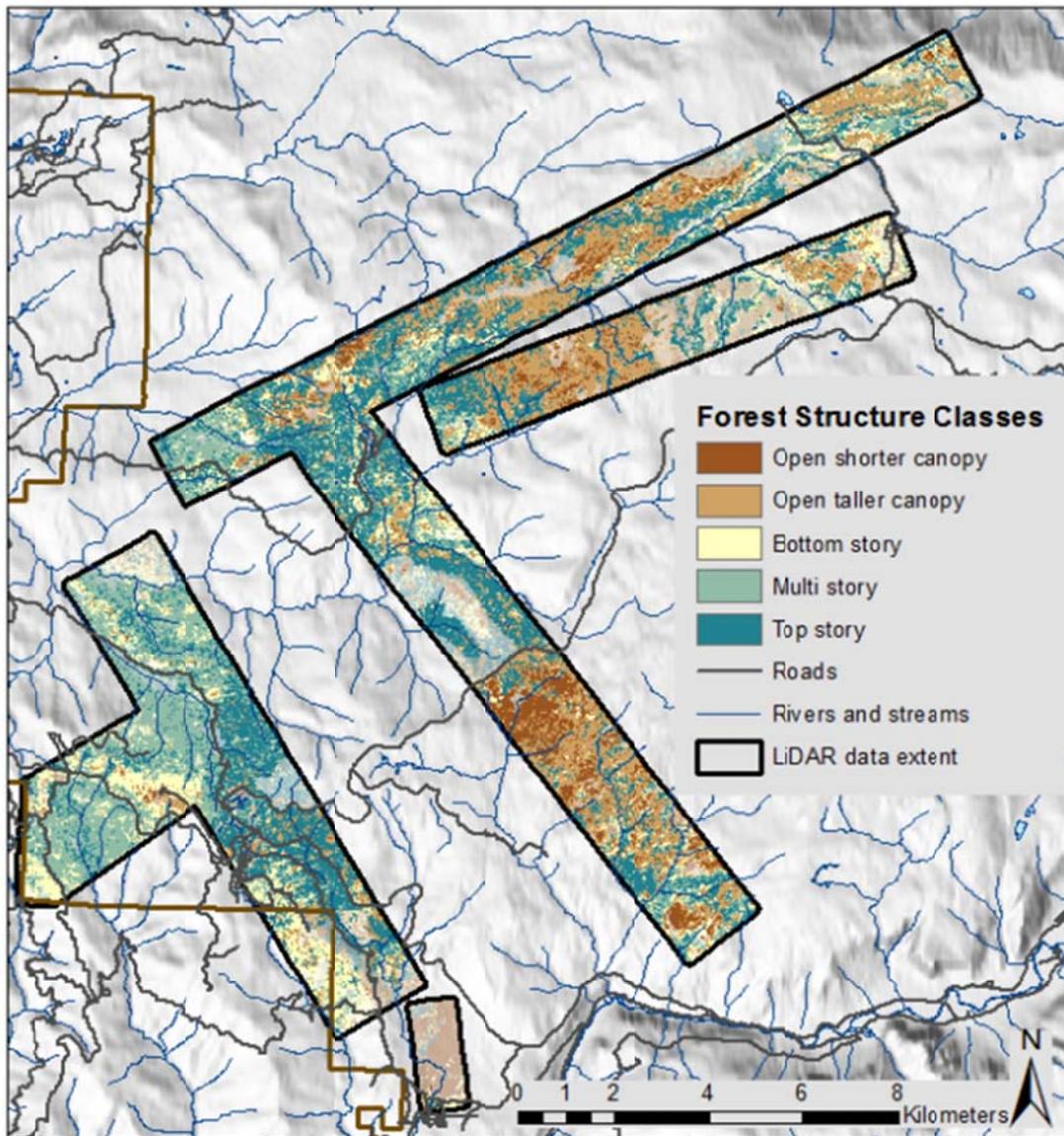


Combining Landsat and LiDAR Remote Sensing Data to Refine Fire Management Objectives for Forest Structural Heterogeneity in Yosemite National Park

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Key Findings

We found differences in vertical canopy structure (height and cover within strata) and horizontal landscape arrangement (canopy patches and gaps) related to fire severity and forest type.

The study area contained five vertical structural classes: 1) open areas with shorter canopy, 2) open areas with taller canopy, 3) bottom story, 4) multi-story, and 5) top story.

The study area contained three landscape patterns of canopy patches and gaps: 1) continuous canopy enclosing small gaps (canopy/gap), 2) forests where the proportion of canopy and gap are similar (patch/gap), and 3) open space surrounding individual trees and small tree clusters (open/patch). The study area had mosaics of fire severity class patches, but the proportion of area in moderate to high severity patches was lower than for all of Yosemite (1984 to 2010).

LiDAR detected changes in vertical forest structure and in gaps for fires of all severities. Low severity fires (both detectable and undetectable by Landsat-derived dNBR values) decreased canopy cover from 2 m to 16 m and increased the number and size of small gaps. Moderate severity fires decreased canopy cover above 16 m, resulting in patch/gap structure. High severity fires increased patch/gap area and created open/patch areas.

Pinus jeffreyi forests and woodlands were unique, with primarily edaphic control of structure. *Pinus jeffreyi* patch structure was mostly unchanged by fire of any severity.

In *Pinus ponderosa*, *Abies concolor*/*Pinus lambertiana*, and *Abies concolor* forests, the proportions of canopy/gap, patch/gap, and open/patch were related to increasing fire severity. The proportions of forest area in each of the five structural classes were related to fire severity, and to a lesser degree, on forest type. Forest patches that were unburned between 1984 and 2010 were characterized by contiguous canopy. Increasing fire severity decreased the proportion of contiguous canopy patches and increased the proportion of gaps until gaps merged into open spaces.

There was no trend in regrowth with time since fire, except for 2 m to 16 m canopy cover in *Pinus ponderosa* patches. In patches that burned at moderate and high severities, tall trees decreased with time since fire, consistent with delayed mortality and the loss of snags.

Burn patches of the same dNBR severity showed considerable structural variation between fires, suggesting complex effects of both pre-fire vegetation and topographic position.

Conclusions and Recommendations

Fires with patches undetectable by Landsat (i.e. many prescribed fires) significantly increase the number of gaps and decrease vegetation cover between 2 m and 16 m.

Low fire severity (in *Abies magnifica* forests) and moderate severity fires (in *Pinus ponderosa* and *Abies concolor*/*Pinus lambertiana* forests) restore vertical forest structure and landscape gap distributions to conditions similar to reconstructed pre-fire-suppression conditions.

We recommend that the park further analyze individual fires and fire management types in conjunction with existing vegetation and topographic data to understand correlates of fire-induced structural change, as well as analyzing LiDAR data from other park regions (e.g., Illilouette basin). We recommend decadal acquisition of LiDAR data over fire-dominated areas of the park to track forest structural change due to fire, wind, and insects.

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INTRODUCTION

Fire shapes the structure of forests (Romme 1982, Agee 1998, Brown et al. 1999) and acts as a keystone process influencing the structural and compositional heterogeneity of forests in western North America (Swetnam 1993, Whitlock et al. 2003). Understanding how fire modifies forest structure, however, is difficult because of the inherent complexity of the interaction between fires and forests. Each fire interacts with the existing template of forest types, forest structures, heterogeneity of fuels, and previous fires to create new templates that influence future forest development and fire behavior (Pyne et al. 1996). The resulting restructuring of forests is inherently complex from the scale of individual trees to stands (Romme 1982, Turner et al. 1994, Turner and Romme 1994, Agee 1998). The mosaics of unburned and burned patches are particularly complex in areas where fires burn with mixed severities such as in the present-day forests of the Sierra Nevada Mountains in California, USA (Collins et al. 2007, Lutz et al. 2009).

Recent work has deepened our understanding of the ecology of mixed severity fires (Perry et al. 2011). These fires are characterized by a patchiness of fire severities that result in mosaics of severity patches with many small patches and relatively few large patches (Hessburg et al. 2005, Hessburg et al. 2007, Collins and Stephens 2010, Moritz et al. 2011). The complex spatial patterns are characteristic of fires in which bottom up controls such as local dominant vegetation, topography, fire history, and fire weather determine severity patterns (Collins et al. 2007, Collins and Stephens 2010, McKenzie and Kennedy 2011). The role of pre-existing forest structures such as the size and arrangement of trees and the laddering of foliage is recognized as an important control for mixed severity fires, and the structural changes created by each fire in turn creates a new template (Moritz et al. 2011, Perry et al. 2011). However, discussions of the relationship between fire and pre-existing forest structure are often at the level of generalities (e.g., Perry et al. 2011), presumably because of the lack of information on both pre and post fire structures present. A method to measure forest structures across the heterogeneous landscape that has experienced mixed severity fires could address this issue.

A better understanding of the relationship between fire and its restructuring of forests in mixed severity regimes also would improve our ecological understanding other aspects of forest ecology. The physical structure of a forest following a fire influences post-fire plant establishment and community composition (Turner et al. 1997, Donato et al. 2009). Gaps are an especially important forest structures that are necessary for species such as *Pinus ponderosa*, *P. lambertiana*, and *P. monticola* (Graham 1990, Kinloch and Scheuner 1990, Oliver and Ryker 1990), which require both available light and moisture, to regenerate. Unnaturally large individual gaps or limited connectivity between forest patches can potentially lead to vegetation type conversions if seed dispersal into them is slow (Turner et al. 1997). The spatial pattern of forest structure created by mixed severity fire regimes influences the composition of wildlife communities (Roberts et al. 2008).

In many forests of the western United States, decades of fuel exclusion has led to a shift in forest patch structure (Hessburg et al. 2005). Prior to Euro-American settlement, these forests experienced frequent, low severity fires that removed many smaller diameter trees and reduced fuel laddering (van Wagtendonk 2007, Scholl and Taylor 2010). Stands often were assemblages of individual trees and small clumps of trees with a high proportion of open space (Larson and Churchill 2012). By contrast, many of these forests today have substantially higher densities of

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small diameter trees leading to fuel laddering and canopy closure is common (Hessburg et al. 2005, Scholl and Taylor 2010, Lutz et al. In review). As a result, managers often seek to return many forests to conditions closer to those that prevailed prior to fire exclusion (Larson and Churchill 2012), and therefore need to understand the effects of current fires on forest structure.

Meeting these needs for a better understanding of how fire restructures forests requires the ability to both map fire severity and forest structure with high resolution and precision. The development of burn severity indices that relate Landsat images to changes in vegetation structure and cover following a fire has allowed quantitative assessment of fires that burned since 1984 at 0.09 ha resolution (White et al. 1996, Key 2006, Key and Benson 2006). Collins and his colleagues examined the fire severity and resulting gap patterns in contemporary natural Sierra Nevada fires and found complex patterns of mixed severity fires influenced by dominant vegetation type, weather during the fire, time since last fire, and slope position (Collins et al. 2007, Collins et al. 2009, Collins and Stephens 2010). Lutz et al. (2009) established that forests burned at higher severities and in more complex patterns in years with lower snow packs. Modern management practices have created a new level of complexity with prescribed fires resulting in larger patches that had no detectable change (as recorded by Landsat) or that burned with low severity in contrast to wildfires that had larger percent areas burned at moderate and high severity (van Wagendonk and Lutz 2007). Thode et al. (2011) used Landsat-derived burn severity records to assign fire regimes to the major vegetation types within and around Yosemite National Park.

To date, we have lacked corresponding measurements of forest structure to relate fire severity to changes in structure. Field studies, such as that of Collins et al. (2011), that relate forest structure to fire severity are rare and can sample only small areas and therefore may under sample the heterogeneity in fire severity and structure. Collins et al.'s (2011) re-sampling of historic surveys, for example, did not include any high severity fire patches. Satellite images such as those from the Landsat satellites offer broad coverage and frequent re-measurement, but have lacked the ability to resolve forests structure beyond broad types with better than moderate structural fidelity (Fassnacht et al. 2006, Bergen et al. 2009, Froelking et al. 2009).

Airborne Light Detection and Ranging (LiDAR) instruments have been research tools for forest studies since the late 1990s (Lefsky et al. 2002, Reutebuch et al. 2005, Hudak et al. 2009). As experience has increased with this technology, research has moved from validation of the LiDAR measurements (e.g., Lefsky et al. 1999, Naesset and Okland 2002) to estimations of continuous variable such as basal area and biomass (e.g., Gobakken and Naesset 2004, Andersen et al. 2005) to studies of forests across large areas (e.g., Asner et al. 2011). Increasingly, LiDAR data has been used to study gaps within forests (Vepakomma et al. 2008, Kellner and Asner 2009, Kane et al. 2011). Several researchers have used LiDAR data to develop regressions to estimate specific fuel parameters such as crown bulk density or height to live crown for use in fire behavior models (Erdody and Moskal, Riano et al. 2004, Andersen et al. 2005, Agca et al. 2011). Kane et al. (2011) used LiDAR to study patterns of patch dynamics within forests.

LiDAR data measure the heights of vegetation surfaces that lie between the instrument mounted on the plane and the ground. The strength of LiDAR measurements is the precise, consistent measurement of forest structure over large areas with greater sensitivity than satellite image and spectral measurements (Asner et al. 2011, Hummel et al. 2011). Because canopies represent the majority of the surface of trees and shrubs, most LiDAR returns measure the 3-D position of canopy material rather than the boles. This is the reverse of many field studies that

focus on measurements of boles with no or few measurements of canopy structure. However, just as field measurements of tree diameters have been regularly used to estimate canopy conditions such as canopy bulk density using allometric equations (Scott and Reinhardt 2001), LiDAR measurements of canopy structure have been used to estimate bole values such as mean diameter and tree height (Naasset 2002, Reutebuch et al. 2005).

A complication of relating differences in fire severity to changes in forest structure is that pre-fire and post-fire measures of structure near the time of a fire are rare except for prescribed fires where managers determine the timing of the fire. Collins et al. (2011), for example, attributed the differences between their low and moderate severity fire plots to the effects of fire and assumed their no fire plots represented the typical pre-fire conditions for their burned plots. While their hypothesis is reasonable given the known effects of fire on forest structure, alternate explanations would be that pre-fire differences in structure caused the differences in fire severity or that the post-fire condition resembled the pre-fire condition. The large samples enabled by LiDAR can test for heterogeneity in structure within no fire patches to test for similarities between patches that did not experience fire and patches burned with different severities. Substantial differences across numerous fires in the equivalent of tens of thousands of plots associated with different fire severities would strengthen the case for fire as the cause.

In this study, we combined Landsat measurements of burn severity with airborne LiDAR measurements of forest structure to examine how fire restructures forests. We looked both at the vertical distribution of foliage and at the spatial characteristics of canopy patches and gaps in unburned and burned patches. We used a 96.9 square kilometer study area that was subjected to 32 fires >40 ha in size between 1984 and 2010 and that contained four forest types that are widely distributed throughout the Sierra Nevada mountain range. We used these datasets to address three questions:

1. What patterns of burn severity were created across our study area?
2. How did different fire severities change the vertical distribution of foliage within each of the forest types and could we distinguish changes in structure from regrowth following the fire?
3. How did different fire severities change the proportion and structure of canopy patches and gaps within each of the forest types?

METHODS

Yosemite National Park

Yosemite National Park (3027 km²) lies in the central Sierra Nevada range, California, USA. This region 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 et al. 2010). The forest vegetation of Yosemite comprises a mosaic of forest types, species, and structural stages (van Wagtenonk et al. 2002, van Wagtenonk and Fites-Kaufman 2006, Fites-Kaufman et al. 2007, Thode et al. 2011). Typical fire intensity and severity vary by forest type (van Wagtenonk et al. 2002, Thode et al. 2011).

Yosemite experiences multiple wildland fires (prescribed and wildfires) each year, and since 1972, many naturally ignited fires have been allowed to burn under prescribed conditions

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(van Wagtendonk and Lutz 2007). The Yosemite fire regime historically was low severity at lower elevations prior to Euro-American settlement (van Wagtendonk and Fites-Kaufman 2006, Perry et al. 2011) but today is characterized as mixed severity (van Wagtendonk and Lutz 2007, Lutz et al. 2011, Thode et al. 2011). The natural fire return interval for the forested ecosystems of Yosemite National Park ranges from 4-187 years (Caprio and Swetnam 1995, Caprio and Lineback 1997, van Wagtendonk et al. 2002, Collins and Stephens 2007) and fires burn with patches of high, moderate, and low severities at intervals ranging from years to centuries (Agee 1993, van Wagtendonk et al. 2002, Sugihara et al. 2006, van Wagtendonk and Fites-Kaufman 2006, van Wagtendonk and Lutz 2007).

Study Area

We selected an area within Yosemite National Park of 10,895 ha to maximize the number of principal forest types, range of fire severities, and the number of fires while providing substantial unburned areas outside the fire perimeters for comparison (Fig. 1-3). We assigned forest types within the study area based on either the 1997 park vegetation map (Keeler-Wolf et al. In press) or the 1937 vegetation map (Wieslander 1935, Walker 2000). 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. Areas delineated as meadow or shrub in both 1937 and 1997 were not included.

Between 1930, when comprehensive park fire records began, and the date of the LiDAR acquisition (21 July 2010), there were 327 fires of all sizes in the acquisition area (4.1 fires/year), with 40 fires ≥ 40 ha. Between 1984 and July 21, 2010, there were 169 fires with 32 fires ≥ 40 ha. The total study area burned by fires between 1984 and July 21, 2010, including reburns, was 7,939.9 ha, with a unique burned area of 6,857.8 ha (Tables 1 and 2). The unburned area between 1984 and July 21, 2010 within the study area was 2,866.6 ha.

To provide sufficient area in all burn severities for meaningful comparison, we limited our final study area to forest types with a total area >1000 ha with our study area - *Pinus ponderosa* (ponderosa pine, PIPO) forest, *Abies concolor/Pinus lambertiana* (white fir/sugar pine, ABCO/PILA) forest, *Pinus jeffreyi* (Jeffrey pine, PIJE) forest, and *Abies magnifica* (red fir, ABMA) forest. The *Pinus ponderosa* forest and *Abies concolor/Pinus lambertiana* forest zones are characterized by deep and well-drained soils (van Wagtendonk and Fites-Kaufman 2006). The *Pinus jeffreyi* and *Abies magnifica* forests lie in the upper montane zone characterized by weakly-developed soils (van Wagtendonk and Fites-Kaufman 2006). Tree densities in the *Abies magnifica* zone vary with soil depth, which effects water availability (North et al. 2002, Meyer et al. 2007). *Pinus jeffreyi* forests were found primarily in expanses of granite outcrops where their spacing was controlled by the availability of soil patches between rocks.

Patterns of Burn Severity

We used the Yosemite fire atlas assembled by Lutz et al. (2011) and processed by the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al. 2007). This atlas includes all fires ≥ 40 ha, which comprise 97% of area within fire perimeters (Lutz et al. 2009).

The differenced Normalized Burn Ratio, dNBR (Key 2006, Key and Benson 2006) calculated from Landsat bands 4 (near infrared) and 7 (mid infrared) was used to stratify fire severity. The dNBR values can range between -2.0 and 2.0, but we followed normal practice and

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scaled these values by a factor of 1000. Higher values of dNBR indicate a decrease in photosynthetic materials and surface materials holding water and an increase in ash, carbon, and soil cover.

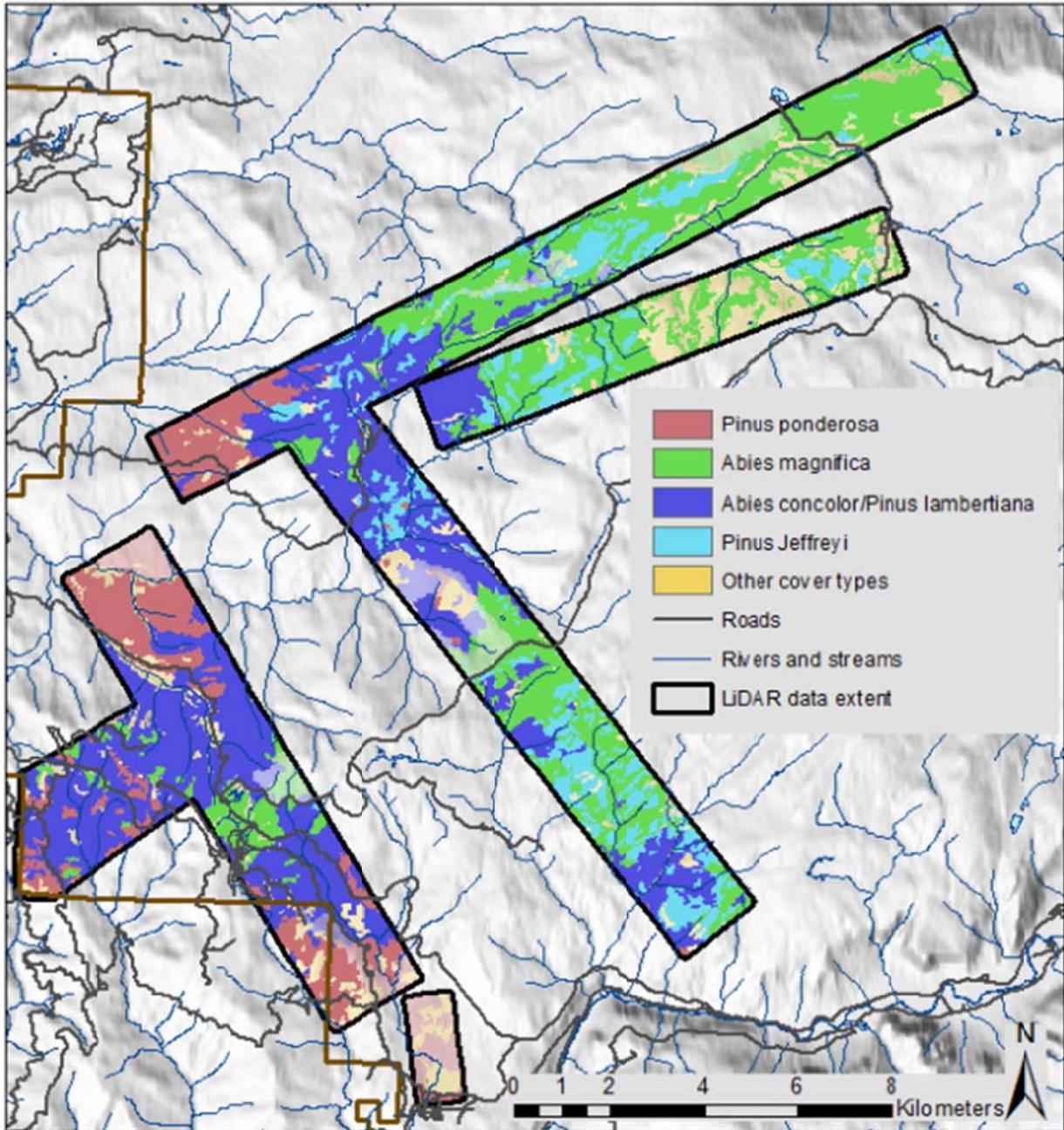


Figure 1. Map of forest types within study area, which included areas that experienced no fire or a single fire and had a forest type of *Pinus ponderosa*, *Abies concolor/Pinus lambertiana*, *Pinus jeffreyi*, or *Abies magnifica*. Areas within the LiDAR data extent that experienced more than a single fire or had a different vegetation cover type are shown in muted colors.

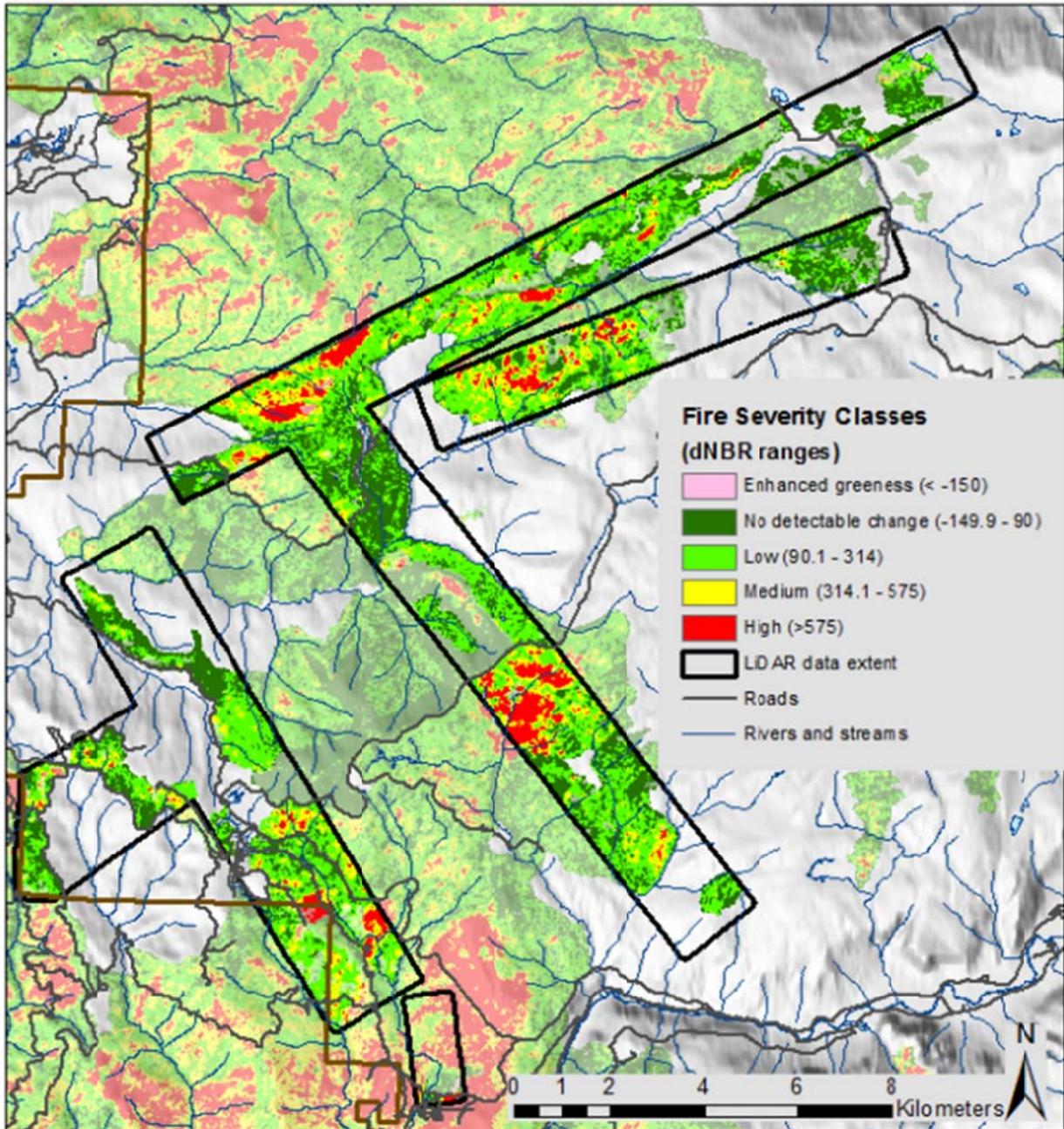


Figure 2. Map of fire severity classes within study area, which included areas that experienced no fire or a single fire and had a forest type of *Pinus ponderosa*, *Abies concolor*/*Pinus lambertiana*, *Pinus jeffreyi*, or *Abies magnifica*. Areas within the LiDAR data extent that experienced more than a single fire or had a different vegetation cover type are shown in muted colors.

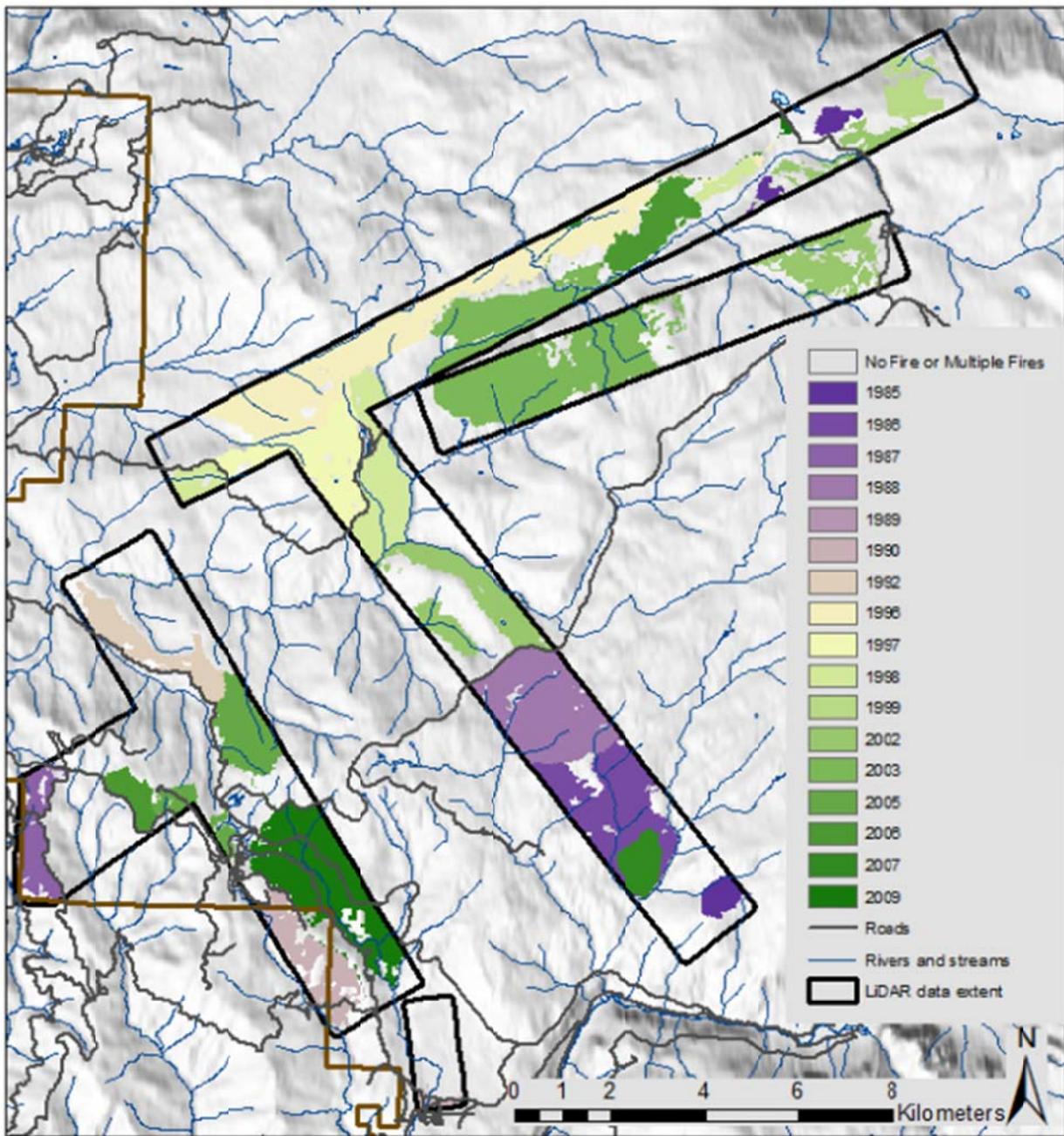


Figure 3. Map of fires dates by year of fire within the area, which included areas that experienced no fire or a single fire and had a forest type of *Pinus ponderosa*, *Abies concolor*/*Pinus lambertiana*, *Pinus jeffreyi*, or *Abies magnifica*. Year of fire is not shown for areas that experienced multiple fires or had a different vegetation cover type.

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Table 1. Vegetation types in the Yosemite study area with their burn characteristics for the study period (1984 – 2010). Burn severity reported is the maximum burn severity for each grid cell. Data based on fires ≥ 40 ha.

Forest type	Area (ha)	Maximum fire severity 1984-2009							
		High severity	Moderate severity	Low severity	No detectable change	No Fire	One Burn	Two burns	Three burns
<i>Abies concolor</i> / <i>Pinus lambertiana</i> forest (ABCO-PILA)	3622.3	5.52%	8.53%	30.83%	18.16%	36.97%	55.62%	6.33%	1.08%
<i>Abies magnifica</i> forest (ABMA)	3365.5	5.32%	9.66%	38.46%	22.75%	23.81%	65.69%	10.47%	0.03%
<i>Pinus ponderosa</i> forest (PIPO)	1527.8	7.17%	16.43%	31.66%	16.28%	28.45%	49.07%	22.11%	0.37%
<i>Pinus jeffreyi</i> woodland (PIJE)	1170.0	3.94%	8.09%	31.00%	32.97%	24.01%	70.40%	5.46%	0.14%
<i>Pinus monticola</i>	314.1	0.03%	0.89%	16.65%	29.11%	53.32%	40.49%	6.16%	0.03%
<i>Pinus contorta</i>	253.1	0.53%	2.42%	11.52%	25.36%	60.17%	39.08%	0.75%	0.00%
<i>Pseudotsuga menziesii</i>	118.2	0.08%	0.61%	13.94%	12.87%	72.51%	25.59%	1.90%	0.00%
<i>Pinus ponderosa</i> woodland	92.3	4.19%	25.54%	46.49%	20.76%	2.92%	62.77%	34.02%	0.29%
<i>Quercus</i> woodland	59.9	11.41%	28.53%	30.63%	7.51%	21.92%	61.86%	16.22%	0.00%
<i>Sequoiadendron giganteum</i>	23.1	0.00%	0.78%	11.67%	22.57%	64.98%	35.02%	0.00%	0.00%
Total forested area	10546.4	5.18%	9.77%	32.42%	21.42%	31.20%	58.41%	9.94%	0.45%
Non-forested area	560.3								

Notes: Burned areas mapped as ‘enhanced greenness’ (dNBR < -150; total area 0.54 ha within forested area; see *Methods: Burn severity*) were excluded.

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Table 2. Fires >40 ha included in study. Fire types are Management Ignited Prescribed Fire (MIPF), Wildland Fire Resource Benefit (WFRB) 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)	Study burned area (ha)	% of fire in study area	Year	Fire name	Fire type	Total burned area (ha)	Study burned area (ha)	% of fire in study area
1985	New Drub	PNF	43	21	48.8%	1999	Pw-2	MIPF	329	116	35.3%
1985	1985YNP-021	PNF	57	55	96.5%	2000	South Fork PW-3	MIPF	89	84	94.4%
1986	Cascade Creek	PNF	838	521	62.2%	2002	Wolf	WFRB	805	416	51.7%
1987	Larson	WF	234	174	74.4%	2002	PW-3 Gin Flat	MIPF	1360	562	41.3%
1988	Walker	PNF	201	14	7.0%	2003	Tuolumne WFU	WFRB	664	478	72.0%
1988	Walker	WF	1073	472	44.0%	2003	Tuolumne WF	WF	789	666	84.4%
1989	Pw3	MIPF	688	276	40.1%	2005	PW5-AD	MIPF	104	74	71.2%
1990	T-Grove 4	WF	231	113	48.9%	2005	PW3-23	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	99.5%	2006	PW5 North C	MIPF	77	77	100.0%
1996	Ackerson	WF	23939	1197	5.0%	2006	MiddleT Sup	WF	140	140	100.0%
1997	Aspen Valley Pw	MIPF	597	333	55.8%	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	MIPF	86	72	83.7%	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%

Satellite-derived dNBR values are commonly classified into burn severity classes after calibration with ground composite burn index plots (Thode 2005, Key 2006, Key and Benson 2006). Analysis of data is then performed using the classification levels (Miller and Thode 2007, Lutz et al. 2009, Miller et al. 2009). We classified the study area into five fire severity classes for areas within fire perimeters: enhanced greenness ($dNBR \leq -150$), no detectable change ($dNBR < 90$), low severity ($90 \leq dNBR < 314$), moderate severity ($314 \leq dNBR < 575$), or high severity ($dNBR \geq 575$; (Lutz et al. 2011). Just six pixels (0.54 ha) were in the enhanced greenness severity class, and these were dropped from the study. We also defined a special class, no fire, as forest patches outside of all fire perimeters for fires ≥ 40 ha between 1984 and the LiDAR acquisition. We treated no fire patches as an additional fire severity class in all analyses representing the reference condition of forests that did not experience fire during the study period.

We identified severity patches as contiguous areas having the same fire severity. We further subdivided the severity patches by forest type and analyzed our data by severity-forest classes. To remove the possible confounding effects of multiple fires, we conducted our analysis using only patches that experienced either no fire or a single fire between 1984 and the LiDAR acquisition in 2010.

LiDAR Data

LiDAR data were collected by Watershed Sciences, Inc. using a dual-mounted Leica ALS50 Phase II instrument on July 21 and 22, 2010. All areas were surveyed with an opposing flight line and scan angles of $\pm 14^\circ$, resulting in a side-lap of $\geq 50\%$ ($\geq 100\%$ overlap) to reduce laser shadowing and increase surface laser painting. Watershed Sciences collected an average pulse density of 10.9 pulses per square meter. The LiDAR instrument recorded up to four range measurements (returns) per pulse, and all discernible laser returns were processed for the output dataset. Average flight height was 1300 m above ground level. Watershed Sciences produced the 1 m resolution digital terrain model (DTM) used in this study from the LiDAR data using the

Table 3. Fire severity classes used in this study with unburned patches outside of fire perimeters listed as a special class, no fire. Field characteristics are from Thode (2005) and Thode et al. (2011). The enhanced greenness fire severity class, indicating a bloom of plant growth following fire ($dNBR$ values < -150), was not used in this study because it was found only in six Landsat pixels within the study area.

Severity Class	Field Characteristics	dNBR ranges
No Fire	Unburned forest patches outside of fire perimeters	
No Detected Change	Unburned or lightly burned	-150 to 90
Low	Fine fuels removed and some scorching of understory trees	90 to 314
Moderate	Some fuels remain on forest floor, mortality of small trees, scorching of crowns for medium and large-sized trees	314 to 575
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	>575

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TerraScan v.10.009 and TerraModeler v.10.004 software packages (Terrasolid, Helsinki, Finland). We processed the LiDAR return point cloud data using the U.S. Forest Service's FUSION software package, beta version derived from version 3.00 (<http://forsys.cfr.washington.edu/fusion.html>). True-color orthographic images with a 15cm resolution also were collected concurrently with the LiDAR data and were used in this study as an interpretive aid.

Analysis of Vertical Foliage Distribution

We measured the vertical foliage distribution using statistical measurements of the distribution of return heights to measure percentile heights, heterogeneity of heights, and canopy cover. Metrics were calculated using all returns for 30 m grid cells to match the resolution of the fire severity and vegetation cover maps. This resulted in a total of 98,267 0.09 ha grid cells (8,844 ha) within our four forest types that either had no fire or a single fire within our study period. With an average return density of 10.9 returns per square meter, the Fusion software had an average of 9,810 returns per 30 m grid cell on which to calculate the metrics.

Height metrics (e.g., 95th percentile return height) were calculated after subtracting the elevation of the underlying ground surface model from each return elevation so that the heights represented height above ground. Canopy cover metrics were calculated as the proportion of returns within a height stratum such as 2-16 m divided by all returns in that stratum and below. We did not include returns below 2 m in the calculation of height measurements, and we did not calculate cover below 2 m. This resulted in these metrics representing the structure of only canopy trees with foliage >2 m in height. For height measurements, this cutoff removed the large number of returns from the ground, shrubs, and saplings from affecting the measurement of the canopy structure. Rumple (canopy surface rugosity) was calculated as a measure of the structural heterogeneity of the canopy surface, which has been shown to correlate with stand structural complexity (Birnbaum 2001, Ishii et al. 2004, Parker et al. 2004, Parker and Russ 2004, Ogunjemiyo et al. 2005, Kane et al. 2008, Kane et al. 2010a, Kane et al. 2010b). Rumple was computed over 30 m grid cells as the surface area a canopy surface model (CSM) within the grid cell divided by the surface area of the underlying ground surface model. Rumple was calculated on a CSM smoothed with a 3×3 moving window so that missing data and microgaps in foliage did not skew the results.

We examined correlation among a candidate set of LiDAR metrics using Pearson correlation (Table 4) and a principal components analysis (PCA) ordination (results not shown) to find a parsimonious set of metrics that could be used to describe the heterogeneity of forest structure within our study area (Lefsky et al. 2005b, Kane et al. 2010a, Kane et al. 2010b). We chose five metrics to analyze vertical structure: 95th percentile return height, which correlates with dominant tree height; 25th percentile return height, which corresponds with the dominant height of lower tree foliage; rumple, which measures the heterogeneity of heights both vertically and horizontally (Kane et al. 2010b); canopy cover in the 2-16 m height strata; and canopy cover >16 m.

Forest Structural Heterogeneity in Yosemite National Park

Table 4. Correlation of LiDAR metrics selected to describe forest structure (columns) among themselves and with other LiDAR metrics considered. Correlations with absolute values ≥ 0.75 in bold for emphasis.

	P25 Return Height	P95 Return Height	Rumple	Canopy Cover 2-16 m	Canopy Cover > 16 m
Mean Height	0.897	0.908	0.764	-0.045	0.756
P05 Height	0.779	0.437	0.444	-0.218	0.537
P25 Height	--	0.674	0.625	-0.189	0.684
P95 Height	0.674	--	0.776	0.134	0.707
SD Height	0.423	0.937	0.676	0.212	0.564
Rumple	0.625	0.776	--	0.229	0.742
Cover 2-16 m	-0.189	0.134	0.229	--	0.411
Cover >16 m	0.684	0.707	0.742	0.411	--
Cover >2 m	0.376	0.527	0.636	0.781	0.859
Cover 2-4 m	-0.290	0.065	0.096	0.791	0.201
Cover 4-8 m	-0.241	0.077	0.152	0.898	0.268
Cover 8-16 m	-0.003	0.162	0.274	0.857	0.487
Cover 16-32 m	0.518	0.462	0.573	0.468	0.903
Cover >32 m	0.684	0.772	0.684	0.129	0.769
% area in gaps > 10 m ²	-0.305	-0.459	-0.600	-0.786	-0.790
% area in gaps > 100 m ²	-0.292	-0.451	-0.599	-0.784	-0.781

We used these metrics to define classes of forest structure based on a random sample of 10,000 grid cells chosen using the sample function without replacement in the R statistical package (R Development Core Team 2007). We used hierarchical clustering, which groups similar observations in a hierarchical fashion (Legendre and Legendre 1998), to classify plot sites. We used Euclidean distances and Ward’s linkage method with the “hclust” function of the R statistical package (release 2.6.1) (R Development Core Team 2007) for this analysis.

Over the 26 year period of our study, regrowth following fire would change the structure of forests. We examined the data by year of fire to determine whether this regrowth was measureable by calculating linear regressions for each metric by time in years since fire.

Analysis of Canopy Patch and Gap Structure

We analyzed the change in gap structure by mapping both areas of canopy, referred to as canopy patches, and gaps. We identified canopy patches and gaps using an unsmoothed 1 m resolution CSM with heights ≥ 2 m in height identified as canopy and heights < 2 m identified as gaps. With this height break, we classified areas with bare ground or herbaceous, shrub, or short saplings cover as gaps. The Fusion software assigned each CSM grid cell the height of the highest return within that grid cell and values could be assigned with just one return within a grid cell. Turbulence during flight causes LiDAR instruments to skip small patches, and the few 1 m grid cells with no returns were marked as no data and not used in the statistical analysis.

We coded each grid cell as either no fire or with the fire severity class experienced and the forest type. The resulting 1 m resolution raster map was converted to an ArcMap polygon

file without shape simplification using ESRI ArcMap 10.0 (ESRI, Redlands, CA, USA). This preserved the resolution of the raster map and identified contiguous canopy patches or gaps as all contiguous grid cells with the same fire severity and forest type. As a consequence, canopy patches and gaps that crossed fire severity patches and/or forest types were identified as separate canopy patches and gaps within each severity-forest combination. We used ArcMap to calculate the area and perimeter of each canopy patch and gap.

RESULTS

Patterns of Burn Severity

The distribution of forest types and fire severities patches resulted in a mosaic landscape across the study area (Fig. 2). No fire patches represented 24% to 37% each forest type (Table 1). For each forest type, the largest percentage of burned area was in low severity patches (31 to 38%) followed by no change detected severity patches (16 to 33%). Medium (8 to 16%) and high (4 to 7%) severity patches represented increasingly smaller portions of the study area.

The cumulative area of no fire patches was dominated by a small number of patches >10 ha (Fig. 4). As fire severity increased from no detectable change through moderate severity, the frequency of patches <10 ha within each severity class increased and developed an increasingly strong log-log distribution. However, for patches that experienced high severity fire, the proportion of area in patches >10 ha increased.

Analysis of Vertical Foliage Distribution

No fire *Pinus ponderosa* and *Abies concolor/Pinus lambertiana* patches had similar median values for all five structural metrics that were higher than the median values for the other two forest types (Fig. 5). No fire patches of *Pinus jeffreyi* were distinct from other forest types with lower values for all metrics. Values for *Abies magnifica* patches fell in between these two groups, but closer to the values for *Pinus ponderosa* and *Abies concolor/Pinus lambertiana* patches.

We found two dominant patterns for change in vertical structure with increasing fire severity. First, change >33% in the height and rumple values generally did not occur except for high, but sometimes also moderate, severity fire patches (except for *Pinus jeffreyi*). Second, cover in each of the two height strata decreased with increasing fire severity (again, except for *Pinus jeffreyi*). However, the specific patterns of change varied by forest type, especially for no change detected and low severity fire. For example, these lower severity patches either had slightly elevated height and rumple values (*Abies concolor/Pinus lambertiana* and *Abies magnifica*), moderately declining values (*Pinus ponderosa*), or increasing values (*Pinus jeffreyi*). *Pinus jeffreyi* also showed several exceptions to the overall patterns such as an increase in canopy cover in the >16 m stratum through moderate fire severity.

We identified nine statistically distinct structural classes using hierarchical cluster analysis (Appendix Fig. A1). Ninety-fifth percentile height, rumple, and canopy closure >16 m, were the primary differentiators between structural groups and were associated with the first axis of the PCA ordination. Canopy closure in the 2-16 m stratum was correlated with the second axis of the ordination and differentiated classes that had similar values for the metrics associated with the first PCA axis.

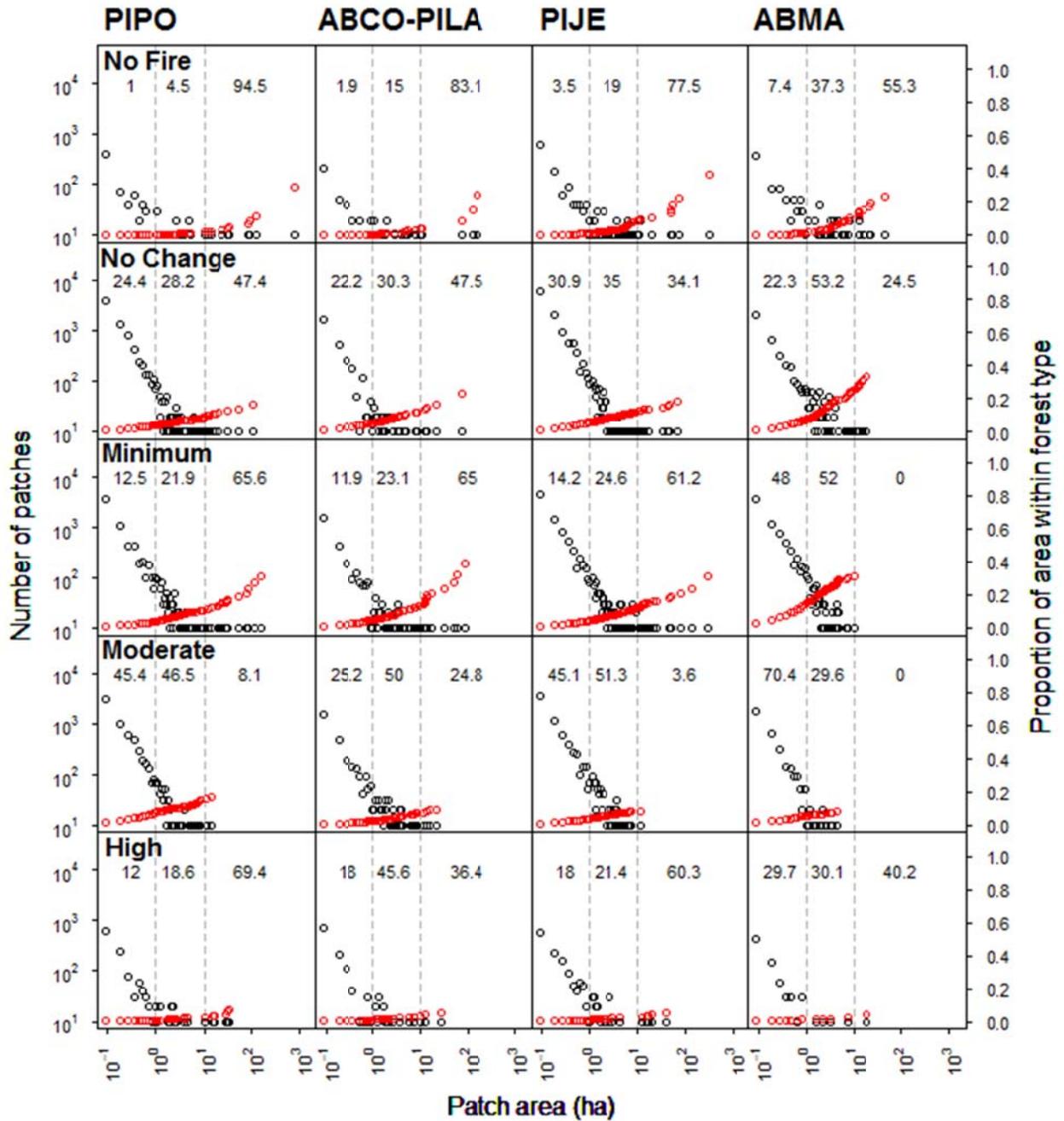


Figure 4. Frequency of fire severity patches by forest type (black circles) and cumulative proportion of area (red circles) for each fire severity and forest type. Cumulative proportions within each forest type sum to 1.0. Legend within each panel shows percentage of area in patches <1 ha, 1-10 ha, and >10 ha. A patch was defined as a contiguous area of the same fire severity class and forest type. The minimum measuring unit was a single Landsat pixel (0.09 ha). Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

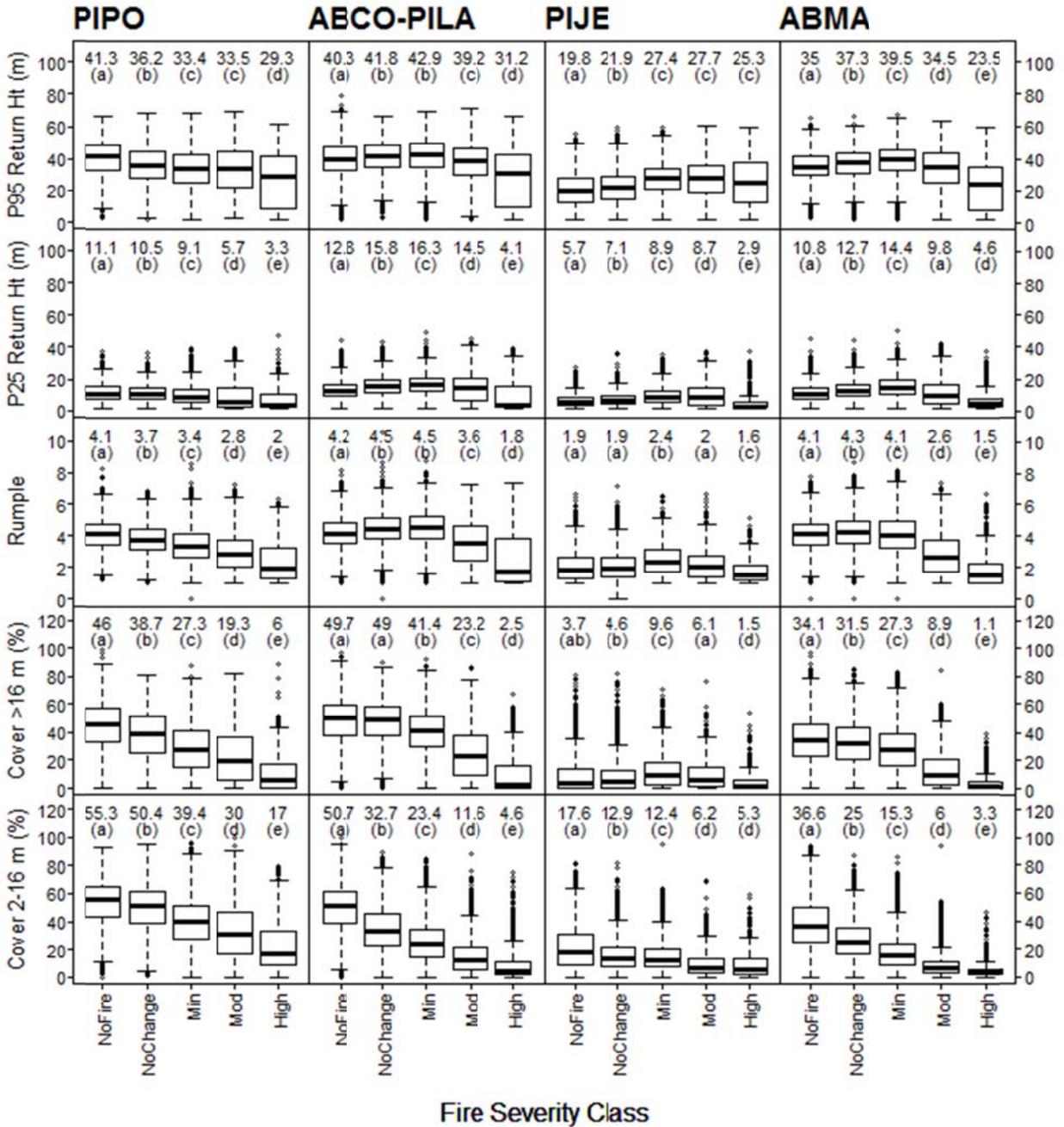


Figure 5. Changes in LiDAR metrics by forest type and fire severity class with median value shown above each boxplot. Letters within each panel indicate statistically distinguishable groups (Tukey HSD $p \leq 0.05$). Species codes are defined in Table 1.

We chose to re-group the classes identified through hierarchical cluster analysis based on similarities in canopy cover in the two height strata because the primary effect of increasing fire severity was to remove canopy cover. This resulted in merging five original classes into two new classes while retaining three of the original classes for a total of five classes (Fig. 6): Open with short canopy, open with taller canopy, bottom story, multistory, and top story. To ensure the classes were still statistically distinct, we performed Tukey HSD analysis on the individual metrics (Fig. 7). All groups were statistically distinct ($P < 0.05$) for all metrics.

Both *Pinus ponderosa* and *Abies concolor/Pinus lambertiana* forests had a preponderance of their no fire patches in the multistory class (65% and 60% respectively) (Fig. 8). For no detectable change and low severity fire patches, both these forest types showed reduced area in the multistory class. However, *Pinus ponderosa* patches showed increases in the open classes while *Abies concolor/Pinus lambertiana* forests showed increases in the top story class for these two fire severity classes. *Pinus jeffreyi* forests were predominantly in the two open forest classes for all fire severities. *Abies magnifica* patches that had not experienced fire were an approximately equal mixture of the open taller, bottom story, multistory, and top story classes (total of 94%). With no detectable change and low severity fire, the percentage of *Abies magnifica* area in the bottom story and multistory classes reduced with corresponding increases in the open taller and the top story classes. All forest types showed an increasing percentage of area in the two open structural classes for moderate and high severity fire patches.

Correlations between metric values and years since fire as measured by linear regression were either not significant ($P > 0.001$) or $R^2 \leq 0.06$ for no detectable change and low severity fires (Table 5). Correlations for moderate severity fires were $R^2 = 0.0-0.18$ except for *Abies concolor/Pinus lambertiana* rumple ($R^2 = 0.32$). Correlations for high severity fires were generally the highest found ($R^2 = 0.14-0.64$) except for cover 2-16 m ($R^2 \leq 0.05$) for all forest types except *Pinus ponderosa* ($R^2 = 0.2$) and for all metrics for *Pinus jeffreyi* ($R^2 = 0.01$). Almost all correlations with $R^2 \geq 0.1$ were for trends where more recent fires had higher values than older fires. The exception was for *Pinus ponderosa* canopy cover 2-16 m, where more recent fires had lower values than older fires.

Analysis of Canopy Patch and Gap Structure

For all forest types except *Pinus jeffreyi*, no fire and lower severity fire patches were 67-87% canopy patches >10 ha and gaps were small inclusions within these patches (Fig. 9 and 10, and Appendix Tables A1-A3). All fire severities, including no change detected, resulted in decreases in canopy patch size and increase in gap sizes. As a result, increasing fire severity led to a reversal of the proportions of canopy and gap. By high severity fire, areas were 78-92% gaps >10 ha (*Abies concolor/Pinus lambertiana*) or 55% gaps >1 ha (*Pinus ponderosa*) and canopy patches were small inclusions within open areas. *Pinus jeffreyi* forests were dominated by large open spaces for no fire and all fire severities patches.

All forest and fire severity combinations had canopy patch and gap area to perimeter regressions with slopes between 0.68 and 1.28 when plotted on log-log scales compared to a slope of 0.5 that would be expected for circular patches and gaps (Fig. 11 and 12). Patches and gaps with higher perimeter lengths for a given area indicate less compact shapes. Higher slope values than 0.5 indicate a trend towards increasingly complex gap shapes as gaps increase in area.

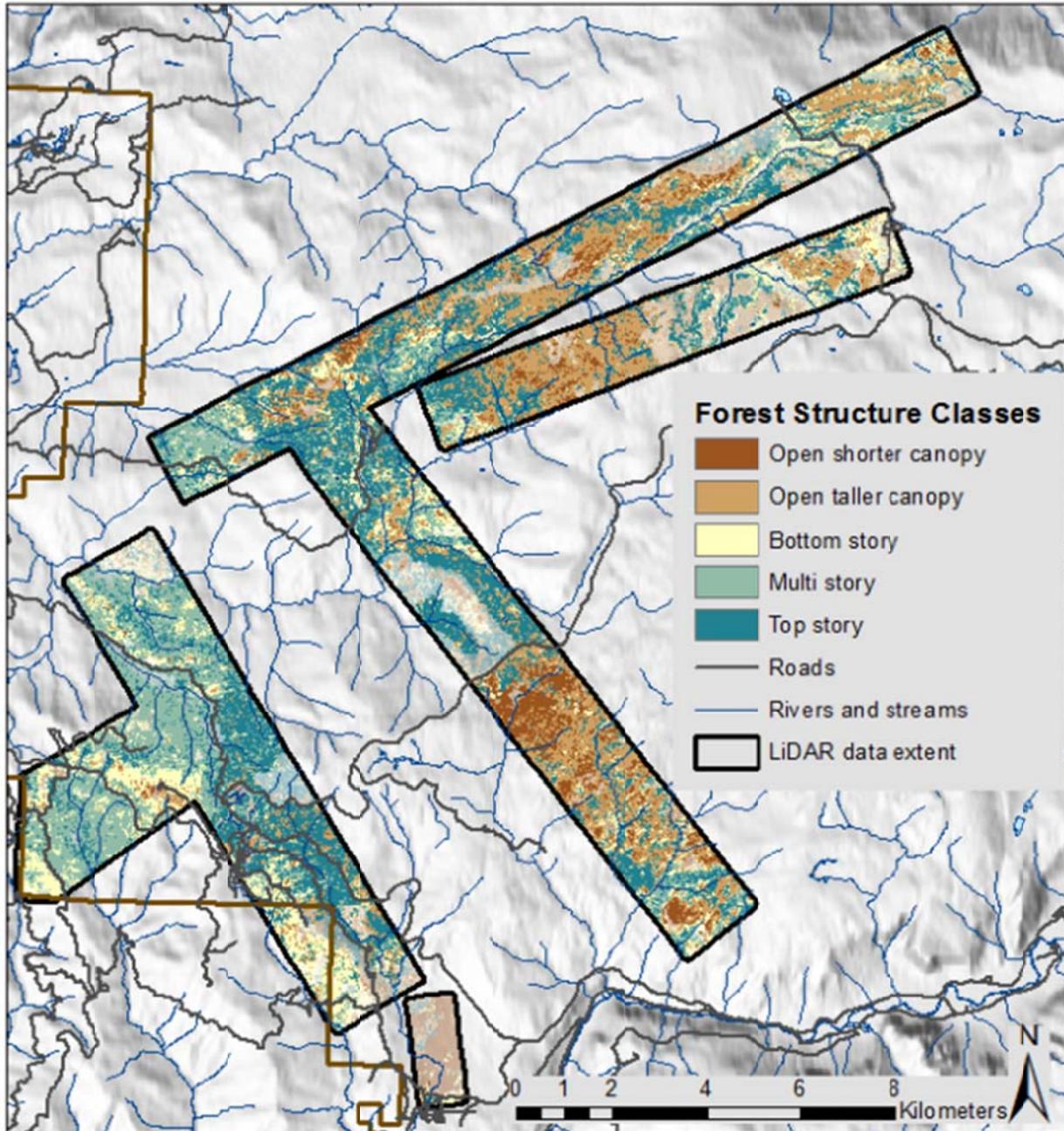


Figure 6. Map of structural classes identified in this study within the study area, which included areas that experienced no fire or a single fire and had a forest type of *Pinus ponderosa*, *Abies concolor*/*Pinus lambertiana*, *Pinus jeffreyi*, or *Abies magnifica*. Areas within the LiDAR data extent that experienced more than a single fire or had a different vegetation cover type are shown in muted colors.

Forest Structural Heterogeneity in Yosemite National Park

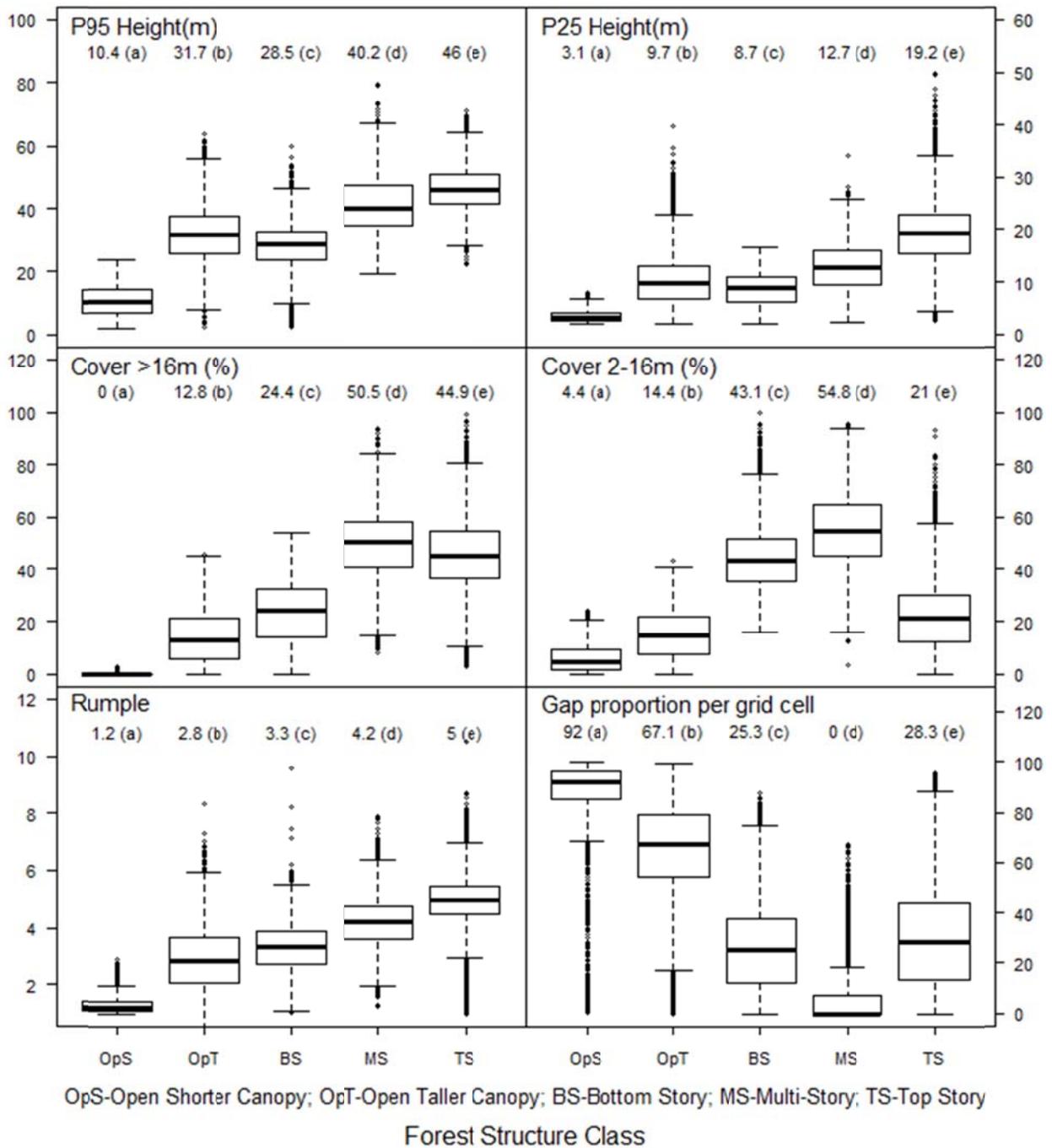


Figure 7. Height and canopy cover characteristics of structural classes identified in this study with median values shown. Letters indicate statistically distinguishable structural classes (Tukey HSD $p \leq 0.05$). Gap proportion was not used in the classification of forest classes but is shown to aid in interpretation of the classes.

Forest Structural Heterogeneity in Yosemite National Park

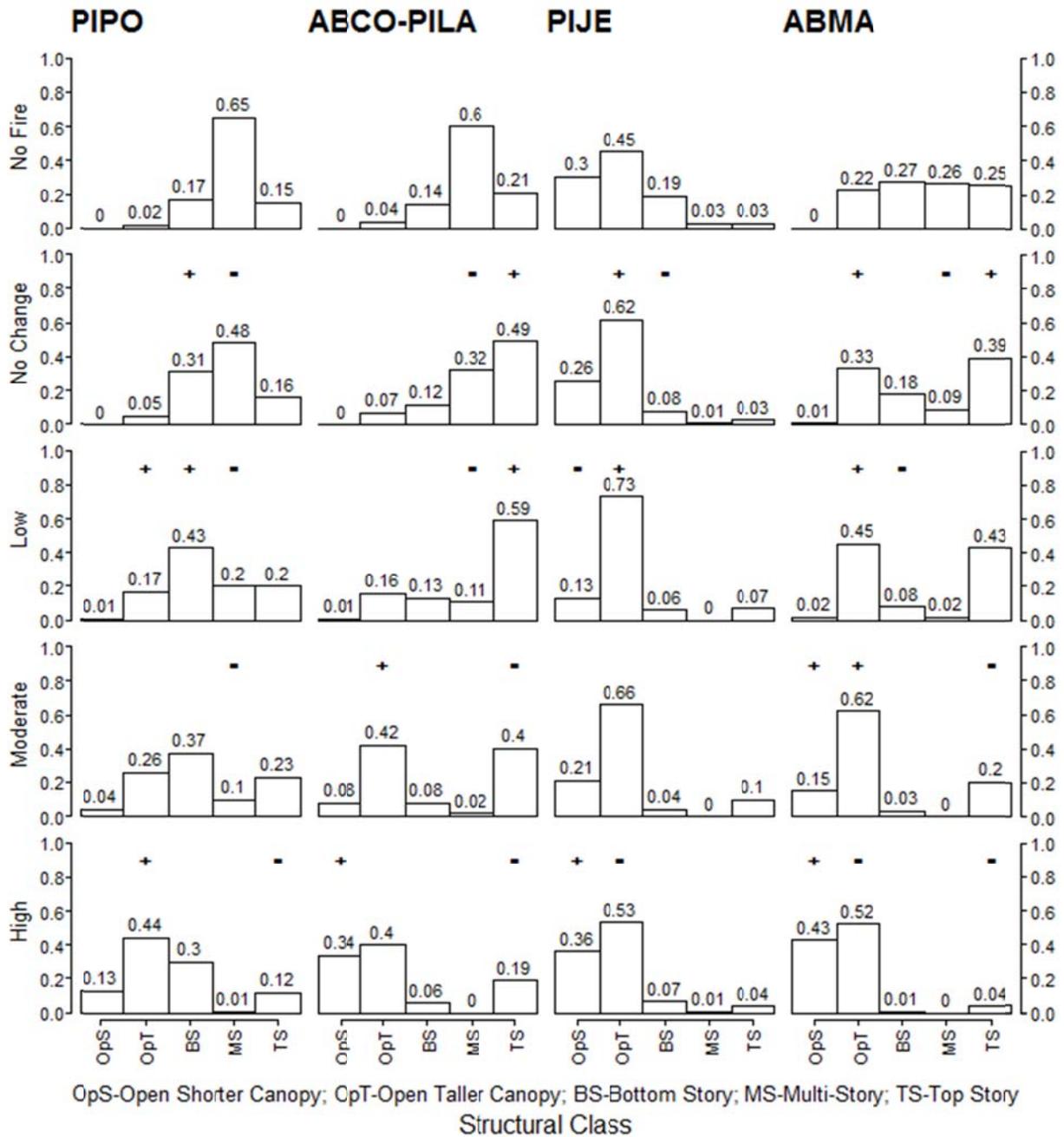


Figure 8. Proportion of structural classes identified in this study present by fire severity class and forest type. Changes greater or equal to an absolute change of 0.1 compared to next lower fire severity class indicated with a plus (+) or minus (-) as an interpretive aide. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

Table 5. Correlation (R^2) of structural metrics with change in metrics with years since fire based on linear regressions. Correlations ≥ 0.30 in bold and underlined for emphasis. Regressions that were not significant at $P < 0.001$ not shown. Correlations > 0.3 for high severity fire patches for 95th percentile height and rumple resulted from decrease in values rather than increase with time since fire. Appendix Fig. A3-A7 show details of values for structural metrics with time since fire. Species codes are defined in Table 1.

	No Detectable Change Severity				Low Severity			
	PIPO	ABCO- PILA	PIJE	ABMA	PIPO	ABCO- PILA	PIJE	ABMA
95th Percentile Height		0.02	0.01		0.05	0.05	0.01	0.01
25th Percentile Height	0.01	0.01			0.04	0.02	0.01	0.02
Rumple		0.01	0.02	0.01	0.04	0.06	0.02	0.04
Cover > 16 m			0.01	0.01	0.01	0.01	0.00	0.02
Cover 2-16 m	0.04	0.05	0.03	0.03	0.11	0.01		0.00
	Moderate Severity				High Severity			
	PIPO	ABCO- PILA	PIJE	ABMA	PIPO	ABCO- PILA	PIJE	ABMA
95th Percentile Height	0.16	0.17	0.02	0.11	<u>0.31</u>	<u>0.33</u>		<u>0.44</u>
25th Percentile Height	0.10	0.13		0.05	0.24	<u>0.33</u>		0.21
Rumple	0.18	<u>0.32</u>	0.02	0.13	<u>0.53</u>	<u>0.64</u>		<u>0.41</u>
Cover > 16 m	0.07	0.17		0.05	0.14	<u>0.51</u>		0.22
Cover 2-16 m	0.18				0.20	0.05		0.02

Forest Structural Heterogeneity in Yosemite National Park

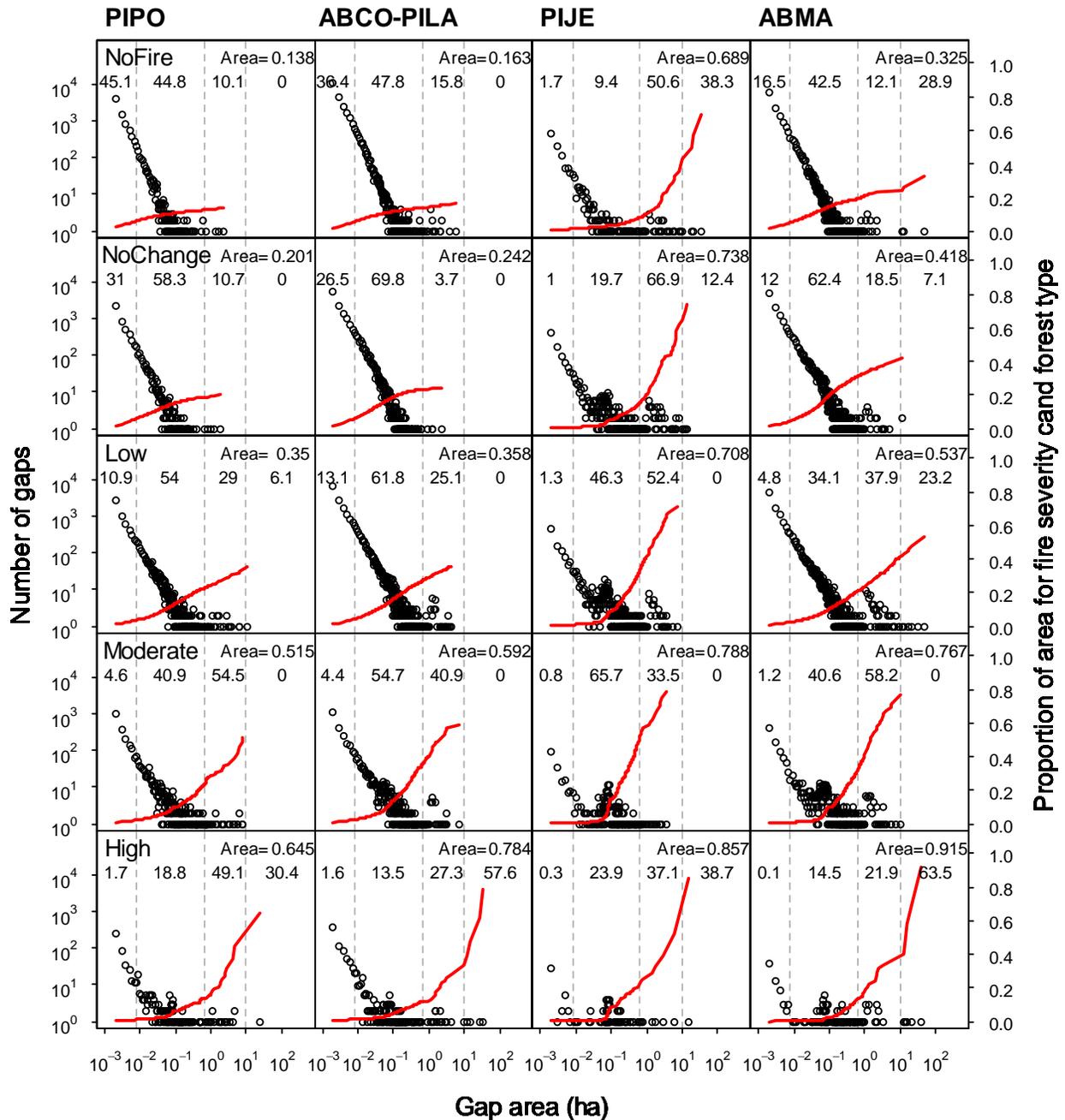


Figure 9. Gap frequency (circles) and cumulative area (line) by fire severity class and forest type. Cumulative area of gaps weighted by proportion of area in gap for each severity class and forest type; maximum cumulative area shown in top right of each panel ("Area="). Legend within each panel shows the percentage of area in gaps that corresponded to <0.008 ha (area of individual trees), 0.008-0.64 ha (area of tree clumps), 0.64-10 ha, and >10 ha. A gap was defined as a contiguous area of the same forest type and fire severity class with no LiDAR returns ≥ 2 m in height. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

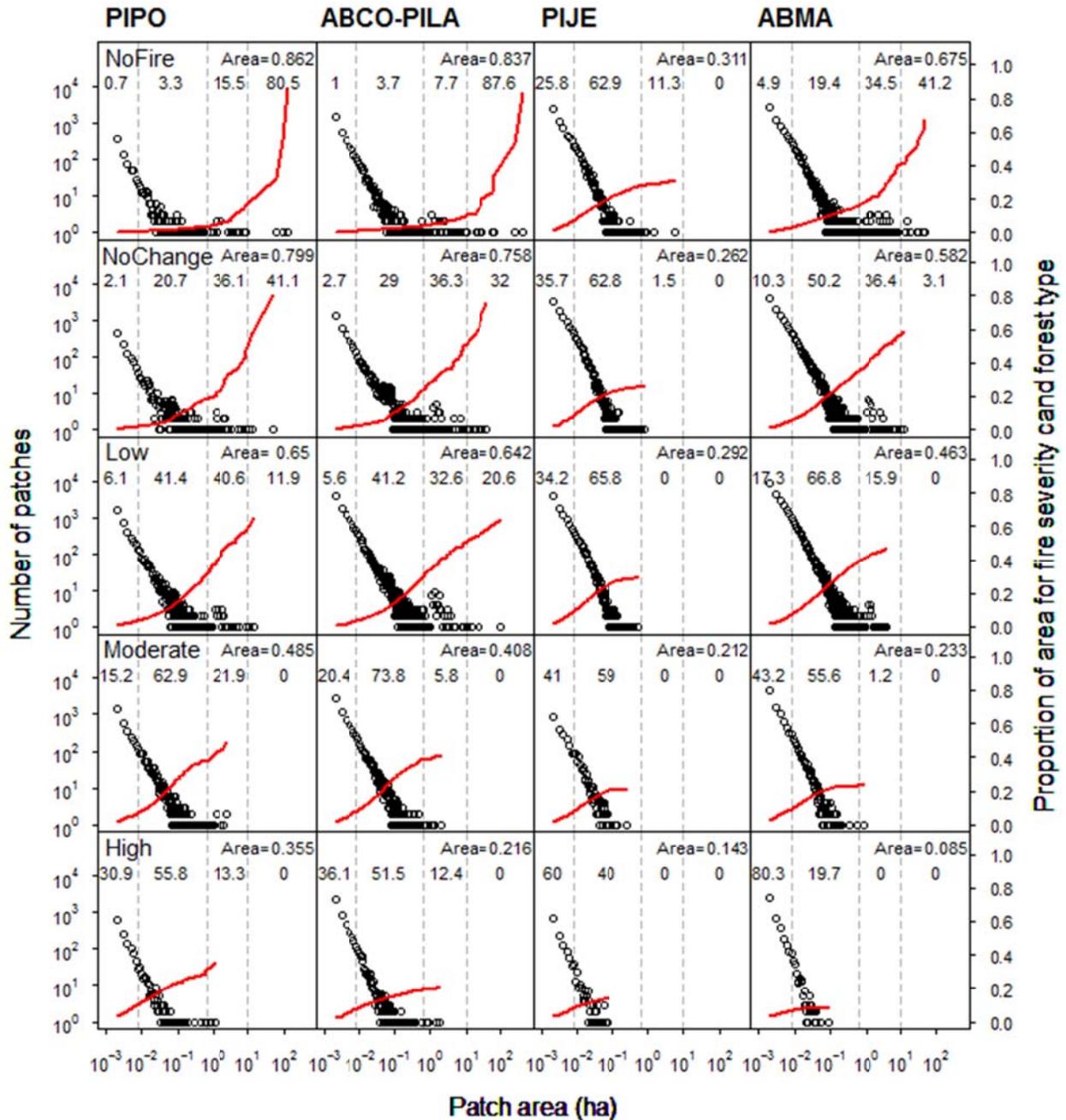


Figure 10. Canopy patch frequency (circles) and cumulative area (line) by fire severity class and forest type. Cumulative area of canopy patches weighted by proportion of area in canopy patches for each severity class and forest type; maximum cumulative area shown in top right of each panel ("Area="). Legend within each panel shows the percentage of area in canopy patches that corresponded to <0.008 ha (area of individual trees), 0.008-0.64 ha (area of tree clumps), 0.64-10 ha, and >10 ha. A canopy patch was defined as a contiguous area of the same forest type and fire severity class with LiDAR returns ≥ 2 m in height. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

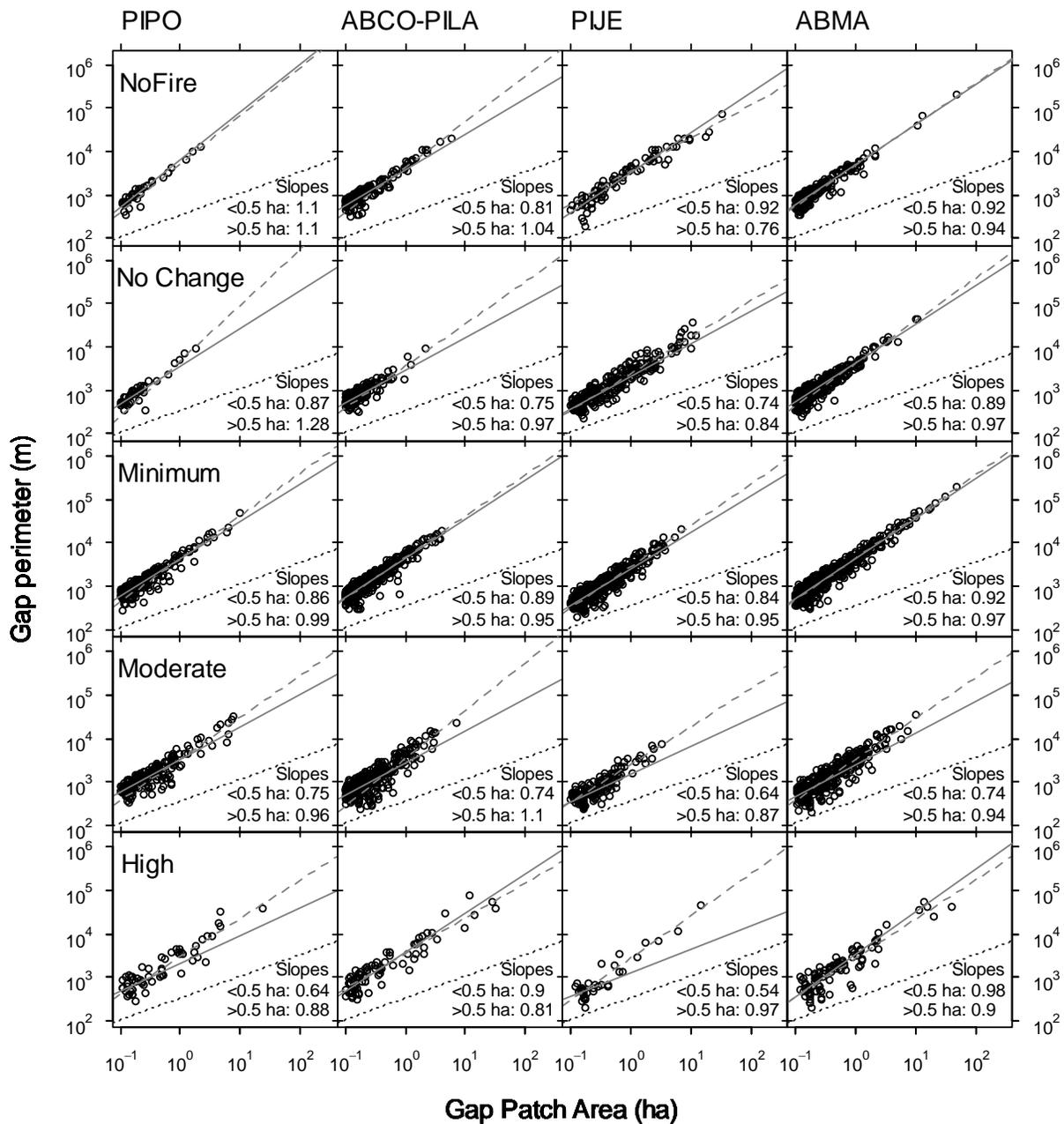


Figure 11. Gap area and perimeter by forest type and fire severity. Gaps with higher perimeter lengths for a given area indicate less compact gap shapes. Linear regression lines shown for gaps 0.1-0.5 ha (solid line) and for gaps >0.5 (dashed line) with slope values shown. Increasing slope values as gap size increases indicate trend for increasingly less compact shapes. Perfectly circular gaps of increasing area plotted on a log-log scale would have a slope of 0.5 for area versus perimeter (dotted line). Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

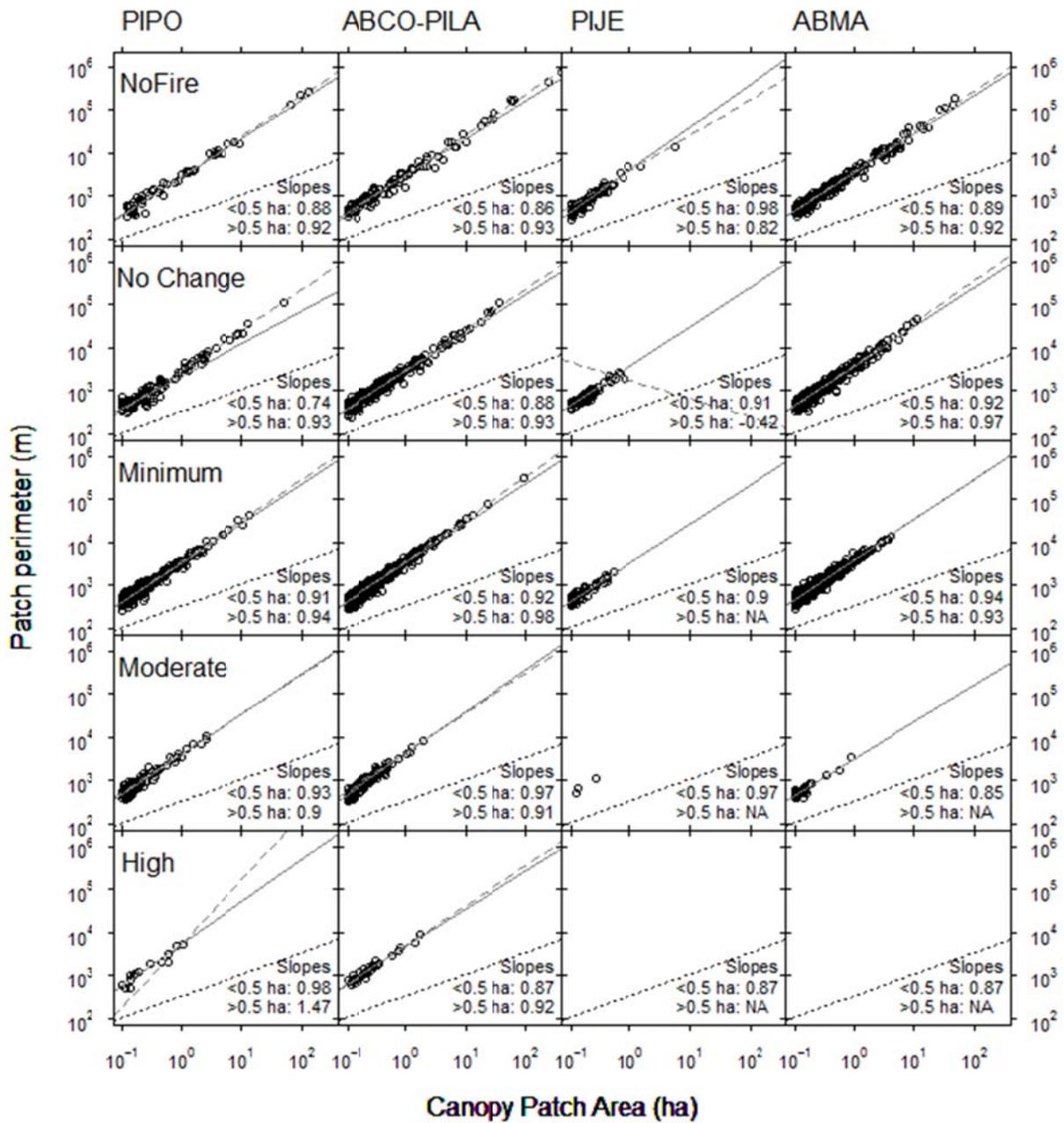


Figure 12. Canopy patch area and perimeter by forest type and fire severity. Canopy patches with higher perimeter lengths for a given area indicate less compact gap shapes. Linear regression lines shown for patches 0.1-0.5 ha (solid line) and for patches >0.5 (dashed line) with slope values shown. Increasing slope values as patch size increases indicate trend for increasingly less compact shapes. Perfectly circular patches of increasing area plotted on a log-log scale would have a slope of 0.5 for area versus perimeter (dotted line). Species codes are defined in Table 1.

DISCUSSION

We had expected that stands that had not recently experienced fire would be dominated by a single structural class either because of species physiology and the moisture gradient (Stephenson 1998, Stephenson et al. 2006) or because a century of fire suppression had led to a homogenization of structure (van Wagtenonk and Fites-Kaufman 2006). We expected little change in structure for areas burned at lower severities, consistent with results from composite burn index plots (Thode 2005, Thode et al. 2011) and more extensive structural change in areas that burned at moderate and especially high severities. We expected that *Pinus jeffreyi* forests would be a special case because they are typically found on rocky expanses within our study area where their wide tree and tree clump spacing is edaphically controlled (Urban et al. 2000). We also had expected to see a clear pattern of recovery following fire with older burns showing clear signs of re-establishment and regrowth since fire.

We were surprised on several accounts. First, no detectable change and low severity were patches had substantially different vertical structure and canopy patch and gap arrangements than did no fire patches (except for *Pinus jeffreyi*). Second, each forest type showed an individual response to increasing fire severity in the vertical structure of its forests. Third, we failed to find a strong sign of regrowth with time since fire, except for a modest pattern for *Pinus ponderosa* patches. And fourth, we found distinct canopy patch and gap arrangements associated with different fire severities (except, again, for *Pinus jeffreyi*). We'll explore each of these findings in the following sections.

Airborne LiDAR to Measure Forest Structure

Statistical measurements of canopy height, standard deviation of height, and canopy closure are commonly used in LiDAR-based studies to estimate stand values such as carbon storage (e.g., Lefsky et al. 2005a) or as primary measurements of forest structure (Falkowski et al. 2009, Kane et al. 2010a, Kane et al. 2011). We chose five LiDAR metrics that represented a parsimonious set that captured the heterogeneity of the structure within our study area. In making our selection, we were guided by the work of Lefsky et al. (2005b) and Kane et al. (Kane et al. 2010b) who found that a parsimonious suite of LiDAR measures of canopy height, heterogeneity of height, and canopy cover correlated strongly with standard suites of field measurements of live tree forest structure. While their studies used a single metric from each group, we chose two height and two canopy cover metrics to allow us to measure the effect of fire on the distribution of canopy foliage. Ninety-fifth percentile height of LiDAR returns was chosen as a measure of dominant tree height within each grid cell, while 25th percentile height of LiDAR returns was selected as a measure of the dominant height of lower foliage. Canopy cover for the 2-16 m strata was correlated with canopy cover within finer height gradations within that range (2-4, 4-8, and 8-16 m) and was selected as a single parsimonious metric representing cover in lower strata. Similarly, canopy cover for >16 m height was chosen to represent cover in higher height ranges. Correlation between cover in the 2-16 m and >16 m was moderate ($R=0.41$). Both cover measurements were negatively correlated with the percent area within each grid cell in gaps $>100 \text{ m}^2$ ($R=-0.78$), indicating that gaps of moderate size or larger were the primary driver of canopy openness. Rumple was selected to represent diversity of canopy heights instead of standard deviation of LiDAR return heights because it had a lower correlation ($R=0.77$) with 95th percentile height than did standard deviation ($R=0.94$). Rumple also

measures both vertical and horizontal heterogeneity of heights, while standard deviation measures only vertical heterogeneity (Kane et al. 2010a).

In evaluating our results, it is important to remember that we used a height cutoff of two meters for calculating our statistical LiDAR metrics and to identify canopy patches and gaps. (The exception was to include the count of LiDAR returns below two meters as part of the calculation of canopy cover.) We chose this cutoff height so that the measurements would reflect the structure of canopy trees and not include measurements of saplings and shrubs and so that any inaccuracies in the computed ground model would be unlikely to result in ground returns being identified as canopy returns. While a study of vegetation below 2 m would be highly valuable, we were unsure that vegetation cover could be reliably identified given ground clutter such as dense shrubs, downed logs, and the inevitable small inaccuracies in the ground model.

Patterns of Burn Severity

With the accumulation of fuel over the last century resulting from fire suppression, recent fires in Sierra Nevada forests are characterized as mixed severity with patches of forests burning at different severities (van Wagtenonk and Fites-Kaufman 2006). While all fires include some variation in severity, mixed severity fire regimes are characterized by substantial portions of burned area in different severities (Perry et al. 2011). Our analysis of burn severity patches supports the characterization of our study area as a mixed severity regime.

For the portion of our study area within fire perimeters, no detectable change and low severity patches made up the majority of our study area with moderate and high severity patches covering 12-24% of each forest type. These results are in contrast to the pattern of burn severity reported by van Wagtenonk and Lutz (2007) and Thode et al. (2011) for the Yosemite park region. They used RdNBR-based fire severity maps and reported larger proportions of area burned in moderate severity fire patches than we found. The much larger area -- all of Yosemite Park plus substantial areas of lower elevation forests in the adjoining Stanislaus National Forest -- used in their studies partially explains the discrepancy with our results. Lower elevation fires burn in vegetation types such as chaparral and live oak (*Quercus wislizenii* and *Quercus chrysolepis*) that typically burn with higher severities and in larger patches. However, even when individual forest types are compared between our study and Thode et al. (2011), our study area was still skewed more toward lower severity fire with less area in moderate severity fire.

On the other hand, our distribution of area in different fire severities was similar to that reported by Collins et al. (2007). Their study area was a higher elevation basin within the Park than more closely matched the range of elevations within our study area than did the other studies. Thode et al.'s (2011) results also included the full extent of several higher severity fires that included extensive areas of the forest types used in our study. Our study area either did not intersect these fires (i.e., 2003 Kibbie fire) or only partially intersected them (e.g., the 1990 A-Rock fire, and 1996 Ackerson Fire). Our study area, therefore, likely represents a particular range of fire regimes with Yosemite National Park characteristic of higher elevation forests experiencing lower severity fires rather than representing the full range of fire regimes across the park and in adjoining forests.

One characteristic of mixed severity fire regimes is a mosaic of fire severity patches (Hessburg et al. 2007, Perry et al. 2011), which we found. Patches with no fire since 1984 were

predominately large (>100 ha for all forest types except *Pinus jeffreyi* and >10 ha patches for the latter)(Fig. 4). With increasing fire severity, severity patch size shifted to increasingly smaller patches, with a partial reversal for high severity fire that increased the area in larger patches. (The exception to this trend for no detectable change patches for forest types except *Abies magnifica* appears to result from the smaller area in this severity class than for the next higher severity class, low. A smaller area cannot hold as many >1 ha patches as a larger area.) This trend partially reversed for high severity fires with the majority of area being dominated by patches in the largest class size present within that severity class (10-100 ha). *Pinus ponderosa* and *Pinus jeffreyi* high severity fire patches, however, continued the pattern of a broader mixture of patch sizes for high severity fires.

Analysis of Vertical Foliage Distribution

We began our analysis of the impact of fire severity on forest structure by examining changes in forest structure for each of the 0.09 ha grid cells covering our four forest types. This grain of measurement captured structure at of the scale of all or a portion of a clump of trees (Larson and Churchill 2012). Because each 0.09 ha grid cell was similar in size to the plot sizes of many field studies, this portion of the study is most directly comparable to the field studies that have studied the impact of fire severity on forest structure. Our large sample size, however, allowed us to observe ranges and heterogeneities in structure that would be impractical in a field study.

Our results show that fires of all severities were associated with differences in vertical canopy structure, and this was especially dramatic for high severity fire. The transition from one severity level to the next higher severity level generally did not cause abrupt changes in ranges of metrics (Fig. 5). Instead, ranges of values for metrics (as measured by the 25th and 75th percentile values on the box plot figure) overlapped, often substantially, between adjacent severity levels. The exception to this pattern for many metrics was the change from moderate to high severity fire, where mean values frequently showed abrupt drops (but not always, as shown by 95th percentile height values for *Pinus jeffreyi*). Abrupt changes occasionally also occurred between low and moderate fire severities, as with canopy cover in the 2-16 m strata for *Abies magnifica* patches.

We identified five statistically distinct classes of canopy structure within our study area (Fig. 7). No standard classification scheme exists for structural classes of Sierra Nevada forests, so far as we are aware, similar to those available for the Douglas-fir-dominated Pacific Northwest forests (Franklin et al. 2002) or the inland Northwest forests (O'Hara et al. 1996). We note similarities between our classes and several of O'Hara et al.'s (1996) classes. Our open shorter class, for example, corresponds in structure to their Stand Initiation class. Similarly our bottom story class is similar to their Closed Stem Exclusion and young-multi-strata classes, our multistory class is similar to their Old Forest Multi-strata class, and our top story class is similar to their Old Forest Single-Stratum class. Because inland Northwest forests are found across a range of productivities associated with drier conifer forests and fire often is a dominant process as in our study area, the correlation of structural classes is not surprising. However, O'Hara et al. (1996) defined their classes from field data, which better allowed them to apply ecological descriptors such as 'old forest' to their classes'. Because we lacked field data, we purposefully named our classes using only structural descriptors.

We found that studying structural change through multivariate classes (Fig. 7 and 8)

better illuminated differences in patch structure between fire severity classes and forest types than did examining individual metrics, which as noted above, often showed broad overlap between fire severity classes. Each of our forest types showed distinct patterns of change with increasing fire severity. For example, *Pinus ponderosa* and *Abies concolor*/*Pinus lambertiana* patches that did not experience fire both were dominated by the Multistory class (65% and 60%, respectively). However, no change detected and low severity patches were associated with greater percentages of the bottom story class for *Pinus ponderosa* forests but with greater percentages of the top story classes for *Abies concolor*/*Pinus lambertiana* forests. For the lower severity fire classes, *Abies magnifica* patches showed losses in the bottom and multi-story classes and gains in the open taller and top story classes. *Pinus jeffreyi* patches showed an increase in open taller class for lower severity fires.

Following a fire, surviving trees will continue to add height, and may show an increase in growth rates in the years immediately following the fire as the result of decreased competition (Sala et al. 2005). Canopy cover will increase both from the establishment of new trees and from remaining trees extending their crowns to fill gaps created by the fire (Fites-Kaufman et al. 2006). When we initially decided to examine the pattern of structural metrics for stands by year of fire, we were using time since fire as a surrogate for repeated LiDAR measurements to measure this regrowth. We expected that the interesting question would be whether different forest types or fire severities impacted the rate of recovery.

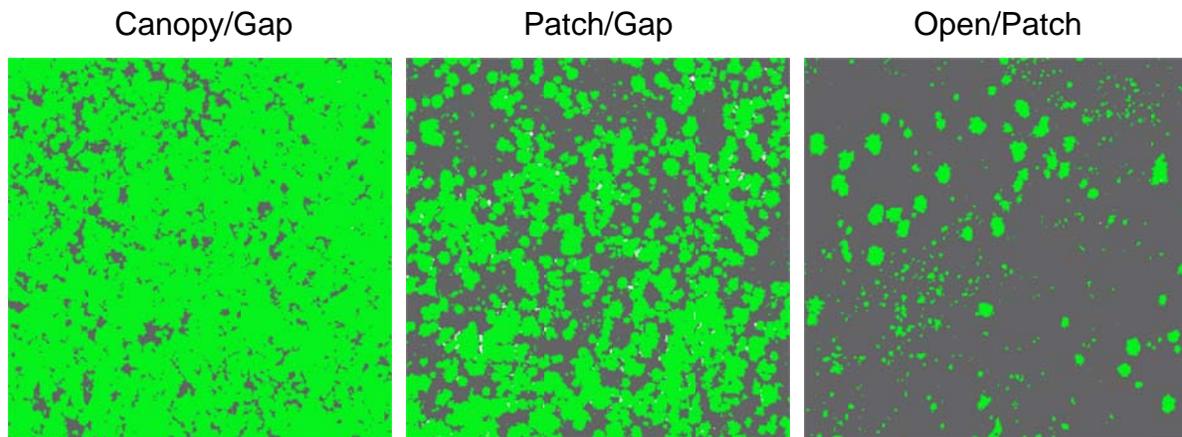
Instead, for most metrics we found no or weak correlations ($R^2 < 0.3$) and time since fire, with two exceptions (Table 6). First, several metrics showed moderate correlations for high severity fire patches. A detailed examination of these regressions (Appendix Fig. A3-A7), however, showed that the pattern was one of loss of structure over time. We believe that these trends may represent both delayed mortality from fire damage and the eventual loss of snags. The second exception was a weak ($R^2 = 0.04-0.2$) increase in canopy cover in the 2-16 m stratum for all *Pinus ponderosa* fire severities. This trend may explain why *Pinus ponderosa* patches showed an increase in the proportion of area in the bottom story structural class for all fire severities compared to no fire patches, which did not occur for any other forest types.

The range in values between individual fires within the same severity class and forest type was surprising and suggests a level of fire heterogeneity not previously captured in discussions of fire severity. Researchers have long known that differences in topography, pre-existing forest structure, ground fuels, and fire weather change the impact of fire on forests (Taylor and Skinner 2003, Stephens and Moghaddas 2005, Stephens et al. 2009). It has generally been thought that these variations in fire conditions would result in different proportions of area in different severity classes. However, it appears that these factors also impact the actual change in forest structure resulting from a given estimated fire severity (Abella and Denton 2009). In this case, our results highlight the variation within each severity class and the individual nature of each fire likely resulting from its unique circumstances of place and weather. Differences in post-fire structure can remain for at least two decades, a result that can guide managers in their plans to use fire to manage forest structure.

Analysis of Canopy Patch and Gap Structure

We found three distinct patterns of canopy patches and gaps (Fig. 13). Canopy/gap patterns have the majority of their area in canopy with gaps as small breaks in the otherwise continuous canopy. Patch/gap patch have similar proportions of canopy and gap with the two interspersed across the area. Open/patch patterns are the reverse of canopy-gap systems with open space essentially a continuous gap interspersed with small patches of canopy that are single trees or small tree clumps. These canopy patch and gap patterns are emergent properties that become recognizable only at scales of approximately 100 m or greater; they cannot be recognized at the scale of 30 m grid cells or most field plots, which sample forests at the scale of individual tree clumps or moderate-sized gaps.

These canopy patch and gap patterns were not unique to any forest type, but rather were associated with different fire severity classes. (The exception was for the *Pinus jeffreyi* patches, which were open-patch patterns for all fire severities.) The canopy-gap pattern typically was found in no fire, no detectible change, and low severity patches, although some *Abies magnifica* patches in these severity classes had patch/gap patterns. In these latter cases, examination of the ortho images suggested these stands were on thin soils and the spatial structure may have been



Gap Proportion	PIPO	ABCO- PILA	PIJE	ABMA
No Fire	0.138	0.163	0.689	0.325
No Change	0.201	0.242	0.738	0.418
Low	0.350	0.358	0.708	0.537
Moderate	0.515	0.592	0.788	0.767
High	0.645	0.784	0.857	0.915

Figure 13. Examples of the ranges of canopy patch and gap patterns present within the study area (figure) and the proportion of gap within each fire severity class and forest type combination (inserted table). Light green represents canopy and black represents gaps (no canopy greater than 2 m in height). Unshaded fire severity-forest type combinations in the table have characteristics of canopy/gap patterns, light shading patch/gap patterns, and dark shading open/patch patterns. Each example pattern is 9 ha (300 x 300 m) from the study area. Canopy and gap areas calculated from a 1 m resolution canopy surface model derived from LiDAR data

edaphically controlled. The patch/gap pattern typically was associated with moderate fire severity for *Pinus ponderosa* and *Abies concolor*/*Pinus lambertiana* patches and with no detectible change and low fire severities for *Abies magnifica*. The open/gap pattern was associated with high severity fire and also moderate severity fire for *Abies magnifica*.

Our finding of distinct canopy-gap patterns extends previous work in Sierra Nevada forests. In forests prone to fires, fire-created gaps are often equated to high severity fire patches because these patches, by definition have had most of their cover removed. Turner et al. (1997), for example, took this approach to analyzing the effects of fire on early succession in Yellowstone National Park. They examined the size of burn patches and their fire severities to analyze their results without using the term 'gap' in their paper. Similarly, Collins and Stephens (2010) equated stand-replacing patches with locations of high severity fire in Yosemite National Park, again without using the term 'gap.' Our LiDAR data that showed that high severity patches had little cover, which supported this interpretation.

In our study, however, we took a more classic approach to the definition of gap as any area without canopy cover greater than 2 m in height (Runkle 1982, 1992). This approach allowed us to include gaps caused by any condition, including edaphic factors, spacing between trees caused by competition for water or other resources, death of trees caused by biotic agents such as insects or abiotic agents such as wind, or loss of trees to fire. We chose this direction based on the hypothesis that locations that experienced fire with lower fire severities would have more areas in gaps due to direct tree mortality in the fire or delayed mortality caused by biotic or abiotic agents acting on fire-weakened trees.

The high resolution of our canopy-gap map allowed us to explore the shape complexity of canopy patches and gaps. We found that as patches and gaps increased in size, the area of their perimeter increased faster than it would have for circular structures of the same size (Fig. 11 and 12). This was the result of both complex exterior shapes and also the shape complexity of inclusions of gaps in patches and vice versa that subtracted area but also added perimeter. We found that the rate at which shape complexity changed varied considerably, and did not find any pattern for how this rate changed between different combinations of forest type and fire severity class.

In themselves, these results indicate a highly complex landscape that becomes more complex as the scale of measurement, and hence the size of structures that can be measured, increases. By identifying patches and gaps only within each forest type and fire severity combinations, these results likely under estimate the true complexity of the landscape. The canopy patches and gaps within each of our fire severity-forest type patches connected with those in adjacent fire severity-forest type patches. In this way, for example, the open space within an open/patch pattern might extend into the gaps in an adjacent patch/gap pattern.

Synthesis and Conclusions

Mixed severity fire regimes are inherently difficult to quantify. A defining characteristic of these landscapes is that the heterogeneity of the fire severities results in a landscape with many small patches and relatively few large patches (a negative power law or Pareto distribution) (Perry et al. 2011). As a result, the key variability in these landscapes lies in the intermediate scales where both top down controls such as weather and bottoms up controls such

as topography and pre-existing forest structure intermix (McKenzie et al. 2011, Moritz et al. 2011). We have good understanding of the behavior of fire at regional scales (van Wagtenonk and Lutz 2007, Lutz et al. 2009, Littell and Gwozdz 2011, Lutz et al. 2011, Miller et al. In press) and at the fines scale such as fire's interaction with individual trees (McKenzie et al. 2011). It is the intermediate scales where the inherent heterogeneity is difficult to measure and model and estimation error propagations are problematic (McKenzie et al. 2011).

Our study examined the relationship between fire severity and forest structure in this intermediate scale. We found differences in forest structure for all fire severities compared to the structure found for no fire patches and these changes generally formed a pattern with increasing fire severity. As noted in the introduction, because we lack pre-fire structural measurements, we cannot prove that fire was responsible for these changes. However, because we found these patterns across many fires and four forest types and they are consistent with the expected behaviors of fire, we accept the hypothesis that fire was the causative agent.

The changes occurred at all three scales we examined: fire severity patches, canopy patches and gaps within fire severity patches, and tree clumps (0.09 grid cells). With increasing fire severity, severity patch size shifted to increasingly smaller patches, with a partial reversal for high severity fire that increased the area in larger patches. Within severity patches, the proportion of area in gaps also increased with increasing fire severity, with a transition from no fire patches dominated by canopy enclosing small gaps (canopy/gap), to approximately equal areas of canopy patch and gap (patch/gap), to open areas with scattered trees and tree clumps (open/patch). At the scale of tree clumps, lower fire severities removed canopy cover from the 2-16 m stratum leading to structural shifts to either the top story or the open taller structural classes. With moderate and high severity fire, canopy cover in the >16 m stratum was removed, leading to increases in the open taller and then the open shorter classes. We found minor exceptions to each of these trends, but as discussed earlier, we believe there are good explanations for them.

The fire regime in Yosemite prior to fire suppression was predominantly low severity with frequent fires removing smaller trees and creating an open forest structure (van Wagtenonk 2007, Scholl and Taylor 2010)). Within our study area, lower severity fires – the no change detected and low severity classes – still predominated. What was unexpected is the degree to which these lower severity fires changed forest structure at all three scales. Thode (2005) characterized dNBR fire severity classes through field work in the Sierra Nevada range and she and her colleagues described low severity fire patches as "lightly burned with only the fine fuels removed and some scorching of the understory trees" (Thode et al. 2011). We found substantial changes between no fire and lower severity patches such as an almost doubling to more than tripling of the proportion of area in gaps, depending on forest type (*Pinus jeffreyi* forest excepted). Measuring the full impact of lower severity fire may require either measurements over large areas or measurements a number of years after a fire for delayed mortality to occur.

Fire has been used as a management tool to thin forests (van Wagtenonk 2007). Our data suggest that even the low severities associated with prescribed burns (van Wagtenonk and Lutz 2007) will thin forests and create new gaps. With our data, we can also examine the question of what level of fire severity is likely needed to return forests to structural conditions prior to fire suppression. Larson and Churchill (2012) analyzed the results of 50 studies that examined tree spatial patterns in western U.S. pine and mixed conifer forests. Their synthesis

identified three structural elements in fire-frequent forests: openings, individual trees, and clumps of trees with overlapping canopies at scales of 0.0003-0.64 ha. Unfortunately, the studies they examined did not use methods to examine the spatial arrangement of these structures. However, we believe that these structures likely were arranged in the patch-gap pattern identified in our study (Hessburg et al. 2005). If this was the case, then the low severity fire would result in the creation of patch-gap structure in *Abies magnifica* forests while moderate severity fire would be needed for *Pinus ponderosa* and *Abies concolor*/*Pinus lambertiana* forests. Our results show that fires in these severity classes also would leave patches of higher density forests that were reported for pre-fire suppression lower montane forests (van Wagtenonk and Fites-Kaufman 2006). Collins et al. (2011) also concluded from plot-based data that moderate severity fire would recreate pre-fire suppression forest structure within the park's forests.

Our data showed that fire in all intensities resulted in substantial forest restructuring. Fires burned in a heterogeneous pattern creating a mosaic of canopy patches, gaps, and vertical forest structures. Fire acted to thin from below with higher intensities increasingly capable of killing progressively larger trees typically resulting in higher severities. This thinning will lead to progressively greater area in gaps and reduced canopy cover first in lower strata and then in higher strata.

This study was the first we are aware of to combine a multi-decade history of fire severity with detailed forest structure measurements over a large contiguous area. We sought to look for dominant patterns that are likely to hold across a number of forest types, a broad range of individual fires, and local conditions of pre-fire forest structures and topographies. Our results then can contribute to developing more refined hypotheses to test the relationships between different top down and bottom up controls on the structure of mixed severity forests. This approach will help create models of how fire restructures forests in the critical intermediate scales.

Recommendations for Future Research

We split our recommendations for future research into two groups, research that can be done using the existing LiDAR dataset and recommendations for research using additional LiDAR acquisitions. The research recommended for the existing data set should also be considered for other acquisitions.

As noted above, within the funding available, we sought to find dominant patterns that apply across a multitude of fires, forest types, and topographies. This approach, however, hides the individual nature of each fire in terms of its weather, pre-existing forest conditions, previous fire history, edaphic controls on forest structure, and topography. We recommend a study that applies our methods (which build upon those of Kane and his colleagues (Kane et al. 2010a, Kane et al. 2010b, Kane et al. 2011)) to analyze forest structure for individual fires and combines them with methods that identify dominant controls on fire severity and forest restructuring such as those used by Lutz and his colleagues (van Wagtenonk and Lutz 2007, Lutz et al. 2009, Lutz et al. 2011) and Collins and his colleagues (Collins et al. 2007, Collins et al. 2009, Collins and Stephens 2010). If funding does not allow the examination of individual fires, we recommend grouping fires by management type: Management Ignited Prescribed Fire (MIPF), Wildland Fire Resource Benefit (WFRB) and Prescribed Natural Fire (PNF). We also did not examine the spatial arrangement of fire severity patches or of canopy patches, gaps, and structure classes with severity patches. Such a study would allow us to better understand the spatial effects of fire in

restructuring forests within severity patches.

We chose our study area to maximize the number of fires and forest types while still providing substantial areas outside of all fire perimeters as reference conditions and ready access for field verification. In doing so, we were not able to include areas that burned with higher average fire severity or for a geomorphically-defined area that would support landscape studies. We recommend that an additional LiDAR acquisition be made to measure the forest structures in areas that burned with higher average severity. In addition, the Forest Service's Southwest Research Station (Malcolm North, PI) has acquired LiDAR data for the Illiouette basin. Because this is a geographically defined area, it would be an ideal candidate for landscape studies of the relationship between topography, forest type, fire severity, and forest restructuring. However, we understand that there is limited funding to conduct a thorough analysis of this data set.

Long term studies in permanent sample plots have proven essential to understanding many dynamics of forest change. We recommend that the area from which we gathered LiDAR data be treated as a large, permanent plot with reacquisition of LiDAR data at least every decade. When combined with the existing Yosemite Forest Dynamics Plot (Lutz et al. In review, James Lutz, PI) and the USGS permanent plots (Nate Stephenson PI), this would be a rich dataset for understanding how fire restructures forests and how forests regrow following fire.

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Appendix

Table A1. Frequency of gaps by gap size ranges normalized to 100 ha for dominant forest types. Smallest gap size reported was 2 m².

	Gap size bins (upper limit) in hectares					
	0.001	0.01	0.1	1	10	100
<i>Pinus ponderosa</i>						
No Fire	1338.5	497.4	51.4	2.2	0.2	0
No Spectral Change	4049.6	1774	345.6	16	0.8	0
Low	2798.8	1118	322.5	47.7	3.5	0.2
Moderate	2243.6	743.6	242	67.6	7.2	0
High	1387	379.6	127.8	39.8	13	0.9
<i>Abies concolor/ Pinus lambertiana</i>						
No Fire	1465.1	602.9	82.6	4.2	0.4	0
No Spectral Change	3559	1734.7	438.3	25.5	0.5	0
Low	2830.6	1243.6	361.7	52.1	3.3	0
Moderate	1891.6	701.9	279.2	91.6	9.4	0
High	1217.7	342.9	81.3	30.8	8.1	2
<i>Pinus jeffreyi</i>						
No Fire	226	77.2	17.2	4.4	2.2	0.3

Forest Structural Heterogeneity in Yosemite National Park

No Spectral Change	608.6	211.4	96.6	47.3	15.8	0.8
Low	716.2	254.7	159.3	103.3	14	0
Moderate	563.8	179.8	211.7	155.3	10.6	0
High	487	82.6	110.9	60.9	8.7	2.2
<i>Abies magnifica</i>						
No Fire	865.7	345.1	74.2	6.1	0.4	0.1
No Spectral Change	3070.5	1324.5	435.6	54.2	3	0.3
Low	1817.9	680.6	219.7	48.8	6.4	0.5
Moderate	877.5	246.9	160.8	96.3	15.7	0
High	252.5	34.5	37.9	41.8	9	2.8

Forest Structural Heterogeneity in Yosemite National Park

Table A2. Ratio of gap count within burn areas normalized to gap count in areas with no fire (1984-2009) for dominant forest and woodland types. Notes indicate that no gaps in that gap size bin were present for patches with no fire. Smallest gap size reported was 2 m².

	Gap size bins (upper limit) in hectares					
	0.001	0.01	0.1	1	10	100
<i>Pinus ponderosa</i>						
No Spectral Change	3.03	3.57	6.72	7.27	4.00	0.00
Low	2.09	2.25	6.27	21.68	17.50	(1)
Moderate	1.68	1.50	4.71	30.73	36.00	0.00
High	1.04	0.76	2.49	18.09	65.00	(2)
<i>Abies concolor/ Pinus lambertiana</i>						
No Spectral Change	2.43	2.88	5.31	6.07	1.25	0.00
Low	1.93	2.06	4.38	12.41	8.25	0.00
Moderate	1.29	1.16	3.38	21.81	23.50	0.00
High	0.83	0.57	0.98	7.33	20.25	(3)
<i>Pinus jeffreyi</i>						
No Spectral Change	2.69	2.74	5.62	10.75	7.18	2.67
Low	3.17	3.30	9.26	23.48	6.36	0.00
Moderate	2.50	2.33	12.31	35.30	4.82	0.00
High	2.50	2.33	12.31	35.30	4.82	0.00
<i>Abies magnifica</i>						
No Spectral Change	3.55	3.84	5.87	8.89	7.50	3.00
Low	2.10	1.97	2.96	8.00	16.00	5.00
Moderate	1.01	0.72	2.17	15.79	39.25	0.00
High	0.29	0.10	0.51	6.85	22.50	28.00

Note: *Pinus ponderosa* and *Abies concolor/Pinus lambertiana* forest patches with no fire had no gaps in the 100 ha class so a ratio could not be computed. The number of 100 ha gaps per 100 ha for these forest types were (1) 0.2, (2) 0.9, and (3) 2.

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Table A3. Percentage of area in gap by gap size bins for each fire severity class for major vegetation alliances. Smallest gap size reported was 2 m².

	Gap size bins (upper limit) in hectares						Sum
	0.001	0.01	0.1	1	10	100	
<i>Pinus ponderosa</i>							
No Fire	1.9	5.1	4.0	1.8	1.2	0.0	14.6
No Spectral Change	1.7	5.7	8.9	3.5	1.2	0.0	21.5
Low	1.1	3.7	10.0	11.7	8.9	2.1	37.8
Moderate	0.9	2.3	8.2	21.1	25.3	0.0	58.2
High	0.5	1.1	5.8	12.5	32.6	22.4	75.2
<i>Abies concolor/ Pinus lambertiana</i>							
No Fire	1.6	5.0	5.0	2.5	2.2	0.0	16.8
No Spectral Change	1.5	5.7	11.4	4.8	0.7	0.0	24.5
Low	1.1	4.1	10.9	12.7	6.4	0.0	35.7
Moderate	0.7	2.3	10.5	25.8	17.6	0.0	57.3
High	0.5	1.1	3.3	7.3	20.1	42.8	75.2
<i>Pinus jeffreyi</i>							
No Fire	0.4	1.0	2.1	6.5	31.7	25.6	67.4
No Spectral Change	0.2	0.7	4.5	15.6	44.2	8.8	74.0
Low	0.3	0.8	8.1	32.4	28.4	0.0	70.1
Moderate	0.2	0.6	13.8	43.3	20.1	0.0	78.1
High	0.2	0.2	7.8	16.5	26.0	31.8	82.7
<i>Abies magnifica</i>							
No Fire	1.4	4.6	8.3	6.2	2.2	9.0	32.2
No Spectral Change	1.2	4.4	13.9	12.4	5.7	2.7	40.8
Low	0.7	2.2	7.2	12.8	17.1	11.8	52.1
Moderate	0.3	0.7	8.4	30.2	34.3	0.0	74.2
High	0.1	0.1	2.4	14.2	15.6	55.9	88.4

Forest Structural Heterogeneity in Yosemite National Park

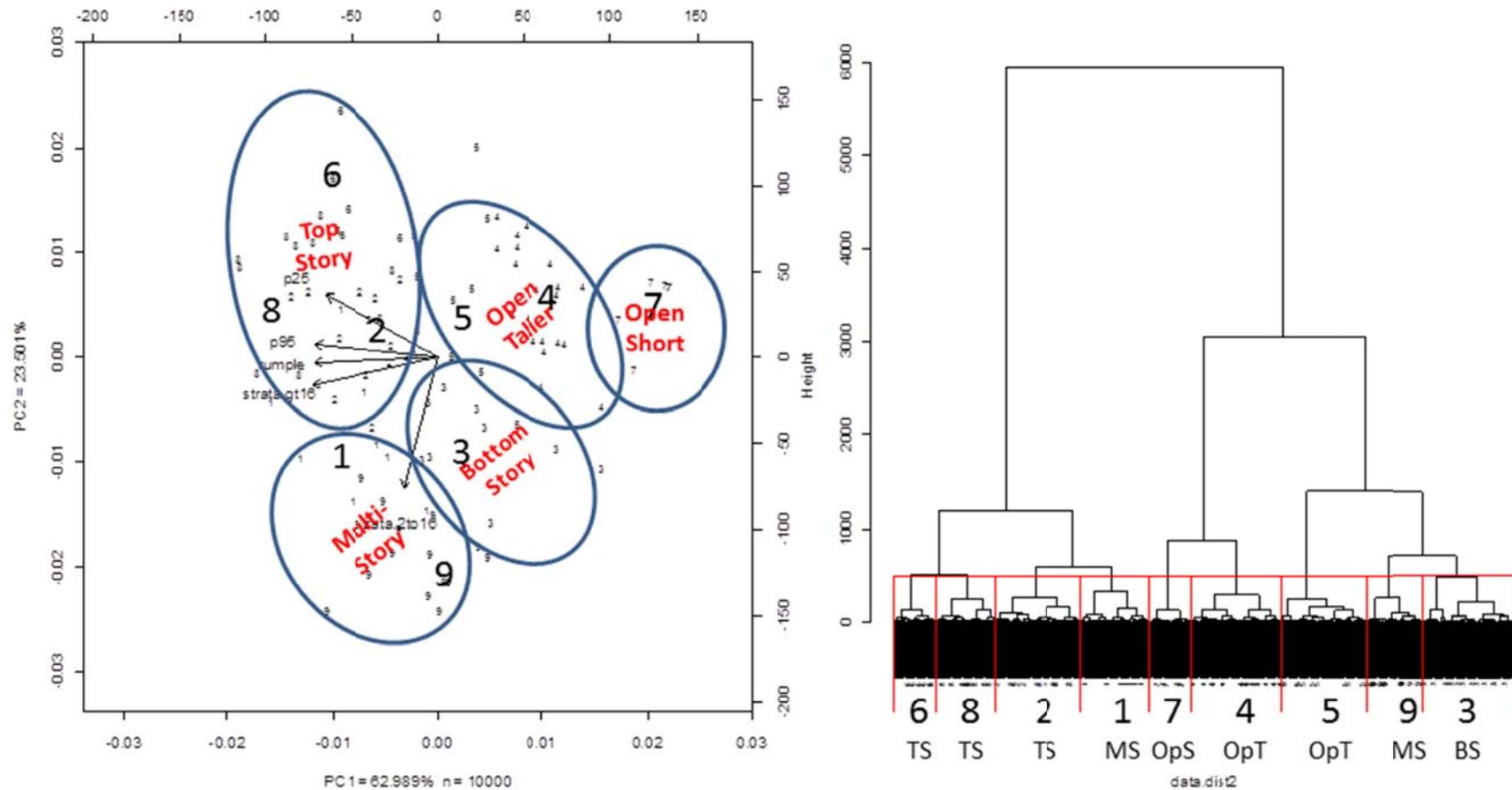


Figure A1. Original classes (numbered) identified by hierarchical cluster analysis displayed in principle components analysis (PCA) and dendrogram. Class numbers were arbitrarily assigned by the classifier and do not imply any ranking. Reclassification of the original nine classes was done by grouping the original classes based on the distribution to canopy cover into five classes: Open short (OpS), open taller (OpT), bottomstory (BS), multistory (MS), and top story (TS).

Forest Structural Heterogeneity in Yosemite National Park

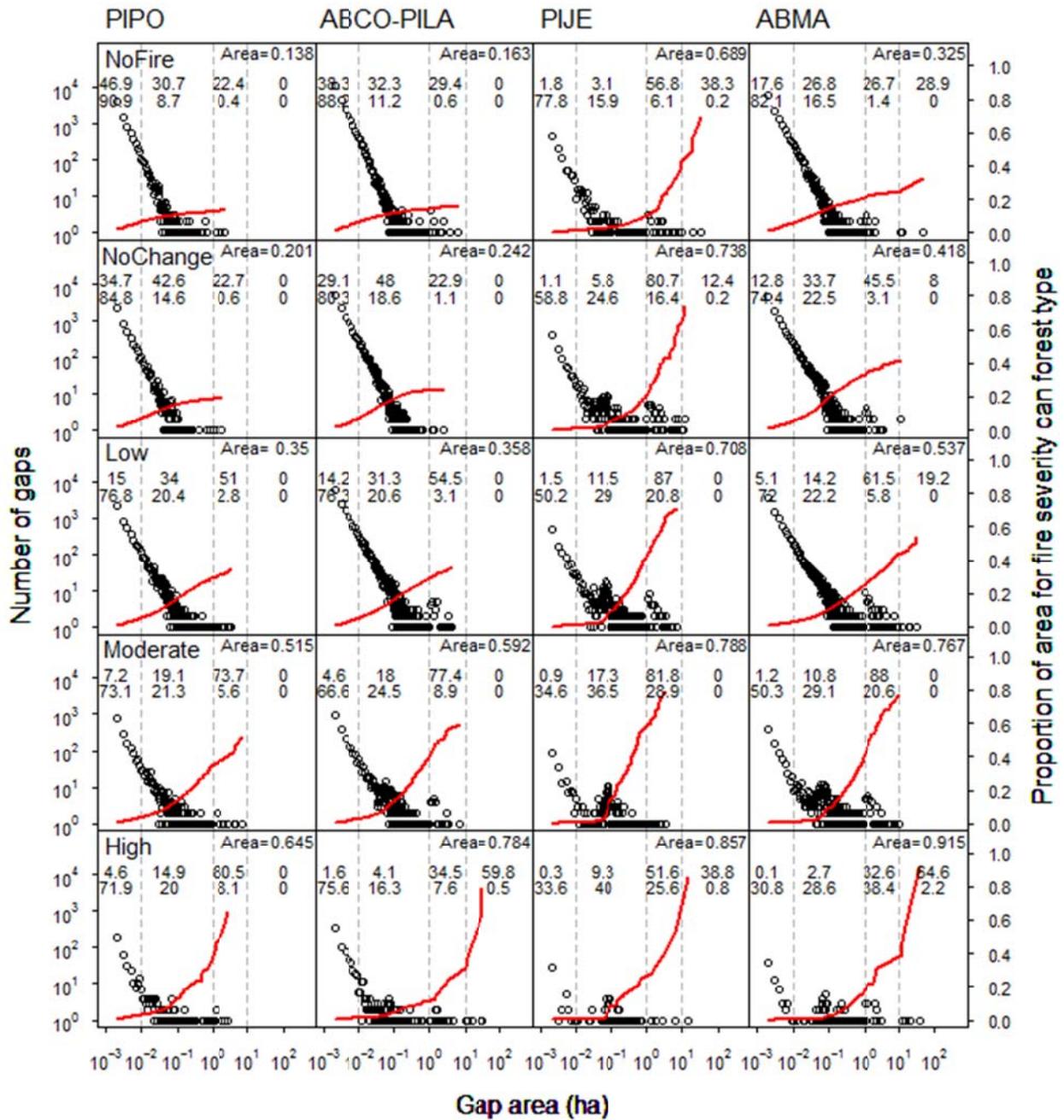


Figure A2. Gap frequency (circles) and cumulative area (line) by fire severity class and forest type using gap distribution size breaks (0.1, 1, 10 ha) from the Yosemite management plan. Cumulative area of gaps weighted by proportion of area in gap for each severity class and forest type; maximum cumulative area shown in top right of each panel. Legend within each panel shows: top line - the percentage of area in gaps <0.1 ha, 0.1-1 ha, 1-10 ha, and >10 ha; bottom line: percentage of gap counts within the same size breaks. A gap was defined as a contiguous area of the same forest type and fire severity class with no LiDAR returns ≥ 2 m in height. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

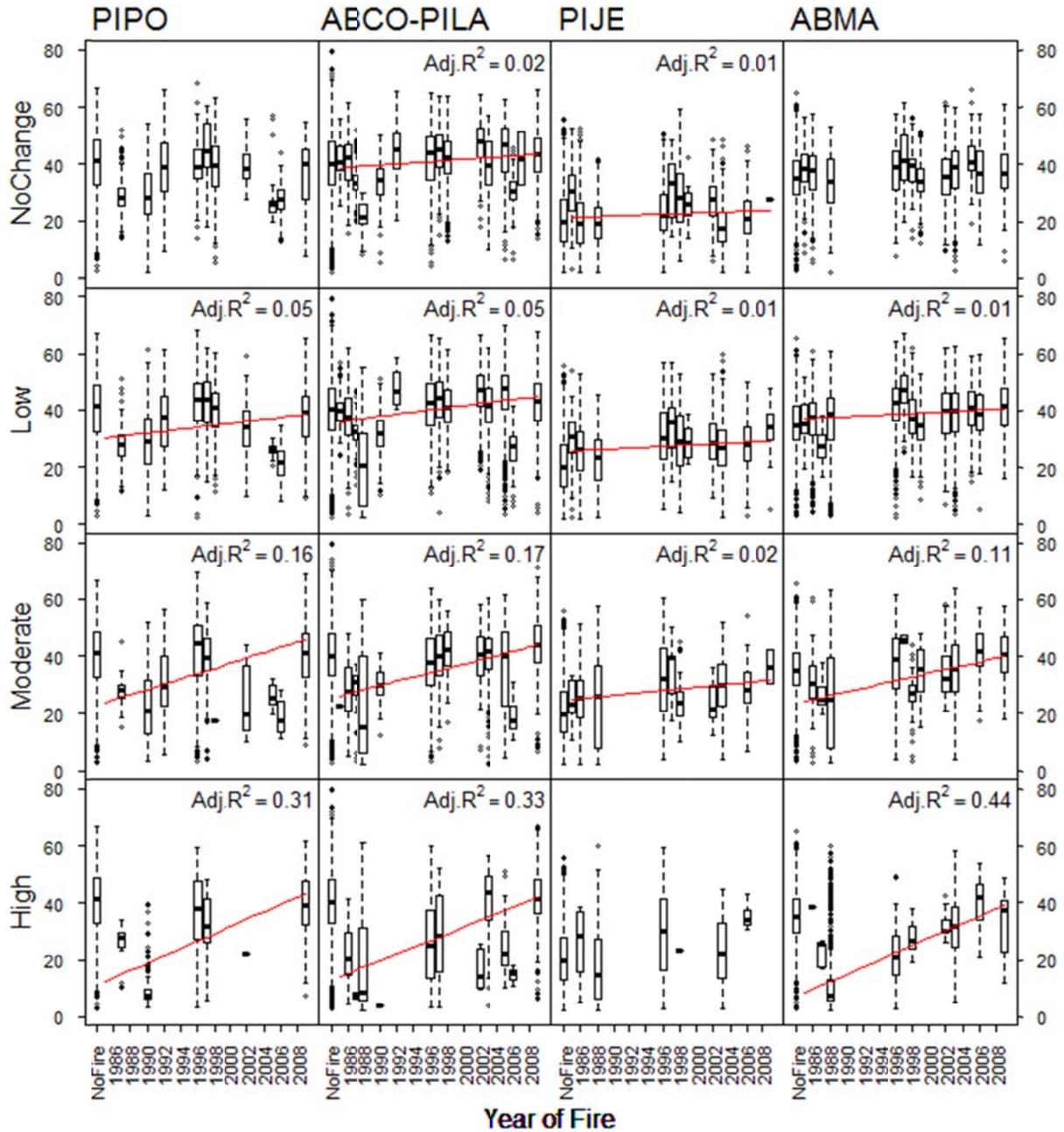


Figure A3: 95th percentile heights (m) by year of fire and fire severity with no fire values also shown for comparison. Only data for locations that experienced one or no fires shown; areas that experienced multiple fires are not shown. Legend for each panel shows adjusted R² value for a linear regression against metric values and number of years since the fire. All regressions shown were significant at P<0.001. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

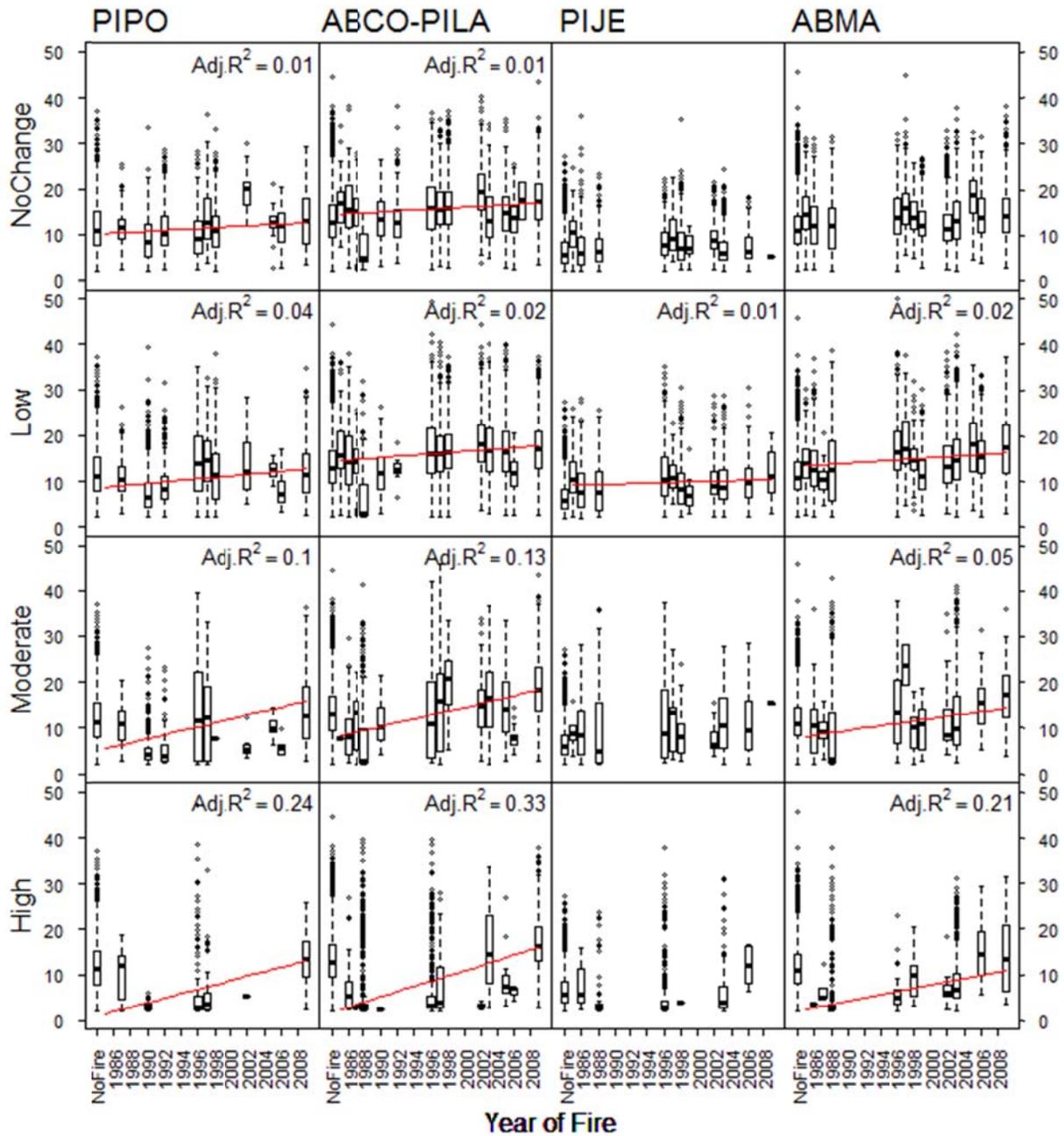


Figure A4: 25th percentile heights (m) by year of fire and fire severity with no fire values also shown for comparison. Only data for locations that experienced one or no fires shown; areas that experienced multiple fires are not shown. Legend for each panel shows adjusted R^2 value for a linear regression against metric values and number of years since the fire. All regressions shown were significant at $P < 0.001$. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

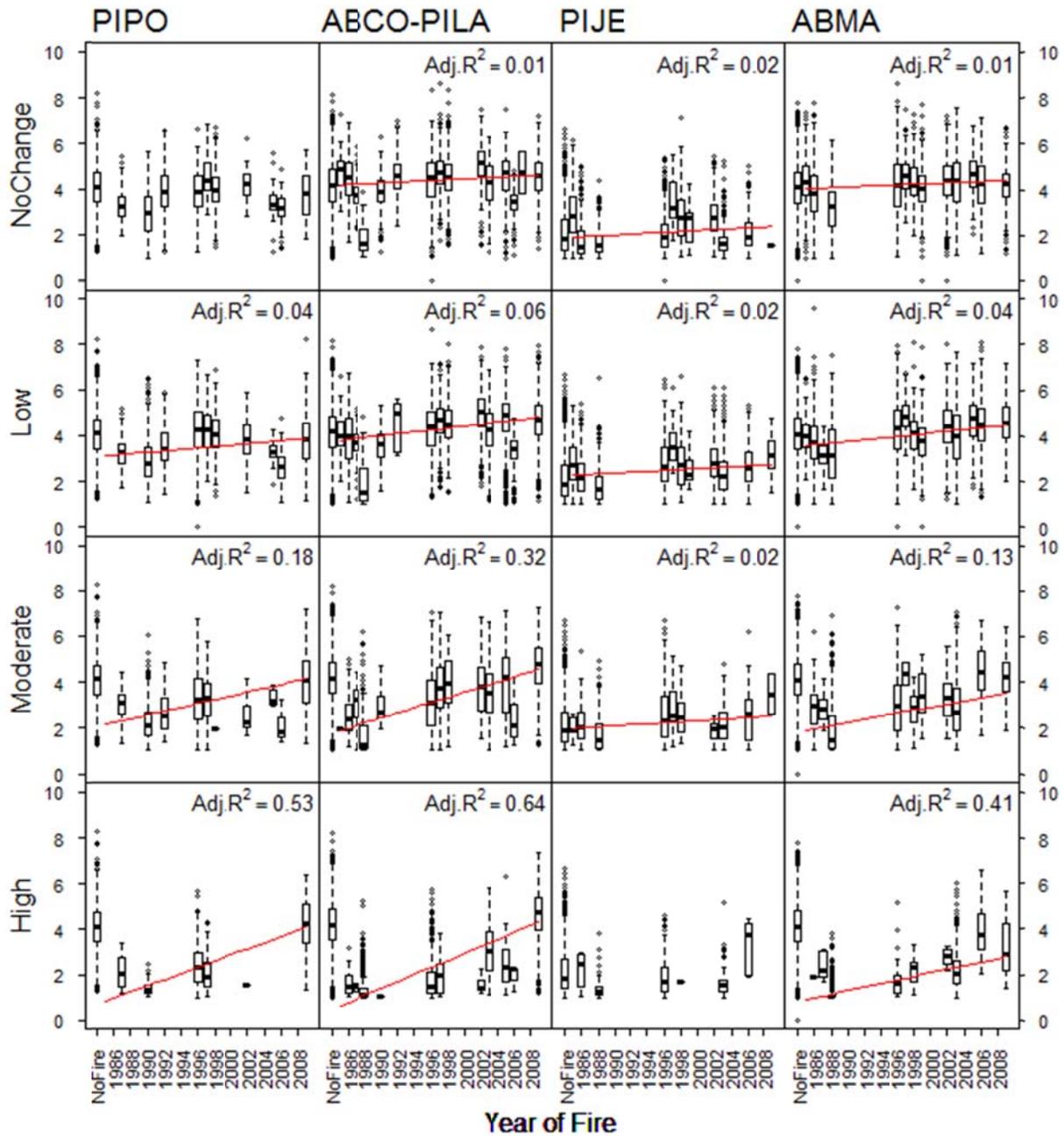


Figure A5: Rumple by year of fire and fire severity with no fire values also shown for comparison. Only data for locations that experienced one or no fires shown; areas that experienced multiple fires are not shown. Legend for each panel shows adjusted R^2 value for a linear regression against metric values and number of years since the fire. All regressions shown were significant at $P < 0.001$. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

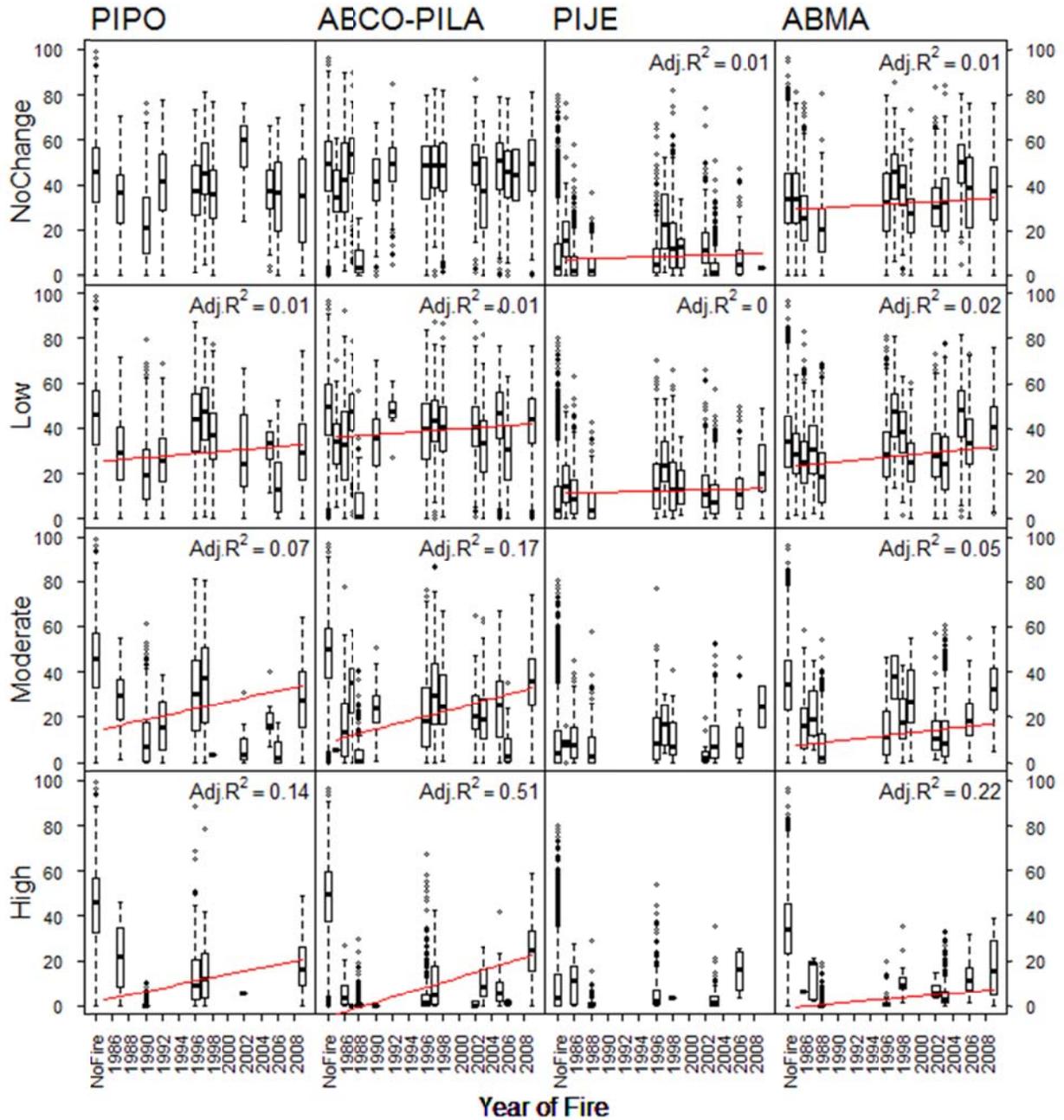


Figure A6: Canopy cover >16 m (percentage) by year of fire and fire severity with no fire values also shown for comparison. Only data for locations that experienced one or no fires shown; areas that experienced multiple fires are not shown. Legend for each panel shows adjusted R² value for a linear regression against metric values and number of years since the fire. All regressions shown were significant at P<0.001. Species codes are defined in Table 1.

Forest Structural Heterogeneity in Yosemite National Park

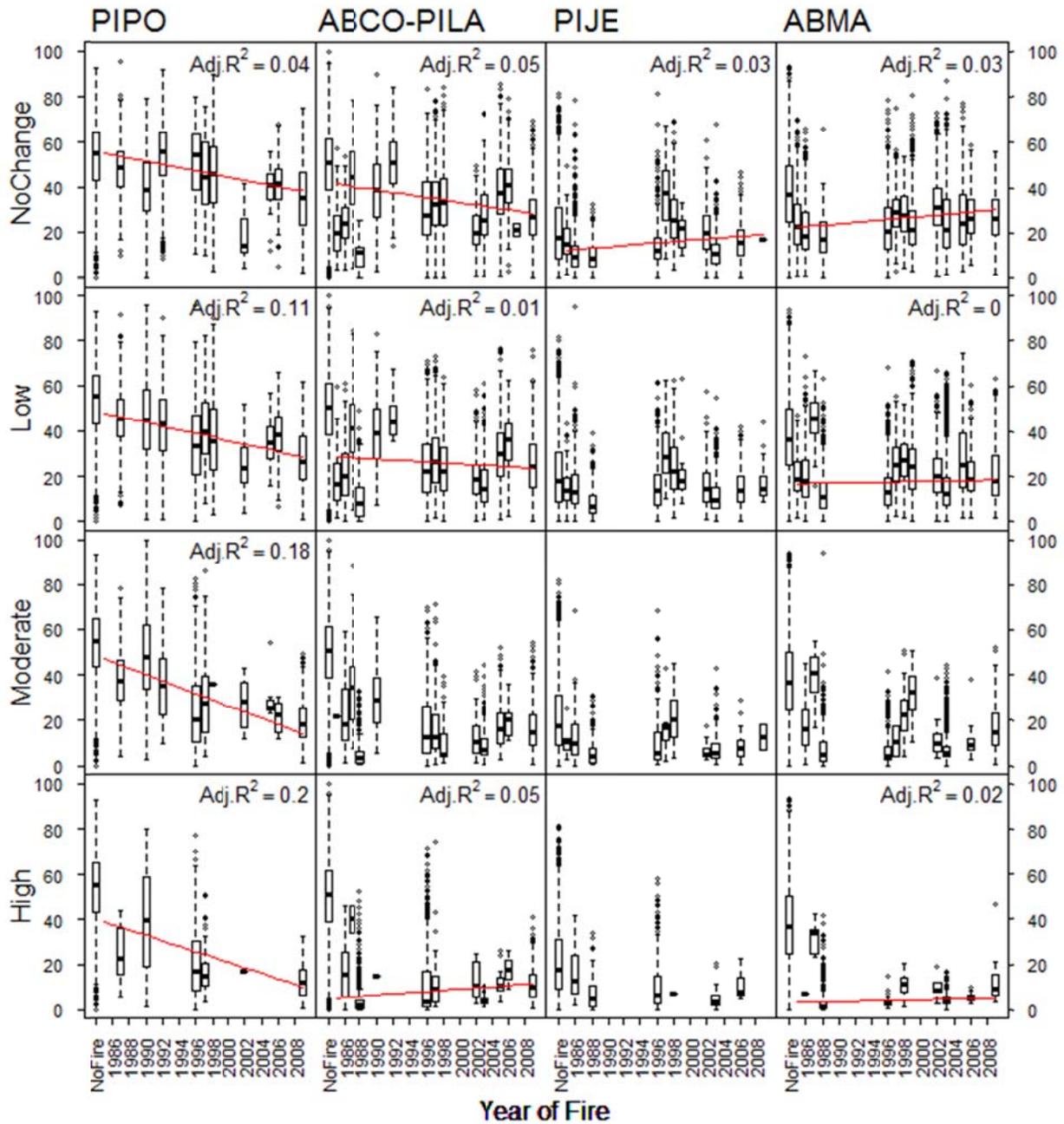


Figure A7: Canopy cover 2-16 m (percentage) by year of fire and fire severity with no fire values also shown for comparison. Only data for locations that experienced one or no fires shown; areas that experienced multiple fires are not shown. Legend for each panel shows adjusted R² value for a linear regression against metric values and number of years since the fire. All regressions shown were significant at P<0.001. Species codes are defined in Table 1.