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# Where are the large trees? A census of Sierra Nevada large trees to determine their frequency and spatial distribution across three large landscapes

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ABSTRACT

Large trees (≥76.2 cm/≥30″ DBH) and especially very large trees (≥101.6 cm/≥40″ DBH) are key structures of Sierra Nevada forests for their ecological function, habitat, and carbon storage. Many of these trees have been lost to historic harvest and more recently to drought and wildfires. Understanding the current frequency and distribution of these large trees is essential to understanding their ecological contribution and management needs. We used airborne lidar to census large trees across three Sierra Nevada landscapes (cumulatively 396 K ha) in lower (dominated by ponderosa pine and mixed conifer) and upper (dominated by red fir) montane forest zones. We used data from a network of Forest Inventory and Analysis (FIA) plots to interpret our lidar-based results for large tree frequency, species, and ages. The lidar data identified > 8 M large and > 2.7 M very large trees, and their mean densities were similar to those from FIA data. Large portions of our study areas had either no or low densities (<20) of large trees per hectare. We found that large and very large tree concentrations were spatially aggregated with most in denser patches containing 20 to 50 + large trees per hectare. Depending on the study area, these often sizable (>1000 ha) patches of dense large trees can cover 20% to 40% of the landscape. (Patches of denser very large trees cover less of the landscape, typically 5% to 10%). However, these large patches are rarely simple blocks. Instead, they typically form complex amorphous matrices interspersed with patches of forests containing shorter trees or non-forest cover. Crucially, almost all large trees were in stands with high canopy cover, suggesting horizontal fuel continuity and low resilience to future wildfires. For lower montane large trees, canopy cover versus large tree density showed almost a unimodal response with canopy cover of 60% to 80% for locations with > 20 large trees per ha. For upper montane large trees, canopy cover versus large tree density showed a more linear relationship for all three study areas. High levels of canopy cover, especially for lower montane forests, suggest settings in which infilling following decades of fire suppression have created overly dense stands with lower resilience to drought and wildfire. Other studies have documented substantial recent losses of these large trees to both factors. The high canopy cover within which almost all large trees exist emphasizes the need for treatment almost everywhere that large trees are present for lower montane forests. This likely will require treatments both within the stands that contain large trees and across the landscapes in which they are found.

## 1. Introduction

In many forested biomes across the world, the largest trees are key anchors of ecosystem structure and function (Lutz et al., 2018). One or more tree species in these biomes have the genetic capability and sufficient time between disturbances to achieve large size (Lindenmayer and Laurance, 2017; Lutz et al., 2018). Generally, the largest trees numerically represent a small fraction of the total tree count, but they collectively comprise most of the local biomass and are defining structural elements (Lutz et al., 2012, 2018). These keystone structures

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modify the local microclimate, provide habitats essential to wildlife species, and influence the patterns of stand composition, tree regeneration, and forest succession (Ali et al., 2019; de Lima et al., 2022; Hessburg et al., 2020; Keeton and Franklin, 2005; Lindenmayer and Laurance, 2017; Lutz et al., 2018; Menshah et al., 2020; Mildrexler et al., 2020; North et al., 2017). Across much of the world, however, the abundance of large trees has been severely reduced over the past century through harvests and land use conversion (Lindenmayer et al., 2012; McIntyre et al., 2015; Thomas et al., 2006). In many cases, the forests containing these trees have been lost through conversion to other uses such as development, farming, or ranching (Ellison et al., 2005; Thomas et al., 2006). Where forests remain, much of the original population of large trees have been harvested, with large trees often remaining only in scattered forest fragments or within designated preserves (Lindenmayer and Laurance, 2017).

These trends also are present in the forested landscapes of the Sierra Nevada, California. The Mediterranean climate and high productivity conditions of the region provide ample growing conditions for some of the world's largest and oldest conifer trees (Kelly and Goulden, 2016; Sugihara et al., 2006). Historical accounts and early forest surveys documented a forested landscape in which large trees with diameters at breast height (DBH) as large as 1.5 m to 2.4 m were reported with more common examples of the larger cohort of trees ranging from 90 cm to 210 cm DBH (Lieberg, 1902; Stephens et al., 2005; Safford and Stevens, 2017).

Today, Sierran forests, which were historically dominated by large trees, have been profoundly restructured. A combination of decades of harvests, fire suppression, and mortality from mass wildfires and drought-induced bark beetle outbreaks have significantly reduced the density and distribution of large trees (Collins et al., 2011; Cova et al., 2023; Franklin and Fites-Kaufmann, 1996; Knapp et al., 2013; McIntyre et al., 2015; Safford and Stevens, 2017; Stephens et al., 2018). Historical logging practices removed large trees across the Sierra Nevada through clearcutting (regeneration harvests) and selective cutting of the largest trees (high grading) (Barbour et al., 1993; Beesley, 1996; McKelvey and Johnston, 1992). As an example of the magnitude of loss, a survey of the historically heavily harvested 82,000 ha Lake Tahoe basin found just 38 surviving old-growth fragments with a mean area of just 25 ha each (Barbour et al., 2002). Where large trees did persist, interruption of Indigenous burning practices and fire suppression has allowed extensive ingrowth leading to historically unprecedented tree densities that increase competitive pressure on existing large trees and make them more susceptible to severe fire (Collins et al., 2011; Knapp et al., 2013; Lydersen et al., 2013). As a result, even in areas that did not experience harvests, the density of large trees appears to have declined severely from combined mortality from wildfires, insects, pathogens, and drought stress (North et al., 2022; Safford and Stevens, 2017; Schwartz et al., 2015; Steel et al., 2021, 2023). Researchers in one study estimated that these factors cumulatively led to the loss of at least 50% of the population of trees $\geq$ 60 cm DBH across the Sierra Nevada since the 1930s (McIntyre et al., 2015) (and many large trees would have been harvested before the 1930s).

However, the story of the current population of large trees in the Sierra Nevada isn't just one of loss. In this highly productive ecoregion, many trees that germinated after initial early harvests have grown to substantial sizes within the decades since fire suppression began in the early 20th century (North et al., 2005; Zald et al., 2022). This has allowed substantial numbers of the fire-intolerant but shade-tolerant species such as white fir (*Abies concolor*) to establish, skewing the species composition of large trees from their historic proportions (North et al., 2007). Because of the presence of large numbers of just decades-old large white fir, many Sierra Nevada ecologists and forest managers distinguish between simply large trees (commonly defined as $\geq$ 76.2 cm or 30 in. DBH) and very large ($\geq$101.6 cm or 40 in. DBH) trees that are more likely to be legacy trees not harvested in the historic period (Collins et al., 2011).

Conservation of large trees has become a central tenet of federal agencies such as the Forest Service and National Park Service that manage a large portion of the forests in this ecoregion (USDA Forest Service, 2023). Operating on the premise that large trees are now rare, federal agencies have applied a "30-inch rule" (76.2 cm DBH) since the 1990's, mandating that trees 30 in. or larger cannot be cut as part of forest management operations regardless of the stand conditions in which they are found (Verner 1992). However, the continuing loss of large trees to drought and wildfire suggests that the context in which these large trees are found is integral to developing effective management strategies designed to protect them (North et al., 2022; Safford and Stevens, 2017; Steel et al., 2021, 2023). Are they found in dense, overstocked stands that would leave them at risk from water stress in droughts or high severity fires? Do managers need to develop plans for populations of large trees dispersed across landscapes or aggregated in large blocks of potentially older and mature forests?

Efforts to map locations of primary forests in the Sierra Nevada have continued from at least the 1940 s to today (Beardsley, 1999; Franklin and Fites-Kaufmann, 1996; USDA Forest Service, 2023). However, the methods to identify these require extrapolating characteristics of known locations of forests that possessed several characteristics of primary forest structure – of which large trees would be just one – using indirect measures of forest structure such as Landsat satellite spectral imagery or geospatial datasets (Barnett et al., 2023; DellaSala et al., 2022; USDA Forest Service, 2023). The methods would neither map variations in densities of large trees within identified primary forest stands nor find the potentially numerous younger large trees found in previously harvested areas that add to local forest structure and could develop into future mature and primary forest stands (Lindenmayer and Laurance, 2017; Lindenmayer, 2017).

Airborne lidar data systematically measures canopy heights over large areas, enabling the direct detection of individual large trees across those areas (Jeronimo et al., 2018; Kramer et al., 2016). With these data, we can directly examine entire landscapes for large trees to determine their frequency, stand setting, and spatial distribution and to use allometric relationships to estimate diameters at breast height (Gorgens et al., 2019; Jeronimo et al., 2018; Jucker et al., 2017; Lines et al., 2022; Zolkos et al., 2013). In this study, we conducted a census of large ($\geq$76.2 cm) and very large ($\geq$101.6 cm) DBH trees using airborne lidar across three large Sierra Nevada landscapes. We investigated the prevalence of these trees, their stand context, and their spatial distribution by addressing these questions:

- What is the frequency of large and very large trees?
- What are the stand and patch characteristics in which these trees are found?
- What do these patterns suggest for future management needs?

## 2. Methods

We used the same methods to separately analyze large and very large tree populations. However, for brevity, we refer to only large trees in the following text.

### *2.1. Study areas*

Our study areas are two key forest zones within three large landscapes in the Sierra Nevada, California (Fig. 1) with airborne lidar data including the Tahoe and portions of the Sierra National Forests and Yosemite National Park. We analyzed a subset of the lidar coverage that included all federal and adjacent state and locally-owned protected areas (with the federal lands constituting the vast majority of the study areas). The forests included in our study areas sample a significant latitudinal gradient of the ecoregion and have experienced a range of harvests and other human management and ecological alteration by policies of fire suppression and fire management (see Discussion Section

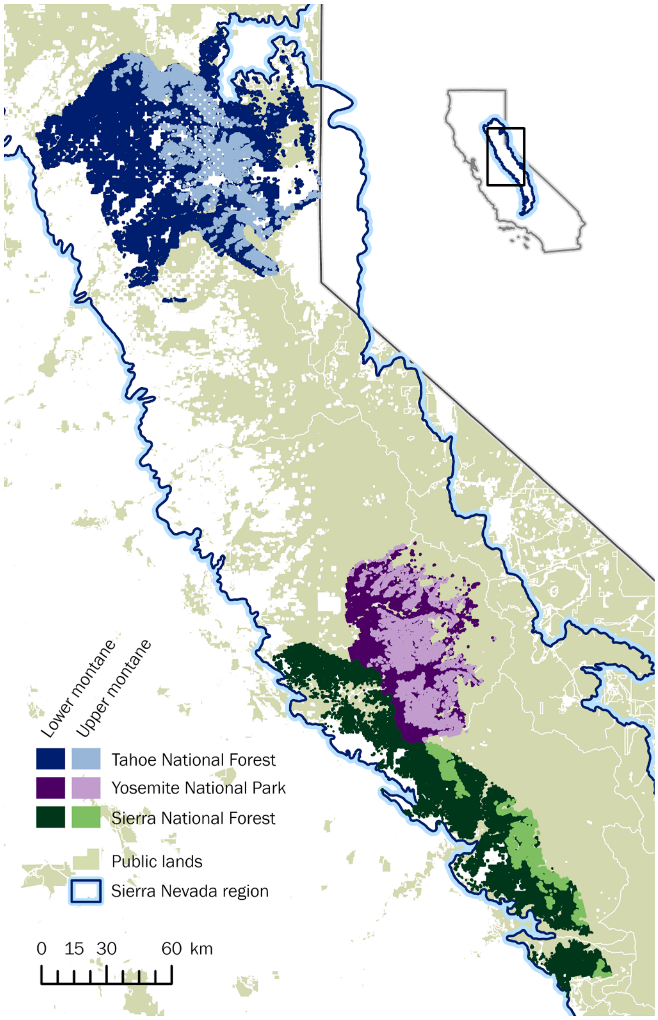


**Fig. 1.** The Tahoe, Yosemite, and southern Sierra areas used in this study with areas of the low and high montane forest zones shown. Study areas are based on airborne lidar acquisitions that were focused on the Tahoe and Sierra National Forests and Yosemite National Park, but we included additional publicly owned federal, state, and local properties within the footprints of the lidar acquisitions. Online interactive maps available at https://arcg.is/8LfW9.

4.2). The study areas are located on the western slope of the Sierra Nevada, which experiences a Mediterranean climate with 85% of the annual precipitation occurring as snow, increasing with elevation, and an annual summer drought (North et al., 2016). The distribution of forest types along the western slope is strongly associated with elevational gradients, emerging from oak woodlands in lower elevations and blending into alpine meadows or rock outcrops at higher elevations (van Wagtendonk and Fites-Kaufmann, 2006).

Within our study areas, we analyzed two forest zones (van Wagtendonk and Fites-Kaufmann, 2006) in our three study areas (Table 1): 1) the lower montane zone dominated by ponderosa pine (*Pinus ponderosa*) and mixed conifer composed of ponderosa pine, sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and Jeffrey pine (*Pinus jeffreyi*); 2) the upper montane zone dominated by red fir (*Abies magnifica*). A third zone, subalpine forests with multiple tree species including the Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), had extensive airborne lidar coverage only in Yosemite National Park. We also analyzed this zone in the park and present partial results in the online supplement. We identified locations of these forest zones in our study areas using the California Department of Forestry and Fire Protection (Cal Fire) FVEG map of Sierra Nevada vegetation cover (https://map.dfg.ca.gov/metadata/ds1327.html, accessed June 2021): lower montane vegetation cover classes: Douglas-fir, ponderosa pine, white fir, Sierran mixed conifer, Jeffrey pine; upper montane vegetation classes: red fir, juniper. We identified ownership using the California Protected Areas Database (https://www.calands.org/, version 2021b accessed February 2023).

**Table 1**
Sizes of datasets in hectares for lidar data and numbers of USDA Forest Inventory Assessment (FIA) plots for the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest Study (SNF) study areas. The study areas were centered on the national forests and park for which each lidar acquisition was acquired, but other public forested land inside the lidar footprint were also included.

| Lower Montane Study Area | Size (ha) | Study Area FIA Plots (n) |
|---|---|---|
| TNF | 156,615 | 100 |
| YNP | 73,663 | 57 |
| SNF | 94,076 | 50 |
| **Upper Montane Study Area** | **Size (ha)** | **Study Area FIA Plots (n)** |
| TNF | 31,387 | 19 |
| YNP | 23,422 | 7 |
| SNF | 17,361 | 11 |

## 2.2. FIA field data

Because an airborne lidar census of large trees is novel, we used data from the USDA Forest Service's Forest Inventory Analysis (FIA) program to interpret our airborne lidar-based results (Bechtold and Patterson, 2005; Smith, 2002; USDA Forest Service, 2022; https://experience.arcgis.com/experience/3641cea45d614ab88791aef54f3a1849/, accessed October 2019). The FIA program has a nationwide set of field plots used to monitor broad-scale forest inventory trends across the United States. Actual locations of FIA field plots are confidential. The Forest Service provides "jittered" plot coordinates to show approximate locations, which we used. We included data from all 244 FIA plots whose publicly available coordinates fell within our study areas (Table 1). From the FIA database, we examined the frequency of large and very large trees, the species of these trees, and tree ages for a field crew-selected sample of these trees.

We also used the FIA data to develop allometric equations to relate our airborne lidar-measured tree heights to DBH. For this, we used a larger sample of 1377 plots with reported public coordinates within a 2 km buffered extent around our study areas (which also made available substantial private inholdings within our study areas). At each plot, a representative (but not statistically random) selection of trees have both their DBH and heights measured. To reflect climate and productivity gradients within our large study areas, we also developed separate allometric models for eighteen of the nineteen Sierra Nevada climate classes identified by Jeronimo et al. (2019) defined on patterns of actual evapotranspiration, climatic water deficit, and January minimum temperature that intersected the study areas. We developed 56 height-to-DBH linear regression models specific to climate classes within each study area with coefficients of determination ranging from 0.57 to 0.86

**Table 2**
Summary statistics for the tree height in meters needed to produce a minimum modeled DBH of 76.2 cm or 101.6 cm (large and very large trees, respectively) using allometric equations derived from FIA field data. Results based on 56 combinations of study areas and climate zones (Jeronimo et al., 2019). Supplement Figs. 1 and 2 provide results for each study area and climate zone combination.

| DBH | 76.2 cm | 101.6 cm |
|---|---|---|
| Minimum (m) | 21.1 | 25.5 |
| Mean (m) | 32.4 | 40.2 |
| Maximum (m) | 45.4 | 55.5 |
| St. Dev. (m) | 4.7 | 5.8 |

with a mean of 0.73 (details on each model presented in the online supplement). For portions of our study area that do not intersect one of the climate classes, we developed separate allometric models for each study area as a whole, with separate models for the two lidar acquisition areas used for the Tahoe study area. We found that the tree heights associated with large and very large tree DBH cutoffs varied considerably based on climate zone and study area (Table 2, Supplement Figs. 1 and 2).

## 2.3. Lidar large tree identification

High density airborne lidar data were acquired across all three of our study sites in the past decade (Table 3). We created canopy height models (CHMs) for the study areas using the US Forest Service's FUSION Lidar Toolkit (McGaughey, 2022). Lidar return heights were normalized to height above ground using the vendor-delivered 1 m resolution ground models for the Tahoe study area and created using the FUSION toolkit for the Yosemite and Sierra study areas. The CHMs were created as a 0.75 m resolution raster in which each cell took on the height of the highest lidar return in each cell. The CHM was smoothed with a 3x3 cell mean filter to remove noise and to improve overstory tree detection (Jeronimo, 2015, Jeronimo et al., 2018).

The FUSION TreeSeg utility identified individual overstory trees from the CSM using an implementation of the watershed transform algorithm (McGaughey, 2022; Vincent and Soille, 1991). This algorithm is computationally efficient to run over large areas and has been shown to have high accuracy approaching 90% for identification of tall trees in Sierra Nevada forests (Jeronimo, 2015, Jeronimo et al., 2018). CSM grid cells with a height $< 2$ m were not used in the tree identification to exclude shrubs, shorter trees, and ground clutter from the tree identification. The watershed transform algorithm, like almost all lidar tree identification algorithms, identifies overstory trees directly visible to the lidar instrument. Subordinate trees, which often are the most numerous on a site, are not detected. For each identified tree, the TreeSeg utility

**Table 3**
Airborne lidar acquisitions used in this study for the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest Study (SNF) study areas. Lidar vendors are the National Center for Airborne Laser Mapping (NCALM; ncalm.cive.uh.edu) and NV5 Geospatial (www.nv5.com/geospatial/technology/lidar/). Table 1 shows the area of the portions of the acquisitions used in the study.

| Study area | Acquisition years | Vendor | Mean pulse density ($m^2$) |
|---|---|---|---|
| TNF | 2013 & 2014 | NCALM | 7.2 & 7.0 |
| YNP | 2019 | NV5 | 23.5 |
| SNF | 2020 | NV5 | 22.0 |

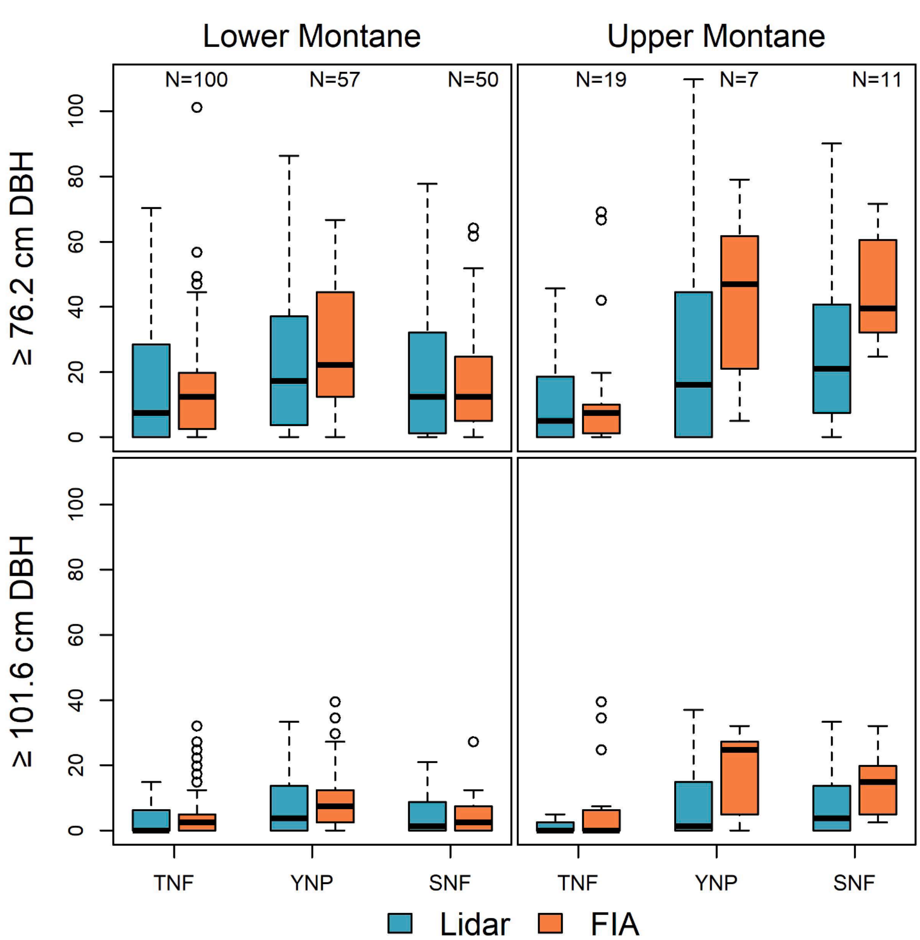


**Fig. 2.** Large (≥76.2 cm DBH) and very large tree (≥101.6 cm DBH) trees per ha from USDA Forest Service Forest Inventory Analysis (FIA) plots and overstory trees identified from airborne lidar data by forest zone and study area. Numbers of FIA plots used is shown above each pair of bar plots; Table 1 gives sizes of areas examined with airborne lidar data. Tree diameters manually measured for FIA plots and modeled from lidar-identified top of tree heights. Study areas are centered on the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest (SNF).

used the highest CSM grid cell associated with each tree to record the tree's height and x,y location.

### 2.4. Large tree frequency

We used the allometric equations developed from the FIA data (Section 2.2) to model DBH for each tree identified from the lidar data. We reported both overall trends in tall density as tall trees per study area and then forest zone. We also recorded the density of lidar-identified large (DBH $\geq$ 76.2 cm) and very large (DBH $\geq$ 101.6 cm) trees per 0.81 ha (90 $\times$ 90 m) grid cells with cell centers 30 m apart (Kane et al., 2015, 2019). This approach is functionally similar to performing a 3x3 smooth and allowed us to provide maps at 30 m scale to allow users to easily compare them to the many Landsat-derived maps prepared at this scale while helping to prevent the calculation of unrealistic values extrapolated from small grid cells (Shugart et al., 2010).

### 2.5. Canopy cover for stand context of large trees

We wanted to examine stand conditions in which large trees were found, which with field data are often expressed as tree density, basal area, and canopy cover. Lidar data, however, cannot identify subordinate trees that are often the most numerous, and basal area modeling of the lidar identified overstory trees essentially replicated the large tree count, and we did not calculate these values. However, airborne lidar can make robust calculations of canopy cover. Canopy cover reflects total tree density and therefore is a surrogate for potential vulnerability to wildfire and drought stress. We used the airborne lidar data to measure canopy cover for each 30x30 m grid cell and then performed a 3x3 focal smooth to match the area over which large tree counts were performed (Section 2.3). Canopy cover was calculated as the percentage of all lidar returns > 2 m in height above the vendor-supplied ground models in each grid cell divided by the total number of lidar returns.

### 2.6. Large tree patch characteristics

We analyzed the spatial distribution of large trees in terms of the structure of higher density patches of large trees. Preliminary analysis showed that substantial portions of our study area had low densities (<20) of large trees per hectare that contributed only a small portion of the total count of large trees (Section 3.1). We therefore analyzed patches of forests with $\geq$ 20 large trees per hectare. We identified a large tree patch as contiguous grid cells that contained at least a density $\geq$ 20 large trees per hectare. We report both the patch sizes and the cumulative area covered by these patches.

To study the shape complexity of the large tree patches identified, we used the Shape Index metric (McGarigal, 1995) as implemented in the R package landscapemetrics (Hesselbarth et al., 2019). The Shape Index calculates the deviation of a patch's shape from that of a perfect square (for raster data). Perfect squares have a value of 1; values increase without limit as shape complexity increases. The calculation of the index corrects for the patch size problem inherent in simple perimeter-area ratio indices by adjusting values for a square standard (McGarigal, 1995).

We were interested in what might be influencing these large tree patch spatial patterns and modeled potential drivers of these patterns using machine learning (random forest) based on topography, local climate, and fire history (Kane et al., 2015, Povak et al., 2000). However, in preliminary analysis the models failed to find any strong predictors possibly because of a complex interplay of disturbances, timber harvests, edaphic conditions, and site conditions for which data was lacking and we do not report these results.

## 3. Results

We identified 8,092,251 large trees (modeled DBH $\geq$ 76.2 cm) and 2,777,423 very large trees (modeled DBH $\geq$ 101.6 cm) from the airborne lidar data across the three study areas in lower and upper montane forests (Fig. 2). In general, we found that trends for the densities and patch structure for these two classes of trees followed similar patterns. The key difference was in the frequency of these two populations, with very large trees occurring in much lower numbers. For brevity below, we discuss large tree trends and then note any significant differences between the two populations by specifically contrasting large versus very large tree results. To assist interpretation of the quantitative results presented below, Fig. 3 provides visualizations of the ranges of large tree densities within our 90 $\times$ 90 m (0.81 ha) grid cells, the structure of large tree patches, and large tree densities across our study areas.

In this paper, we report results for lower and upper montane forests across our three study areas. In supplement Fig. 5 we also provide frequency results for subalpine forests in Yosemite National Park (the other two areas had too little subalpine forest within the area of the lidar acquisitions to provide useful results).

### 3.1. Large tree frequency

Both FIA plot data and airborne lidar data generally showed similar trends in overall large tree frequencies and both show variations by forest zone and study area (Fig. 2). The match between the two datasets was closest for lower montane forests for both large and very large trees. However, the FIA data showed a larger density of both tree populations in upper montane forests for both the Yosemite and Sierra study areas but not the Tahoe study area. (The online supplement Figs. 3 and 4 also provide information from the FIA data on large tree species and field estimated ages to aid interpretation of our results).

We found that low densities of large trees were widely dispersed but that most of these trees were spatially aggregated. Based on our lidar count of large trees, substantial portions of our study areas had either no or low densities (<20 large TPH) of large trees $\geq$ 76.2 cm (Fig. 4). Despite their large extent, these areas contributed few large trees to the cumulative count of this population. The remaining grid cells with $\geq$ 20 and especially $\geq$ 50 large trees per hectare represented approximately one-half to one-quarter of our study areas and cumulatively accounted for the majority of large trees. We found similar trends for the cumulative frequency of very large trees, but the portion of area with very large tree densities $\geq$ 20 covered a much smaller portion of the landscape, ranging from approximately a fifth to a twentieth of the area depending on the study area and forest zone.

### 3.2. Canopy cover stand context of large trees

To examine the context of the stands containing large trees, we plotted large tree density by canopy cover for 90x90 m (0.81 ha) grid cells (Fig. 5). For lower montane large trees, canopy cover versus large tree density showed almost a unimodal response with canopy cover of 60% to 80% for large tree densities of approximately > 20 large TPH for the Tahoe and Sierra study areas and approximately > 40 large TPH for the Yosemite study areas. However, for upper montane large trees, canopy cover versus large tree density showed a more linear relationship for all three study areas. Canopy cover for very large trees generally followed similar patterns (results not shown).

### 3.3. Large tree patch characteristics

Because grid cells with < 20 large TPH contributed little to the cumulative count of large trees (Section 3.1), we examined the patch structure only for contiguous grid cells with large TPH $\geq$ 20. The most common patches of large trees were isolated single grid cells and 2–10 ha patches (Fig. 6). Patches > 50 ha were numerically rare. However, the largest tall tree patches (500 + ha and especially 1000 + ha) represent the majority of the area in each of our three study sites with large trees. All three study areas had similar cumulative area in large

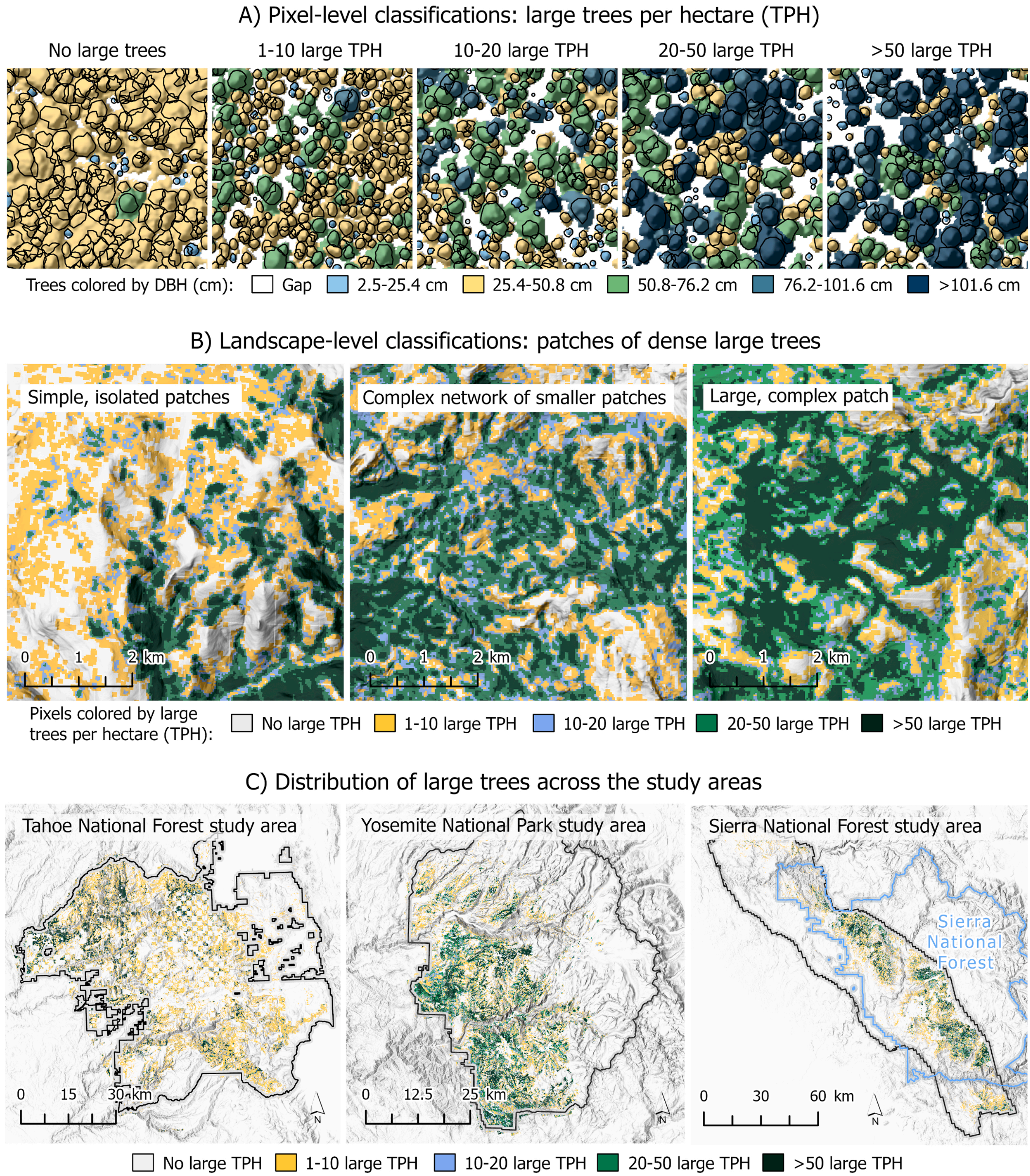


**Fig. 3.** Visualizations of the data used in this study. A) Individual trees identified from the airborne lidar data for different densities of large (≥76.2 cm) trees per hectare with ranges of modeled diameters at breast height. Areas shown are 90 × 90 m. (Breaks correspond to to 1–10, 20–30, 30–40, and > 40 in..) B) Examples of different patterns of large tree patches found in our study areas. C) Patterns of patches with different densities of large trees across our study areas. Interactive maps of large trees .
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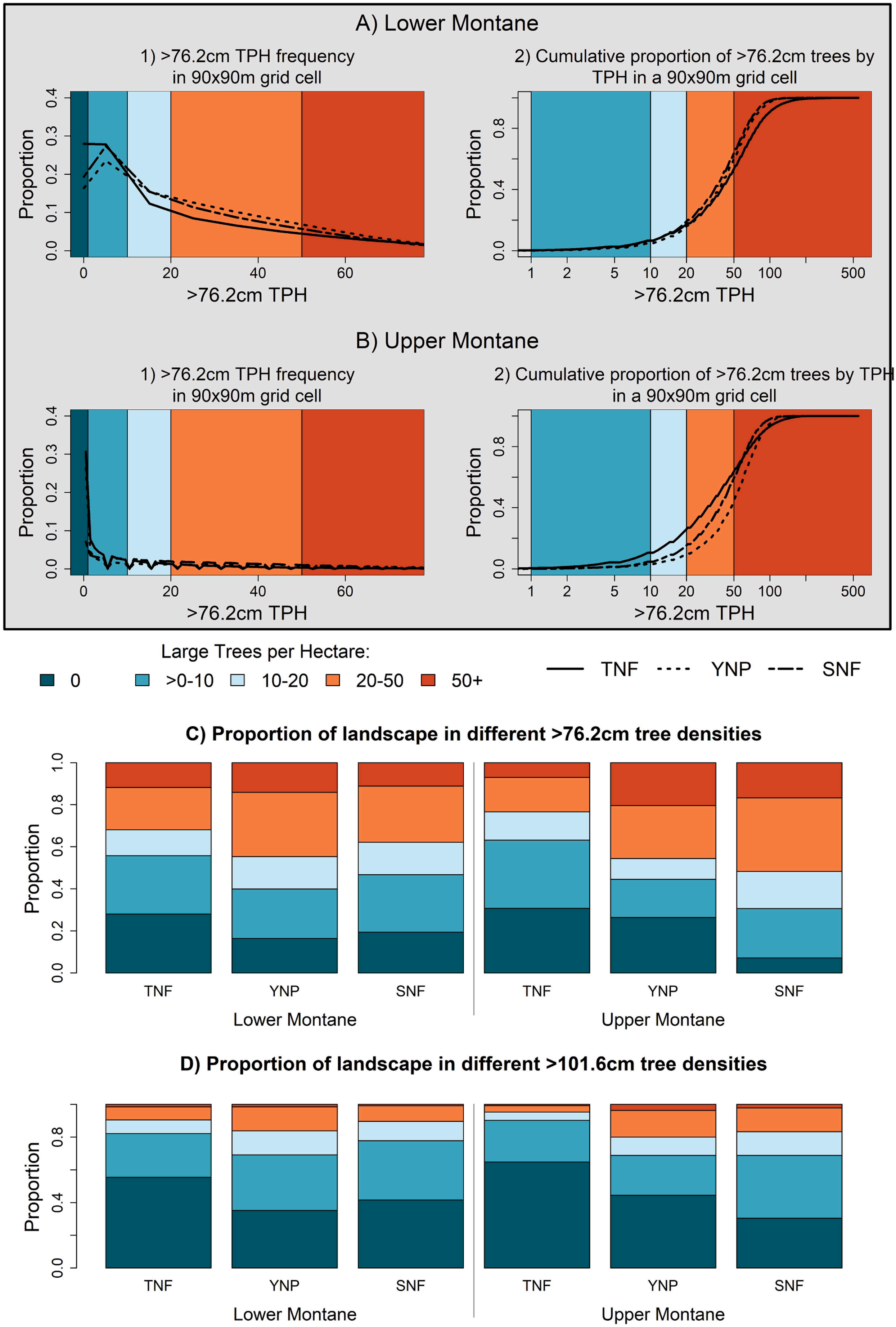


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**Fig. 4.** Patterns of large tree (>76.2 cm DBH) densities. A) and B) show frequencies of large (≥76.2 cm) trees per hectare for all 90 × 90 m grid cells and cumulative counts of large trees for the lower and upper montane forest zones of study areas centered on the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest Study (SNF) study areas. Patterns of frequencies and cumulative counts similar for very large trees (≥101.6 cm; data not shown). C) and D) show proportions of each study area covered by grid cells with different densities of large and very large trees by forest zone. Supplement Fig. 6 provides equivalent results for very large (>101.6 cm DBH) trees for Panels A and B.

tree patches for lower montane forests, but the Tahoe study area had substantially less cumulative area in large tree patches than the other two areas for upper montane forests. As patches became larger, their shapes rapidly became more complex as reflected in higher values for the Shape index for larger patches (Fig. 3 panel B and Fig. 7).

## 4. Discussion

Large trees (≥76.2 cm DBH) are key backbone structures of Sierra Nevada forests for their ecological function, habitat, and carbon storage. We used airborne lidar data acquired over three large landscapes to identify more than eight million individual canopy dominant large trees. In this first census of large trees over large areas of the Sierra Nevada, we found that the distribution of large trees was spatially aggregated with most in patches containing 20 to 50+ large trees per hectare. However, large portions of our study area had either no or low densities (<20) large trees per hectare.

Two factors will make protecting large trees challenging. First, these trees are usually found in locations with high canopy cover exceeding 60%, which suggests that many are likely in overstocked stands. Second, while large trees are typically found in high density patches of large trees > 1000 ha, these patches were not compact but instead appeared to be highly interspersed with patches of no or low densities of large trees. As a result, managers will need to manage for improved resilience against future wildfires and droughts across large landscapes containing interspersed patches of primarily shorter trees and patches with high densities of large trees. 4.1 Airborne lidar for censusing large tree populations.

Airborne lidar has long been used to study variation in heights in forest canopies including identifying locations with tall canopies that indicate the presence of large trees within study areas (e.g., Fricker et al., 2019). Understanding the strengths and limitations of our methods is essential to interpreting the results of this study.

Our tree identifications from lidar data are models subject to errors of omission and commission in segmenting tall (and therefore also likely large DBH) trees. We used a computationally efficient tree segmentation algorithm whose accuracy has been tested against field data collected within our Yosemite and Sierra study areas (Jeronimo, 2015; Jeronimo et al., 2018). For the large overstory trees that are the focus of this study, identification accuracy approaches 90% (Jeronimo et al., 2018).

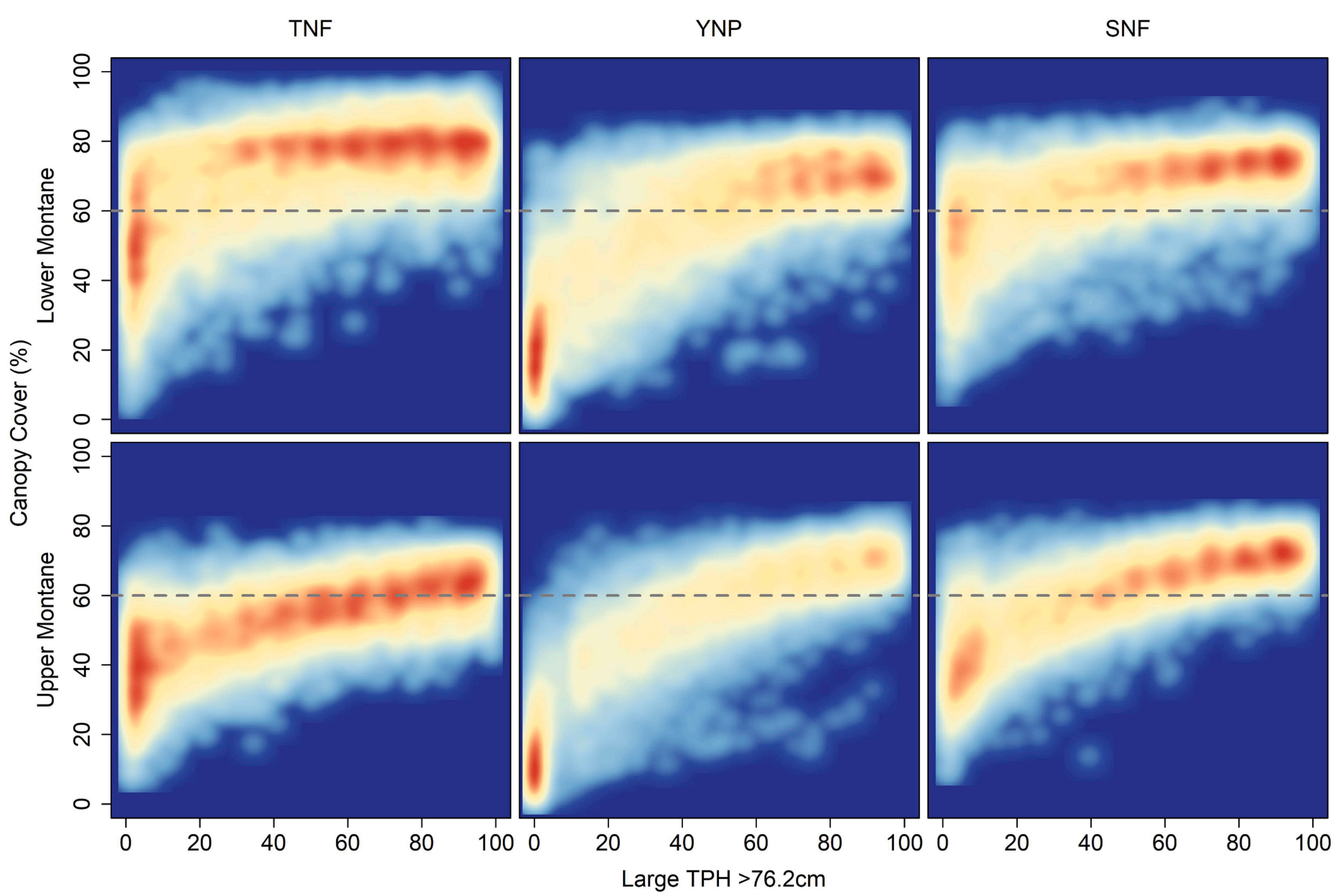
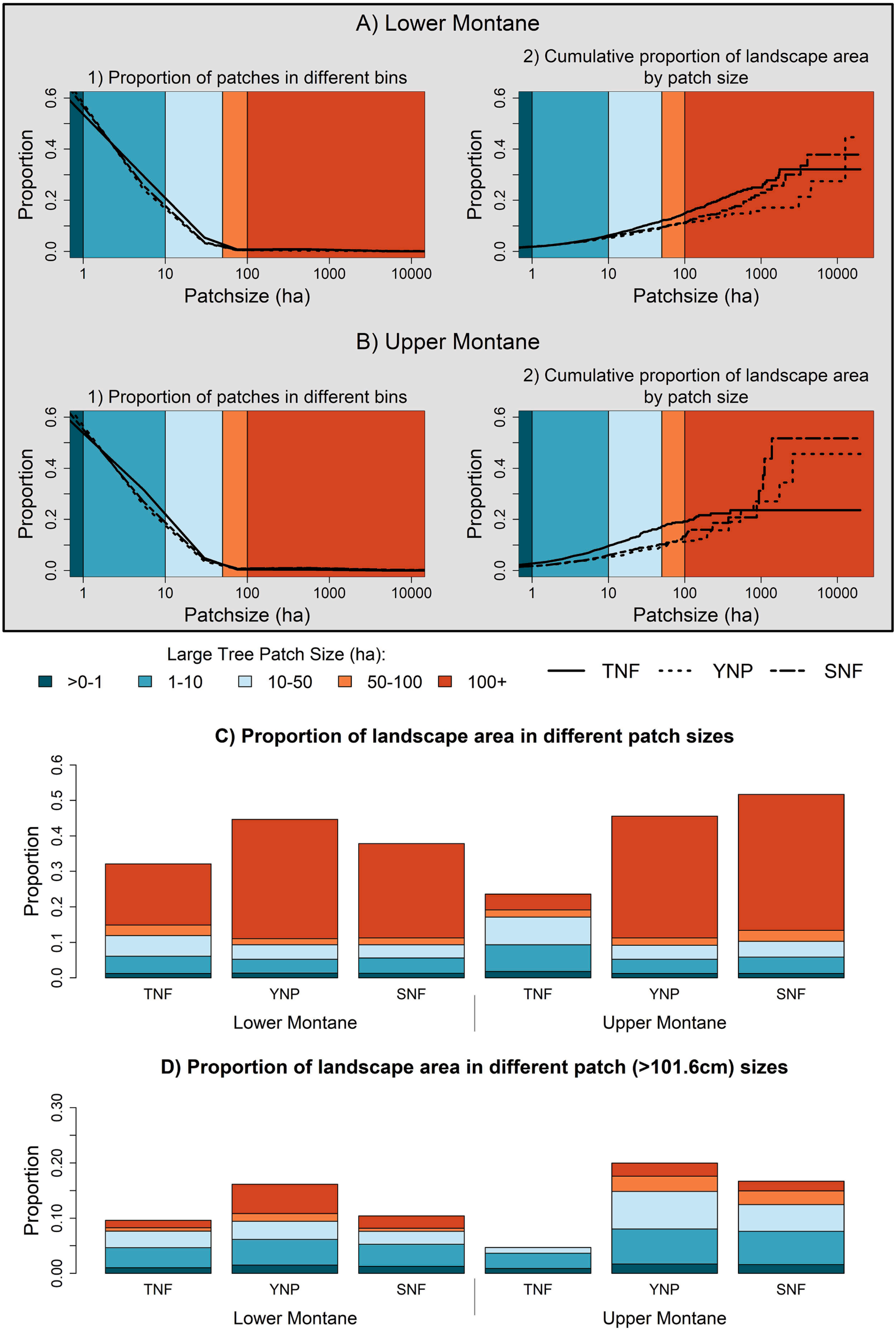



**Fig. 5.** Relationship of airborne lidar-identified large tree (>76.2 cm) density per hectare (TPH) to canopy cover calculated from the airborne lidar data for 90 × 90 m grid cells used in our study. Canopy cover measurements include contributions from trees of all sizes within a grid cell. To create a balanced visualization of all ranges of tree densities, a stratified random sample of tree densities (x axis) was performed in increments of 10 tall trees per hectare, n = 1000 per bin. This allows us to understand how canopy cover varies with density per se, rather than observing the frequency of various density-canopy cover combinations. Without this sampling, high values of large tree densities, which are proportionally rare, would not be visible in the color ramp. Study areas are centered on the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest (SNF).




(caption on next page)

**Fig. 6.** Structure of large tree patches where a patch is one or more contiguous 90x90 m grid cells with a large tree density of 20 or more large trees per hectare. A) and B) show frequencies and cumulative area of large tree (≥76.2 cm) patches for the lower and upper montane forest zones of study areas centered on the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest Study (SNF) study areas. Patterns of patch sizes and cumulative areas similar for very large trees (≥101.6 cm; data not shown). C) and D) show proportions of each study area by forest zone covered by different sizes of patches of large trees where the large tree density was > 20 large trees per hectare for both large and very large (≥101.6 cm) trees. Panels C and D vertical axes have different scales because very large tree patches are much rarer. Supplement Fig. 7 provides equivalent results for very large (>101.6 cm DBH) trees for Panels A and B.

To provide an independent check on our lidar-derived results, we also used FIA data to assess how common large trees were. Both datasets reported substantial numbers of large trees. How well they agreed on specifics such as median or interquartile ranges of large tree densities varied by study area and forest zone and diverged most for upper montane forests (Fig. 3). One explanation for divergence could be that the FIA plots cumulatively sample just 0.00004% of our study areas and therefore cannot fully represent large tree populations across our study areas. Another explanation is that we noticed that the predictions from the allometric equations tend to asymptote, which would lead to lower DBH estimates for the tallest trees. Also, the accuracy of our models relating lidar-measured tree heights to DBH may vary across our study sites. For example, these models are based on many fewer FIA plots for upper montane forests than for lower montane forests (Table 1). Also,

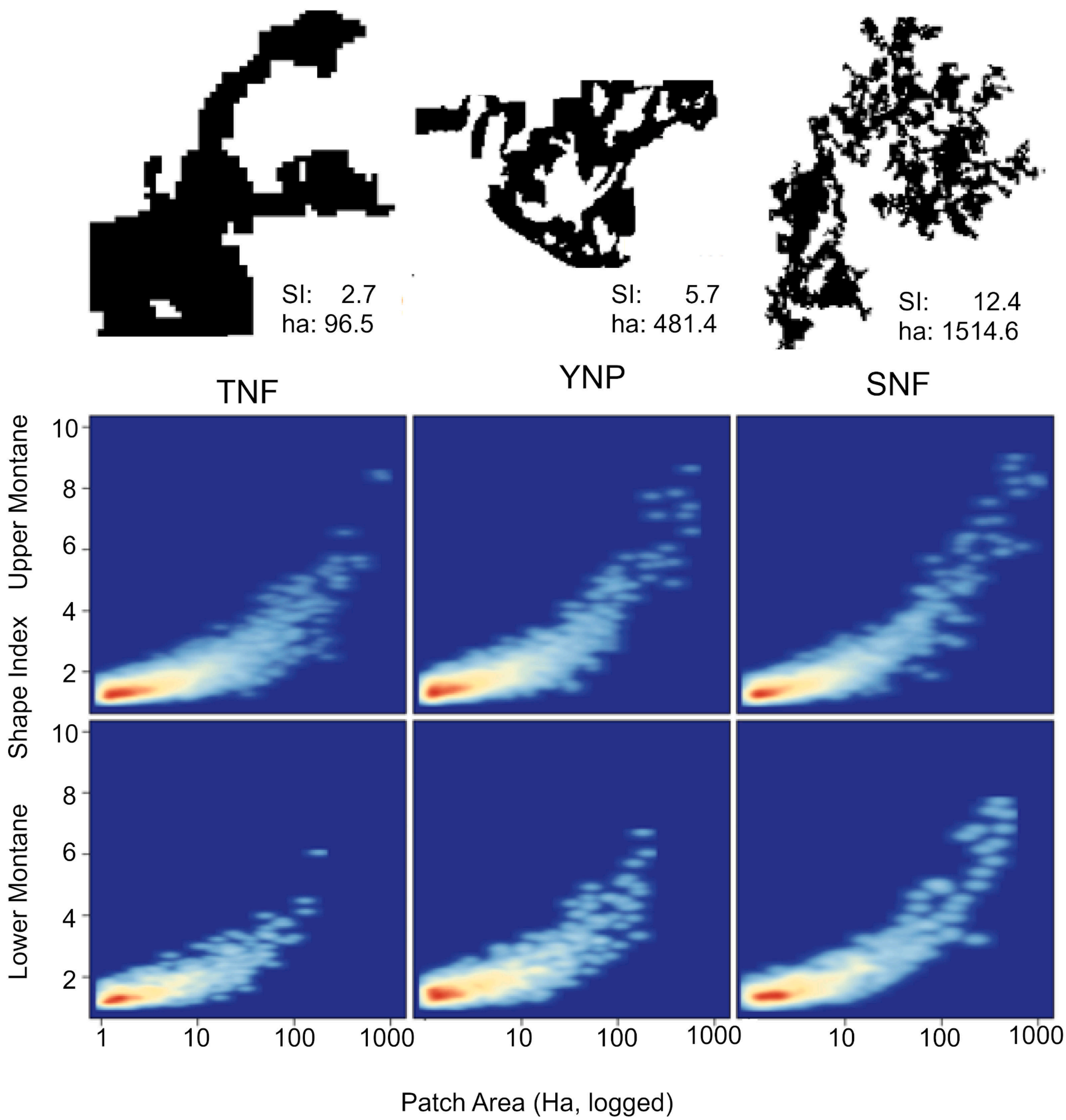



**Fig. 7.** Complexity of large tree (≥76.2 cm) patches (large tree density > 20 large trees per hectare) by patch size. Top row shows examples of large tree patches for different sizes and shape indices (SI). Lower rows show relationship of patch size to shape index for all large tree patches identified in this study. The shape index calculates a unitless measure of the deviation of a patch's shape from that of a perfect square, which has a value of 1, increasing with patch complexity (unbounded). Study areas are centered on the Tahoe National Forest (TNF), Yosemite National Park (YNP), and Sierra National Forest (SNF).

lightning is more common at higher elevations (van Wagtendonk and Cayan, 2008) leading more upper montane large trees to have been struck and lost their tops, skewing height to DBH relationships.

A key limitation to our methods is that we cannot distinguish between living and dead (snag) overstory trees. While airborne lidar intensity data can be used to distinguish the two (Kane et al., 2019; Wing et al., 2015), technical issues with the Yosemite lidar data made applying these methods problematic. We therefore did not attempt to identify snags in any of our three study areas. As a result, our census of large trees will overstate the frequency of living large trees, especially in the two southern study areas that were harder hit by the mid-2010s drought (Young et al., 2017). However, given the rate at which snags typically fall to the ground (Morrison and Raphael, 1993, Ritchie et al., 2013), most snags still standing at the time of our lidar acquisition likely were living a decade or so before their respective lidar acquisitions and therefore still represent large tree trends for the last few decades. Future work likely will be able to use contemporaneous airborne lidar and field or high-resolution aerial imagery to address mortality trends.

### 4.1. Biophysical and management context for large tree distributions

The high number of large trees we identified demonstrates that conditions exist across our study areas that have both the productivity and time between disturbances to grow large trees. The lower and upper montane forest zones (between approximately 900 m and 2500 m elevation) lie in a “sweet spot” where precipitation, warmth, and the availability of groundwater supports high productivity (Kelly and Goulden, 2016; Sugihara et al., 2006). Many of the dominant tree species are also physiologically adapted to enable year-round photosynthesis (Kelly and Goulden, 2016). Historically, these conditions allow the growth of truly giant trees that were reported by early Euro-American settlers (Lieberg, 1902, Stephens et al., 2005). These conditions also have allowed the growth of trees exceeding 76.2 cm DBH in the time since harvests of many legacy large trees in the late 19th and early 20th centuries (North et al., 2005; Online Supplement Fig. 4).

Historical fire regimes also supported the growth of large trees (Coppoletta et al., 2021; Meyer et al., 2019; North et al., 2022; Safford and Stevens, 2017). In lower montane forests, frequent fires ignited by Indigenous peoples and lightning typically burned at low intensity serving to keep tree densities low, allowing adult surviving trees to grow large with thick fire-resistant bark (Safford and Stevens, 2017). The low stocking densities also reduced water competition allowing large trees to survive the periodic droughts (North et al., 2022). In upper montane forests, the fire return interval was longer, allowing denser populations of large trees to establish (Coppoletta et al., 2021; Merriam et al., 2022; Meyer et al., 2019a,b).

Harvests in the lower montane forests following Euro-American settlement removed most large trees and reshaped forest structure across much of the Sierra Nevada (our summary follows Beesley (1996) and McKelvey and Johnston (1992)). The earliest, most intensive, and longest history of harvesting centered on our Tahoe study area. Harvesting in areas later added to Yosemite National Park (Chad Anderson, personal communication) and in our Sierra study area, however, developed more slowly, in early decades often to only supply local timber needs. More intensive harvesting within these study areas did not begin until the interwar era and was largely confined to selection (high grading) harvests of the largest trees. In the southern Sierra, including our Sierra study area, intensifying harvests gradually expanded to higher elevations initially as selection harvests but transitioning to clearcutting following World War II, again starting at lower elevations (Keane, 2017).

### 4.2. Present frequency and density of large trees

The current broad patterns of large tree densities for our study areas could be extrapolated from patterns of historic fire regimes and harvests. Across our three study areas, lower montane forests show similar values for median large and very large trees per hectare and similar interquartile ranges (Fig. 3). This could reflect harvest histories for each study area that removed most legacy large trees followed by the establishment of a new cohort of now large trees following harvest (Beesley, 1996; McKelvey and Johnston, 1992). Yosemite’s somewhat higher large tree frequencies could reflect areas of lower montane forest originally in the park and therefore protected from harvests. Previous work based on field studies similarly found higher frequencies of large trees in this park than in national forests (Collins et al., 2017). On the other hand, both datasets show that upper montane forests had higher frequencies of large trees. This could reflect both historically less-frequent fire regimes allowing greater densities of large trees (Meyer et al., 2019) and protection from harvests in the Yosemite study area and late introduction of harvests in the Sierra study area (Beesley, 1996; McKelvey and Johnston, 1992). The exception was the Tahoe study area with its low number of large trees in the upper montane forests, which likely reflects the intense early harvests of this forest zone (Beesley, 1996; McKelvey and Johnston, 1992).

We found that the densities of large and very large trees varied considerably within each of our study areas and forest zones (Fig. 4 Panels C and D). Most of our 0.81 ha grid cells had either no or low densities of these trees, and these locations contributed little to the cumulative count of large and very large trees. However, most large trees were found in the grid cells with > 20 and especially > 50 large trees per ha, demonstrating the spatially aggregated distribution of large trees. This was true for both the historically harvested lower montane forests in all three study areas as well as the unharvested (Yosemite) or lightly harvested (Sierra) upper montane forests.

### 4.3. Spatial patterns of large tree patches

We found similar patterns of large tree patches across all our forest zones and study areas (Figs. 6 and 7). Across the three areas, large numbers of these patches were isolated single 0.81 ha grid cells or were patches < 10 ha in size. The landscape-scale ecological impact of these scattered patches of large trees – in terms of providing habitat or moderating local conditions – is likely diminished by their small sizes. Locally, however, these sparsely distributed large trees likely are key structures that can be the focus of local conservation and resilience planning (Lindenmayer, 2017). In landscapes that were subject to harvests, these small patches of large trees may represent locations, for example on steep slopes, that escaped any harvest or that were not reharvested following a historically early harvest. In other locations, these small patches may represent favorable topographic or edaphic conditions within larger areas of lower productivity.

The dominant settings for large trees, however, were patches of several hundred to several thousands of hectares in size. Depending on the study area, these large patches can cover 20% to 40% of the landscape in a forest zone. These patches are extensive enough for large trees to modify local climatic conditions over large areas, provide continuous blocks of habitat for species that require large trees, and retain substantial stores of carbon (Hurteau et al., 2019).

The lower montane forests in all three study areas generally had similar distributions of large tree patch sizes and cumulative area covered by these large tree patches (Fig. 6 Panel A and B). The similarity was surprising. The three study areas had different harvest histories and portions of the lower montane forests of Yosemite had experienced decades of a restored fire regime (van Wagtendonk, 2007); at the time of their lidar acquisitions, the other two study areas had experienced relatively little wildfire. This contrasts with the upper montane forests where the Yosemite and Sierra study areas had similar distributions of large patch sizes and cumulative areas, but the Tahoe upper montane forests had both smaller large patches and less cumulative area. The two different stories for the Tahoe large tree patches could be a simple one of productivity – the higher productivity of the lower montane forests may have allowed faster recovery of a large tree population following intense harvests than in the upper montane forests.

Both visual inspections (e.g., Fig. 3) and analysis with the shape index (Fig. 7) shows that these large patches are rarely simple large blocks. Instead, they form complex matrices interspersed with patches of forests with shorter trees. Obvious contributors to these complex patterns would be local biophysical factors such as topography, edaphic conditions, and local climatic conditions. In some cases, the highest densities of large trees appear to follow valleys where productivity would be expected to be locally high. In other cases, the mosaic of large tree presence may result from patterns of historic harvests or, especially in Yosemite with its decades-old restored fire regime (van Wagtendonk and Lutz, 2007), patterns of wildfires. Both harvest decisions and fire progression may in turn be influenced by underlying biophysical patterns.

The recent availability of airborne lidar provided the first opportunity in which we have the technical means to census rather than sparsely sample the distribution of large and very large trees. So, we cannot tell whether the distribution of large trees we found in these large amorphously-shaped patches covering a third to half of landscapes reflects underlying biophysical controls or is an accidential happenstance of approximately 150 years of intense modification of these forested landscapes by Euro American management. Finding similar patterns across a national park and two national forests with very different harvest histories gives support to the present distribution of large trees reflecting underlying biophysical conditions. Understanding the factors that led to and may work to maintain or change these distributions would be an important area for future research to help us know how to manage this legacy in a changing climate and future human use of these landscapes.

### 4.4. Current threats to large trees

A common belief, implicit in the 30-inch rule meant to preserve all remaining large trees (McKelvey and Weatherspoon, 1992; Stephens et al., 2016), is that these key trees are rare. Similar rules are in place for federal interior Pacific Northwest forests (21 in./53.3 cm), the southwest (5 to 18 in./12.7 to 45.7 cm), other areas within California (6 to 30 in./15.2 to 76.2 cm) (Abella et al., 2006; Johnston et al., 2021). Across large portions of the landscapes we examined, our results show that large trees indeed are rare or exist in low densities. However, substantial portions of our three study landscapes had > 20 large trees per hectare with small patches having densities of 50 to 100 + large trees per hectare. Depending on the location examined, large trees are both rare and abundant.

However, our study may have documented a peak in contemporary large tree numbers for lower montane forests, and managers likely will struggle to retain much of the current population. Historical data showed that these original stands contained a fraction of the stocking density of today's forests because the then-frequent wildfires removed smaller trees (Larson and Churchill, 2012; Lydersen and North, 2013; North et al., 2022). The lower stocking density reduced competition and the buildup of fuels, increasing the chances that large trees would survive the periodic droughts and fires would be lower intensity (North et al., 2022). However, most of these historic large trees were harvested, especially in the more productive lower montane forests (Beesley, 1996; McKelvey and Johnston, 1992).

However, today's large trees (many of which are less than a century old, (North et al., 2005; Supplement Fig. 4)) exist in historically unprecedented stand conditions with fire suppression having allowed infilling to create high stocking levels (Collins et al., 2011, 2017; Meyer et al., 2019; Stephens et al., 2015, 2018a, 2018b, 2022; Dolanc et al., 2014). Forests in 1911 averaged 12% − 28% canopy cover compared to the common 60% − 80% canopy cover we found for current locations with large trees (North et al., 2022). Increased stocking densities creates stress that can reduce vigor and increase susceptibility to stress (Cailleret et al., 2017; Das et al., 2011; Franklin et al, 1987;). Under the climate commonly present over the last few decades, increased competition at local scales seems to have little or no effect on rates of large tree mortality (Das et al., 2011; Smith et al., 2005).

However, more extreme droughts such as those projected to occur with climate change are expected to bring increased tree mortality (Allen et al., 2015; Hammond et al., 2022; Madakumbura et al., 2020; Senf et al., 2020). As an example, a severe warm drought in the Sierra Nevada from 2012 to 2016 demonstrated the vulnerability of its forests, especially its large trees. Overall, an estimated 80 to 120 million trees died in the region (USDA Forest Service 2020). Severity of tree mortality was strongly associated with stand densities and basal area (Restaino et al., 2019; Young et al., 2017), and increased densities of large trees especially contribute to increased basal area. Overall, larger trees disproportionately died during the drought compared to smaller trees (Furniss et al., 2020; Hemming-Shroeder et al., 2023; Stephenson and Das 2022; Stovall et al., 2019). However, the relationship between tree size and mortality intensity was species specific with height being a strong predictor of mortality for the numerous large pines but a weaker one for other large conifers (Stephenson and Das, 2020).

Uncharacteristically severe wildfires represent another growing threat to contemporary large trees. Over the last decades, wildfires in the Sierra Nevada have become more numerous and a class of large fires with unprecedented large high severity burn patches have emerged (Cova et al., 2023; Parks and Abatzoglou, 2020; Stephens et al., 2022; Williams et al., 2023). The contemporary, overly dense, infilled forests with their high fuel loads and continuous horizontal and vertical canopies are widely believed to be associated with this emerging fire regime (Hagmann et al., 2021; Knapp et al., 2017; Lydersen et al., 2013; North et al., 2021; Prichard et al., 2021; Safford and Stevens, 2017; Stephens et al., 2009). Within these high severity patches, most to all of the trees, including large trees, can be lost leading to conditions where conversion of forests to other vegetation cover can occur (Coop et al., 2020, Steel et al., 2023). (A visual inspection of large patches with few to no large trees in the Yosemite study area – the only one of our three study areas to have had substantial fire prior to the collection of the lidar data we used – showed that several of them corresponded with large high severity burn patches of fire from before the lidar acquisition.) Lower intensity burns also appear to remove large trees in approximate proportion to their pre-fire presence (Kane et al., 2013, 2014, 2019). Unlike large high severity patches, however, these lower severity effects reduce tree density by creating patterns of intermixed tree clumps and openings that together should increase resilience to both future drought and wildfires (Churchill et al., 2013; Davis et al., 2023; Kane et al., 2019).

Combined, severe drought and wildfires can remove high percentages of large tree populations. In a recent analysis, change in large tree cover from 2011 to 2020 was modeled based on the presence of tall (>30 m) trees across the southern Sierra, which would have included our Yosemite and Sierra study areas (Steel et al., 2023). The combined effects of severe drought and wildfire removed almost 50% of the identified mature forest cover (based on dominant tree height) in this period and, importantly, large trees in settings with higher canopy cover were at higher risk of loss (Steel et al., 2023).

Between fire and drought, the forests of the Sierra Nevada are in constant change. Any inventory of large trees (or any forest characteristic) over large landscapes is likely to be out of date by the time the data to measure it is analyzed and published. We recognize that this is true for our analysis of the frequency and distribution of large trees. These results will need to be regularly updated with new data, and our results can provide a baseline for understanding future change. However, large swaths of these forests would still benefit from active management to improve resilience (Cova et al., 2023) and we believe that our results and their management implications can inform management to preserve large trees.

### 4.5. Management implications

The high canopy cover observed around most large trees within our study suggests that protecting large trees will require treatments both within the stands that contain them and across the landscapes in which they live. The high canopy cover within which almost all large trees exist (Fig. 5) emphasizes the need for treatment almost everywhere that large trees are present for lower montane forests. (Upper montane forests are considered to have higher than historic densities but not to be as departed as lower montane forests and therefore at less risk (Meyer et al., 2019a)). However, plans to increase resilience for large trees cannot just focus on high density large tree patches. Our analysis shows that these patches typically exist in complex mosaics intermixed with patches of smaller trees. Given widespread infilling, these shorter tree patches also likely are overly dense (Lydersen et al., 2013, North et al., 2016) and therefore could carry higher intensity wildfires into patches with large trees. Defending patches of large trees, therefore, likely will require approaches that increase the resilience of complex mosaics of stand patches at the landscape scale to create buffers around the stands with the largest trees. Management options for both treatments within stands to reduce competition and for landscape scale management to increase resilience have been identified (e.g., Hessburg et al., 2015; Larson et al., 2022; Lindenmayer et al., 2008; North et al., 2009, 2012, 2021).

A question that has arisen in recent years is whether managers should have the option to remove large trees in certain circumstances. The 30″ (76.2 cm) limit on cutting large trees on federal lands in the Sierra Nevada (and similar DBH-based rules in other western U.S. forests) was initially viewed as a temporary solution to halt immediate further loss of large trees until more flexible rules could be agreed upon between federal forest managers and stakeholders (Hessburg et al., 2020). Instead, it has become an ongoing rule. Some researchers argue that retention of larger trees, regardless of age, is important for wildlife habitat quality and forest health (e.g., Allen et al., 2002). Others have argued that an inflexible rule can make it more difficult to meet targets for tree species composition, basal area, or forest structural heterogeneity (Abella et al., 2006; Coughlan et al., 2003; Hessburg et al., 2021; Triepke et al., 2011).

While our results can help identify locations where managers and stakeholders may want to focus these discussions, our data alone cannot resolve this question. We found locations where the apparent density of large trees is high, 50 to 100 or more large trees per hectare. While these densities could be associated with overstocking depending on local moisture availability, these dense stands also are considered key habitat for the California spotted owl (*Strix occidentalis*) and the Pacific fisher (*Pekania pennanti*) as well as other wildlife and botanical diversity (Blomdahl et al., 2019; North et al., 2017; Purcell et al., 2009). Ultimately, managers and stakeholders need to individually examine each location with a dense population of large trees, determine whether local conditions can support the population given the inevitability of future drought and wildfire, and determine whether retaining the full population of large trees meets other goals including habitat requirements, desired tree species mixes, and views of stakeholders. (Interactive maps showing our results for large and very large tree densities and canopy cover are available at https://arcg.is/8LfW9).

## 5. Conclusions

Our study shows that large trees are not rare across three large landscapes in the Sierra Nevada, but their distribution is spatially aggregated primarily in large amorphous patches. However, the present population is vulnerable because its large trees occur in overly dense stands and homogenous landscapes enabled by decades of fire suppression. Other studies have documented large losses of these trees to both drought and wildfire. Protecting these ecological keystones will require managers to treat both within stands with large trees and across landscapes that are matrices of large and shorter tree patches. As with any first census of a population, we expect that this study sets the foundation for more focused follow-up studies. New airborne lidar acquisitions will allow the area censused to be expanded. Other studies may focus on conditions that lead to the current distribution of large trees, threats to their survival, or management options to sustain them.

## CRediT authorship contribution statement

**Van R. Kane:** Conceptualization, Methodology, Formal analysis, Investigation, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Bryce N. Bartl-Geller:** Conceptualization, Methodology, Formal analysis, Software, Visualization, Investigation, Writing – review & editing. **Gina R. Cova:** Visualization, Writing – review & editing. **Caden P. Chamberlain:** Writing – review & editing. **Liz van Wagtendonk:** Writing – review & editing, Visualization. **Malcolm P. North:** Conceptualization, Formal analysis, Methodology, Writing – review & editing.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Van R. Kane reports financial support was provided by USDA Forest Service Pacific Southwest Research Station. Van R. Kane reports financial support was provided by USDA Forest Service Pacific Northwest Research Station. Bryce Bartl-Geller reports financial support was provided by USDA Forest Service Pacific Northwest Research Station. Bryce Bartl-Geller reports was provided by USDA Forest Service Pacific Southwest Research Station.

## Data availability

GIS maps of large and very large tree density, canopy cover, and forest zones used in our study are available at https://arcg.is/8LfW9.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121351.

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