



Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park



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ABSTRACT

Mosaics of tree clumps and openings are characteristic of forests dominated by frequent, low- and moderate-severity fires. When restoring these fire-suppressed forests, managers often try to reproduce these structures to increase ecosystem resilience. We examined unburned and burned forest structures for 1937 0.81 ha sample areas in Yosemite National Park, USA. We estimated severity for fires from 1984 to 2010 using the Landsat-derived Relativized differenced Normalized Burn Ratio (RdNBR) and measured openings and canopy clumps in five height strata using airborne LiDAR data. Because our study area lacked concurrent field data, we identified methods to allow structural analysis using LiDAR data alone. We found three spatial structures, canopy-gap, clump-open, and open, that differed in spatial arrangement and proportion of canopy and openings. As fire severity increased, the total area in canopy decreased while the number of clumps increased, creating a patchwork of openings and multistory tree clumps. The presence of openings >0.3 ha, an approximate minimum gap size needed to favor shade-intolerant pine regeneration, increased rapidly with loss of canopy area. The range and variation of structures for a given fire severity were specific to each forest type. Low- to moderate-severity fires best replicated the historic clump-opening patterns that were common in forests with frequent fire regimes. Our results suggest that managers consider the following goals for their forest restoration: 1) reduce total canopy cover by breaking up large contiguous areas into variable-sized tree clumps and scattered large individual trees; 2) create a range of opening sizes and shapes, including ~50% of the open area in gaps >0.3 ha; 3) create multi-story clumps in addition to single story clumps; 4) retain historic densities of large trees; and 5) vary treatments to include canopy-gap, clump-open, and open mosaics across project areas to mimic the range of patterns found for each forest type in our study.

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1. Introduction

In frequent-fire pine and mixed-conifer forests in western North America (hereafter, *dry forests*), historic accounts (Dunning, 1923; Show & Kotok, 1924) and studies of forests with active fire regimes (Collins & Stephens, 2010; Collins, Kelly, van Wagtendonk, & Stephens, 2007; Larson & Churchill, 2012; Stephens & Collins, 2004; Stephens & Gill, 2005) have emphasized the importance of spatial variability in forest structure to maintain ecosystem process and resilience. A recent review of studies of stand-level structure found that fire-frequent dry forests were composed of mosaics of widely-spaced individual trees, tree clumps (two to 20+ trees), and openings (Larson & Churchill,

2012). Historically, these patterns of individual trees, tree clumps, and openings were maintained by fire and insect-driven mortality, and once established, tended towards self-perpetuation. Openings would act to moderate fire and inhibit bark-beetle dispersal (Finney et al., 2007; Pimont, Dupuy, Linn, & Dupont, 2011; Stephens, Fry, & Franco-Vizcaino, 2008) while the fine-scale local variation in canopy height and continuity would impede crown fires (Beatty & Taylor, 2007; Parisien, Miller, Ager, & Finney, 2010; Pimont et al., 2011; Stephens et al., 2008; Thaxton & Platt, 2006). Openings also provided areas for subsequent regeneration, particularly of shade-intolerant, fire-resistant species, creating a fine-scale shifting mosaic maintained by frequent fire (Agee, 1993; Boyden, Binkley, & Shepperd, 2005; Cooper, 1960; Sánchez Meador, Moore, Bakker, & Parysow, 2009).

Today, decades of fire exclusion have altered forest structure and often led to forests with nearly continuous canopies (Hessburg, Agee,

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& Franklin, 2005). Openings, especially large ones that can act as fire breaks and regeneration sites, are less prevalent than they were a century ago (Hessburg et al., 2005; Lutz, Larson, Swanson, & Freund, 2012; Scholl & Taylor, 2010). To restore structure, maintain resilience, and mitigate the possibility of large areas of high-severity fire, managers use mechanical thinning and prescribed and wildland fire across hundreds of thousands of hectares of public forests annually (Miller et al., 2012; North, Collins, & Stephens, 2012; Schoennagel & Nelson, 2011).

Researchers and managers need spatially-explicit measurements of tree clumps and openings over large areas to understand the ecological relationships between fire and the spatial structure of forests. Stem maps of reconstructed pre-Euro-American era forests or active-fire regime sites have been the primary source of information (e.g., Harrod, McRae, & Hartl, 1999). However, only 22 stem-map studies have been conducted on dry forest reference sites from 1960 to 2011 covering a cumulative 294.7 ha (Larson & Churchill, 2012; Lutz et al., 2012). The limited area suggests that the full diversity of spatial structures on western landscapes has been under sampled. Most spatially explicit tree maps are of small areas (0.5 to 4 ha) and thus do not inform managers on how pattern varies over spatial extents commonly used in restoration treatments (10 to 100 ha), or intact landscapes (>1000 ha). In addition, few stem map studies contain height information, and little is known about the vertical structure of tree clumps. Silvicultural methods are being developed to restore stand-level patterns of tree clumps and openings (Churchill et al., 2013; North & Sherlock, 2012), but these lack high resolution spatial reference information over large scales (Larson & Churchill, 2012).

Airborne Light Detection and Ranging (LiDAR) data can assess forest structure over large areas (Hudak, Evans, & Stuart Smith, 2009; Lefsky, Cohen, Parker, & Harding, 2002; Reutebuch, Andersen, & McGaughey, 2005) including patterns of gaps and tree clumps. LiDAR's strength is the high resolution (typically several measurements per square meter) and consistent measurement of ground elevation and canopy heights over large areas with greater fidelity to structural attributes than possible with satellite images (Asner et al., 2011; Hummel, Hudak, Uebler, Falkowski, & Megown, 2011). Researchers have traditionally correlated LiDAR canopy measures with extensive ground-based tree measurements (e.g., for biomass or cubic volume). However, many forest LiDAR acquisitions lack concurrent field data. Lefsky, Hudak, Cohen, and Acker (2005) and Kane, McGaughey, et al. (2010) laid out the theoretical basis and provided a practical example (Kane, Bakker et al., 2010) for interpreting relative differences in forest structure using LiDAR data as a primary data source. Recently, researchers have begun to use LiDAR as a primary data source to study forest canopy structure without reference to field data over large areas (Asner et al., 2013; Kane et al., 2011, 2013; Kellner & Asner, 2009; Whitehurst, Swatantran, Blair, Hofton, & Dubayah, 2013). One of our goals is to identify methods to

study openings and tree clumps for acquisitions that lack field data and demonstrate potential use for ecological analysis. Building on methods of Kane et al. (2011), we examine spatial structure of unburned stands and stands following fire. We used Landsat images to estimate fire severity across a 26 year period (1984 to 2010).

In this study, we use LiDAR data to examine the effects of different fire severities on the range of opening and tree clump structures (Fig. 1) found in three unburned and burned forest types (ponderosa pine, white fir-sugar pine, and red fir) common on the Sierra Nevada's western slope. While the role of fire in shaping and maintaining dry forests with active fire regimes is well documented (Collins & Stephens, 2010; Collins et al., 2007; Larson & Churchill, 2012; Stephens & Collins, 2004; Stephens & Gill, 2005), the effect of re-introduced fire following decades of fire exclusion is less well understood (but see Collins, Everett, & Stephens, 2011; Lydersen & North, 2012; Miller & Safford, 2012).

We used the methods identified for this study to address three questions related to the spatial structure of forests with increasing fire severity:

1. How do the spatial structures of clumps and openings change with increasing fire severity for these three forest types?
2. Which model(s) of forest restructuring (thin from below, dispersed mortality of all tree heights, or patchy mortality of all tree heights) best explains changes in structure with increasing fire severity?
3. What are the management implications for forest structural restoration?

2. Methods

We developed new methods for this study to analyze the spatial structures of tree clumps and openings for different fire severities and forest types. We reused the Landsat fire severity measurements and LiDAR data of Kane et al. (2013), who performed complementary analyses focused on changes in canopy profiles with fire, the landscape patterns of fire severity in a mixed severity landscape, and a rudimentary spatial structure analysis that demonstrated the need for this follow on study. In an effort to standardize terminology, our definitions of forest spatial structure are listed in Table 1.

2.1. Study area: Yosemite National Park

Yosemite National Park (3027 km²) lies in the central Sierra Nevada, California, USA. As a protected area, the forests in Yosemite currently experience no pre- or post-fire logging. A small portion of the land now within park boundaries was logged in the early 20th century, but there has been limited thinning and development since the finalization of the park boundaries in 1937. As a result, Yosemite is one of the best remaining

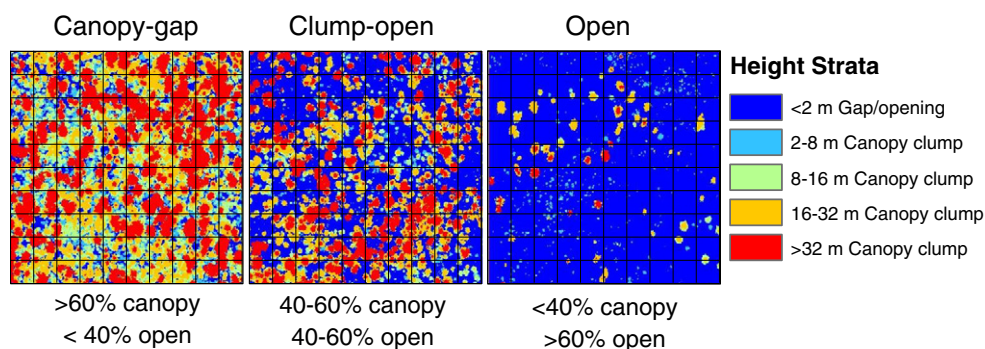


Fig. 1. Examples of the canopy-gap (canopy clumps dominate area and enclose gaps), clump-open (similar area of canopy clumps and openings), and open areas (openings dominate area and enclose small canopy clumps). Each example area is 300 m × 300 m (9 ha) and grid lines show areas of 30 m × 30 m (0.09 ha). Canopy and gap characteristics of individual 30 m × 30 m areas often are not representative of the context at larger scales such as the 90 m × 90 m (0.81 ha) sample areas used in this study.

Table 1
Terminology used in this paper.

Term	Definition
Sample area	A 90 m × 90 m area used as the basic analysis unit of this study
Unburned	An area outside all fire perimeters since 1930
Low, moderate, high severity	Estimated categorical fire severity classifications based on the Landsat-derived Relativized differenced Normalized Burn Ratio (RdNBR)
Opening	A contiguous area with no canopy >2 m in height
Gap	Opening entirely enclosed by surrounding canopy
Canopy clump	A contiguous area with canopy >2 m. Assumed to be composed of one or more trees with interlocking or adjacent crown of similar height. Clumps were further classified by height strata: 2–8 m, 8–16 m, 16–32 m, and >32 m.
Canopy-gap	A sample area with canopy >60% of the area; openings typically were gaps entirely enclosed by surrounding canopy.
Clump-open	A sample area with canopy 40–60% of the area; neither gaps/openings nor canopy clumps dominated.
Open	A sample area with gaps/openings >60% of the area; openings dominated the area and canopy patches typically were entirely enclosed by surrounding open area.
Patch	Landscape ecology term for a continuous area with the same classification. In this study, a patch could be a gap, open area, or one of the four canopy clump strata.

natural laboratories to evaluate the effects of fire severity on forest structure with minimal confounding influences.

The western portion of Yosemite possesses a Mediterranean climate with July mean minimum and maximum temperatures of 2 °C to 13 °C at higher elevations and 16 °C to 35 °C at lower elevations. Most precipitation falls as snow with annual precipitation ranging from 800 mm to 1720 mm (Lutz, van Wagtenonk, & Franklin, 2010). The forest vegetation of Yosemite comprises a mosaic of forest types, species, and structural stages (Fites-Kaufman, Rundel, Stephenson, & Weixelman, 2007; Thode, van Wagtenonk, Miller, & Quinn, 2011; van Wagtenonk & Fites-Kaufman, 2006; van Wagtenonk, van Wagtenonk, Meyer, & Painter, 2002). Each forest type, as well as woodlands and shrub fields, exhibits a characteristic fire severity distribution (Thode et al., 2011; van Wagtenonk et al., 2002).

Yosemite experiences multiple wildland fires each year, and since 1972 many lightning ignited fires have been allowed to burn under prescribed conditions (van Wagtenonk & Lutz, 2007). The historic fire return interval for the forested ecosystems of Yosemite ranges from 4 to 187 years, depending on the forest type (Caprio & Lineback, 1997; Caprio & Swetnam, 1995; Collins & Stephens, 2007; van Wagtenonk et al., 2002).

2.2. Site selection

Our study area within Yosemite National Park sampled a number of forest types that experienced a diverse fire history since 1984 (Fig. 2 and Supplement Figs. 1 and 2). This LiDAR acquisition covered 10,895 ha ranging in elevation from 1290 m to 2526 m. To minimize the impact of human disturbance, our study area was primarily designated wilderness area that had experienced minimal human impacts. We excluded two small areas that were harvested in the early 20th century prior to their incorporation into the park.

Between 1930, when comprehensive park fire records began, and the date of the LiDAR acquisition (21 July 2010), there were 327 fires in the acquisition area (4.1 fires per year), with 40 fires ≥ 40 ha (Supplement Table S1). We used only areas that had not burned since 1930 (outside all fire perimeters) or burned just once since 1984 (the earliest date for data from the Landsat Enhanced Thermal Mapper (ETM and ETM+)).

We assigned forest types within the study areas based on either the 1997 park vegetation map (Keeler-Wolf et al., 2012) or the 1937 vegetation map (Walker, 2000; Wieslander, 1935). We knew that a number

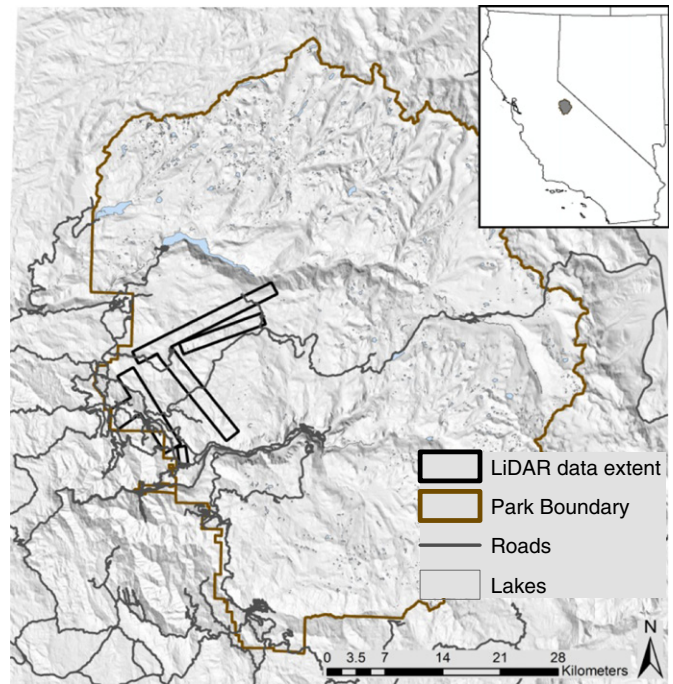


Fig. 2. Location of LiDAR data collection (bold black lines) within Yosemite National Park. Inset shows location of park within the state of California. Supplement Fig. S1 and Fig. S2 show higher resolution maps of the study area.

of previously forested areas that had burned since 1984 had become either meadow or shrubland. To include these areas in our study, we compared cover reported in both the 1937 and 1997 maps. We used the 1997 vegetation map if the area was forested in 1997. We used the 1937 map for areas delineated as meadow or shrub in 1997 but delineated as forested in 1937 under the assumption that fire had caused a shift in vegetation type. We did not include areas that were delineated as meadow or shrub in both 1937 and 1997.

To make meaningful comparisons among forest types, we limited our analysis to forest types covering > 1000 ha within the LiDAR acquisition area. These were ponderosa pine (*Pinus ponderosa*), white fir-sugar pine (*Abies concolor*/*Pinus lambertiana*), and red fir (*Abies magnifica*) forests (Supplement Table S2). Jeffrey pine (*Pinus jeffreyi*) forests and woodlands, prevalent within the study area, occurred on rocky outcrops where the spatial structure of landscape patches was primarily controlled by the unburnable area between trees (Kolden, Lutz, Key, Kane, & van Wagtenonk, 2012), and were excluded.

2.3. Estimating fire severity with Landsat data

We used the Yosemite fire atlas assembled by Lutz, Key, Kolden, Kane, and van Wagtenonk (2011), processed by and available from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al., 2007). This atlas includes all fires ≥ 40 ha from 1984 through June 2010 prior to the LiDAR acquisition, which comprised 97% of area within fire perimeters (Lutz, van Wagtenonk, Thode, et al., 2009). The minimum measuring unit was a single Landsat pixel (0.09 ha).

We used the Relativized differenced Normalized Burn Ratio, RdNBR, (Miller & Thode, 2007) which is an extension of the differenced Normalized Burn Ratio, dNBR (Key & Benson, 2006). These severity measurements calculate normalized burn ratios (NBR) from Landsat bands 4 (near infrared) and 7 (mid infrared) to stratify estimated fire severity:

$$NBR = (Band4 - Band7) / (Band4 + Band7). \quad (1)$$

The dNBR values for each pixel were calculated by subtracting the post fire NBR from the pre-fire NBR:

$$dNBR = \text{prefireNBR} - \text{postfireNBR}. \quad (2)$$

Miller and Thode (2007) determined that the estimate of fire severity could be enhanced by calibrating severity measurements by removing the biasing of the pre-fire vegetation using the square-root of the pre-fire NBR:

$$RdNBR = dNBR / (\text{SQRT}(\text{ABS}(\text{prefireNBR}/1000))). \quad (3)$$

Higher RdNBR values of these satellite-derived burn indices signify a decrease in photosynthetic materials and surface materials holding water and an increase in ash, carbon, and soil cover. Miller and Thode (2007) and Miller, Safford, Crimmins, and Thode (2009) demonstrated that RdNBR produced more accurate classifications of fire severity in Sierra Nevada forests, particularly for areas with lower pre-fire canopy cover. We classified the satellite-derived RdNBR values into standard burn severity classes calibrated with ground composite burn index plots (Key, 2006; Key & Benson, 2006; Lutz, van Wagendonk, Thode, et al., 2009; Miller & Thode, 2007; Miller et al., 2009; Thode et al., 2011).

We classified forest patches outside of all fire perimeters for fires between 1930 and July 2010 as 'unburned.' We classified patches within fire perimeters using the five standard MTBS fire severity classes: enhanced greenness, undifferentiated (no detectable change), low, moderate, and high. Miller and Thode (2007) established RdNBR thresholds for each severity class (Supplement Table S3) using field plots from the central Sierra Nevada range including plots in Yosemite. We excluded from this study areas with a classified severity of enhanced greenness because they were found only in 8.4 ha within the study area. Preliminary analysis of the LiDAR data showed that undifferentiated burn severity areas showed an intermediate level of change between unburned areas and low-severity burn areas. We chose not to report results from undifferentiated severity areas to better focus on the changes between unburned and among the low- to high-severity continuum.

2.4. LiDAR data collection and processing

Watershed Sciences, Inc. (Corvallis, OR) collected LiDAR using dual-mounted Leica ALS50 Phase II instruments. They collected the data on 21 and 22 July 2010 with an average pulse density of 10.9 pulses m^{-2} and up to four returns per pulse. Watershed Sciences used the TerraScan

v.10.009 and TerraModeler v.10.004 software packages (Terrasolid, Helsinki, Finland) to create the 1 m resolution digital terrain models (DTM) from the LiDAR data. We processed the LiDAR return point cloud data to generate metrics relevant to the measurement of forest canopies using the USDA Forest Service's FUSION software package, beta version derived from version 3.00 (<http://forsys.cfr.washington.edu/fusion.html>). Orthographic images (15 cm resolution) were acquired concurrently with the LiDAR data and used for interpretation.

We normalized the height of each LiDAR return to height above ground by subtracting the elevation of the DTM below each point. We then created a canopy surface model using the maximum height of LiDAR returns within each 1 m grid cell. We classified each grid cell of the canopy surface model into the following height strata: <2 m, >2 m, 2 to 8 m, 8 to 16 m, 16 to 32 m, and >32 m (Fig. 3), with some additional analysis of the strata >48 m. This provided us with a classified raster map of the height of the dominant vegetation that could be analyzed as openings (<2 m) or as clumps of canopy, and clumps of canopy within each height strata. We selected these canopy clump height breaks to identify tree canopies in key phases of regeneration and succession on the continuum from early regeneration to large, mature trees.

2.5. Sample area processing

Because of the large number of canopy clumps and openings (many millions) within the study area, we analyzed a sample of non-overlapping 90 m $\times$ 90 m areas. This area was large enough to detect characteristic canopy clump and opening patterns (Kane et al., 2013; Larson & Churchill, 2012) while small enough to enable a large number of samples to fit within single forest type-fire severity patches. The sample size also was a multiple of the 30 m grain for the forest type and fire severity data.

We selected samples from all possible 90 m $\times$ 90 m areas that were entirely classified as one or more of our three target forest types (ponderosa pine, white fir-sugar pine, or red fir). We assigned the forest type reported for the center of each sample area to the entire sample area. Preliminary analysis showed that requiring each sample area to have experienced only one fire severity would have severely limited the sample size for moderate- and high-severity fire patches. Therefore, we retained areas that were classified entirely as unburned (outside all fire perimeters) or that were within one fire severity class across the sample area (e.g., undifferentiated and low-severity fire, or moderate- and high-severity fire, but not low- and high-severity fire). We assigned

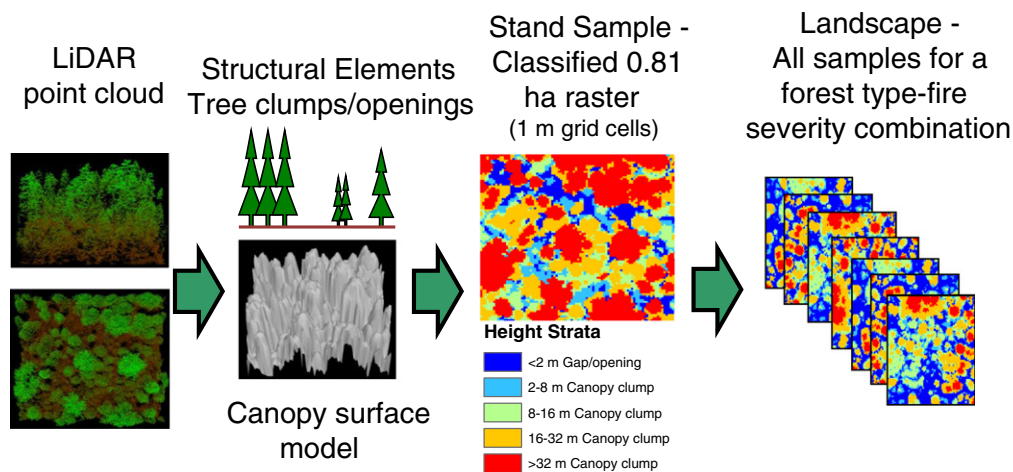


Fig. 3. Methods used to identify gaps/openings and canopy patches in different strata—and to analyze spatial structure. Individual tree clumps and openings were identified from 90 $\times$ 90 m canopy surface models produced from the LiDAR point cloud (sample areas). Each 1 m CSM grid cell was classified into a height stratum to identify canopy clumps and openings. Analysis was done on patterns of structural elements within each sample area to understand structure within stands. Analysis of all sample areas for a given forest type and fire severity combination was done to reveal landscape patterns.

the fire severity class reported for the center of each sample area to the entire sample area.

For forest type-fire severity combinations with larger areas, we selected a random pool of 200 sample areas. For combinations with smaller areas from which 200 samples could not be drawn, we used all available

sample areas. We then eliminated any sample area found to be on the edge of the acquisition and therefore had an area <0.81 ha. These criteria resulted in 1937 sample areas covering a cumulative 1569 ha.

2.6. Forest structure analysis

We identified contiguous areas of the canopy surface model classified into the same stratum as individual patches corresponding to specific openings or canopy clumps. This resulted in sample areas containing discrete patches that could be correlated with tree clumps of different heights and openings visible in the LiDAR point cloud and canopy surface model (Fig. 4). We measured the cumulative area of each class by patch size. We analyzed the canopy clump area within each height stratum as the proportion of total canopy area for its sample area.

We analyzed the spatial pattern of each sample area individually using landscape ecology metrics in the R SDMTools (VanDerWal,

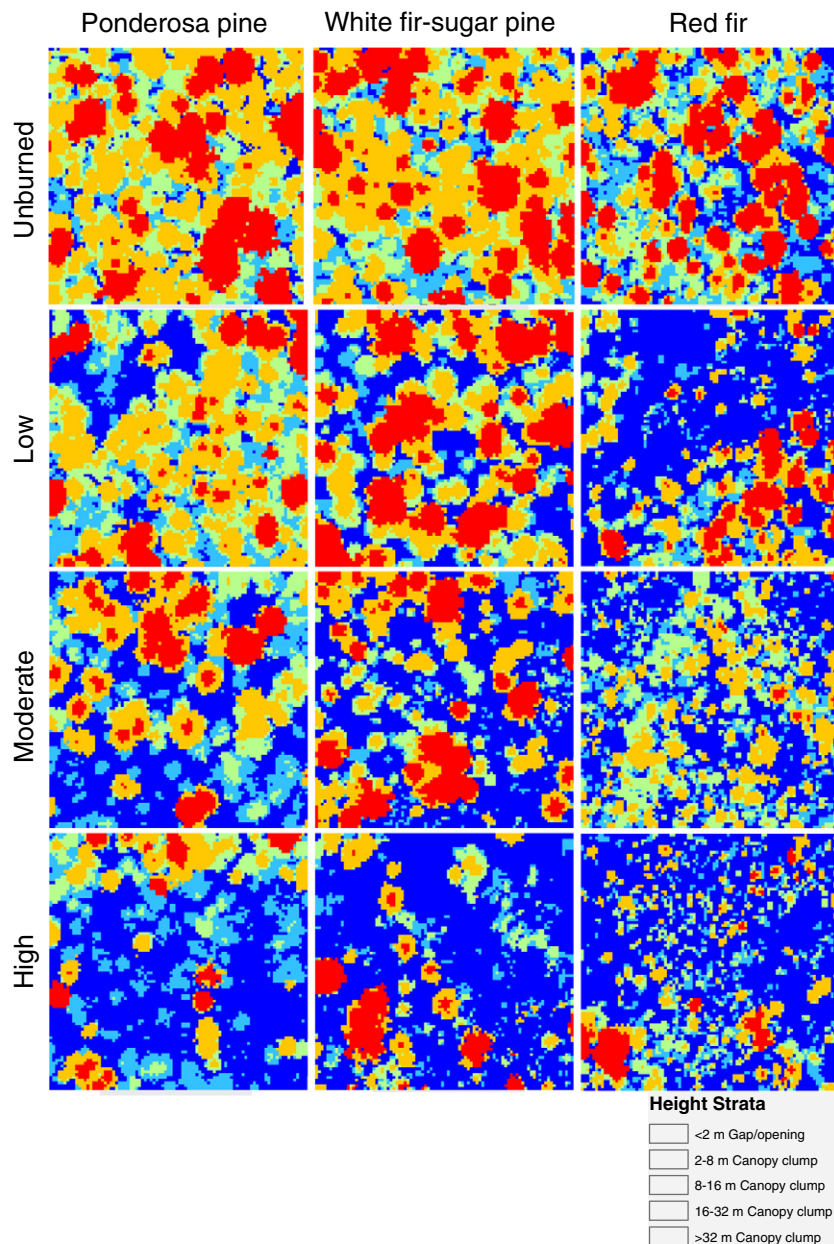


Fig. 4. Example sample areas (0.81 ha) for each forest type-fire severity combination. Examples illustrate common spatial patterns but not the range of variation found for each combination.

Falconi, Januchowski, Shoo, & Storlie, 2012) (<http://cran.r-project.org/web/packages/SDMTools/index.html>) package and the Fragstats software package (McGarigal & Marks, 1995) (<http://www.umass.edu/landeco/research/fragstats/fragstats.html>). We calculated area for each stratum both by patch and by class, and used the aggregation and clumpiness indices to assess the dispersion pattern of clumps and openings.

For all canopy >2 m, we calculated two canopy measurements for each height stratum: canopy cover and canopy area. We calculated canopy cover by dividing the number of returns in each height strata by the number of returns in that stratum and all lower strata. We calculated canopy area as the proportion of 1 m canopy surface model grid cells in each height strata divided by the area of each sample area. Canopy cover uses the total vertical distribution of returns as an estimate of the canopy profile and estimates the presence of canopy at all heights whether or not there is foliage above a given height. Canopy area measures only the top of canopy foliage in each 1 m grid cell and ignores lower foliage and therefore measures the area of dominant tree clumps. Even when foliage is found at a single narrow height, the two measurements may produce different values. A single spray of needles may cause a return to be measured within a 1 m grid cell even though most of the area of that grid cell would be empty. In this case, canopy cover would report a low value while canopy area would report an area of 1 m².

3. Results

As fire severity increased, the total area in canopy decreased while the number of clumps increased, indicating progressive canopy fragmentation into smaller clumps (Fig. 5 and Supplement Fig. S3). As canopy area decreased, the dominant pattern transitioned from a single, nearly continuous clump, to a small number of clumps, and then to many clumps (Fig. 1). The proportion of area in openings ≥ 0.3 ha increased rapidly with increasing fire severity (Fig. 6) with a corresponding decrease in the area of canopy. Once the area in openings was

greater than approximately 40% of a sample area, almost all opening area was in openings ≥ 0.3 ha. While the absolute area of all canopy and for each canopy stratum decreased with increasing fire, the proportion of canopy area for strata >8 m relative to remaining absolute canopy area was similar to the proportions for unburned sample areas (Fig. 7).

For all canopy >2 m, both canopy cover and canopy area generally declined with increasing fire severity (Supplement Table S4). For the 2 to 8 m stratum, however, canopy cover showed a steep decline with increasing fire severity, but canopy area either increased or decreased at a slower rate at moderate and high severities (Fig. 8).

As fire severity increased, the total area in canopy decreased while the number of clumps increased indicating progressive fragmentation of remaining canopy into smaller clumps (Fig. 9). Aggregation values measured across all patches in the sample areas (landscape aggregation) had values of 73 to 87%, indicating an overall tendency towards aggregation of openings and canopy patches in larger patches rather than dispersal of small patches across the sample areas (Fig. 10). All canopy patches and openings had inverse aggregation relationships with the former decreasing with increased fire severity and the latter increasing. The 2 to 8 m and 8 to 16 m canopy strata had the lowest aggregation values. The 16 to 32 m and >32 m strata had the highest aggregation values in that order. Increasing fire severity was associated with little change in median aggregation values for the canopy strata, although the range of values increased. The Fragstats CLUMPY index results showed similar patterns (data not shown), indicating that the aggregation patterns were distinct from those expected from a random pattern.

4. Discussion

The LiDAR data revealed three spatial structures, canopy-gap, clump-open, and open (Fig. 1) that differed in the proportion of canopy and opening and in spatial arrangement. We found that fire increased open area and number of tree clumps, but the relationship between fire

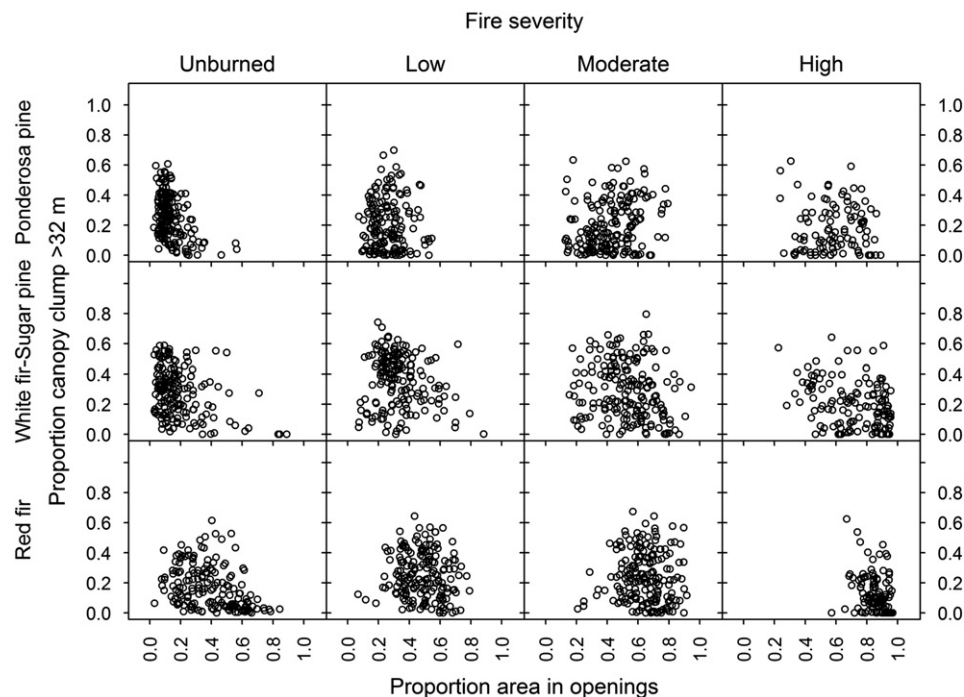


Fig. 5. Heterogeneity in total opening area and tall-tree (>32 m) patch areas by fire severity and forest type with the proportion of the total area in openings (x axis) and the proportion of total canopy area in tall tree (>32 m) clumps (y axis). Wider point dispersal indicates a greater range of structural heterogeneity for a given fire severity-forest type combination. Increased fire severity resulted in a greater range of opening area for ponderosa pine and white fir-sugar pine forests but resulted in a narrow range for red fir. Increased fire severity had little effect on the range of sample area proportions in tall tree clumps for either ponderosa pine or white fir-sugar pine forests but resulted in a narrower range for red fir. Supplemental Fig. S3 shows change in heterogeneity for other canopy strata.

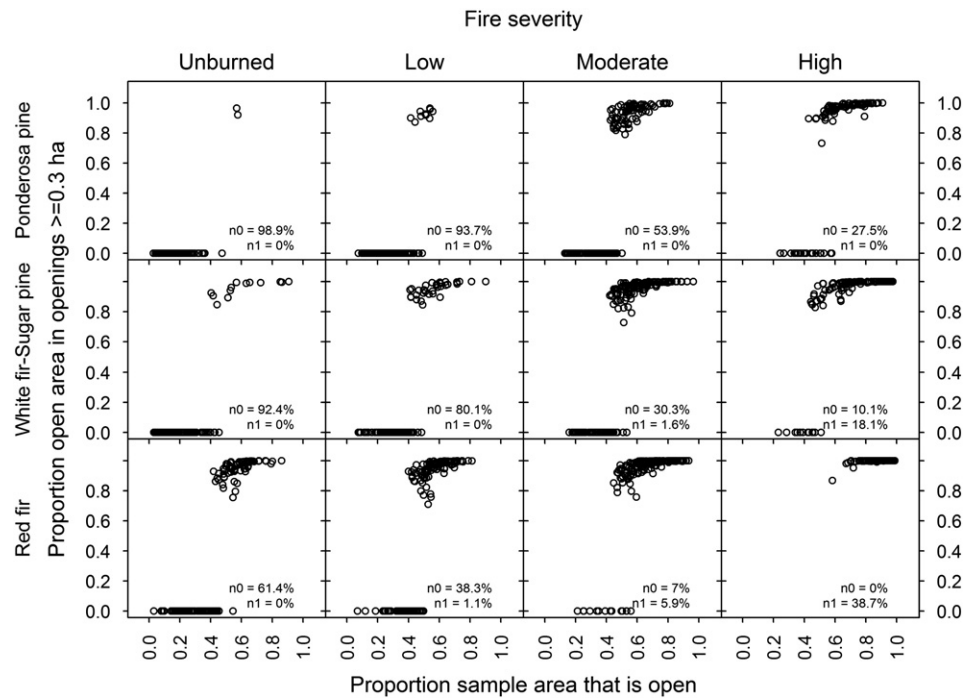


Fig. 6. Proportion of openings that are ≥ 0.3 ha (needed for regeneration of tree species requiring high sunlight exposure) plotted against proportion of the total sample area in openings by fire severity and forest type. The percentage of sample areas where there are no gaps ≥ 0.3 ('N 0 ='), and the percentage of sample areas where all openings are ≥ 0.3 ha ('N 1 =') are shown.

severity and forest change was not linear. A given fire severity could result in a range of spatial structures. In general, unburned forests and high-severity patches had the least variation in spatial structures while low- and moderate-severity patches had the greatest variation. The range of variation for a given fire severity was specific to each forest type.

Fires 'thinned from below' to remove large proportions of cover in the 2 to 8 m strata, a trend that was partially masked by extensive

regeneration. In strata > 8 m, however, fire acted in a heterogeneous manner, leaving multistory clumps in some places and removing them in others. The presence of large openings (> 0.3 ha) increased rapidly with loss of canopy area indicating that openings were created in an aggregated pattern.

Kane et al. (2013) performed complementary analyses that focused on fire effects on canopy profiles using the same LiDAR data set as this study. They found clear signs of low- and moderate-severity fire thinning

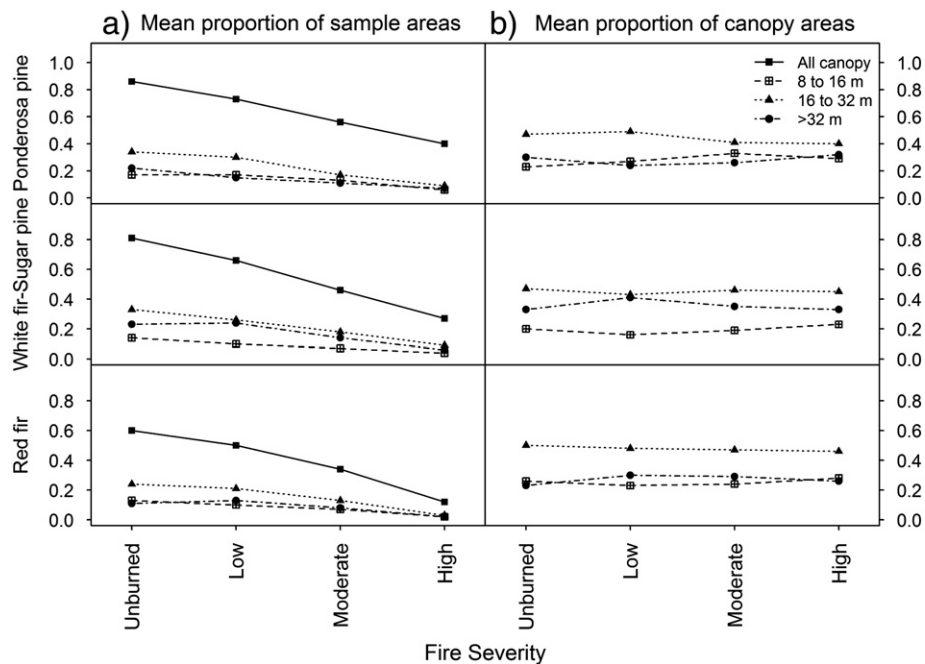


Fig. 7. Change in proportion of canopy area by forest type and fire severity. As fire severity increases, the absolute area of canopy cover decreased in all strata (a). However, within the remaining canopy area, the proportion of area in different strata showed little change (b), indicating that fire left multistory tree clumps. Because the absolute area of 2–8 m canopy increased for two forest types with increasing fire severity, the method for calculating proportion of canopy area (b) was calculated using canopy area minus the 2–8 m canopy area. See Fig. 8 for changes in the 2 to 8 m canopy stratum.

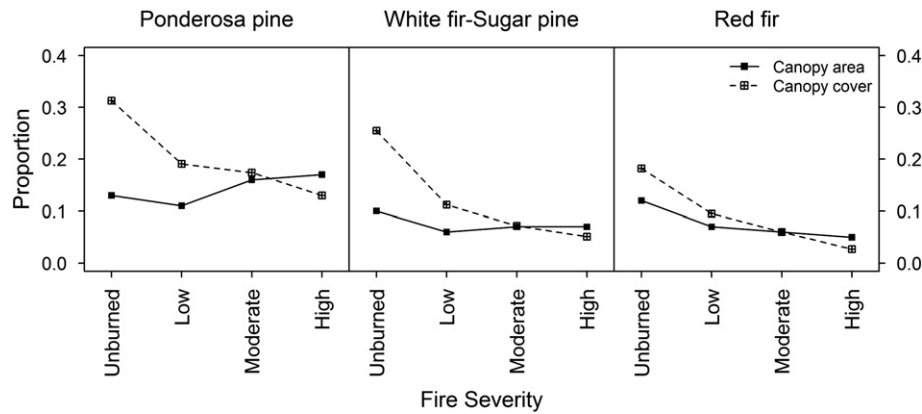


Fig. 8. Change in proportion of canopy area and canopy cover by forest type and fire severity in the 2 to 8 m stratum. Canopy cover trends suggest ‘thinning from below’ in this stratum as fire removes smaller trees under larger trees and standalone tree clumps in this stratum. Increases in canopy area with increased fire severity suggests establishment of new tree clumps in this stratum through regeneration. Canopy cover uses the total vertical distribution of returns as an estimate of the canopy profile and estimates the presence of canopy at all heights whether or not there is foliage above a given height. Canopy area measures only the top of canopy foliage in each 1 m grid cell and ignores lower foliage and therefore measures the area of top-of-canopy trees within clumps.

from below with resulting canopy profiles transitioning from multiple canopy layers to single overstory canopies. They found that burned patches that showed too little change to be distinguished from unburned (the RdNBR no detectable change fire severity class) or with low severity showed clear structural differences compared to unburned patches. This effect was unexpected given the previous work characterizing fire severity and correlating it with Landsat measurements (Miller & Thode, 2007; Thode, 2005; Thode et al., 2011).

4.1. Landsat and LiDAR to study forest response to fire

Kane et al. (2013) were the first to use LiDAR data with Landsat-derived measures of fire severity to measure the impact of fire on forest

structure over a large area. That work and this study confirm the utility of Landsat fire severity estimates to measure fire as an ecological process and the high resolution of LiDAR data to measure the structural change resulting from that process. The wide variation in spatial structures found within low- and moderate-severity fires shows the value of monitoring actual changes from fire with LiDAR rather than depending on models to predict changes.

We were able to use simple LiDAR measures of top of canopy height and canopy cover and area to study the complex process of forest restructuring with increasing fire severity. Our study area, like many LiDAR forest acquisitions, lacked concurrent field data to use in interpreting the LiDAR measurements. However, we believe that we have demonstrated that using simple, well proven LiDAR measurements

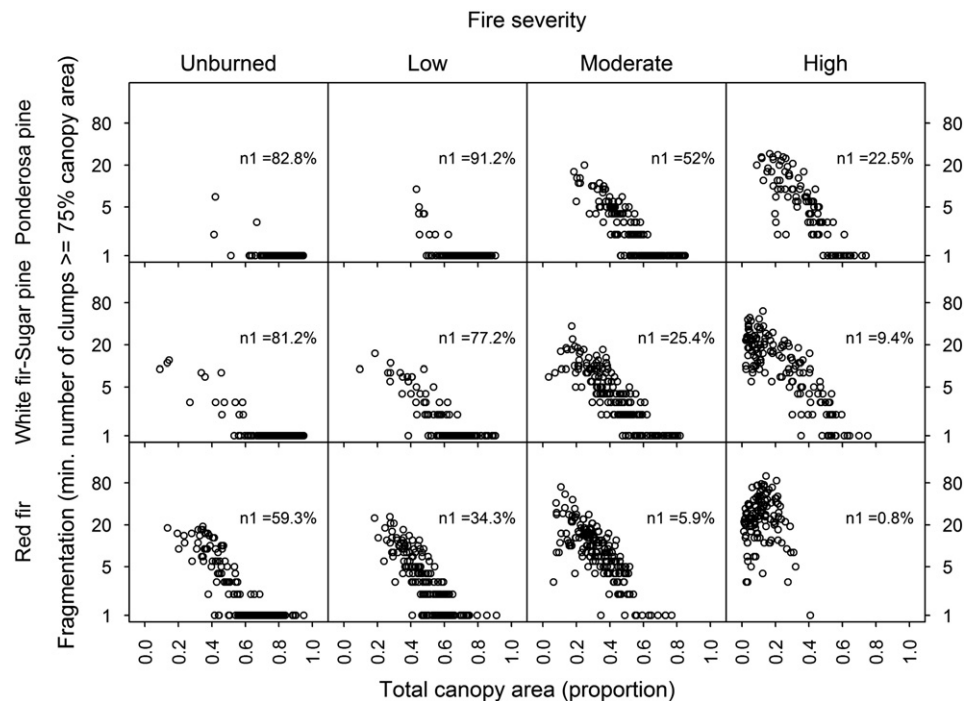


Fig. 9. Fragmentation of canopy clumps within sample areas. As fire severity increased, the total area in canopy (x axis) decreased while the number of clumps (y axis) increased indicating progressive fragmentation of remaining canopy into smaller clumps. Each point represents one sample area. To exclude small clumps that made little contribution to total canopy area, clump count was calculated by determining the minimum number of clumps within each sample area required to account for 75% of canopy area with clumps added in order of size (largest first). The percentage of sample areas where all canopy in a single continuous clump (‘N1 =’), usually percolated with enclosed gaps, is shown.

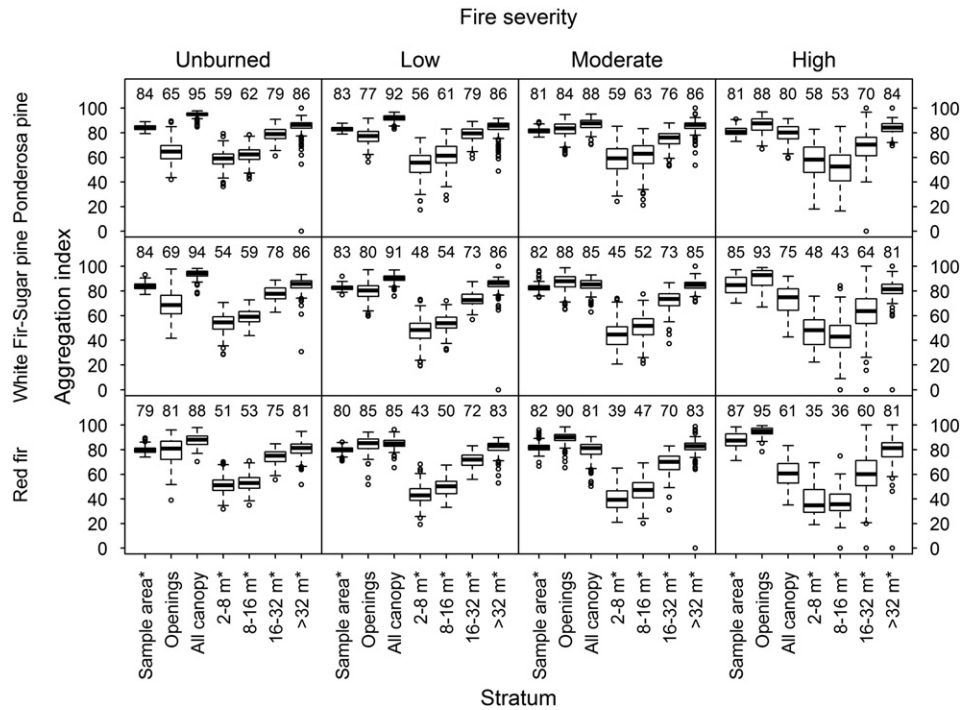


Fig. 10. Clumping of openings and canopy strata (class types) within larger patches as opposed to dispersion based on the Fragstats aggregation index. Aggregation value (numerical value above each bar and whisker plot) was calculated as the likelihood that an adjacent cell is of the same patch type. Higher values indicate greater clumping into fewer, larger patches. As fire severity increased, openings became more aggregated while overall canopy patches became smaller and more dispersed. Aggregation of patches within individual canopy strata, however, showed only modest changes. Results calculated for each sample area are based on a classification of only openings (<2 m) and all canopy (>2 m) and by height strata (indicated with an asterisk in legend). Bold lines show median values; the bottom and top of the boxes show the 25th and 75th percentile values; the upper and lower whiskers show either minimum and maximum values or 1.5 times the interquartile range (approximately two standard deviations), whichever is nearer to the mean; and circles show outliers. See Supplement Fig. S5 for aggregation values calculated relative to a random distribution of cells by height strata.

alone can enable a serious ecological study over a large forested area. This work joins a small but growing body of studies that have taken this approach (Asner et al., 2013; Kane et al., 2011, 2013; Kellner & Asner, 2009; Whitehurst et al., 2013).

Field studies of forest spatial structure typically use a spatially-explicit census of tree trunks to enable point pattern analysis, but usually lack measurements of the openings that separate the trees (Larson & Churchill, 2012). Current methods to census individual trees with LiDAR data have accuracies that can vary considerably within and between stands based on juxtaposition of different tree heights and differences in canopy cover (Kaartinen et al., 2012; Li, Guo, Jakubowski, & Kelly, 2012; Vauhkonen et al., 2012). We adopted an alternative approach that focused on tree clumps (trees with interlocking crowns or solitary trees) and openings, which are basic structural units in dry forests (Larson & Churchill, 2012). The canopy surface models we used provided high resolution mapping of these structures. Our measurements of canopy area in different strata complemented this approach by estimating canopy foliage profiles below the overstory canopy. We believe that our methods could be readily applied to other LiDAR acquisitions that also lack concurrent field data.

As with all studies that use a chronosequence, we cannot completely account for differences in pre-fire vegetation that could be affecting our interpretation of post-fire structure. With the large datasets enabled by LiDAR, we can measure the range and heterogeneity of forest structures for stands that were unburned and that burned with different severities. As severity increased, we found changes in spatial structure that were consistent with existing conceptual models of fire severity (Agee, 1993). Consequently, we believe that our unburned sample areas were representative of the range and heterogeneity of pre-fire conditions for our burned sample areas. In analyzing our results, however, we focused on dominant trends to avoid both the limitations of no pre-fire structural measurements and limitations in the accuracy of estimated fire severity (Kane et al., 2013).

4.2. How did spatial structure of clumps and openings change with fire severity?

We found that increasing fire severity fragmented the nearly continuous canopies typical in unburned stands into either (1) mosaics of a few large, multistory clumps (typically low-or moderate-severity fire) or into (2) open areas with many small scattered clumps that likely were individual trees or snags (typically moderate-or high severity) (Fig. 9) (see also Larson, Belote, Canaler, Parks, & Dietz, 2013). Moderate and high severity fires increased both the cumulative area and size of individual openings (Fig. 6). As fire severity increased, overall canopy patches became smaller and more dispersed, but within those canopy patches, patches within canopy strata >8 m retained similar aggregation as in unburned samples (Fig. 10).

Fire, however, is just one of many processes (e.g., climate, pests, and pathogens) that shape forest structure. We used a large study area in an effort to sample the range of structures and fuel conditions in unburned forests that were likely to represent the variation caused by these processes. This variation, in turn, likely influences combustion and fire intensity affecting burn severity patterns and the resulting forest structure. We cannot disentangle those processes and in this paper treat them as part of the natural range of forest conditions interacting with fire to alter forest composition and spatial structure. In our analysis we focused on changes in the range of variation between unburned and burned samples. Since the non-fire processes operate on unburned and burned forests, we ascribed differences in the range of variation between unburned and burned samples to fire.

We had expected unburned and low-severity fire patches to be dominated by canopy-gap spatial structures, moderate-severity fire patches to be dominated by clump-open spatial structures, and high-severity fire patches to be dominated by open spatial structures (Kane et al., 2013). Instead, only a few forest type-fire severity combinations were clearly dominated by a single spatial structure (e.g., ponderosa

pine and white fir-sugar pine unburned patches (canopy-gap) and red fir high-severity patches (open)). Low- and moderate-severity fires resulted in an increase in the heterogeneity of spatial structures present compared to unburned and high-severity fire patches.

The key changes in spatial structure occurred with thresholds of total canopy area (Fig. 9). With decreasing canopy area, the spatial structure transitioned from single large clumps with enclosed openings (>65% canopy area), to two to five larger clumps (45 to 65% canopy area), then to five to ten smaller clumps (25 to 45% canopy area), and then to tens of very small clumps (<25% canopy area). These results are in contrast to possible alternative patterns. For example, sample areas with 20% canopy area theoretically could have some areas with a single large clump, some with two to five clumps, and some with tens of clumps. Instead, sample areas with ~20% canopy area always had at least five and usually tens of clumps. We observed this relationship between canopy area and clump number across forest types and fire severities. This suggests that canopy area-clump number thresholds may result from fire behavior at local scales, a hypothesis worth examining in future studies.

We found that the larger canopy clumps in our study area were complexes of smaller clumps in different height strata, resulting in spatially segregated multistory clumps that likely indicate multiple tree cohorts growing in close proximity. This is evident from visual inspection of site data (Figs. 1 and 4) and from the distribution of clump sizes and cumulative strata area with no stratum predominating (Fig. 5 and Supplement Fig. S3). Clump complexes appear to be the dominant structural element for unburned, low, and moderate-fire severity sample areas. They are less apparent for high-severity sample areas where individual trees and patches of early regeneration are more common. Prior to fire exclusion, the extent to which clumps were predominantly even-aged and single story versus multi-aged and multistory is poorly understood. Both have been found in reconstruction studies (Cooper, 1960; Sánchez Meador et al., 2009; White, 1985).

Each forest type showed a different rate of change with increasing fire severity and range of spatial structures (Fig. 11). Unburned ponderosa pine patches were dominated by the canopy-gap structure. With increasing fire severity, all three spatial patterns were common, but the open structure never became dominant even with high-severity fire. Conversely, unburned red fir patches had all three spatial structures, but increasing

fire severity increased the proportion of the open structure, which became strongly dominant with high-severity fire. White fir-sugar pine forests showed the widest range of structure types, spanning from canopy-gap for unburned and low severity, to a mixture of the three with moderate-severity fire, and then to open with high-severity fire. These differences show that the interaction of fire with forests varies between forest types.

The creation of openings >0.3 ha has been a management goal to provide locations for the regeneration of shade-intolerant, fire-resilient pines that require high light levels. These larger openings are an important structure because they provide sufficient understory light to favor pine regeneration (Bigelow, North, & Salk, 2011; York, Heald, Battles, & York, 2004) and sustain shrub cover, preferred habitat for several bird (e.g., Greenlaw, 1996; Raphael, Morrison, & Yoderwilliams, 1987) and small mammal species (e.g., Coppeto, Kelt, Van Vuren, Wilson, & Bigelow, 2006; Roberts, van Wagendonk, Kelt, Miles, & Lutz, 2008). Our data show that openings this size are uncommon when the total opening area is less than 40%, but common when total opening area is greater than 40% (Fig. 6). While we did not statistically examine opening shapes, our visual inspection of canopies suggests that each of the three spatial patterns has distinct opening shapes. In canopy-gap stands, openings tend to be more compact and circular; in clump-open stands, openings tend to be more sinuous and amorphous and interspersed with canopy clumps; and in open stands, openings tend to be a continuous open area with scattered enclosed individual trees and tree clumps.

We were surprised by the post-fire decrease in taller trees in the >32 m stratum that was similar to the loss of shorter trees in the 8 to 16 and 16 to 32 m strata (this pattern was also found in the >48 m stratum; data not shown). Large trees have thicker bark and generally a greater height to their crown base. We assumed that this would imply that the taller trees should be more resistant to low-and moderate-severity fire. Decades of fire suppression exclusion may have created fuel ladders that carried fire into the crown of the taller trees or allowed litter and duff to accumulate around the boles of trees with fire subsequently girdling the trees from long, hot residence times. The pattern of loss for the >32 m stratum was greater for ponderosa pine than for the other two forest types (see Kane et al. (2013) for a discussion of possible explanations for the loss of very tall trees in ponderosa pine forests).

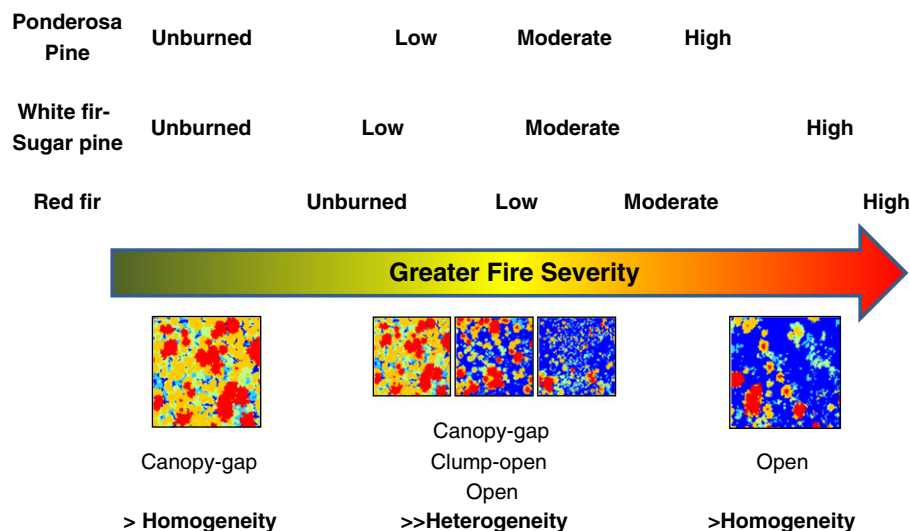


Fig. 11. Changes in spatial structure comparing unburned (outside all fire perimeters since 1930) and burned areas with increasing fire severity. While the direction of change with fire severity was consistent across forest types, each forest type was unique in the range of structures found along this general continuum. Forest types are shown above the line. Fire severities shown for each forest type line up with the characteristic canopy and opening structures shown below the arrow for that forest type and fire severity.

4.3. Which models of fire behavior best explain structural changes?

We hypothesized that reintroducing fire to forests that had experienced decades of fire exclusion might thin from below, remove trees of all heights in a patchy pattern, or remove trees of all heights in a dispersed pattern. We found evidence for all three patterns, but for different structures and/or fire severities.

In the 2 to 8 m stratum, the steep loss of canopy cover (total vertical profile of LiDAR returns as an estimate of the canopy profile) with increasing fire severity is evidence that fire removed a considerable proportion of the smallest trees and/or lower foliage on taller trees across our sample areas. This is consistent with the widespread observation that fire thins from below by removing smaller trees (Kane et al., 2013; Nesmith, Caprio, Pfaff, McGinnis, & Keeley, 2011). The data suggest that fire also thinned from below for the 8 to 16 m stratum, but the trends were not as conclusive. On the other hand, we interpret the increase or slower decline of canopy area (only the top of the canopy foliage in each 1 m grid cell, ignoring lower foliage) in the 2 to 8 m stratum with increasing fire severity as evidence of regeneration following fire, consistent with several field studies (Moghaddas, York, & Stephens, 2008; Scholl & Taylor, 2006; Zald, Gray, North, & Kern, 2008).

We found strong evidence for fire acting in a patchy, aggregated pattern that removed trees of all heights. For each stratum > 8 m, the *absolute area* of canopy decreased with increasing fire severity while the *proportion* of strata within the remaining canopy area showed only small changes from the unburned proportions (Table 2). We interpret this as evidence of fire removing trees of all heights in a patchy pattern that left other multistory clump complexes intact other than the loss of foliage in the 2 to 8 m stratum. Visual inspection of low- and moderate-severity sample areas shows that post-fire canopy clumps were organized in multistory clump complexes (Figs. 1 and 4). Similarly, median values for aggregation by canopy clump strata showed little change with increasing fire severity (Fig. 10). These two lines of evidence suggest that the internal spatial arrangement of surviving clump complexes changed little following fire.

We also found that fire could remove trees in all strata in a dispersed pattern. High fire severity tended to produce open areas with canopies in tens of clumps, many of which represented individual trees or dispersed regeneration.

4.4. Management implications

The spatial patterns following a single fire in our study area are far more complex than patterns created by commonly used commercial thinning and fuel reduction treatments, such as basal area or spacing-based prescriptions (Churchill et al., 2013). Similarly, burn intensity and tree mortality are generally kept low in prescribed fire treatments, resulting in only thinning from below and little mortality in medium and large size classes (Schwilke et al., 2009; Stephens et al., 2009). It is unclear whether current mechanical restoration treatments that explicitly seek to restore reference spatial patterns are effective at creating the level of variation in vertical and horizontal structure found in our study (Churchill et al., 2013; Waltz, Fule, Covington, & Moore, 2003). The practice of leaving untreated patches with multistory clumps of trees (North, Stine, O'Hara, Zielinski, & Stephens, 2009), typically for wildlife habitat, is consistent with the presence of multistory clumps post-fire. However, it is not clear that these restoration treatments leave similar proportions in openings. Our results show that a third to half of areas would need to be in openings to replicate conditions for low- and moderate-severity fire, respectively, in the white fir-sugar pine type. Periodic monitoring of treatments with pre-treatment and post-treatment LiDAR will be useful to evaluate restoration treatments.

For large tree retention across the landscape, an important management implication emerges from our study. Patches of high-severity fire in red fir and white fir-sugar pine forests reduce the number of clumps containing taller and, therefore, presumably larger, trees to numbers

lower than pre-Euro-American conditions. In landscapes where high-severity fire patches are prevalent, large-diameter trees have declined (Lutz, van Wagendonk and Franklin, 2009). However, in landscapes where fire remains low- or moderate-severity, large-diameter tree density is equivalent to pre-Euro-American conditions (Collins et al., 2011; Scholl & Taylor, 2010). Therefore, avoiding large areas of high-severity fire in these forest types through a combination of prescribed fire or lightning-ignited fires under cooler conditions will help retain large trees (North et al., 2012). Patches of high-severity fire in ponderosa pine forests did not proportionately reduce tall tree density as much as other forest types we examined. Taller ponderosa pine tree clumps may be composed of one to a few individual trees that have experienced many fires, or those tree clumps occur in a landscape with more natural barriers to fire spread (Stephens & Collins, 2004; Taylor, 2010).

Our results and those in Kane et al. (2013) suggest that low- to moderate-severity fires best replicate the clump-opening patterns that were common in dry forests with natural, frequent fire regimes (Larson & Churchill, 2012). Based on our results, managers might want to consider the following goals for their restorations: 1) reduce total canopy area over project areas by breaking up large areas of canopy leaving variable-sized tree clumps and scattered large individual trees; 2) create a range of opening sizes and shapes, including ~50% of the open area in gaps > 0.3 ha; 3) create multistory clumps (all trees > 2 m) in addition to single story clumps; 4) retain historic densities of large trees; and 5) vary treatments to include canopy-gap, clump-open, and open mosaics across project areas to mimic the range of patterns found in our study.

Our results also suggest that low- and moderate-severity fires generally increase heterogeneity, but optimal forest conditions are produced by different severities for specific forest types. In remote areas away from the wildland urban interface, land managers in the Sierra Nevada might consider letting wildfire in ponderosa pine burn under higher percentile weather conditions to achieve the higher severity level associated with the greatest heterogeneity. In contrast, more moderate weather conditions may be desirable for wildfire burning in red fir to produce low-severity burn conditions for optimal heterogeneity. Our analysis shows that fire produces highly heterogeneous forest conditions at multiple scales, challenging managers to significantly vary treatments to increase forest complexity and possible resilience.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rse.2013.07.041>.

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Supplement to

Kane, V.R., et al., Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park, Remote Sensing of Environment (2013), <http://dx.doi.org/10.1016/j.rse.2013.07.041>

This paper reuses the same LiDAR and fire severity databases as Kane et al. (2013). Tables S1, S2, and S3 and Figures S1 and S2 are reproduced with permission from Kane et al. (2013) or its online supplement.

Kane, V.R., Lutz, J.A., Roberts, S.L., Smith, D.F., McGaughey, R.J., Povak, N.A., & Brooks, M.L. (2013). Landscape-scale effects of fire severity on mixed-conifer and red fir forest structure in Yosemite National Park. *Forest Ecology and Management*, 287, 17-31.

Table S1. Fires ≥ 40 ha included in LiDAR acquisition area. Fire types are Management Ignited Prescribed Fire (MIPF), Wildland Fire Resource Benefit (WFRB, including “Fire Use”) and Prescribed Natural Fire (PNF) which were allowed to burn with little or no control activity, and Wildfire (WF) which were actively suppressed.

Year	Fire name	Fire type	Total burned area (ha)	LiDAR acquisition burned area (ha)	% of fire in study area	Year	Fire name	Fire type	Total burned area (ha)	LiDAR acquisition burned area (ha)	% of fire in study area
1985	New Drub	PNF	43	21	48.8%	1999		MIPF	329	116	35.3%
1985	1985YNP-021	PNF	57	55	96.5%	2000	Pw-2 South Fork	MIPF	89	84	94.4%
1986	Cascade Creek	PNF	838	521		2002	Wolf	WFRB	805	416	51.7%
1987	Larson	WF	234	174	74.4%	2002	PW-3 Gin Flat Tuolumne	MIPF	1360	562	41.3%
1988	Walker	PNF	201	14	62.2%	2003	WFU	WFRB	664	478	72.0%
1988	Walker	WF	1073	472	7.0%	2003	Tuolumne WF	WF	789	666	84.4%
1989	Pw3	MIPF	688	276	40.1%	2005		MIPF	104	74	71.2%
1990	T-Grove 4	WF	231	113	44.0%	2005	Pw-3 AD-23	MIPF	699	287	41.1%
1990	A-rock	WF	7191	654	9.1%	2006	MiddleT WFU	WFRB	52	52	100.0%
1992	South Fork	MIPF	210	209	48.9%	2006	PW5 North C	MIPF	77	77	100.0%
1996	Ackerson Aspen Valley	WF	23939	1197	5.0%	2006	MiddleT Sup	WF	140	140	100.0%
1997	Pw	MIPF	597	333		2007	Devil	WFRB	97	97	100.0%
1998	Harden	WFRB	48	48	100.0%	2007	Bald WFU	WFRB	134	6	4.5%
1998	Aspen Valley		86	72	55.8%	2009	Harden	WFRB	670	132	19.7%
1998	Pw-2 Av	MIPF	877	296	33.8%	2009	Big Meadow	WF	3059	864	28.2%
1999	Morrison	WFRB	152	144	94.7%	2010	PW-05 Seg D	MIPF	84	81	96.4%

Table S2. Vegetation types in the study area by hectares for each RdNBR fire severity class for the study period 1984 through July 2010. Percentages refer to area within the burned area for specific RdNBR fire severity classifications or to total area burned or unburned (outside all fire perimeters between 1930 and July 2010) within the forest type during the study period within each forest type. This study used only grid cells that were unburned or had one fire. Data based on fires ≥ 40 ha between 1984 and July 2010. The enhanced greenness and Landsat undifferentiated severity patches were not used in this study.

Forest type	Total Area (ha)	High severity	Moderate severity	Low severity	Landsat-undifferentiated	Enhanced Greenness	Total burned (single fire)	Unburned
Ponderosa pine	1089	9.4%	30.5%	40.2%	19.8%	0.1%	60.6%	39.4%
White fir-Sugar pine	2972.5	13.1%	19.3%	53.5%	14.1%	0.1%	55.7%	44.3%
Red fir	2900	12.7%	20.7%	49.8%	16.5%	0.3%	73%	27%
Totals (ha)	6961.5	547.6	956.8	2204.3	7131.4	8.48.4	2531 4430.5	2531

Table S3. Fire severity classes used. Field characteristics are from Thode *et al.* (2011) and associated ranges for Relativized differenced Normalized Burn Ratio (RdNBR) from Miller and Thode (2007). Areas with a classified severity of enhanced greenness class and Landsat-undifferentiated (no change detected) were not used in this study.

Severity Class	Field Characteristics	RdNBR ranges
Unburned	Unburned forest patches outside of fire perimeters	
Enhanced greenness	Bloom of plant growth following fire	< -150
Landsat-undifferentiated	No detected change in post-fire vegetation	-150 to 68
Low	Fine fuels removed and some scorching of understory trees	69 to 315
Moderate	Some fuels remain on forest floor, mortality of small trees, scorching of crowns for medium and large-sized trees	316 to 640
High	Near-complete combustion of ground fuels, near total mortality of small and medium-sized trees, and severe needle scorch and/or mortality of large trees	≥ 641

Table S4. Mean canopy cover and canopy area by forest type and fire severity. We calculated canopy cover by dividing the number of returns in each height strata by the number of returns in that stratum and all lower strata. We calculated canopy area as the proportion of 1 m canopy surface model grid cells in each height strata divided by the area of each sample area. Canopy cover uses the total vertical distribution of returns as an estimate of the canopy profile and estimates the presence of canopy at all heights whether or not there is foliage above a given height. Canopy area measures only the top of canopy foliage in each 1 m grid cell and ignores lower foliage and therefore measures the area dominant tree clumps.

		Canopy Cover (mean)					Canopy Area (mean)					Difference (cover - area)				
		8 to 16		16 to 32		>32 m	8 to 16		16 to 32		>32 m	8 to 16		16 to 32		>32 m
		>2 m	2 to 8 m	m	m		>2 m	2 to 8 m	m	m		>2 m	2 to 8 m	m	m	
Ponderosa pine	Unburned	0.728	0.313	0.292	0.336	0.161	0.862	0.125	0.170	0.343	0.224	-0.134	0.188	0.121	-0.007	-0.063
	Low	0.601	0.191	0.232	0.276	0.110	0.731	0.108	0.169	0.304	0.151	-0.130	0.083	0.063	-0.027	-0.041
	Moderate	0.444	0.174	0.140	0.155	0.081	0.565	0.159	0.132	0.168	0.106	-0.120	0.015	0.008	-0.013	-0.025
	High	0.287	0.130	0.059	0.083	0.054	0.398	0.172	0.064	0.090	0.072	-0.111	-0.042	-0.006	-0.006	-0.017
White fir-Sugar pine	Unburned	0.686	0.255	0.270	0.340	0.159	0.805	0.097	0.144	0.332	0.232	-0.119	0.157	0.125	0.009	-0.073
	Low	0.556	0.112	0.166	0.282	0.175	0.658	0.065	0.096	0.255	0.242	-0.102	0.047	0.071	0.027	-0.067
	Moderate	0.375	0.072	0.100	0.181	0.100	0.460	0.066	0.075	0.182	0.138	-0.085	0.006	0.025	-0.001	-0.038
	High	0.187	0.051	0.042	0.075	0.042	0.265	0.075	0.043	0.085	0.062	-0.079	-0.024	-0.001	-0.010	-0.020
Red fir	Unburned	0.503	0.182	0.176	0.223	0.077	0.602	0.118	0.128	0.243	0.113	-0.099	0.064	0.048	-0.021	-0.036
	Low	0.422	0.095	0.129	0.199	0.092	0.505	0.074	0.097	0.206	0.128	-0.083	0.021	0.032	-0.007	-0.035
	Moderate	0.283	0.060	0.076	0.127	0.061	0.340	0.062	0.066	0.131	0.081	-0.057	-0.002	0.011	-0.005	-0.020
	High	0.078	0.027	0.015	0.026	0.013	0.123	0.053	0.020	0.032	0.018	-0.045	-0.026	-0.005	-0.006	-0.005

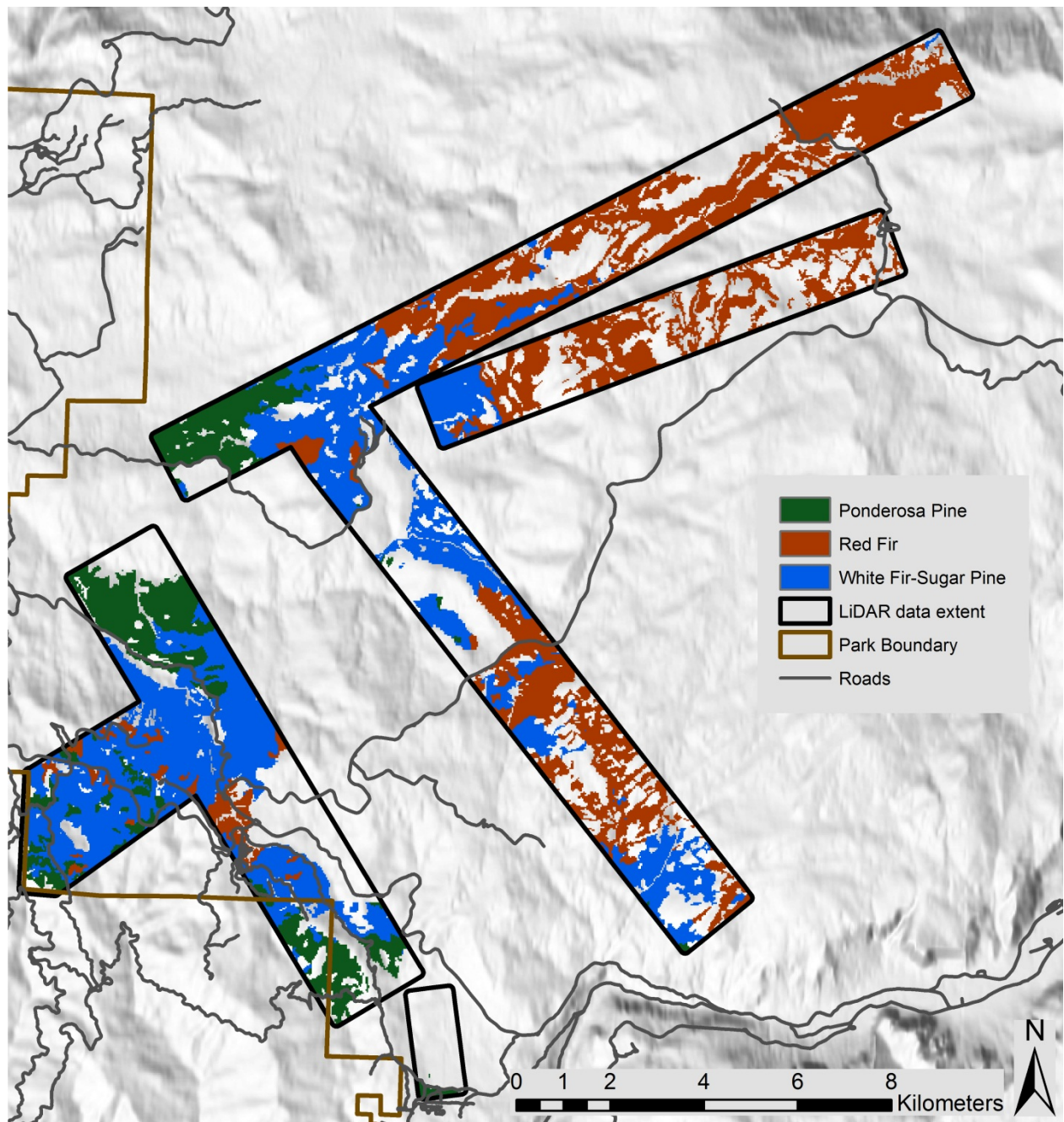


Figure S1. Map of forest types within study area, which included unburned areas outside all fire perimeters that did not experience a fire between 1930 and July 2010 or experienced a single burn between 1984 and July 2010 and had a forest type of ponderosa pine, white fir-sugar pine, or red fir.

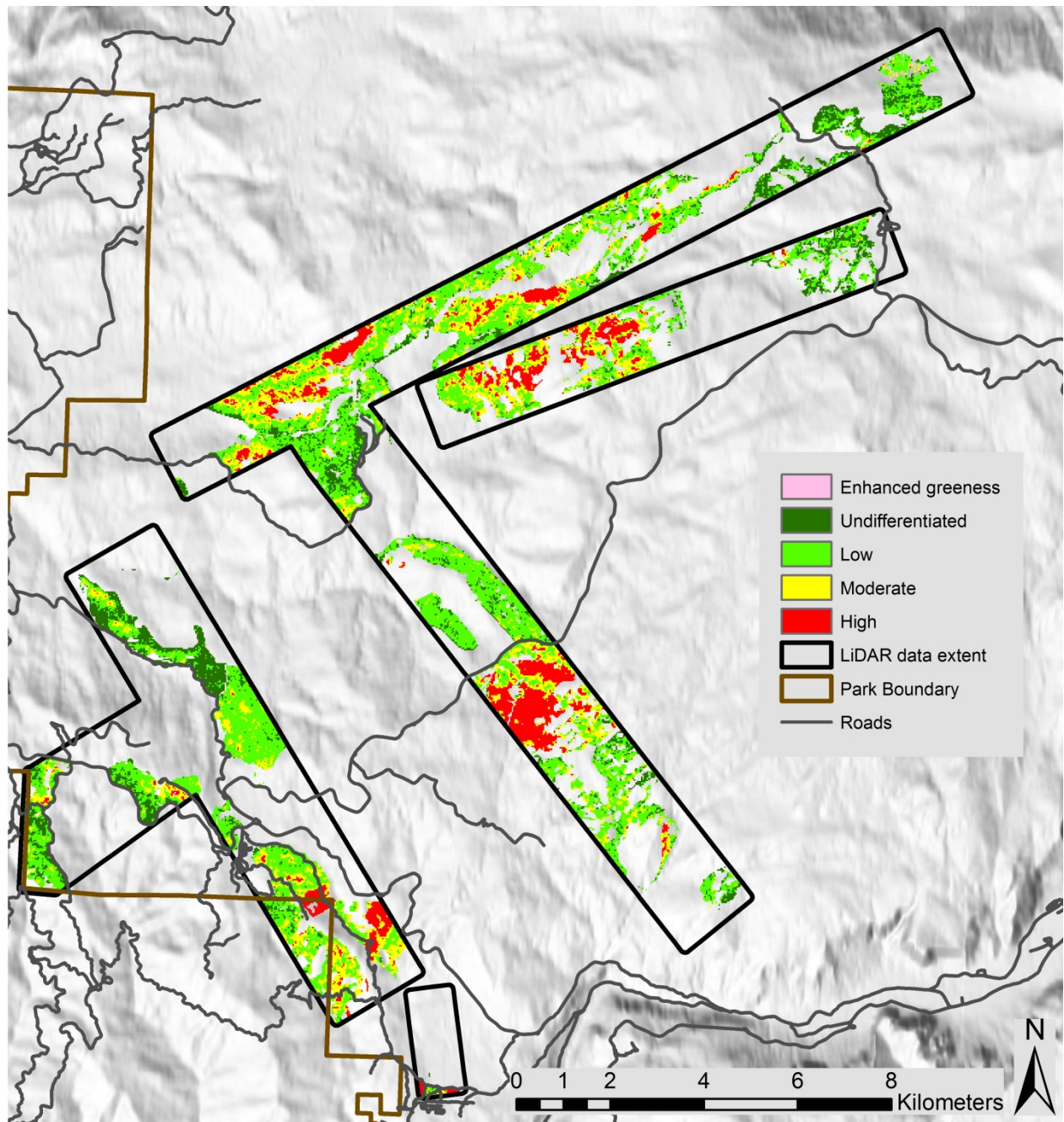


Figure S2. Map of fire severity classes within study area, which included unburned areas outside all fire perimeters that did not experience a fire between 1930 and July 2010 or experienced a single burn between 1984 and July 2010 and had a forest type of ponderosa pine, white fir-sugar pine, or red fir.

Fig. S3a) 2 to 8 m stratum

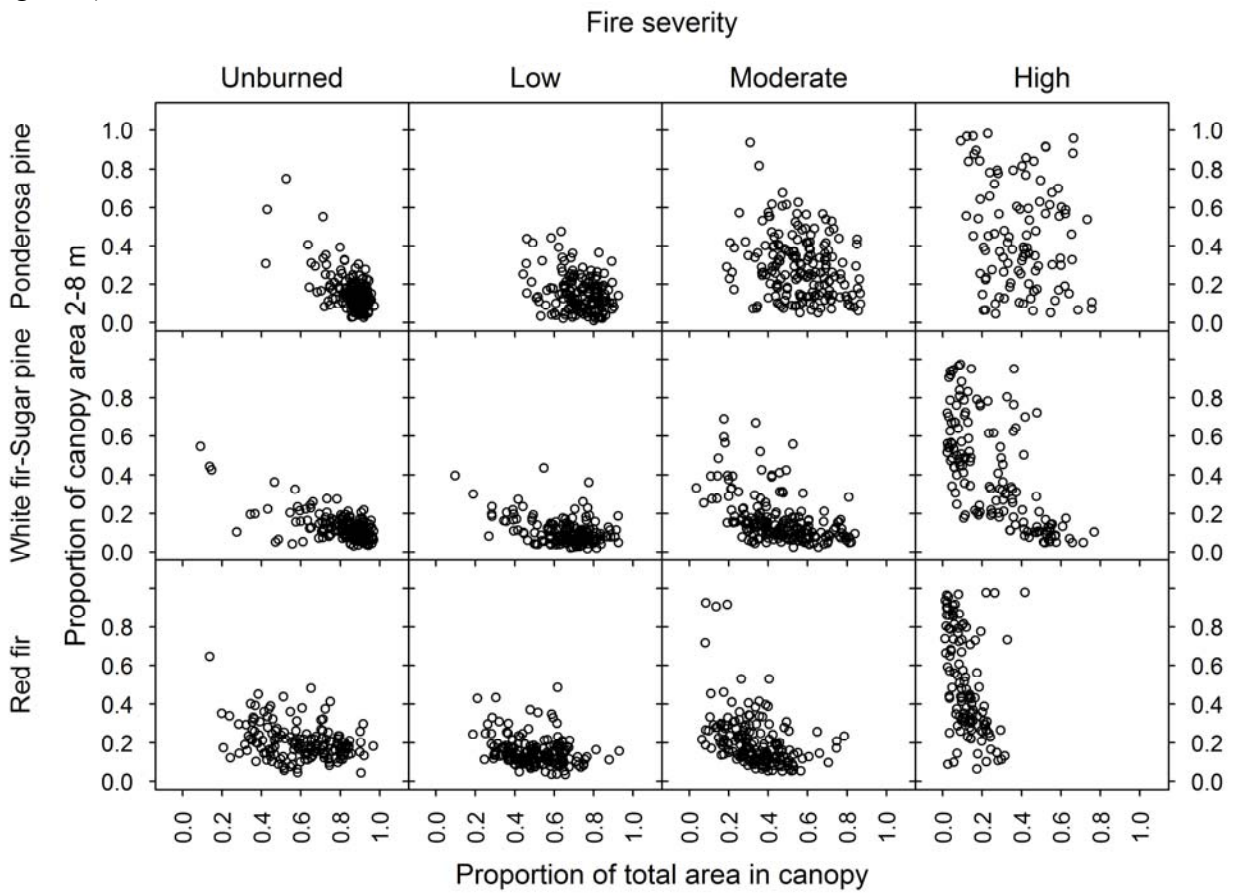


Fig. S3b) 8 to 16 m stratum

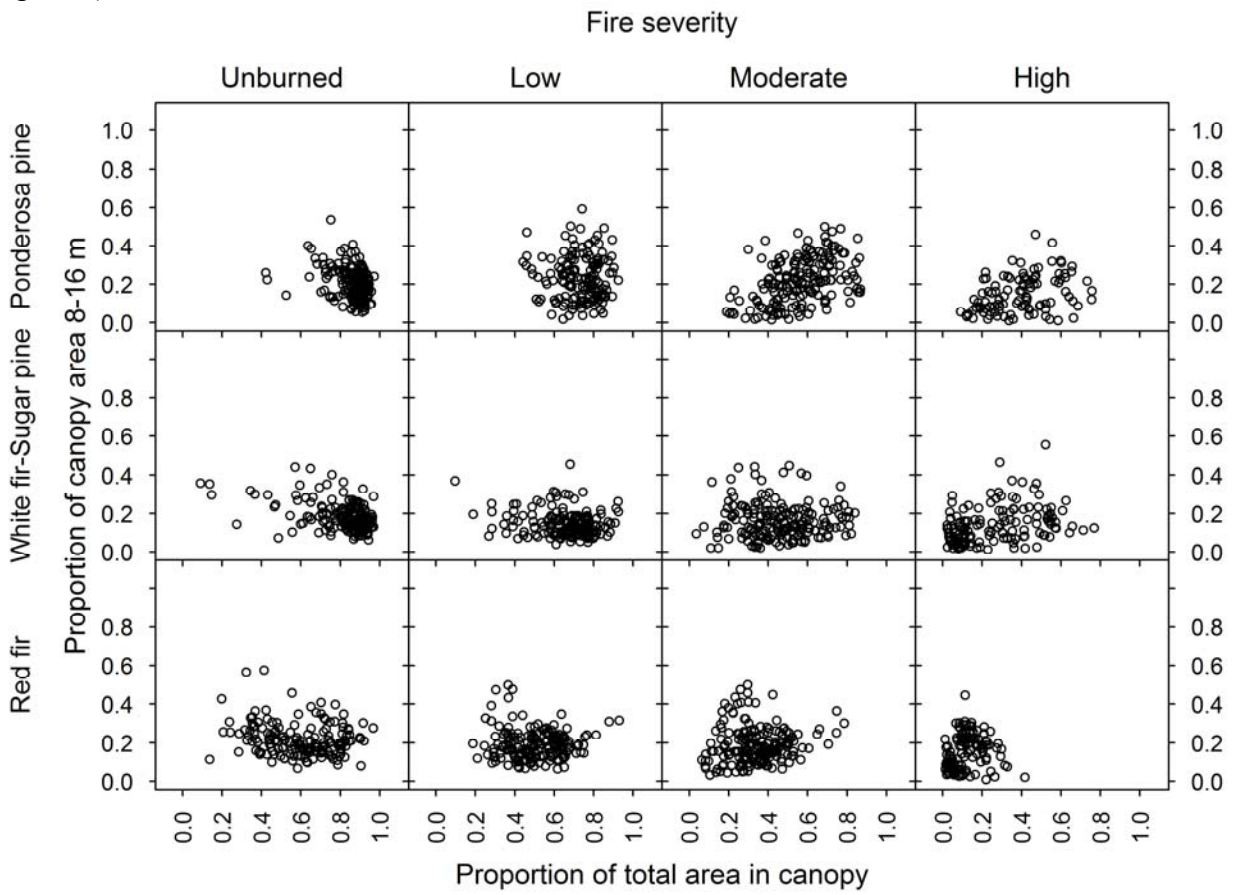


Fig. S3c) 16 to 32 m stratum

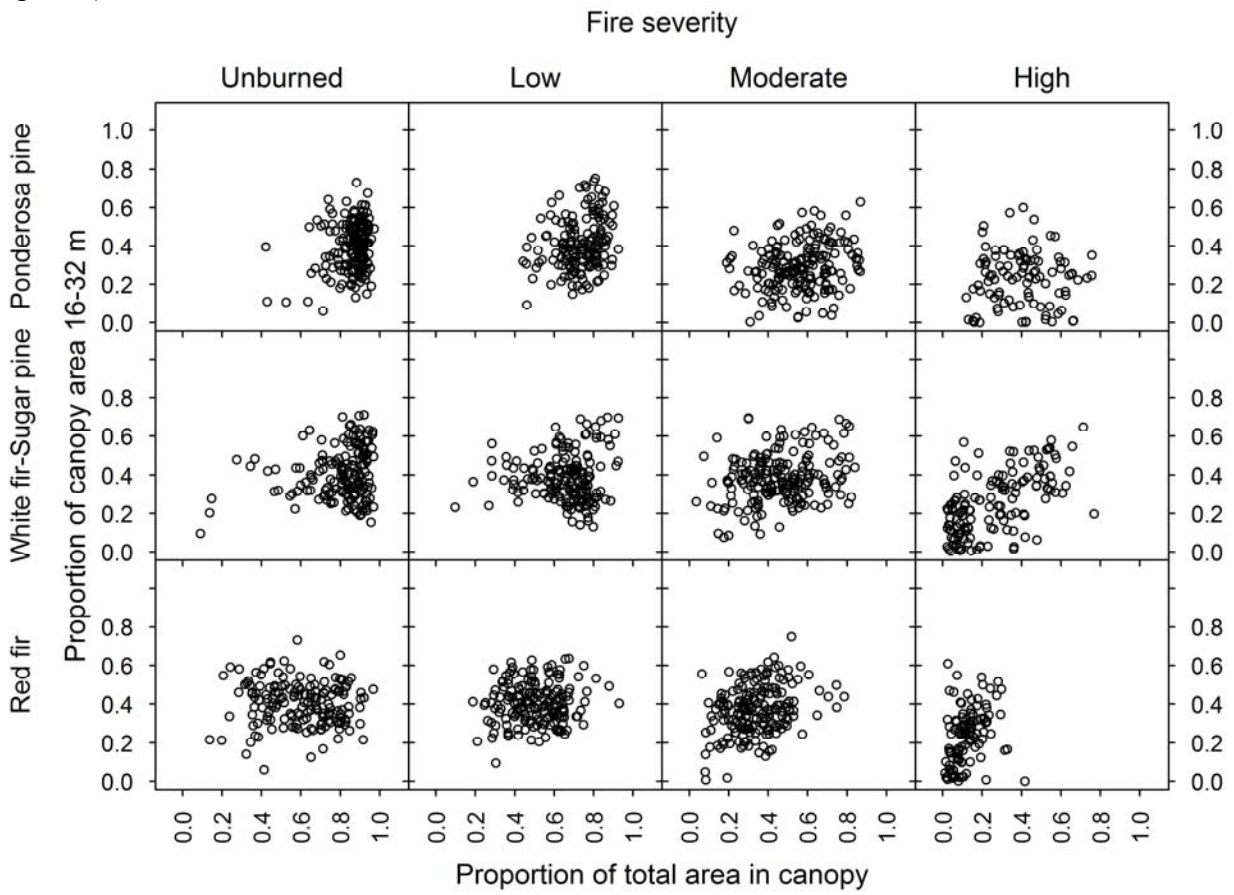


Fig. S3d) > 32 m stratum

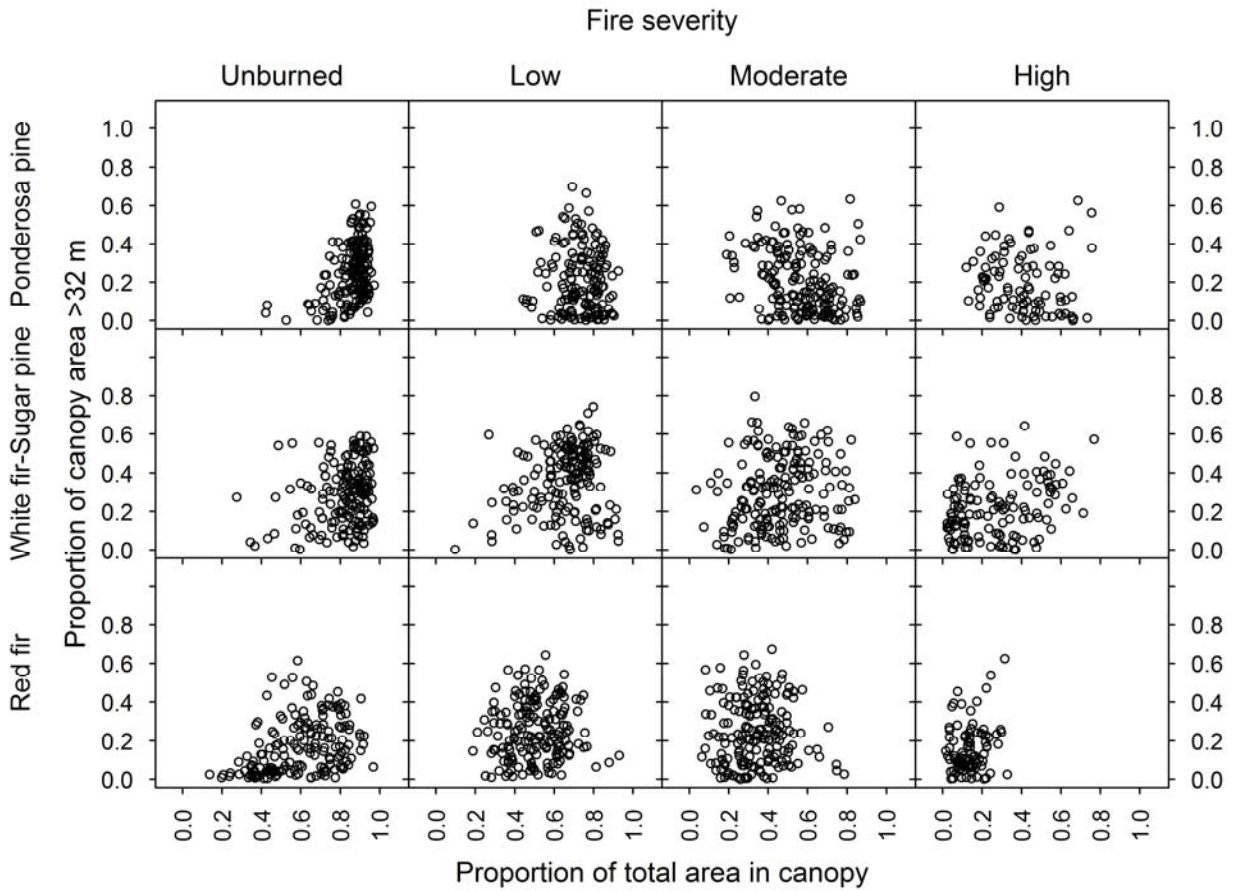


Figure S3. Heterogeneity of overall canopy and canopy patches by strata and by fire severity and forest type with total area within openings (x axis) shown for each sample area and total proportion of canopy area in clumps height stratum (y axis). Wider dispersal of points indicates a wider range of structural heterogeneity for a given fire severity-forest type combination. Increased fire severity resulted in a wider range of area in canopy for ponderosa pine and white fir-sugar pine forests but resulted in a narrow range for red fir. Increased fire severity had little effect on the range of proportion of canopy area in clumps >32 for ponderosa pine and white fir-sugar pine forests but resulted in a narrow range for red fir.