánchez Meador and Moore, 2010). While historic data sets usually incorporate 20–40 years of post-settlement forest modifications (e.g., fire suppression and livestock grazing), they still are assumed to be representative of the functional pre-settlement overstory conditions. Other sources of reference condition data are relict forests (*sensu* Stephens and Fulé, 2005) with intact fire regimes, and sites where fire regimes and forest structure have been restored (e.g., Taylor, 2010). To capture the complete spectrum of available information on tree spatial patterns in fire-frequent forests, we also examined data and analyses of contemporary tree spatial patterns at sites with altered fire regimes and past timber harvest or other land uses.

Interpretation of reference conditions provides guidance on specific management actions to include, as well as avoid, in restoration treatments (Larson and Churchill 2008). Tree spatial patterns are dynamic through time: the objective is not to precisely recreate

and maintain historic tree spatial patterns with restoration treatments. Rather, spatial reference conditions are used to inform management actions that directly manipulate forest structure such that spatiotemporal feedbacks between pattern and process can be restored and maintained (Hessburg et al., 1999; Fry and Stephens, 2010). Reference conditions also provide benchmarks for evaluating the outcomes of restoration treatments (Moore et al., 1999; Allen et al., 2002; North et al., 2007; Larson and Churchill, 2008), as well as a framework for interpreting and applying lessons learned from experiments (e.g., Wayman and North, 2007; Schwilk et al., 2009) and models (e.g., Stephens et al., 2009; Johnson et al., 2011), which by definition only approximate the structural, compositional and functional diversity of natural forests.

1.4. Spatial pattern concepts and definitions

Here we introduce some spatial pattern concepts in order to establish a vocabulary for the review and synthesis that follow. We emphasize terms and concepts relevant to point pattern analysis techniques—the primary methods for analyzing stem map data. We examine the two common usages of the concept of spatial scale; global versus local spatial pattern analysis; pattern type and strength; and pattern elements. This summary is necessarily brief, and specific to our objectives; the review by Perry et al. (2006) provides an accessible introduction to spatial point pattern concepts and the texts by Cressie (1993), Diggle (2003), and Fortin and Dale (2005) contain more detailed information.

Two usages of spatial scale are commonly encountered in the point pattern analysis literature; both are closely tied to the methods with which spatial data are collected and analyzed. The one-dimensional or linear definition of scale is used with methods that characterize the spatial relationships between mapped points, such as distance-based spatial point pattern statistics (e.g., Ripley's K), spatial correlation analysis and geostatistics. In the one-dimensional sense scale refers to the interpoint (or lag) distance, d , typically reported in meters in forest ecology and management studies. Studies that delineate and measure patches in the field (e.g., Stephens and Fry, 2005), or that use quadrat-based point pattern analysis methods such as Morisita's I or the Greig-Smith continuous quadrat technique, use a two-dimensional or area-based definition of spatial scale, which is usually expressed in square meters or hectares. The area-based definition of scale is equivalent to the landscape ecology concept of spatial grain (Wiens, 1989).

We use both the linear and area-based definitions of spatial scale throughout this review, reflecting methods used the original studies. Authors occasionally convert between the linear and area-based measures of spatial scale by using the formula for the area of a circle, where the interpoint distance d is used as the radius. We strongly discourage this practice as it easily leads to incorrect interpretation of spatial analysis results. For example, statistically significant clustering at a scale of 6 m with Ripley's K statistic is not necessarily equivalent to a patch size of 113 m².

Following Fortin and Dale (2005) we recognize two classes of spatial pattern analysis: global pattern analysis and local pattern analysis. Global spatial pattern analysis summarizes the dominant pattern (i.e., the average pattern) over the entire study area; local spatial pattern analysis characterizes the variation of spatial pattern within the study area (Fotheringham and Brunsdon, 1999; Péliissier and Goreaud, 2001). Local pattern analysis is particularly well suited to detecting regions of clustering within a point pattern (Getis and Franklin, 1987; Fotheringham and Brunsdon, 1999). Fortin and Dale (2005) provide an introduction to this topic, including a detailed explanation of the difference between global and local spatial pattern analysis.

Pattern type refers to the average (global) pattern across the entire study area. Pattern type is usually defined with respect to a

pattern-generating stochastic spatial point process model (Loosmore and Ford, 2006; Perry et al., 2006). The simplest and most frequently used point process model is complete spatial randomness (CSR). A CSR (or random) pattern is one where the location of each point is independent of all other points in the pattern. Spatial randomness is used as a benchmark to define two other commonly used pattern types, spatial aggregation (also called clumping or clustering) and spatial uniformity (also called regularity or inhibition). Points in an aggregated pattern have, on average, more neighbors within a specified interpoint distance, d , than a random pattern containing the same total number of points. Conversely, points in a uniform pattern have, on average, fewer neighbors within d than a random pattern containing the same total number of points. Pattern strength refers to the degree to which a pattern differs from those generated by a null point process model (such as CSR). For example, points in a weakly aggregated pattern will have slightly more neighbors within d than a random pattern while points in a strongly aggregated pattern will have many more neighbors within d than a random pattern.

The concept of a spatial pattern element is closely tied to local spatial pattern analysis and the idea of spatial heterogeneity: pattern elements are subsets of (or subregions within) the overall pattern. We recognize three spatial pattern elements within maps of tree locations: tree clumps, single trees, and openings. Tree clumps (also called clusters or groups) are subsets of trees within the study area that have neighbors closer than a specified intertree distance, d . Single trees have no neighbors closer than d . Openings (also called gaps) are subregions within the study area where no trees occur within d of an arbitrary location. Single trees and tree clumps

are also defined ecologically: clumps are groups of trees with interlocking or adjacent crowns (Long and Smith, 2000; Graham et al., 2006) while the crowns of single trees do not overlap with those of neighbors. In the ecological definition of single trees and clumps the sums of the crown radii within each unique tree pair is used instead of the intertree distance d , which is held constant across all trees in the pattern in the spatial definition of clumps and single trees.

2. Literature review

We aspired to obtain a complete census of all studies reporting spatial data and spatial analyses of within-stand (i.e., within areas $<10^2$ ha in extent) forest structure and tree patterns in fire-frequent pine and mixed-mixed conifer forests of western North America. Because our objective was a complete census of the literature in our focal subject area we used every means possible to locate qualifying studies. We exhaustively searched the peer reviewed literature using multiple electronic databases and search engines and a wide variety of search terms. We reviewed studies cited in qualifying studies, and also searched forward citations of qualifying studies. We searched library catalogues and used web-based search engines to identify unpublished theses, dissertations and government documents that met our criteria. Most, but not all, studies reporting spatial data at these scales were based on stem map data; however we did not restrict our review to only include studies based on stem maps. Other sources of spatial data at the scale of interest include remote sensing imagery and aerial photography,

Table 1
Studies reporting spatial reference conditions in fire-frequent pine and mixed conifer forests in western North America.

Region and Location	Plots (n)	Size (ha) ^a	Analysis methods	Citation
<i>Pacific Northwest</i>				
Eastern Cascades, Oregon	2	1.0	Morisita's I	Morrow (1985)
Eastern Cascades, Washington	48	0.5	Ripley's K	Harrod et al. (1999)
Eastern Cascades, Oregon Southern Cascades, California	27	1.0	Ripley's K	Youngblood et al. (2004)
Southern Cascades, California	7	1.0	Moran's I	Taylor (2010)
<i>Sierra Nevada and Sierra San Pedro Martir</i>				
Kings Canyon National Park, California	NA	NA	Classified forest structural aggregation types	Bonnicksen and Stone (1982)
Lake Tahoe Basin, Nevada	20	0.5	Ripley's K	Taylor (2004)
Lake Tahoe Basin, California	12	0.5	Moran's I	Beatty and Taylor (2007)
Teakettle Experimental Forest, California	18	4.0	Ripley's K	North et al. (2007)
Baja California, Mexico	NA	NA	Delineated regeneration patches; semivariogram analysis	Stephens and Fry (2005), Fry and Stephens (2010)
Baja California, Mexico	NA	NA	Winkelmass index	Stephens et al. (2008)
<i>American Southwest and Northern Mexico</i>				
Fort Apache and San Carlos Indian Reservations, Arizona	4	1.0	Greig-Smith contiguous quadrat	Cooper (1960)
Gus Pearson Natural Area, Arizona	1	7.3	Subjectively delineated tree groups	White (1985)
Sierra Madre Occidental, Durango, Mexico	4	0.2	Ripley's K	Fulé and Covington (1998)
Mt. Trumbull, Arizona	1	0.3	None	Moore et al. (1999)
Coconino National Forest, Arizona	53	1.0	Percolation-based spatial clump detection; Ripley's K	Abella and Denton (2009)
Fort Valley Experimental Forest, Arizona	1	2.6	Ripley's K, semivariogram analysis and kriging; Moran's I	Sánchez Meador et al. (2009)
Fort Valley Experimental Forest, Arizona	9	1.1	Ripley's K	Sánchez Meador and Moore (2010)
Coconino National Forest, Arizona	6	2.6	Percolation-based spatial clump detection; Ripley's K	Dyer et al. (2008), Sánchez Meador et al. (2011)
<i>Southern and Central Rockies</i>				
Rocky Mountain Front Range, Colorado	12	0.4	Ripley's K; Moran's I	Mast and Veblen (1999)
Uncompahgre National Forest, Colorado	26	0.3	Ripley's K	Binkley et al. (2008)
<i>Northern Rockies</i>				
Western Montana	11	1.0	None	Arno et al. (1995, 1997)
Boise Basin Experimental Forest, Idaho	10	0.4	Delineated tree groups with adjacent or interlocking crowns	Graham and Jain (2005)

^a Mean plot size given for studies that used plots of variable area.

georeferenced fixed area plots, and indices based on inter-tree spacing such as the Winkelmass index (Schmidt et al., 2006).

2.1. Overview and geographic distribution of studies

Fifty studies spanning a half-century of research (1960–2011) were identified that included data on tree spatial patterns in fire-frequent pine and mixed conifer forests in western North America. Of these, 25 studies provided information reasonably interpreted as reference spatial conditions (Table 1), 21 of which included spatially explicit data for individual tree locations (stem map data). Another 25 studies (Table 2) report data characterizing tree patterns at sites with a significantly altered fire regime or otherwise modified conditions (e.g., timber harvest), of which 23 include stem map data. These additional studies of non-reference tree patterns do provide useful information but require greater caution in interpretation. Several of the reference studies (Table 1) also include data characterizing contemporary tree spatial patterns.

The majority of reference studies were samples of topographically uniform upland forest sites, although a few included plots located on steep, rough terrain (e.g., Arno et al., 1995). The types that are best represented are mixed-conifer forests in the Sierra Nevada and ponderosa pine forests in northern Arizona, followed by mixed conifer forests in the Cascade Range in the Pacific Northwest (Table 1). Spatial reference information for fire-frequent forests in the Rocky Mountains are provided in six studies but they account for only 10% of the total area sampled across all spatial reference stud-

ies (i.e., the sum of stem mapped plots) and only two of the six reference studies from the Rocky Mountains reported quantitative analyses of tree spatial patterns.

2.2. Sampling effort and replication

Plot sizes and replication varied widely across studies (Tables 1 and 2). Several published studies were based on a single stem-mapped plot. The spatial extent of stem mapped plots (mapped using ground-based techniques) ranged from 0.1 (Mast and Wolf, 2004) to 9.3 ha (Boyden et al., 2005); average stem mapped plot size across all studies was 1.1 ha. Only 13 of the 43 stem map studies included ten or more replicate plots; Youngblood et al. (2004), Harrod et al. (1999) and Abella and Denton (2009) achieved the highest level of replication, with sample sizes (n plots) of 27, 48, and 53, respectively. North et al. (2007) sampled the largest cumulative area, 72 ha, with 18 replicate 4 ha plots.

The size of stem map plots used in most studies was apparently determined by available resources, or simply set at an arbitrary convenient size. Of the studies reviewed here, only one determined sample plot area based on a prior analysis of forest spatial structure: North et al. (2007) used variogram analysis of a pilot data set to determine that a 4 ha plot was necessary to capture the range of spatial variation present in their study area. We are unaware of any published analyses of plot size effects on sensitivity of spatial pattern detection or statistical power of spatial hypothesis tests in fire-frequent forests.

Table 2

Studies reporting contemporary tree spatial patterns in fire-frequent pine and mixed conifer forests in western North America.

Region and location	Plots (n)	Size (ha) ^a	Analysis methods	Reference
<i>Pacific Northwest</i>				
Okanagan Valley, British Columbia, Canada	3	0.5	Various distance and quadrat-based spatial statistics.	Pielou (1960, 1961, 1962)
Warm Springs Indian Reservation, Oregon	12	1.1	Greig-Smith contiguous quadrat method	West (1969)
Southern Cascades, California	6	11.3	Nearest neighbor, spectral, and autocorrelation analysis	Franklin et al. (1985)
Southern Cascades, California	1	1.4	Local second-order neighborhood analysis	Getis and Franklin (1987)
Klamath National Forest, California	NA	NA	Fractal dimension, shape index	Skinner (1995)
<i>Sierra Nevada and Sierra San Pedro Martir</i>				
Sierra Nevada, California	3	0.6	Various distance and quadrat-based spatial statistics	Bonnicksen and Stone (1981)
Sequoia National Park, California	1	2.5	Ripley's K, G statistic, F statistic	Knight (1997)
Sequoia National Park, California	1	2.0	Ripley's K	Van Pelt and Franklin (2000)
Sierra Nevada, California	NA	NA	Ripley's K	Knight (2003)
Teakettle Experimental Forest, California	1	8.4	Ripley's K	North et al. (2004)
Blodgett Forest Research Station, California	NA	NA	Winkelmass index	Schmidt et al. (2006)
Sequoia and Yosemite National Parks, California	14	1.3	Ripley's K	Das et al. (2011)
Sequoia National Park, California	5	1.0	Ripley's K	van Mantgem et al. (2011)
<i>American Southwest and Northern Mexico</i>				
Fort Apache and San Carlos Indian Reservations, Arizona	14	NA	Nearest neighbor analysis	Cooper (1961)
Gus Pearson Natural Area, Arizona	1	4.0	Variograms and kriging	Biondi et al. (1994)
Grand Canyon National Park, Arizona	5	0.1	Ripley's K; Moran's I	Mast and Wolf (2004)
Grand Canyon National Park, Arizona	5	0.1	Ripley's K; Moran's I	Mast and Wolf (2006)
<i>Southern and Central Rockies</i>				
Black Hills, South Dakota	1	0.9	Stand structure metrics summarized in 7 × 7 m quadrats	Olsen et al., (1996)
Rocky Mountain Front Range, Colorado	9	0.3	Ripley's K	Ehle and Baker (2003)
Rocky Mountain Front Range, Colorado	1	9.3	Ripley's K with Poisson (random) and Neyman-Scott (clumped) spatial point process models	Boyden et al. (2005)
<i>Northern Rockies</i>				
Eastern Montana	14	0.2	Ripley's K; Moran's I	Woodall (2000)
Flathead Indian Reservation, Montana	10	0.1	Ripley's K	Fajardo et al. (2006)
Flathead National Forest, Montana	3	1.0	Morisita's I	Stover (2011)

^a Mean plot size given for studies that used plots of variable area.

2.3. Spatial analysis methods

A remarkable diversity of analytic techniques were used across the studies reviewed, reflecting a diversity of objectives and the emergence of new techniques over time. Sixty separate spatial analyses were conducted in the 44 studies utilizing stem map data; individual studies sometimes used more than one method. Analyses were tallied at the study level, not the sample plot level; here an instance of spatial analysis refers to the decision by an investigator to use a particular analytic technique, not the number of times a particular technique was applied in a given study. At least 18 unique spatial analysis methods were used across the 44 stem map studies.

Global pattern analysis techniques (54 of 60 analyses) were used far more frequently than local pattern analysis (6 of 60 analyses). Ripley's K statistic was the most frequently used spatial analysis method (23 of 60 analyses), consistent with the findings from an informal survey of the plant ecology literature (Perry et al., 2006); Moran's I was the second most popular analytic technique (7 of 60 analyses). Ripley's K and Moran's I are both examples of global pattern analysis.

Different methods of spatial pattern analysis yield different results, and interpretations, even when applied to the same data set (Perry et al., 2006). The review and synthesis that follow are constrained by the diversity of plot sizes and analytic methods used in the original studies and the fact that many of the methods used return non-comparable results; for example, results of Ripley's K analysis and Moran's I analysis are not directly comparable.

2.4. Reference spatial patterns in fire-frequent forests

The spatial structure of fire-frequent forests visited by low and moderate severity fires is a mosaic of three elements: openings, widely-spaced single trees, and tree clumps (Fig. 2). This within-stand mosaic structure typically manifests at scales <0.4 ha (Agee, 1998). The relative abundance and area occupied by these three elements within stands varies widely within and between fire-frequent forest types, but this basic spatial structure appears broadly characteristic of fire-frequent forests throughout western North America (Agee, 2003; Spies, et al., 2006; Kaufmann et al., 2007; Binkley et al., 2008; North et al., 2009).

Woolsey (1911) provided an early description of this mosaic structure for southwestern ponderosa pine forests, "The typical yellow pine forest of the Southwest is a pure park-like stand made up of scattered groups of from 2 to 20 trees, usually connected by scattering individuals. Openings are frequent and vary greatly in size." Other early 20th Century descriptions of fire-frequent pine and mixed conifer forest spatial structure throughout western North America echoed Woolsey's (1911) observations, variously noting widely spaced trees, tree clumps or groups, small dense patches of seedlings and saplings, and non-forested openings, shrubfields or meadows (Munger, 1917; Sparhawk, 1918; Korstian, 1924; Show and Kotok, 1925; Meyer, 1934; Weaver, 1943; Rummell, 1951; Hallin, 1959; see also the review of Forest Reserve Reports and associated discussion in Baker, 2009). The seminal works of Cooper (1960, 1961), Pielou (1960, 1961, 1962) and West (1969) brought quantitative analyses to bear on the striking spatial heterogeneity of fire-frequent forests and, along with Weaver (1943) and Rummell (1951), stimulated the early scientific discourse on mechanisms of spatial pattern formation in fire-frequent forests. Modern quantitative analyses (Tables 1 and 2) and qualitative descriptions (Covington and Moore, 1994; Agee, 2003; Franklin and Van Pelt, 2004; Spies et al., 2006; Baker, 2009) confirm these descriptions by early forest scientists, and repeatedly characterize fire-frequent forest spatial structure as a fine-grained mosaic (Fig. 2). Fire suppression and other land management activities have resulted in



Fig. 2. The three element fine-grained mosaic of openings, widely-spaced individual trees and closely-spaced tree clumps exemplified by a relict ponderosa pine forest with a resumed fire regime in the Bob Marshall Wilderness, Montana, USA (2010 photo, A.J. Larson). Fire was restored to this site by the 2003 Little Salmon Creek complex fire—which was not suppressed—after an approximately 75-year-long absence during the 20th Century era of fire suppression (Arno et al., 2000; Keane et al., 2006).

alteration of tree spatial patterns from reference conditions in most fire-frequent forests (e.g., Morrow, 1985; Harrod et al., 1999; Sánchez Meador et al., 2009).

2.4.1. Global spatial pattern

Spatial aggregation (clumping) is the dominant spatial pattern type identified in global analyses of reference tree patterns in fire-frequent forests. The majority of studies that used an analysis technique suitable for detecting spatial aggregation did, in fact, result in detections of spatial aggregation, usually in most replicate plots within individual studies. Spatial aggregation was apparent most frequently at spatial scales <20 m. This means that in fire-frequent forests, trees tend to have—averaged across an entire mapped study plot—more neighbors rooted within 20 m than would be counted if the trees were rooted in locations completely independent of each other. Some studies did document random or uniform tree patterns (e.g., Bonnicksen and Stone, 1981; Youngblood et al., 2004; North et al., 2007), usually within particular tree size classes (e.g., large trees [Bonnicksen and Stone, 1981]) or at restricted spatial scales (e.g., <1.5 m, Youngblood et al. (2004)). Some studies reported global spatial aggregation at scales larger than 20 m (e.g., North et al., 2007). The finding that clustering was most common at spatial scales <20 m is in part due to the fact that small plot sizes were used in several studies—there is simply less information available in the literature on patterning at larger scales.

The results under discussion are from global analyses of tree patterns, which characterize the average pattern across a study

area. In forests, tree patterns that are on average clumped will virtually always contain local areas of spatial randomness and uniformity; similarly, tree patterns in unmanaged forests that are on average spatially uniform typically also include regions of randomness and clumping within the study area. This is exemplified in the analysis of a 1.44 ha plot of ponderosa pine forest in northern California (Getis and Franklin, 1987). The spatial arrangement of trees in the study area did not differ statistically from spatial randomness at scales of 1–36 m using Ripley's K analysis. However, local spatial pattern analysis revealed areas of clumping and inhibition (i.e., open areas) within the study plot across the same range of spatial scales.

2.4.2. Local pattern: tree clumps

Tree clumps are the most frequently identified spatial pattern element in studies of reference tree spatial patterns in fire-frequent forests, consistent with finding that spatial aggregation is the most common global (average) pattern. Some authors have based their entire framework for characterizing tree patterns on tree clumps (e.g., White, 1985; Graham and Jain, 2005).

Three types of tree clumps are apparent in fire-frequent forests. Dense patches of seedlings and saplings comprise the first type of tree clump (Fig. 3). Such regeneration patches appear to be a broadly characteristic feature of fire-frequent forests with intact

fire regimes (Munger, 1917; Stephens and Fry, 2005; Taylor, 2010), especially for the long-needled species ponderosa pine and Jeffery pine. Regeneration patch sizes vary across studies (range: 0.001–0.64 ha); mean regeneration patch size is usually <0.15 ha (Stephens and Fry, 2005 and studies reviewed therein).

Clumps formed of overstory trees are another distinctive element of fire-frequent forest spatial structure (Fig. 4). Reports of overstory tree clump sizes range from 2 to 44 trees clump⁻¹, and areas of 0.003–0.4 ha clump⁻¹ (Cooper, 1960; Bonnicksen and Stone, 1982; Morrow, 1985; White, 1985; Graham and Jain, 2005; Abella and Denton, 2009; Sánchez Meador et al., 2011; Sánchez Meador and Moore, 2010). Estimates of overstory tree clump density range from 10 to 27 clumps ha⁻¹ (Graham and Jain, 2005; Sánchez Meador et al., 2011).

Clumps composed of trees with a variety of tree sizes and ages are the third clump type (Bonnicksen and Stone, 1982; White, 1985; Arno, et al., 1995; Arno et al., 1997; Sánchez Meador et al., 2011); such mixed aged clumps are probably quite common. White's (1985) study of the spatial age structure of pre-settlement ponderosa pine in the Gus Pearson Natural Area near Flagstaff, Arizona provides the most compelling evidence for mixed-age tree clumps: he reported age ranges of 33 to 268 years within overstory tree clumps. Mixed-age tree clumps may have received less attention in interpretations of fire-frequent forest dynamics because they are more difficult to detect visually (Bonnicksen and Stone, 1981, 1982) and because of the strong legacy of Cooper's (1960) conceptual model of even-aged groups in southwestern ponderosa pine forest dynamics.

Numerous studies have found evidence for spatial aggregation and tree clumps in fire-frequent forests; the spatial distribution of trees within clumps is also of interest (Cooper, 1961). Intra-clump spatial distribution has long been an interest of ecologists (Morisita, 1959; Pielou, 1960): competition within clumps between closely spaced trees is expected to result in small-scale spatial regularity. Several studies detected spatial regularity at the smallest scales analyzed (e.g., <1.5 m, Youngblood et al., 2004) in fire-frequent forests. Following dense establishment in regeneration patches (Cooper, 1960; West, 1969; Stephens and Fry, 2005), self-thinning and non-competitive mortality lead to increasing small-scale uniformity within the clump (Cooper, 1961; Pielou, 1960; Mast and Veblen, 1999; Mast and Wolf, 2004, 2006) while aggregation is conserved at larger scales; the clump persists even while mortality alters the intra-clump density and spatial distribution of trees (Morrow, 1985).

2.4.3. Local pattern: widely-spaced single trees

Widely-spaced individual trees are a second component of fire-frequent forest spatial structure (Fig. 2). The largest trees in fire-frequent forests are frequently widely-spaced individuals (Pearson, 1950; Pielou, 1960). In southwestern ponderosa pine forests the mean diameter of trees in clumps was consistently smaller than widely-spaced individual trees (Pearson, 1950; Sánchez Meador et al., 2011); widely-spaced individual trees also had higher diameter growth rates than trees growing in clumps (Pearson, 1950). Consistent with these observations, the largest tree size classes frequently exhibit global spatial uniformity or randomness when analyzed separately from smaller tree size classes (e.g., Bonnicksen and Stone, 1981; North et al., 2004; Boyden et al., 2005).

The most detailed information on the proportion of trees occurring as widely-spaced individual trees as opposed to members of tree clumps comes from southwestern ponderosa pine forests. For the majority of southwestern ponderosa pine forests more than 50% and as many as 88% of trees occur as members of clumps based on available information (White, 1985; Abella and Denton, 2009; Sánchez Meador et al., 2011). However, some southwestern ponderosa forests exhibit a lesser degree of clumping; for example,



Fig. 3. Dense ponderosa pine regeneration patch at the Beaver Creek Pinery, a pine-oak woodland with a resumed frequent fire regime within the Ishi Wilderness, Lassen National Forest, California, USA (2002 photo, A.J. Larson). The Beaver Creek Pinery burned five times during the 20th Century, most recently in 1990 and 1994 (Taylor, 2010). The seedlings and saplings in the foreground established following the 1990s wildfires.



Fig. 4. Openings and a mixed-species clump of old-growth sugar pine, ponderosa pine and incense-cedar trees in southwestern Yosemite National Park, California, USA (2011 composite photo stitched from two originals, A.J. Larson). A regime of frequent fire has been restored to this site through an active prescribed fire program that augments wildfires.

Abella and Denton (2009) found that trees growing on black cinder and clay basalt soil types were relatively less clumped (as few as 28% of trees in clumps at an intertree distance of 6 m) compared to other soil types. In pre-settlement southwestern ponderosa pine forests, tree density and degree of clumping appear to increase along a gradient of available moisture (Abella and Denton, 2009). The proportion of trees occurring as widely spaced individuals versus members of tree clumps are not currently available in the literature for other fire-frequent forests in western North America. In ponderosa pine – mixed conifer forests of the eastern Washington Cascades between 30% and 85% of trees occurred in clumps at an intertree distance of 6 m (D. Churchill, unpublished analysis of data from Harrod et al. (1999)).

2.4.4. Local pattern: openings

Openings unoccupied by trees are the third and most poorly quantified component of fire-frequent forest spatial structure

(Fig. 5). We are aware of only a single quantitative spatial analysis of opening characteristics in fire-frequent forests of western North America. Based on analysis of repeat aerial photography Skinner (1995) concluded that, in forests of the Klamath Region of northern California, total area in openings as well as perimeters and areas of individual opening decreased, while opening shape complexity (as measured by fractal dimension and an index of patch shape) did not change between 1944 and 1985. Skinner (1995) attributed changes in opening characteristics to a disruption of the historic low-moderate severity fire regime due to fire suppression during the 41-year study period.

Many authors explicitly mention openings as an element of fire-frequent forest reference spatial structure (e.g., Woolsey, 1911; Rummell, 1951; Youngblood et al., 2004) and openings are readily apparent in maps of reference tree locations (Arno et al., 1995; Moore et al., 1999; Beaty and Taylor, 2007; Abella and Denton, 2009). A few studies provide information on opening size ranges



Fig. 5. Openings and tree clumps in the ponderosa pine – Douglas-fir forest at Meeks Table, William O. Douglas Wilderness, Wenatchee National Forest, Washington, USA (2009 photo, D. Churchill). Meeks Table is unique in that it has never been subject to livestock grazing, and thus supports an intact native understory plant community (Rummell, 1951). Fire scars attest to lightning strikes and a historic regime of frequent fires (Rummell, 1951; Tiedemann et al., 1972); however fires have been actively suppressed at Meeks Table beginning in the early 20th Century and continuing to the present. Nevertheless, the forests of Meeks Table have remained relatively open despite fire suppression. Rummell (1951) interpreted the open stand structure and low density of tree regeneration (relative to similar adjacent grazed forests) as evidence for inhibition of tree seedling establishment by native understory plants.

(e.g., Piirto and Rogers, 2002), but we are unaware of any spatial analyses of openings that utilize ground-based measurements such as stem maps. Drawing on a wide range of published and unpublished sources, Piirto and Rogers (2002) argued that most openings in pre-settlement giant sequoia – mixed conifer forests ranged from 0.04 to 0.8 ha.

There are at least two reasons why spatial aspects of openings in fire-frequent forests are poorly characterized. First, the majority of methods used to analyze forest spatial structure (Tables 1 and 2) are based on how trees are arranged with respect to each other (e.g., inter-tree spacing) and do not explicitly consider openings or the relationship of tree locations to unoccupied sites within forest stands. Second, in many fire-frequent forests open areas are not clearly defined canopy gaps; instead openings are the matrix or background in which individual trees or tree clumps are distributed, making open areas difficult to delineate and quantify.

2.5. Moderate severity fire regimes

The literature provides few data for tree spatial patterns in forests with a history of moderate-severity fires. Results from the few studies of tree spatial patterns at sites with evidence of past moderate severity fires (Morrow, 1985; Arno et al., 1995; Arno, et al., 1997; Boyden et al., 2005; Ehle and Baker, 2003) are consistent with a spatial structure composed of a mosaic of openings, single trees and tree clumps with adjacent or interlocking crowns. For example, Boyden et al. (2005) concluded that the spatial structure of the Colorado Front Range ponderosa pine forest they studied was very similar to that of Arizona ponderosa pine forests studied by Cooper (1960) and White (1985), even though the fire histories of these regions and the individual study sites differ substantially. Based on visual interpretations of stem maps and qualitative assessments of stand structure Arno et al. (1995) concluded that some reference dry-site ponderosa pine – Douglas-fir forests as well as some moist western larch forests in western Montana exhibit a fine-grained mosaic of tree clumps. However, similar

adjacent forests of both types sometimes exhibited patterns at somewhat larger scales—a within-stand patch mosaic with a grain of about 0.2–1.2 ha. The small plot sizes (0.03–1.0 ha) and diverse analytic techniques used in the few reference studies with clear evidence for past moderate severity fires (Arno et al., 1995, 1997; Ehle and Baker, 2003) limit quantitative comparisons of forest spatial structures arising from strictly low-severity fire regimes and fire regimes that include both low- and moderate-severity events.

2.6. Mechanisms of pattern formation and maintenance

The mosaic structure of fire-frequent forests with intact fire regimes emerges from interactions between fires, and tree regeneration and mortality. More than any other factor, the development and maintenance of the tree clumps and the associated fine-grained mosaic structure appears to depend on spatially aggregated tree regeneration mediated by small-scale variability of fire behavior and effects (Stephens and Fry, 2005; Taylor, 2010). The conceptual model presented here is most relevant to sites that experienced a regime of frequent, low-severity fire, and builds on ideas presented by Weaver (1943), Rummell (1951), Cooper (1960, 1961) and West (1969) with elaborations reflecting recent syntheses (Agee 1993, 1998, 2003; Spies et al., 2006; Kaufmann et al., 2007; Baker, 2009) and new information from the studies reviewed here (Tables 1 and 2).

1. The formation of safe sites for tree regeneration in an intact low-severity fire regime appears related to local areas of high-intensity surface fire associated with accumulations of surface fuels originating from the death of individual (West, 1969; White, 1985) or groups (Cooper, 1960; West, 1969; Stephens and Fry, 2005; Taylor, 2010) of overstory trees. A spectrum of overstory tree mortality, from individual trees (both isolated trees and members of clumps) to the near synchronous mortality of overstory clumps (Agee, 1993), is recognized. Overstory tree mortality occurs due to a variety of possible agents, including attack by bark beetles and other insects, windthrow, structural failure due to basal fire scars, lightning, fire, pathogens or a combination of these and other agents (Weaver, 1943; Johnson, 1966; Boyden et al., 2005). When future fires visit the site these accumulations of coarse fuels burn with relatively greater intensity and duration than the majority of the stand, creating local patches of exposed mineral soil and understory plant mortality.
2. Given adequate seed supply and suitable climatic conditions, tree seedlings preferentially establish and survive in fire-created patches of bare mineral soil (Fig. 3). Fire-created patches of mineral soil reduce belowground competition with herbaceous understory plants, promoting initial seedling establishment and survival (Rummell, 1951; Agee, 1993). Exposed mineral soil also provides a more favorable moisture regime than tree litter, promoting initial seedling survival. Individuals and small groups of seedlings constantly establish throughout the stand; regeneration is not necessarily limited to fire-created patches of exposed mineral soil. Rather, establishment and initial survival is concentrated in the fire-created patches, leading to an overall aggregated distribution of tree seedling establishment set against a background of open areas and occasional isolated seedlings and saplings. Other mechanisms, such as seed caching by small mammals (Briggs et al., 2009) or birds (Lorenz et al., 2011), and facilitation by shrubs (Keyes et al., 2009) or overstory trees (Dyer et al., 2008) may contribute to spatially aggregated tree regeneration as well.
3. When regeneration clumps are not overshadowed by residual overstory trees surface fuels accumulate slowly, providing seedlings in the clump some protection from fire (Cooper, 1960;

- Agee, 1993; Stephens et al., 2008). Microclimatic and fuel moisture conditions within dense seedling and sapling clumps may limit fire spread, conferring some additional protection from surface fires (Harrington, 1982). As seedlings within the regeneration clump age and surface fuels accumulate, subsequent fires burn through the regeneration clump. These surface fires, along with competitive and other non-competitive mortality agents, kill a fraction of the trees within an initially dense regeneration patch. The process of fire-caused thinning is accelerated and more severe when regeneration clumps are intermingled with residual overstory trees, which suppress seedling growth rates while increasing surface fuel accumulation rates (Cooper, 1960; Agee, 1993). Depending on the severity of intra-patch mortality new cohorts of seedlings establish, leading to the development or exaggeration of an uneven age structure in some tree clumps, while preserving the spatially aggregated tree distribution (White, 1985; Morrow, 1985; Beaty and Taylor, 2007; Taylor, 2010).
4. Within both even-aged and uneven-aged tree clumps competition leads to the development of a range of tree sizes within the clump (Pearson, 1950; Cooper, 1960; Mast and Veblen, 1999; Woodall, 2000; Sánchez Meador et al., 2011; Taylor, 2010). Trees on the perimeter of clumps tend to maintain higher diameter growth rates and attain larger sizes than trees in the interior of the clump (Pearson, 1950). Position within the clump also causes differentiation of tree crown attributes: trees growing on the outer edge of clumps may develop asymmetrical crowns with large limbs and tend to lean away from the clump center, while trees in the center of the clump tend to have relatively smaller symmetrical crowns (Pearson, 1950).
 5. Competition and intra-clump mortality can cause a gradual transition from aggregated to uniform tree spacing within tree clumps (Das et al., 2008, 2011), leading to reduced intra-clump tree density and development of spatial uniformity at scales less than about 1.5 m (Pielou, 1960; Mast and Veblen, 1999; Woodall, 2000; Youngblood et al., 2004; Mast and Wolf, 2004, 2006). As regeneration patches age they become increasingly diffuse and indistinct, and may ultimately be represented by clumps of 2–6 large old-growth trees (Morrow, 1985; White, 1985, Fig. 4), and may even deteriorate into individual widely-spaced single trees if subsequent recruitment does not

occur in close proximity. However some large overstory tree clumps composed of as many as 10 to 40 trees may persist (White, 1985; Sánchez Meador et al., 2011).

6. Mortality of individual or groups of large, old trees leads to local accumulations of coarse surface fuels, setting the stage for the creation of new safe sites for tree regeneration. This cyclic repetition of fires, tree regeneration, and tree mortality perpetuates a shifting mosaic of tree clumps in different stages of development, with variable intra-clump tree age and size structures, set against a background of widely spaced individual trees and non-forested open areas.

Other mechanisms influence the spatial distribution of tree mortality and recruitment. For example, micro-environmental heterogeneity is a potentially important driver of tree spatial patterns at some sites. At Teakettle Experimental Forest in the southern Sierra Nevada post-settlement tree regeneration primarily occurred in patches of existing trees, maintaining historic openings; this was apparently due to elevated seedling mortality in openings due to high radiation loads and associated physiological stress (North et al., 2004, 2007). This contrasts with some Arizona ponderosa pine forests, where tree seedlings successfully established and filled historic openings (Sánchez Meador and Moore, 2010), and tended to be negatively associated with overstory trees (Sánchez Meador et al., 2009). The invasion of historic openings by ponderosa pine at many sites in Arizona was likely facilitated by domestic livestock grazing, which reduced competition with understory grasses and forbs (Weaver, 1950; Cooper, 1960), an interpretation consistent with observations of persistent openings at a fire-excluded but ungrazed site (Fig. 5) in the eastern Washington Cascades (Rummel, 1951).

Areas of overstory tree mortality at sites that experience moderate severity fire events extend the range of scales at which spatial patterning manifests, up to about 4 ha (Arno et al., 1995; Agee, 1998; Kaufmann et al., 2007). Moderate severity fire events result in areas of overstory tree mortality (Fig. 6), thereby creating relatively larger areas suitable for tree regeneration compared to those created when local accumulations of coarse fuels burn in low-severity surface fires. Consequently, tree regeneration following moderate severity fire is less strongly aggregated, but aggregated at larger scales compared to regeneration following low-severity



Fig. 6. An area that burned with moderate severity within an old-growth western larch-mixed conifer forest, Bob Marshall Wilderness, Flathead National Forest, Montana, USA (2010 composite photo stitched from four originals, A.J. Larson). Moderate-severity fires induce a broader range of fire effects and resultant structural development pathways within forest stands than low-severity surface fires.

fires. Because a fraction of overstory trees survive moderate-severity fire events, some existing overstory tree clumps persist (e.g., site Lolo-4 in Arno et al., 1997): moderate-severity events edit, but do not completely overwrite pre-fire tree patterns, generating a wider range of within-stand spatial patterns and structural development pathways compared to strictly low-severity fire regimes (Agee, 1993, 1998; Lundquist and Negron, 2000; Kaufmann et al., 2007; Baker, 2009).

3. Discussion

3.1. Characterizing spatial heterogeneity within forests

Based on this review, a principal remaining challenge for forest scientists is to provide managers with clear, operationally-relevant information about spatial heterogeneity within forest stands. Quantifying spatial heterogeneity is tantamount to local spatial pattern analysis (Pélissier and Goreaud, 2001; Fortin and Dale, 2005). Global spatial statistics, such as Ripley's K , are often appropriate for developing hypotheses about mechanisms of pattern formation (e.g., Kenkel, 1988). However, global spatial pattern analysis is not well suited to the very different objective of providing information about spatial heterogeneity within forest stands to forest managers and restoration practitioners. This is unfortunate, because the majority of analyses reviewed here fall into the category of global pattern analysis.

The limitations of global pattern analysis are clearly exemplified by the most common spatial analysis method used in the studies reviewed here, Ripley's K (38% of all analyses). In essence, the empirical K statistic is simply the number of trees within a circle with radius d centered on the i th tree, averaged over all trees in the study area (Fortin and Dale, 2005; Perry et al., 2006). Spatial heterogeneity within the pattern—such as clumps of closely spaced trees or widely spaced single trees—is masked by the pattern-wide summary K statistic which averages across all points (trees) and returns a single value for each scale at which analysis is conducted (Dale and Powell, 2001; Fortin and Dale, 2005; Perry et al., 2006).

The spatial ecology literature offers methods of local point pattern analysis suitable for detecting heterogeneity within maps of tree locations. Here we describe two approaches, one based on

continuum percolation, the other a relative of the familiar Ripley's K statistic.

3.1.1. Continuum percolation to detect clumps and single trees

Characterizing tree spatial patterns in a way that partitions the overall pattern into discrete groups of trees (i.e., individual trees and clumps) enables more effective use of reference spatial information in restoration prescriptions (Larson and Churchill, 2008). Such a method brings quantitative detail to the intuitive and operationally relevant idea of tree clumps used by so many authors to describe tree spatial patterns in fire-frequent forests of the western United States (White 1985; Harrod et al., 1999; Long and Smith, 2000; Lynch et al., 2000; Youngblood et al., 2004; Graham and Jain, 2005; Dodd et al., 2006; Taylor 2010).

Continuum percolation (Meester and Roy, 1996) was first applied to spatial analysis of individual mapped tree locations by Plotkin et al. (2002), who introduced a method to detect spatial clusters (clumps) in tree maps, and used the approach to investigate habitat associations of Malaysian tree species. Recently, forest scientists working to characterize reference spatial patterns to inform forest restoration have independently converged on this approach (Larson and Churchill, 2008; Abella and Denton, 2009; Sánchez Meador et al., 2011). White (1985) and Graham et al. (Graham and Jain, 2005; Graham et al., 2006) used closely related methods to delineate tree clumps.

The basic clump detection algorithm (Plotkin et al., 2002; Larson and Churchill, 2008; Sánchez Meador et al., 2011) works as follows. At a given spatial scale—the intertree distance, d —the map of tree locations is partitioned into a set of unique tree clumps: trees $\leq d$ of each other are members of the same clump (Fig. 7). Every tree in a clump need not be within d of every other tree in the clump; trees belong to the same clump as long as a chain of pairwise distances $\leq d$ is maintained among the clump members. The tree clump size distributions for different d provide a scale-dependant characterization of spatial heterogeneity within the pattern (Larson and Churchill, 2008). The clump size distribution (Fig. 7) is directly applicable to restoration prescription design: it provides reference information useful for determining the number and sizes of tree clumps (groups of trees spaced closer than a threshold intertree distance, d), and the number of individual trees (trees further

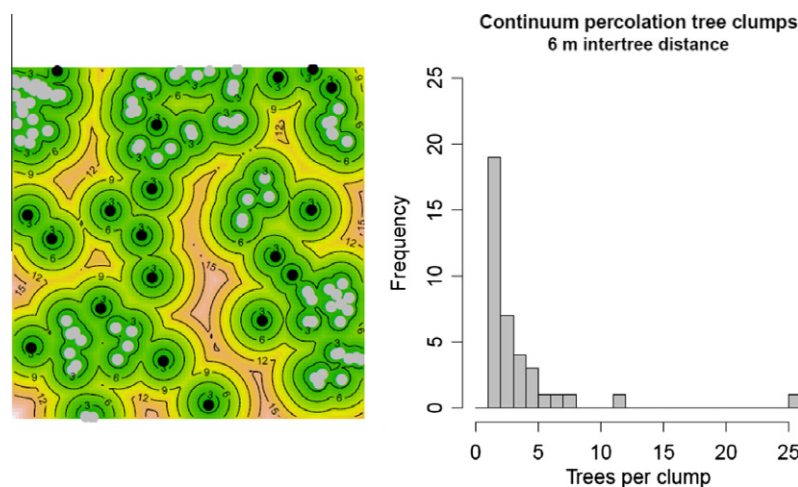


Fig. 7. Stem map (left panel) and tree clump size distribution (right panel) for reconstructed 1900 tree spatial patterns for a 1.0 ha (100 m × 100 m) plot within a ponderosa pine - Douglas-fir forest, Lolo National Forest, Montana. This figure based on data from "Lolo Plot 2" in Arno et al. (1995). Contour lines show distance from nearest tree at 3 m intervals; the color gradient shows a continuous gradient of distance to nearest tree, with distance increasing from green to brown. Solid black symbols mark trees with no neighbors within 6 m—widely-spaced single trees. Solid gray symbols show trees with neighbors within 6 m—trees that members of multi-tree clumps at an intertree distance of 6 m. Note the numerous openings and dense tree clumps. The intertree distance of 6 m was chosen because it approximates twice the crown radius of a typical overstory tree, and thus approximates the functional definition of tree clumps: trees with interlocking or adjacent crowns.

than d from their nearest neighbor) to retain within the treatment area.

3.1.2. Second order neighborhood analysis

Getis and Franklin (1987) introduced a method useful for detecting spatial heterogeneity in point patterns which they termed second-order neighborhood analysis. Just as with Ripley's K , second-order neighborhood analysis is based on the count of trees occurring within a circle of radius d centered on each respective tree in the pattern. The principal difference is that the local spatial structure (i.e., the number of neighbors within d) around *each individual tree* is the result of interest in the Getis method, not the pattern-wide average provided by the K statistic. Maps showing variation in the local spatial structure and frequency distributions of neighbor counts (Fig. 8), respectively, characterize spatial heterogeneity at a given scale, the intertree distance d , within the pattern (Getis and Franklin, 1987; Pélissier and Goreaud, 2001; Dale and Powell, 2001; Fortin and Dale, 2005; Perry et al., 2006).

Dale and Powell (2001) introduced a related method (circumcircle analysis) and showed how it could be used to delineate dense patches of trees (clumps) and openings (see Fig. 2.38 in Fortin and Dale (2005)). The Dale and Getis methods, respectively, could be extended to develop area-based size distributions for tree clumps and openings, data that could directly inform prescription development and tree marking guidelines by providing estimates of the number, size and geometry of tree clumps and openings to be created with restoration treatments.

3.1.3. A balanced approach to characterizing tree patterns

Here, we outline some general recommendations for exploratory and descriptive analyses of spatial point pattern data (i.e., stem map data). These recommendations are intended help ensure that future analyses fill information gaps revealed by this review, and generate information that directly informs restoration targets and prescriptions.

Exploratory or descriptive studies of tree spatial patterns (such as reference condition studies) should seek to quantify three fundamental attributes of tree patterns: (1) global pattern across

scales within a site (within a stem map); (2) variation of local pattern across scales within a site; and (3) variation of global and local pattern among different replicate study sites, at (or up to) specific scales of interest, such as twice the median overstory tree crown radius. Quantifying variation of local pattern among sites will permit development of quantitative “envelopes” or ranges of variability that will provide managers with a scientific basis for determining among-site variability of spatial restoration targets.

We recommend that, whenever possible, investigators use (and report) both the global and local forms of any analytic technique selected. For example, if Ripley's K is used to characterize global patterns, also report Getis' local adaptation of the K statistic (Getis and Franklin, 1985). Similarly, if the continuum percolation method is used, report both the global summaries, such as plot-wide mean clump size (Abella and Denton, 2009; Sánchez Meador et al., 2011), as well as local variation, such as the clump size distribution within the study plot (Larson and Churchill, 2008). Combining global and local versions of a particular analytic technique facilitates a richer interpretation of the individual results: local pattern analysis helps the investigator identify ecologically interesting departures from average conditions within the study area. Local analysis also bridges the gap between point pattern analysis and tree neighborhood effects theory (Frelich et al., 1998; Woodall et al., 2003; Das et al., 2008, 2011), providing opportunities to test and refine ecological hypotheses that global pattern analysis does not.

Finally, we concur with the recommendation of Perry et al. (2006) to use multiple different analytic techniques, specifically because most individual techniques do not simultaneously provide information about the three basic pattern elements. For example, while the continuum percolation method efficiently quantifies global and local attributes of tree clumps and single trees at multiple scales, the method does not directly quantify openings. In studies where providing spatial reference information to managers is an explicit objective we recommend including methods that quantify local spatial structure (i.e., within-stand variability) of clumps, single trees and openings, respectively, in the suite of analytic techniques used.

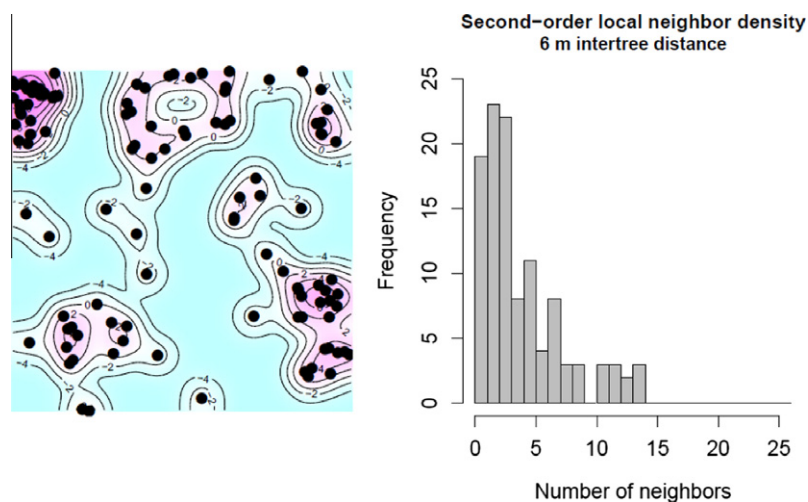


Fig. 8. Getis map (left panel) and local second-order neighbor frequency distribution (right panel) calculated at a neighborhood scale of 6 m for the same 1.0 ha stem map as shown in Fig. 7. A Getis map shows spatial variation of local second-order neighbor density (\hat{L}_i) within a point pattern (Getis and Franklin, 1987; Perry et al., 2006). Tree locations are shown by solid black circles. Contours show spatial variation in \hat{L}_i values across the study area; contours are based on a 1 m grid of points overlaid on the map of tree locations (see Getis and Franklin, 1987 for details). Positive \hat{L}_i values (warm colors) indicate local clumping and negative \hat{L}_i values (cool colors) indicate local inhibition (openings); \hat{L}_i values near zero suggest areas of local spatial randomness. The null hypothesis of spatial randomness was rejected for this pattern ($P = 0.001$) at scales up to 6 m based on $n = 1999$ simulated random patterns using Ripley's K analysis (implemented following the method of Loosmore and Ford, 2006). A plot of the empirical K function indicated global spatial clumping at these scales. In other words, Ripley's K analysis indicates the pattern shown here is, on average, significantly clumped at distances up to 6 m. However, Ripley's K analysis does not explicitly quantify the regions occupied by widely-spaced single trees and openings quantified with the Getis map.

4. Application to management

4.1. Current barriers

Forest managers and restoration practitioners are aware of the need to maintain or enhance spatial heterogeneity with restoration and fuel reduction treatments (Lynch et al., 2000; Egan, 2008; Binkley et al., 2008; North et al., 2009; Okanogan-Wenatchee National Forest, 2011). Empirical studies and reviews of spatial reference conditions generally conclude with recommendations to create random or aggregated tree spatial patterns (e.g., Harrod et al., 1999; Taylor, 2004; Youngblood et al., 2004; Fiedler et al., 2007; North et al., 2007, 2009) and some explicitly state that uniform tree spacing should be avoided (e.g., Woodall, 2000). Yet examples of restoration treatments that implement these recommendations are rare (Stephens et al., 2008; Sánchez Meador et al., 2009) and restoration prescriptions based on average tree density and uniform tree spacing or crown bulk density targets (e.g., Johnson, 2008; Powell, 2010) continue to be used. While globally uniform patterns have been found in a few sample plots (generally <1.0 ha in extent), such patterns represent only a small fraction of the range of pattern types documented in this review. Globally clumped tree patterns were most common reference spatial pattern type identified; treatments that leave trees uniformly spaced over areas exceeding about 1.0 ha in extent appear to be outside known reference conditions (Fig. 9).

Multiple factors contribute to the continued use of spatially homogenous restoration treatments in fire-frequent forests, but three are outstanding: (1) Legacy effects of the timber management silvicultural paradigm (Puettmann et al., 2009); (2) Perpetuation of a non-spatial view of forest structure by fuel management planning tools; and (3) Communication by forest scientists of spatial information in formats not readily incorporated into restoration prescriptions and tree-marking protocols.

4.1.1. Legacy of timber management silviculture

Fuel reduction and restoration treatments fall under the broad rubric of forest density management and thinning. Thinning treatments directly manipulate tree density, and indirectly influence individual tree growth and forest development, thereby achieving a variety of management objectives such as aesthetics, wildlife habitat, wood production, and potential fire behavior (Tappeiner et al., 2007).



Fig. 9. A uniformly-thinned, second-growth ponderosa pine forest on US Forest Service lands in northern California, USA (2007 photo, A.J. Larson). Compare to Fig. 1.

In North American silviculture, density management has, until recently, been used primarily to control inter-tree competition and utilization of growing space in order to promote individual tree vigor, stand volume growth and economic return (Davis, 1954; Stiel, 1978; Smith et al., 1997). Thinning treatments designed to optimize these timber management objectives create structurally simple forests composed of evenly-spaced, similarly-sized trees (Smith et al., 1997). This wood production approach to forest density management remains deeply ingrained in silvicultural practice (Puettmann et al., 2009), as well as in contracting rules and contractor performance evaluation criteria. Consequently, spacing-based thinning prescriptions that reduce spatial heterogeneity are often the default approach used in fuel reduction and restoration treatments, despite the differences in objectives compared to those of a timber management paradigm.

4.1.2. Fuel and fire management planning tools reinforce a non-spatial view of forest structure

Widely used fuel and fire behavior models (e.g., BEHAVE, NEXUS, FVS-FFE) are based on stand-level averages of forest structure and fuel conditions and do not incorporate within-stand spatial variation (Schaaf et al., 2007). These models are used extensively in the planning of fuel management and forest restoration treatments, and assessment of treatment effectiveness (e.g., Stephens et al., 2009). Despite some deficiencies (Cruz and Alexander 2010), these models are important management tools. However, as with any model or decision support tool, their appropriate use requires thoughtful interpretation of model results in the context of model assumptions and limitations.

Researchers and managers alike tend to reify the non-spatial representation of forest structure used in fire behavior models because the data input and output formats do not accommodate the spatial complexity of natural forests (Stover, 2011). Simulation studies (e.g., Johnson et al., 2011) and management guidelines (e.g., Johnson et al., 2007) based on these non-spatial models necessarily default to non-spatial thinning prescriptions, typically expressed in terms of the number of residual trees or basal area to be retained per unit area. Because fire behavior models available to managers do not consider spatial aspects of within-stand forest structure, a uniform tree distribution is typically assumed. Target residual tree densities are converted to equilateral tree spacing and incorporated into tree marking guidelines, propagating the assumed, but uncharacteristic, uniform tree patterns onto the landscape (Fig. 9).

4.1.3. Non-informative management recommendations

Researchers have generally not communicated information about tree spatial patterns in terms applicable to management (see discussion in Fry and Stephens, 2010). Most methods used by forest scientists to quantify spatial aspects of forest structure, such as spatial correlation analysis (Larson and Franklin, 2006), geostatistics (Fry and Stephens, 2010), stochastic point process models (Boyden et al., 2005), and point pattern statistics (Diggle, 2003) return derived data products that are distant abstractions of actual tree patterns. *These methods do not generate information that can be directly used by forest managers and restoration practitioners.* The pervasive use of global spatial pattern analysis techniques such as Ripley's *K* further compounds this problem, as global analysis masks spatial heterogeneity within the study area (Fortin and Dale, 2005; Perry et al., 2006), similar to the way that the arithmetic mean masks the variability within a heterogeneous sample.

When researchers report spatial reference conditions in terms of global spatial statistics, parameterized spatial models, or even verbal summaries (i.e., clumped, random or uniform) they place the burden of back-transforming mathematical abstractions of tree patterns into restoration prescriptions entirely on managers. A

simple example illustrates this problem. A common management recommendation in the peer-reviewed literature is to create random tree patterns with restoration treatments. But how might a silviculturist actually go about designing and implementing a restoration treatment that creates random tree patterns, and how will success be judged? Tree patterns that are on average (globally) random will almost always include dense tree clumps as well as openings and widely spaced individual trees (Getis and Franklin, 1987; Fortin and Dale, 2005; Perry et al., 2006) but these important elements of forest spatial structure are not explicitly acknowledged with a recommendation to create random tree patterns. This example makes obvious the current mismatch between management recommendations provided by researchers and the operational realities faced by practitioners.

4.2. Recommendations for forest managers and restoration practitioners

Restoring fire-frequent pine and mixed conifer forests requires treatments that introduce or retain spatial variation within the treatment area. Fundamentally, this requires a view of forest structure that accommodates within-stand variability (Puettmann et al., 2009). This section outlines five principles to help guide the restoration of spatial aspects of fire-frequent forest structure. Specific management recommendations (Table 3) compliment these principles.

4.2.1. Adopt a view of forest structure that accommodates spatial heterogeneity within forest stands

Based on the studies reviewed here, fire-frequent forest spatial structure can be understood as a mosaic of openings, individual trees and tree clumps resolved at spatial scales <0.4 ha. Restoration treatments, however, are usually designed and implemented at scales of 10–100 ha. This mismatch argues strongly against

describing fire-frequent forest restoration targets only in terms of treatment unit averages.

4.2.2. Incorporate within-stand spatial heterogeneity into restoration targets and prescriptions

Within stands, restoration treatments should seek to create or maintain a range of clump and opening sizes, and variable densities of widely-spaced single trees. To achieve this outcome, express desired conditions and tree marking guidelines in terms of the numbers and sizes of the three pattern elements—clumps, openings and single trees—to be created and retained within the treatment area. Existing conditions, especially the presence of old-growth trees or major forest health issues, will influence the possible types, numbers and locations of pattern elements to be left within the treatment unit.

4.2.3. Use spatial reference conditions to define a range of restoration targets among stands

Studies based on a large number of replicate sample plots (e.g., Harrod et al., 1999; Youngblood et al., 2004; Abella and Denton, 2009) consistently report a range of reference tree patterns. Based on the studies reviewed, we infer that clumping is the dominant pattern type in fire-frequent forests. However, the strength of clumping varies among sites. For example, in Arizona ponderosa pine forests the proportion of trees in clumps, mean clump size and maximum clump size depended on soil parent material (Abella and Denton, 2009). A forest restoration strategy for any fire-frequent landscape should incorporate a variety of restoration targets (i.e., prescriptions) that reflect the diversity of reference spatial patterns and structural development stages within the landscape (Hessburg et al., 1999; Okanogan-Wenatchee National Forest, 2011). Practically, this means varying among treatment units the number and sizes of clumps and openings, and the density of widely-spaced single trees, in a manner that reflects variation in local reference conditions, subject to site-specific constraints.

Table 3
Management recommendations for restoring spatial heterogeneity to fire-frequent pine and mixed conifer forests.

Recommendation	Basis
Vary marking guidelines and prescribed fire intensity within stands to create or enhance a mosaic of openings, single trees and clumps of overstory trees with adjacent or interlocking crowns	The characteristic spatial structure of fire-frequent pine and mixed conifer forests is a fine-grained mosaic
Retain live old-growth trees	Densities of large, old trees have declined during the 20th Century due to timber harvest, and have also declined in some protected areas as well (Lutz et al., 2009). Live old-growth trees are difficult to replace, provide unique structural and functional attributes, and are typically the most fire resistant trees in the stand (Agee and Skinner 2005)
Avoid arbitrary upper diameter limits for tree removal, especially in second-growth stands and plantations	Prescriptions with upper diameter limits that are not based on site-specific assessments can prevent restoration of a mosaic structure, especially openings (Abella et al., 2006)
Leave larger clumps (more trees per clump) in second-growth stands and plantations than reference estimates derived from old-growth stands	Competitive and non-competitive mortality thins clumps through stand development
Retain some clumps of seedlings and saplings where they do not function as ladder fuels	Leaving some seedling and sapling clumps will help restore stand development processes and long-term pattern maintenance. (Stephens and Fry 2005; Taylor 2010)
When shade-intolerant species (<i>Pinus</i> spp., western larch) have been eliminated from the site, consider planting some seedlings in a clumped spatial pattern	Planting fire-resistant species in their characteristic spatial pattern enables restoration of functioning fire-stand development linkages (Thomas and Agee 1986)
Allow some local accumulations of coarse fuels to burn during prescribed fires, especially in areas of relatively low overstory stocking	Patches of exposed mineral soil with limited competition from understory plants originating from long-burning coarse fuels are thought to promote spatially-clumped tree seedling establishment and survival
Include occasional patches of moderate and high severity, as well as unburned refugia within prescribed fire units	Prescribed fires that uniformly burn dense forests at low severity do not appear to restore spatial heterogeneity to fire-frequent forests (Schmidt et al., 2006, van Wagtenonk and Lutz 2007, Collins et al., 2011)
Where appropriate, use slashing and hand piling to create a spatially heterogeneous fuel distribution	Long fire-free intervals have homogenized the distribution of surface and canopy fuels. Heterogeneous surface fuels are thought to cause small-scale variation in fire intensity, duration and severity, maintaining a patchy forest structure (Stephens et al., 2008)

4.2.4. Fire-frequent forest restoration treatments need not optimize tree growth or wood production

Prescriptions that strictly prioritize the largest and most vigorous trees for retention and emphasize uniform allocation of growing space to residual trees have a low likelihood of restoring spatial aspects of fire-frequent forest structure, and the associated linkages between pattern, process and ecosystem function. In most fire-frequent forests restoring spatial heterogeneity requires a tradeoff with respect to tree crown development, growth rate and wood production (Pearson, 1950; Pielou, 1960). Such a tradeoff is acceptable and appropriate when management objectives are to reduce fuel loads or restore characteristic forest structures: fire-frequent forests with intact fire regimes contain trees in a variety of conditions, including slow-growing, low-vigor, and “defective” trees (e.g., Munger, 1917; Korstian, 1924). Restoring tree clumps and ecologically-significant openings (Abella et al., 2006) while simultaneously meeting fuel reduction objectives will sometimes require removal of relatively fast-growing large-diameter trees—what might be considered crop trees in a timber management program—especially in second-growth stands and plantations. We do not, however, endorse cutting old-growth trees that established prior to widespread Euro-American settlement in restoration and fuel reduction treatments (Agee and Skinner, 2005).

4.2.5. Monitor spatial outcomes of treatments to guide adaptive management

Published information on how thinning and prescribed fire treatments affect tree spatial patterns is limited to only three empirical studies (Schmidt et al., 2006; North et al., 2007; van Mantgem et al., 2011). Both the Healthy Forest Restoration Act and the Collaborative Forest Landscape Restoration Program require monitoring to evaluate whether projects achieve the stated goals. Monitoring effects of treatments on tree spatial patterns should be part of these efforts when restoration of characteristic forest structure is an objective: the efficacy of restoration treatments at achieving this objective cannot be determined if monitoring does not include spatial aspects of forest structure. Writing and implementing prescriptions that create within-stand spatial heterogeneity is outside the formal training of many silviculturists and restoration practitioners. Monitoring spatial outcomes of restoration treatments will help refine prescription development and implementation techniques, thereby building capacity and improving the likelihood of success through adaptive management.

5. Future research

We perceive the need for two fundamentally different types of research. Over the short-term, additional analyses of existing and new reference data sets will increase the likelihood of successful restoration of fire-frequent forest spatial structure. Over the medium- to long-term, likelihood of restoration success will be improved by investing in experimental studies of mechanisms of pattern formation and maintenance.

Reanalysis of existing spatial reference datasets using local spatial analysis methods should be a priority. This is the most cost-effective method to increase spatial reference information available to managers over the short term.

New datasets characterizing spatial reference conditions are also needed. Spatial reference conditions are provided from less than 300 ha of forests (the sum of areas on which tree locations were mapped in the studies listed in Table 1) and these are distributed in an unbalanced pattern across the fire-frequent forests of western North America. This limited body of information is the current empirical basis for designing treatments to restore forest spatial structure across literally millions of hectares throughout

the western United States. Reference tree spatial patterns in fire-frequent forests throughout the Rocky Mountains and in forests with moderate-severity fire regimes represent major gaps in current knowledge, limiting development of defensible, science-based restoration targets in these forests (Kaufmann et al., 2007; Crist et al., 2009).

The current scientific understanding of mechanisms originating and maintaining spatial patterns in fire-frequent forests—including the conceptual model outlined in section 2.6—constitutes a collection of untested hypotheses developed from observational studies. After a half century of study little progress has been made to address the situation described by Cooper (1960), that tree clumps are a conspicuous feature of fire-frequent forests, “... but surprisingly little attention has been given to the structure of these groups or to their mode of origin”. The numerous studies (Tables 1 and 2) since the pioneering work of Cooper (1960, 1961) have added rich detail to descriptions of the spatial structure of fire-frequent forests—a basis for initial guidelines to restore spatial aspects of fire-frequent forest structure, and for developing hypotheses about mechanisms of pattern formation. Ultimately, however, restoration targets and management regimes based on an experimentally-verified understanding of pattern-generating mechanisms will be more robust than targets based on inferences from observational studies, and will enable a forward-looking restoration paradigm.

6. Conclusions

The characteristic structure of fire-frequent pine and mixed-conifer forests throughout the western North America can be understood as a mosaic of three elements: openings, single trees, and clumps of trees with adjacent or interlocking crowns. This mosaic structure typically manifests at scales <0.4 ha, but sometimes extends to scales as large as 4 ha, particularly on sites with fire regimes that include both low- and moderate-severity fires. There is considerable variation, both within and among forest types, of the sizes and numbers of tree clumps and openings in reference forests. An important remaining advance is to develop more detailed and operationally meaningful characterizations of this variability.

Our most significant finding is the preferential use of global spatial pattern analysis techniques. This finding is important because global pattern analysis subsumes the spatial heterogeneity present within the study area—the very thing spatial reference studies seek to quantify and one of the core structural attributes treatments aim to restore—into a single value that summarizes average spatial structure. Based on this finding we infer that seemingly innocuous decisions about which analytic techniques to use have exerted strong control on the type, quantity and usability of spatial reference information available to managers. The near-exclusive use of global spatial pattern analysis techniques found here, and in the broader plant ecology literature (Perry et al., 2006), has likely limited the development and testing of novel ecological hypotheses about pattern-generating mechanisms. Consequently, we recommend that forest scientists change how they quantify and communicate information about tree spatial patterns. Complementing the traditional global analysis methods with techniques that characterize local spatial structure will enable the delivery of usable spatial reference information to managers and facilitate novel ecological insights.

Managers cannot afford to ignore tree spatial patterns in fire-frequent forest restoration and fuel reduction treatments given the vast geographic scope of ongoing and future operations, and potential consequences for ecosystem function. Restoration of both the spatial and non-spatial aspects of forest structure is the surest way to return fire-frequent forest ecosystems to a resilient condition, and position them to adapt to future climates and disturbance regimes.

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