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Tree and opening spatial patterns vary by tree density in two old-growth remnant ponderosa pine forests in Northern Arizona, USA

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A B S T R A C T

Forest spatial patterns influence many ecological processes in dry conifer forests. Thus, understanding and replicating spatial patterns is critically important in order to make these forests sustainable and more resilient to fire and other disturbances. The labor and time required to stem-map trees and the large plot size (> 0.5 ha) needed to study tree spatial patterns have limited our examination of how these patterns change as a function of site conditions and tree densities. We stem-mapped all trees > 40 cm DBH within two large relict (minimally logged) pure ponderosa pine study sites on experimental forests at Long Valley (73 ha) on sedimentary soils and Fort Valley (32 ha) on basalt soils in northern Arizona, USA. We also simulated 1,000 4-ha plots from models of each study site incorporating field data parameters. Using cluster analysis and field data, we found that an inter-tree distance (ITD) of 9–11 m best separated single trees and groups within our study sites. Using a fixed 10-m ITD, the more productive Long Valley (LV) site had 62 trees ha^{-1} and groups of up to 113 trees, compared to the Fort Valley (FV) site, which averaged 41 trees ha^{-1} and had 22 trees in the largest group. However, the sites differed only slightly in terms of single trees ha^{-1} (LV 7.3; FV 5.6) and group of tree ha^{-1} (LV 7.2; FV 8.1). Simulation results indicated that when tree densities are equal, the spatial patterns were very similar between the two sites, suggesting that tree spatial pattern variability is a function of tree densities and only indirectly related to site productivity. As the number of trees increased, the additional trees integrated into existing groups rather than creating new groups. In addition to tree spatial patterns, we quantified gaps (defined as > 30 m wide stem-to-stem) and openings (defined as ≥30 m wide stem-to-stem) within the two study sites. Although both sites were dominated by small openings most of the open area was found within a few large openings. Our large plots allowed us to incorporate variability and capture a larger range of tree and openings spatial patterns than have been captured in previous studies to provide insights on spatial heterogeneity that can inform management of this important forest type in North America.

1. Introduction

Across the western United States, dry forests historically evolved with frequent low severity fires every 5–25 years (Swetnam and Baisan, 1996; Covington et al., 1997). Since the exclusion of these fires and subsequent logging, these forests have become increasingly dense with young trees, reducing open space and herbaceous production (Weaver, 1951; Cooper, 1960; Covington and Moore, 1994). Unlike historical forests, these novel dense conditions are characterized by abundant fuels, including fuel ladders that can, under dry and windy conditions, support both passive and active crown fires. The extent of area characterized by these conditions has in some places resulted in large uncharacteristic stand-replacing fires (Graham, 2003; Finney, et al., 2005; Mallek et al., 2013). The increase of fuels at the stand level and the increased homogeneity of forest conditions at landscape levels are among the most pressing management issues across frequent-fire-adapted forests in the western United States (Agee and Skinner, 2005; Stephens et al., 2016). Moreover, if seasonal average temperatures increase as projected, these forests are likely to be subjected to fires of greater severity and other disturbances exacerbated by climate impacts (Seager et al., 2007; Jolly et al., 2015; McDowell et al., 2016; Singleton et al., 2019). To minimize such disturbances and their effects on ecosystems, managers are emphasizing fuels reduction as well as restoration of the historical spatial structure of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson var. *scopulorum* Engelmann) forests across the western United States (Moore et al., 1999; Allen et al., 2002; Graham et al., 2004; Agee and Skinner, 2005).

Trees within ponderosa pine forests have long been noted to have a unique spatial pattern that has only recently been quantified. For example, scientists working in the western United States in the first half of the 20th century often commented on the open nature of these forests (Pearson, 1933; Cooper, 1960). The open conditions were due to low tree densities and an aggregated spatial pattern. Historical tree densities in ponderosa pine forest ranged from 10 to 200 trees ha^{-1} (TPH), as documented by numerous studies (Fulé et al., 1997; Covington et al., 1997; Mast et al., 1999). Tree spatial patterns in ponderosa pine forests have also been described using traditional spatial pattern analysis and were summarized by Larson and Churchill (2012). These studies found that ponderosa pine forests were most often dominated by trees aggregated at scales between 2 and 40 m. However, some studies have

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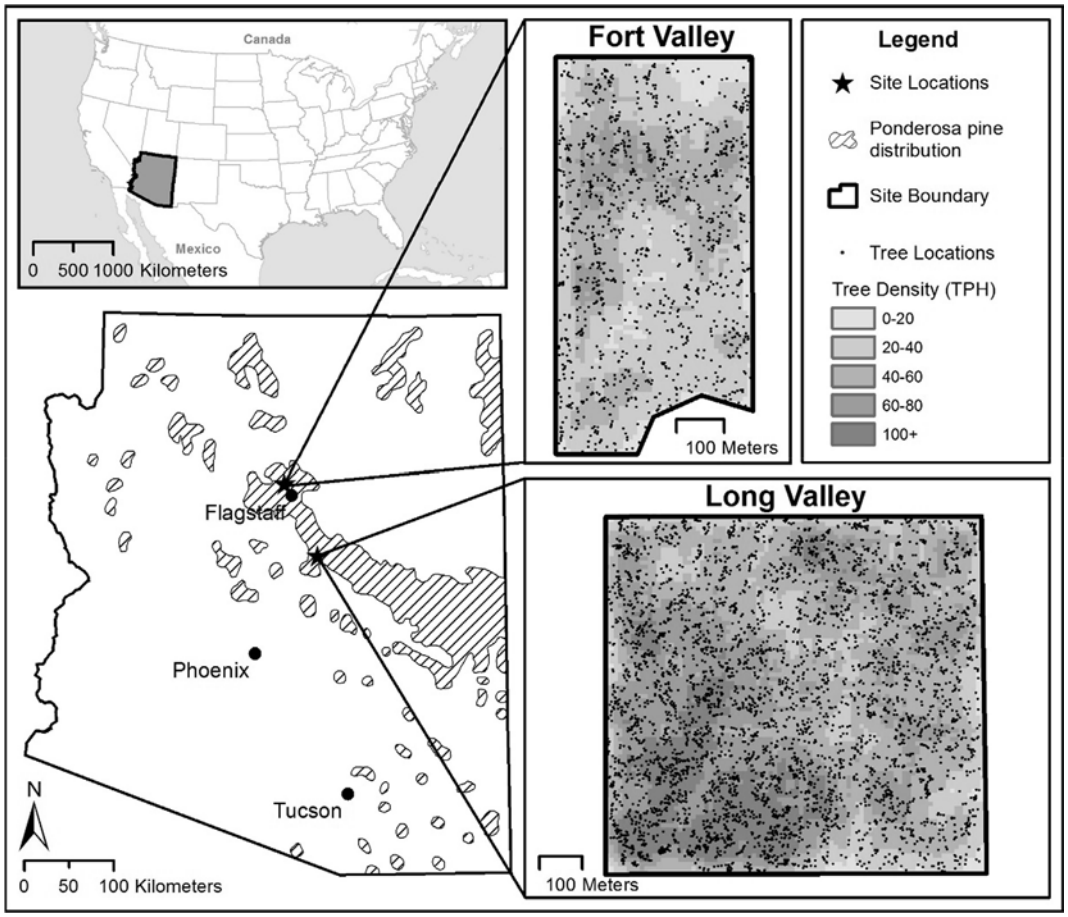

Fig. 1. Map of tree locations within the Long Valley and Fort Valley study sites in Northern Arizona. Along with stem map locations (black dots in inset maps of each site) and tree density (trees ha^{-1}; TPH), microsite variability is represented by different shades of gray.

also found global random spatial patterns in forests, particularly among larger and older groups (Youngblood et al., 2004; Schneider et al., 2016).

Gaps and openings are also recognized as important components within frequent fire forests because of the understory plant diversity they support (Matonis and Binkley, 2018) and wildlife habitat they provide (Reynolds et al., 2013). Quantifying the shape and size of these components, however, has been notoriously difficult (Larson and Churchill, 2012). This non-forested space has been broadly described by other studies using simple metrics such as percent open, while more recent studies have used the "empty space" concept (Clyatt et al., 2016; Matonis and Binkley, 2018; Pawlikowski et al., 2019). The empty space method is easy to understand and a good broad or global method to describe the amount of open space, but fails to quantify the distribution of these open spaces. Therefore, in addition to the open space method, some studies differentiate the open space into gaps and large openings (Churchill et al., 2017). Identifying large openings as a distinct component facilitates assessing the size distribution to determine if the open space is concentrated in one large opening or in several smaller ones.

Understanding and replicating tree and openings spatial patterns is critically important, but research on the subject has yet to capture the variability and factors responsible for pattern variability. These patterns directly influence ecological processes such as fire behavior (Graham et al., 2004), tree competition and growth (Biondi et al., 1994; Boyden and Binkley, 2015), regeneration (Sánchez Meador et al., 2009, Malone et al., 2018; Pawlikowski et al., 2019), understory development (Matonis and Binkley, 2018), wind flow, and creation of wildlife habitat (Reynolds et al., 2013). Only relatively recently, however, have attempts been made to quantify and replicate this pattern in treatment prescriptions (Churchill et al., 2013). One unique aspect of quantifying spatial pattern within frequent-fire forests has been the need to capture and implement these patterns at larger scales compared to traditional silvicultural or other forestry activities (Sánchez Meador et al., 2009). For instance, typical forestry studies use 0.01- to 0.1-ha plots to sample tree densities and basal area, based on the assumption that trees are arranged in a random spatial pattern (Smith et al., 1997). Yet, small plot analyses may underestimate the size of the largest groups of trees as well as the size of openings. The aggregated spatial pattern of most dry forests (Larson and Churchill, 2012) requires sampling using larger plots (> 0.5 ha) (Knapp et al., 2013, White, 1985). Larger plots, and the time-consuming process of stem-mapping trees, has limited replication across sites and conditions. As a result, sampling across a wide range of conditions and tree densities is needed to understand their impact on tree and opening spatial patterns (Sánchez Meador et al., 2009; Reynolds et al., 2013).

Tree and open space metrics often differ between sites; however, it is not clear whether these differences are directly due to site conditions (e.g., soils, precipitation, topography, region, or past disturbances) or indirectly related to changes in tree densities. For example, Abella and Denton (2009) compared spatial pattern between "ecosystem types," defined as areas with similar parent material and precipitation patterns. They found strong relationships between tree density and certain tree spatial metrics, but also found substantial variation within ecosystem types. Following the recommendations by Larson and Churchill (2012), recent papers have introduced new metrics to describe tree spatial patterns (Lydersen et al., 2013; Clyatt et al., 2016; Tinkham et al., 2017). These new metrics have been largely focused on the density, frequency, and distribution of single trees and groups. While studying

multiple plots in Montana, USA, Clyatt et al. (2016) found a positive relationship between tree density and group size as well as percentage of trees within groups. Clyatt et al. (2016) also noted differences in the group size frequency distribution between regions and attributed those differences to changes in tree density related to historical fire regimes. In general, there is still a need to determine how forest spatial metrics differ within and between sites, and better understand the main drivers responsible for these differences (Sánchez Meador et al., 2010). Managers and researchers need this information to make adjustments when implementing or evaluating treatments across varying site conditions and tree densities. Understanding the spatial pattern and variability of ponderosa pine forests is critical for providing guidance to land management plans designed to create the desired forest structural and spatial patterns that are less prone to stand-replacing crown fires (Churchill et al., 2013).

By sampling two large relict (minimally logged) pure ponderosa pine study sites the goal of this study was to assess tree and opening spatial patterns both between and within sites. Our intent was to capture the heterogeneity within each site including sub-areas with similar densities (Fig. 1). The objectives of the study were to: (1) establish definitive characteristics for the grouped arrangement of ponderosa pine trees greater than 40 cm DBH in old-growth (yellow-barked) stands in the Southwest, (2) compare overall tree spatial pattern between the two sites, (3) determine how spatial patterns change as a function of tree densities within and between sites, and (4) quantify the area of openings, gaps and "empty space" in each study site.

2. Methods

2.1. Study area

To study the historical spatial structure of ponderosa pine forests, we selected a study site within each of two experimental forests with similar species composition and disturbance history. The Fort Valley site was within the Fort Valley Experimental Forest and the Long Valley site was within Long Valley Experimental Forest, both in the Coconino National Forest in northern Arizona, USA (Fig. 1). Fort Valley is 11 km northwest of Flagstaff, Arizona at an elevation of 2 250 m on soils derived from basalt and cinders (Avery et al., 1976) with an average annual precipitation of 51 cm (Western Regional Climate Center, 2019). The Long Valley site is 90 km southwest of Flagstaff at an elevation of 2 100 m on soils developed from weathered sandstone with limestone inclusions (Wheeler and Williams, 1974); annual precipitation averages 67 cm (Western Regional Climate Center, 2019). In general, the precipitation pattern in this region is bimodal, received primarily as late summer rain and winter snow.

Within Fort Valley we sampled a 32-ha area that was set aside as the "control" for other studies shortly after the experimental forest was established in 1906. Within Long Valley we sampled a 73-ha site that was first inventoried in 1937. At Fort Valley, livestock grazing was eliminated in 1926 and there has been no logging except for localized firewood cutting (Covington and Sackett 1984; Sutherland et al. 1991). At Long Valley, a light "sanitation cut" removed diseased or insect-infested trees in 1967 (Sackett 1980). Both sites still contain most trees that established during a period of natural frequent fires (prior to 1880) and are part of the few remaining "intact" old-growth forests in the Southwest. Between 1700 and 1900 the mean fire-return interval for widespread fires (fires that scarred 25% of the fire scar samples) was 7 and 5 years at Long Valley and Fort Valley, respectively (Swetnam and Baisan, 1996). Both study sites are dominated by ponderosa pine with scattered alligator juniper (*Juniperus deppeana* Steud.) and Gambel oak (*Quercus gambelii* Nutt.) shrubs.

2.2. Field methods

The tree populations of interest within each relict site were old-growth ponderosa pine trees that established under a frequent fire regime. We defined "old growth" as trees > 40 cm diameter at breast height (DBH: at 1.45 m height) with "old morphology characteristics" such as yellow bark, flattened top, and tall crown base height (sensu Brown et al., 2019). The DBH cutoff was based on guidelines adopted in restoration projects in the Southwestern United States (e.g., Coughlan, 2003; Abrams and Burns, 2007). When we started fieldwork, the two most commonly mentioned cutoff definitions for old-growth were 37 or 40 cm DBH (White, 1985; Abella et al., 2006; Schneider et al., 2016). We chose 40 cm DBH for stem-mapping data collection even though some old-growth, yellow-barked trees are less than 40 cm DBH, and some relatively young trees are less than 40 cm DBH but not yellow-barked.

Within each study site we recorded DBH and the geographic position, in meters, as Universal Transverse Mercator (UTM zone 12N) coordinates using North American Datum (NAD 83) projection, of all ponderosa pine trees with a DBH less than 40 cm. The stem-mapping process began by first establishing a reference point within a relatively open area for improved satellite reception using high precision (submeter) global positioning system (GPS) units (Trimble® Geo XH, Trimble, USA). Once the reference point was established, this location was "off-set" using a laser rangefinder (TruePulse™ 360° B, Laser Technology Inc., USA) to determine the distance and direction to the outermost edge of individual trees. Each GPS point was differentially corrected to an estimated average accuracy of less than 0.2 m. In addition, canopy measurements were conducted for 156 randomly selected trees (> 40 cm DBH) at each site. Canopy radius was measured from the stem to the edge of the canopy, and canopy intersection with another canopy was documented. These were measured and recorded along the four cardinal directions as well as the maximum and minimum canopy distances.

2.3. Simulation model

We were also interested in evaluating changes in spatial pattern metrics as a function of tree density within each study site. We therefore simulated 1,000 4-ha plots from fitted models of each study site incorporating field data parameters. For the fitted models, we assumed that points were distributed as a Neyman-Scott process such that tree groupings are formed as clusters of points arising from spatially Poisson-distributed cluster center points (Diggle 2014). The cluster member points in turn have a specified spatial distribution about the cluster center points. The distribution of cluster center points within both Long Valley and Fort Valley were spatially inhomogeneous with no simple eastward or northward trend. This precluded the use of stem density models containing linear directional trends. We therefore adopted a flexible nonparametric third-order spline function that allowed for greater complexity in the trend surface (Hastie 1992).

To simulate the spatial distribution of cluster members about each cluster center, we adopted a variance-gamma relationship with a cross-sectional density that is greater near the cluster center and attenuates as a function of distance from the cluster center (Baddeley et al. 2015). From available cluster models, the variance gamma model showed the best fit between the fitted model and the actual Long Valley and Fort Valley observed stem locations. We confirmed the goodness of fit of the final model using the following three metrics, which compared observed and model-predicted spatial point distributions: (1) $G(r)$, the nearest neighbor distance function; 2) $L(r)$, Besag's transformation of Ripley's $K(r)$; and 3) $g(r)$, the pair correlation function (Schabenberger and Gotway, 2005). For each metric, we performed Diggle-Cressie-Loosmore-Ford (DCLF) tests to assess goodness of fit (Baddeley et al., 2014). The DCLF test evaluates the probability that the observed and modeled point patterns are from the same distribution. Therefore, a small p-value is indicative of a poor fit (Table 1). Modeled and observed point intensities are shown in Appendix A. All models were estimated using the R statistical computing platform (R Core Team, 2018) and R

Table 1
p-values for G(r), L(r), and g(r) for Diggle-Cressie-Loosmore-Ford test confirming model used for simulations. Smaller p-values represent poor fit between the predicted and observed spatial distributions.

Summary Function	Long Valley	Fort Valley
G(r)	0.236	0.071
L(r)	0.970	0.660
g(r)	0.510	0.770

library spatstat (Baddeley et al., 2015).

2.4. Defining trees and groups

Tree spatial pattern descriptions must differentiate between single trees and tree groups. Defining groups is rooted in the idea that trees within a group are "connected," thereby facilitating migration or spread between trees within the group. For example, in the context of fire spread, a group could be defined where crown fire could spread between crowns under certain conditions. A group could also be defined by the distance needed for dwarf mistletoe (*Arceuthobium* spp.) seeds to spread between trees (Robinson and Geils, 2006). One often cited group definition is in regards to wildlife habitat, where a group is defined as two or more trees with interlocking or nearly interlocking crowns within which tree squirrels could travel while avoiding the forest floor (Reynolds et al., 2013). A number of recent studies that have described reference tree spatial patterns use this definition, although it is still unclear how and when tree canopies are measured. Tree canopy radius varies as a function of tree diameter and competition (Sánchez Meador et al., 2011). Most of the recent literature has defined groups based on a fixed inter-tree distance (ITD), meaning that two trees are within a group when the distance between them is less than or equal to the ITD (Lydersen et al. 2013; Brown et al. 2015; Clyatt et al. 2016).

To narrow in on possible threshold inter-tree distance levels for use in defining the final group, we considered statistical and ecological factors. Statistically we first created groups using hierarchical cluster analysis based on the geographic locations (UTM easting and northing) for each tree. The distance matrix of (Euclidian) inter-tree distances between all trees was created using PROC Cluster in SAS/STAT 90.4 based on the single linkage method. In this analysis, initially each tree is an individual, then the two trees separated by the shortest distance are joined to form a group. This process is repeated until all trees are part of a single group, similar to a method used by Larson and Churchill (2008) to create tree groups. Proc TREE in SAS/STAT 9.4 was then used to produce a dendrogram which included all trees to visually identify the most distinct tree groups and to determine possible threshold distance levels. The groups identified using cluster analysis were ecologically evaluated in the field and compared to canopy measurements before we decided on the final ITD group criteria.

2.5. Comparison between sites

Global tree spatial patterns within each site were analyzed using Ripley's K point pattern analysis in the spatstat package (Baddeley et al., 2015) in R v.3.4.1. The null hypothesis of this test is that points are randomly distributed. To determine whether trees were distributed in a random, clustered or dispersed fashion, we used the inhomogeneous Ripley's K(r). Due to the spatial trend within both sites we used univariate L_{inhom} *(r)* function specifically designed for inhomogenous point processes. The K-function was normalized to L(r)-r in order to simplify interpretation (Besag, 1977). The neirnorbohood radius r about each point was limited to distances of 0–100 m in Fort Valley and 0–200 m in Long Valley (half the shortest plot dimension; sensu Dixon, 2002) to minimize the influence of unobserved points near observed points close to the plot edge (Boots and Getis, 1988). Significant clustering or dispersion was determined by comparing observed L_{inhom} *(r)* - r transformation values to a 95% confidence envelope based on 999 permutations of simulated complete spatial randomness (Upton and Fingleton, 1985).

To compare tree spatial patterns between the two study sites we conducted two distinct but complementary analyses. The first analysis compared the two sampled study sites using the collected field data. The second analysis focused on simulations generated from the fitted model for each study area. For each of the two study sites, we randomly located 1,000 4-ha plot (200 m × 200 m). Each randomly located plot was therefore characteristic of the modeled density of cluster centers at that location. The simulations were then used to calculate various spatial metrics. Four hectares has previously been identified as the optimal plot size for measuring tree spatial pattern in dry forests (North et al. 2007; Larson and Churchill 2012). For both the field data and the modelled iterations we defined a tree group as two or more trees within a specified ITD (stem-to-stem). Trees that did not have neighboring trees within the specified distance were identified as singles. Single trees were described according to the following spatial metrics: singles ha^{-1}, and % singles. Tree group spatial metrics included: groups ha^{-1}, % of trees within groups, mean group size, maximum group size, and mean nearest neighbor distance (NND) within groups. The spatial relationship between trees was compared using the mean NND between all trees within each site, mean NND among trees within groups, and mean NND among singles.

In addition to tree spatial patterns we also quantified gaps and openings within the two sites. We defined openings as non-canopy areas that include a core without tree competition. According to Boyden and Binkley (2015) , competition is strongest within 14 m from ponderosa pine trees; therefore we first created a polygon of all areas greater than 15 m from any tree stem. We then delineated openings by buffering the polygon by 10 m which expanded the area of the opening to the edge of the tree canopy (5 m away from the tree stem). Intersecting and adjoining polygons were then merged to form continuous polygons. This method, described by Churchill et al. (2017), ended up identifying openings that were at least 30 m wide on all sides (tree-stem to tree-stem). The number and size of openings was then calculated for each site, and described in terms of opening size distribution, total area within openings and percent of total site area within openings. In addition to openings we also measured gaps, defined as areas beyond the tree canopy (> 5 m from a tree stem) and not part of an opening. Therefore by definition gaps are less than 10 m from a tree canopy (or < 15 m from a tree stem).

In addition to gaps and openings, we also quantified the distance to the nearest tree for each site by creating buffers at different distances (Matonis and Binkley, 2018; Churchill et al., 2017). We then calculated the "empty areas" within each of the following distance from tree classes: 0–3 m, 3–5 m 5–10 m, 10–15 m, and 20 + m. The percentage of area within each of these classes was then calculated for each site and compared graphically.

3. Results

In general, both Long Valley and Fort Valley exhibited similar global tree spatial patterns, but at different scales (Fig. 2). That is, both sites showed a clustered spatial pattern at short distances, a random pattern at medium distances, and a dispersed pattern at long distances. In Long Valley, the clustered pattern was exhibited up to 70 m, with a random pattern from 70 to 90 m, and a dispersed spatial pattern at distances greater than 90 m. In Fort Valley, the clustered pattern was between 1 and 50 m, while the dispersed pattern extended beyond 60 m.

The cluster analysis showed that a 9–11 m (threshold) ITD was optimal for separating tree groups across both sites. This 2-meter range was judged to best meet descriptive statistical separation on the dendrogram and visual separation between tree groups in the field. With these large data sets, a 2-meter variation was necessary to prevent

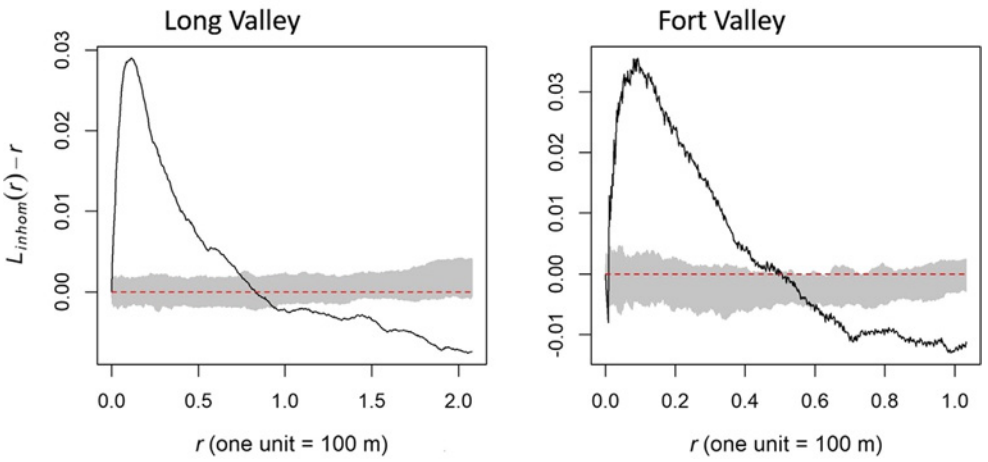

Fig. 2. Global tree spatial pattern within Long Valley and Fort Valley study sites. Ripley's K transformed values (L_{inhom} *(r)* – r) across lag distances in meters. Observed (solid line) above the shaded area indicated distances at which trees are clustered, while observed values within the shaded area are considered random and observed values below the shaded are considered dispersed.

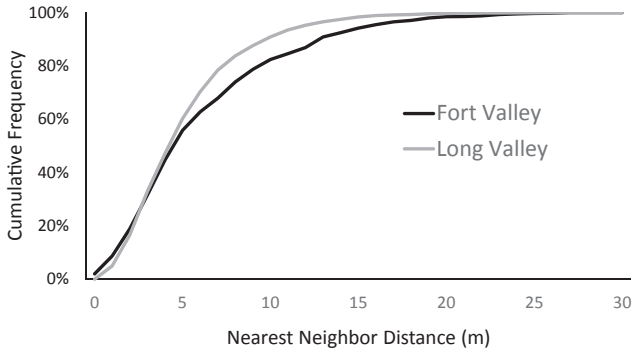

Fig. 3. Percent cumulative frequency of trees within Long Valley and Fort Valley based on nearest neighbor distance (meters).

splitting a group, or combining two groups that were distinct graphically on the dendrogram as well as visually in the field. The cumulative number of trees placed in groups also tended to flatten out at the 9–11 m ITD threshold (Fig. 3). For the following analyses, we defined groups using an ITD of 10 m based on two considerations (Fig. 4). First, field data collected within both sites show that the maximum canopy radius was 4.3 m among non-interlocking crowns. Moreover, 60% of these trees had a maximum canopy radius of at least 5 m (Appendix B). Hence, we consider this to be the potential achievable canopy radius for mature ponderosa pines in the absence of crown competition. Second, we observed during field visits that a 10-m ITD best represented tree groups with overlapping canopies. Thus, we define a group as all trees less than 10 m from other trees. Trees less than 10 m from its nearest neighbor are classified as single trees (Fig. 4). To facilitate comparisons with other studies we also used a 6-m ITD and calculated the same tree spatial metrics.

3.1. Tree spatial patterns compared between sites

Tree spatial metrics are sensitive to the methods used to identify groups. In some respects the ITD is directly related to the NND. For example, 82% of trees in Fort Valley are less than 10 m from another tree (Fig. 3), meaning that at an ITD of 10 m, 82% of trees are in groups while 18% of trees are singles. Moreover, in Fort Valley the average TPH was 41, so on average there were 7.3 singles ha^{-1} (Table 2). Using the same 10-m ITD to define groups in Long Valley, 91% of trees are within groups and 9% are singles, or an average of 5.6 singles ha^{-1} (Table 2). At an ITD of 6 m, in Fort Valley 63% of trees would be in

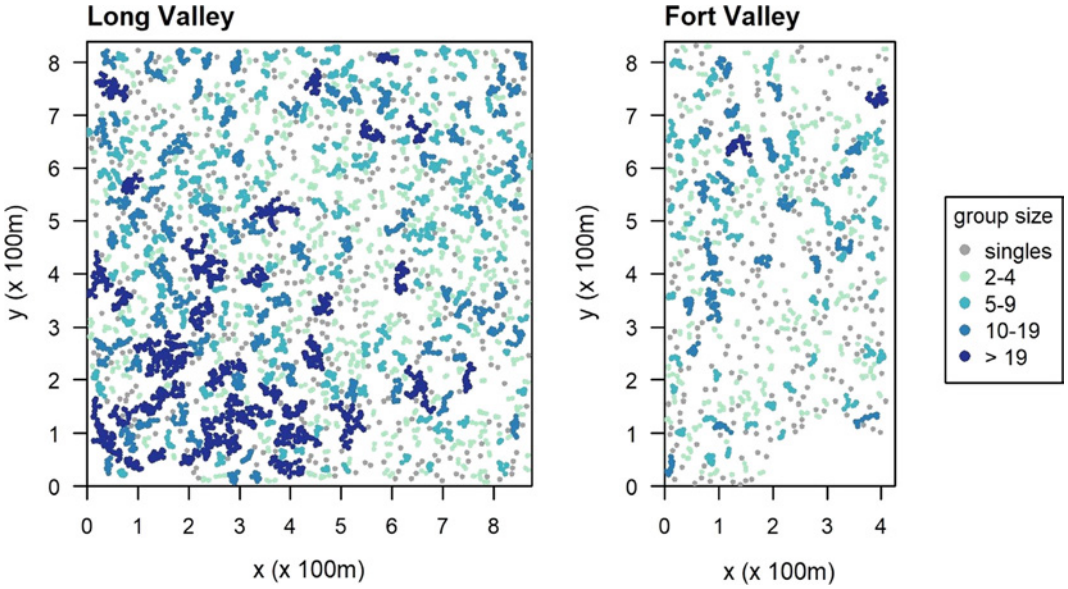

Fig. 4. (color). Tree groups in Long Valley (left) and Fort Valley (right) sites based on 10 m inter-tree distance (5-m buffer around each point) with overlapping buffers creating tree groups. Each dot represents an individual tree location (all *Pinus ponderosa*) and adjacent dots with similar colors are members of the same group. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Comparison of tree spatial pattern metrics between Fort Valley and Long Valley based on stem-mapped tree data.

	Fort Valley	Long Valley
Total trees ha^{-1}	40.9	61.7
Singles ha^{-1}	7.3	5.6
% Singles	17.9%	9.1%
Groups ha^{-1}	7.2	8.1
Trees within Groups ha^{-1}	33.6	56.1
% trees within groups	82.1%	90.9%
Maximum Group Size	22	113
Mean Group Size	4.7	6.9
Mean NND (all trees)	6	5
Mean NND (trees within groups)	4.1	4.2
Mean NND (just singles)	14.3	13

groups, meaning that 37% of trees would be classified as singles, while in Long Valley the split would be 70%/30% between trees in groups versus singles (Fig. 3). These dramatic differences between spatial metrics based on the same spatial data highlight the sensitivity of these metrics to definitions of groups and singles. However, Fig. 3 also illustrates a potentially simple but powerful method for comparing spatial patterns between studies and inter-tree distance definitions (Sánchez Meador et al., 2011).

Overall the number of groups per area was similar, but the group size distribution differed between sites. The average number of groups ha^{-1} was similar between Long Valley and Fort Valley (Table 2); however, Long Valley generally had more trees per group. In Long Valley groups averaged 6.9 trees per group, or > 2 additional trees per group compared to Fort Valley (Table 2). The group size distributions were skewed toward smaller groups (2–4 trees group^{-1}) at both sites (Fig. 5). Long Valley had a greater proportion of larger groups (≥10 trees group^{-1}) compared to Fort Valley. Long Valley contained 24 groups with ≥24 trees, and the largest group had 113 trees, while the largest group we found in Fort Valley contained 23 trees. Based on the field data, the mean NND for all trees differed by 1 m between the two sites (Table 2). When considering only the trees within groups, the maximum NND is of course < 10 m, thereby reducing the mean NND to 4.1 m within Fort Valley and 4.2 m within Long Valley. Therefore the total NND difference between sites was mainly due to singles, which were on average 1 m farther apart in Fort Valley (Table 2).

The diameter distribution pattern was relatively similar between the two sites, but differed for single trees and trees within groups (Fig. 6). In Fort Valley, single trees averaged 61 cm DBH compared to trees within groups which averaged 59 cm DBH. Similarly, in Long Valley single trees had an average diameter of 59 cm while trees within groups averaged 56 cm DBH. In regards to the diameter distributions, in Fort Valley 18% of single trees were larger than 80 cm DBH, whereas such

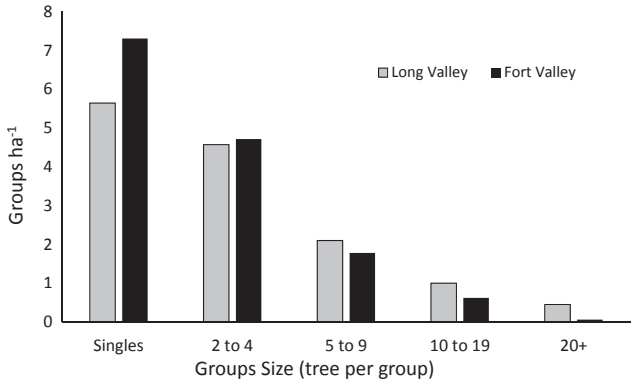

Fig. 5. Singles and group size distribution on a ha^{-1} basis for Long Valley and Fort Valley sites in northern Arizona.

large trees made up only 7% of the total trees within groups. Similarly, in Long Valley, trees larger than 80 cm DBH accounted for 12% of all singles, but only 5% of all trees within groups (Fig. 6). At Fort Valley the total basal area was 11.8 m^2 ha^{-1}, 80.5% of which was in trees within groups and 19.5% in singles. In Long Valley basal area was 16.2 m^2 ha^{-1}, and 90% was in trees that were part of a group.

3.2. Changes across tree densities within and between sites

By generating 1,000 model simulations of each study site based on the same spatial attributes as the original field data and sampling each iteration using 4-ha plots, we examined how ponderosa pine spatial metrics change as a function of tree density at each site. We found that in Long Valley tree densities ranged from 35 to 100 TPH, while in Fort Valley densities ranged from 10 to 70 TPH (Fig. 7). Despite differences in the range of tree densities, spatial pattern metrics changed consistently across tree densities at both sites. In terms of singles ha^{-1}, Long Valley and Fort Valley differed only slightly (< 1 single ha^{-1}) at any given tree density (Table 3). In Fort Valley, at tree densities between 10 and 30 TPH, singles ha^{-1} increased as total tree densities increased (Fig. 7a). Where the TPH ranges overlap (40–60 TPH) between sites, singles ha^{-1} decreased at a general rate of one fewer single for every increase of 15–20 TPH. In Long Valley at densities greater than 70 TPH, singles ha^{-1} continued to decrease with increasing tree densities, but at a slower rate (Fig. 7a). Differences in singles ha^{-1} were more pronounced when we consider singles as a percentage of all trees. For example, in Fort Valley, singles on average constituted 37.5% of all trees at 20 TPH, but only10% at 60 TPH (Table 3).

The number of groups ha^{-1} tended to increase from low to mid tree densities and decline from mid to high densities (Fig. 7b) within both sites. Between 20 and 40 TPH, the number of groups ha^{-1} increased with increasing overall tree densities from 4.2 to 8 groups ha^{-1} (Table 3). Where their ranges overlapped group ha^{-1} differed between the two sites by less than 1 group ha^{-1} for any given TPH. The number of groups ha^{-1} peaked at tree densities around 60 TPH, but started to decrease at higher densities. The average number of groups ha^{-1} peaked at slightly different tree densities within each site. Moreover, Long Valley, which had sub-sites with higher TPH, showed a slight decrease in groups ha^{-1} at higher tree densities (Fig. 7b).

Our simulation results suggest that increasing tree densities did not result in more groups or singles but instead resulted in larger groups. That is, in both sites, the number of trees within groups increased proportionally with increasing tree densities (Table 3). The relationship between the number of trees within a group and TPH is essentially the same between the two sites (Fig. 7c). Increasing tree densities also resulted in significant changes to the group size distribution. The general pattern of these changes was again consistent between the two sites. In general, areas with the lowest tree density were dominated by small groups consisting of 2–3 trees group^{-1} (Fig. 8). In addition, larger groups (10 trees group^{-1}) were generally underrepresented in areas with low tree densities (< 40 TPH). As tree densities increased, the proportion of small groups generally declined and the frequency of larger groups increased. Plots with the highest tree densities (80 TPH) had an almost flat group size distribution; no size group was dominant (Fig. 8). In such cases, however, most trees not only were part of a group but were more likely to be part of a large group (> 15 trees group^{-1}).

3.3. Gaps and openings

The area not occupied by tree canopies (> 5 m from a tree stem) accounted for 68% and 77% of the total area within Long Valley and Fort Valley, respectively. In Long Valley 42% of the total area was in openings and 26% in gaps, whereas in Fort Valley 58% of the area was openings and 19% percent gaps. At both sites, the size distribution of openings was dominated by small openings with more than half of all

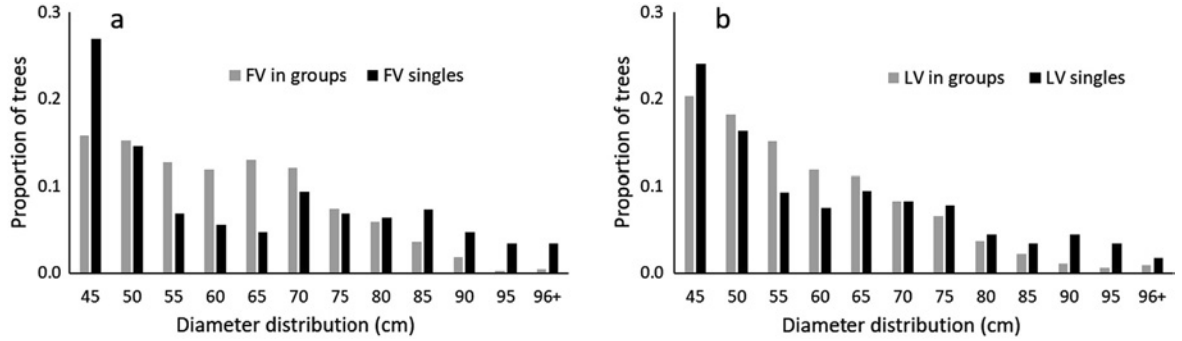

Fig. 6. Diameter distribution of single trees and trees within groups in (a) Fort Valley and (b) Long Valley.

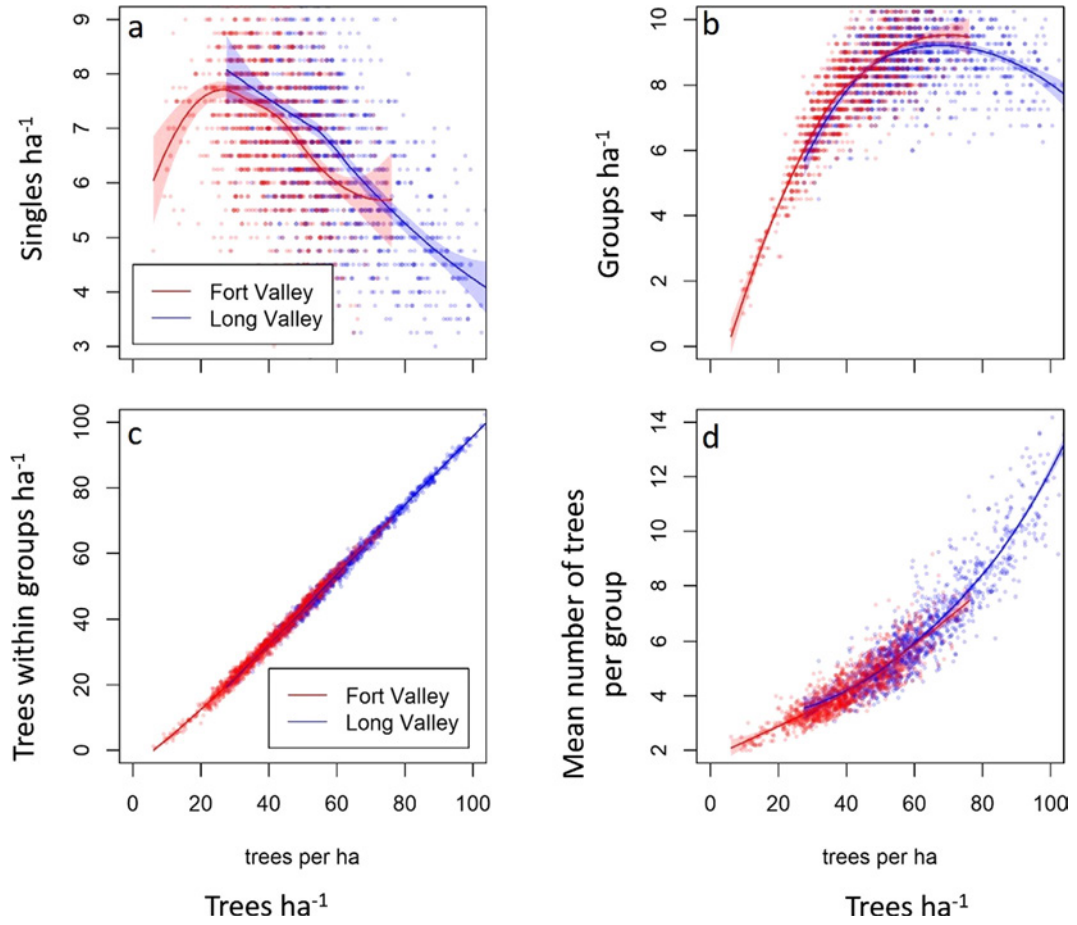

Fig. 7. (color). Relationship between tree densities (trees ha^{-1}) and (a) singles ha^{-1}, (b) groups ha^{-1}, (c) trees within groups ha^{-1} and (d) mean group size within Long Valley and Fort Valley based on 1,000 simulations modelled using field data. Each point represents a value sampled using 4-ha plots within each simulated landscape.

openings being < 0.1 ha (Fig. 9a). Although large openings were less common, they occupied more than one third of the total area in Fort Valley (Fig. 9b). Small openings tended to be round, whereas medium openings tended to be elongated and large openings tended to be interconnected and sinuous (Appendix C).

Due to the greater tree density at Long Valley, this site tended to have more of the total area within 5 m of a tree compared to Fort Valley (Fig. 10). Conversely, Fort Valley had a greater percentage of areas that were > 15 m away from trees (Appendix D). However, at both sites the majority of the site was 5–15 m from a tree stem.

4. Discussion

4.1. Tree spatial pattern differences between sites

Our results based on field data showed differences between the two sampled sites. As expected, the difference between sites was most obvious in terms of total tree densities; Long Valley had on average 20 more trees ha^{-1} than Fort Valley. Although the two sites differed slightly in singles and groups ha^{-1}, the difference in tree density was manifested most sharply in the shift from the dominance of singles and small groups in the low tree-density Fort Valley site to the dominance of large and extra-large groups in the Long Valley site. If we consider solely the field data collected over large areas, the two sites appear to

Table 3
Comparison of average forest spatial pattern based on different tree densities within Fort Valley and Long Valley. These average estimates are based on conditions sampled within 1,000 simulations of each site sampled using 4-ha plots within each simulated site.

	Fort Valley			
Total trees ha^{-1}	20	40	60	
Singles ha^{-1}	7.5	7.3	6.0	
% Singles	37.5%	18.3%	10.0%	
Groups ha^{-1}	4.2	8.0	9.3	
Trees w-in Groups ha^{-1}	12.5	32.7	54	
% trees w/in groups	62.5%	81.8%	90.0%	
Mean Group Size	3.0	4.1	5.8	
	Long Valley			
Total trees ha^{-1}		40	60	80
Singles ha^{-1}		7.6	6.6	5.3
% Singles		19.0%	11.0%	6.6%
Groups ha^{-1}		7.8	9.1	9.0
Trees w-in Groups ha^{-1}		32.4	53.4	74.7
% trees w/in groups		81.0%	89.0%	93.4%
Mean Group Size		4.2	5.9	8.3

have very different tree spatial patterns. Moreover, these differences could have been attributed to productivity differences related to parent material and precipitation. Such differences have also been found on other studies in the southwestern United States (Abella and Denton, 2009; Rodman et al., 2017). For example, Schneider et al. (2016) sampled limestone soils in northern Arizona and found higher tree densities compared to sites adjacent to Fort Valley sampled previously by Sánchez Meador et al. (2011). Results of both studies also show some spatial pattern differences, with more groups ha^{-1} found in the limestone site compared to the basalt site. However, the analysis of our field data and simulations provides other insights into the drivers of tree spatial patterns.

4.2. Comparison across similar tree densities within each site

As previously noted, sedimentary soils tend to hold more moisture, supporting greater tree densities. Within each site, however, we found that tree densities are highly inhomogeneous due to a combination of factors including topography and past disturbances such as fire, insects, or mistletoe (Abella and Denton, 2009). Stem-mapping of relatively large sites allowed us to capture this microsite variability and better understand how spatial patterns vary within each site as a function of tree density. The sub-sampling results suggest that the range of tree densities overlap between the two sites, meaning that some sub-areas within the two sites share similar tree densities. The overlap between sites occurred at tree densities between 35 and 65 TPH. Therefore, within this overlapping range we can compare spatial tree patterns

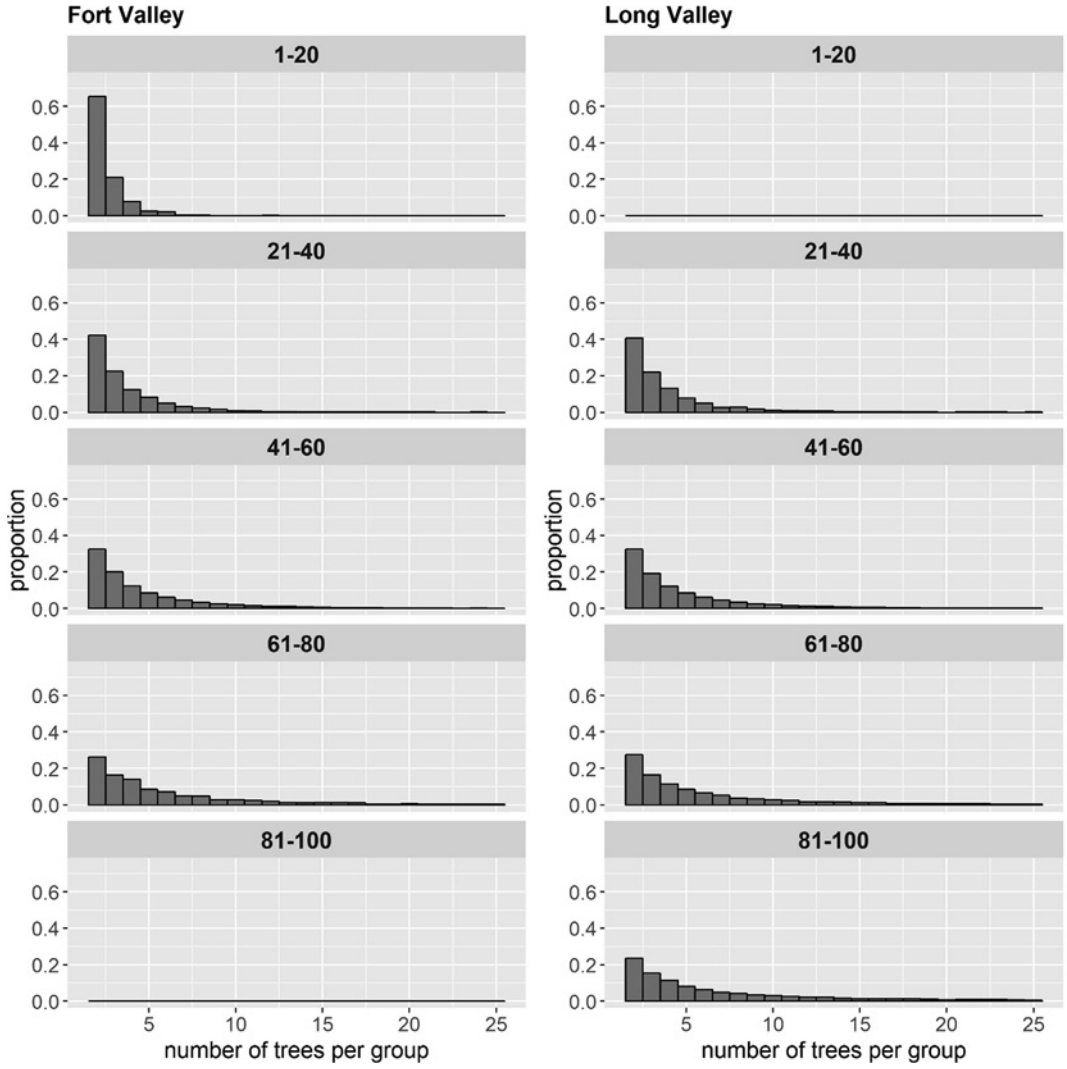

Fig. 8. Group size (number of trees group^{-1}) distribution as a function of different tree density (trees ha^{-1}) classes for (a) Fort Valley and (b) Long Valley based on 1,000 simulations models of the field data. Each graph is based on a 4-ha sample area within each simulation.

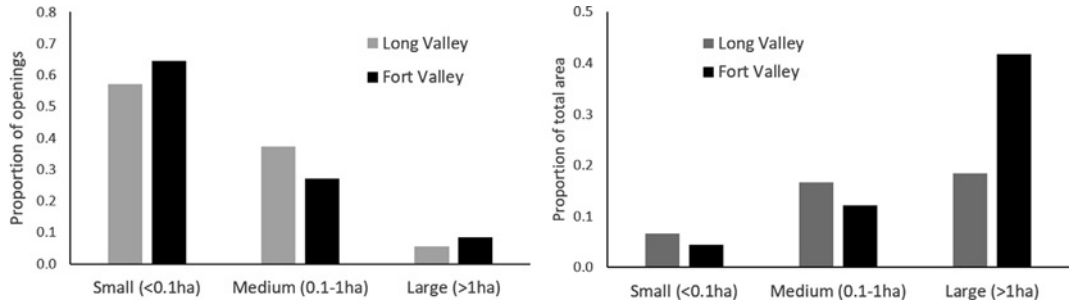

Fig. 9. Opening size distribution and proportion of the total area occupied by different sized openings within Long Valley and Fort Valley.

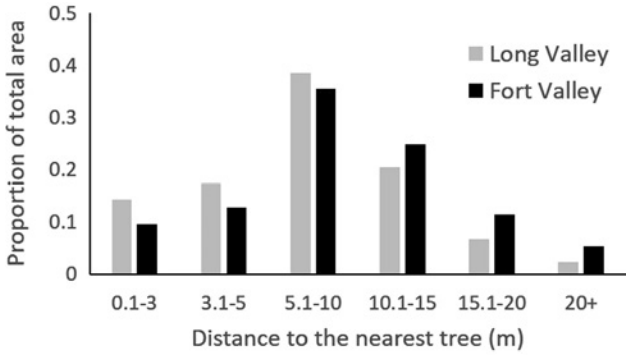

Fig. 10. Empty space distribution described as the distance from the nearest tree (m) within Long Valley and Fort Valley.

between sites while controlling for tree density. Averaged results from the simulations indicate that when tree densities are equal, the spatial patterns are actually very similar between the two sites. For example, at a density of 35 and 65 TPH, the difference between the two sites is less than one single and one group ha^{-1} (Table 3). The percentage of trees within groups is similar when TPH are equal and decrease at a similar rate as tree densities increase at both sites. For example, at a TPH of 40 both Long Valley and Fort Valley average about 81% of trees within groups, while at 60 TPH that increases to around 90%. The same synchronous relationship applies to mean group size, which increases with increasing tree densities (Table 3).

The within-site subsampling suggests that the differences in spatial pattern observed between sites is actually a function of tree density rather than site properties such as parent material or precipitation. That is, each site showed high within-site variability in tree density, yet at similar densities, spatial patterns were similar on the two sites. Likely due to sedimentary soils and greater precipitation, a larger portion of Long Valley had high tree densities compared to Fort Valley (Fig. 1). However, when we examined spatial patterns at similar tree densities on the two sites, the spatial attributes were very similar. These results suggest that it is important to consider microsite variability within sites and adjust spatial patterns according to the desired tree densities to produce more heterogeneous and resilient landscapes (Churchill et al., 2013).

4.3. Where do the "additional trees" go?

As tree density increases, we need to understand how "additional trees" are distributed among singles and tree groups. In theory, the additional trees could result in more singles, more groups, or larger groups. Our field data indicated that despite large differences in total tree densities, the two sites differed only marginally in singles and groups ha^{-1}. These results suggest that as the number of trees increased, these additional trees integrated into existing groups (Fig. 7c) rather than creating new groups. This pattern led to a general increase in group size (Fig. 7d), hence fewer small groups and more large groups at Long Valley (Fig. 8). Further, as groups become larger, they are more likely to "merge" with other groups, creating the extra-large groups of ≥ 20 trees. This pattern is also apparent in the simulated data, where tree density increases tend to result in an increase in the number of large groups at both sites (Fig. 8). That is, areas with greater tree densities tend to have group size distributions with "longer tails". In general, singles ha^{-1} marginally increase with increasing tree density, whereas singles as a percentage of all trees drastically decrease with increasing tree density (Table 3). For example, at low tree densities, up to 50% of all trees are singles, but at high densities singles can account for less than 10% of all trees (Table 3). This sizable difference in the percentage of singles with increasing tree density has also been found in other studies (Table 4) of tree spatial patterns (Brown et al., 2015).

4.4. Tree spatial patterns comparisons to other studies

Compared to other recent studies that have described tree spatial patterns using trees and groups, our results have both commonalities and new insights. In this study we have defined tree groups using an ITD of 10 m, however we have also included the same spatial metrics based on a 6-m ITD (Table 4; Fig. 11). This information is useful for comparing with other published studies as well as for considering management implications. A number of studies have previously provided attributes on singles and tree groups in dry forests across the western United States. All of these studies consistently report trees and groups ha^{-1}, yet there is no consistent use of other spatial metrics. For example, Brown et al. (2015) also reported % trees within groups, while Clyatt et al. (2016) reported % singles. To better understand general trends in tree spatial patterns across these studies, we used the values provided by these authors to calculate a standard set of spatial metrics and facilitate comparisons among studies from different sites (Table 4). Compared to these other studies, the tree densities we found at our two sites are on the lower end of a continuum ranging from 25 to 170 TPH. Contrary to our simulation results, the pattern among the literature appears to show a general increase in both singles and groups ha^{-1} with increasing tree density, although these values are highly variable. In relative terms, the proportion of trees within groups appears to increase (and % singles decreases) as total tree densities increase (Table 4). This pattern is identical to our findings based on the model simulations (Table 3) and support the idea that spatial patterns are a function of tree densities and are only indirectly related to site conditions.

4.5. Open spaces

Similar to tree spatial metrics, our results show that empty space is influenced by tree density. That is, Fort Valley had a greater percentage of areas greater than 5 m from a tree compared to Long Valley, where higher tree densities made it difficult to find areas greater than 15 m away from a tree. In some ways the distribution of openings was the inverse of the tree group size distribution. That is, the dominance of singles and small tree groups allowed for a greater proportion of the

Table 4
Tree spatial patterns found in Long Valley (LV) and Fort Valley (FV) compared to other studies across the western United States that have reported spatial pattern using metrics related to single trees and groups. The sites selected for this comparison were based on species composition similar to the sites sampled in this study and are presented from increasing tree densities from left to right. Each column represents the results for a specific plot provided within a study as follows: FV and LV are the same as provided in Table 2 except in this table those metrics are based on 6-m ITD. S1B and S1A were reported in Sánchez Meador et al. (2011), SCH was reported in Schneider et al. (2016), PRE was reported in Tuten et al. (2015), HE19, HE20, and HA01 were reported in Brown et al. (2015), L1 (LOLO1), B2 (Bitterroot 2), B3 (Bitterroot 3) were reported in Clyatt et al. (2016); and LYS is based on 3 plots reported in Lydersen et al. (2013).

Site	HE19	FV	S1B	LV	S1A	SCH	L1	HE20	B2	B3	LYS	PRE	HA01
Trees ha^{-1}	**25**	**41**	**44**	**62**	**67**	**77**	**102**	**110**	**125**	**129**	**133**	**142**	**170**
Singles ha^{-1}	*10*	**15**	*11*	**18**	*16*	**24**	*23*	*18*	*29*	*28*	**17**	**37**	*22*
% singles	*41%*	*37%*	*25%*	*30%*	*24%*	*31%*	**23%**	*16%*	**23%**	**22%**	**13%**	*26%*	*13%*
Groups ha^{-1}	**14**	**26**	**10**	**31**	**11**	**18**	**46**	**20**	**49**	**54**	**23**	**27**	**22**
Trees w/in groups ha^{-1}	*15*	*26*	*33*	*43*	*51*	*54*	*79*	*92*	*96*	*101*	*117*	*105*	*148*
% trees w/in groups	**59%**	*63%*	*75%*	*70%*	*76%*	*69%*	*77%*	**84%**	*77%*	*78%*	*88%*	*74%*	**87%**
Mean trees per group	*1.1*	*1.0*	**3.6**	*1.4*	**5.4**	*2.9*	**2.2**	*4.6*	**2.6**	**2.4**	**5.2**	*3.8*	*6.7*
Max trees per group	**5**	**11**	**12**	**27**	**19**	**7**		**15**			**27**	**16.3**	**11**
Reference Year	**1860**	**2009**	**1874**	**2009**	**1874**	**1883**	**1900**	**1860**	**1900**	**1900**	**1929**	**2015**	**1860**
Min DBH (cm)	**25**	**40**	**9.4**	**40**	**9.4**	**12.5**	**1.4**	**25**	**1.4**	**1.4**	**25**	**44**	**25**
Inter-tree distance (m)	**6**	**6**	**5.2**	**6**	**5.2**	**5.2**	**6**	**6**	**6**	**6**	**6?**	**5.2**	**6**
Plot size (ha)	**0.5**	**30**	**1**	**71**	**1**	**4**	**1**	**0.5**	**1**	**1**	**4**	**2.02**	**0.5**

Bold numbers were reported within each paper. Italic numbers were not provided in the paper but were calculated based on the reported figures. Blank fields indicate where data was not provided and could not be calculated.

total area in large openings within Fort valley, where as the dominance of large groups in Long Valley prohibited large openings. These and other similar methods (Lydersen et al., 2013) are still subjective, in that the user has to define what constitutes a large opening. These more detailed methods, however are likely to be useful in development and evaluation of treatment prescriptions.

The normal distribution of empty space across distances to nearest tree we found at both sites is consistent with other studies that have reported such values (Clyatt et al., 2016; Churchill et al., 2017; Matonis and Binkley, 2018; Pawlikowski et al., 2019). This suggests that most of the empty space within these frequent-fire forests was at distances between 5 and 15 m from a tree. Functionally, gaps or areas 5–15 m from a tree are where most regeneration is likely to occur given that regeneration is closely associated with distance to seed source (Owen et al., 2017; Malone et al., 2018). These areas are also more likely to be influenced by root competition and associated tree microclimates such as shadows and snow retention (Boyden and Binkley, 2015). Conversely, openings or areas beyond 15 m from a tree are likely to have the greatest plant species diversity and more likely to restrict crown fire spread (Matonis and Binkley, 2018). It is clear, however, that the amount and distribution of empty space, gaps and openings is influenced by tree density. That is, low density sites will have less area at short distances from trees and more area at long distances from trees, such as Fort Valley. In turn, this pattern also results in a greater proportion of the area in large openings.

4.6. Limitations

One limitation of this study is that we sampled only trees that were > 40 cm DBH. Using this size cut-off likely underestimates tree densities and may explain why the tree densities we report are generally lower than those reported for other ponderosa pine forests (Table 4). White (1985) actually sampled age structure within a small section of the Fort Valley site and cored yellow bark trees less than 37 cm DBH finding that half of the trees established under a frequent fire regime (prior to 1880). This suggests that by excluding trees less than 40 cm, we underestimated tree densities, while including yellow bark < 40 cm would overestimate tree densities. Another limitation of this study is that we described tree spatial patterns, groups and gaps but did not explore how these features developed or changed over time. We could potentially explore such topics in the future by separating trees into different size/age classes similar to other studies (Youngblood et al., 2004; Boyden et al., 2005; Knapp et al., 2013). Such analysis however, were beyond the scope of the current study. Finally, there is also a need to further explore the minimum plot size required to capture spatial patterns in this forest type. Our use of a 4-ha plot for the analyses allowed us to capture large tree groups and openings, but it is possible that the spatial patterns could be captured with less effort in smaller plots.

4.7. Management Implications

The 10-m ITD is best at defining trees and groups within mature forests such as the sites sampled here. However, expecting the same tree

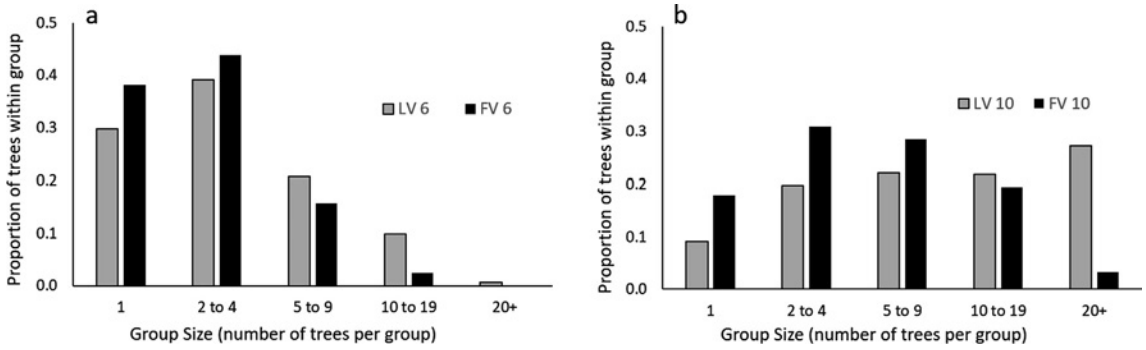

Fig. 11. The distribution of trees among singles and groups of different sizes changes drastically depending on whether they are based on ITD of (a) 6-m or (b) 10-m when comparing spatial patterns between Fort Valley and Long Valley. (Based on field data).

spatial pattern after restoration treatments within a typical second-growth fire-excluded forest would not be realistic because those trees lack the large canopies found within our sites. Instead we would suggest replicating the tree spatial pattern provided in Table 4 and Fig. 11a, where we calculated the same tree spatial matrices, but using an ITD of 6 (Fig. 11), which better matches the actual maximum canopy radius of immature forests.

Although no study has been conducted expressly to determine the optimal plot size for sampling dry forests, the recent literature and our own analysis (not presented here) suggest that 4-ha is the minimum plot size to observe unique spatial patterns (North et al., 2007; Larson and Churchill, 2012). One of the main advantages of larger plots is that they allow us to capture a greater proportion of large tree groups (5+ trees) and openings. That is, these components are likely to be "cut off" if smaller plots are used, unless they happen to be in the middle of the plot. Similarly, we believe that attempting to replicate these spatial patterns on the ground will be best served by creating heterogeneous conditions at spatial scales of at least 4 ha because many of these spatial metrics are difficult to interpret at the per hectare scale. For example, it would be difficult to replicate 0.38 groups ha^{-1}. Implementing these spatial patterns at larger scales will also result in more heterogeneous landscapes that incorporate both macro and micro-scale variability.

In regards to replicating these natural tree spatial patterns it is important to emphasize single trees and the overall group size distribution of both tree groups and openings. The lack of a normal group size distribution translates to a greater number of small tree groups and openings. Conversely, although large tree groups and openings are not frequent they actually account for a large portion of area and should therefore by emphasized according to the desired density. Overall our results suggest a range of conditions from a savanna matrix with small group-tree islands and large openings in low density conditions to areas dominated by large tree-patches and smaller openings in more dense forests.

5. Conclusions

Based on stem maps from two large sites, each with different soil parent material and precipitation, we conclude that these two sites differed in terms of tree groups, gaps and openings. Overall, the more productive Long Valley site had higher tree densities and slightly fewer singles ha^{-1}, but similar numbers of groups ha^{-1} compared to the Fort Valley site. The most important difference between the two sites was in regards to the tree group size distribution, where large (10–19 trees) and extra-large (20+ trees) tree groups were more frequent in Long Valley compared to Fort Valley. Another major difference was that the largest group in Fort Valley included 22 trees, whereas a group of 113 trees was found in Long Valley.

Despite these overall differences between sites, sub-sampling of simulated sites based on the field data showed high inter-site variability with some overlap in the range of tree densities between the two sites. Our simulated sub-sampling also showed that the spatial pattern (groups and singles) varied according to tree density, with similar rates of change between sites. Furthermore, sub-sites with similar tree densities tended to have similar spatial patterns across both Long Valley and Fort Valley. These results suggest that the overall differences we observed between sites were due to differences in tree densities and were only indirectly related to productivity. Tree densities vary at macro and microscales due to both biotic and abiotic factors; therefore spatial patterns should also be adjusted accordingly.

In general, areas with lower tree densities to have a greater proportion of trees as singles, smaller tree groups and more open space including gaps and larger openings. On the contrary, more productive areas with higher tree densities will support a greater proportion of trees in large and very large groups, with open spaces closer to trees and smaller openings. Furthermore, these results suggest that it is important to consider microsite variability within sites and adjust spatial patterns according to the desired tree densities to produce the variation in spatial patterns that characterized these old-growth forest remnants. Managers can use this variation to create heterogeneous, and hence, potentially more resilient, landscapes to better cope with an uncertain climatic future.

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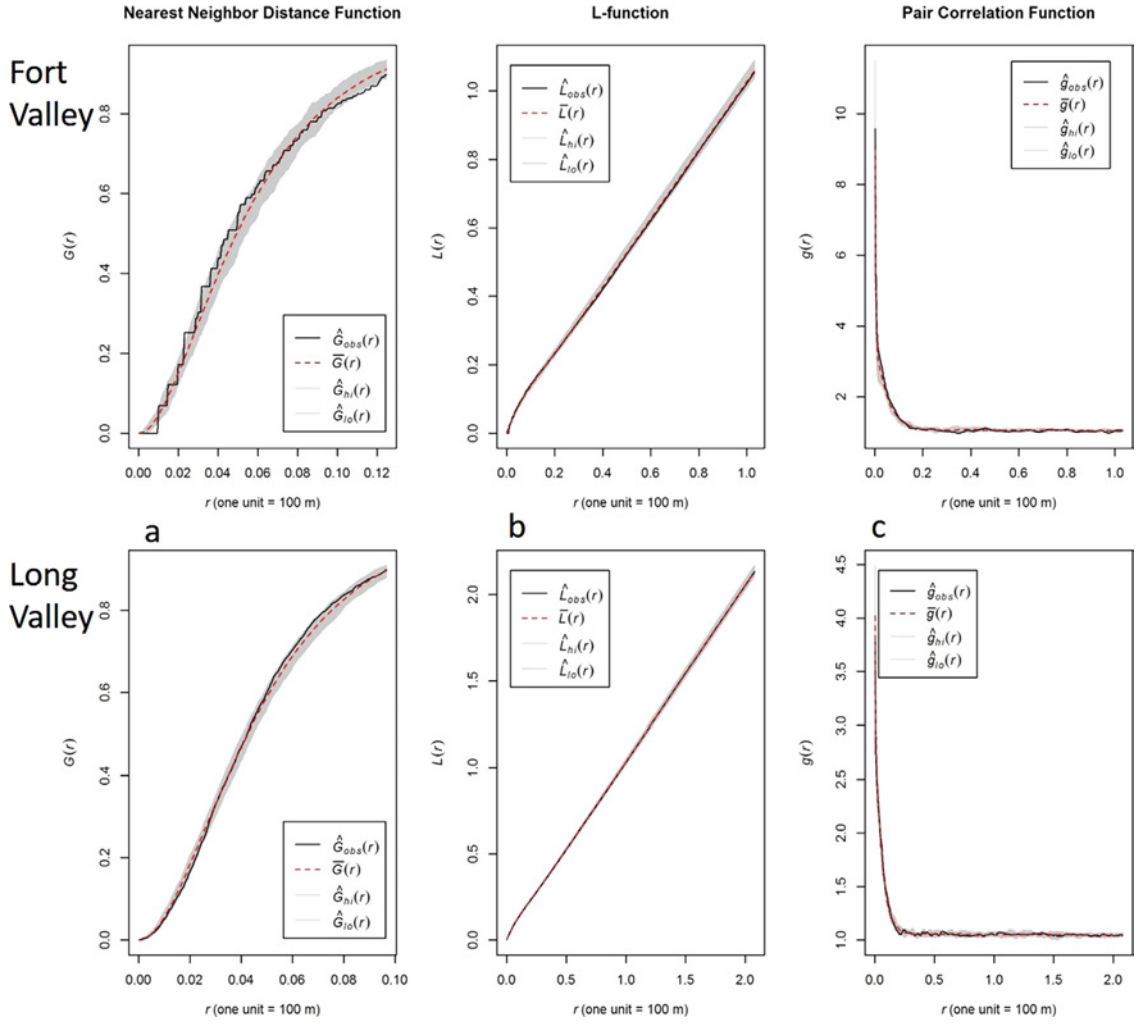
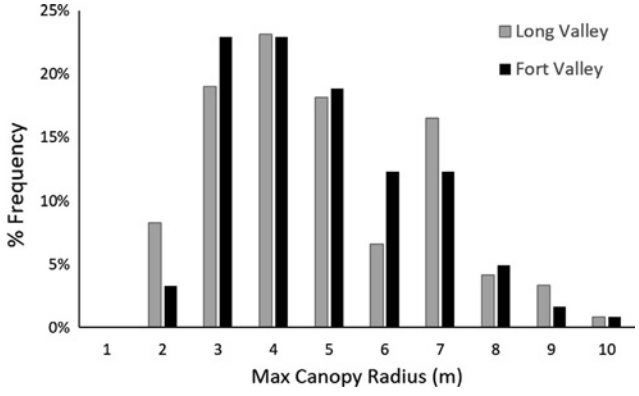
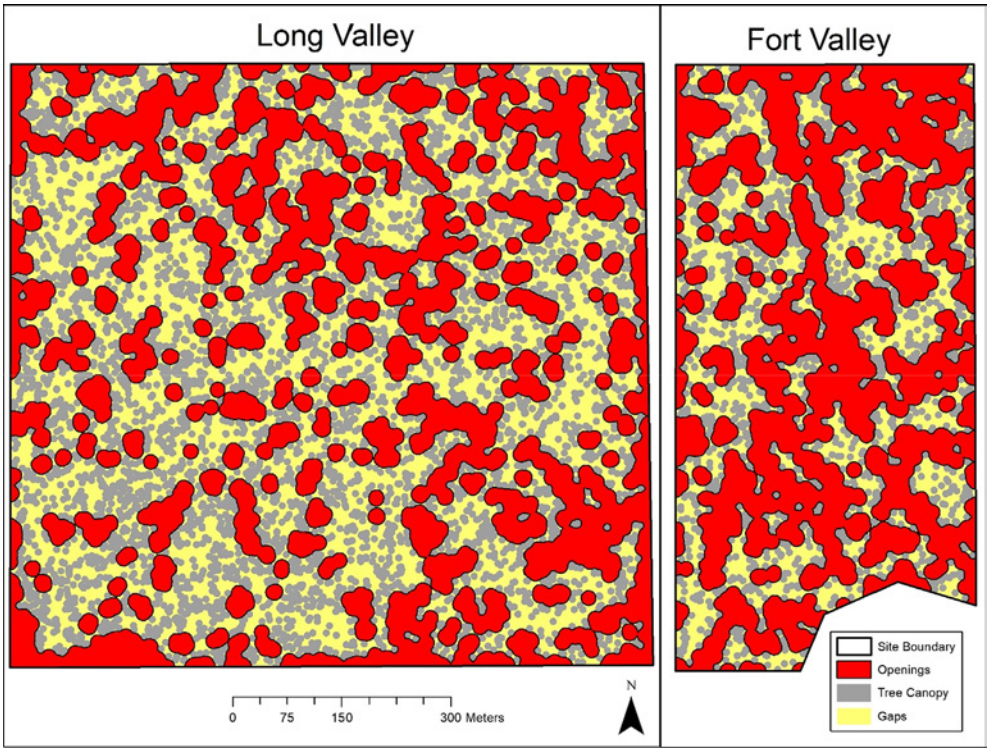
Appendix A. Evaluation of goodness of fit for the final model based on three metrics comparing observed and model-predicted spatial point distributions: (a) *G(r)*, the nearest neighbor distance function; (b) *L(r)*, Besag's transformation of Ripley's *K(r)*; and (c) *g(r)*, the pair correlation function, for Fort Valley and Long Valley spatial data sets.



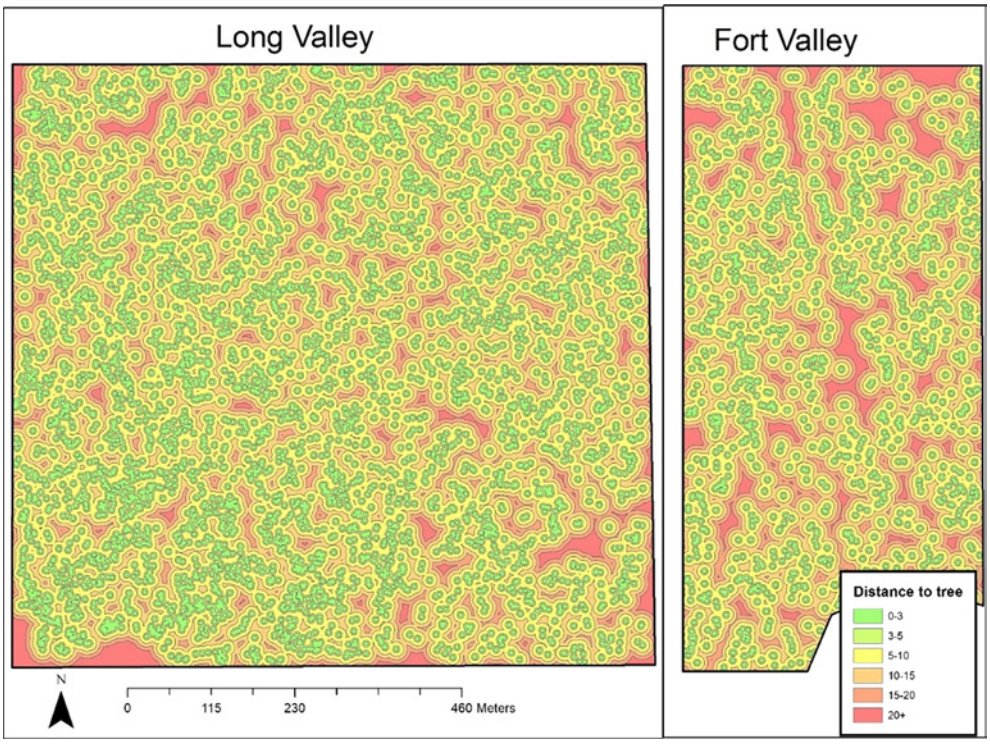
Appendix B. Maximum canopy radius percent frequency distribution for tree canopies not intersecting another tree canopy in ponderosa pine forest in Long Valley and Fort Valley sites in northern Arizona.



Appendix C. Visual of areas dominated by tree canopies (5 m from tree stem), gaps (less than 30 m wide stem-to-stem) and openings (opening at least 30 m wide stem-to-stem) within Long Valley and Fort Valley.



Appendix D. Empty space defined as the distance to the nearest tree in both Long Valley and Fort Valley.



Appendix E. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117502.

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