Can low-severity fire reverse compositional change in montane forests of the Sierra Nevada, California, USA?

KENDALL M. L. BECKER† AND JAMES A. LUTZ

Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, Utah 84322 USA

Abstract. Throughout the Sierra Nevada, nearly a century of fire suppression has altered the tree species composition, forest structure, and fire regimes that were previously characteristic of montane forests. Species composition is fundamentally important because species differ in their tolerances to fire and environmental stressors, and these differences dictate future forest structure and influence fire regime attributes. In some lower montane stands, shade-tolerant, fire-sensitive species have driven a threefold increase in tree density that may intensify the risk of high-severity fire. In upper montane forests, which were historically characterized by longer fire return intervals, the effects of fire exclusion are both less apparent and less studied. Although land managers have been reintroducing fire to lower and upper montane forests for >4 decades, the potentially restorative effects of these actions on species composition remain largely unassessed. We used tree diameter and species data from 51 recently burned and 46 unburned plots located throughout lower and upper montane forests in Yosemite National Park and Sequoia & Kings Canyon National Parks to examine the effects of low- to moderate-severity (hereafter, lower-severity) fire on the demography of seven prevalent tree species. The density of *Abies concolor* <30 cm diameter at breast height (dbh) was significantly lower in burned plots than unburned plots; densities of *A. concolor* 30–45 cm dbh, *A. magnifica* <30 cm dbh, and *Calocedrus decurrens* <15 cm dbh were lower in burned plots than unburned plots at a marginal level of significance. These diameter thresholds represent the maximum size at which each species is likely to experience significant mortality from lower-severity fire. We overlaid these thresholds on historical and contemporary diameter distributions to show that: (1) lower-severity fire has reduced mean tree density to historical levels for *A. concolor* but not for *C. decurrens,* and (2) variability in tree density among plots that burned at lower severity exceeded the range of tree densities reported in historical data sets. High proportions of shade-tolerant species in some postfire stands may increase the prevalence of shade-tolerant species in the future, a potential concern for managers who seek to minimize ladder fuels and promote forest structure that is less prone to high-severity fire.

† **E-mail:** kendall.becker@aggiemail.usu.edu

INTRODUCTION

Across the dry forests of western North America, a century of fire suppression has resulted in widespread change in tree species composition (i.e., the proportion and abundance of tree species; hereafter, composition) and structure (i.e., the density, basal area, and spatial arrangement of stems), driven by greater abundance of fire-sensitive, shade-tolerant tree species (Parsons and DeBenedetti 1979, Dolanc et al. 2014, Stephens et al. 2015). Although fire is now viewed as an inevitable disturbance and key ecological process in these systems (Smith et al.

2016), fire reintroduction is hindered by accumulations of ground and ladder fuel that increase the risk of high-severity fire (Thode et al. 2011). Management objectives in this context have focused on restoring fire, reducing fuels, and creating forest structure that can support a low-severity fire regime (North et al. 2007, Schwilk et al. 2009).

Composition and forest structure are interrelated and both are integral to managing fire-suppressed forests (Stephenson 1999, North et al. 2007). High shade tolerance enables some species to reach high densities in understory positions, and the high level of shade in dense forests further promotes regeneration of shade-tolerant species. Thus, species composition affects the trajectory and pace of forest structural development (Kobe et al. 1995) and should factor in to management strategies to reduce tree density.

Land managers have reintroduced fire to fire-suppressed forests in the past four decades (van Wagtendonk 2007), but few studies have assessed the impact of this management action on species composition (North et al. 2007, Webster and Halpern 2010, Collins et al. 2011). Here we examine the effects of fire on the diameter distributions of individual tree species to facilitate fire use management decisions that consider both forest structure and composition.

Compositional change enabled by fire exclusion has increased tree density, which may heighten the risk of high-severity fire and decrease the survival of large-diameter trees. Previous studies have temporally linked fire exclusion to a threefold increase in tree density, driven by positive feedbacks that are associated with burgeoning populations of fire-sensitive, shade-tolerant *Abies concolor* (white fir) and *Calocedrus decurrens* (incense-cedar; tree species' relative tolerances are provided in Appendix S1: Table S1; Vankat and Major 1978, Scholl and Taylor 2010, Knapp et al. 2013, Dolanc et al. 2014, Stephens et al. 2015). Shade precludes the establishment of shade-intolerant *Pinus* species and facilitates the further recruitment of shade-tolerant *Abies* and *Calocedrus* species, thereby perpetuating the dominance of shade-tolerant species (Keeley 2012). Attempts to use low-severity fire to disrupt this cycle may be stymied by the fuel bed characteristics of shade-tolerant species, such as the short leaf length of *A. concolor* that promotes less severe fire behavior

and thus facilitates the survival of the current constituents (Stephens et al. 2004, Schwilk and Caprio 2011). When weather conditions are conducive to high-severity fire, however, the fire-damping effect of short needles may be overshadowed by the high density of understory trees, the crowns of which can spread fire from the ground to the canopies of mature trees, thereby transforming low-severity surface fires to high-severity crown fires (Menning and Stephens 2007).

As tree density and risk of high-severity fire have increased, large-diameter trees have decreased in abundance, potentially due to greater susceptibility to native and introduced pathogens (e.g., *Heterobasidium annosum* and *Cronartium ribicola*), bark beetles (e.g., *Scolytus ventralis* and *Dendroctonus* spp.), and competition for limited resources in high-density neighborhoods (Sherman and Warren 1988, Guarín and Taylor 2005, Lutz et al. 2009*a*, Das et al. 2011). Large-diameter trees contribute disproportionately to the amount and heterogeneity of forest biomass (e.g., Lutz et al. 2012, 2013) and the annual sequestration of carbon (e.g., Stephenson et al. 2014). Importantly, large-diameter trees have well-developed root systems and thick bark, attributes that confer drought tolerance and fire resistance. Thus, maintaining forests that include large-diameter constituents is a key management objective, particularly considering that warmer temperatures and more variable precipitation patterns are projected to increase fire size, frequency, and severity (Appendix S1: Table S1; Westerling et al. 2006, Littell et al. 2009, Lutz et al. 2009*b*).

Wildland fires and prescribed burns have been utilized to reduce tree density and remove surface and ladder fuels that facilitate high-severity fire and increase the competitive stresses on large-diameter trees (van Wagtendonk 2007). In general, the survivorship of trees reflects species' tolerances: higher proportions of small-diameter (<10 cm) *Abies* have been killed in prescribed burns than small-diameter *Pinus* (Appendix S1: Table S1; Kilgore 1973, Schwilk et al. 2006, Collins et al. 2011, van Mantgem et al. 2013, but see North et al. 2007). Few studies, however, have addressed whether current fire use practices in fire-suppressed forests effectively restart the process of compositional change at the historical baseline. Collins et al. (2011) found that moderate-severity fire within a >4000-ha area

reduced density of trees >30.5 cm dbh to historical levels but that low-severity fire did not. This suggests that some individuals that established during the fire suppression era have attained fire-resistant size and "escaped" from restorative efforts to reduce tree density with low-severity fire (Kilgore 1973, Miller and Urban 2000, North et al. 2005). Understanding the extent of this phenomenon at the species level could have important management implications if disproportionate numbers of shade-tolerant individuals have indeed attained fire-resistant size.

We analyzed recently burned and unburned forests in Yosemite National Park and Sequoia & Kings Canyon National Parks to quantify the effects of low- to moderate-severity fire (hereafter, lower-severity fire) on individual tree species. We sampled along a compositional gradient that spanned both lower and upper montane forests—areas altered by marked departures from historical disturbance regimes and areas that still reside within their historical range of variability, respectively (Fulé and Laughlin 2007, Dolanc et al. 2013). Our objectives were to: (1) identify which tree species and diameter classes exhibited a reduction in density following lower-severity fire; and (2) compare tree density at burned plots with historical data sets to determine whether the reintroduction of lower-severity fire effectively reversed the compositional changes observed since the onset of fire suppression. We also compared the satellite-derived severity of successive fires in our data set to determine whether fire reintroduction reduced the severity of subsequent fires as some studies have shown (e.g., van Wagtendonk et al. 2012).

STUDY AREA

Physical environment

Yosemite National Park (37°42′ N, 119°39′ W) and Sequoia & Kings Canyon National Parks (36°47′ N, 118°40′ W) are located on the western slope of the central Sierra Nevada (Fig. 1). The climate is Mediterranean, with cool, wet winters and warm, dry summers. Orographic effects cause temperature and precipitation to vary with elevation. Soil water-holding capacity also varies with elevation; low-elevation, unglaciated soils are deeper, having undergone a longer period of development, while high-elevation

soils are shallower and less developed. Montane forest cover extends from 861 to 3385 m in Yosemite (study plot range: 1338–2705 m) and from 1125 to 3522 m in Sequoia & Kings Canyon (study plot range: 1600–2645 m). At the lower limit of contiguous forest cover 20–25% of annual precipitation falls as snow, whereas in the upper montane zone 70–90% falls as snow (Fites-Kaufman et al. 2007). Cooler temperatures in the upper montane zone maintain snow coverage for up to 200 d/yr, and maximum snow depths typically vary between 2.5 and 4.0 m (van Wagtendonk and Fites-Kaufman 2006). Among the Yosemite plots, mean modeled January temperatures ranged from −4.0° to 5.8°C, mean July temperatures ranged from 12.5° to 22.6°C, and annual precipitation ranged from 983 to 1370 mm. Among the plots in Sequoia & Kings Canyon, mean January temperatures ranged from −2.4° to 5.1°C, mean July temperatures ranged from 14.6° to 22.4°C, and annual precipitation ranged from 778 to 1196 mm (1981–2010 climate normals; PRISM 2012).

Vegetation

Lower montane mixed-conifer stands predominate between 1500 and 1650 m (van Wagtendonk and Fites-Kaufman 2006). Principal tree species are *Abies concolor*, *Calocedrus decurrens*, *Pinus jeffreyi* (Jeffrey pine), *P. lambertiana* (sugar pine), *P. ponderosa* (ponderosa pine), and *Quercus kelloggii* (California black oak). *Pinus ponderosa* and *Q. kelloggii* generally occupy lower elevations, where decreased water availability restricts *A. concolor* abundance. Subdominant *C. decurrens* and *P. lambertiana* extend throughout lower montane forests. Minor constituents include *Cornus nuttallii* (Pacific dogwood), *Q. chrysolepis* (canyon live oak), and *Pseudotsuga menziesii* (Douglas-fir).

Upper montane stands generally occur above 1800 m in Yosemite and above 2200 m in Sequoia & Kings Canyon (Fites-Kaufman et al. 2007). *Abies magnifica* (red fir) coexists with *A. concolor* at lower elevations and with *P. jeffreyi*, *P. contorta* (lodgepole pine), *P. monticola* (western white pine), and *Tsuga mertensiana* (mountain hemlock) at higher elevations. *Juniperus occidentalis* (Sierra juniper) and *P. jeffreyi* woodlands occupy granitic outcrops. Plant nomenclature follows Flora of North America (Flora of North America Editorial Committee 1993+).
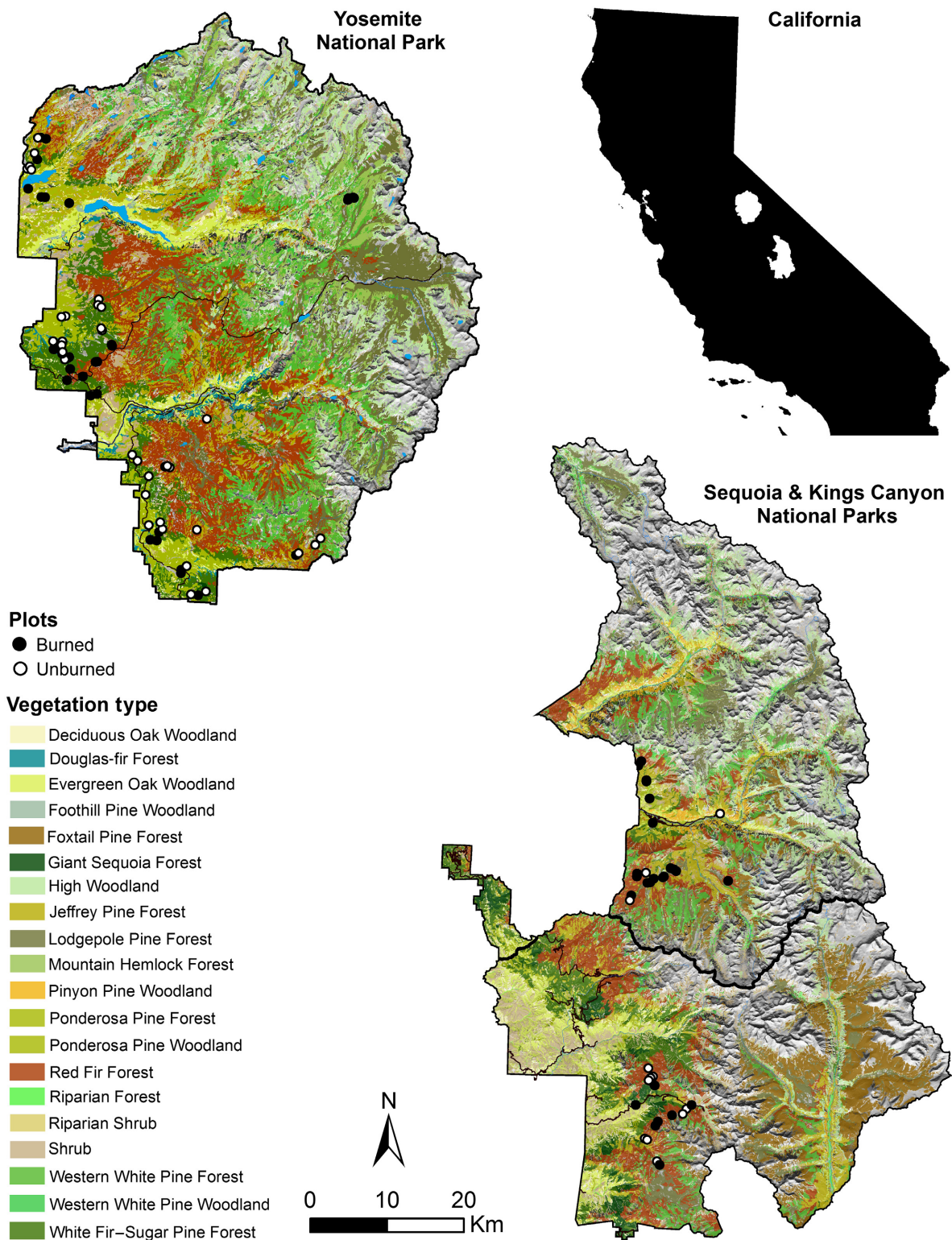
Fig. 1. Locations of 105 study sites in Yosemite and Sequoia & Kings Canyon National Parks, California, USA, superimposed on lower and upper montane vegetation types.

Disturbance history

Historically, mean fire return intervals (FRIs) of 5 to 80 yr characterized the lower montane zone, while mean FRIs ranged from 15 to 290 yr in upper montane forests (Skinner and Chang 1996, van Wagtendonk and Fites-Kaufman 2006, Van de Water and Safford 2011). Longer snow-pack retention at higher elevations reduced the likelihood of ignition despite the higher density of lightning strikes (Lutz et al. 2009*b*).

Fire suppression in Yosemite and Sequoia & Kings Canyon began in 1890 (van Wagtendonk 2007), causing fuel to accumulate and precipitating a shift toward higher-severity fires relative to historical fire regimes (van Wagtendonk and Lutz 2007, Thode et al. 2011). Park managers have used prescribed burns and lightning ignitions to restore fire in these areas since 1968 in Sequoia & Kings Canyon and since 1972 in Yosemite (Kilgore and Briggs 1972, van Wagtendonk 2007). A mosaic of forest patches has resulted, including some patches that have burned up to five times in the last 40 yr and others that have not burned since before the adoption of fire suppression policies.

Between 1968 and 2010, 188 fires (management-, lightning-, or human-ignited) >400 ha burned 83,525 ha in Sequoia & Kings Canyon. In Yosemite, between 1972 and 2010, 182 fires >40 ha burned 106,106 ha (Eidenshink et al. 2007, Lutz et al. 2011). According to satellite-derived indices, fires that occurred in the lower montane zone of Yosemite between 1984 and 2003 burned over a third of *P. ponderosa* stands at low to moderate severity and nearly a third of *A. concolor* stands at low severity, likely due to the controlled severity of prescribed fires and the short needles of *A. concolor* that form compact litter and resist ignition (Thode et al. 2011). During the same period (1984–2003), fires in the upper montane zone of Yosemite burned 23% of *A. magnifica* stands and 28% of *P. jeffreyi*–shrub stands at mostly low to moderate severity, and 4% of *P. contorta* stands at mostly low severity (Thode et al. 2011).

Methods

Site selection and field methods

We used a geographic information system (ESRI ArcGIS version 10) to position plots a priori in burned and unburned forests dominated by *A. concolor*, *A. magnifica, P. jeffreyi,* and *P. ponderosa*. We selected plot locations based on forest type (Sequoia and Kings Canyon National Parks Photo Interpretation Report 2007, Keeler-Wolf et al. 2012); burn status; fire severity; slope; and distance from streams, roads, and trails. Plots were located at least 50 m within the intended forest type and burned or unburned patch; had slopes between 0° and 35°; and were at least 100 m from streams, roads, and trails.

Between June and September of 2011, we established 105, 0.1-ha circular plots, 46 that had not burned since at least 1930 (hereafter, unburned; Yosemite: 35 plots; Sequoia & Kings Canyon: 11 plots; Fig. 1) and 59 that had burned between one and five times since 1946 (hereafter, burned; Yosemite: 32 plots; Sequoia & Kings Canyon: 27 plots). To characterize species composition and diameter distributions, we recorded species and diameter at breast height (1.37 m; dbh) of all live trees and snags ≥15 cm dbh. We divided each plot into four equal quadrants and recorded stems between 2.5 and 15 cm dbh in one or more quadrants, depending on stem abundance, and scaled these abundance values up to the whole plot. For each quadrant, we visually estimated percent cover by woody species that occupied ≥2.5 m^2 (1% of the quadrant area) to inform plot assignments to forest alliance and association.

Climate and fire variables

Because water availability influences fire severity and forest structure (e.g., Kane et al. 2014, 2015), we calculated mean annual actual evapotranspiration (AET) and climatic water deficit (Deficit; sensu Stephenson 1998) from 1980 to 2010 for the 67 plots in Yosemite based on the Thornthwaite-type methods of Lutz et al. (2010). We used climate normals from PRISM (2012), soil data from NRCS (2012), latitude, and local topography. High-resolution soil data were unavailable for Sequoia & Kings Canyon so we were unable to calculate AET and Deficit for the remaining 38 plots.

The fire history of each plot was expressed in number of fires since 1930 and fire severity. We obtained these data from the Yosemite fire atlas compiled by Lutz et al. (2011) and the Monitoring Trends in Burn Severity database (Eidenshink et al. 2007). We used the Relative differenced Normalized Burn Ratio (RdNBR), a satellite-derived metric developed by Miller and Thode

(2007), to characterize fire severity. RdNBR data were available for fires that occurred in or after 1984 and were >40 ha in Yosemite and >400 ha in Sequoia & Kings Canyon. We created 1-ha circular buffers around each plot center and extracted all 30 × 30 m RdNBR pixels with centers that fell within each buffer. We averaged the pixel values associated with each plot to obtain RdNBR values that minimized the potential effects of geo-rectification error (ESRI ArcGIS version 10; Key and Benson 2006, Kolden et al. 2012).

Data reduction

All unburned plots and the 51 burned sites with maximum RdNBR values <641 (i.e., moderate severity and below; Fig. 2) were retained for analysis (97 plots: 46 unburned, 28 burned once, 16 burned twice, six burned three times, and one burned four times). The burned plots were located within the perimeters of 33 different fires, 22 of which were management-ignited and 11 of which were caused by lightning or accidental human ignition. Seven plots were located where management-ignited fires overlapped with lightning- or human-ignited fires. The remaining 44 burned plots were split evenly between areas associated only with management ignitions and areas associated only with lightning or human ignitions. We used the percent canopy and shrub cover data to assign each plot to a forest alliance and association based on park-specific vegetation community identification keys (Sequoia and Kings Canyon National Parks Photo Interpretation Report 2007, Keeler-Wolf et al. 2012). We report these classifications because we were only able to sample some forest associations within each alliance, and this should be considered when extrapolating from our results. We classified the stems of each species by diameter into nine 15-cm bins, stratified the data into four categories by mortality status (live tree vs. snag) and burn status (burned plot vs. unburned plot), and calculated slope-corrected basal area and stem density for each diameter class at each plot.

Ordination

We illustrated variation in species composition among plots by ordinating species basal area using nonmetric multidimensional scaling (NMDS) and the Bray–Curtis distance measure. We standardized by the total basal area of each plot so site positions in ordination space would reflect the proportional contribution of each species to plot basal area (hereafter, relative basal area). We depicted the total tree density, burn status, and most recent fire severity of each plot in ordination space to illustrate the distribution of these key variables across the compositional gradient we sampled. Ordination was executed in the R statistical language (version 3.0.2; R Development Core Team 2013) with the function "metaMDS" from the vegan package (version 2.0-10; Oksanen et al. 2013).

Diameter distributions

We generated diameter distributions of tree and snag density for the seven most common species. Burned and unburned plots were represented separately to illustrate the potential effects of fire on species abundance. Snag data were graphically displayed to provide a complete account of standing stems at each site, but the data were not analyzed because snag age and cause of death were unknown. For each species, we selected plots that contained ≥1 live tree or snag of the focal species and performed Mann–Whitney U tests on tree density of that species in each diameter class to identify significant differences between burned and unburned populations. We applied a Bonferroni correction to these tests based on the total number of species by diameter class categories we examined (63; modified $\alpha = 0.00079$).

We then categorized burned plots for each species by: (1) number of fires and (2) most recent fire severity to assess whether these fire regime attributes affected tree density. We performed pairwise comparisons on tree density in each diameter class among: (1) plots burned different numbers of times and unburned plots and (2) plots burned at different severities and unburned plots (Mann–Whitney U test). The single plot that burned four times was not included in this analysis. We applied a Bonferroni correction to these tests based on the total number of species by diameter class categories we examined (63) and the number of comparisons made on each species by diameter class category (6; modified $\alpha = 0.00013$).

We tested our assumption that differences in density could be attributed to recent fire occurrence by comparing the distribution of elevation, slope, aspect, AET, and Deficit across each pair of
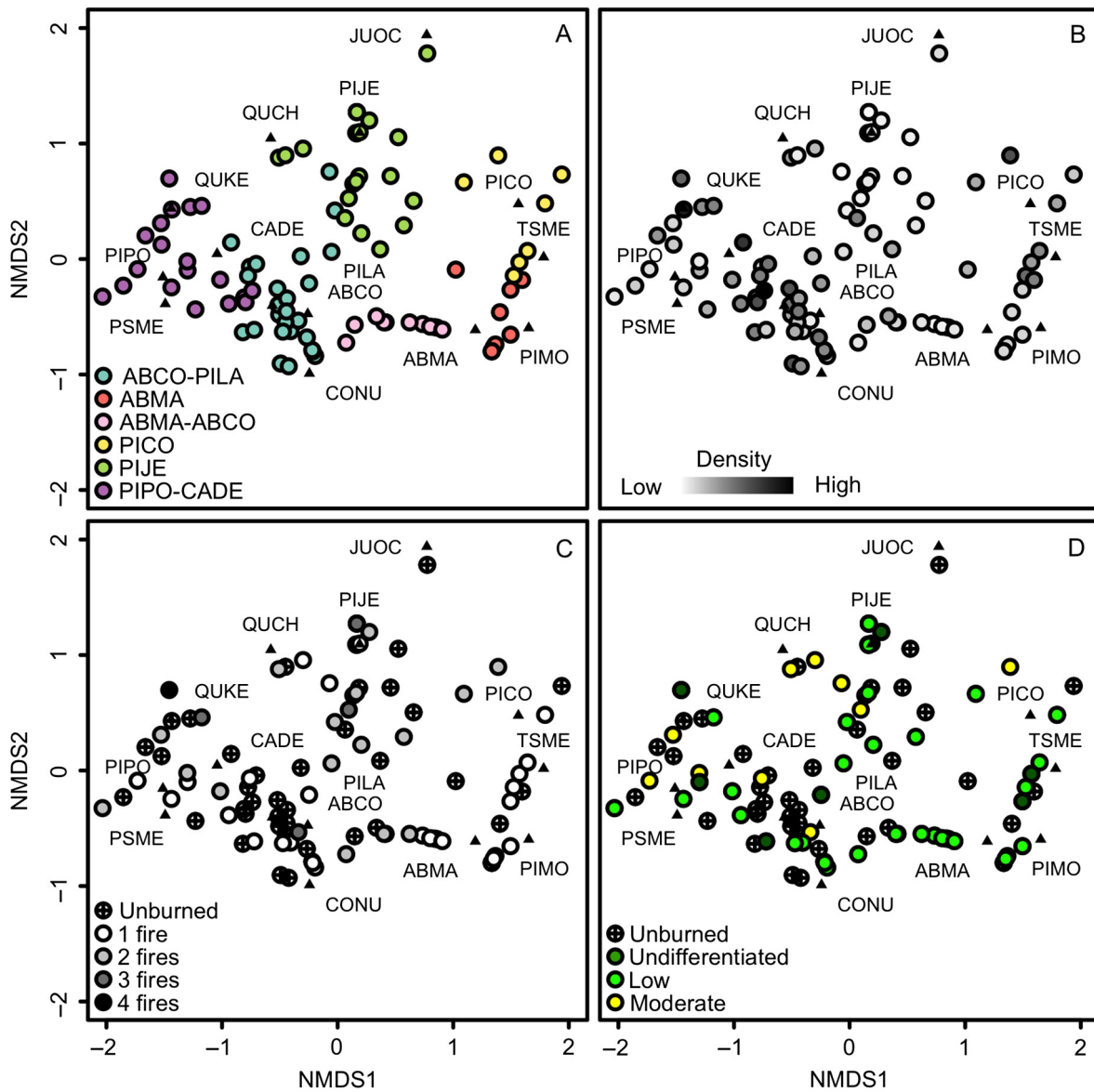
Fig. 2. Forest alliances (A), tree density (B), number of fires (C), and fire severity (D) superimposed on a nonmetric multidimensional scaling (NMDS) ordination of the relative basal area attributed to each of 14 tree species in 97 montane forest plots in Yosemite and Sequoia & Kings Canyon National Parks. Density ranged from 30 to 2082 trees/ha. The Relative differenced Normalized Burn Ratio severities shown in panel D are defined in Fig. 3B. Alliances: ABCO–PILA, *Abies concolor–Pinus lambertiana* alliance; ABMA, *Abies magnifica* alliance; ABMA–ABCO, *Abies magnifica–Abies concolor* alliance; PICO, *Pinus contorta* alliance; PIJE, *Pinus jeffreyi* alliance; PIPO–CADE, *Pinus ponderosa–Calocedrus decurrens* alliance. Other species: CONU, *Cornus nuttallii*; JUOC, *Juniperus occidentalis*; PILA, *P. lambertiana*; PIMO, *P. monticola*; PSME, *Pseudotsuga menziesii*; QUCH, *Quercus chrysolepis*; QUKE, *Q. kelloggii*; TSME, *Tsuga mertensiana*.

plot groups that we analyzed for density differences (Mann–Whitney U test). For the burned vs. unburned tests, we applied a Bonferroni correction based on the number of environmental variables we examined (5; modified $\alpha = 0.01$). Between the burned and unburned plots that contained each species, we detected no significant differences in physical site attributes. Plots that included *P. jeffreyi* exhibited a marginally significant difference in slope ($P = 0.04$; $\mu_{burned} = 10°$; $\mu_{unburned} = 15°$). For the tests among plots burned different numbers of times and among plots burned at different severities, we applied a Bonferroni correction based on the number of environmental variables we examined (5) and the number of comparisons made on each pair of plot groups (6; modified $\alpha = 0.0017$), at which level no results were significant. All Mann–Whitney U tests were unpaired, two-sided, and performed with the function "wilcox.test" in the R statistical language (version 3.0.2; R Development Core Team 2013).

Comparisons with historical, reconstructed, and contemporary data sets

We graphically compared mean tree density by species and diameter class at burned and unburned plots with historical and contemporary mean diameter distributions published by Lutz et al. (2009*a*) to: (1) determine the extent to which fire reintroduction reduced mean tree density to historical levels and (2) evaluate the representativeness of our unburned plots by comparing them with contemporary data from another source. Lutz et al. (2009*a*) described vegetation change by comparing data collected by the Vegetation Type Mapping (VTM) Project within Yosemite (1932–1936; Wieslander et al. 1933) with data from plots established by the Yosemite Vegetation Inventory, the US Geological Survey, and The Nature Conservancy between 1988 and 1999. We used mean diameter distributions to assess landscape-scale differences between our study, which spanned two national parks, and data from Lutz et al. (2009*a*), which extended throughout Yosemite.

We also graphically compared diameter distributions from our burned and unburned plots with reconstructed and contemporary diameter distributions published by Scholl and Taylor (2010). The geographic scope of Scholl and Taylor (2010) was confined to a 2125-ha unburned lower montane forest dominated by *P. ponderosa*, *C. decurrens*, *P. lambertiana*, *A. concolor*, *P. menziesii*, *P. jeffreyi*, and *Q. kelloggii*. Scholl and Taylor (2010) used dendrochronological techniques to reconstruct the forest in 1899 and compared their results with contemporary data from 2002. We excluded plots from our study that contained conifer species not present in the study area of Scholl and Taylor (2010) and rebinned our diameter classes and those of Scholl and Taylor (2010) to match the historical data set used by Lutz et al. (2009*a*; 10–30 cm, 31–60 cm, 61–91 cm, >91 cm) for ease of comparison among figures. We considered the study by Scholl and Taylor (2010) local-scale relative to our data set, which sampled across a much larger area, and juxtaposed their density values against the distribution of values we observed among our plots, rather than our mean values.

Lastly, we graphically compared tree density at our burned and unburned plots to non-species-specific diameter distributions from allegedly unbiased historical and contemporary data sources. We presented data from the 1911 timber inventory reported in Collins et al. (2011; >4000-ha area) and Stephens et al. (2015; 11,500-ha area) and from three 4-ha pretreatment "Methods of Cutting" plots established in 1929 (Knapp et al. 2013). We also included the reconstructed (1899) tree density values from Scholl and Taylor (2010) to assess the validity of their estimates relative to historical values. Because the geographic extents of these studies were substantially smaller than the extent of our study, we considered these comparisons local-scale and juxtaposed their density values against the distribution of values we observed among our plots, rather than our mean values. We also included contemporary (2005–2007) diameter distributions from unburned plots (Collins et al. 2011), contemporary (2001–2008) Forest Inventory and Analysis (FIA) data (Stephens et al. 2015), a contemporary (2012) control plot (Knapp et al. 2013), and data from a contemporary (2002) survey (Scholl and Taylor 2010) to assess the representativeness of our unburned plots. Finally, we included contemporary (2005–2007) diameter distributions from recently burned plots reported in Collins et al. (2011) to assess the representativeness of our burned plots. The study areas in this comparison collectively included *A. concolor*, *A. magnifica*, *C. decurrens*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*,

P. menziesii, *Q. chrysolepis*, and *Q. kelloggii*. Plots from this study that contained other tree species were excluded from the tree density distributions (n_{burned} = 37; $n_{unburned}$ = 38). We compared across studies by pooling the species in each of our plots, summing the Scholl and Taylor (2010) values across species, rebinning our diameter classes to match the 1911 inventory (15.2–30.4 cm, 30.5–61.0 cm, 61.1–91.4 cm, >91.4 cm), and rebinning diameter classes from Knapp et al. (2013) and Scholl and Taylor (2010) to match those of the 1911 inventory as closely as possible.

RESULTS

Species composition

We sampled six forest alliances and 19 forest associations (Appendix S1: Tables S2 and S3). NMDS ordination of the relative basal area of 14 tree species revealed a gradient relationship along NMDS axis 1 from lower montane species (*P. ponderosa*, *P. menziesii*, *Q. kelloggii*, and *C. decurrens*) to upper montane constituents (*P. contorta*, *P. monticola*, and *T. mertensiana*; Fig. 2; stress = 0.120). *Pinus lambertiana*, *A. concolor*, *C. nuttallii*, and *A. magnifica* were located midway along NMDS axis 1 but were associated with lower values of NMDS axis 2; *Q. chrysolepis*, *P. jeffreyi*, and *J. occidentalis*, which were also located midway along NMDS axis 1, were associated with higher values of NMDS axis 2. The *A. concolor* centroid was centrally located, marking the convergence of two lower montane and two mid-elevation forest alliances, *Pinus ponderosa–Calocedrus decurrens*, *Abies concolor–Pinus lambertiana*, *Abies magnifica–Abies concolor*, and *Pinus jeffreyi*, and reflecting that *A. concolor* was present in more plots (63) than any other species (Fig. 2A).

Tree density varied within and among alliances. Density ranges were large within the *Pinus ponderosa–Calocedrus decurrens* (range: 150–2082 trees/ha), *Abies concolor–Pinus lambertiana* (range: 70–1523 trees/ha), and *Pinus contorta* alliances (range: 386–1280 trees/ha) but were narrower within the *Abies magnifica–Abies concolor* (range: 71–621 trees/ha), *Abies magnifica* (range: 140–899 trees/ha), and *Pinus jeffreyi* alliances (range: 30–909 trees/ha; Fig. 2A, B).

Higher AET and Deficit characterized the lower montane and mid-elevation alliances, while the upper montane alliances, *Abies magnifica*

and *Pinus contorta*, were associated with lower AET and Deficit (Fig. 3A). Ranges of climatic water balance parameters were approximately equivalent between burned and unburned plots in Yosemite (AET_{burned} = 237–422 mm; $AET_{unburned}$ = 230–453 mm; $Deficit_{burned}$ = 103–361 mm; $Deficit_{unburned}$ = 160–330 mm; Fig. 3A). Among all burned plots, RdNBR ranged from −174 to 548, representing areas where greenness increased after fire (negative RdNBR values) to areas burned at moderate severity (Fig. 3B). Although burned and unburned plots spanned the full compositional gradient (Fig. 2C), the distribution of fire history attributes was heterogeneous, particularly with respect to plots dominated by *A. magnifica*, which were exclusively associated with single, undifferentiated- or low-severity fires (Figs. 2C, D and 3B; Appendix S1: Table S3).

Diameter distributions

Density by diameter class for three species, *A. concolor*, *A. magnifica*, and *C. decurrens*, exhibited a reverse-J distribution among unburned plots and a truncated reverse-J distribution among burned plots due to the low density of trees <15 cm dbh at burned sites (Fig. 4). *Pinus contorta* represented a counterexample to this pattern, exemplifying a reverse-J distribution among burned plots and low density of trees <15 cm dbh among unburned plots (Fig. 4). The distributions of *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* were relatively uniform among both burned and unburned plots, with the exception of some unburned plots where the density of *P. lambertiana* and *P. ponderosa* <15 cm was greater (Fig. 4).

Fire sensitivity of tree species

Tree density was significantly lower at burned plots than unburned plots for *A. concolor* (2.5–30 cm dbh; $P < 0.0079$). Lower density at burned plots was marginally significant for *A. concolor* (30–45 cm dbh, $P = 0.0081$), *A. magnifica* (2.5–15 cm dbh, $P = 0.0160$; 15–30 cm dbh, $P = 0.0036$), and *C. decurrens* (2.5–15 cm dbh, $P = 0.0042$; Table 1, Fig. 4). No *Pinus* spp. exhibited significant differences in any diameter class ($P > 0.05$; Table 1, Fig. 4). Density of individuals >45 cm dbh of any species did not differ significantly between burned and unburned plots ($P > 0.05$; Table 1, Fig. 4). Neither number of fires nor fire
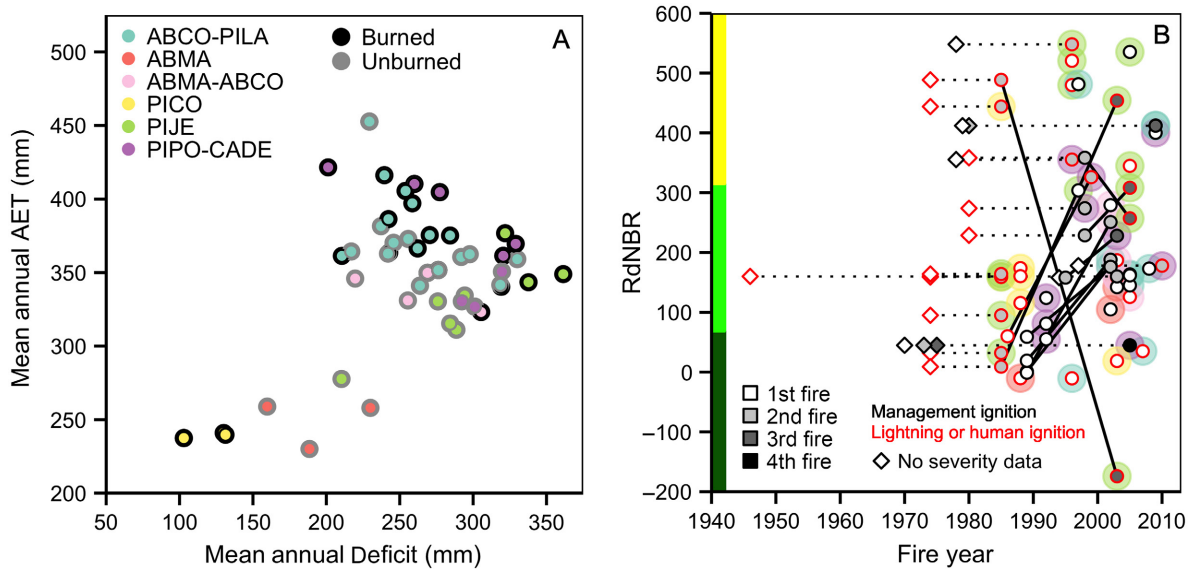
Fig. 3. Climate defined by modeled actual evapotranspiration (AET) and climatic water deficit (Deficit) of 63 forest plots in Yosemite (plots in Sequoia & Kings Canyon National Parks could not be included due to lack of soil data; A). Fire history of 51 burned plots is delineated by fire year and severity (quantified by the satellite-derived Relative differenced Normalized Burn Ratio [RdNBR]; B). Lines connect fires that occurred at the same plot. Unburned plots (not pictured) had not experienced fire since at least 1930. Solid lines: RdNBR data were available for the fires at both endpoints of the line. Dotted lines: RdNBR data were not available for at least one of the fires at the endpoints of the line. Colored bars denote fire severity: dark green—enhanced greenness (greater vegetative cover one year after fire [sensu Kane et al. 2013]) and undifferentiated (areas within fire perimeters with RdNBR values that do not differ from adjacent unburned areas [sensu Kolden et al. 2012]); light green—low; yellow—moderate. See Fig. 2 for the alliance abbreviations in panel A.

severity significantly affected density of any species in any diameter class. We do not interpret these results to mean that number of fires and fire severity are unimportant variables in determining changes in tree density (see Collins et al. 2011) but instead posit that our sample size was too small to robustly withstand the many subdivisions required to address these multilevel questions.

Comparisons with historical, reconstructed, and contemporary data sets

Mean tree density of *A. concolor* 10–60 cm dbh in burned plots was comparable to historical data from the VTM survey (1932–1936) and in unburned plots was comparable to the contemporary data (1988–1999) synthesized in Lutz et al. (2009*a*; Fig. 5). In burned plots, mean density of *C. decurrens* 10–30 cm dbh was higher than VTM observations, mean densities of *P. jeffreyi* and

P. lambertiana 10–30 cm dbh were comparable to VTM observations, and mean densities of *A. magnifica* and *P. ponderosa* 10–30 cm dbh were lower than the VTM data (Fig. 5). Mean densities for most species and diameter classes at unburned plots were comparable to the contemporary data in Lutz et al. (2009*a*; Fig 5).

Reconstructed and contemporary mean density values from Scholl and Taylor (2010) fell within the range of values detected in our burned and unburned plots, respectively (Fig. 6). Total tree density values from historical data and the recently burned plots from Collins et al. (2011) fell within the density range of our burned plots (Fig. 7). Contemporary tree density values fell within the density range of our unburned plots (Fig. 7).

Multiple fires and fire severity

Ten plots had RdNBR records for the two most recent fires. In eight of these instances, the more
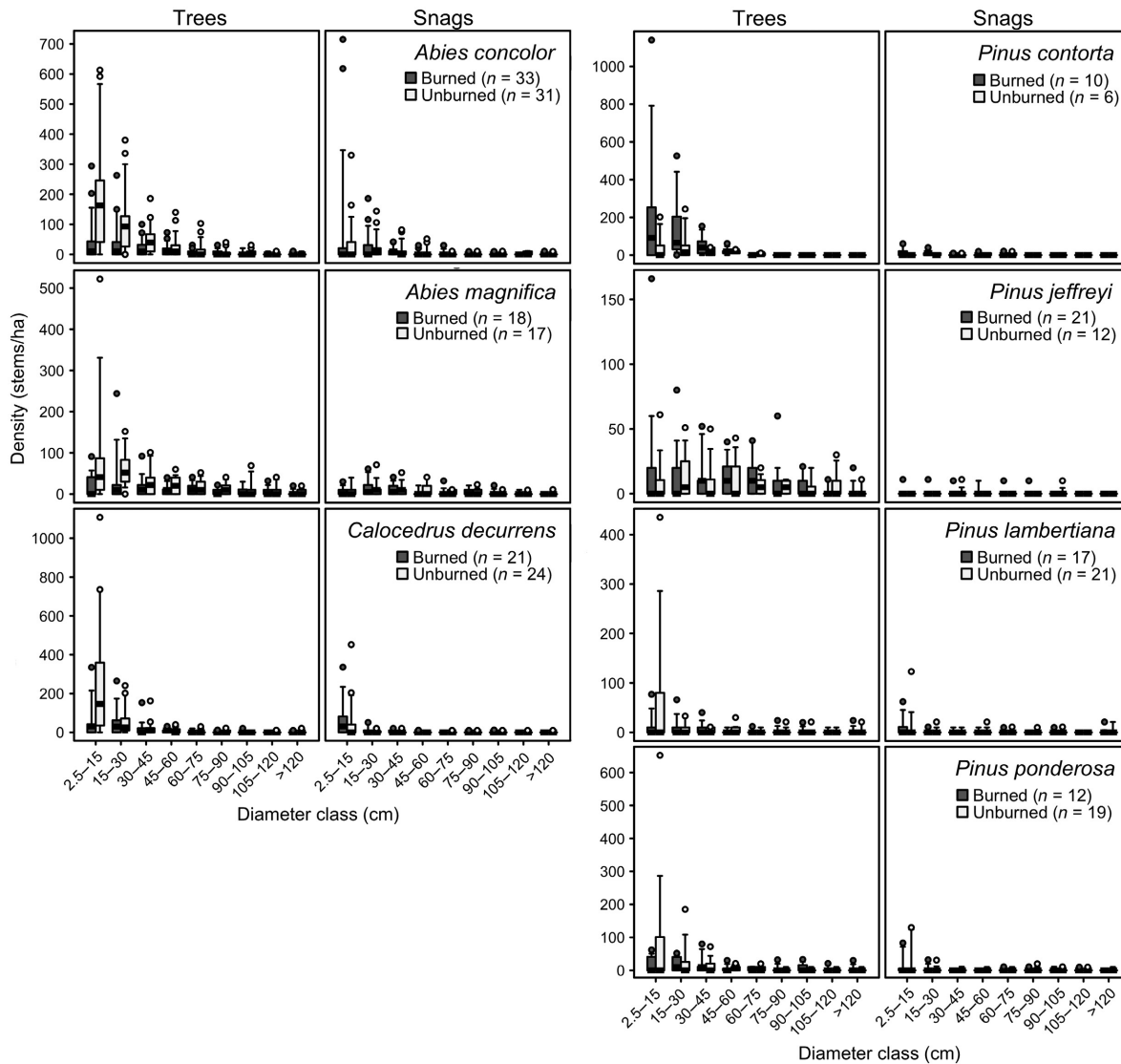
Fig. 4. Distributions of density by diameter class for seven conifer species in lower and upper montane forests of Yosemite and Sequoia & Kings Canyon National Parks. For each species, plots were included that contained ≥1 tree or snag of the focal species. Horizontal bars in each boxplot represent the 25th, 50th, and 75th percentiles; whiskers extend from the 5th to the 95th percentile; circles represent outliers that exceed the whisker threshold.

recent fire burned at higher severity (Fig. 3B). We compared the years of these fires to Yosemite fire normals for number of fires, RdNBR, and area burned (Lutz et al. 2011). All later fire years were ranked above the 25th percentile in the three categories of Yosemite fire activity proposed by Lutz et al. (2011) and maintained or exceeded the percentile ranking of the year of the previous fire (Table 2).

DISCUSSION

Fire sensitivity of tree species

We observed that lower-severity fire reduced the density of shade-tolerant species in the smaller-diameter classes, a result that is consistent with prior studies. We found that *A. concolor* <30 cm dbh exhibited significantly lower densities at burned sites relative to unburned sites

Table 1. Effect sizes from Mann–Whitney U tests that compared the tree density in nine diameter classes of burned and unburned plots for seven species sampled in Yosemite and Sequoia & Kings Canyon National Parks.

			Diameter class (cm)								
Species	n_b	n_{ub}	<15	30	45	60	75	90	105	120	>120
Abies concolor	33	31	**0.79***	**0.76***	0.69***	0.53	0.54	0.48	0.56	0.52	0.48
Abies magnifica	18	17	0.74****	0.79**	0.58	0.63	0.53	0.67	0.55	0.53	0.53
Calocedrus decurrens	21	24	0.75**	0.54	0.55	0.47	0.52	0.59	0.50	0.52	0.58
Pinus contorta	10	6	0.27	0.27	0.30	0.56	0.67	0.67	0.50	0.50	0.50
Pinus jeffreyi	21	12	0.45	0.56	0.42	0.46	0.37	0.56	0.42	0.60	0.49
Pinus lambertiana	17	21	0.56	0.56	0.45	0.56	0.52	0.48	0.47	0.48	0.48
Pinus ponderosa	12	19	0.58	0.46	0.47	0.63	0.44	0.49	0.34	0.48	0.49

Notes: Effect size $\hat{p}$ estimates the probability that the density of a sample randomly drawn from the unburned population will exceed the density of a sample randomly drawn from the burned population or $\hat{p}_{ub>b} = U/(n_{ub} \times n_b)$. The n values enumerate unburned (n_{ub}) and burned (n_b) plots with ≥1 tree or snag of the focal species. Diameter classes are denoted by their upper bound. Only trees ≥2.5 cm dbh were included.

Selected P-values: 0.05>****, 0.01>***, 0.005>**, 0.001>*; values with $P < 0.00079$ are in bold.

See Fig. 4 for the diameter distributions of each species.

(Table 1). Lower densities in burned plots were observed at a marginal significance level for *A. concolor* 30–45 cm dbh, *A. magnifica* <30 cm dbh, and *C. decurrens* <15 cm dbh. These results corroborate previous work in this region on burned (Fig. 3; Minnich et al. 1995, Schwilk et al. 2006, Webster and Halpern 2010, Collins et al. 2011, van Mantgem et al. 2013) and unburned forests (Vankat and Major 1978, Beaty and Taylor 2007, Lutz et al. 2009*a*, Scholl and Taylor 2010, Dolanc et al. 2014, Stephens et al. 2015).

Fire reintroduction, in contrast, had a negligible effect on *P. contorta*, *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*, evidenced by the lack of significant differences in densities between burned and unburned populations of any diameter class (Table 1, Fig. 4). Among *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*, lack of fire effects is likely explained by the low abundance of fire-susceptible individuals (e.g., <15 cm dbh) across all plots and the thicker bark, relative to *Abies*, of the young individuals that were present (Appendix S1: Table S1). Median density values of trees <15 cm dbh of all three species were zero in unburned plots, suggesting that ≥50% of the unburned plots that contained these species did not support their regeneration (Fig. 4). These *Pinus* spp. are shade intolerant, and widespread regeneration is improbable unless preceded by a disturbance that sufficiently alters the light environment (Keeley 2012). Subsequent studies are needed to determine whether lower-severity fire is sufficient to stimulate regeneration of *Pinus* spp. and to better establish diameter thresholds of sensitivity to

lower-severity fire for *Pinus* spp. in instances where regeneration has occurred.

The diameter distributions of *P. contorta* were unique in that burned sites were characterized by a reverse-J distribution and unburned sites were associated with a lower density of trees <45 cm dbh (Fig. 4). This likely reflects a combination of three factors: (1) the capacity of *P. contorta* to rapidly germinate postfire and eventually self-thin on more productive sites; (2) the ability of *P. contorta* to persist, albeit at diameters <15 cm, on unproductive sites where fire severity is minimal due to lack of fuel; and (3) the lack of unburned *P. contorta*-dominated sites in this data set (Fig. 2A, C), such that our sample primarily included instances where *P. contorta* was a minor constituent in unburned forest. Greater sampling of both burned and unburned forests dominated by *P. contorta* is needed to fully represent the spectrum of fire effects on this species.

Lack of fire effects on trees >45 cm dbh of any species supports the utility of lower-severity fire as a management tool to reduce high tree density and relieve stress on large-diameter trees, which sequester the majority of forest carbon (Table 1; Das et al. 2011, Lutz et al. 2012).

Efficacy of lower-severity fire

The effectiveness of lower-severity fire as an instrument to control populations of shade-tolerant species hinges on whether the decrease in density of shade-tolerant species due to fire occurrence adequately compensates for the
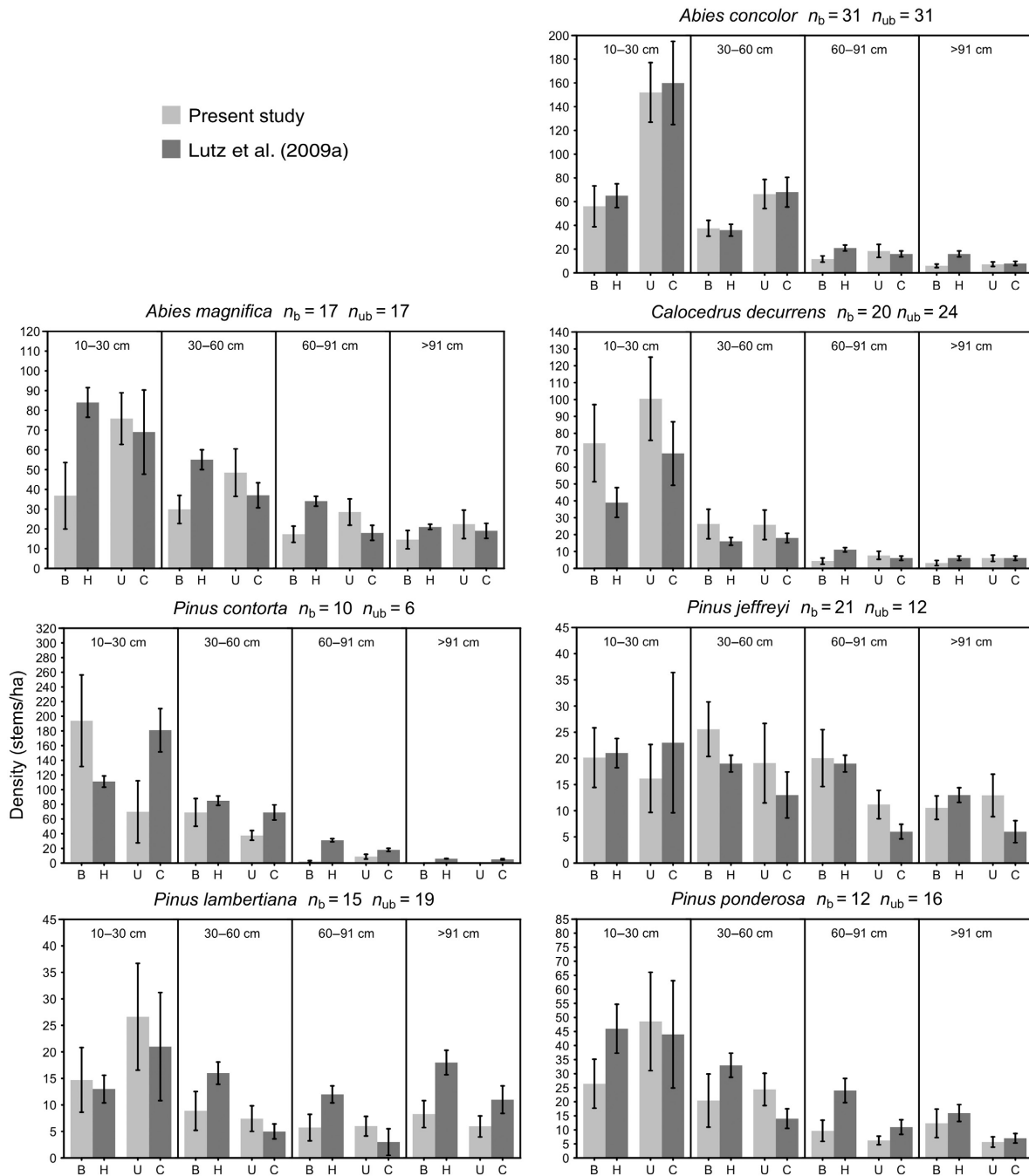
Fig. 5. Comparison of tree density (mean ± SE) in burned and unburned plots with historical Wieslander (1932–1936) and contemporary (1988–1999) surveys from Lutz et al. (2009*a*). Tree density calculations for this study and Lutz et al. (2009*a*) included plots containing ≥1 tree (≥10 cm dbh) of the focal species; n_b and n_{ub} denote the number of burned and unburned plots, respectively, for each species from this study. B, burned; H, historical; U, unburned; C, contemporary.
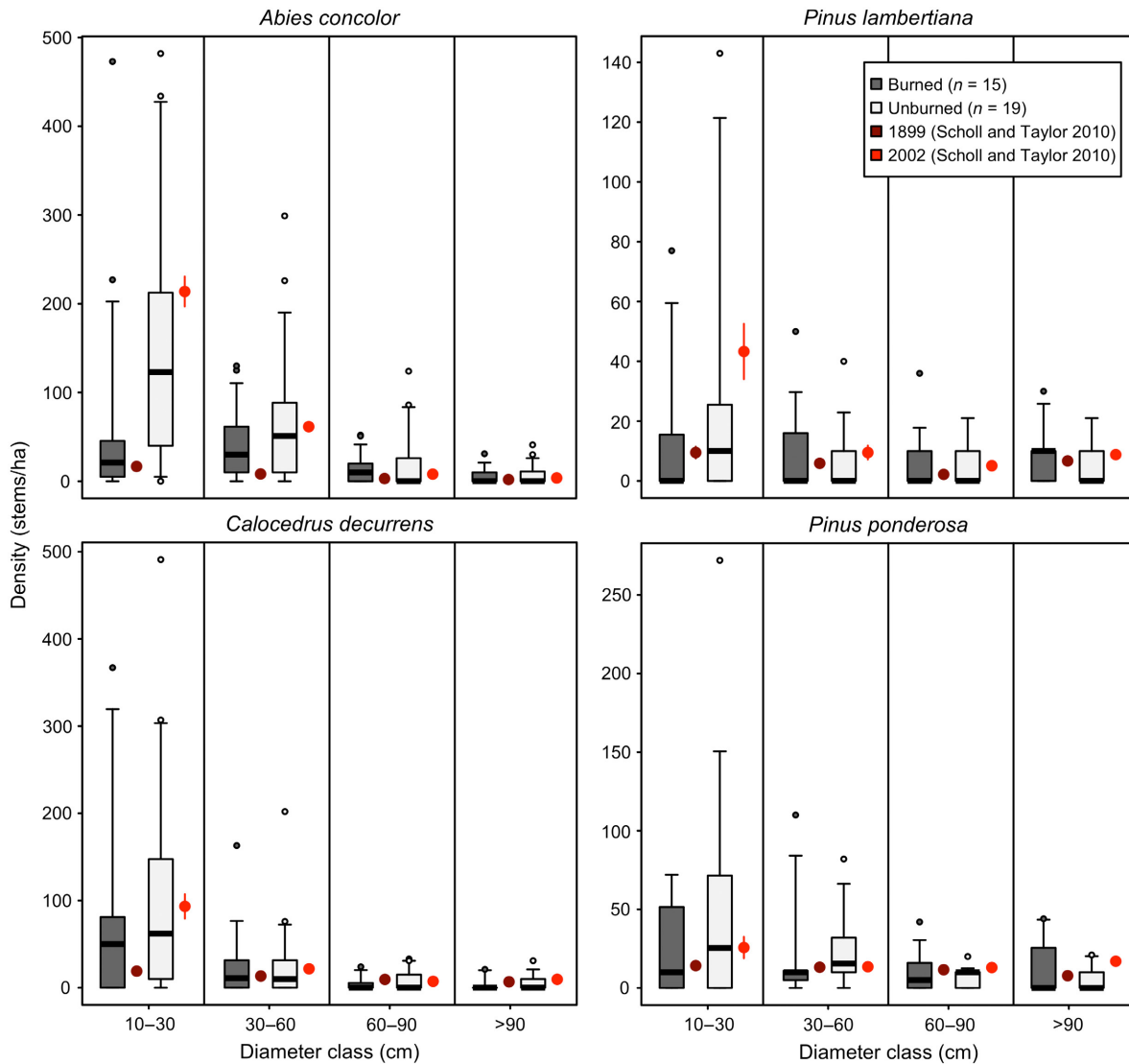
Fig. 6.   Comparison of tree density in burned and unburned plots with reconstructed (1899) and contemporary (2002) data from Scholl and Taylor (2010; mean ± SE; diameter classes rebinned). Scholl and Taylor (2010) calculated tree density within a 2125-ha forest of *Abies concolor*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Pinus lambertiana*, *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Quercus kelloggii*. Plots from this study that contained other tree species were excluded from the tree density distributions. Tree density distributions from this study were based on plots containing ≥1 tree (≥10 cm dbh) of the focal species.

increase in density that was enabled by the period of fire exclusion. We use the graphical comparisons of tree density in our burned plots with historical and reconstructed tree densities to assess the efficacy of lower-severity fire in reducing populations of shade-tolerant species.

Because of spatial variability in historical and contemporary tree density, the spatial scale at which these comparisons are interpreted is important. We used mean tree density values when comparing with VTM data at a landscape scale, but we displayed the distributions of our density data beside values derived from smaller areal extents when comparing with Scholl and Taylor (2010), Collins et al. (2011), Stephens et al. (2015), and Knapp et al. (2013) at a local scale.
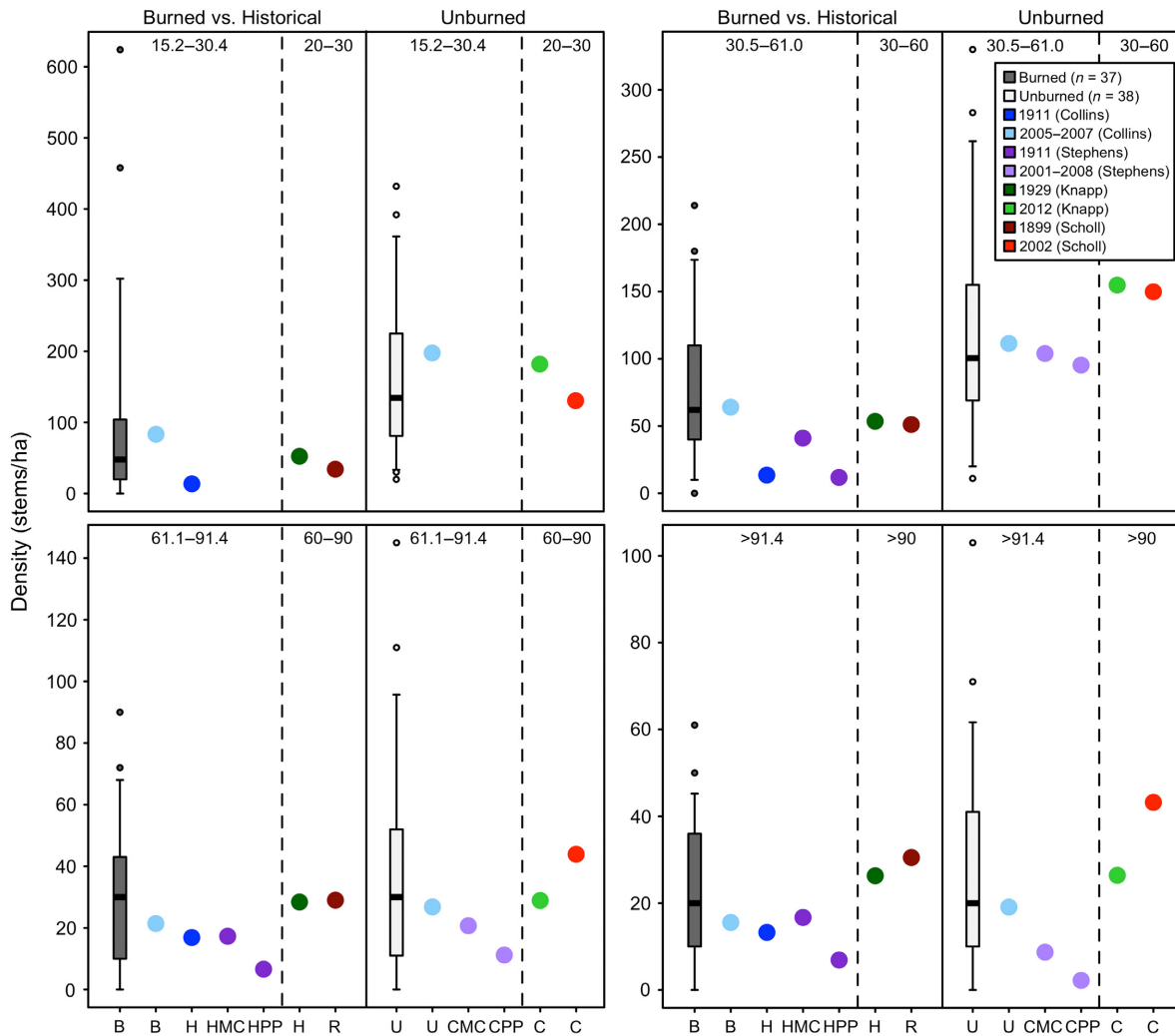
Fig. 7. A comparison of tree density by diameter class (cm) in burned and unburned plots with mean tree density values from a historical timber inventory (1911; Collins et al. 2011, Stephens et al. 2015), a historical "Methods of Cutting" pretreatment survey (1929; Knapp et al. 2013, diameter classes rebinned), a dendro-chronological reconstruction (1899; Scholl and Taylor 2010, diameter classes rebinned), a contemporary survey (2005–2007; Collins et al. 2011), Forest Inventory and Analysis plots (2001–2008; Stephens et al. 2015), a contemporary control plot (2012; Knapp et al. 2013, diameter classes rebinned), and another contemporary survey (2002; Scholl and Taylor 2010, diameter classes rebinned). These study areas collectively included *Abies concolor*, *A. magnifica*, *Calocedrus decurrens*, *Pinus jeffreyi*, *P. lambertiana*, *P. ponderosa*, *Pseudotsuga menziesii*, *Quercus chrysolepis*, and *Q. kelloggii*. Plots from this study that contained other tree species were excluded from the tree density distributions. Collins et al. (2011) presented historical and recent postfire inventory data separately depending on recent site history; we present the same data here as weighted averages. B, burned; H, historical; HMC, historical mixed-conifer; HPP, historical *P. ponderosa*; R, reconstructed; U, contemporary unburned; CMC, contemporary mixed-conifer; CPP, contemporary *P. ponderosa*; C, contemporary unburned, not from a study that differentiated between burned and unburned.

Table 2. Comparison of Yosemite National Park fire normals with successive fire events, each with Relative differenced Normalized Burn Ratio (RdNBR) fire severity records, that occurred at 10 plots in forests of Yosemite and Sequoia & Kings Canyon National Parks.

Plot	Alliance	Year	R†	RdNBR	R	Size (ha)	R	Cause‡	Name
P061	ABMA–ABCO	1989	L	1	L	688	L	MI	Pw3
		2002	M	179	M	1360	M	MI	PW-3 Gin Flat
P062	ABMA–ABCO	1989	L	−1	L	688	L	MI	Pw3
		2002	M	251	M	1360	M	MI	PW-3 Gin Flat
P068	PIPO–CADE	1986	M	60	M	584	M	LTG	Eleanor
		1999	H	326	M	1042	H	LTG	Eleanor
P087	ABCO–PILA	1989	L	19	L	688	L	MI	Pw3
		2002	M	188	M	1360	M	MI	PW-3 Gin Flat
P088	ABCO–PILA	1989	L	59	L	688	L	MI	Pw3
		2002	M	176	M	1360	M	MI	PW-3 Gin Flat
P148	PIPO–CADE	1995	L	158	M	843	L	MI	Mineral 1
		2003	H	228	H	1098	H	MI	Atwood
P168	PIJE	1998	L	358	L	645	L	MI	Lewis Creek
		2005	H	257	M	3947	M	LTG	Comb
P170	PIJE	1998	L	229	L	645	L	MI	Lewis Creek
		2005	H	308	M	3947	M	LTG	Comb
P195	PIJE	1985	H	9	M	1152	M	LTG	Sugarloaf
		2003	H	454	H	1405	H	LTG	Williams
P251	PIJE	1985	H	489	M	1152	M	LTG	Sugarloaf
		2003	H	−174	H	1405	H	LTG	Williams

Notes: ABMA–ABCO, *Abies magnifica–Abies concolor*; PIPO–CADE, *Pinus ponderosa–Calocedrus decurrens*; ABCO–PILA, *Abies concolor–Pinus lambertiana*; PIJE, *Pinus jeffreyi*.

† Letters in the ranking columns (R) that follow fire year, RdNBR, and fire size values indicate, respectively, whether the number of fires, RdNBR, or area burned associated with that year fell in the upper quartile (H), the middle two quartiles (M), or the lower quartile (L) of fire normals developed from 26 yr of Yosemite fire history (Lutz et al. 2011).

‡ Fires were ignited by management (MI) or lightning (LTG).

Our comparison of mean density in burned plots with VTM data from Lutz et al. (2009*a*) suggests that lower-severity fire effectively results in a mean diameter distribution of *A. concolor* that is similar to historical conditions (Fig. 5). In contrast, lower-severity fire failed to reduce the density of *C. decurrens* <30 cm dbh to historical levels, implying that some shade-tolerant species may be less responsive to lower-severity fire at the landscape scale (Fig. 5). The reconstructed diameter distributions of *A. concolor* and *C. decurrens* from Scholl and Taylor (2010) are well within the range of densities we observed in each diameter class among our burned plots, suggesting that the range of diameter distributions produced by lower-severity fire overlaps with the historical range of variability (Fig. 6). The diameter distributions from the 1911 timber inventory and "Methods of Cutting" plots similarly fall within the range of densities we observed in each diameter class at burned plots, further supporting that lower-severity fire restores some stands to

forest conditions within their historical range. Because our plots were 0.1 ha in size, greater variability would be expected among many small plots relative to the mean or complete tree density records from larger areas.

Both the historical VTM and the reconstructed Scholl and Taylor (2010) data sets may introduce biases that compromise the validity of these comparisons. The field crews that gathered the VTM data set may have preferentially sampled low-density, old-growth stands, despite the mandate in their protocol to select representative areas (Wieslander et al. 1933, Lutz et al. 2009*a*, Dolanc et al. 2014). If old-growth stands were over-sampled, this could lead to an underestimate of the density of small-diameter trees in historical times, making it more likely that we would detect higher tree density in our burned plots relative to historical data. Dolanc et al. (2014; their Figure 2) compared scatterplots of density by elevation of all VTM plots with contemporary FIA plots and density by latitude of mixed-conifer plots from

each data set. Although their analysis does not preclude the possibility of a preference for low-density, old-growth stands in the VTM survey, it does show that both studies captured similar ranges of tree density (Lutz et al. 2009*a*, Dolanc et al. 2014).

The Scholl and Taylor (2010) reconstruction is subject to another type of bias, that of missing wood. Scholl and Taylor (2010) report a gap of 30 yr from 1899 to 1929, during which any *P. lambertiana* that may have died were not detectable in their sample due to decay. It is likely that dead *A. concolor*, which have a shorter decay half-life of 14 yr, were underrepresented in their reconstruction to an even greater degree (Harmon et al. 1987, North et al. 2007, Barth et al. 2015). Thus, Scholl and Taylor (2010) present a known underestimate of the density of small-diameter trees in historical times. In this analysis, such an underestimate could increase the likelihood of detecting a higher density of small-diameter trees in burned plots relative to the reconstructed density. We note, however, that despite this bias, the densities in each diameter class of all species combined at the site of Scholl and Taylor (2010) actually exceed the densities in each diameter class reported in a reputedly unbiased timber survey conducted in 1911 in the same region (Collins et al. 2011), even when only stems >20 cm dbh from the Scholl and Taylor (2010) study are compared with stems >15.2 cm dbh from the 1911 inventory (Fig. 7). To our knowledge, Lutz et al. (2009*a*) and Scholl and Taylor (2010) are the only relevant studies that examine tree density by species and diameter class simultaneously. Thus, we included them in our analysis despite these potential biases.

Comparisons of recently burned plots to historical data provide a framework to evaluate forest change but do not imply that reinstating historical tree density conditions across Yosemite and Sequoia & Kings Canyon National Parks is or should be the object. We show that mean historical diameter distributions can largely be attained through the application of lower-severity fire and that the areas that have experienced lower-severity fire over the past four decades represent the portion of Yosemite and Sequoia & Kings Canyon National Parks that most closely resembles historical composition and structure. Repeated fire application will likely be necessary to maintain these

conditions that are considered to be more resilient to fire (e.g., Larson et al. 2013), partly because lower-severity fires have been observed to stimulate high levels of *A. concolor* regeneration (Webster and Halpern 2010, Collins et al. 2011).

Precise restoration to historical conditions is an impossibility because historical heterogeneity is inadequately documented. Some burned plots in our study far exceed historical density values, which may suggest that lower-severity fire is ineffective at restoring some stands due to: (1) the heterogeneity of fire at small spatial scales, or (2) the trees that established during the fire suppression era and have attained fire-resistant size (Figs. 6 and 7; Collins et al. 2011). Alternatively, however, the higher density values we observe at some burned plots relative to historical data could be an artifact of: (1) the large number of small (0.1-ha) plots included in our study relative to the fewer, larger areas where historical data were summarized, or (2) the limited coverage of historical data that, as a result, may inadequately represent the historical range of stand density.

Fire and upper montane species composition

The structural and compositional response to fire exclusion is less pronounced in upper montane forests, where the growing season is shorter and wind supersedes fire as a dominant disturbance (Oosting and Billings 1943, Parker 1986). Rapid growth is required for *A. magnifica* saplings to transition to subcanopy status from a niche beneath the surface of the snowpack that is protected from high-speed winds (Oosting and Billings 1943, Parker 1984, 1986). Saplings are therefore already the most vulnerable demographic, even before fire is considered. A comparison of historical (1932–1936) and contemporary (1988–1999) populations of *A. magnifica* by Lutz et al. (2009*a*) found that mean density declined across all diameter classes. Our unburned plots also showed a decline in mean density of individuals ≤91 cm dbh relative to historical levels (Fig. 5). Whereas the removal of shade-tolerant individuals <30 cm dbh was viewed as restorative in lower montane forests, the advancement of *A. magnifica* regeneration may therefore be an important objective in upper montane stands. Gap formation in *A. magnifica* forests, potentially by fire, should be a primary management focus

to provide high-light conditions for saplings. Long FRIs may be equally important to enable *A. magnifica* saplings to attain fire-resistant size (>30 cm dbh; Table 1). Diminishing snowpack in the future, however, may negate such management strategies (Hayhoe et al. 2004). Reduced recruitment of *A. magnifica* could presage a compositional change in upper montane forests as the adaptations to deep snow that have been beneficial to *A. magnifica* no longer provide a competitive advantage.

Comparison with other contemporary data sets

Previous studies have published contemporary data that provide a basis to evaluate the representativeness of our plots. Lutz et al. (2009*a*) and Scholl and Taylor (2010) included diameter distributions of mean tree density for individual species, allowing the most detailed comparison. Mean tree density at our unburned plots fell within one standard error of the contemporary Yosemite-wide data of Lutz et al. (2009*a*) for most species and diameter classes (Fig. 5). Scholl and Taylor (2010) reported contemporary mean density by diameter class for *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa* in a 2125-ha forest. Their values fall within the density range we observed at our unburned plots that contained ≥1 stem of the focal species (Fig. 6). Dolanc et al. (2014) summarized FIA data from Yosemite to Plumas National Forest and reported mean density values by forest type for *A. concolor* (range: 11.8–161.4 trees/ha), *A. magnifica* (range: 16.3–322.1 trees/ha), *C. decurrens* (range: 17.2–107.1 trees/ha), *P. contorta* (range: 22.4–175.0 trees/ha), *P. jeffreyi* (range: 10.5–108.2 trees/ha), *P. lambertiana* (range: 11.7–18.3 trees/ha), and *P. ponderosa* (range: 31.4–209.3 trees/ha). These values generally fall within the density ranges observed in our unburned plots that contained ≥1 stem of the focal species (*A. concolor*: 10–952 trees/ha; *A. magnifica*: 30–722 trees/ha; *C. decurrens*: 11–1338 trees/ha; *P. contorta*: 40–356 trees/ha; *P. jeffreyi*: 10–182 trees/ha; *P. lambertiana*: 10–468 trees/ha; *P. ponderosa*: 10–870 trees/ha). We conclude that our data are representative of montane forests in Yosemite and Sequoia & Kings Canyon National Parks.

Multiple fires and fire severity

The impact of multiple fires on forests is an area of growing relevance to land managers (Westerling et al. 2006, Lutz et al. 2009*b*). Previous work by van Wagtendonk et al. (2012) has shown that multiple intersecting fires in the Illilouette Creek basin of Yosemite can reduce subsequent fire severity. The 10 plots in our study that experienced two fires that were each associated with satellite-derived fire severity did not exhibit the same pattern. In eight of the 10 instances, five in Yosemite and three in Sequoia & Kings Canyon, multiple fires were linked to slightly higher subsequent severity, as measured by RdNBR (Fig. 3B, Table 2). The two plots that experienced moderate-severity fire in the earlier burn exhibited lower severity in the subsequent burn, likely due to fuel combustion followed by lack of fuel in the later fire (van Wagtendonk et al. 2012). We present three viable explanations for the higher severity of later fires in the eight remaining plots. First, differences in annual fire behavior could have reflected short-term fluctuations in climate; this is supported by the higher rankings of later fire years relative to Yosemite fire normals for number of fires, fire severity, and area burned (Table 2; Lutz et al. 2011). Alternatively, antecedent fires could have stimulated shrub species, which then burned in the subsequent fire; although higher prefire NBR would lower the RdNBR value, complete ignition of shrub cover could potentially yield a higher RdNBR (Lydersen et al. 2014, Lauvaux et al. 2016). This second hypothesis is supported by the greater proportion of burned plots (76.5%) than unburned plots (39.1%) with ≥2.5-m² shrub cover. Third, previous fires could have accelerated the accumulation of ground fuels due to the deposition of scorched needles and other debris, thereby increasing the intensity of subsequent fires (van Wagtendonk et al. 2012).

CONCLUSIONS

Management that aims to duplicate historical levels of forest density and species composition has become less relevant because the climate that gave rise to the forests of the Sierra Nevada several centuries ago no longer exists (e.g., Lutz et al. 2010). Instead, forest management has begun to focus on more general concepts of resistance and resilience to hedge against high uncertainties. We examined the effects of fire reintroduction on tree species communities at the broad scale of the

central Sierra Nevada, using the relatively undisturbed forests of Yosemite and Sequoia & Kings Canyon National Parks. We found that lower-severity fire significantly reduced the density of shade-tolerant *A. concolor* <30 cm dbh and reduced the density at a marginal level of significance of *A. concolor* 30–45 cm dbh, *A. magnifica* <30 cm dbh, and *C. decurrens* <15 cm dbh. Comparisons of diameter distributions from our burned plots with landscape-scale historical data showed that lower-severity fire reduced mean tree density of *A. concolor* 10–60 cm dbh to the historical mean and that mean density of *C. decurrens* <30 cm dbh was greatly reduced but still exceeded historical mean values. Comparisons with local-scale historical and reconstructed data showed that lower-severity fire successfully produced some stands that align with historical diameter distributions but that the range of outcomes from lower-severity fire exceeds the range observed in historical forests. This could be due to the small number of historical data sets and how they are summarized or due to the variation in the effects of lower-severity fire on tree density that we captured in our study. Possible decreases in snowpack in this century (e.g., Hayhoe et al. 2004) along with the small number of trees <45 cm dbh that survive fires imply that reintroducing and maintaining an active fire regime (e.g., Churchill et al. 2013, Larson et al. 2013) will help lower and control overall tree density. It is important, however, that reintroduced fire not kill the large-diameter trees that help define the structure of Sierra Nevada forests (e.g., Lutz et al. 2009*a*, Collins et al. 2011, Kane et al. 2014). Maintaining this balance of fire severities and return intervals will remain a challenge for fire and forest managers in the Sierra Nevada.

Acknowledgments

Literature Cited

Barth, M. A. F., A. J. Larson, and J. A. Lutz. 2015. A forest reconstruction model to assess changes to Sierra Nevada mixed-conifer forest during the fire suppression era. Forest Ecology and Management 354:104–118.

Beaty, R. M., and A. H. Taylor. 2007. Fire disturbance and forest structure in old-growth mixed conifer forests in the northern Sierra Nevada, California. Journal of Vegetation Science 18:879–890.

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291: 442–457.

Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2:1–14.

Das, A., J. Battles, N. L. Stephenson, and P. J. van Mantgem. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. Forest Ecology and Management 261:1203–1213.

Dolanc, C. R., H. D. Safford, S. Z. Dobrowski, and J. H. Thorne. 2014. Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US. Applied Vegetation Science 17:442–455.

Dolanc, C. R., J. H. Thorne, and H. D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography 22:264–276.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–21.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fites-Kaufman, J., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 456–501 *in* M. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Berkeley, California, USA.

Flora of North America Editorial Committee, editors. 1993+. Flora of North America north of Mexico. 16+ volumes. FONA, New York, New York, USA.

Fulé, P. Z., and D. C. Laughlin. 2007. Wildland fire effects on forest structure over an altitudinal

gradient, Grand Canyon National Park, USA. Journal of Applied Ecology 44:136–146.

Guarín, A., and A. H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. Forest Ecology and Management 218:229–244.

Harmon, M. E., K. Cromack Jr., and B. G. Smith. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Canadian Journal of Forest Research 17:1265–1272.

Hayhoe, K., et al. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences USA 101: 12422–12427.

Kane, V. R., J. A. Lutz, C. A. Cansler, N. A. Povak, D. Churchill, D. F. Smith, J. T. Kane, and M. P. North. 2015. Water balance and topography predict fire and forest structure patterns. Forest Ecology and Management 338:1–13.

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

Kane, V. R., M. North, J. A. Lutz, D. Churchill, S. L. Roberts, D. F. Smith, R. J. McGaughey, J. T. Kane, and M. L. Brooks. 2014. Assessing fire-mediated change to forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. Remote Sensing of Environment 151:89–101.

Keeler-Wolf, T., P. E. Moore, E. T. Reyes, J. M. Menke, D. N. Johnson, and D. L. Karavidas. 2012. Yosemite National Park vegetation classification and mapping project report. Natural Resource Report NPS/YOSE/NRTR-2012/598. National Park Service, Fort Collins, Colorado, USA.

Keeley, J. E. 2012. Ecology and evolution of pine life histories. Annals of Forest Science 69:445–453.

Key, C. H., and N. C. Benson. 2006. Landscape assessment: sampling and analysis methods. USDA Forest Service General Technical Report RMRS-GTR-164-CD. USDA Forest Service, Rocky Mountain Research Station. Logan, Utah, USA.

Kilgore, B. M. 1973. Impact of prescribed burning on a sequoia-mixed conifer forest. Proceedings of the Tall Timbers Fire Ecology Conference 12:345–375.

Kilgore, B. M., and G. S. Briggs. 1972. Restoring fire to high elevation forests in California. Journal of Forestry 70:266–271.

Knapp, E. E., C. N. Skinner, M. P. North, and B. L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 310:903–914.

Kobe, R. K., S. W. Pacala, J. A. Silander Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5:517–532.

Kolden, C. A., J. A. Lutz, C. H. Key, J. T. Kane, and J. W. van Wagtendonk. 2012. Mapped versus actual burned area within wildfire perimeters: characterizing the unburned. Forest Ecology and Management 286:38–47.

Larson, A. J., R. T. Belote, C. A. Cansler, S. A. Parks, and M. S. Dietz. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. Ecological Applications 23:1243–1249.

Lauvaux, C. A., C. N. Skinner, and A. H. Taylor. 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. Forest Ecology and Management 363:74–85.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications 19:1003–1021.

Lutz, J. A., C. H. Key, C. A. Kolden, J. T. Kane, and J. W. van Wagtendonk. 2011. Fire frequency, area burned, and severity: a quantitative approach to defining a normal fire year. Fire Ecology 7(2): 51–65.

Lutz, J. A., A. J. Larson, J. A. Freund, M. E. Swanson, and K. J. Bible. 2013. The importance of large-diameter trees to forest structural heterogeneity. PLoS ONE 8:e82784.

Lutz, J. A., A. J. Larson, M. E. Swanson, and J. A. Freund. 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS ONE 7:e36131.

Lutz, J. A., J. W. van Wagtendonk, and J. F. Franklin. 2009a. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. Forest Ecology and Management 257:2296–2307.

Lutz, J. A., J. W. van Wagtendonk, and J. F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936–950.

Lutz, J. A., J. W. van Wagtendonk, A. E. Thode, J. D. Miller, and J. F. Franklin. 2009b. Climate, lightning ignitions, and fire severity in Yosemite National Park, California, USA. International Journal of Wildland Fire 18:765–774.

Lydersen, J. M., M. P. North, and B. M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. Forest Ecology and Management 328:326–334.

Menning, K. M., and S. L. Stephens. 2007. Fire climbing in the forest: a semi-qualitative, semi-quantitative

approach to assessing ladder fuel hazards. Western Journal of Applied Forestry 22:88–93.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Miller, C., and D. L. Urban. 2000. Modeling the effects of fire management alternatives on Sierra Nevada mixed-conifer forests. Ecological Applications 10: 85–94.

Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau. 1995. Sixty years of change in California conifer forests of the San Bernardino Mountains. Conservation Biology 9:902–914.

North, M., M. Hurteau, R. Fiegener, and M. Barbour. 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. Forest Science 51:187–197.

North, M., J. Innes, and H. Zald. 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Canadian Journal of Forest Research 37:331–342.

NRCS. 2012. Soil Survey Staff, Natural Resources Conservation Service (NRCS), United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minckin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2013. vegan: community ecology package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Oosting, H. J., and W. D. Billings. 1943. The red fir forest of the Sierra Nevada: *Abietum magnificae*. Ecological Monographs 13:259–274.

Parker, A. J. 1984. Mixed forests of red fir and white fir in Yosemite National Park, California. American Midland Naturalist 112:15–23.

Parker, A. J. 1986. Environmental and historical factors affecting red and white fir regeneration in ecotonal forests. Forest Science 32:339–347.

Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.

PRISM. 2012. Climatological normals, 1981–2010. The PRISM Group, Oregon State University, Oregon, USA. http://prism.oregonstate.edu

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org

Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20:362–380.

Schwilk, D. W., and A. C. Caprio. 2011. Scaling from leaf traits to fire behaviour: Community composition predicts fire severity in a temperate forest. Journal of Ecology 99:970–980.

Schwilk, D. W., E. E. Knapp, S. M. Ferrenberg, J. E. Keeley, and A. C. Caprio. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 232:36–45.

Schwilk, D. W., et al. 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecological Applications 19:285–304.

Sequoia and Kings Canyon National Parks Photo Interpretation Report. 2007. USGS-NPS vegetation mapping program. Environmental Systems Research Institute, Inc, Redlands, California, USA.

Sherman, R. J., and R. K. Warren. 1988. Factors in *Pinus ponderosa* and *Calocedrus decurrens* mortality in Yosemite Valley, USA. Vegetatio 77:79–85.

Skinner, C. N., and C. Chang. 1996. Fire regimes, past and present. Pages 1041–1069 *in* Sierra Nevada ecosystem project final report to congress. Wildland Resources Center Report 37. University of California, Davis, California, USA.

Smith, A. M. S., et al. 2016. The science of firescapes: achieving fire resilient communities. BioScience 66:130–146.

Stephens, S. L., M. A. Finney, and H. Schantz. 2004. Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. Northwest Science 78:93–100.

Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the southern Sierra Nevada. Ecosphere 6:1–63.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25:855–870.

Stephenson, N. L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9:1253–1265.

Stephenson, N. L., et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93.

Thode, A. E., J. W. van Wagtendonk, J. D. Miller, and J. F. Quinn. 2011. Quantifying the fire regime distributions for severity in Yosemite National Park, California, USA. International Journal of Wildland Fire 20:223–239.

Van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26–58.

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, and M. Brooks. 2013. Tree mortality patterns following prescribed fire for *Pinus* and *Abies* across the southwestern United States. Forest Ecology and Management 289:463–469.

van Wagtendonk, J. W. 2007. The history and evolution of wildland fire use. Fire Ecology 3(2):3–17.

van Wagtendonk, J. W., and J. A. Fites-Kaufman. 2006. Sierra Nevada bioregion. Pages 264–294 *in* N. G. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

van Wagtendonk, J. W., and J. A. Lutz. 2007. Fire regime attributes of wildland fires in Yosemite National Park, USA. Fire Ecology 3(2):34–52.

van Wagtendonk, J. W., K. A. van Wagtendonk, and A. E. Thode. 2012. Factors associated with the severity of intersecting fires in Yosemite National Park, California, USA. Fire Ecology 8(1):11–31.

Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia National Park, California. Journal of Biogeography 5:377–402.

Webster, K. M., and C. B. Halpern. 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. Ecosphere 1:1–27.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

Wieslander, A. E., H. S. Yates, A. E. Jensen, and P. L. Johannsen. 1933. Manual of field instructions for vegetation type map of California. USDA Forest Service Memorandum.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1484/full