

Topographic variation in tree group and gap structure in Sierra Nevada mixed-conifer forests with active fire regimes

Jan Ng^{a,c,*}, Malcolm P. North^{b,c}, Alec J. Arditti^c, Monica R. Cooper^c, James A. Lutz^d

^a Graduate Group in Ecology, University of California, Davis, One Shields Ave., Davis, CA 95616, USA

^b USDA Forest Service Pacific Southwest Research Station, 2500 Highway 203, Mammoth Lakes, CA 93546, USA

^c John Muir Institute of the Environment, University of California, Davis, One Shields Ave., Davis, CA 95616, USA

^d Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, USA

ARTICLE INFO

Keywords:

Fire resilience
Forest gaps
Forest restoration
ICO
Topography
Tree spatial patterns

ABSTRACT

In Sierra Nevada mixed-conifer forests, heterogeneity in overstory tree spatial patterns is an important ecological characteristic associated with resilience to frequent fires. Regional managers often emphasize this heterogeneity as a key component of forest treatments. There is a lack of information about how the dimensions of fire-resilient tree spatial patterns might vary with topography, which is an important influence on forest structure. We mapped, analyzed, and compared overstory tree spatial patterns across three topographic slope positions (ridges, mid-slopes, and valleys) in unlogged stands with multiple recent lower/mixed-severity burns. Using analysis of Individual trees, Clumps of trees, and Openings (ICO), we found significant differences in a number of spatial pattern metrics, including stand-level tree density and maximum clump size (highest in valleys), forest opening size (largest on ridges), and species composition (percent shade-intolerant stems highest on ridges). We found notably non-significant differences in within-clump tree densities at all spatial scales. Additionally, stand-level averages for forest structure across topography did not consistently capture spatial patterns for individual trees or smaller clump sizes, but often matched trends for clumps and openings in the largest size classes. As “megafires” become more common, prescribed fire and thinning treatments will be used more often to increase forest resilience. By quantifying variable tree spatial patterns across topographic positions in frequent-fire forests, we provide general guidelines for marking prescriptions that may increase resilience of treated forests to increasing fire intensity.

1. Introduction

In western North America, management of forests with historical or active frequent-fire regimes often emphasizes maintaining or restoring fire-resilient forest structure (Clyatt et al., 2016; Roccaforte et al., 2010; Stephens et al., 2008). Overstory tree spatial patterns form a major component of fire-resilient forest structure and, in these ecosystems, have been described as a relatively low-density mosaic of Individual trees, Clumps of trees, and Openings – “ICO” (*sensu* Larson and Churchill, 2012). Multiple studies have now quantified ICO patterns for fire-dependent forests (e.g., Churchill et al., 2013; Fry et al., 2014; Jeronimo et al., 2019; Lydersen et al., 2013; Pawlikowski et al., 2019), but thus far there have been no field-based studies of how ICO patterns might vary with topography. Topography is known to influence forest structure at both local and landscape scales in this region (Kane et al., 2015; Perry et al., 2011; Tuten et al., 2015), and is advantageous for

forest management because it is easily observable by field personnel (Underwood et al., 2010). We conducted an extensive field-based stem mapping study in contemporary active-fire forests in Yosemite National Park, California to characterize and compare ICO patterns across slope positions. Distinguishing ICO patterns across topographic gradients could be valuable to forest and fire managers in order to guide ecologically appropriate targets for thinning, prescribed burns, and other activities to promote fire and drought resilience.

1.1. Background

Fire is an integral feature in Sierra Nevada mixed-conifer forests (Kilgore and Taylor, 1979; Show and Kotok, 1924; Skinner and Chang, 1996; Sugihara et al., 2006). Active-fire areas – both pre-settlement and contemporary – are often studied to gain insights into conditions associated with resilience to centuries of frequent-fire disturbance and

* Corresponding author at: Graduate Group in Ecology, 2132 Wickson Hall, University of California, Davis, One Shields Ave., Davis, CA 95616, USA.

E-mail address: jnyng@ucdavis.edu (J. Ng).

<https://doi.org/10.1016/j.foreco.2020.118220>

Received 4 September 2019; Received in revised form 5 May 2020; Accepted 6 May 2020

0378-1127/ © 2020 Elsevier B.V. All rights reserved.

climate fluctuations (Allen et al., 2002; Collins et al., 2011; Larson and Churchill, 2012; Scholl and Taylor, 2010). In this context, we define resilience (*sensu* Walker et al., 2004) as the capacity of a system to adapt and reorganize during and after disturbances and thereby, “still retain essentially the same function, structure, identity, and feedbacks”.

An important characteristic of frequent-fire forests is horizontal complexity in their overstory tree spatial patterns (Harrod et al., 1999; Moustakas, 2015). This spatial pattern complexity has been associated with habitat for sensitive species (Apigian et al. 2006; Humple and Burnett, 2010; Underwood et al., 2010), secure carbon storage (Hurteau and North, 2009), and greater resilience to drought and wildfire (Fulé, 2008; Stephens et al., 2008). As fires burn across these landscapes, they leave behind a spatially heterogeneous patchwork of surviving trees and lowered fuel loads (Keifer et al., 2006; Larson and Churchill, 2012; Skinner and Taylor, 2006; Sugihara et al., 2006; Taylor, 2010). This in turn creates a positive feedback loop in the system, maintaining lower/mixed severities during future fires (Mitchell et al., 2009; Stephens and Moghaddas, 2005; Thaxton and Platt, 2006). Outside of extreme weather conditions – where intense crown fires can overwhelm common impediments like high fuel moisture and fuel discontinuity (Lydersen et al., 2014) – horizontal complexity in local forest structure tends to have a strong negative correlation with wildfire severity (Koontz et al., 2020).

Characterizing these complex horizontal spatial patterns using ICO methods has become increasingly common, enabling comparisons of spatial patterns before and after fire suppression, following thinning treatments, and among different latitudes and elevations (Churchill et al., 2013; Clyatt et al., 2016; Fry et al., 2014; Lydersen et al., 2013; Sánchez Meador et al., 2011). For fuels treatment marking guidelines that aim for heterogeneous overstory tree spatial patterns, managers need metrics for desired ranges of residual forest structure that ICO analysis can provide (e.g., targets for density, composition, and size of tree clumps and openings) (Churchill et al., 2013; Lydersen et al., 2013; North and Sherlock, 2012). They also need to know how these metrics vary with key environmental factors.

Studies from mixed-conifer forests indicate that overstory forest structure is substantially influenced by site productivity, water balance, and fire behavior, all of which are linked to topography (Holden and Jolly, 2011; Lydersen and North, 2012; Kane et al., 2015; Urban et al., 2000). Topographic variation in moisture availability is particularly influential on forest structure at finer (25–50 m) spatial scales (Fricker et al., 2019). At these scales, not only does topography strongly influence solar radiation and soil drainage (Dubayah and Rich, 1995; Urban et al., 2000), but it also affects fuel conditions (e.g., fuel moisture and density of ladder fuels) and thereby fire behavior (Holden and Jolly, 2011; Perry et al., 2011). Fuel arrangement and weather conditions being equal, fires often spread more readily in steeper and/or drier areas (van Wagtenonk, 2006).

Because fire behavior shifts across topographic slope positions, and because growth environments do as well, topography becomes a useful filter for subdividing forested landscapes into sections that are structured similarly by the interaction of those two dominant influences (Lydersen and North, 2012). Several studies have reported topographic differences in landscape and stand-level forest structure (e.g., canopy cover, basal area) (Kane et al., 2015; Lydersen and North, 2012; Urban et al., 2000). The few we could identify that did not find topographic differences in forest structure (e.g., Beaty and Taylor, 2007; Scholl and Taylor 2010) relied on spatial autocorrelation analyses (e.g., Moran's I) that did not explicitly capture tree spatial patterns (North et al., 2007; Scholl and Taylor 2010; Larson and Churchill, 2012).

We know of no field-based studies that currently exist for ICO patterns across topography, although one study (Jeronimo et al., 2019) has used remote sensing (lidar) to compare ICO metrics for “tree approximate objects” by topography and climate across large landscapes. Lidar, with its canopy-focused output, currently has some technical limitations in informing stem-focused, ground-based forest

management (Jeronimo et al., 2019). In addition to providing structure metrics that may help managers to increase post-treatment forest resilience, our field-based study may also contribute to building translational linkages between lidar output and ground-based metrics over time.

1.2. Objectives

We characterized overstory tree spatial patterns across topography under a contemporary frequent-fire regime in non-logged, old-growth Sierra Nevada mixed-conifer forests. Specifically, we asked whether ICO metrics would differ across three topographic slope positions (ridge, mid-slope, and valley) for: size and density of tree clumps, species composition, size and frequency of forest openings, and percent area in open space or under canopy cover. Additionally, because within-stand spatial scales are relatively understudied but have been identified as the scale at which fire-resilient ICO patterns manifest (Larson and Churchill, 2012), we also examined whether plot-level (approximating stand-level, more commonly studied) trends would be consistent with and representative of within-plot (approximating within-stand) trends.

2. Methods

2.1. Study area

Our study areas were mixed-conifer forests with active (restored) fire regimes in Yosemite National Park, California (hereafter, Yosemite; Fig. 1). The northwestern quadrant of the park where our plots were located has a characteristic Mediterranean climate of hot, dry summers and cold, wet winters (van Wagtenonk and Lutz, 2007). For montane coniferous forests in Yosemite, mean mid-summer maximum temperatures range from 22 to 27 °C and annual precipitation ranges from 1422 to 1066 mm for higher to lower elevations, respectively (Lutz et al., 2010). Most of these forests were fire-suppressed from the late 1800s onward in keeping with national policy (Rothman, 2007; Stephens and Ruth, 2005), but Yosemite began to allow wildfires again starting in the 1970s (van Wagtenonk and Lutz, 2007).

Prior to Euro-American settlement, Sierra Nevada mixed-conifer forests experienced frequent low- to moderate-severity fires—commonly due to lightning strikes and the landscape practices of Native Peoples (Anderson and Moratto, 1996; Lewis, 1973; McKelvey et al., 1996). Our study areas fall in the traditional territory of the Sierra Mewuk who, historically in this region and continuing today where possible, commonly apply burning techniques for the production of basketry materials, tending of food resources, and management of higher-severity fire hazard (Anderson, 1993; Bates and Lee, 1990; B. Cunningham-Summerfield, Mtn. Maidu and Turtle Mtn. Chippewa, pers. comm., May 2020). Fire history studies near our study area have reported mean fire return intervals of 6–30 years between the dates 1575–1900 (Barth et al., 2015; Knapp et al., 2013; Scholl and Taylor, 2010), while a meta-analysis for this forest type in general reported a median fire return interval of 9 years (Van de Water and Safford, 2011).

The most abundant overstory tree species in our sites were ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertiana*) (Table A.1). Some of our plots contained Jeffrey pine (*Pinus jeffreyi*), which we combined in our analyses with *P. ponderosa* as the two overlapped in the field and are known to sometimes hybridize (Conkle and Critchfield, 1988). In smaller quantities, we also found black oak (*Quercus kelloggii*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), red alder (*Alnus rubra*), and canyon live oak (*Quercus chrysolepis*).

All sites selected for this study had no history of thinning or salvage logging and had experienced at least two low- to moderate-severity burns in the 60 years prior to 2013, including one within 30 years prior (Table 1). All sites subsequently returned at low- to moderate-severity

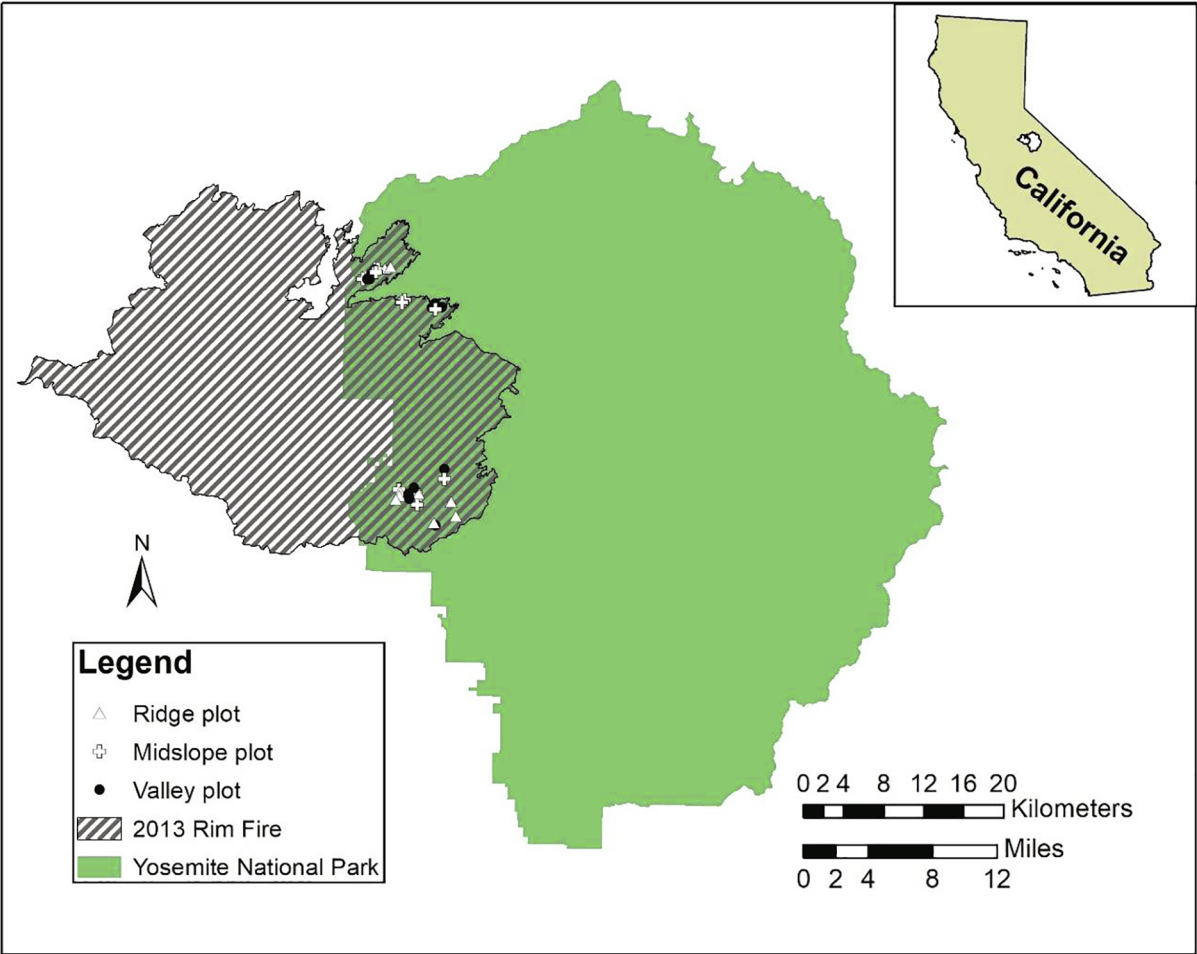


Fig. 1. Map of study areas within California's Yosemite National Park.

Table 1
Study site characteristics as measured from plot center. RdNBR for 2013 Rim Fire: median taken across plots; individual plot values calculated as an area-weighted average (by pixel). For aspect, NE: 293° to 112°; SW: 113° to 292°. Fire record represents years 1953–2012; all plots re-burned in 2013.

Topography	Elevation (m)	Slope (°)	RdNBR	Aspect (# of plots)	Fire record (# of plots)
Ridge	1,563–2,051	0–30	221	NE (4) SW (8)	1989, 2002 (2) 1989, 2000, 2002 (1) 1986, 1999 (4) 1983, 1998 (3) 1983, 1990, 1990 (2)
Mid-slope	1,648–1,932	10–21	254	NE (3) SW (9)	1986, 1999 (4) 1983, 1998 (5) 1978, 1996 (2) 1978, 1991, 2005 (1)
Valley	1,554–2,004	4–22	173	NE (2) SW (10)	1989, 2002 (1) 1986, 1999 (4) 1983, 1998 (4) 1978, 1991, 2005 (3)

during the 2013 Rim Fire, determined at a coarse scale by relativized delta Normalized Burn Ratio (RdNBR; [Tables 1, A.2–A.4](#)) ([Miller and Thode, 2007](#)) and verified by visual assessment in the field. For visual assessment, we defined low-severity as $\leq 25\%$ and moderate-severity as 25–75% overstory mortality. The Rim Fire is currently the fifth largest fire on record for California at roughly 104,000 ha ($\approx 257,000$ ac) ([CalFire, 2019](#)). These restored fire areas should not be viewed as explicit pre-settlement analogs or representative of forests that have never experienced suppression ([Lydersen and North, 2012](#)), however research

suggests that two low- to moderate-severity burns can substantially shift overstory spatial structures towards resembling those found historically in frequent-fire coniferous forests ([Larson et al., 2013](#); [Taylor, 2010](#); [Webster and Halpern, 2010](#)).

2.2. Field methods

In summers 2014–2015, we established 36 plots stratified by topography: 12 plots in each of three topographic slope positions

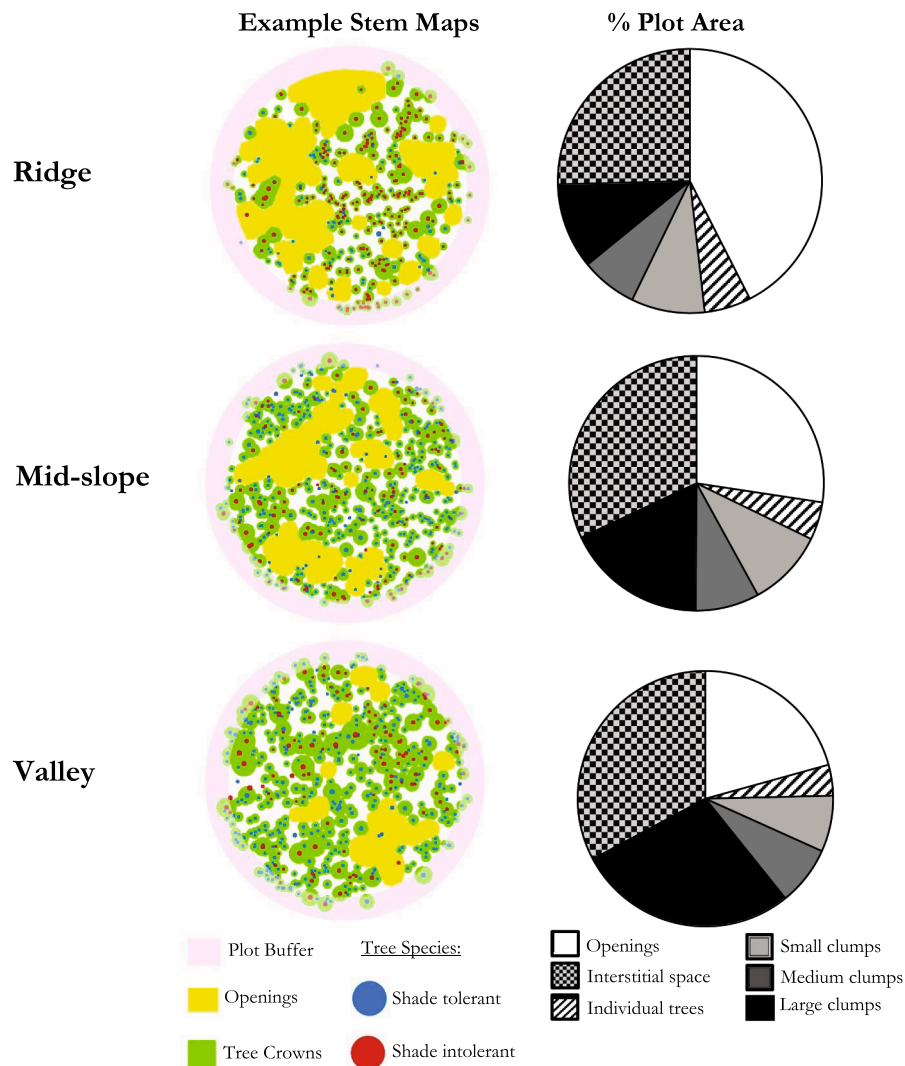


Fig. 2. Example stem maps for each topography type and comparison of mean percent area (out of total plot area, 2 ha) for all ICO components. Trees include all live and dead stems ≥ 20 cm DBH. In stem maps: minimum opening size is 80 m^2 ; plot buffer shown is 15 m (5 m inward from plot boundary, 10 m outward); white space within plot boundary is interstitial space. In pie charts: clump area is defined by crown overlap; small clumps are 2–4 trees; medium clumps are 5–9 trees; large clumps are ≥ 10 trees.

(Table 1, Fig. 1). Topography was classified as either valley, mid-slope, or ridge—a simplified version of the system described by Parker (1982) and used by multiple studies in montane coniferous forests thereafter (e.g. Lydersen and North, 2012; Taylor, 2010; Underwood et al., 2010). Plots were 80 m horizontal-distance radius circles (≈ 2 ha, not accounting for effects of slope angles), excluded roads and major trails, and in cases where plots were located in the same general area, had intervening features that would reasonably cause a shift in fire behavior, e.g. creeks, crevices, or changes in topography (Perry et al., 2011; Pettit and Naiman, 2007). Plots spanned a 500 m range in elevation, had slope angles of 0 – 30° , and included the four major cardinal directions for aspect, although more aspects faced southward than northward (Table 1).

For each plot, we mapped all live and dead stems ≥ 20 cm in diameter at breast height (DBH, 1.37 m). Mapping trees in the field was completed using a Criterion 400 total station (Laser Technology Inc.) with an allowed spatial margin of error up to 0.5 m. For each tree, we recorded DBH, species, and live/dead status. For dead trees, we recorded a decay class rating from 1 to 5 (following Harmon and Sexton, 1996).

2.3. Defining individual trees and tree clumps

We built stem maps by plotting the point locations of trees based on field data, then buffering each point by circles representing the tree bole (using DBH) and the tree crown (Figs. 2, A.1–A.3). Stem maps were built using ArcGIS Desktop v10.5 (Esri, 2016). Crown diameters were estimated using published species-specific allometric equations for conifers (Gill et al., 2000, their Table 9) and hardwoods (Bechtold, 2004, their Table 3) based on DBH. We chose Gill et al. (2000) because their samples came from forests adjacent to our study area and because Lydersen et al. (2013) found their calculations to be nearly identical to site-specific crown allometries from sites close to our study area. We used Bechtold (2004) equations for hardwoods because they were the best available for the western U.S. There were no parameters available for *P. jeffreyi*, so we used parameters for *P. ponderosa* in their place based on personal observation of growth form. Dead trees with decay ratings > 1 (indicating no foliage or fine branches) were given crowns reduced to the size of their boles so as not to be considered in recent competition with live trees but still be included in the stem count for clumps. Across all plots, crown radii ranged from 1.5 m (for a 20 cm

DBH *A. magnifica*) to 9.9 m (for a 225 cm DBH *P. lambertiana*), with a median of 2.5 m.

We defined tree clumps as groups of two or more trees with overlapping crowns (following Fry et al., 2014; Lydersen et al., 2013; Sánchez Meador et al., 2011). These methods derive from Plotkin et al.'s (2002) idea of grouping trees by the overlap of radii of influence around each stem. We then categorized the clumps as small (2–4 trees), medium (5–9 trees), or large (≥ 10 trees) for comparability with other published studies.

To control for edge effects, we applied a 5 m buffer inward from the plot edge so as to allow crowns straddling the inner boundary of the buffer to contribute to clumps, but exclude effects from potential (unmapped) crowns/clumps extending into the buffer whose associated trees were outside of the plots (Lydersen et al., 2013; Fry et al., 2014). Buffer size was selected relative to the larger crown radii expected for our system (Lydersen et al., 2013), and in our case over 96% of all trees in our plots had crown radii < 5 m (Fig. 2).

2.4. Defining forest openings and interstitial space

We defined openings in the canopy using modified Python scripts for the *PatchMorph* spatial sorting algorithm described by Girvetz and Greco (2007), which can be used to sort between canopy, openings, and leftover open space (hereafter, “interstitial space”; Figs. 2, A.1–A.3) based on parameters for several spatial thresholds. These parameters include a “gap threshold”, “spur threshold”, and “minimum patch area”. In our case, the gap threshold specified a minimum required canopy size for a given patch of canopy to remain influential when surrounded by open space. Open space would still be considered a candidate for canopy opening designation if the occasional tree(s) intruded, so long as that patch of tree canopy was smaller than the gap threshold. The gap threshold prevents overlap of substantial tree crowns with openings and is commonly set close to the minimum diameter for crowns across all plots (Lydersen et al., 2013). We set ours to 3 m, as all but one tree in our plots had a crown radius > 1.5 m. Spur threshold, for our purposes, specified a minimum width for openings and is commonly set to be at least the diameter of a large tree crown (Lydersen et al., 2013). We set our spur threshold to 10 m so as to be $> 96\%$ of tree crowns in our dataset. Likewise, we set our minimum patch area for openings to be 80 m^2 , or roughly equivalent to the area of a 10 m diameter crown.

2.5. Calculating ICO structure metrics by plot

For all ICO tree components (individuals, small/medium/large clumps, and at the plot-level), we calculated tree density, quadratic mean diameter (QMD), basal area, and the percentage of shade-intolerant trees out of total trees. We defined shade-intolerants as all *Pinus* and *Quercus* species (Table A.1).

For tree components falling at within-plot spatial scales (individuals, small/medium/large clumps), we calculated each as a percentage of total trees in the plot and did the same for percentage of total basal area. We also calculated a “within-clump” percentage for shade-intolerants, i.e. the percentage of shade-intolerant trees for a given clump size. For individual trees, this was notated as a “within-individuals” percentage. Although excluded from topographic comparisons due to predetermined tree densities, we calculated median clump area as a two-dimensional measure of canopy area within dripline.

At the plot-level and for all clump sizes, we calculated the density of clumps per hectare and a “within-clump” tree density, i.e. the tree density per hectare for a given clump size based on canopy area within dripline.

At the plot-level, we further calculated the mean and maximum number of trees per clump, the frequency of openings, and percent of total plot area under canopy cover, in openings, and in interstitial space.

Equations for all ICO metrics (excluding standard forestry equations) can be found in Table A.5.

2.6. Comparing ICO metrics across topography

To assess if any ICO metrics differed significantly among topographic slope positions (ridges, mid-slopes, and valleys), we averaged the values for each ICO metric (in each spatial category: individuals, small/medium/large clumps, and at the plot-level) across the 12 plots in each topography type. We then compared means across topography for each metric using generalized linear models (GLMs, means modeled as a function of topography) with a likelihood ratio test followed by pairwise Tukey's HSD (Honest Significant Difference) post hoc tests ($\alpha = 0.05$). We fit GLMs using the following model families: Poisson for count data (e.g. number of trees), binomial for percentages comparing two count values (e.g. percent of total trees), and gamma for continuous data (e.g. QMD).

Due to technical limitations for computing GLMs with beta distributions in R, percentages comparing two continuous, 0–1 constrained values (e.g., percent of total basal area) were an exception to the GLM protocol above. For these data, we compared means using beta regression models with a likelihood ratio test followed by evaluation of 95% confidence intervals (CI) for pairwise comparisons of model coefficients. Coefficients were simulated 1,000 times using the beta model's covariance matrix and a multivariate normal distribution.

Computation and statistical analyses for all ICO metrics were performed in R v3.5.2 (R Core Team, 2014) via the user interface RStudio v1.1.463 (RStudio Team, 2018). Data analyses were performed using the packages 'betareg' v3.1-1 (Cribari-Neto and Zeileis, 2010), 'car' v3.0-2 (Fox and Weisberg, 2011), 'data.table' v1.12.2 (Dowle and Srinivasan, 2019), 'dplyr' v0.7.5 (Wickham et al., 2018), 'lme4' v0.9-36 (Zeileis and Hothorn, 2002), 'multcomp' v1.4-8 (Hothorn et al., 2008), 'plyr' v1.8.4 (Wickham, 2011), 'rcompanion' v2.1.7 (Mangiafico, 2019), 'tidyverse' v1.2.1 (Wickham et al., 2019), and 'xlsx' v0.5.7 (Dragulescu, 2014).

3. Results

3.1. Individual tree, clump, and plot-level structure across topography

At the plot-level: Tree density and maximum trees per clump were lowest on ridges, increasing to become highest in valleys ($p < 0.001$; Table 2). Basal area was lowest on ridges ($p < 0.05$) and average trees per clump was highest in valleys ($p < 0.01$). Clump density peaked on mid-slopes ($p < 0.05$).

At the plot-level, for individual trees, and for all clump sizes: QMD and within-clump tree density showed no significant differences across topography ($p > 0.05$; Table 2). Pooled across all plots, the frequency of trees in each DBH class was lowest on ridges and highest in valleys (Fig. 3). The proportion of plot basal area allocated to the smallest DBH class (20–40 cm) was greatest for ridges and mid-slopes (both 14%; Fig. 4). For intermediate DBH classes (40–80 cm), the proportion was highest on ridges (20–21%), whereas at the largest DBH class (> 100 cm) it was highest in valleys (34%).

For large clumps: Tree density increased from ridges to valleys ($p < 0.001$; Table 2), as did percent of total trees and basal area ($p < 0.001$ and $p < 0.05$, respectively). Percent of total basal area was highest in valleys (simulation CI = 95%).

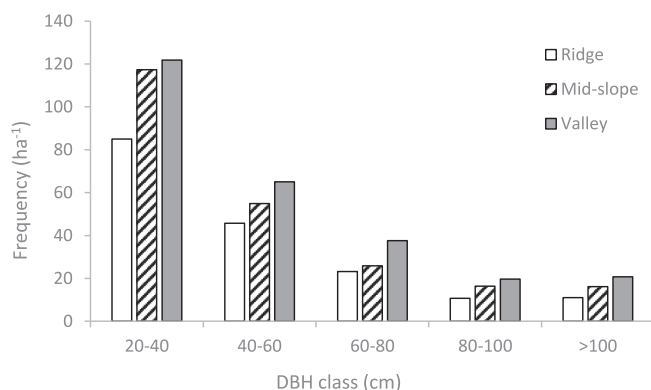
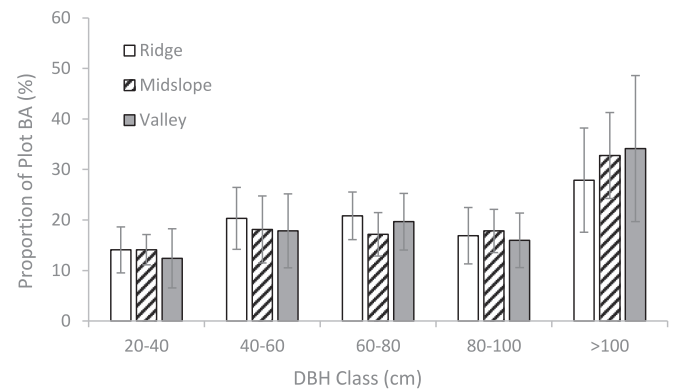
For medium clumps: Tree density peaked on mid-slopes ($p < 0.01$; Table 2). The percent of total trees was lowest in valleys ($p < 0.001$). Medium clumps showed no significant topographic differences for basal area, percent of total basal area, or clump density ($p > 0.5$, simulation CI = 95%, and $p > 0.1$, respectively).

For small clumps: Tree density peaked on mid-slopes ($p < 0.01$; Table 2). The percent of total trees as small clumps decreased from ridges to valleys ($p < 0.001$). Small clumps showed no significant

Table 2

Diameter and density metrics for individual trees, tree clumps, and at plot-level (2 ha). Values are expressed as means (and standard deviations). Means with differing superscripts are significantly different ($\alpha = 0.05$). Trees include all live and dead stems ≥ 20 cm DBH. % of total trees (or total BA): proportion out of total trees (or total BA) in a plot. BA: Basal Area. QMD: Quadratic Mean Diameter. * Units for within-clump tree density are (ha^{-1}) based on area bounded by canopy dripline.

	Ridge		Mid-slope		Valley	
<i>Individual Trees</i>						
# Trees (ha ⁻¹)	30.2	(5.5)	31.5	(5.4)	29.7	(7.1)
% of total trees	19.1 ^a	(7.3)	14.0 ^b	(2.8)	11.4 ^c	(3.0)
QMD	58.0	(4.1)	58.0	(5.5)	57.6	(9.4)
BA (m ² ·ha ⁻¹)	8.0	(1.9)	8.3	(1.8)	7.7	(2.3)
% of total BA	20.9 ^a	(7.9)	14.8 ^b	(3.5)	10.9 ^c	(3.8)
<i>Small Clumps (2–4 trees)</i>						
# Trees (ha ⁻¹)	46.0 ^a	(9.2)	52.3 ^b	(11.3)	39.8 ^c	(14.4)
% of total trees	28.3 ^a	(8.6)	23.3 ^b	(5.9)	15.5 ^c	(6.6)
QMD	54.1	(7.4)	55.0	(4.5)	57.1	(7.1)
BA (m ² ·ha ⁻¹)	10.6	(3.0)	12.5	(3.1)	9.9	(3.4)
% of total BA	27.0 ^a	(10.6)	22.3 ^b	(6.4)	14.6 ^c	(6.6)
# Clumps (ha ⁻¹)	18.1 ^{a, b}	(3.6)	19.3 ^a	(4.5)	15.1 ^b	(5.6)
w/in-clump tree density*	679.7	(101.0)	684.6	(58.1)	774.4	(273.9)
<i>Medium Clumps (5–9 trees)</i>						
# Trees (ha ⁻¹)	36.9 ^a	(21.0)	45.9 ^b	(11.6)	39.8 ^a	(10.1)
% of total trees	20.1 ^a	(5.5)	20.1 ^a	(5.0)	15.6 ^b	(5.5)
QMD	57.0	(8.9)	55.4	(7.0)	60.1	(10.2)
BA (m ² ·ha ⁻¹)	9.3	(5.0)	11.2	(4.1)	11.4	(4.3)
% of total BA	20.9	(5.9)	19.6	(6.7)	15.8	(5.9)
# Clumps (ha ⁻¹)	5.8	(2.9)	7.2	(1.7)	6.0	(1.7)
w/in-clump tree density*	659.8	(135.8)	686.0	(106.5)	608.1	(99.5)
<i>Large Clumps (≥10 trees)</i>						
# Trees (ha ⁻¹)	62.8 ^a	(39.3)	101.1 ^b	(39.7)	155.7 ^c	(49.5)
% of total trees	32.6 ^a	(13.1)	42.6 ^b	(9.6)	57.6 ^c	(12.8)
QMD	52.0	(10.2)	57.2	(6.5)	60.0	(8.2)
BA (m ² ·ha ⁻¹)	14.9 ^a	(10.6)	25.2 ^b	(8.4)	44.6 ^c	(19.8)
% of total BA	31.2 ^a	(15.8)	43.4 ^a	(9.3)	58.6 ^b	(13.2)
# Clumps (ha ⁻¹)	3.8 ^a	(2.0)	5.2 ^{a, b}	(1.6)	6.4 ^b	(2.0)
w/in-clump tree density*	693.7	(157.8)	624.3	(105.9)	609.7	(106)
<i>Plot-level</i>						
# Trees (ha ⁻¹)	175.9 ^a	(60.2)	230.8 ^b	(45.3)	264.9 ^c	(41.0)
QMD	55.6	(4.9)	56.5	(3.8)	59.3	(7.7)
BA (m ² ·ha ⁻¹)	42.9 ^a	(15.9)	57.2 ^b	(9.4)	73.7 ^b	(19.3)
# Clumps (ha ⁻¹)	27.6 ^a	(6.4)	31.7 ^b	(5.1)	27.5 ^a	(7.1)
w/in-clump tree density*	675.7	(89.7)	676.7	(54.5)	699.7	(179.6)
Mean # trees/clump	5.1 ^a	(1.2)	6.3 ^a	(1.2)	9.3 ^b	(3.9)
Max. # trees/clump	24.1 ^a	(10.6)	37.1 ^b	(11.2)	73.3 ^c	(41.8)

**Fig. 3.** Frequency distribution of trees ≥ 20 cm DBH across all plots.**Fig. 4.** Distribution of basal area for trees ≥ 20 cm DBH, expressed as means across 12 plots (2 ha) in each of three topography types. Error bars correspond to standard deviation.**Table 3**

Median clump area (and median absolute deviation) pooled across topography types, calculated as canopy area within dripline.

ICO Category	Clump Area (m^2)	
Individual Trees	16.9	(7.9)
Small Clumps (2–4 trees)	40.1	(22.1)
Medium Clumps (5–9 trees)	100.9	(50.1)
Large Clumps (≥ 10 trees)	262.0	(141.0)

differences for basal area ($p > 0.1$), but percent of total basal area was highest on ridges, decreasing to become lowest in valleys (simulation CI = 95%), and clump density was higher on mid-slopes than in valleys ($p < 0.01$).

In absolute numbers, median clump area increased with clump size (number of trees), although variance in clump area was especially high for large clumps (Table 3). The absolute frequency of clump sizes across all topography types was highest for smaller clump sizes and decreased as clump size increased (Fig. 5).

For individual trees: Tree density and basal area showed no significant differences across topography ($p > 0.5$ and $p > 0.7$, respectively; Table 2). However, percent of total trees and percent of total basal area were both highest on ridges and decreased to become lowest in valleys ($p < 0.001$ and simulation CI = 95%, respectively).

3.2. Species composition across topography

For individual trees, small and medium clumps, and at the plot-level: The percentage of shade-intolerant trees was highest on ridges and decreased to become lowest in valleys ($p < 0.01$, Table 4). For large clumps: The percentage of shade-intolerants was significantly lower in valleys than on ridges ($p < 0.01$).

For individual trees and all clump sizes: Within-individuals and within-clump percent shade-intolerants was highest on ridges and decreased to become lowest in valleys ($p < 0.01$; Table 4).

3.3. Forest openings and percent cover across topography

The frequency of openings did not show any significant differences across topography ($p > 0.9$), but the percentage of area in openings did, with ridges having a higher percentage of area in openings (43%) than either mid-slopes or valleys (27% and 21%, respectively; simulation CI = 95%; Table 5, Fig. 2). Percent canopy cover was higher in valleys (47%) compared to either mid-slopes or ridges (41% and 32%, respectively; simulation CI = 95%). Percentage of area in interstitial space increased moving from ridges to valleys (simulation CI = 95%), although the absolute values were quite close for mid-slopes and valleys

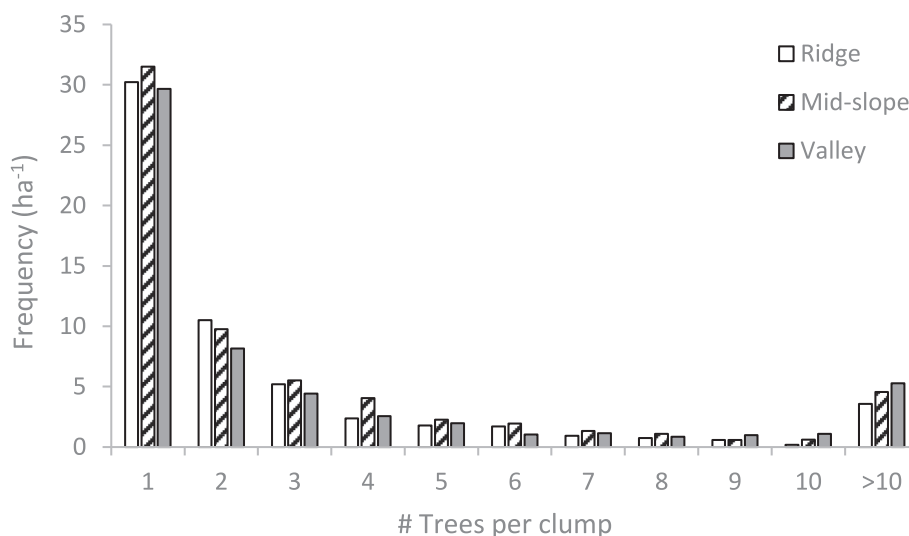


Fig. 5. Frequency distribution of clump sizes by number of trees (≥ 20 cm DBH) per clump. Clumps defined by overlap of crowns. Crowns determined by species-specific allometric equations based on DBH.

Table 4

Species composition: percent shade-intolerants for individual trees, tree clumps, and at plot-level (2 ha). Values are expressed as means (and standard deviations). Means with differing superscripts are significantly different ($\alpha = 0.05$). Trees include all live and dead stems ≥ 20 cm DBH. Shade-intolerants: *Pinus* and *Quercus* species. % of total trees: proportion out of total trees in a plot. % w/in individuals (or clump): proportion out of individual trees (or trees in specified clump size) in a plot.

	Ridge		Mid-slope		Valley	
<i>Individual Trees</i>						
% of total trees	9.8 ^a	(6.5)	3.8 ^b	(2.6)	1.6 ^c	(1.0)
% w/in individuals	46.5 ^a	(23.7)	27.0 ^b	(17.5)	14.5 ^c	(8.8)
<i>Small Clumps (2–4 trees)</i>						
% of total trees	17.2 ^a	(12.9)	7.2 ^b	(5.7)	3.0 ^c	(2.7)
% w/in clump	54.9 ^a	(30.5)	29.7 ^b	(18.2)	19.4 ^c	(15.9)
<i>Medium Clumps (5–9 trees)</i>						
% of total trees	9.8 ^a	(5.0)	7.0 ^b	(4.2)	3.4 ^c	(2.8)
% w/in clump	53.4 ^a	(27.8)	35.3 ^b	(20.1)	22.4 ^c	(17.7)
<i>Large Clumps (≥ 10 trees)</i>						
% of total trees	16.1 ^a	(9.3)	14.9 ^{a, b}	(7.9)	13.3 ^b	(10.2)
% w/in clump	55.4 ^a	(29.7)	35.5 ^b	(19.8)	23.2 ^c	(16.4)
<i>Plot-level</i>						
% of total trees	52.9 ^a	(27.6)	32.9 ^b	(18.2)	21.2 ^c	(15.6)

Table 5

Plot-level metrics for frequency of openings (80 m² minimum area) and percent out of total plot area (2 ha) as openings, canopy cover, and interstitial space. Values are expressed as means (and standard deviations). Means with differing superscripts are significantly different ($\alpha = 0.05$).

	Ridge		Mid-slope		Valley	
<i>Plot-level</i>						
# Openings (ha ⁻¹)	5.8	(1.6)	5.9	(1.2)	6.0	(1.5)
% Area - opening	42.5 ^a	(16.7)	27.4 ^b	(9.8)	20.7 ^b	(8.0)
% Area - canopy cover	32.1 ^a	(8.9)	40.6 ^a	(5.3)	46.5 ^b	(6.9)
% Area - interstitial space	25.4 ^a	(8.2)	32.0 ^b	(5.1)	32.8 ^c	(3.4)

(32% and 33%, respectively).

In absolute numbers, the highest frequency of openings across all topography types occurred for openings less than 250 m² in size (Fig. 6). For increasingly larger opening sizes, the frequency then dropped steeply for valleys, less steeply for mid-slopes, and less steeply still for ridges, such that ridges ultimately had the highest frequency of

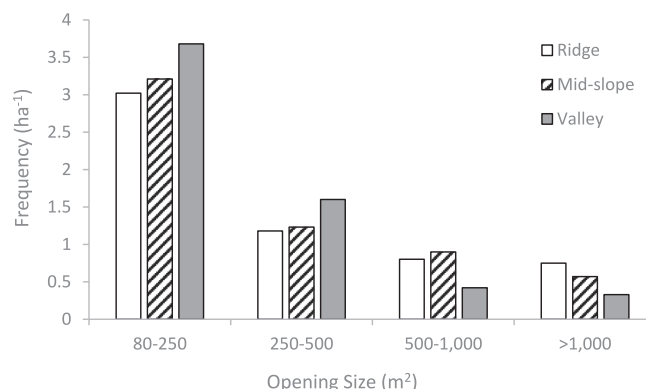


Fig. 6. Frequency distribution of forest openings ≥ 80 m² across all plots.

openings $> 1,000$ m² in size.

4. Discussion

4.1. Overview

We found that plot-level averages for overstory forest structure corroborated available literature but did not necessarily capture shifts in spatial structure that occurred at within-plot spatial scales across topography. Plot-level trends for tree density, basal area, canopy cover, and percent of area in openings were driven primarily by the density of clumps and openings in the largest size classes. Within-clump tree density, on the other hand, did not differ significantly across topography at any of the spatial scales we examined. And species composition trends showed a decrease in percent shade-intolerants moving from ridges down to valleys, consistent across nearly all spatial scales. These topographic patterns emerged despite variation in slope angle and aspect among plots, supporting the argument for using topography as a discriminating landscape feature when managing for overstory heterogeneity in frequent-fire forests (Jeronimo et al., 2019; Lydersen and North, 2012; Underwood et al., 2010). For managers, our findings suggest that much of the topographic differences in stand structure and spatial pattern might be achieved by focusing on the number and size of large tree clumps and large openings. For readers interested in discussion of other results or additional literature comparisons (e.g. for percent basal area allocations, QMD, clump size), please refer to the Supplementary Text (Appendices B.1–B.5).

4.2. Limitations

We caution that our study design has several limitations. First, setting a minimum DBH at 20 cm precludes our ability to capture elements of spatial structure that vary with the presence of smaller trees (e.g., absolute tree density). However, this DBH threshold was selected to effectively capture overstory trees in our plots, which was our target for pattern analysis in this study. Frequent fires tend to keep understory fuel levels relatively low in this system (Keifer et al., 2006; Skinner and Chang, 1996), nevertheless future studies might wish to examine spatial patterning of smaller trees in order to assess their impact as ladder fuels (Ziegler et al., 2017). If so, we would recommend sampling around a decade post-fire for this system, at minimum, in order to accurately capture pre-fire understory fuel levels.

Second, defining our largest clump size as “ ≥ 10 trees” reduces our ability to recognize patterns that only manifest at larger clump sizes. We chose our clump sizes for comparability to prior literature and because preliminary histograms did not suggest more logical divisions.

Third, our plot selection process permitted the presence of (non-forested) creeks in valleys, which impacts open space metrics for those areas. That said, because valleys and creeks do commonly co-occur, our results are still likely representative of general spatial structure in valleys for the central Sierra Nevada.

Fourth, we defined tree clumps based on overlap of allometrically sized tree crowns. This likely causes our results to differ from those in studies that used fixed inter-tree distances (Barth, 2014; Tuten et al., 2015). However, allowing our crowns to vary by tree size and species might be more ecologically relevant (Fry et al., 2014; Rodman et al., 2016), especially given that unlike most studies using fixed distances, our study system is not dominated by any one overstory species.

Lastly, the geographic extent of this study was limited to the northwest quadrant of Yosemite National Park and thus does not capture the full range of variability in factors like climate, physiography, etc. that are known to correlate with shifts in structure for this forest type (Jeronimo et al., 2019). Therefore, any translation of our results to other locations should take local biophysical conditions into account.

4.3. Individual tree, clump, and plot-level structure across topography

Plot-level tree density and basal area increased moving from ridges down to valleys (Table 2) as expected, corroborating contemporary studies evaluating topographic effects on stand-level forest structure in Sierra Nevada mixed-conifer forests (Jeronimo et al., 2019; Lydersen and North, 2012; Underwood et al., 2010). This likely reflects topographically-influenced variation in conditions that impact forest growth, such as solar radiation, soil depth, and water balance (Fricker et al., 2019; Kane et al., 2015; Urban et al., 2000). In our study, it appeared that topographic trends at the plot-level were driven primarily by the finer spatial scale trends of large clumps. Plot-level trends and large clump trends mirrored one another, and tree allocation to large clumps was disproportionately high – both in absolute numbers as well as in percentage of total trees. Within any topography type, tree allocation to large clumps constituted anywhere from 50% to 500% more trees per ha on average than that of any other clump size (Table 2).

In contrast, for individual trees and smaller clump sizes, topographic trends in tree density and basal area were not mirrored at the plot-level. This was the case despite plot-level mean clump size falling within the “medium” range (5–9 trees) for all topography types (Table 2). Frequencies of different clump sizes (Fig. 5) supported the “many small, few large” power law distribution that is not uncommon for forests with mixed-severity fire regimes (Perry et al., 2011). That the most frequent clump sizes did not drive plot-level trends indicates that the wide range in clump size, more so than clump frequency, was what influenced plot-level topographic trends in tree density. At the plot-level, valleys did not have more clumps on average compared to mid-

slopes or ridges, but valleys did have more large clumps, as well as a significantly greater maximum clump size (nearly two-fold that of mid-slopes, and nearly three-fold that of ridges) (Table 2). Overall, this suggests that commonly assessed stand-level averages may do a good job of capturing forest structure associated with large clumps (and vice versa) but might not be reliable for capturing structure – and any ecological phenomena – associated with individual trees, small clumps, or medium clumps.

Surprisingly, topographic distinctions in tree density were erased when analyzed at the within-clump spatial scale. This was true at every clump size and at the plot-level (Table 2). This could indicate that the typically influential forces of water availability and fire behavior acting across slope positions (Jeronimo et al., 2019) were insufficient to create substantial heterogeneity within clumps. Rather, while those principal drivers might create and maintain characteristic patchy forest structure throughout a stand (Larson and Churchill, 2012; Skinner and Taylor, 2006; Sugihara et al., 2006), perhaps within a given clump (i.e. more locally), forces like competition and facilitation that are known to govern spacing (Pielou, 1962; Shreve, 1931) might be the primary regulators.

4.4. Species composition across topography

Unlike trends for tree density, trends for species composition were largely consistent and significantly different across topography for individual trees, all clump sizes, and at the plot-level (Table 4). The decrease in percent shade-intolerants moving downslope corroborates literature from the study region (Lydersen and North, 2012) and matched our expectations given the increase in tree density moving downslope. Higher tree densities typically translate to increased clump size and canopy area, and therefore shade (Rodman et al., 2016) (Table 3). Shade from the land itself (landform topographic shading) might also have contributed, as valleys are regularly associated with cooler nighttime temperatures and higher humidity that maintain higher moisture levels (Holden and Jolly, 2011). This enables ingrowth from more shade-tolerant, less drought-tolerant species. Landform shading may be important for explaining patterns of within-clump percent shade-intolerants, as these adhered to the decreasing-downslope trend even for restricted clump sizes (individuals, small & medium clumps), for which stem counts by definition did not increase.

Overall, species composition in our plots varied as expected relative to results from other frequent-fire sites (Lydersen et al., 2013; Rodman et al., 2016), with percent shade-intolerants comparatively higher for whichever sites were likely to have higher light availability (due to lower stem densities and/or landform shading effects). Topography-mediated differences in light and moisture conditions at a site (Kane et al., 2015) might explain why active-fire systems can still have locally high percentages of fire-intolerant – often shade-tolerant – species (e.g. smaller-diameter *A. concolor*). There has been some discrepancy in the literature over the occurrence of these supposed fire-intolerants regularly burning at lower severities (Lydersen et al., 2014). Our results indicate that fire-intolerant, shade-tolerant species are more strongly associated with valleys in this frequent-fire system, where environmental factors (e.g. moisture) may outweigh biotic factors (e.g. species-specific fire susceptibility) in keeping fire intensities and severities low.

4.5. Forest openings and percent cover across topography

We found that the mean frequency of openings did not differ significantly across topography (Table 5), but that ridges nevertheless had a higher percentage of area in openings (in absolute terms: by 50–100% compared to mid-slopes or valleys, Fig. 2). These results suggest that topographic distinctions in percent area in openings for this ecosystem are driven by variation in the size of openings rather than variation in frequency. In absolute numbers, whereas mid-slopes and/or valleys had more openings in smaller size classes ($< 1000 \text{ m}^2$), ridges had more

openings in the largest size class ($> 1000 \text{ m}^2$) (Fig. 6). The effect of these topographic distinctions on cover type might underlie patterns found across broader spatial scales, as ridges are described as having comparatively greater open space throughout frequent-fire forests in the Sierra Nevada (Jeronimo et al., 2019). Our results also corroborate trends for active-fire (versus fire-suppressed) sites in the existence or greater presence of mid-sized openings ($250\text{--}1000 \text{ m}^2$) and in values for percent area in openings (Fry et al., 2014; Lydersen et al., 2013).

In our study, the topographic trend for percent canopy cover ran opposite to that of percent area in openings, with higher percent canopy in valleys compared to mid-slopes or ridges (Fig. 2, Table 5). This followed expectations that percent canopy cover would match trends in plot-level tree density. However, the trend for percent area in interstitial space also followed the trend for tree density – running opposite to the trend for percent area in openings despite interstitial space being a form of open space (Table 5). This illustrates a spatial arrangement of valleys having smaller openings and larger clumps, where larger clump sizes are associated with smaller and more sinuous types of open space (Lydersen et al., 2013). Results for interstitial space also highlight a potentially large range of discrepancy in the literature concerning open space values – up to 33% of total area (Fig. 2, Table 5) – depending on how open space is defined and measured. We were unable to find literature for comparison of interstitial space, but in future research it could be derived from lidar data and may prove useful for studying regeneration. Interstitial space may provide an important microsite for tree regeneration in an ecosystem where water and light availability are both major driving factors. Full-canopy and full-opening areas could be inhospitable (personal observation) on the basis of lacking light or water, especially under climate change.

5. Management implications

When managing for future fire resilience in forests with a history of frequent fire, it may be especially important to consider ecologically informed targets for stand structure (Churchill et al., 2013; Hessburg et al., 2016). These targets include overstory tree spatial patterns at both stand-level and within-stand spatial scales (Clyatt et al., 2016; Larson and Churchill, 2012; Lydersen et al., 2013; Pawlikowski et al., 2019). If 2 ha plots can approximate small stands, our results indicate that within-stand patterns are not immediately achievable by focusing on stand-level metrics alone, but rather that specific differences in structure within stands can scale up to differences in stand-level spatial patterns across topographic slope positions.

Topography can affect overstory stand structure through its influences on ecological processes, particularly the frequency and intensity of fire, as well as water availability (Fricker et al., 2019; Holden and Jolly, 2011; Kane et al., 2015; Urban et al., 2000). Our results suggest that average tree diameter (QMD; Appendix B.2) and within-clump tree densities are fairly consistent across different topographic positions, but that significant differences do exist in stand-level structure and those are often driven by the sizes of forest openings and tree clumps. Therefore, if considering topography in treatments for tree spatial patterns in these ecosystems, we recommend that managers base structural variability around the results summarized in Tables 2, 4, and 5 and Fig. 6. In particular, we recommend focusing on the percentages of overstory trees and basal area allocated to different clump sizes (Table 2), the relative proportion of shade-intolerant species (Table 4), and the frequencies of large tree clumps (≥ 10 trees) and largest openings ($> 1000 \text{ m}^2$) across topography types (Tables 2 & 5, Fig. 6).

Variation in climate and physiography correlates with shifts in forest structure for frequent-fire mixed-conifer forests (Clyatt et al., 2016; Fry et al., 2014; Jeronimo et al., 2019). Therefore, use of our results to inform treatments in other locations will need to adjust for local biophysical conditions. When determining appropriate adjustments, information from lidar-based studies of climate, topography, and forest structure across landscapes (e.g., Jeronimo et al., 2019) may

be helpful. There is currently a need for better translation across spatial scales between canopy-focused, large-area lidar output and stem-focused, ground-based forest management. While lidar can efficiently collect data on topography, canopy height, and area-/volume-based elements of stand structure (Reutebuch et al., 2005), there are often inherent complications with distinguishing species, tree diameters, and general sub-canopy structure (Falkowski et al., 2008; Jakubowski et al., 2013; Jeronimo et al., 2018; Wiggins et al., 2019). The process of more effectively translating lidar output for future forest management may be a matter of linking it with ICO metrics from field-based studies like this one. For this purpose, we recommend that future lidar and ICO studies standardize and regularly report metrics that are comparable across both lidar and field-based methods – e.g., clump area, canopy cover, and percent of area in openings and interstitial space (Tables 3 & 5).

Overstory tree spatial patterns in frequent-fire forests are also of importance in wildlife conservation efforts (Latif et al., 2015; Perry et al., 2011; Tuten et al., 2015; Underwood et al., 2010). It may initially seem as though management for sensitive, closed-canopy species such as the California spotted owl (*Strix occidentalis occidentalis*) or Pacific fisher (*Martes pennanti*) is at odds with heterogeneous tree spatial pattern goals for fire resilience (Gaines et al., 2010). However, our research supports key strategies for managing both interests simultaneously. Multiple studies have found closed-canopy specialists to occur more often in valley sites compared to mid-slopes or ridges (Blomdahl et al., 2019; Ganey and Balda, 1989; Underwood et al., 2010), or to associate specifically with higher canopy cover of the tallest trees (North et al., 2017). Our findings indicate that ICO patterns in valleys – where on average there are higher stem densities, higher canopy cover, and more large trees compared to other topographic slope positions – may naturally support closed-canopy specialists and can therefore be managed accordingly.

Topographies where biophysical conditions and fire behavior combine to reinforce lower canopy cover and patchy forest structure (Perry et al., 2011) also provide important habitat for wildlife that are rare, fill ecosystem engineering roles, or serve as the food base for higher trophic levels in frequent-fire forests (Franklin et al., 2000; Humple and Burnett, 2010; Latif et al., 2015). For example, certain prey species for spotted owls and northern goshawks require patchy openings interspersed with dense canopy, and owls have been known to prefer open areas for hunting (Bond et al., 2009; Perry et al., 2011; Youtz et al., 2008). Our research suggests that managing within-stand spatial patterns by topography can guide a feasible overlap of species conservation goals with fire resilience goals in an age of increasing fire intensity and frequency in the Sierra Nevada.

CRedit authorship contribution statement

Jan Ng: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Malcolm P. North:** Conceptualization, Methodology, Resources, Writing - review & editing, Funding acquisition. **Alec J. Arditti:** Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Monica R. Cooper:** Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **James A. Lutz:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Data collection for this project was conducted under Yosemite National Park research study # 00603 and associated permits. Funding was provided by the University of California, Davis, the Henry A. Jastro Research Scholarship Fund, and the USDA Forest Service Pacific Southwest Research Station. The authors also gratefully acknowledge the following people: Alexandra Weill, Jessica Kathan, and Rita Loudermilk for field assistance. Anu Kramer for coding initial Python scripts for PatchMorph analysis (which we later modified). Jamie

Lydersen for consulting on PatchMorph scripts, on ArcGIS protocols for ICO analysis, and on field site selection criteria. Jay Miller and Kent van Wagtenonk for assistance with determining historical fire severity. Ben Cunningham-Summerfield and M. Kat Anderson for consulting on traditional territories and Indigenous burning practices in our study region. Derek Young and Andrew Latimer for statistics consultation on beta-regression simulation models. Grace Ha for overall statistics consultation and review of early manuscript drafts. Two additional, anonymous reviewers for providing feedback on our manuscript during the review process.

Appendix A

See [Figs. A1–A3](#) and [Tables A1–A5](#).

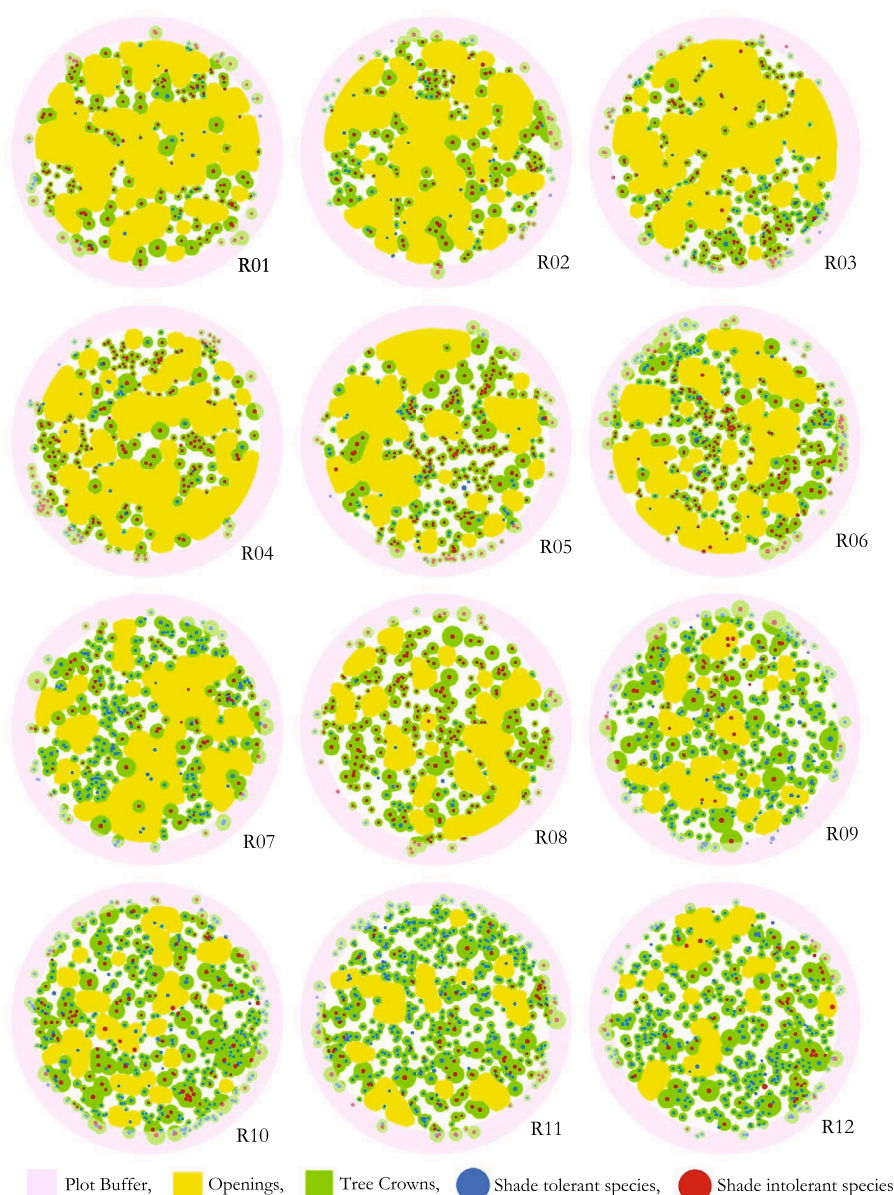


Fig. A.1. All ridge topography stem maps. White space within plot buffers is interstitial space.

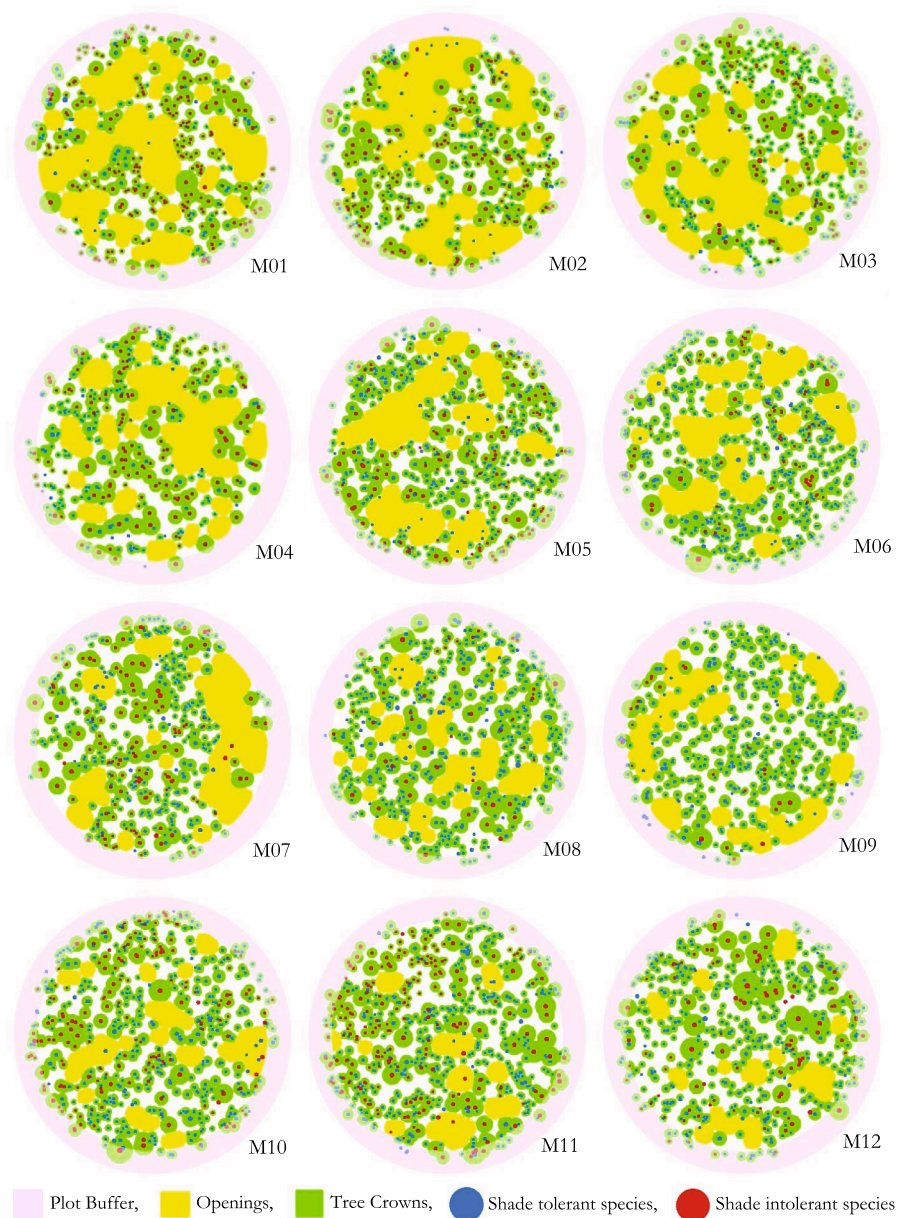


Fig. A.2. All mid-slope topography stem maps. White space within plot buffers is interstitial space.

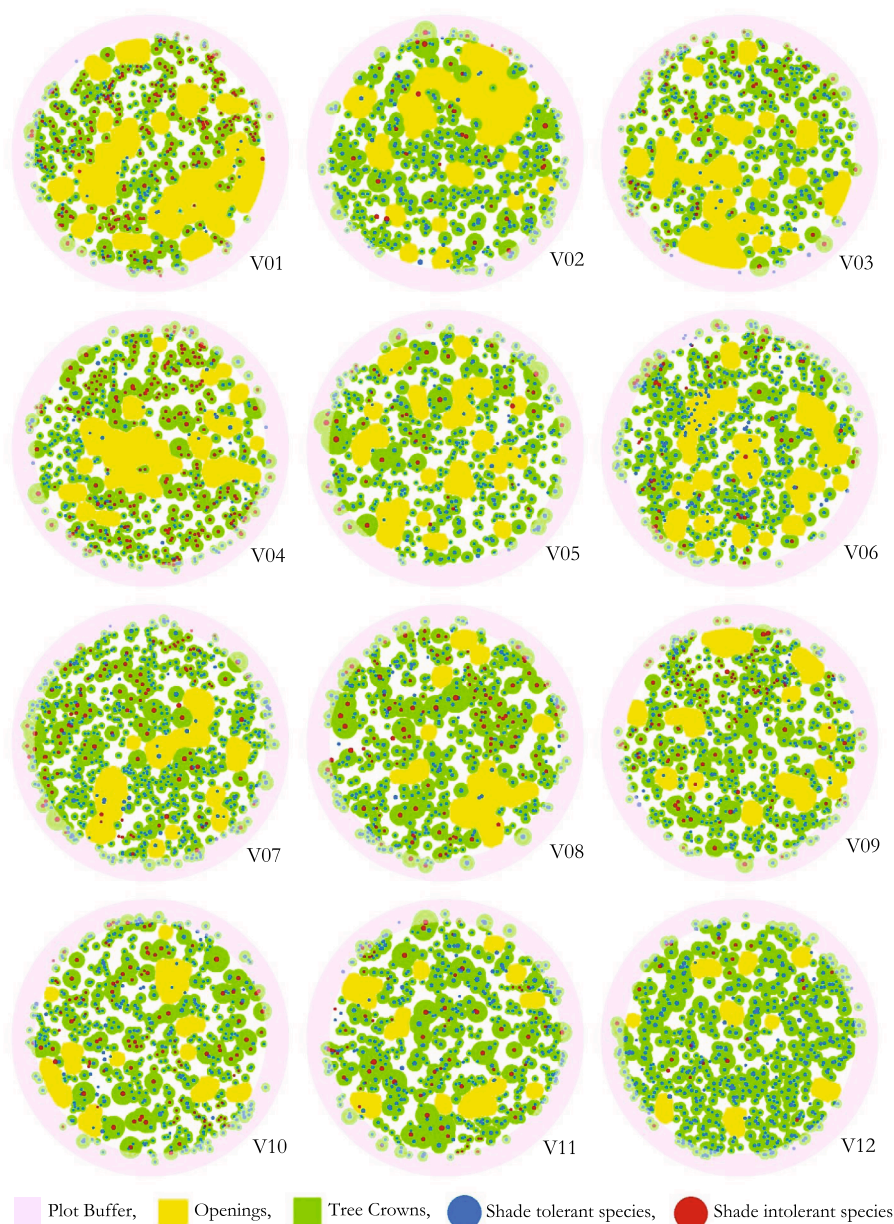


Fig. A.3. All valley topography stem maps. White space within plot buffers is interstitial space.

Table A.1
Tree species demographics pooled across all plots.

Tree species	Density (stems·ha ⁻¹)	Basal Area (m ² ·ha ⁻¹)	Shade Status
<i>Abies concolor</i>	95.9	19.10	Tolerant
<i>Calocedrus decurrens</i>	50.7	11.13	Intermediate
<i>Pinus ponderosa</i>	33.6	11.06	Intolerant
<i>Pinus lambertiana</i>	21.1	10.15	Intolerant
<i>Pinus jeffreyi</i>	8.0	3.18	Intolerant
<i>Quercus kelloggii</i>	4.2	0.45	Intolerant
<i>Abies magnifica</i>	2.6	0.54	Tolerant
<i>Quercus</i> spp.	1.3	0.18	Intolerant
<i>Pinus</i> spp.	0.6	0.41	Intolerant
<i>Quercus chrysolepis</i>	0.5	0.03	Intolerant
<i>Pseudotsuga menziesii</i>	0.2	0.07	Intermediate
<i>Alnus rubra</i>	0.2	0.01	Intermediate
Unknown	5.1	1.61	Unknown

Table A.2

Ridge topography RdNBR summary for the 2013 Rim Fire. Plot IDs match stem maps in Fig. A.1. Topography-level median, minimum, and maximum based on area-weighted averages for each plot. Plot-level area-weighted averages (by pixel, 30 m spatial resolution), minimum, and maximum based on data obtained from the U.S. Monitoring Trends in Burn Severity project (<https://www.mtbs.gov>) (Eidenshink et al., 2007). Burn severity thresholds: Increased/equivalent greenness: < 90; Low: 90 to 313; Medium: 314 to 574; High: ≥ 575 .

	Median	Minimum	Maximum
Ridge plots:	221	− 6	393
Plot ID	Weighted Avg.	Minimum	Maximum
R01	273	163	505
R02	334	195	484
R03	− 6	− 210	602
R04	275	199	452
R05	393	247	586
R06	287	85	458
R07	165	− 58	457
R08	132	33	325
R09	221	23	414
R10	130	− 9	296
R11	242	52	622
R12	202	21	512

Table A.3

Mid-slope topography RdNBR summary for the 2013 Rim Fire. Plot IDs match stem maps in Fig. A.2. Topography-level median, minimum, and maximum based on area-weighted averages for each plot. Plot-level area-weighted averages (by pixel, 30 m spatial resolution), minimum, and maximum based on data obtained from the U.S. Monitoring Trends in Burn Severity project (<https://www.mtbs.gov>) (Eidenshink et al., 2007). Burn severity thresholds: Increased/equivalent greenness: < 90; Low: 90 to 313; Medium: 314 to 574; High: ≥ 575 .

	Median	Minimum	Maximum
Mid-slope plots:	254	86	511
Plot ID	Weighted Avg.	Minimum	Maximum
M01	359	214	469
M02	173	39	462
M03	398	120	684
M04	339	174	628
M05	321	45	608
M06	131	33	395
M07	511	205	1,033
M08	173	22	369
M09	286	110	665
M10	117	11	252
M11	86	8	175
M12	158	− 16	475

Table A.4

Valley topography RdNBR summary for the 2013 Rim Fire. Plot IDs match stem maps in Fig. A.3. Topography-level median, minimum, and maximum based on area-weighted averages for each plot. Plot-level area-weighted averages (by pixel, 30 m spatial resolution), minimum, and maximum based on data obtained from the U.S. Monitoring Trends in Burn Severity project (<https://www.mtbs.gov>) (Eidenshink et al., 2007). Burn severity thresholds: Increased/equivalent greenness: < 90; Low: 90 to 313; Medium: 314 to 574; High: ≥ 575 .

	Median	Minimum	Maximum
Valley plots:	173	74	293
Plot ID	Weighted Avg.	Minimum	Maximum
V01	252	− 24	646
V02	101	24	320
V03	241	− 47	572
V04	293	50	535
V05	74	− 15	275
V06	112	8	280
V07	172	21	305
V08	185	1	545
V09	251	82	437
V10	118	9	444
V11	79	16	176
V12	203	− 8	510

Table A.5

Equations for ICO metrics (excluding standard forestry equations). Equations for medium clumps (5–9 trees) and large clumps (≥ 10 trees) were the same as for small clumps, substituting appropriate clump size. All calculations listed here were performed at the plot-level (and later averaged across topography types). All percentages were calculated as proportions, then multiplied by 100. Trees included all live and dead stems ≥ 20 cm DBH. #: number. BA: basal area. Shade-intolerants: *Pinus* and *Quercus* species. *Clump canopy area calculated as area within canopy dripline.

	Equation
Individual Trees	
<i>Diameter & Density metrics</i>	
% of total trees	total # individual trees/total # trees
% of total BA	total BA of individual trees/total plot BA
<i>Species composition (% shade-intolerants) metrics</i>	
% of total trees	total # shade-intolerant individual trees/total # trees
% w/in individuals	total # shade-intolerant individual trees/total # individual trees
Small Clumps (2–4 trees)	
<i>Diameter & Density metrics</i>	
% of total trees	total # trees in small clumps/total # trees
% of total BA	total BA of trees in small clumps/total plot BA
w/in-clump tree density	total # trees in small clumps/total canopy area of small clumps*
<i>Species composition (% shade-intolerants) metrics</i>	
% of total trees	total # shade-intolerant trees in small clumps/total # trees
% w/in clump	total # shade-intolerant trees in small clumps/total # trees in small clumps
Plot-level	
<i>Diameter & Density metrics</i>	
w/in-clump tree density	total # trees in clumps/total canopy area of clumps*
<i>Species composition (% shade-intolerants) metrics</i>	
% of total trees	total # shade-intolerant trees/total # trees
<i>Frequency of openings & Percent area metrics</i>	
% Area - opening	total area in PatchMorph-determined openings/total plot area
% Area - canopy cover	total canopy area*/total plot area
% Area - interstitial space	100% – % area in openings – % canopy cover

Appendix B. Supplementary material

Supplementary text to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118220>.

References

- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of south-western ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12 (5), 1418–1433.
- Anderson, M.K., 1993. Indian fire-based management in the sequoia-mixed conifer forests of the central and southern Sierra Nevada. Final report to the Yosemite Research Center, Yosemite National Park. United States Department of Interior. National Park Service. Western Region. Cooperative Agreement Order Number 8027-002.
- Anderson, M.K., Moratto, M.J., 1996. Native American Land-Use Practices and Ecological Impacts. Chapter 9, Pages 187 – 206 in Sierra Nevada Ecosystem Project, Final Report to Congress, vol. 2: Assessments and Scientific Basis for Management Options. Wildland Resources Center Report No. 37. Davis: University of California, Centers for Water and Wildland Resources.
- Apigian, K.O., Dahlsten, D.L., Stephens, S.L., 2006. Fire and fire surrogate treatment effects on leaf litter arthropods in western Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 221, 110–112.
- Barth, M.A., 2014. Use of a Forest Reconstruction Model to Assess Changes to Sierra Nevada Mixed-Conifer Forest Conditions During the Fire Suppression Era (Master's thesis). University of Montana, Missoula, Montana.
- Barth, M.A., Larson, A.J., Lutz, J.A., 2015. A forest reconstruction model to assess changes to Sierra Nevada mixed-conifer forest during the fire suppression era. *For. Ecol. Manage.* 354, 104–118.
- Bates, C.D., Lee, M.J., 1990. Tradition and innovation: a basket history of the Indians of the Yosemite-Mono Lake area. Yosemite Assn.
- Beatty, M.R., Taylor, A.H., 2007. Fire disturbance and forest structure in old-growth mixed conifer forests in the northern Sierra Nevada, California. *J. Vegetation Sci.* 18 (6), 879–890.
- Bechtold, W.A., 2004. Largest-crown-width prediction models for 53 species in the western United States. *West. J. Appl. For.* 19 (4), 245–251.
- Blondahl, E.M., Thompson, C.M., Kane, J.R., Kane, V.R., Churchill, D.J., Moskal, L.M., Lutz, J.A., 2019. Forest structure predictive of fisher (*Pekania pennanti*) dens exists in recently burned forest in Yosemite, California, USA. *Forest Ecology and Management* 444, 174–186. <https://doi.org/10.1016/j.foreco.2019.04.024>.
- Bond, M.L., Lee, D.E., Siegel, R.B., Ward Jr, J.P., 2009. Habitat use and selection by California spotted owls in a postfire landscape. *J. Wildl. Manag.* 73 (7), 1116–1124.
- CalFire, 2019. Top 20 Largest California Wildfires. Accessed at < https://www.fire.ca.gov/media/5510/top20_acres.pdf > on 21 July 2019.
- Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *For. Ecol. Manage.* 291, 442–457.
- Clyatt, K.A., Crotteau, J.S., Schaedel, M.S., Wiggins, H.L., Kelley, H., Churchill, D.J., Larson, A.J., 2016. Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. *For. Ecol. Manage.* 361, 23–37.
- Collins, B.M., Everett, R.G., Stephens, S.L., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2 (4), art51.
- Conkle, M.T., Critchfield, W.B., 1988. Genetic variation and hybridization of ponderosa pine. In: *Ponderosa Pine: the species and its management*. Washington State University Cooperative Extension, pp. 27–43.
- Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. *J. Stat. Softw.* 34 (2), 1–24.
- Dowle, M., Srinivasan, A., 2019. data.table: Extension of 'data.frame'. R package version 1.12.2.
- Dragulescu, A.A., 2014. xlsx: Read, write, format Excel 2007 and Excel 97/2000/XP/

- 2003 files. R package version 0.5.7.
- Dubayah, R., Rich, P.M., 1995. Topographic solar radiation models for GIS. *Int. J. Geograph. Inform. Syst.* 9 (4), 405–419.
- Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.L., Quayle, B., Howard, S., 2007. A project for monitoring trends in burn severity. *Fire Ecol.* 3 (1), 3–21.
- Esri, 2016. ArcGIS Desktop v10.5. Environmental Systems Research Institute, Redlands, CA.
- Falkowski, M.J., Smith, A.M., Gessler, P.E., Hudak, A.T., Vierling, L.A., Evans, J.S., 2008. The influence of conifer forest canopy cover on the accuracy of two individual tree measurement algorithms using lidar data. *Can. J. Remote Sens.* 34 (sup2), S338–S350.
- Fox, J., Weisberg, S., 2011. *An R Companion to Applied Regression*, second ed. Sage, Thousand Oaks CA.
- Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol. Monogr.* 70 (4), 539–590.
- Fricker, G.A., Synes, N.W., Serra-Diaz, J.M., North, M.P., Davis, F.W., Franklin, J., 2019. More than climate? Predictors of tree canopy height vary with scale in complex terrain, Sierra Nevada, CA (USA). *For. Ecol. Manage.* 434, 142–153.
- Fry, D.L., Stephens, S.L., Collins, B.M., North, M.P., Franco-Vizcaino, E., Gill, S.J., 2014. Contrasting spatial patterns in active-fire and fire-suppressed mediterranean climate old-growth mixed conifer forests. *PLoS ONE* 9 (2), e88985.
- Fulé, P.Z., 2008. Does it make sense to restore wildland fire in changing climate? *Restor. Ecol.* 16 (4), 526–531.
- Gaines, W.L., Harrod, R.J., Dickinson, J., Lyons, A.L., Halupka, K., 2010. Integration of Northern spotted owl habitat and fuels treatments in the eastern Cascades, Washington, USA. *For. Ecol. Manage.* 260 (11), 2045–2052.
- Ganey, J.L., Balda, R.P., 1989. Distribution and habitat use of Mexican spotted owls in Arizona. *The Condor* 91 (2), 355–361.
- Gill, S.J., Biging, G.S., Murphy, E.C., 2000. Modeling conifer tree crown radius and estimating canopy cover. *For. Ecol. Manage.* 126 (3), 405–416.
- Girvetz, E.H., Greco, S.E., 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. *Landscape Ecol.* 22 (8), 1131–1142.
- Harmon, M.E., Sexton, J., 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. LTER Network Office: University of Washington, Seattle, WA, USA.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *For. Ecol. Manage.* 114 (2), 433–446.
- Hessburg, P.F., Spies, T.A., Perry, D.A., Skinner, C.N., Taylor, A.H., Brown, P.M., Stephens, S.L., Larson, A.J., Churchill, D.J., Povak, N.A., Singleton, P.H., 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *For. Ecol. Manage.* 366, 221–250.
- Holden, Z.A., Jolly, W.M., 2011. Modeling topographic influences on fuel moisture and fire danger in complex terrain to improve wildland fire management decision support. *For. Ecol. Manage.* 262 (12), 2133–2141.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. *Biometrical J.* 50 (3), 346–363.
- Humple, D.L., Burnett, R.D., 2010. Nesting ecology of Yellow Warblers (*Dendroica petechia*) in montane chaparral habitat in the northern Sierra Nevada. *Western North Am. Naturalist* 70 (3), 355–363.
- Hurteau, M., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front. Ecol. Environ.* 7 (8), 409–414.
- Jakubowski, M., Li, W., Guo, Q., Kelly, M., 2013. Delineating individual trees from LiDAR data: A comparison of vector-and raster-based segmentation approaches. *Remote Sens.* 5 (9), 4163–4186.
- Jeronimo, S.M., Kane, V.R., Churchill, D.J., Lutz, J.A., North, M.P., Asner, G.P., Franklin, J.F., 2019. Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada. *For. Ecol. Manage.* 437, 70–86.
- Jeronimo, S.M., Kane, V.R., Churchill, D.J., McGaughey, R.J., Franklin, J.F., 2018. Applying LiDAR individual tree detection to management of structurally diverse forest landscapes. *J. Forest.* 116 (4), 336–346.
- Kane, V.R., Lutz, J.A., Cansler, C.A., Povak, N.A., Churchill, D.J., Smith, D.F., Kane, J.T., North, M.P., 2015. Water balance and topography predict fire and forest structure patterns. *Forest Ecol. Manage.* 338, 1–13.
- Keifer, M., van Wagtenonk, J.W., Buhler, M., 2006. Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the central and southern Sierra Nevada, CA (USA). *Fire Ecol.* 2 (1), 53–72.
- Kilgore, B.M., Taylor, D., 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60 (1), 129–142.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understorey change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 310, 903–914.
- Koontz, M.J., North, M.P., Werner, C.M., Fick, S.E., Latimer, A.M., 2020. Local forest structure variability increases resilience to wildfire in dry western US coniferous forests. *Ecol. Lett.* 23 (3), 483–494.
- Larson, A.J., Belote, R.T., Cansler, C.A., Parks, S.A., Dietz, M.S., 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecol. Appl.* 23 (6), 1243–1249.
- Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manage.* 267, 74–92.
- Latif, Q.S., Saab, V.A., Mellen-Mclean, K., Dudley, J.G., 2015. Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forest. *J. Wildl. Manage.* 79 (2), 263–273.
- Lewis, H., 1973. *Patterns of Indian Burning in California: Ecology and Ethnohistory*. Ballena Press, Ramona.
- Lydersen, J., North, M., 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15 (7), 1134–1146.
- Lydersen, J.M., North, M.P., Collins, B.M., 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328, 326–334.
- Lydersen, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. *For. Ecol. Manage.* 304, 370–382.
- Lutz, J.A., van Wagtenonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *J. Biogeogr.* 37, 936–950.
- Mangiafico, S., 2019. rcompanion: Functions to Support Extension Education Program Evaluation. R package version 2 (1), 7.
- McKelvey, K.S., Skinner, C.N., Chang, C., Erman, D.C., Husari, S.J., Parsons, D.J., van Wagtenonk, J.W., Weatherspoon, C.P., 1996. An overview of fire in the Sierra Nevada. Pages 1033–1040 in *Sierra Nevada ecosystem project: final report to Congress, vol.2: Assessments and Scientific Basis for Management Options*. Wildland Resources Center Report No. 37. Davis, California: University of California, Centers for Water and Wildland Resources.
- Miller, J.D., Thode, A.E., 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sens. Environ.* 109 (1), 66–80.
- Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G., 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. *J. Forest.* 107 (8), 391–397.
- Moustakas, A., 2015. Fire acting as an increasing spatial autocorrelation force: Implications for pattern formation and ecological facilitation. *Ecol. Complexity* 21, 142–149.
- North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. *Can. J. For. Res.* 37 (2), 331–342.
- North, M.P., Kane, J.T., Kane, V.R., Asner, G.P., Berigan, W., Churchill, D.J., Conway, S., Gutiérrez, R.J., Jeronimo, S., Keane, J., Koltunov, A., 2017. Cover of tall trees best predicts California spotted owl habitat. *For. Ecol. Manage.* 405, 166–178.
- North, M., Sherlock, J., 2012. Marking and assessing forest heterogeneity. In: M. North (ed.) *Managing Sierra Nevada Forests*. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-237, pp. 95–105.
- Parker, A.J., 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Phys. Geogr.* 3, 160–168.
- Pawlikowski, N.C., Coppoletta, M., Knapp, E., Taylor, A.H., 2019. Spatial dynamics of tree group and gap structure in an old-growth ponderosa pine-California black oak forest burned by repeated wildfires. *For. Ecol. Manage.* 434, 289–302.
- Perry, D.A., Hessburg, P.F., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J.F., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *For. Ecol. Manage.* 262 (5), 703–717.
- Pettit, N.E., Naiman, R.J., 2007. Fire in the riparian zone: characteristics and ecological consequences. *Ecosystems* 10 (5), 673–687.
- Pielou, E.C., 1962. The use of plant-to-neighbour distances for the detection of competition. *J. Ecol.* 357–367.
- Plotkin, J.B., Chave, J., Ashton, P.S., 2002. Cluster analysis of spatial patterns in Malaysian tree species. *Am. Nat.* 160 (5), 629–644.
- R Core Team, 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reutebuch, S.E., Andersen, H.E., McGaughey, R.J., 2005. Light detection and ranging (LiDAR): an emerging tool for multiple resource inventory. *J. Forest.* 103 (6), 286–292.
- Roccaforte, J.P., Fule, P.Z., Covington, W.W., 2010. Monitoring landscape-scale ponderosa pine restoration treatment implementation and effectiveness. *Restor. Ecol.* 18 (6), 820–833.
- Rodman, K.C., Sánchez Meador, A.J., Huffman, D.W., Waring, K.M., 2016. Reference conditions and historical fine-scale spatial dynamics in a dry mixed-conifer forest, Arizona, USA. *Forest Sci.* 62 (3), 268–280.
- Rothman, H.K., 2007. *Blazing heritage: a history of wildland fire in the National Park Service*. Oxford University Press, New York, NY.
- RStudio Team, 2018. *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Sánchez Meador, A.J., Parysow, P.F., Moore, M.M., 2011. A new method for delineating tree patches and assessing spatial reference conditions of ponderosa pine forests in northern Arizona. *Restor. Ecol.* 19 (4), 490–499.
- Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecol. Appl.* 20 (2), 362–380.
- Show, S.B., Kotok, E.I., 1924. The role of fire in the California pine forests. *USDA Depart. Bull.* 1294, 80 pp.
- Shreve, F., 1931. Physical conditions in sun and shade. *Ecology* 12 (1), 96–104.
- Skinner, C.N., Chang, C.R., 1996. Fire regimes, past and present. *Sierra Nevada ecosystem project: final report to Congress, vol.2: Assessments and Scientific Basis for Management Options*. Wildland Resources Center Report No. 37. Wildland Resources Center Report No. 37. Davis: University of California, Centers for Water and Wildland Resources, Davis, California, pp. 1041–1069.
- Skinner, C.N., Taylor, A.H., 2006. Southern cascades bioregion. In: Sugihara, N.G., VanWagtenonk, J.W., Fites-Kaufman, J., Shaffer, K.E., & Thode, A.E. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, pp. 195–224.
- Stephens, S.L., Fry, D.L., Franco-Vizcaino, E., 2008. Wildfire and spatial patterns in forests in northwestern Mexico: the United States wishes it had similar fire problems. *Ecol. Soc.* 13 (2), 10.
- Stephens, S.L., Moghaddas, J.J., 2005. Experimental fuel treatment impacts on forest

- structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *For. Ecol. Manage.* 215 (1–3), 21–36.
- Stephens, S.L., Ruth, L.W., 2005. Federal Forest-Fire Policy in the United States. *Ecol. Appl.* 15, 532–542.
- Sugihara, N.G., van Wagtendonk, J.W., Fites-Kaufman, J., 2006. Fire as an Ecological Process. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, California, pp. 58–73.
- Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *J. Veg. Sci.* 21 (3), 561–572.
- Thaxton, J.M., Platt, W.J., 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. *Ecology* 87 (5), 1331–1337.
- Tuten, M.C., Meador, A.S., Fulé, P.Z., 2015. Ecological restoration and fine-scale forest structure regulation in southwestern ponderosa pine forests. *For. Ecol. Manage.* 348, 57–67.
- Underwood, E.C., Viers, J.H., Quinn, J.F., North, M., 2010. Using topography to meet wildlife and fuels treatment objectives in fire-suppressed landscapes. *Environ. Manage.* 46 (5), 809–819.
- Urban, D.L., Miller, C., Halpin, P.N., Stephenson, N.L., 2000. Forest gradient response in Sierran landscapes: the physical template. *Landsc. Ecol.* 15 (7), 603–620.
- Van de Water, K.M., Safford, H.D., 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecol.* 7 (3), 26–58.
- van Wagtendonk, J.W., 2006. Fire as a physical process. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, California, pp. 38–57.
- van Wagtendonk, J.W., Lutz, J.A., 2007. Fire regime attribute of wildland fires in Yosemite National Park, USA. *Fire Ecol.* 3, 34–52.
- Walker, B., Holling, C.S., Carpenter, S.R., Kinzig, A., 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecol. Soc.* 9 (2), 5.
- Webster, K.M., Halpern, C.B., 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* 1 (5), 1–27.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4 (43), 1686. <https://doi.org/10.21105/joss.01686>.
- Wiggins, H.L., Nelson, C.R., Larson, A.J., Safford, H.D., 2019. Using LiDAR to develop high-resolution reference models of forest structure and spatial pattern. *For. Ecol. Manage.* 434, 318–330.
- Wickham, H., 2011. The Split-Apply-Combine Strategy for Data Analysis. *J. Stat. Softw.* 40 (1), 1–29.
- Wickham, H., François, R., Henry, L., Müller, K., 2018. dplyr: A Grammar of Data Manipulation. R package version 0.7.5.
- Youtz, J.A., Graham, R.T., Reynolds, R.T., Simon, J., 2008. Implementing northern goshawk habitat management in Southwestern forests: a template for restoring fire-adapted forest ecosystems. In: *Integrated restoration of forested ecosystems to achieve multiresource benefits: Proceedings of the 2007 national silviculture workshop*. Gen. Tech. Rep. PNW-GTR-733, vol. 733. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 173–191.
- Zeileis, A., Hothorn, T., 2002. Diagnostic Checking in Regression Relationships. *R News* 2 (3), 7–10.
- Ziegler, J.P., Hoffman, C., Battaglia, M., Mell, W., 2017. Spatially explicit measurements of forest structure and fire behavior following restoration treatments in dry forests. *For. Ecol. Manage.* 386, 1–12.