Forest Ecology and Management 507 (2022) 120004

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Operational resilience in western US frequent-fire forests

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ARTICLE INFO

Keywords:
Competition
Drought
Fire suppression
Stand density index
Tree vigor

ABSTRACT

With the increasing frequency and severity of altered disturbance regimes in dry, western U.S. forests, treatments promoting resilience have become a management objective but have been difficult to define or operationalize. Many reconstruction studies of these forests when they had active fire regimes have documented very low tree densities before the onset of fire suppression. Building on ecological theory and recent studies, we suggest that this historic forest structure promoted resilience by minimizing competition which in turn supported vigorous tree growth. To assess these historic conditions for management practices, we calculated a widely-used measure of competition, relative stand density index (SDI), for two extensive historical datasets and compared those to contemporary forest conditions. Between 1911 and 2011, tree densities on average increased by six to seven fold while average tree size was reduced by 50%. Relative SDI for historical forests was 23–28% of maximum, in the ranges considered 'free of' (<25%) to 'low' competition (25–34%). In contrast, most (82–95%) contemporary stands were in the range of 'full competition' (35–59%) or 'imminent mortality' (≥60%). Historical relative SDI values suggest that treatments for restoring forest resilience may need to be much more intensive then the current focus on fuels reduction. With the contemporary increase in compounding stresses such as drought, bark beetles, and high-severity wildfire, resilience in frequent-fire forests may hinge on creating stands with significantly lower densities and minimal competition. Current management practices often prescribe conditions that maintain full competition to guide development of desired forest conditions. Creating stands largely free of competition would require a fundamental rethinking of how frequent-fire forests can be managed for resilience.

1. Introduction

The increasing frequency and severity of novel disturbance patterns and climatic conditions has stressed many ecosystems, sometimes leading to degradation or loss of essential ecological processes (Stephens et al., 2018). In many western US dry conifer forests, severe drought and large, high-intensity wildfires have produced sizeable (i.e., >500 ha) mortality patches (Stevens et al., 2017) including loss of large, old trees and associated ecosystem services (Stephens et al., 2016). In response, current forest management practices have focused on reducing fuels and tree density, sometimes using forests conditions prior to the onset of fire suppression for general guidance (Innes et al., 2006). Given current changing conditions, however, most management practices do not attempt to strictly recreate historical forest conditions (Safford et al., 2012), but instead try to enhance ecosystem resilience and reduce type conversion (Coop et al., 2020).

While intuitively appealing as a long-term management goal, resilience has proven difficult to operationally implement for several reasons. In the research literature, definitions have often varied between different disciplines such as engineering (Holling, 1996; Bergen et al., 2001), ecology (Peterson et al., 1998; Gunderson, 2000), and silviculture (Larsen, 1995; DeRose and Long, 2014). Furthermore, definitions have often overlapped between similar concepts such as resistance, resilience, and response (Harrison, 1979; Grimm and Wissel, 1997; Millar et al., 2007). This can make it unclear, for example, whether a forest treatment such as fuels reduction is a resistance or resilience

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https://doi.org/10.1016/j.foreco.2021.120004
Received 16 November 2021; Received in revised form 28 December 2021; Accepted 30 December 2021

0378-1127/Published by Elsevier B.V.

strategy, and how objectives may vary depending on whether the focus is on the tree, ecosystem, or landscape (Stephens et al., 2021). Compounding these definition problems is the challenge that resilience will differ between ecosystems, their disturbance regimes, and constraints on growth resources (Hessburg et al., 2019). Predictably, a recent survey of southwestern U.S. forest managers found many barriers to applying the resilience concept including ambiguities about the appropriate scale, management specificity, adaptive landscape approaches, and a lack of applied metrics (Greiner et al., 2020).

This ambiguity is an urgent problem as forest landowners try to adapt to severe wildfires and drought. For example, most of US's 155 National Forests are developing new forest plans as guided by the 2012 Forest Plan Rule (USDA-FS, 2012). The planning rule emphasizes the stress of changing climate conditions and the need to restore forest resilience. While resilience's ambiguity makes it appealing as a boundary concept ("a [malleable] term that facilitates communication across disciplinary borders by creating shared vocabulary… [bridging] the gap between science and policy" [Brand and Jax, 2007]), it can dilute the term's utility as a well-defined, measurable scientific concept (Higuera et al., 2019). To help guide forestry practices, resilience needs specific metrics based on both silvicultural dynamics and ecological processes (DeRose and Long, 2014).

Defining and operationalizing resilience, however, may become more tractable when applied to a forest type's specific ecological context, such as dry forests that historically had frequent fire regimes. Our objective is to propose a resilience metric for frequent-fire forests based on both ecological theory and recent forest research emphasizing density-dependent competition and its influence on tree vigor[1]. We evaluate a common management metric, stand density index, as a potential means for assessing resilience in frequent fire forests. Using two extensive datasets with individual tree records, we examine whether unharvested, historical forests with an intact fire regime had low relative SDI, how that may have changed in contempory forests, and what this potential change suggests about forest ecological dynamics. Finally, we discuss how this measure of resilience might alter current treatment practices, and its management implications.

1.1. *Conceptual foundation*

Forests that historically had low to moderate severity frequent-fire regimes (i.e., <35 years) occur in areas with regular ignition sources (i.e., Indigenous populations that use fire and/or lightning), sufficient productivity to rapidly accumulate surface fuels, and seasonal aridity to propagate fire. Before European colonization many dry, low to mid-elevation western U.S. conifer forests had frequent-fire regimes (i.e., ponderosa [*Pinus ponderosa*] and Jeffrey pine [*P. Jeffreyi*], and mixed conifer), and make up much of the area that now has problematic large high-severity wildfires (Hagmann et al., 2021; Prichard et al., 2021) and large areas of drought/bark beetle mortality in part resulting from decades of fire suppression (Stephens et al., 2018). Thinning and prescribed fire are often used to reduce accumulated fuel loads (Agee and Skinner, 2005), and their effectiveness at moderating potential fire behavior and intensity are readily understood from modeling and empirical studies (Stephens et al., 2009; Kalies and Yocom Kent, 2016). While these treatments enhance forest resistance to fire, restoring resilience is an effort to retain fundamental ecological structure, composition and processes, which requires an understanding of the historical role of frequent-fire in the dynamics of these ecosystems.

Fire's ecological effects have conceptually been compared to herbivory, in which consumer control alters ecosystem biomass and species composition (Bond and Keeley, 2005). One prediction about herbivore-controlled ecosystems is that when predators are scarce, there is relatively little plant competition because herbivores proliferate, limiting plant growth more than resources (Hairston et al., 1960). An analogous condition may occur in some forests, where fire is frequent in the absence of suppression (similar to herbivory in the absence of predators), limiting tree density more than growth resource availability (i.e., water, light, and nutrients), significantly reducing competition. Such a forest would appear 'understocked' to an observer focused on maximizing the occupancy of tree growing space. For example, an early timber survey of northern California's forests when they still had an active-fire regime remarked "Suppression of the young growth has always been one of the serious results of fires…The land does not carry more than 35 per cent of the quantity of timber it is capable of supporting" (Leiberg, 1902, p. 42).

A corollary to this theory, is that in the absence of fire, live tree density and biomass accumulate, increasing competition for growth resources which can reduce tree vigor (Das et al., 2016). Many factors can episodically reduce tree vigor (i.e., surface fire, dry years, bark beetle outbreaks), but inter-tree competition can create chronic growth reductions which, in gymnosperms (Cailleret et al., 2017, 2019), increase tree susceptibility to stress and potential mortality (Franklin et al., 1987; Das et al., 2011). While dendrochronology studies and historical records document frequent-fire forests' resistance to stress 'pulses', these forests may not be as well adapted to continuous internal stress 'presses' that result from sustained and widespread competition for resources. Recent meta-analyses of growth patterns and tree mortality found that long-term reductions in gymnosperm radial growth from density-dependent competition were associated with chronic deterioration of a tree's carbon and water economies (Cailleret et al., 2017, 2019). This response may explain why some restoration studies in dense, fire-suppressed forests, have recorded mortality of large, long-lived trees following low-intensity treatments such as thinning small neighboring trees or re-introduction of surface fire (Das et al., 2011; Collins et al., 2014; van Mantgem et al., 2018; Stevens et al., 2020; Steel et al., 2021b).

1.2. *Working definition of resistance and resilience*

Resistance is a measure of persistence when exposed to a stress and in forests is often assessed by an ecosystem component such as large trees or canopy cover. Because this strategy is focused on minimizing change, resistance treatments are often designed for specific stresses. For example, fuels reduction is a resistance treatment designed to reduce fire severity and focused on increasing overstory tree survival. The emphasis in long-lived conifer forests on large trees, sometimes termed the ecosystem's backbone, is because they support many key services such as wildlife habitat, stable carbon stores, and diversified microclimates (Lutz et al., 2009).

Resistance is one element of resilience, which is a broader community-level response, when an ecosystem is impacted by stress but retains its essential structure and composition. As such, resilience is a measure of the forest's adaptability to a range of stresses and reflects the functional integrity of the ecosystem. To reduce ambiguity, some researchers (Carpenter et al., 2001; Westman, 1978; DeRose and Long, 2014) have suggested resilience should be defined as resilience of what, to what, at appropriate spatial and temporal scales. In this context, we assess resilience as the ability of frequent-fire forests to retain their inherent structure, composition and functional integrity in response to stresses common to this forest type (i.e., fire, drought, insects, and pathogens) at the ecosystem to landscape level over the age span of the dominant trees (i.e., 300–400 years).

Fundamental to this definition is the recognition that, beside fire, other stresses can reduce tree vigor (Das et al., 2008, 2011, 2016) and significantly alter or type convert a frequent-fire forest (Fettig et al., 2019; Stevens-Rumann et al., 2018). We propose that resilience treatments need to restore tree vigor by creating the very low densities

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[1] Tree vigor is defined by tree physiologists as the annual growth of stem wood per unit leaf area or 'growth efficiency'. In our context, we define it more generally as a tree's ability to persist and resist stressors.

characterized by little resource competition that sustained frequent-fire forests. To examine this idea, we analyze historical datasets of unlogged, frequent-fire forest conditions focusing on the stand density index, a measure of resource competition widely used by silviculturists. We compare historical and current forest conditions, and what these conditions imply about ecological dynamics and resilience in frequent-fire forests.

2. Methods

2.1. Study site

We used data from two timber inventories conducted in 1911 that span the southern and central Sierra Nevada (latitude 36°–38°) at elevations ranging from 1433 m to 1832 m. One inventory was conducted in the Sequoia National Forest (formerly Kern National Forest), while the other was conducted within the Stanislaus National Forest (including a small area of Yosemite National Park) (Fig. 1), with both sites under federal ownership at the time of the surveys. Both areas have a Mediterranean climate consisting of cool, wet winters and hot, dry

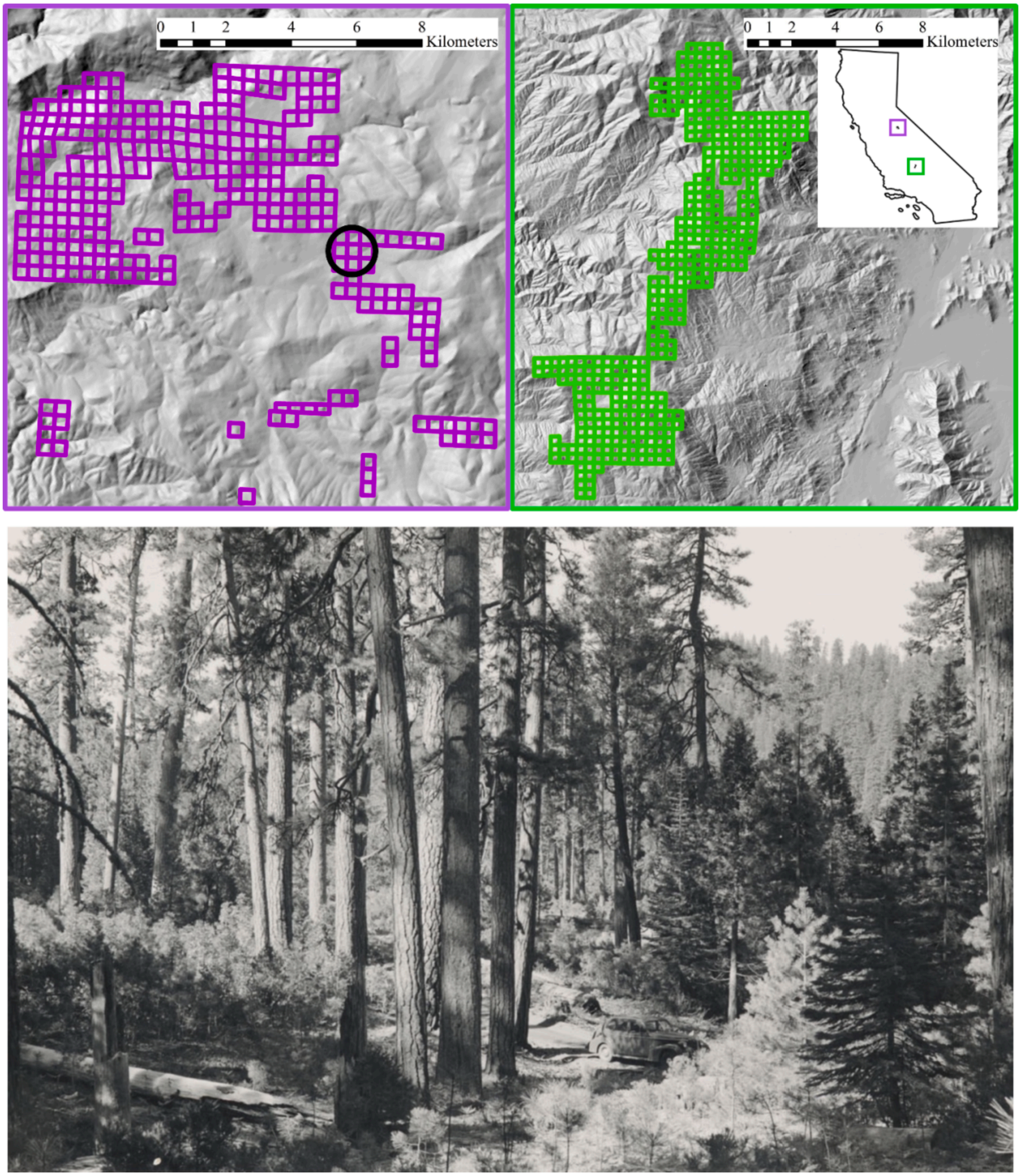

Fig. 1. Location and overall extent of the individual quarter-quarter sections (unit of sampling) in the 1911 timber inventories in the Stanislaus National Forest (top left panel) and Sequoia National Forest (top right panel). The circle in the Stanislaus NF panel indicates the approximate location for the 1941 photo (bottom row). Note the clump of large pines in the photo center and the surrounding small tree ingrowth, showing how forest conditions are starting to transition from historical to contemporary conditions. This photo was taken as part of the Wieslander vegetation type mapping project in California (Kelly et al., 2005).

summers (North et al., 2016). Modeled estimates of annual precipitation during the year the inventories were conducted ranged from 83 cm to 145 cm, while mean annual temperatures ranged from a minimum of 2.5 °C to a maximum of 18.4 °C (PRISM Climate Group, 2021). For both sites, the mixed-conifer forest type consisted of sugar pine (*Pinus lambertiana*), ponderosa pine, white fir (*Abies concolor*), and incense-cedar (*Calocedrus decurrens*). In the Stanislaus inventory area, mixed conifer also included Douglas-fir (*Pseudotsuga menziesii*). While hardwoods, particularly black oak (*Quercus kelloggii*), commonly occur in mixed-conifer forests (albeit at generally low proportions), both historical inventories do not record any hardwoods. In all liklihood hardwoods were present in the overstory in 1911, but not tallied due to their low commercial value. For consistency in our comparison, we also excluded hardwoods from our analysis of the 2011 data, resulting in a slight downward bias in our estimates of tree density and basal area for both time periods.

Prior to 1900, low- to moderate-severity fire was common across these areas, with mean fire return intervals ranging from 5 to 20 years (Kilgore and Taylor, 1979; Caprio and Swetnam, 1993). Areas surrounding our sites varied in land-use practices but consisted of some logging operations. With the exception of 14 sites that were documented as harvested and that we excluded from our analysis, there is no evidence suggesting the remainder of our sites were logged prior to the timber surveys we analyzed (Collins et al., 2015; Stephens et al., 2015).

Each historical inventory was located systematically based on the Public Land Survey System (PLSS) – the primary method used to survey rural and undeveloped land in the western United States. Both inventories used belt transects ranging from 20.1 m to 40.2 m wide by 402 m long and spanned the length of one 16.2 ha quarter-quarter (QQ) section. This resulted in a sampling intensity of either 5% (0.8 ha; Stanislaus) or 10% (1.6 ha; Sequoia) within each individual QQ section. Within transects, all conifers >15.2 cm diameter at breast height (DBH; 1.37 m above ground) were tallied by species and measured for DBH (cm). We standardized the tree lists to per hectare values for each sampling unit (QQ section), resulting in 644 samples distributed across the Sequoia ($n = 379$) and the Stanislaus ($n = 265$). We removed an additional 6 QQ sections from the Sequoia dataset ($n = 373$; 18,041 tree records) and 1 QQ section from the Stanislaus dataset ($n = 264$; 20,630 tree records) due to the low number of trees present within those sites (<5 trees tallied; Long and Shaw, 2005) and because the vegetation characteristics of those sites were not representative of our entire dataset.

Using the location of each 1911 QQ plot, we extracted data for 2011 forest conditions from F3, a 30-m resolution raster dataset. F3 integrates Forest Inventory and Analysis data and uses the Forest Vegetation Simulator to model initial stand conditions and project succession over time (Huang et al., 2018). It then uses those model outputs within Field and Satellite for Ecosystem Mapping to incorporate remotely-sensed data (Light Detection and Ranging data and Landsat imagery) to simulate spatiotemporal forest patterns across larger scales. Although uncertainties associated with F3 data may underrepresent non-forested areas (i.e., shrub-dominated sites) in its estimates (Huang et al., 2018), these sites were not a major component in our study areas (Stephens et al., 2015; Collins et al., 2015). For comparability with the 1911 QQ dataset, which inventoried all trees > 15.2 cm DBH, we used a similar minimum diameter in the F3 data (all trees > 12.7 cm DBH). While the lack of small tree data due to the 1911 sampling protocol will underestimate total stem densities, it will have less bias on basal area and SDI estimates (Burkhart et al., 2019; Murphy et al., 2021).

2.2. Data analysis

For each QQ section, we estimated tree density (trees ha^{-1}) and total basal area (m^2 ha^{-1}) by species. Total basal area is the cross-sectional area of all trees measured at DBH and represents the amount of area occupied by live tree stems. We also categorized each QQ section into a particular forest type based on the percentage of basal area dominated by pine (>50% pine; pine-mixed conifer), fir (>50% fir; mesic-mixed conifer), or not dominated by either pine or fir (≤50% pine and ≤50% fir; xeric-mixed conifer). Using the F3 dataset we derived 2011 tree density and basal area for the same area identified in each QQ section. For consistency, and to avoid mistyping forest conditions impacted by fire suppression, we binned the 2011 F3 data into forest types using the designation identified for each QQ section from the historical data.

Stand density index (SDI) is widely used by foresters as a measure of stocking level because its calculation, based on a combination of the size and number of trees, can be used as a relative measure of inter-tree competition or how 'crowded' a stand is. We estimated SDI by forest type using the summation method:

$$SDI = \sum TPH_i \left(\frac{D_i}{25.4}\right)^{1.6}$$

where TPH_i is the trees ha^{-1} represented by $tree_i$ and D_i represents the DBH (cm) of $tree_i$. The summation method is a derivative of Reineke's original SDI equation (Reineke, 1933) that uses the summation of individual tree diameters (Long and Daniel, 1990) instead of quadratic mean diameter. The summation method limits aggregation bias as tree diameters increase and can be applied to stands with uneven-age or irregular structure (Shaw, 2000).

A stand's absolute SDI is compared to a maximum value, estimated for different forest types, that is based on the concept of a maximum size-density relationship (Drew and Flewelling, 1979; Long, 1985). That maximum is calculated from a sampling of many stands, which are plotted on logarithmic scales of mean tree size against stem density from which an upper bounds line is calculated with a slope approximating $-3/2$. The $-3/2$ self thinning law, familiar to plant ecologists (Yoda, 1963), is mathematically equivalent to Reineke's stand density index (Burkhart et al., 2019) and forms the basis for stand management diagrams. These diagrams are used to estimate how changes in tree density affect tree size and to characterize competition benchmarks in forest development based on a stand's percent of maximum SDI [hereafter referred to as relative SDI] (Drew and Flewelling, 1979; Long, 1985). These benchmarks include the onset of competition (25% of maximum SDI), the lower limit of full site occupancy (35% of maximum SDI) and the 'zone of imminent mortality' driven by density-dependent competition (≥60% of maximum SDI) for a particular forest type (Long, 1985; Long and Shaw, 2005). A general forestry practice is to maintain stand stocking above 35% of maximum SDI to sustain stand growth, and schedule thinning harvests before a stand SDI reaches 60% of the maximum SDI to 'capture' density-dependent mortality (Drew and Flewelling, 1979).

Using these principles, we calculated the absolute and relative SDI of each 1911 QQ plot by forest type to assess the competitive environment under historical conditions. For pine-mixed conifer, maximum SDI was designated as 902 trees ha^{-1} (365 trees ac^{-1}; Zhang et al., 2013, 2019), for xeric-mixed conifer 1112 trees ha^{-1} (450 trees ac^{-1}) (Long and Shaw, 2005), and for mesic-mixed conifer 1359 trees ha^{-1} (550 trees ac^{-1}) (Long and Shaw, 2012). Absolute SDI values change according to the units of measurement used (VanderSchaaf, 2013), with maximum SDI values generally given in English units representing the number of trees per acre with a quadratic mean diameter (QMD) of 10 in. (25.4 cm). Since our data were calculated using metric units, we calculated relative SDI by converting our data to English units and used the following equation to calculate our observed SDI values compared to maximum estimates for each forest type:

$$SDI = \sum TPA_i * \left(\frac{D_i}{10}\right)^{1.6}$$

where TPA_i is trees $acre^{-1}$ represented by $tree_i$ and D_i represents the DBH (in) of $tree_i$.

We repeated these calculations in the same locations as the 1911 QQ plots using the F3 dataset to assess current forest conditions in 2011. The F3 data were only available in 25-cm diameter classes and did not identify the percentage of stems by species. Therefore, our estimates of SDI for the 2011 F3 data are reported based on the midpoints of these classes, while SDI estimates for our historical QQ dataset are based on individual tree DBH.

3. Results

Our forest type classifications of the historical data (QQ plots) were generally supported by species composition of each type. By frequency, pines made up 57% of stems in pine-mixed conifer, incense-cedar made up 42% of stems in xeric mixed conifer and fir made up 68% of stems in mesic-mixed conifer. In the historic data, there were slight differences in tree density and absolute SDI values between the Stanislaus and Sequoia study sites, but consistent differences between the forest types in both areas. For Sequoia, mean absolute SDI in pine-mixed conifer (205 trees ha^{-1}; 83 trees ac^{-1}) was 47% lower than what we observed in mesic-mixed conifer (391 trees ha^{-1}; 158 trees ac^{-1}) (Table 1).

This difference was less pronounced in Stanislaus, but mean absolute SDI in pine-mixed conifer (207 trees ha^{-1}; 84 trees ac^{-1}) was still 27% lower than what we estimated for mesic-mixed conifer (285 trees ha^{-1}; 115 trees ac^{-1}) (Table 1). For Sequoia, mean absolute SDI for xeric-mixed conifer (312 trees ha^{-1}; 126 trees ac^{-1}) was higher than pine-mixed conifer but was still 20% lower than absolute SDI in mesic-mixed conifer (Table 1). This difference was more pronounced in Stanislaus, with mean absolute SDI for xeric-mixed conifer (186 trees ha^{-1}; 75 trees ac^{-1}) 35% lower than absolute SDI observed in mesic-mixed conifer (Table 1). Absolute SDI$_{metric}$ in 2011 (473–632) had increased from 1911 values (186–391) by 1.6–2.5 times (Table 1). Following these results, in subsequent analyses, we combined the data from both sites while keeping the distinction of the different forest types.

Tree density and QMD for 1911 forest conditions were 47 trees ha^{-1} and 75 cm, 62 trees ha^{-1} and 66 cm, and 72 trees ha^{-1} and 70 cm for pine-mixed conifer, xeric-mixed conifer, and mesic-mixed conifer forest types respectively (Fig. 2). In contrast, contemporary (2011) tree densities and QMD were estimated as 347 trees ha^{-1} and 35 cm, 365 trees ha^{-1} and 35 cm, and 422 trees ha^{-1} and 34 cm for pine-, xeric-, and mesic-mixed conifer forest types, respectively. Overall, between 1911 and 2011, tree densities on average increased by six to seven fold while average tree size was reduced by 50%. This shift in contemporary forest conditions resulted from ingrowth with very high densities (>300 stems ha^{-1}) in the two smallest diameter classes (<51 cm DBH) in contrast to 1911′s low densities (≤25 stems ha^{-1}) and relatively even diameter distribution (Fig. 2).

All forest types in 1911 had mean relative SDIs that were much lower than the threshold associated with the onset of competition (Table 2) and the vast majority of stands (73–85% of stands) have densities that fell below the level of full site occupancy. Only one 1911 inventory was in the zone of imminent mortality (relative SDI ≥ 60%) (Table 2). In contrast, most (82–95%) contemporary stands were in the range of 'full competition' (35–59%) or 'imminent mortality' (≥60%). This shift in the competitive environment between historic and contemporary conditions is evident in the distribution of sample plots by time period and forest type. 'Violin' plots suggest contemporary forest conditions (2011) have an inverted distribution of relative SDI values compared to 1911 conditions (Fig. 3).

Table 1
Mean (interquartile range) absolute SDI for each forest type within historical (1911) and contemporary (2011) datasets in metric (trees ha^{-1}) and English (trees ac^{-1}) units.

Forest type	SDI (metric)		SDI (English)	
Stanislaus NF	1911	2011	1911	2011
Pine MC	207 (144–266)	585 (596–699)	84 (58–109)	237 (201–283)
Xeric MC	186 (120–236)	576 (501–676)	75 (49–95)	233 (203–274)
Mesic MC	285 (200–389)	628 (551–736)	115 (80–157)	254 (223–298)
Squoia NF				
Pine MC	205 (111–273)	473 (381–568)	83 (45–110)	191 (154–230)
Xeric MC	312 (219–395)	540 (426–666)	126 (89–160)	218 (173–270)
Mesic MC	391 (254–509)	632 (572–672)	158 (103–206)	256 (235–272)

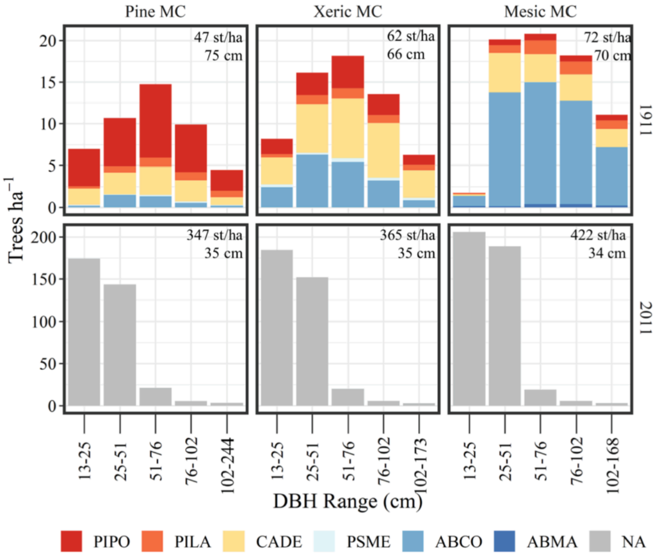

Fig. 2. For pine-mixed conifer, xeric-mixed conifer, and mesic-mixed conifer forest types the diameter distribution of the 1911 historical (top panels) and 2011 contemporary (bottom panels) datasets by DBH size classes (indicated by the range in DBH values) and species (1911 only). Density (st/ha) and quadratic mean diameter (QMD) (cm) values are shown in the upper right corner of each graph. Note the difference in the Y axis scale for tree density between the 1911 (top row, range 0–20) and 2011 (bottom row, range 0–200) data sets. Species codes are PIPO: *Pinus ponderosa*; PILA: *Pinus lambertiana*; CADE: *Calocedrus decurrens*; PSME: *Pseudotsuga menziesii*; ABCO: *Abies concolor*; ABMA: *Abies magnifica*; and NA: not available (F3 data only).

Table 2
For historical (1911) and contemporary (2011) datasets in each forest type; a) mean and interquartile range of relative SDI values (% of SDI$_{max}$); and b) the percentage of relative SDI observations within each competitive benchmark (free, partial, full, and imminent mortality).

	Pine MC		Xeric MC		Mesic MC	
a) Relative SDI (% of SDI$_{max}$)						
	1911	2011	1911	2011	1911	2011
Mean	23	59	25	50	28	46
(Range)	(14–30)	(48–73)	(16–33)	(42–60)	(18–36)	(42–50)
b) % of Relative SDI Observations In Each Competitive Benchmark						
Free (<25% SDI$_{max}$)	64	4	58	9	44	0
Partial (25–34% SDI$_{max}$)	21	6	21	9	29	5
Full (35–59% SDI$_{max}$)	14	42	20	57	27	95
IM (≥60% SDI$_{max}$)	<1	48	0	25	0	0

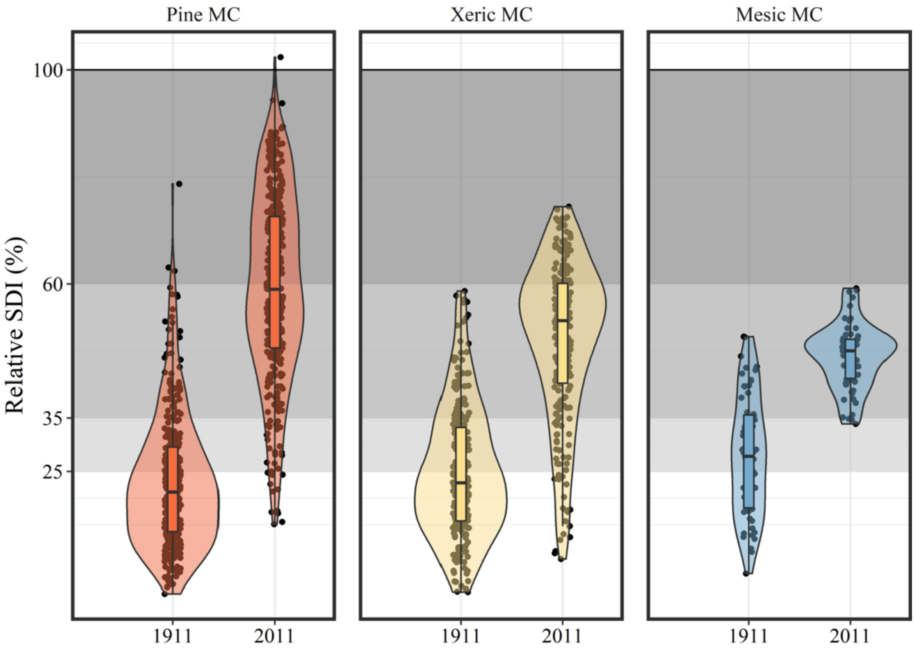

Fig. 3. 'Violin' plots of the relative stand density index (% of maximum SDI) within the historical (1911) and contemporary (2011) datasets by forest type. The colored region around each 'violin' plot illustrates the proportion of data located at that given value and dots represent the actual dataset observations. The gradient of gray shaded boxes indicate relative SDI benchmarks for free competition (in white; <25%), partial competition (25–34%), full site occupancy (35–59%) and imminent mortality (≥60%). The solid black horizontal line represents maximum SDI.

4. Discussion

Historically, dry western U.S. conifer forests persisted through recurrent fires, periodic severe droughts, and insect/pathogen outbreaks exhibiting resilience to an array of stresses. In contrast, contemporary forests have been prone to large-scale mortality often in areas with heavy fuel loads and high stand densities (Lydersen et al., 2014; Young et al., 2017). While resistance treatments, such as fuels reduction, can decrease large tree loss from fire, such specific prescriptions may not restore the forest's resilience to the broad array of interacting stresses and evolving disturbance regimes (Steel et al., 2021b). Our analysis of historical forest conditions produced by an active-fire regime suggest stand densities were so low that vigorous tree growth from a lack of competition may have been the essential characteristic of their ecological resilience. Many dry western U.S. forests historically had similar frequent, low-intensity fire regimes suggesting our results may be more broadly applicable to a larger geographic extent than the Sierra Nevada. Ecological theory and empirical field studies have associated robust growth rates with forest resilience to a range of stresses (Das et al., 2011, 2016; Cailleret et al., 2017; Zhang et al., 2019). In frequent-fire forests, the competitive environment can be indirectly but readily assessed using relative stand density index, a standard forest management metric that can be used to assess potential forest resilience.

We caution that our analysis is an observational, correlation study that infers ecological mechanisms driving resilience but did not directly test them. Furthermore, our calculations of stand conditions are constrained by the lack of a tally of the number and size of trees <15.2 cm DBH in the 1911 data, and the specific size and species composition of trees in the 2011 data. Abiotic factors such as edaphic conditions, local water balance, higher temperatures, and snow pack persistence can influence tree size-density relationships, affecting stand densities in ways that do not necessarily confer resilience to ecosystem stressors (van Mantgem et al., 2009; Stephenson et al., 2011; Paz-Kagan et al., 2017). Abiotic factors, however, are largely beyond the influence of management actions. Consequently, density management may be the best operational tool for forest managers to mitigate stress susceptibility at stand to landscape scales.

While relative SDI may be a valuable metric for assessing tree vigor and potential ecosystem resilience, it is a compliment to, but not replacement for, several important management measures currently used. Elevated fuel loads (Agee and Skinner, 2005) increase fire severity and can lead to extensive overstory mortality and potential type conversion even in forests with low SDI values. Recent research has found homogenous tree spatial patterns can increase wildfire severity, highlighting the importance of spatial variability in restoration treatments (Knapp et al., 2017; Koontz et al., 2020). Process-related metrics such as fire regime departure indicators (e.g., FRID) are also useful for understanding how antecedent management decisions and disturbance events can influence forest resilience (Safford and Van de Water, 2014). Although, it should be noted that fire regime departure metrics are indirect measures of conditions 'on the ground', and as such, may have limited applicability at finer spatial scales (Collins et al., 2018). At landscape-scales, heterogeneity measures of seral stages, fuel continuity, and pyrodiversity can help assess a fireshed's potential resistance to large, contiguous high severity fire (Loudermilk et al., 2012; Steel et al., 2021a). Resilience is a measure of forest adaptability to a range of stresses and as such no single metric can assess all potential scenarios, but our SDI work provides an efficient method to define resilience using a metric used in forest management for >75 years.

SDI is readily derived from field data that tallies the number and diameter of trees within a sampled area (Daniel et al., 1979). When expressed as a percentage of a maximum carrying capacity by forest type, it can provide a relative measure of site occupancy and the potential competitive environment. While SDI has most often been used to manage timber stands to maximize stand growth (i.e., thinning to capture mortality and influence stand development), it could also be used to maximize individual tree growth and vigor by creating a low competition environment which minimizes density-driven stress and mortality. By evaluating multiple stands, it can be applied to larger landscapes to assess competitive variability in forest conditions and whether that variability is aligned with resource availability and potential stresses. In the historical mixed-conifer forests we evaluated, mean relative SDI values were 23–28% of maximum, but interquartile ranges spanned 14–36% (Table 2). Managers could use this range to create stands with higher relative SDIs on sites with greater soil moisture availability and lower potential fire intensity, and lower relative SDI values on drier, steeper slopes more prone to drought and higher intensity burns.

Historical relative SDI values suggest that treatments for restoring forest resilience may need to be much more intensive then current forest management practices. The vast majority of historical stand conditions maintained by frequent, low-severity fire were at relative densities well below full site occupancy (35% of maximum SDI) and most were below the onset of competition (25% of maximum SDI). Nearly three quarters or more of all historical stands in each forest type had relative densities below the lower limit of full site occupancy (35% of maximum SDI). Using relative SDI as an approximate measure of the competitive environment can quantify the efficacy of forest treatments, providing resilience targets based on the competitive environment that may be more attuned to process and function than simpler structural metrics.

Reducing a forest's density and competitive environment has also been suggested by studies of forest carbon dynamics (Hurteau et al., 2016) and drought induced tree mortality (Maloney et al., 2008). Examining the carbon storage capacity of forests, Keith et al. (2009) suggested forests with historically frequent but now interrupted disturbance regimes, can temporarily 'pack on' more carbon from ingrowth. This additional biomass, however, destabilizes total forest carbon stocks due to increased susceptibility to drought and fire mortality (Earles et al., 2014; Hurteau et al., 2019). Keith et al. (2009) suggest secure carbon stores, or carrying capacity, is well below the higher but unstable carbon stocks that result from suppressing disturbances. Other current research has suggested an analogous pattern exists in forest adaptability to drought. During wet periods, trees can increase their photosynthetic surface beyond what can be supported during drought onset. This response, resulting in 'structural overshoot' (Jump et al., 2017), can increase drought induced mortality and reduce forest resilience (Goulden and Bales, 2019; Goodwin et al., 2020). Both of these concepts support the theory that frequent-fire forests are more resilient to these two most common stresses when forest density and competition are significantly reduced.

4.1. Management implications

If forests that historically had frequent-fire disturbance regimes were characterized by minimal competition, many current post-treatment targets are probably misaligned with creating resilience. Competition is the driver of how managed forest stands develop, when thinning occurs, and which trees are favored due to their size and capture of growth resources. For example, relative SDI and its competition benchmarks are the basis for models such as the Forest Vegetation Simulator (FVS), widely used by the U.S. Forest Service to estimate forest growth, yield, and mortality. As a predictive tool, SDI is used to determine the timing and intensity of prescriptions guiding harvests. A general practice when managing for harvest yields is to reduce stocking to no less than 35% of maximum SDI, and schedule thinnings as a stand SDI approaches 60% of the maximum SDI to 'capture' density-dependent mortality (Drew and Flewelling, 1979). Relative SDI for historical forests that we evaluated, however, was 23–28% of maximum, where competition is considered to be non-existent (<25%) or in a range of low competition (25–34%). Instead of 35% representing a *minimum* stocking level, our analysis suggests that it may more appropriately represent a *maximum* stocking level.

This perspective shift in maximum stand-level stocking would also impact landscape management if current standards are significantly underestimating the forest area needing density reduction. In the U.S. Forest Service's Region 5, for example, priority areas for fuels and density reduction treatments are identified as having a relative SDI $\geq$ 60%. If thinnings were being applied to the areas we assessed with the 2011 data using this criteria, only 48%, 25% and 0% of contemporary pine, xeric, and mesic mixed-conifer plots, respectively, would receive treatment. However, using a relative SDI maximum of 35%, treatment levels to minimize competition would increase to 96%, 91% and 100%, respectively, for each of the forest types we assessed.

Another current management practice, maintaining high levels of canopy cover (>40–50%) to provide sensitive species habitat, would need to become more congruent with local biotic conditions that could support higher canopy cover. Species such as the spotted owl (*Strix occidentalis*) and their principal prey (Meyer et al., 2007) have been associated with dense stands of large, old trees and high canopy cover (Verner et al., 1992). These stands are often in steep, inaccessible areas that weren't logged (Peery et al., 2017), and at current tree densities may not be resilient unless they are located in highly productive (often wet) sites (North et al., 2017; Fricker et al., 2019). Managers may need to create lower tree densities and canopy cover conditions across the larger landscape, but could still foster owl habitat in relatively compact, more productive areas such as existed in some of the stand inventories in the 1911 data represented by points in the upper portion of the 'violin' plots (Fig. 3). Using FVS to assess canopy conditions in our historical data set, we estimated the 1911 forests averaged between 12 and 28% canopy cover (Collins et al., 2015; Stephens et al., 2015) across most of the landscape. Current management guidelines for canopy cover, if widely applied, may attempt to perpetuate contemporary habitat conditions that resulted from fire suppression, but which lack resilience to changing climate and disturbance patterns.

Resilience is an ecosystem attribute of community persistence and stress tolerance, and in western dry conifer forests, should not be conflated simply with fire resistance (Stephens et al., 2021). The first two decades of the new century have demonstrated that disturbance complexes including drought, insect epidemics, and landscape-level, high-severity fire will be stressing and in some places, type converting dry, western U.S. conifer forests. For example, the 2012–2016 drought in overstocked Sierra Nevada forests, produced unprecedented tree mortality (>150 million), particularly of large trees (Young et al., 2020). Although the impacts of this mortality event are significant on their own, the potential for compounded disturbance interactions may occur when the massive pulse of large dead fuels subsequently burns (Goodwin et al., 2021), possibly leading to widespread type conversion (Stephens et al., 2018). Managing forests to minimize competition is a significant departure from current practices that use competitive dynamics to guide the development of forest composition, tree size, and stem spatial pattern (Fry et al., 2014). If forests are to be resilient to a variety of stresses, including climate change, robust tree vigor resulting from 'free' growth may be needed. SDI provides a widely-used measure of a forest's competitive environment and may help managers operationalize resilience in western US frequent fire forests.

CRediT authorship contribution statement

Malcolm P. North: Conceptualization, Methodology, Writing – original draft, Supervision, Project administration. **Ryan E. Tompkins:** Conceptualization, Methodology, Writing – review & editing. **Alexis A. Bernal:** Formal analysis, Methodology, Writing – review & editing, Visualization. **Brandon M. Collins:** Conceptualization, Methodology, Writing – review & editing. **Scott L. Stephens:** Conceptualization, Methodology, Writing – review & editing. **Robert A. York:** Conceptualization, Methodology, 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

We thank two anonymous reviewers whose edits and comments improved manuscript clarity. We appreciate conversations and feedback on the concept of resilience from Mark Schwartz, U.C. Davis and Pat Manley, USFS PSW Research Station. We also thank Jan van Wagtendonk, Yosemite N.P., for introducing use to the QQ historical datasets, and Lee Tarnay and Carlos Ramirez, USFS Region 5 Remoting Sensing, for providing the F3 data and patiently answering our questions. We greatly appreciate the help of Julia Murphy for providing us with the initial R code for estimating SDI. Funding for the initial analysis of these historic datasets was provided by the NPS Pacific West Region, USFS Pacific Southwest Research Station, US Joint Fire Sciences Program, and the UC Agriculture and Natural Resources Division.

References

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211 (1-2), 83–96.

Bergen, S.D., Bolton, S.M., L. Fridley, J., 2001. Design principles for ecological engineering. Ecol. Eng. 18 (2), 201–210.

Bond, W., Keeley, J., 2005. Fire as a global `herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20 (7), 387–394.

Brand, F.S., Jax, K., 2007. Focusing the meaning(s) of resilience: Resilience as a descriptive concept and a boundary object. Ecol. Soc. 12.

Burkhart, H.E., Avery, T.E., Bullock, B.P., 2019. Forest Measurements, sixth ed. Wavelend Press, Inc. Long Grove, Illinois.

Cailleret, M., Jansen, S., Robert, E.M., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Change Biol. 23, 1675–1690.

Cailleret, M., Dakos, V., Jansen, S., Robert, E.M., Aakala, T., Amoroso, M.M., Antos, J.A., Bigler, C., Bugmann, H., Caccianaga, M., Camarero, J.J., 2019. Front. Plant Sci. 9, 1964.

Caprio, A., Swetnam, T.W., 1993. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In: 5th Proceedings: Symposium on Fire in Wilderness and Park Management, Missoula, MT, pp. 173–179.

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4 (8), 765–781.

Collins, B.M., Das, A.J., Battles, J.J., Fry, D.L., Krasnow, K.D., Stephens, S.L., 2014. Beyond reducing fire hazard: Fuel treatment impacts on overstory tree survival. Ecol. Appl. 24 (8), 1879–1886.

Collins, B.M., Lydersen, J.M., Everett, R.G., Fry, D.L., Stephens, S.L., 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecol. Appl. 25 (5), 1167–1174.

Collins, B.M., Miller, J.D., Kane, J.M., Fry, D.L., Thode, A.E., 2018. Characterizing fire regimes. In: van Wagtendonk, J.W., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites, J. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, USA.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A., Fornwalt, P.J., Fule, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.A., Prichard, S., Rodman, K.C., 2020. Wildfire-driven forest conversion in western North American landscapes. Bioscience 70, 659–673.

Daniel, T.W., Helms, J.A., Baker, F.S., 1979. Principles of silviculture (No. Ed. 2). McGraw-Hill Book Company.

Das, A., Battles, J., van Mantgem, P.J., Stephenson, N.L., 2008. Spatial elements of mortality risk in old-growth forests. Ecology 89 (6), 1744–1756.

Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manage. 261 (7), 1203–1213.

Das, A.J., Stephenson, N.L., Davis, K.P., 2016. Why do trees die: Characterizing the drivers of background tree mortality. Ecology 97 (10), 2616–2627.

DeRose, R.J., Long, J.N., 2014. Resistance and resilience: A conceptual frameowrk for silviculture. For. Sci. 60, 1205–1212.

Drew, T.J., Flewelling, J.W., 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25, 518–532.

Earles, J.M., North, M.P., Hurteau, M.D., 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol. Appl. 24 (4), 732–740.

Fettig, C.J., Wuenschel, A., Balachowski, J., Butz, R.J., Jacobsen, A.L., North, M.P., Ostoja, S.M., Pratt, R.B., Standiford, R.B. 2019. Drought management recommendations for California. In: Vose, J., Patel-Weynand, T., Peterson, D.L., Luce, C.H. (Eds.), Drought impacts on U.S. forests and rangelands: Translating science into management responses. WO-GTR-98. U.S. Department of Agriculture, Forest Service, Washington Office, Washington, DC, pp. 71–93.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37 (8), 550–556.

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. https://doi.org/10.1371/journal.pone.0088985.

Goodwin, M.J., North, M.P., Zald, H.S.J., Hurteau, M.D., 2020. Changing climate reallocates the carbon debt of frequent-fire forests. Glob. Change Biol. 26 (11), 6180–6189.

Goodwin, M.J., Zald, H.S.J., North, M.P., Hurteau, H.D., 2021. Climate-driven tree mortality and fuel aridity increase wildfire's potential heat flux. Geophys. Res. Lett. 48.

Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. Nat. Geosci. 12 (8), 632–637.

Greiner, S.M., Grimm, K.E., Waltz, A.E.M., 2020. Managing for resilience? Examining management implications of resilience in southwestern National Forests. J. Forest. 118 (4), 433–443.

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323–334.

Gunderson, L.H., 2000. Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. 31 (1), 425–439.

Hagmann, R.K., Hessburg, P.F., Prichard, S.J., Povak, N.A., Brown, P.M., Fulé, P.Z., Keane, R.E., Knapp, E.E., Lydersen, J.M., Metlen, K.L., Reilly, M.J., Sánchez Meador, A.J., Stephens, S.L., Stevens, J.T., Taylor, A.H., Yocom, L.L., Battaglia, M.A., Churchill, D.J., Daniels, L.D., Falk, D.A., Henson, P., Johnston, J.D., Krawchuk, M.A., Levine, C.R., Meigs, G.W., Merschel, A.G., North, M.P., Safford, H.D., Swetnam, T. W., Waltz, A.E.M., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol. Appl. 31 (8) https://doi.org/10.1002/eap.v31.810.1002/eap.2431.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. Am. Nat. 94, 421–425.

Harrison, G.W., 1979. Stability under environmental stress: Resistance, resilience, persisitence, and variability. Am. Nat. 113, 659–669.

Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V.R., Churchill, D.J., Hagmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Slater, R.B., 2019. Climate, environment, and disturbance history govern resilience of western North American forests. Front. Ecol. Evol. 7, 239.

Higuera, P.E., Metcalf, A.L., Miller, C., Buma, B., McWethy, D.B., Metcalf, E.C., Ratajczak, Z., Nelson, C.R., Chaffin, B.C., Stedman, R.C., McCaffrey, S., Schoennagel, T., Harvey, B.J., Hood, S.M., Schultz, C.A., Black, A.E., Campbell, D., Haggerty, J.H., Keane, R.E., Krawchuk, M.A., Kulig, J.C., Rafferty, R., Virapongse, A., 2019. Integrating subjective and objective dimensions of resilience in fire-prone landscapes. Bioscience 69, 379–388.

Holling, C.S. 1996. Engineering resilience versus ecological resilience. In: Schulze, P. (Ed.) Engineering within ecological constraints. National Academy of Engineering, pp. 31–43.

Huang, S., Ramirez, C., McElhaney, M., Evens, K., 2018. F3: Simulating spatiotemporal forest change from field inventory, remote sensing, growth modeling and management actions. For. Ecol. Manage. 415, 26–37.

Hurteau, M.D., Liang, S., Martin, K.L., North, M.P., Koch, G.W., Hungate, B.A., 2016. Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. Ecol. Appl. 26 (2), 382–391.

Hurteau, M.D., North, M.P., Koch, G.W., Hungate, B.A., 2019. Managing for disturbance stabilizes forest carbon. Proc. Natl. Acad. Sci. 116, 10193–10195.

Innes, J.C., North, M.P., Williamson, N., 2006. Effect of thinning and prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth mixed-conifer forest. Can. J. For. Res. 36 (12), 3183–3193.

Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Glob. Change Biol. 23 (9), 3742–3757.

Kalies, E.L., Yocom Kent, L.L., 2016. Tamm Review: Are fuel treatments effective at achieving ecological and social objectives? A systematic review. For. Ecol. Manage. 375, 84–95.

Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proc. Natl. Acad. Sci. 106 (28), 11635–11640.

Kelly, M., Allen-Diaz, B., Kobzina, N., 2005. Digitization of a historic dataset: the Wieslander California vegetation type mapping project. Madroño 52 (3), 191–201.

Kilgore, B.M., Taylor, D., 1979. Fire history of a sequoia-mixed conifer forest. Ecology 60, 129–142.

Knapp, E.E., Lydersen, J.M., North, M.P., Collins, B.M., 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. For. Ecol. Manage. 406, 228–241.

Koontz, M.J., North, M.P., Werner, C.M., Fick, S.E., Latimer, A.M., Swenson, N., 2020. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. Ecol. Lett. 23 (3), 483–494. https://doi.org/10.1111/ele.13447.

Larsen, J.B., 1995. Ecological stability of forests and sustainable silviculture. For. Ecol. Manage. 73 (1-3), 85–96.

Leiberg, J.B., 1902. Forest conditions in the northern Sierra Nevada, California. U.S.G.S. Professional Pager 8, Series H, Forestry, 5. Washington D.C. Government Printing Office.

Long, J.N., 1985. A practical approach to density management. For. Chron. 61 (1), 23–27.

Long, J.N., Daniel, T.W., 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For. 5 (3), 93–96.

Long, J.N., Shaw, J.D., 2005. A density management diagram for even-aged ponderosa pine stands. West. J. Appl. For. 20 (4), 205–215.

Long, J.N., Shaw, J.D., 2012. A density management diagram for even-aged Sierra Nevada mixed-conifer stands. West. J. Appl. For. 27 (4), 187–195.

Loudermilk, E.L., O'Brien, J.J., Mitchell, R.J., Cropper, W.P., Hiers, J.K., Grunwald, S., Grego, J., Fernandez-Diaz, J.C., 2012. Linking complex forest fuel structure and fire behaviour at fine scales. Int. J. Wildland Fire 21 (7), 882. https://doi.org/10.1071/WF10116.

Lutz, J.A., van Wagtendonk, J.W., Franklin, J.F., 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. For. Ecol. Manage. 257 (11), 2296–2307.

Lydersen, J., North, M., Collins, B., 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. For. Ecol. Manage. 328, 326–334.

Maloney, P.E., Smith, T.F., Jensen, C.E., Innes, J., Rizzo, D.M., North, M.P., 2008. Initial tree mortality, and insect and pathogen response to fire and thinning restoration treatments in an old growth, mixed-conifer forest of the Sierra Nevada, California. Can. J. For. Res. 38 (12), 3011–3020.

Meyer, M., Kelt, D., North, M., 2007. Microhabit associations of northern flying squirrels in burned and thinned stands of the Sierra Nevada. Am. Midl. Nat. 157, 202–211.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecol. Appl. 17 (8), 2145–2151.

Murphy, J.S., York, R., Rivera Huerta, H., Stephens, S.L., 2021. Characteristics and metrics of resilient forests in the Sierra de San Pedro Martír, Mexico. For. Ecol. Manage. 482, 118864. https://doi.org/10.1016/j.foreco.2020.118864.

North, M., Collins, B., Safford, H., Stephenson, N., 2016. Montane Forests. In: Mooney, H., Zavelta, E. (Eds.), Ecosystems of California, U.C. Press, Berkeley, CA. 984, pp. 553–578.

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., Mark, T., Moskal, M., Munton, T., Peery, Z., Ramirez, C., Sollmann, R., White, A., Whitmore, S., 2017. Cover of tall trees best predicts California spotted owl habitat. For. Ecol. Manage. 405, 166–178.

Paz-Kagan, T., Brodrick, P.G., Vaughn, N.R., Das, A.J., Stephenson, N.L., Nydick, K.R., Asner, G.P., 2017. What mediates tree mortality during drought in the southern Sierra Nevada? Ecol. Appl. 27 (8), 2443–2457.

Peery, M.Z., Gutiérrez, R.J., Manley, P.N. Stine, P.A., North, M.P. 2017. Synthesis and interpretation of California spotted owl research within the context of public forest management. In: Bioregional Assessment of the California Spotted Owl. USDA Forest Service, PSW-GTR-254, pp. 216–237.

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity and scale. Ecosystems 1, 6–18.

Prichard, S.J., Hessburg, P.F., Hagmann, R.K., Povak, N.A., Dobrowski, S.Z., Hurteau, M. D., Kane, V.R., Keane, R.E., Kobziar, L.N., Kolden, C.A., North, M., Parks, S.A., Safford, H.D., Stevens, J.T., Yocom, L.L., Churchill, D.J., Gray, R.W., Huffman, D.W., Lake, F.K., Khatri-Chhetri, P., 2021. Adapting western North American forests to climate change and wildfires: ten common questions. Ecol. Appl. https://doi.org/10.1002/eap.2433.

PRISM Climate Group, 2021. Data explorer: Annual precipitation, minimum temperature, and maximum temperature [data].

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.

Safford, H.D., North, M.P., Meyer, M.D. 2012. Climate change and the relevance of historical forest conditions. In: North, M. (Ed.), Managing Sierra Nevada Forests, General Technical Report PSW-GTR-237. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. 184 pp. 23–45.

Safford, H.D., Van de Water, K.M., 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California. Res. Pap. PSW-RP-266. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 59.

Shaw, J.D., 2000. Application of stand density index to irregularly structured stands. West. J. Appl. For. 15 (1), 40–42.

Steel, Z.L., Collins, B.M., Sapsis, D.B., Stephens, S.L., 2021a. Quantifying pyrodiversity and its drivers. Proc. Roy. Soc. B 288 (1948). https://doi.org/10.1098/rspb.2020.3202.

Steel, Z.L., Goodwin, M.J., Meyer, M.D., Fricker, G.A., Zald, H.S.J., Hurteau, M.D., North, M.P., 2021b. Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality? Ecosphere 12 (1). https://doi.org/10.1002/ecs2.v12.110.1002/ecs2.3344.

Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecol. Appl. 19, 305–320.

Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., Meyer, M.D., 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the southern Sierra Nevada. Ecosphere 6 (5), art79. https://doi.org/10.1890/ES14-00379.1.

Stephens, S.L., Miller, J.D., Collins, B.M., North, M.P., Keane, J.J., Roberts, S.L., 2016. Wildfire impacts on California spotted owl nesting habitat in the Sierra Nevada. Ecosphere 7 (11), e01478. https://doi.org/10.1002/ecs2.1478.

Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North, M.P., Safford, H., Wayman, R.B., 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68, 77–88.

Stephens, S.L., Battaglia, M.A., Churchill, D.J., Collins, B.M., Coppoletta, M., Hoffman, C. M., Lydersen, J.M., North, M.P., Parsons, R.A., Ritter, S.M., Stevens, J.T., 2021. Forest restoration and fuels reduction: Convergent or divergent? Bioscience 71, 85–101.

Stephenson, N.L., van Mantgem, P.J., Bunn, A.G., Bruner, H., Harmon, M.E., O'Connell, K.B., Urban, D.L., Franklin, J.F., 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. Ecol. Monogr. 81 (4), 527–555.

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. For. Ecol. Manage. 406, 28–36.

Stevens, J.T., Boisramé, G.F.S., Rakhmatulina, E., Thompson, S.E., Collins, B.M., Stephens, S.L., 2020. Forest vegetation change and its impacts on soil water following 47 years of managed wildfire. Ecosystems 23 (8), 1547–1565.

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., Lloret, F., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21 (2), 243–252.

USDA-FS. 2012. The Forest Planning Rule. Online http://www.fs.usda.gov/detail/planningrule.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323 (5913), 521–524.

van Mantgem, P.J., Falk, D.A., Williams, E.C., Das, A.J., Stephenson, N.L., 2018. Pre-fire drought and competition mediate post-fire conifer mortality in western U.S. National Parks. Ecol. Appl. 28 (7), 1730–1739.

VanderSchaaf, C.L. 2013. Reineke's stand density index: a quantitative and non-unitless measure of stand density. In: Proceedings of the 15th Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS-GTR-175:577–579.

Verner J., McKelvey, K.S., Noon, B.R., Gutiérrez, R..J, Gould Jr., G.I., Beck, T.W., 1992. The California spotted owl: A technical assessment of its current status. USDA Forest Service Gen. Tech. Rep. PSW-GTR-133.

Westman, W.E., 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28 (11), 705–710.

Yoda, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants. XI). J. Inst. Polytech. Osaka City Univ. Ser. D. 14, 107–129.

Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., Lloret, F., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20 (1), 78–86.

Young, D.J., Meyer, M., Estes, B., Gross, S., Wuenschel, A., Restaino, C., Safford, H.D., 2020. Forest recovery following extreme drought in California, USA: natural patterns and effects of pre-drought management. Ecol. Appl. 30, e02002.

Zhang, J., Oliver, W.W., Powers, R.F., 2013. Reevaluating the self-thinning boundary line for ponderosa pine (*Pinus ponderosa*) forests. Can. J. For. Res. 43, 963–971.

Zhang, J., Finley, K.A., Johnson, N.G., Ritchie, M.W., 2019. Lowering stand density enhances resiliency of ponderosa pine forests to disturbances and climate change. For. Sci. 65 (4), 496–507.