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Multi-scale reference conditions in an interior pine-dominated landscape in northeastern California

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ABSTRACT

A plot-based census was conducted of trees >8.9 cm in breast height diameter in a 4000 ha forest in northeastern California in 1933 and 1934, prior to any harvest activity. The trees were tallied by size class and species on contiguous plots specified to be 1.01 ha in size, although some plots had a forested area less than this specification due to natural openings in the forest. In general, variability in all metrics declined as scale increased across a range from 1 ha to 244 ha, although much of this variability was in the tails; the inner quartile range appeared to be more stable, particularly so for crown area. Although metrics were derived at a smaller scale (<1 ha) from partial plots, these may be unreliable due to the study design and possible confounding factors. The landscape distribution of tree sizes was bimodal and skew positive with a maximum tree size of 189.2 cm. However locally the distribution of tree sizes was more ragged and variable in shape. Species distribution appears to have shifted in a direction away from pine dominance in the years since the census was conducted. Historically, these stands were approximately 86 percent pine by basal area, with some variation depending on slope position. The stem density was dominated by young, thrifty-mature trees of good or moderate vigor but basal area and crown area was dominated by mature or over-mature trees with moderate or poor vigor. Crown area tended to be low with 90 percent of observations between 13 and 35 percent at the 1 ha scale.

1. Introduction

Land managers often consider historic condition metrics, including range of variability, in guiding decision making. Forest restoration efforts may benefit from reference condition metrics describing the range of variability of stands from a time when stands exhibited greater resiliency to disturbance (Swetnam et al., 1999). Reference conditions also provide insight into processes that have shaped forest dynamics and may help managers gain an understanding of influence of past activities on the landscape (Safford et al., 2012).

Although reference conditions are important in understanding how forests functioned in the past, and can be used in guiding management today (Higgs et al., 2014; Fulé, 2008) they are not without limitations. Our understanding of reference conditions are often shaped by data which are limited in geographic scope and in total area dedicated to sample plots (e.g. Fulé et al., 1997 roughly 2.5 ha in sample plots over 700 ha). Furthermore, climate change effects may require consideration of a more process-based approach to restoration, rather than one heavily dependent on historic metrics (Safford et al., 2012).

In ponderosa pine forests of the southern Cascades, general trends have been toward more closed forests with smaller trees (Taylor, 2000) and species shifts to late seral dominance (Hessburg et al., 2000; Agee, 2003). These same types of trends may be inferred from other regions as well (Moore et al., 2004; Fulé et al., 1997). The primary reason cited for these general trends is the change in fire regime over the last century, although livestock grazing and past harvest practices have also contributed.

Any discussion of reference condition variability should be framed in the context of scale. Scale can have a major impact on the interpretation of reference data (White and Walker, 1997). Much of the work that has been done was derived from observations at a very limited scale (e.g. Harrod et al., 1999; Lydersen et al., 2013). While there has been a good deal of focus on local patch dynamics (e.g. Lydersen et al., 2013), less research conducted on larger scale inferences, primarily because of the difficulty in obtaining historic data over a large landscape (Baker, 2014; Stephens et al., 2015).

The objective of this analysis is to present historic metrics covering a 4000 ha forest reflecting pre-harvest conditions, with particular emphasis on variability across the landscape and the relationship between variability and scale of observation. These observations were also compared to a limited area for which we

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have more current data to indicate changes over time in areas with no influence of harvesting. The historic data come from a census of trees conducted at Blacks Mountain Experimental Forest (BMEF) by Austin Hasel in 1933 and 1934 (Hasel, 1938).

Austin Hasel was a researcher at the California Forest and Range Experiment Station in Berkeley, California in the late 20s and 30s. Hasel initiated an effort to collect data on BMEF that would serve two primary purposes. The first was to provide detailed volume and vigor estimates for trees across the entire forest by administrative compartments. The second objective was to develop an understanding of sampling concepts as applied in western forests (Hasel, 1938). Hasel was specifically interested in the practical effects of random vs. systematic sampling on the estimation of error (Hasel, 1938, 1942b), and the effects of plot configuration (strips vs. plots) or plot size (Hasel, 1942a). With this in mind, Hasel established a complete census for all trees on the Experimental Forest above 8.9 cm (3.5 in.) breast height diameter (dbh) by contiguous 1.01 ha (2.5 acre) plots. This census was done in such a way as to facilitate grouping into various size plots and a variety of sample intensities and strategies.

2. Methods

2.1. Location

Blacks Mountain Experimental Forest (BMEF) was formally designated in 1934, although some preliminary research work began prior to this designation. It is located on the Lassen National Forest (40.72° N, 121.18° W) in northeastern California with elevations ranging from 1700 to 2100 m. The southwest portion is a flat basin (Halls Flat) while most of the rest of the forest has gentle slopes, <15 percent (Fig. 1). The climate is characterized by warm, dry summers and median annual precipitation is approximately 500 mm, about 75 percent of which falls, primarily as snow, from November to April. BMEF is currently 4300 ha but the original configuration was slightly smaller because of several patented in-holdings (~400 ha) which have since been added. The forested acreage is reduced further by several hundred ha of small non-timbered openings, these are primarily grasslands with no recent evidence of trees (Fig. 1).

Today, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) can be found throughout the forest while Jeffrey pine (*Pinus Jeffreyi* Balf.) occurs primarily at the lower elevation. In some areas the pines reside in a mix with white fir (*Abies concolor* (Gord. and Glendl.) Lindl. ex Hildebr.), and incense-cedar (*Calocedrus decurrens* (Torr.) Florin). Western juniper (*Juniperus occidentalis* Hook.) is sparsely distributed in the lower elevations of the forest and are found only rarely. Junipers were not recorded in the Hasel study.

Fire was once a frequent occurrence at Blacks Mountain. Historically the fire return interval on sites <40 ha ranged from 5 to 17 years (Norman, 2002). Fire has been effectively excluded from the Experimental Forest during the 20th century (Skinner, 2005). The first disruption in the historic fire regime was due to widespread sheep grazing in the late 1800s; later in the early 1900s the Forest Service began instituting aggressive fire suppression policies.

2.2. The Hasel data

Hasel's observations at Blacks Mountain predate management and provide a remarkable compilation of stand structure on contiguous plots across a large forested area. The trees recorded (those >8.9 cm in diameter) largely reflect conditions that exclude ingrowth from fire exclusion. The primary pulse of regeneration in this region dates to the turn of the century (Taylor, 2000; Youngblood et al., 2004). This pulse in regeneration is linked to the introduction of sheep grazing in the late 1800s (Norman and Taylor, 2005; Skinner and Taylor, 2006).

Prior to the commencement of observations of the forest conditions by Hasel, a compartment mapping exercise was completed

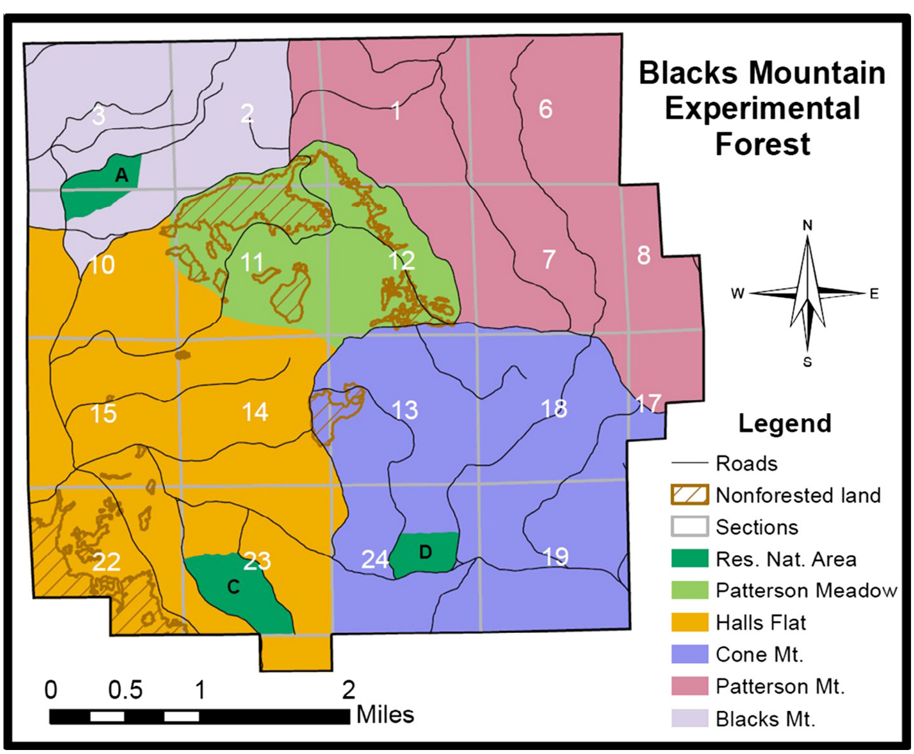

Fig. 1. Map of Blacks Mountain Experimental Forest with two basin regions and three up-slope regions; numbered square sections displayed are 1609 m on each side. Most roads displayed were not present at the time of 1933–1934 tree census.

which formed 100 administrative compartments within the forest. Furthermore these compartments were grouped into 5 distinct regions within the forest. These regions were identified as the Blacks Mountain footslope (B), Patterson mountain slope (P), Cone mountain slope (C), the southwest basin (G) and the interior basin (A).

Hasel divided the forest area into sections and quarter sections so that each quarter section was a manageable quantity for survey. Each quarter section was then divided into 16 sub-quarters that were 4.05 ha (10 acres) in size. The sub-quarters were numbered in a serpentine fashion starting in the northwest corner of the quarter. Each sub-quarter was divided into four 1.01 ha (2.5 acre) strips running east to west and numbered 1–4 from north to south.

Three crews of three persons each (one compass man and two recorders) completed the survey. They began work in summer 1933 and finished in the fall of 1934. No data were collected in winter months. Crews averaged somewhere around six hectares per day.

Within each individual rectangular plot, all trees >8.9 cm (3.5 in.) were tallied by 5.08 (2 in.) wide diameter classes so each diameter tally class was labelled by even inches (4, 6, 8, 10...). The only variance in this is the width of the first diameter class, which is actually slightly narrower (3.81 cm) because the starting point for tally was 3.5 in. rather than 3 in.

For each plot, the crew estimated the timbered area of the plot. Since the plots were done by moving through the strip, when boundaries were encountered, the distances from starting point was determined to estimate the area. To be considered at least partly timbered any given 1 ha strip had to have at least 1 tree >27.9 cm in dbh. With few exceptions those areas classed as "non-timbered," and given a timbered area of zero, were in permanent meadows. Those areas so designated in 1933 appear the same today. One exception to this is a small area in the northeast quarter of section 14 which today has some openings with a cover of junipers. A plot falling in this juniper woodland would have been classed "non-timbered" in 1933.

Each tree was tallied by diameter class, species, and vigor class (Dunning, 1928). Dunning's classification is detailed in Table 1. Species were identified as pine, or fir or cedar; no distinction was made between Jeffrey and ponderosa pine. Diameters were confirmed by diameter tape or Biltmore stick until the recorder developed an eye for ocular estimation of the diameter. Periodically, observers would re-confirm diameters with tape or Biltmore stick. Dunning's tree seven tiered classification system was based primarily on age (young, thrifty mature, mature and over mature), tree position (independent, dominant, codominant, intermediate and suppressed) and tree vigor (good, moderate, or poor).

Table 1
Dunning (1928) tree class definition summary. Age classes at Blacks Mountain can be approximated as young (<50), thrifty mature (50–100), mature (100–200), and overmature (>200).

Class	Age	Position	Vigor
1	Young or thrifty mature	Dominant or isolated	Good
2	Young or thrifty mature	Codominant, rarely dominant	Good or moderate
3	Mature	Codominant, rarely dominant	Moderate
4	Mature	Codominant, rarely dominant	Moderate or poor
5	Over mature	Dominant, rarely codominant	Poor
6	Young or thrifty mature	Intermediate or suppressed	Moderate or poor
7	Mature or over mature	Intermediate or suppressed	Poor

Original field sheets were located in the Pacific Southwest Research Station library in Redding, California. These files were then checked for species consistency, range of diameters and range of vigor class. Diameter class tallies were also checked for extreme values to see if they matched the field sheets. Incorrect or suspect data entries were then checked against the field sheets and corrected to correspond with the record on the field sheet.

Crown area for each tree was estimated by application of crown width equations (Fig. 2) developed for BMEF from a sample of 1953 trees with measured crown widths (Wing et al., 2015). Where crown width was measured in two dimensions (long and short axis) and dbh was measured with a diameter tape. Crown width was obtained as the geometric mean. A random normal deviate was added to each crown width corresponding to the estimated weighted root mean squared error for each tree. The inclusion of this term was inconsequential in the final analysis, as there were sufficient trees on most plots for the sum of deviations to be very close to zero for each strip. Crown area percentage adjusted for

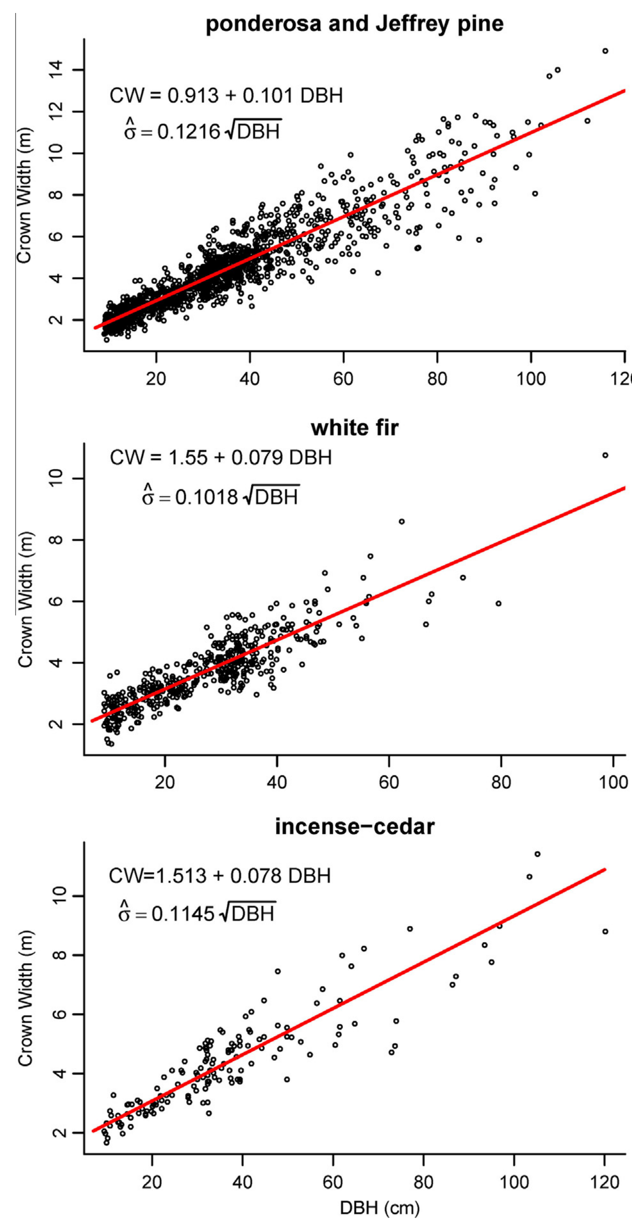

Fig. 2. Crown width estimation using weighted linear regression for Blacks Mountain Experimental Forest.

overlap *CA* was derived from the nonlinear transformation of unadjusted crown area percentage (*CAS*). *CAS* derived as a percentage of unit area of the sum of individual tree crown areas (Crookston and Stage, 1999):

$$CA = 100[1 - \exp(-CAS/100)].$$

Above-ground biomass was calculated with a function dependent on species. Ponderosa pine biomass equations were developed locally at BMEF (Ritchie et al., 2013) and applied for all pine, with heights estimated from local height-diameter equations. Equations of Jenkins et al. (2004) were used for white fir and incense-cedar.

Aggregation across a range of scales was completed for 1, 2, 4, 8, 16, 32, 64, 128, and 244 ha using Hasel's original protocol. For example, summaries by quarter-sections yield calculations at a scale of approximately 64. The effects of scale on both tree density by size class as well as quadratic mean diameter, above ground biomass, and crown area were then related to these scales graphically.

There was some variability in the size of the individual plots in the Hasel data. The variation in plot size arises because some plots landed on the boundary of natural openings. In these instances the protocol directed that plots be bounded at that point and the crew then estimated the "timbered area" of the plot. While for most plots the timbered area was the designed 1.01 ha (2.5 acres), there were also a small proportion of plots that had a smaller timbered area and these may not be representative of the variability at the 1 ha scale. Furthermore, in some instances plots were slightly >1 ha, although these were quite uncommon. These were most likely due to variation in section boundaries as surveyed at Blacks Mountain.

2.3. Current observations at Blacks Mountain Experimental Forest

For comparison, three subunits of the Blacks Mountain Research Natural Area (Cheng, 2004) were used to develop current metrics. The Research Natural Area is 211 ha in total area, and divided into 5 separate subunits. The Research Natural Area has been withdrawn from active management and has no history of timber harvest. An array of permanent nested plots has been established (0.08 ha for dbh > 29.2 cm/0.02 ha for $8.9 < \text{dbh} \leqslant 29.2$ cm/0.004 ha for dbh $\leqslant$ 8.9 cm) on a grid spacing of 1 plot every 2 ha (Oliver, 2000). Tree diameter, heights and species were recorded on each plot. The most recent observation in the Research Natural Area was in 2012.

2.4. Tree classification

Dunning's tree classification ratings were compared between upslope and basin areas of the forest to see if there were differences at the 1 ha scale. A two sample *t*-test was conducted for differences in stem density and crown area percent unadjusted for crown overlap. The unadjusted values were used because the transformation is nonlinear and the resultant values would be inconsistent with the sum.

3. Results

Of the 3959 plots established only 74 had less than two overstory trees (>29.2 cm dbh) per plot. Furthermore, all aggregations of these open plots, about 75 percent of the total, were associated either with forest property boundaries or with permanent openings shown in Fig. 1; these are meadows or ephemeral pond basins. The remainder were isolated plots scattered throughout the forest. About 96 percent of the 3779 ha area covered in the Blacks Mountain Experimental Forest census was represented by plots 0.8 and larger, averaging 1.01 ha (Table 2). These tend to have a higher occupancy as reflected in basal area than the smaller partial or fractional-plots (with lower timbered area) that tended to fall on the border of natural openings in the forest (see Fig. 1).

Table 2
Distribution of forested plot area and basal area (BA), by size class, in the 1933–34 tree census of 3779 ha at Blacks Mountain Experimental Forest.

Variable	Plot size (ha)			
	0–0.1	0.1–0.4	0.4–0.8	0.8+
Number of plots	57	107	217	3576
Mean area (ha)	0.05	0.23	0.63	1.01
Total area (ha)	2.99	25.56	136.34	3614.61
BA (m^2 ha^{-1})	16.2	14.7	14.7	20.87
BA s.e. (m^2 ha^{-1})	2.2	1.1	0.6	0.1

3.1. Landscape-level distribution of trees

Ignoring scale and plot size entirely, and just viewing the overall distribution of tree sizes across the observed 3779 ha timbered landscape (excluding grassy meadows and juniper woodland) yields a total number recorded trees of 596,357 (Fig. 3). The largest tree observed was 182.9 cm (72 in.). The most common size class

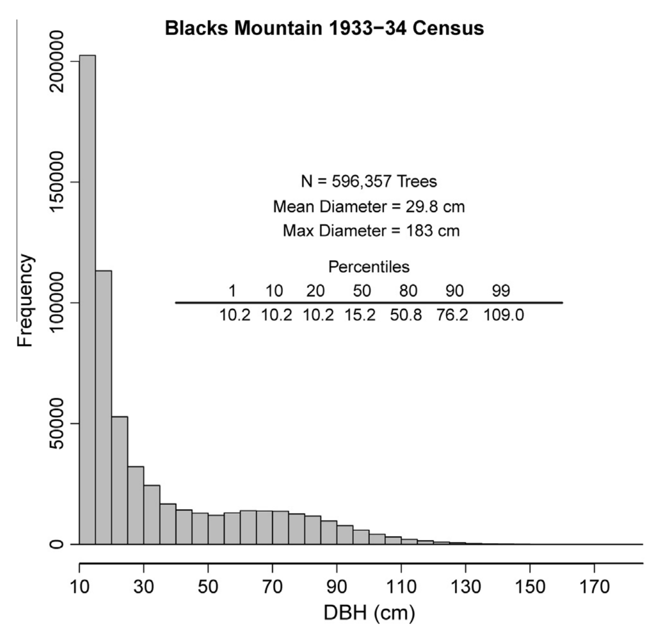

Fig. 3. Distribution of all trees >8.89 cm observed on 3779 ha classified as timbered in the Blacks Mountain in 1933/34 census, note that these are 5.08 cm width classes as the original observations were made in English units.

Table 3
Distribution of trees ha^{-1} by size (lower diameter limit sampled of 8.9 cm) and species across the 3779 ha Blacks Mountain Experimental Forest in the 1933–1934; the census total mean trees ha^{-1} (>8.9 cm) was 167.

	Breast-height diameter		
	8.9–27.9 cm	27.9–58.4 cm	>58.4 cm
Pine	86.72	20.85	24.82
White fir	22.40	4.60	2.06
Incense-cedar	3.04	0.68	1.75
Total	112.16	26.13	28.63

recorded, by far, was the smallest class. There is evidence of a bimodal diameter distribution at BMEF, with a second peak, although somewhat muted, between 60 and 80 cm dbh (Fig. 3). A total of only 115 (0.02 percent) of observed trees were in excess of 152 cm (60 in.). The total number of trees greater than or equal to 127 cm (50 in.) was 1572. Across the landscape, this distribution of tree size per hectare is simplified in Table 3.

3.2. Scale and variation

The range of variability generally decreased with increasing scale of observation for stem density (Fig. 4). Although much of this effect of scale was observed in the outer quartiles while the inner-quartile range was relatively stable across the range of observed scales from 1 to 244 ha. Density of small trees appeared to exhibit a stronger skew-positive distribution, particularly at smaller scales, whereas mid-size and large tree densities were relatively symmetric. The mean is relatively stable, as it must be, since variability in the mean density is only associated with slight variation in plot size within a given scale. However, the median varies to a greater degree than the sample mean.

The separation between the median and mean is an indicator of the degree of skewness in a distribution, it is thus evident from this separation that there was some degree of positive skew in tree density for smaller trees at a scale below about 20 ha. The skewness statistic (Sk) was derived from the third moment about the sample mean and standard deviation (sd), with sample size correction:

$$Sk = \frac{n}{(n-1)(n-2)} \sum_{i}^{n} \left(\frac{x_i - \bar{x}}{sd} \right)^3$$

This indicates decreasing skewness in small and medium sized tree density, while for large trees the skewness statistic was uniformly small, with the absolute value below 0.20 regardless of scale (Fig. 5). Other metrics considered (QMD, Crown Area and Biomass) were generally negatively skewed although not strongly so.

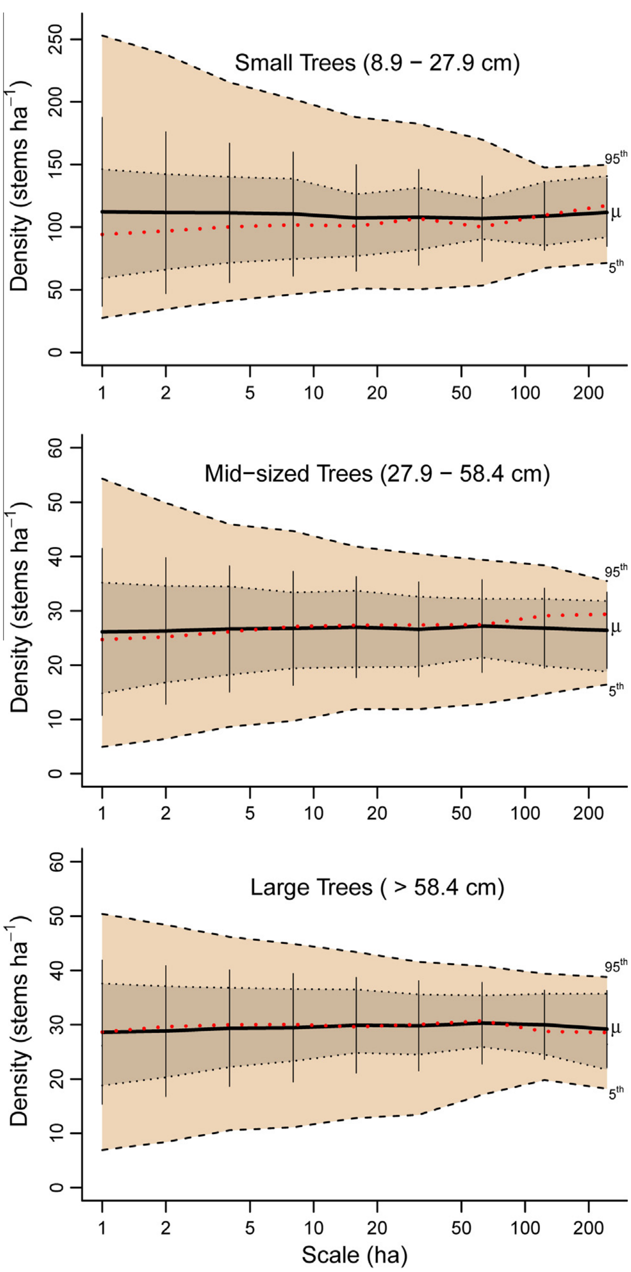

Fig. 4. Distribution of number of stems ha^{-1}, by broad diameter ranges, across a range of scales (in log scale) at Blacks Mountain Experimental Forest in the 1933–34 census with 5th to 95th percentile shaded and inner-quartile range shown as dotted line; sample median is shown with the red dotted line. Mean is black line with standard deviations (±1) shown as vertical bars.

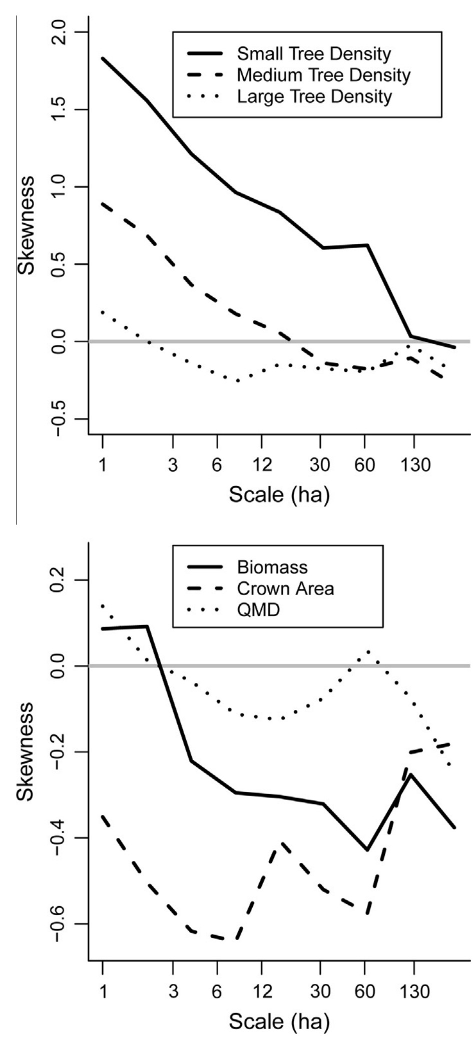

Fig. 5. Skewness statistics, adjusted for sample size, for forest metrics expressed as a function of scale in the Blacks Mountain 1933–1934 census.

For above-ground woody biomass, the inner quartile range of 84–14 at 1 ha scale diminished only slightly with increasing scale and the mean of 112, again, exhibited stability (Fig. 6). For crown area, the mean was 25 percent and the inner-quartile range was in the vicinity of 21–29. About 80 percent of the observations were between 15 and 33 percent crown area at the smallest whole-plot scale. The distribution of tree size, as reflected in quadratic mean diameter, displayed a slightly more pronounced flaring at smaller scales as exhibited in the 5th and 95th percentiles.

Biomass, crown area and QMD all tended to be symmetric with small skewness values, regardless of scale. As with tree density the log-scale produced a nearly linear relationship with the extremes (5th and 95th percentile) associated with biomass, crown area and quadratic mean diameter.

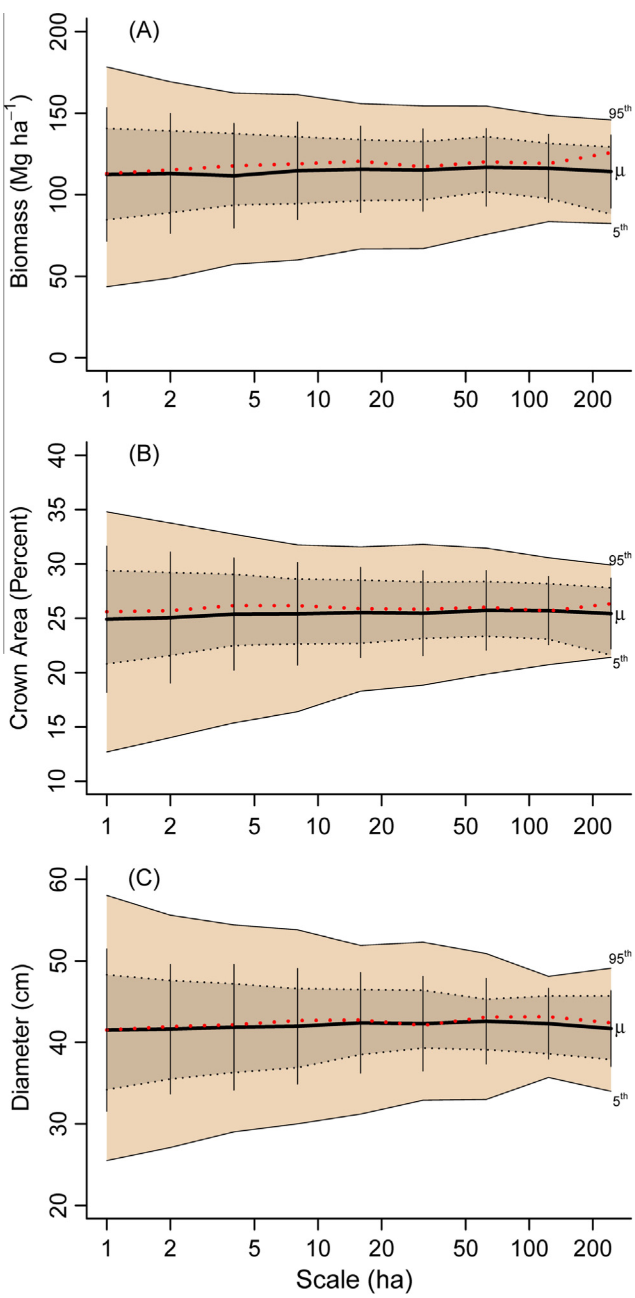

Fig. 6. Distribution of above ground biomass (A), crown area adjusted for overlap (B), and quadratic mean diameter (C) across a range of scales (in log scale) at Blacks Mountain Experimental Forest in the 1933–34 census with 5th to 95th percentile shaded and inner-quartile range shown as dotted line; the sample median is shown with a red dotted line. Mean is black line with standard deviations (±1) shown as vertical bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. ha scale metrics

The smallest scale that can be evaluated consistently with these data is at the design-specified 1.01 ha level. Unfortunately the study design does not provide for anything below that scale with the exception of the partial plots.

For these results all plots in the data set >0.8 ha in size (3546 of the 3959 plots in the data set) were selected. By selecting a threshold of 0.8 ha and above for these whole plots, a relatively homogeneous plot size was established (mean = 1.01 ha, s.d. = 0.056 ha).

Total stem density all for trees >8.9 cm in dbh varied widely, with a range from 9 to 932 stems ha^{-1} (Table 4). This skew positive distribution for this metric (skewness coefficient = 1.67) masks somewhat the underlying dynamic with regard to tree size. The skewness is primarily reflected in small trees, where the maximum is roughly ten times the median (skewness = 1.83), while the maximum density for mid-sized trees is only about seven times the median (skewness = 0.89) and the maximum density for large trees is about three times the median (skewness = 0.19).

Initially, an attempt was made to fit a Weibull function for diameter distributions at the 1 ha scale. However, it was common to find that individual 1 ha plots did not meet the underlying assumption of a unimodal distribution (Fig. 7). That is, diameter distributions at this scale were often quite ragged and highly variable in shape and the Weibull was usually not a good fit because of bimodality. Density of small trees was highly variable even in adjacent plots. Further attempts at fitting individual plot distributions were abandoned.

All metrics considered showed a negative relationship between variability, as expressed by coefficient of variability, and plot scale. This was trend most notable among tree density metrics, particularly for small (8.9–27.9 cm dbh) trees (Fig. 8).

When looking at the distribution of densities of large trees (>58.5 cm in diameter) and mid-sized trees (28.0–58.5 cm) it is evident that there was a wide range of conditions across the forest. Although the most common range was that where both mid-sized trees and large tree densities were between 20 and 40 stems ha^{-1} (24 percent), observations both above and below this range were not uncommon (Table 5). Almost 30 percent had a density of large trees below 20 stems ha^{-1}. Approximately 87 percent of the plots fell in the shaded area shown in Table 5, and 62 percent were in the dark shaded area.

Ponderosa and Jeffrey pine dominated the forest in the 1933–34 census. When expressed as trees ha^{-1}, pine constituted 79 percent (Table 4). The median species composition across the forest was 91 percent pine by basal area with an inter-quartile range of 16.1–25.7 (Table 4), and over 25 percent of the plots were pure pine (Table 4).

A comparison with current conditions can be made only on a very limited scale based on recent field data from the Blacks Mountain Research Natural Area (Cheng, 2004). All other areas of the forest with more current observations have a history of harvest over the last 80 years and comparisons with these would exhibit confounding effects. On the three subunits within the Research Natural Area for which we have current data, the proportion of pine by basal area has been reduced over the 80 year observation period (Table 6). When comparisons are made with stem density the trend is very similar. The reduction in proportion of pine by stem density over time range from 8 to 23 percent.

Above-ground (living) tree biomass varied from 0.6 to 313 Mg ha^{-1}, with a mean of 112. A comparison within the unmanaged Research Natural Area shows living biomass has been reduced substantially while at the same time stem density has increased

Table 4
Univariate summary metrics (T = stem density for small (*s*), mid-size (*m*) and large trees (*l*), BA = basal area for small, mid-size and large trees, SDI_r = Reineke stand density index, SDI_s = summation stand density index, CA = crown area) for trees 7.6 cm and larger in dbh on 3546 forested plots at least 0.8 ha in size at Blacks Mountain observed in 1933 and 1934; average plot size = 1.01 ha and standard deviation of plot size = 0.05 ha.

Variable	Units	Mean	Min	5th	25th	50th	75th	95th	Max
T	stems ha^{-1}	166.9	8.9	73.1	116.6	152.2	203.6	301.1	932.3
T_s	stems ha^{-1}	112.2	2.0	27.7	59.3	94.1	146.2	253.0	834.6
T_m	stems ha^{-1}	26.1	0	4.9	14.8	24.7	35.2	54.4	146.3
T_l	stems ha^{-1}	28.6	0	6.9	18.8	28.7	37.6	50.4	85.3
BA	m^2 ha^{-1}	20.8	0.3	8.8	16.1	20.9	25.7	32.0	51.9
BA_s	m^2 ha^{-1}	2.0	0.0	0.5	1.1	1.8	2.6	4.5	14.9
BA_m	m^2 ha^{-1}	3.7	0.0	0.5	2.0	3.5	5.0	7.5	18.7
BA_l	m^2 ha^{-1}	15.1	0.0	4.8	10.9	15.1	19.3	25.2	45.2
Pine BA	percent	86	6	57	74	91	100	100	100
SDI_r	stems ha^{-1}	337	8	158	272	342	407	494	818
SDI_s	stems ha^{-1}	291	7	131	229	295	354	437	648
QMD	cm	42	14	26	34	41	48	56	78
CA	percent	25	1	13	21	26	29	35	52
Biomass	Mg ha^{-1}	112	0.6	44	84	113	140	178	313

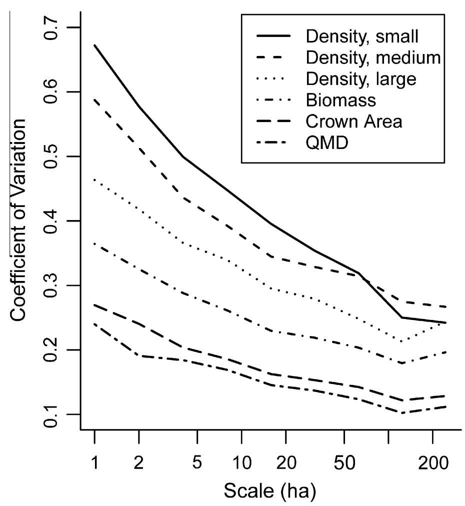

Fig. 7. Diameter distributions with fitted Weibull function for four adjacent 1 ha plots at Blacks Mountain in the south east quarter of section 1 in the 1933–1934 census.

(Table 7). Tree size, expressed as mean biomass per living tree has therefore shrunk. There is a 10-fold difference between the two over time.

3.4. Crown area

Crown area expressed as an estimated vertical projection of tree crowns with adjustment for crown overlap, varied between 1 and 52 percent forest-wide on 1 ha plots at BMEF in the 1933–1934 census with a mean of 25 (Table 4). Comparisons at the RNA, again, show a significant difference over time. In the three Research Natural Areas the crown area has more than doubled, in the absence of any harvesting and with little fire activity at Blacks Mountain during the 20th century. Although it should be noted that RNA C had one recent entry of prescribed fire with a fall burn in 1998.

Table 5
Bivariate distribution of stems per hectare (expressed as a percentage) in mid-size trees (27.9–58.4 cm in diameter) and large trees (>58.4 cm) among 3546 forested plots at least 0.8 ha plots in size at Blacks Mountain Experimental Forest. Dark shading indicates cells with at least 15 percent and light shading indicates areas between 5 and 10 percent.

	Trees ha^{-1}	Mid-size trees				Total
		0–20	20–40	40–60	60+	
Large trees	0–20	18.1	7.2	1.8	0.3	27.4
	20–40	17.3	25.4	8.4	1.9	53.0
	40–60	3.8	10.5	3.6	0.6	18.5
	60+	0.1	0.6	0.2	0.2	1.1
	Total	39.3	43.7	14.0	3.0	100

Table 6
Comparison of species compositions, as expressed by percent of basal area by species in three unmanaged units in the Blacks Mountain Research Natural Area.

Year	Pine/fir/incense-cedar		
	Unit A (35 ha)	Unit C (57 ha)	Unit D (25 ha)
1933	87/4/9	96/2/2	74/17/8
2012	73/9/18	89/9/2	45/40/15

3.5. Tree classification

For evaluation of Dunning's (1928) tree classification I used the slope position post stratification. The plots in the basin compartments were separated from the upslope compartments.

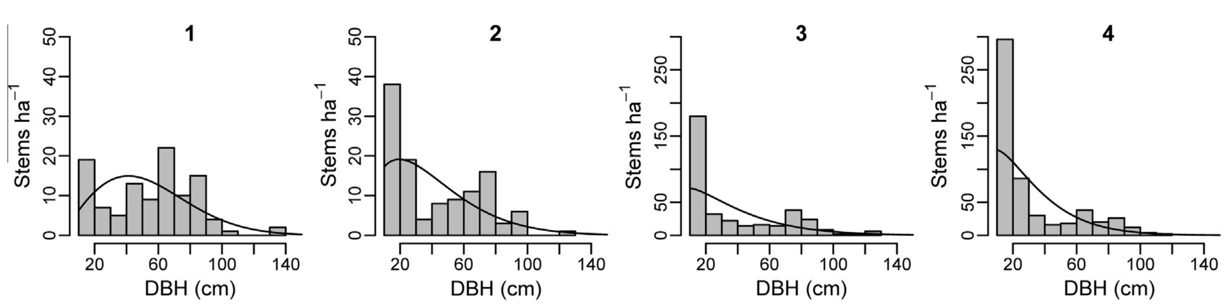

Fig. 8. Coefficient of variation for all six metrics considered: tree density for three size classes of trees (8.9–27.9 cm, 27.9–58.4 cm, and >58.4 cm), above-ground biomass, crown area and quadratic mean diameter.

Table 7
Comparison of total stem density and above ground biomass (branch and bole) as expressed by percent of basal area by species in three units in the Blacks Mountain Research Natural Area; the 2012 sample estimates include standard error. All comparisons of recent sample estimate and the 1933/1934 census are statistically significant ($P < 0.001$).

Year	Biomass (Mg ha^{-1})		
	Unit A	Unit C	Unit D
1933	107	100	142
2012	57 (5.6)	49 (3.6)	67 (17)
	Density (Stems ha^{-1})		
1933	284	257	202
2012	958 (147)	618 (67)	1173 (187)
	Crown area (Percent)		
1933	26	25	28.0
2012	49 (3.8)	40 (2.2)	52 (5.2)

This distinction was possible because when the original plots were established, the field crews identified the compartment or if the plot straddled two or more compartments; for this post-stratification, border plots were discarded. Also crown area remains unadjusted for overlap because that adjustment is a nonlinear transformation and the individual crown areas would not be consistent with the sum. There were subtle differences between the upslope and basin stands. The most notable difference was in species composition. Basin units had a mean percentage of pine by basal area of 98 percent (s.d. = 7.1 percent); these are primarily pure stands with the only white fir and incense-cedar being found along the transition margins. In contrast the upslope stands had a mean of 80 percent (s.d. = 15.7 percent). While total stem density was essentially the same for the two areas, the total basal area differed. Upslope areas tended to carry, on average, about 32 percent more basal area (p-value < 0.001) than basin areas. Similarly upslope unadjusted crown area (31 percent) tended to exceed that in the basin (25 percent), and this difference was statistically significant (p-value < 0.001). Also, within tree classes, there were some subtle but statistically significant differences. Class 3, 5 and 6 trees were all more common upslope (Table 8) while there tended to be fewer Class 1 trees. This distinction of Dunning Class 3 and 5 trees is attributable to their larger size on average (Table 8). These tended to be the largest trees and while there were only a few more stems per acre among upslope areas, they contributed to a substantial increase in basal area and crown area. Yet, at 31 percent mean crown cover, these stands were still quite open. Dunning class 7 and 4 trees were found infrequently across the forest. The large old Dunning Class 5 trees, while only accounting for roughly 10 percent of the stems contributed approximately 50 percent of the crown area in these stands.

3.6. Fine scale metrics

The 413 fractional plots observed in the 1933 census give an opportunity to investigate metrics at an even smaller scale than the 1.0 ha plots. The fractional plots were those where, often due to their representation of areas bordering openings, the fraction accounted as forested was <0.8 ha. Fractional plots had a forested area of 0.42 ha and a standard deviation of 0.42 and ranged from 0.04 to 0.8 ha in size. However, the limitation is that these areas appear to exhibit confounding, as the plots may be located in ecotones between forest and meadows and, as such, they tend to have lower median densities (Fig. 9).

The variability of the observations are quite high in the fractional plots, particularly with respect to small tree density where the standard deviation is 143 trees ha^{-1} for small fractional plots and 75 for 1 ha plots; most of this variability is expressed in the long positive tail where the maximum observed small tree density was 835 for full plots and 1013 in fractional plots.

The increase in variability can also be seen in other metrics as well. Crown area, for example, had a 5th and 95th percentiles of 2 percent and 49 percent respectively. While the median was only 20 percent, down from 30 percent for whole plots.

4. Discussion

In the early 1930s, prior to the onset of harvesting activity, Blacks Mountain Experimental forest was dominated by pine and characterized by open conditions with few (mean of 55 ha^{-1}) large- (>58.4 cm) and medium-sized (27.9–58.4 cm) trees across the forest. These observations are consistent with other findings (e.g. Fulé et al., 1997; Youngblood et al., 2004) in the ponderosa pine forest type. The presence of bimodality of the tree-size distribution was somewhat unexpected and may be attributed to an earlier period of favorable regeneration conditions at a point in time past that resulted in a higher number of trees between 50 and 80 cm observed in the census of the early 1930s. This bimodality was found for the forest at large (Fig. 3), but also was observed commonly, though not uniformly when looking at individual 1 ha plots (e.g. Fig. 7).

A median basal area of 21 m^2 ha^{-1} is consistent with the observations reported by Stephens and Gill (2005) for pine-dominated forests in the Sierra San Pedro Mártir, but almost twice that reported by Stephens et al. (2015) for pine-dominated dry forests in the southern Sierra Nevada. Although it is important to note, for such comparisons, that Stephens et al. (2015) did not include trees below 30 cm. This value is also consistent with that observed in high basal area ponderosa pine plots of the Sierras (Collins et al., 2015). The inner-quartile range (at the 1 ha scale) was 16–26 m^2 ha^{-1} at the 1 ha plot scale meaning that half the one-ha plots fell within this range.

Although the variability with respect to numerous metrics as reflected in the 5th and 95th percentiles certainly decreased with increasing scale, the inner-quartile range appeared to be less influenced by scale and was relatively stable across a wide range of scales for most of the metrics considered, indicating that the scale influence on variability was reflected more in the tails of the

Table 8
Upslope and basin distribution of stem density (T, stems ha^{-1}), basal area (BA m^2 ha^{-1}), crown area unadjusted for overlap (CA, percent) and quadratic mean diameter (QMD, cm) by Dunning (1928) tree class with two-sample t-test p-value for comparisons of stem density and crown area.

Tree	Basin plots				Upslope plots				P value	
Class	T	BA	CA	QMD	T	BA	CA	QMD	ΔT	ΔCA
1	85.1	2.8	5.7	20.6	68.0	3.1	5.8	24.2	<0.001	0.155
2	41.9	1.0	2.2	17.2	42.3	1.3	2.8	19.8	0.715	<0.001
3	6.1	2.4	3.1	70.4	12.0	4.2	5.3	66.6	<0.001	<0.001
4	4.2	1.1	1.5	57.0	5.8	1.5	1.9	56.8	<0.001	<0.001
5	15.9	9.6	11.7	87.8	21.1	12.2	14.3	85.6	<0.001	<0.001
6	11.3	0.2	0.5	15.5	17.3	0.4	0.9	16.1	<0.001	<0.001
7	1.1	0.1	0.5	39.7	1.3	0.2	0.2	39.0	<0.001	0.008

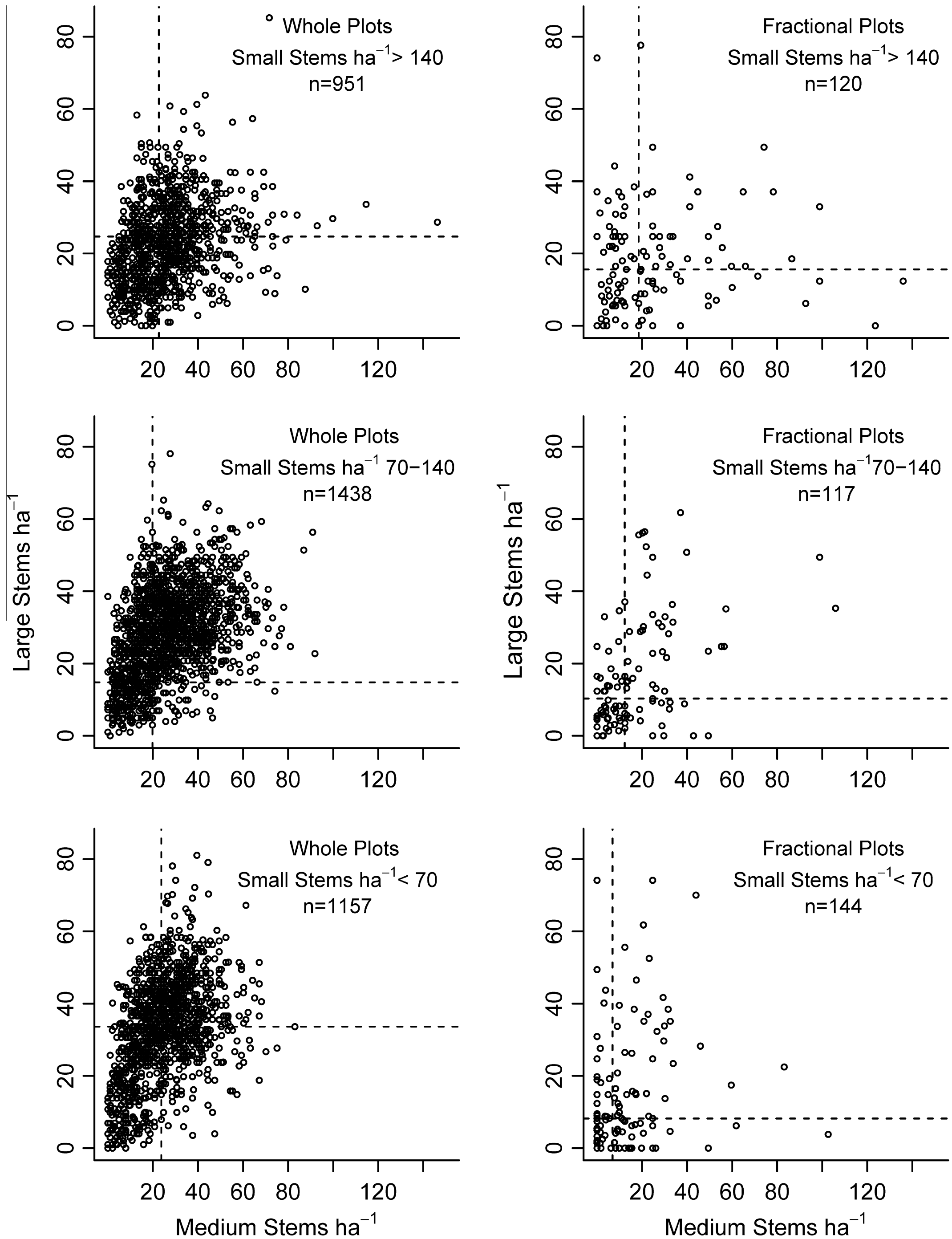

Fig. 9. Comparison of stem densities for three different tree sizes (Small 8.9–27.9 cm, Medium 37.9–58.4 and Large >58.4) compared for both the whole plots (mean size 1.0 ha) and the fractional plots (mean size 0.6 ha) in the 1933–1934 census at BMEF. Median at dashed lines.

distribution. This highlights the need to fully consider scale and variability when evaluating reference condition metrics. It also is important, therefore, that managers consider the scale of treatment when developing prescriptions guided or influenced by some reference metrics; such treatments may reasonably be allowed to exhibit a much greater range of variability within a treatment, at the 1 ha or smaller scale, than may be reasonable across a 20 ha treatment unit, for example.

The density of small (sapling-sized) trees varied much more and was more highly skewed (positively) than the larger size classes at Blacks Mountain, and this was true across the range of scales considered in this analysis. This may be indicative of patches or aggregations of smaller-sized trees distributed across this landscape. This suggests that forest management objectives of building resilient forest conditions in this region could reasonably include denser patches of smaller trees at small scales (less than 1 ha) among more widely spaced large- and medium-sized trees. However, these observations were taken after some years of fire exclusion and perhaps this contributes to a slightly higher density of small trees than would be expected had frequent low-intensity fire continued unabated up until the time of measurement.

From the limited comparisons made with current conditions in unmanaged stands at Blacks Mountain on three Research Natural Areas, it appears that fir and cedar are more common now than in the early 1930s. This is reflected both in terms of the proportion by basal area (Table 6) and stem density. This is consistent with an expectation that, in the absence of fire during the interim at Blacks Mountain, fir and cedar may find a more favorable environment for establishment and survival than under the historic fire regime. Show and Kotok (1924) noted the increased susceptibility of fir and cedar regeneration to succumb to fire, thus under repeated low-severity fires these species would tend to be kept at lower levels of density. Under an altered fire regime, a similar shift in species composition over time has been reported elsewhere (e.g. Skinner and Taylor, 2006; Stephens et al., 2015). It should be noted that the change over time may have been influenced by elevation within the forest as Unit C is the in the basin (1740 m), where historically fir was at very low levels, whereas the other two areas are in an upslope transition, with Unit D being the highest elevation (1830 m) area showing the greatest change in species composition.

The elevational gradient observed across the Research Natural Area appears to be influential in this regard. This gradient, although limited to a range of only approximately 100 m on average, is reflected both in the overstory composition, and in the understory as well at Blacks Mountain. There is a noticeably higher concentration of *Arctostaphylos patula* and *Ceanothus velutinus* in unit D, while the basin unit, C, the understory is dominated by *Purshia tridentata* with presence of *Artemisia tridentata* as well (recent field data and early vegetation maps on file, PSW Redding Laboratory). Some of the lower elevation areas at Blacks Mountain appear impervious to fir encroachment over the last century and still remain dominated by ponderosa and Jeffrey pine.

Interestingly, with the current drought conditions at Blacks Mountain over the last several years, the tenuous nature of the increase in fir density may have been exposed. White fir mortality rate is elevated at Blacks Mountain during the recent drought; particularly in those areas which have had some density management featuring retention of this species. The species has poor stomatal control (Hinkley et al., 1982) and maintaining fir on sites such as Blacks Mountain for the long term is therefore problematic (Cochran, 1998). Thus restoration efforts that feature retention of fir may be ill-advised, depending on elevation and slope position.

The number of trees by tree vigor, position and age was dominated by young "thrifty-mature" trees of good or moderate vigor as defined by the Dunning (1928) rating (Dunning Class 1 and 2), with far fewer stems classed as mature or over-mature with moderate or poor vigor (Dunning Class 3 and 5). However, in contrast crown area and basal area were dominated by Dunning Class 3 and 5 owing to the much larger size of these trees. Because of the slow growth rates of these trees, once the Dunning 3 and 5 trees are lost due to disturbance, replacement with the younger cohort takes many decades at Blacks Mountain (Ritchie et al., 2008). So, while the stands at Blacks Mountain now have, generally, higher levels of basal area and crown area, these stands are often very different structurally because of the paucity of mature and over mature trees.

The forests at Blacks Mountain prior to harvest were very open; estimated crown area among trees >8.9 cm dbh, expressed as a vertical projection of tree crowns with adjustment for overlap, rarely exceeded 35 percent at the 1 ha scale. Only 5 percent of the plots are above this value. These values of observed cover are fairly consistent with the range of values cited by Reynolds et al. (2013) for ponderosa pine in the southwest.

The structures observed across this landscape before any harvesting are an indication, in part, of the influence of fire on these forests. While the historic median fire return interval for this area was 6–17 years (Norman, 2002), the absence of any areas without an overstory of mature trees suggests the fires were of sufficiently low severity to maintain tree cover among mature trees at scales above 1 ha. Therefore, any high severity fire from historic fire regime must then have occurred in patches below 1 ha in size. The observations on this landscape were not consistent with a past of mixed severity fire as described by Odion et al. (2014). With past of mixed-severity fire, one would expect to see a much higher frequency of openings exceeding 1 ha in size. The openings in forest that we do see at Blacks Mountain appear to be low-lying meadows associated with poor drainage.

Not surprisingly, consideration of the partial plots (those below 0.8 ha in size) indicates an even greater variability than at the larger scale of the whole plots. However, these observations appear to be confounded by the finding of generally more open conditions as the median densities of both large and medium sized trees was found to be lower in the partial (<1 ha) plots. This highlights the difficulty in drawing inferences about the expectations of range of variability at scales that may be consistent with the disturbance dynamics influencing regeneration before European settlement in this region. Taylor (2010) demonstrated that before European settlement, frequent low-severity fire influenced patch dynamics and led to regeneration occurring at a scale below 0.1 ha in ponderosa pine forests of the southern cascades. This value is well below the smallest average plot size that could be evaluated with these data.

Managers should be aware that generally, stem density metrics from interior pine-dominated stands in California exhibited substantial variability but that the variability was inversely related to scale. One aspect of these stands that was actually quite uniform is that they exhibited low crown cover. Across a range of scales from 1 to 244 ha, crown cover associated with trees >8.9 cm in diameter had an IQR consistently of about 21–29 percent (Fig. 6). Furthermore, the greatest contributors to crown cover were the large Class 3 and 5 trees that Dunning referred to as over mature (Dunning, 1928).

The strength of this data set is in the scope of the effort. It is a complete census of a large area, conducted in such a manner that one may evaluate variability in forest metrics at different scales at a point in time prior to any harvesting activity and fairly early in the era of fire exclusion.

However, the data also have some limitations that may bear on interpretation of results. Grazing had been taking place in this region since the late 1800s and this likely had impacts on understory vegetation, conifer regeneration and on the fire regime leading up to the 1933–34 census. We know the current densities of the cohort of trees originating after European settlement (roughly 1000–1500 trees ha^{-1}) would represent approximately four million trees that apparently did not show up in the smallest diameter class, since there were only about 200,000 such trees found in the census (Fig. 3). The lower limit of observed diameter (8.9 cm) likely excluded regeneration encouraged by the initiation of grazing and fire suppression in this region. Observed past periodic annual dbh increment of approximately 0.30 cm (Dolph et al., 1995) suggests few trees in this cohort would have reached Hasel's lower diameter threshold by the early 1930s. This diameter growth rate was confirmed independently by a review of data from Ritchie et al. (2013). Also, recent observations of natural regeneration of pine seedlings growing in openings after a wildfire at Blacks Mountain showed that trees reached a mean height of 1.19 m in 12 years, with an inter-quartile range of 0.64–1.64 m (Data on file at PSW Research Station, Redding CA). Thus, one would expect that a majority of natural seedlings at Blacks Mountain will take over a decade just to reach breast height and then about another thirty years to achieve a diameter of 9 cm. So it is likely that the trees observed by Hasel in 1933 and 1934 excluded most of the regeneration from the turn of the century cohort. This is certainly so for all but the smallest diameter class observed.

Biomass and crown width estimation are derived from current observations so that if the relationship between crown width and diameter or biomass and diameter have changed over time, these equations could mis-represent to some degree the true biomass and crown area. It is not possible to know the degree or even direction of any changes in these relationships over time. For example, more open conditions might have produced trees with wider crowns for a tree of a given diameter. At the same time, a historic frequent fire regime may have produced trees that had a higher average base to live crown which would tend to produce trees with a narrower crown.

One other limitation is that standing dead trees were not included in these data. Thus we have no indication of recent mortality or the distribution of snags by species or size at the time of the 1933–34 census.

Finally, the 1-ha plots tend to be on the interior because partial edge plots are excluded. Only full edge plots were kept. In order to maintain scale-fidelity it was necessary to use only whole plots and these are generally on the interior. This may also lead to slight over estimates of stand density and cover in the 1933 census because edge conditions tended to be more open than those on the interior.

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References

Agee, J.K., 2003. Historical range of variability in eastern Cascades forests, Washington, USA. Landscape Ecol. 18, 725–740.

Baker, W.L., 2014. Historical conifer forest structure and fire in Sierran mixed-conifer forests reconstructed from general land office survey data. Ecosphere 5, 1–70. http://dx.doi.org/10.1890/ES14-00046.1.

Cheng, S., 2004. Forest Service Research Natural Areas in California Technical Report PSW-GTR-188 U.S. Forest Service. Pacific Southwest Research Station.

Cochran, P.H., 1998. Examples of mortality and reduced annual increments of white fir induced by drought, insects, and disease at different stand densities. Research Note PNW-RN-525. USDA Forest Service Pacific Northwest Research Station, p. 18.

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. http://dx.doi.org/10.1890/14-1797.1.

Crookston, N.L., Stage, A.R., 1999. Percent canopy cover and stand structure statistics from the forest vegetation simulator General Technical Report RMRS-GTR-24, USDA Forest Service. Rocky Mountain Research Station, Berlin.

Dolph, K.L., Mori, S., Oliver, W.W., 1995. Long term response of old-growth stands to varying levels of partial cutting in the eastside pine type. Western J. Appl. Forestry 10, 101–108.

Dunning, D., 1928. A tree classification for the selection forests of the Sierra Nevada. J. Agric. Res. 36, 755–771.

Fulé, P.Z., 2008. Does it make sense to restore wildland fire in changing climate? Restor. Ecol. 16 (4), 526–531.

Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecol. Appl. 7, 895–908. http://dx.doi.org/10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2.

Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. For. Ecol. Manage. 114, 433–446. http://dx.doi.org/10.1016/S0378-1127(98)00373-9.

Hasel, A.A., 1938. Sampling error in timber surveys. J. Agric. Res. 57, 713–736.

Hasel, A.A., 1942a. Estimation of volume in timber stands by strip sampling. Ann. Math. Statist. 13, 179–206.

Hasel, A.A., 1942b. Sampling error of cruises in the California pine region. J. Forest. 40, 211–217.

Hessburg, P.F., Smith, B.G., Salter, R.B., Ottmar, R.D., Alvarado, E., 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. For. Ecol. Manage. 136, 53–83. http://dx.doi.org/10.1016/S0378-1127(99)00263-7.

Higgs, E., Falk, D.A., Guerrini, A., Hall, M., Harris, J., Hobbs, R.J., Jackson, S.T., Rhemtulla, J.M., Throop, W., 2014. The changing role of history in restoration ecology. Front. Ecol. Environ. 12 (9), 499–506.

Hinkley, T.M., Teskey, R.O., Waring, R.H., Morikawa, Y., 1982. The water relations of true firs. In: Oliver, C.D., Kenady, R.M. (Eds.), Proceedings of the Biology and Management of True Fir in the Pacific Northwest Symposium. University of Washington, College of Forest Resources, Seattle, WA.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2004. Comprehensive database of diameter-based biomass regressions for North American tree species General Technical Report NE-319. USDA Forest Service, Northeastern Research Station, <http://www.treesearch.fs.fed.us/pubs/7058>.

Lydersen, J., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. For. Ecol. Manage. 304, 370–382. http://dx.doi.org/10.1016/j.foreco.2013.05.023.

Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Sci. 50, 162–176.

Norman, S.P., 2002. Legacies of Anthropogenic and Climate Change in Fire Prone Pine and Mixed Conifer Forests of Northeastern CALIFORNIA Ph.D. Dissertation. Pennsylvania State University, State College.

Norman, S.P., Taylor, A.H., 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. For. Ecol. Manage. 215, 51–68. http://dx.doi.org/10.1016/j.foreco.2005.05.003.

Odion, D.C., Hanson, C.T., Arsenault, A., Baker, W.L., DellaSala, D.A., Hutto, R.L., Klenner, W., Moritz, M.A., Sherriff, R.L., Verblen, R.L.T.T., Williams, M.A., 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. PLoS ONE 9 (2), e87852. http://dx.doi.org/10.1371/journal.pone0087852.

Oliver, W.W., 2000. Ecological research at the Blacks Mountain Experimental Forest in northeastern California General Technical Report PSW-GTR-179. USDA Forest Service, Pacific Southwest Research Station, <http://www.fs.fed.us/psw/publications/documents/psw_gtr179/>.

Reynolds, R.T., Sánchez Meador, A.J., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P. L., DeLorenzo, D.G., Graves, A.D., 2013. Restoring composition and structure in southwestern frequent-fire forests: a science-based framework for improving ecosystem resiliency General Technical Report RMRS-GTR-310. USDA Forest Service Rocky Mountain Research Station, <http://www.treesearch.fs.fed.us/pubs/44885>.

Ritchie, M.W., Wing, B.M., Hamilton, T.A., 2008. Stability of the large tree component in treated and untreated late-seral interior ponderosa pine stands. Can. J. For. Res. 38, 919–923. http://dx.doi.org/10.1139/X07-242.

Ritchie, M.W., Zhang, J., Hamilton, T.A., 2013. Aboveground tree biomass for *Pinus ponderosa* in northeastern California. Forests 4, 179–196. http://dx.doi.org/10.3390/f4010179.

Safford, H.D., North, M., Meyer, M.D., 2012. Chapter 3: Climate change and the relevance of historical forest conditions General Technical Report PSW-GTR-237. In: North, M. (Ed.), Managing Sierra Nevada Forests. U.S. Forest Service, Pacific Southwest Research Station, <http://www.fs.fed.us/psw/publications/documents/psw_gtr237/>.

Show, S.B., Kotok, E.I., 1924. The Role of Fire in the California Pine Forests Department Bulleting 1294. U.S. Department of Agriculture.

Skinner, C.N., 2005. Reintroducing fire into the Blacks Mountain Research Natural Area: Effects on fire hazard. In: Ritchie, M.W., Maguire, D.M., Youngblood, A. Tech. Coordinators, (Eds.), Proceedings of the Symposium on Ponderosa Pine: Issues, Trends and Management. General Technical Report PSW-GTR-198. USDA Forest Service, Pacific Southwest Research Station.

Skinner, C.N., Taylor, A.H., 2006. Southern cascades bioregion. In: Sugihara, N.G., Van Wagtendonk, J.W., Fites-Kauffmann, J., Shafter, K.E., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press.

Stephens, S.L., Gill, S.J., 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in north-western Mexico. For. Ecol. Manage. 205, 15–28. http://dx.doi.org/10.1016/j.foreco.2004.10.003.

Stephens, S.L., Lydersen, J.L., 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, 1–63. http://dx.doi.org/10.1890/ES14-00379.1.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. Ecol. Appl. 9, 1189–1206. http://dx.doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2.

Taylor, A.H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. J. Biogeogr. 27, 87–104. http://dx.doi.org/10.1046/j.1365-2699.2000.00353.x.

Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. J. Veg. Sci. 21, 561–572. http://dx.doi.org/10.1111/j.1654-1103.2009.01164x.

Wing, B.M., Ritchie, M.W., Boston, K., Cohen, W.B., Olsen, M.J., 2015. Individual snag detection using neighborhood attribute filtered airborne lidar data. Remote Sens. Environ. 163, 165–179. http://dx.doi.org/10.1016/rse.2015.03.013.

White, P.S., Walker, J.L., 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restor. Ecol. 5, 338–349. http://dx.doi.org/10.1046/j.1526-100X.1997.00547.x.

Youngblood, A.J., Max, T., Coe, K., 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. For. Ecol. Manage. 199, 191–217. http://dx.doi.org/10.1016/j.foreco.2004.05.056.