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Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests

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Abstract. We re-sampled areas included in an unbiased 1911 timber inventory conducted by the U.S. Forest Service over a 4000 ha study area. Over half of the re-sampled area burned in relatively recent management- and lightning-ignited fires. This allowed for comparisons of both areas that have experienced recent fire and areas with no recent fire, to the same areas historically based on early forest inventories. Our results indicate substantially altered present forest conditions, relative to the 1911 data, and can largely be attributed to the disruption of the key ecosystem process for these forests, fire. For areas that burned recently there was a noticeable difference in forest structure based on fire severity. Current tree density and canopy cover in areas burned recently with moderate severity did not differ from 1911 estimates, while areas that burned recently with low severity or were unburned had higher tree density and canopy cover relative to the 1911 estimates. This emphasizes an important distinction with regard to using fire to restore forests, resting primarily on whether fires kill trees in the lower and intermediate canopy strata. Our results also demonstrate nearly a doubling of live tree carbon stocks in the present forest compared to the historical forest. The findings presented here can be used by managers and ecologists interested in restoring Sierra Nevada mixed conifer systems.

Key words: fire ecology; fire management; forest ecology; restoration.

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Introduction

Past harvesting practices and livestock grazing, coupled with over a century of fire suppression have shifted the structure and composition of many dry, mid- to low-elevation forests throughout the western U.S. This shift is generally characterized by increased tree densities, smaller average tree diameters, increased proportions of shade-tolerant tree species, and elevated surface fuel loads relative to historical or pre-European settlement forest conditions (Parsons and Debenedetti 1979, Naficy et al. 2010, Scholl and Taylor 2010). These changes have substantially increased the vulnerability of many contemporary forests to uncharacteristically high disturbance intensities and extents, particularly from fire and insects/disease (Allen 2007). Following such disturbances these forests, and the species dependent on them, have limited capacity to return to pre-disturbance states. As a result, forest managers are tasked with mitigating the potential for uncharacteristic disturbances, primarily through the modification of tree densities and surface fuels (Agee and Skinner 2005, Stephens et al. 2009*a*). Much of the ecological basis for these mitigation efforts comes from studies that reconstruct historical, or pre-Euro American settlement, forest conditions (Swetnam et al. 1999). These reconstruction studies characterize the structure and composition of forests for a period in which low- to moderate-intensity fire was the dominant process. Under these conditions forests were largely resistant to extensive, high-intensity fire (Brown et al. 2008), and were generally resilient to other disturbances and stressors (e.g., insects, disease, and drought) (Fulé 2008). However, there is evidence from some forest types that historical fires did occur at higher intensities as well, resulting in discrete patches of high tree mortality throughout the landscape (Beaty and Taylor 2001, Hessburg et al. 2007, Beaty and Taylor 2008); such patterns continue today where wildfires have been managed for resource benefit (Collins and Stephens 2010).

Most historical forest reconstructions rely on information inferred from tree rings, which allows for temporal depth and spatial precision that often exceeds other historical data sources (e.g., written accounts, maps, plot data, and photographs) (e.g., Fulé et al. 1997, Taylor 2004, Brown et al. 2008, Scholl and Taylor 2010). However, tree-ring based reconstructions are subject to an inherent limitation brought about by only using extant data. When there is a considerable amount of time between the reconstruction period and data collection, as there is with most historical forest reconstructions (>100 years), uncertainty increases owing to losses from fire, insects and disease, and decomposition. This uncertainly has not been studied extensively (but see Moore et al. 2004) and its impacts on reconstructed tree densities and tree size distributions are largely unknown.

Historical datasets, data collected from the field and archived, are an alternative source of information used in forest reconstructions (e.g., Leiberg 1902, Wieslander et al. 1933). These datasets allow for detailed quantitative comparisons of current vs. historical forest structure and composition (Stephens 2000, Lutz et al. 2009). However, there are a number of concerns associated with historical datasets: (1) limited geographic extent, (2) unknown or unrepeatable study site selection/inventory methodologies, (3) uncertainty in accurately re-locating sampled areas (Kelly et al. 2008), and (4) limited temporal depth. Finding a historical dataset that addresses all of these concerns would be extremely difficult, if not impossible. That stated, we have identified a historical dataset that covers a large geographic extent (>4000 ha), has unbiased sampling locations, and can be re-located reasonably well. This particular dataset consists of early timber inventories conducted by the U.S. Forest Service (USFS). In California, these inventories were conducted ca. 1910 and were part of the first organized assessment of all timber resources within the then, new agency.

In this study we take advantage of a unique portion of these early USFS timber inventories that were conducted on what was then part of the Stanislaus National Forest, but which subsequently became incorporated into Yosemite National Park (YNP). As a result of being included within YNP this area did not experience timber harvesting intensities that occurred in surrounding areas and throughout much of the mixed-conifer region in the Sierra Nevada. Livestock grazing may have occurred prior to the timber inventories, but likely ceased upon incorporation into YNP, ca. 1930. Thus, for this area a comparison of current forest conditions to those based on the early inventories could provide information on potential change driven primarily by 20th century fire exclusion policies. In addition, by being part of YNP, which has maintained an active fire management program for the last 30 years, over half of this area burned relatively recently (10–20 years) in lightning- and/or management-ignited fires. This allows for comparisons of both areas that have experienced recent fire and areas with no recent fire, to the same areas historically based on early unbiased forest inventories. Such comparisons can provide information on how close forest structure and composition under more active recent fire management approximates that for historical forests. Our objectives were to: (1) identify usable historical timber inventory records, (2) locate historical inventory areas 'on the ground' and sample current forest stand conditions, and (3) perform statistical analyses comparing current to historical forest stand conditions, both overall and partitioned based on recent fire activity. This study is novel in that it re-samples the same forest areas approximately 100 years later, uses unbiased sampling methods, and occurs at relatively large spatial scales.

Our study is not the first to use data from the 1911 timber inventories. Scholl and Taylor (2010) summarized forest structure using the 1911 data and compared that to reconstructed historical forest structure based on tree rings. They did this for an area that overlaps our study area. Our study goes beyond what Scholl and Taylor (2010) did by: (1) including a higher number of 1911 timber inventory areas, (2) intentionally re-measuring the areas where historical inventories were conducted, and (3) analyzing the impact of recent fire management activities on forest structure and composition relative to the 1911 data.

Study Area

The historical timber inventory data we use only exists for the western portion of YNP, which is situated in the central Sierra Nevada (Fig. 1). Elevation in our study area ranges between 1460 and 2130 m. The forest within the study area is characterized as west-slope Sierra Nevada mixed conifer, consisting of: sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), red fir (*A. magnifica*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepsis*). The climate is Mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation, primarily as snow, ranges from 25 to 155 cm/year, with an average just over 100 cm/year. Mean monthly temperatures range from 2°C in January to 18°C in July (Crane Flat Remote Automated Weather Station).

Prior to 1900 fire was common in this forest, with a mean point fire return interval reported for an adjacent area of 12 years (Scholl and Taylor 2010). With the onset of fire suppression ca. 1900 fire was largely excluded from the study area until 1983, which marked the first of seven management- and lightning-ignited fires that burned through 2009. These fires were part of the YNP Fire Management Plan, with the objectives of both returning a natural process to these forests and reduction of hazardous fuels (Martin 2009).

Methods

Historical forest inventory data

All of the historical forest inventories within our study area were conducted in 1911. At that time the Stanislaus National forest extended over 10 km farther east than its modern boundary, and included the Gin Flat and Crane Flat areas of YNP. The inventories within our study area were conducted by two-person crews, with one person compass & distancing and the other assessing the timber. Their assessments involved recording all conifer trees within belt transects that were 40.2 m (132 ft or 2 chains) wide and 402 m (1320 ft or 20 chains) long. Trees were tallied by species into diameter at breast height (dbh) and total height classes. The dbh classes consisted of poles (15.2–30.4 cm), and then for trees $\geq$30.5 cm were 5.1 cm (2 in) (Appendix). Smaller trees ($<$15.2 cm dbh) were tallied into sapling or seedling classes, but the actual dbh/height break values were not recorded on the inventory forms and are unknown to us (Appendix). Height was recorded in 4.9 m (16 ft) classes (Appendix). In addition to inventorying trees, the following observations were made in each transect: rock type and exposure, soil texture, forb cover, shrub cover, stand development stage, and stand age. Transect locations were based on the Public Land Survey System (PLSS), which is the primary method used to survey rural or undeveloped land in the western U.S. Transects started and ended at the mid-points of quarter-quarter sections, which are referred to as lots (Fig. 1). Transects were oriented either N–S or E–W, against dominant contour within the lot. Each transect covered 1.6 ha (4 ac).

21st century reconstruction

From historical data available at the National Archive and Records Administration archives we were able to find forest inventory data sheets for over 50 lots that are now within the YNP boundary. We used a PLSS layer in ArcGIS, which contained lot boundaries, to obtain Universal Transverse Mercator coordinates for the starting and ending points of these transects. These points defined the theoretical centerline of the historical belt transects. We use the term 'theoretical' to point out uncertainty in the exact transect locations due to potential errors incurred

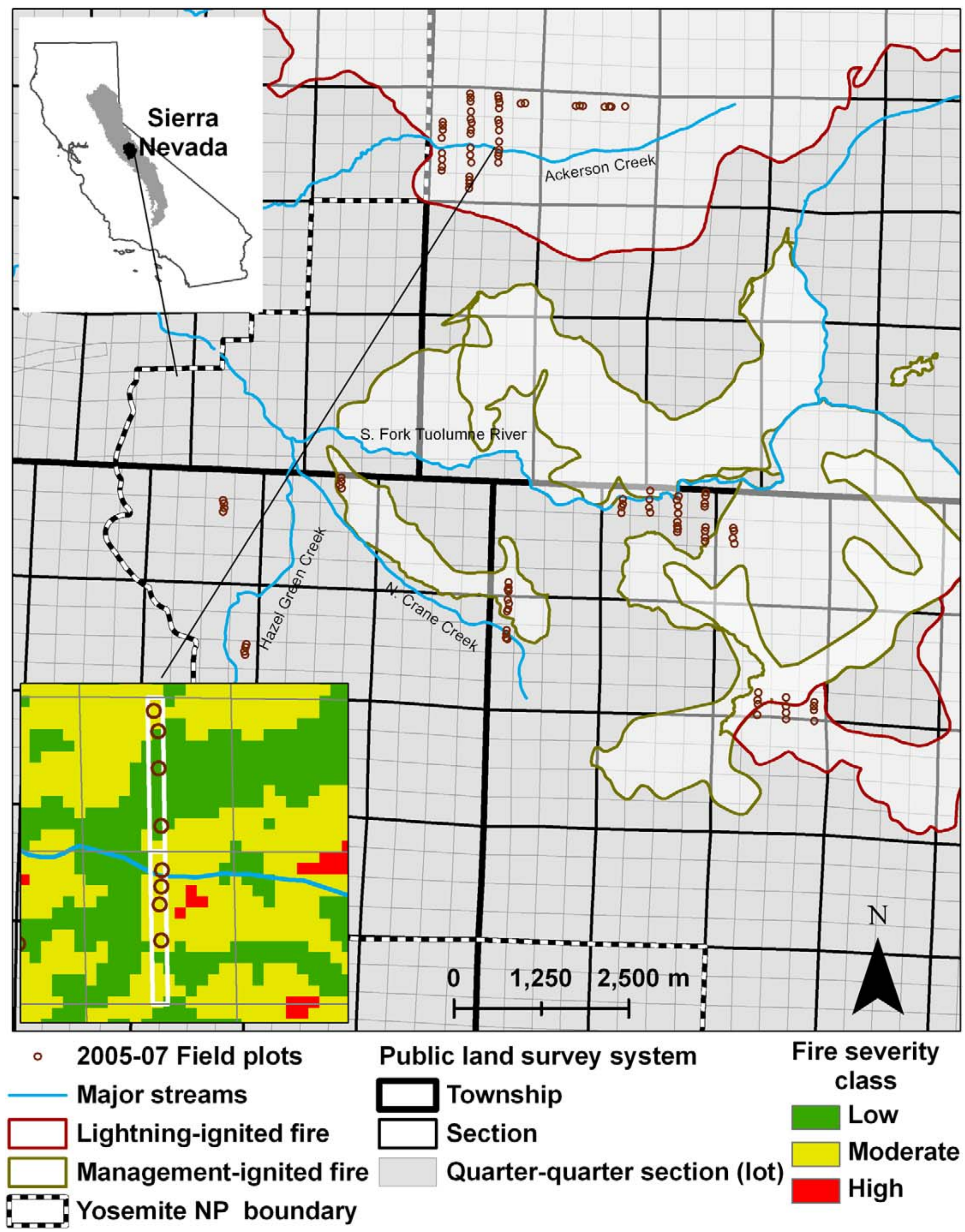

Fig. 1. Locations of lots included in the 1911 timber inventories that were re-sampled between 2005 and 2007 within Yosemite National Park, California, USA. Portions of the study area have burned in seven management- and lightning-ignited fires, occurring between 1983 and 2002. The lower left frame demonstrates both the re-sampling effort within the estimated historical belt transect (white rectangle outline), and the satellite-derived fire severity classification used to broadly capture fire effects on dominant vegetation (see Methods).

in locating (compassing and distancing) transects originally. In order to re-measure a greater number of lots we opted to subsample from within the original belt transects. Our 2005–2007 subsamples entailed establishing four 1/10th ha circular plots centered at random, non-overlapping distances along the theoretical historical transect centerline (Fig. 1). In each plot we recorded tree species, height, dbh, and crown position for all trees 5.1 cm dbh and above. In addition we recorded shrub cover, aspect, and slope at each plot. Due to time and access constraints we were only able to sample from 30 lots. We removed two of the sampled lots because of inconsistencies between the historical descriptions of transect physiographic features (aspect, proximity to streams, rock outcrops) and our observations in the field, leaving 28 lots for the comparative analysis: 1911 to 2005–2007. The 2005–2007 sampling effort is referred to hereafter as 'recent'.

Fire information

Nineteen of our 28 sampled lots were burned in either management- or lightning-ignited fires. Rather than arbitrarily separate out lots that burned in management- vs. lightning-ignited fires, or simply burned lots vs. unburned lots, we opted to take advantage of an existing dataset containing satellite-derived estimates of fire severity for all fires >40 ha within YNP (Thode 2005) to characterize fire effects on each individual lot. These fire severity estimates are based on the relative differenced Normalized Burn Ratio, which is computed from Landsat TM imagery (see Miller and Thode 2007, Miller et al. 2009*a*). This index has been used extensively to characterize contemporary fires and fire regimes (Holden et al. 2007, van Wagtendonk and Lutz 2007, Collins et al. 2009, Miller et al. 2009*b*). We used three fire severity classes: low, moderate, and high, which were based on the classification thresholds reported by Miller and Thode (2007), to broadly represent the extent of fire-caused change in burned lots. The actual fire severity class assigned to each lot was based on the majority of classified pixels within and immediately adjacent our 1/10th ha plots (see Fig. 1 for an example). This resulted in 9 lots in the low severity category, 10 lots in the moderate severity, and 0 lots in the high severity category. Recall there were 9 lots that were unburned. This relatively even distribution among the low severity, moderate severity, and no fire categories was purely serendipitous, i.e., our lot sampling scheme was driven by both broadening the sampling area and access rather than attempting to evenly capture recently burned and unburned areas.

The time between the last fire and the recent sampling of these 19 burned lots ranged between 3 and 17 years. However, for 74% of these lots the time since fire ranged between 11 and 13 years. The lack of a more even distribution among times since fire precluded any use of this variable for potentially explaining differences in observed forest structure and composition.

Data analysis

We assembled a suite a variables to characterize forest structure and composition using tree lists generated from the 1911 belt transects and our recent plots. The tree lists were standardized for area sampled such that outputs represented per hectare values. The constructed variables were: tree density for all trees and partitioned into four dbh classes, proportion of stand basal area by four species groups, derived canopy cover, live tree carbon, and density of large pines. The four dbh classes used to report partitioned tree density were: 15.2–30.4 cm, 30.5–61.0 cm, 61.1–91.4 cm, >91.4 cm, and were based on a stand classification scheme used in forest management throughout the Sierra Nevada (USDA 2004) and in previous work (Lutz et al. 2009). The four species groups that we investigated for potential changes in proportion of stand basal area were: (1) pine–ponderosa pine and sugar pine, (2) true fir–white fir and red fir, (3) incense-cedar, and (4) Douglas-fir. The derived canopy cover was calculated with the Forest Vegetation Simulator (Dixon 2002), using the belt transect/plot tree lists as inputs. This calculation represents the percentage of ground area directly covered with tree crowns. It uses species specific estimates for crown radius and corrects for canopy overlap (Dixon 2002). To investigate the impact of excluding smaller trees (<15.2 cm dbh) on our canopy cover estimates we additionally calculated derived canopy cover for all live conifers ≥5.1 cm dbh from the recent sampling effort. Differences between the two estimates

(≥5.1 cm dbh and ≥15.2 cm dbh) ranged between 0 and 14%, with the average across all lots being 4%. This indicates that on average our canopy cover estimates based on trees ≥15.2 cm dbh may slightly under represent actual canopy cover. Note that this calculation of underestimation is entirely based on recent forest conditions, and would likely be reduced for historical stand conditions due to increases in tree densities resulting from fire exclusion (Scholl and Taylor 2010).

Tree carbon estimates were obtained by first calculating biomass using the genus-specific allometric equations presented by Jenkins et al. (2004), then multiplying biomass by 0.5. This method has been used in previous studies of Sierran forests (North et al. 2009*a*, Stephens et al. 2009*b*) and allows for direct comparisons across different study areas. The density of large pines was the per hectare aggregation of ponderosa and sugar pine >61.0 cm and is investigated in response to concern over possible under representation of large pines throughout Sierra Nevada forests (USDA 2004).

The constructed stand structure and composition variables were limited to live conifers that were ≥15.2 cm dbh. This truncated tree information was a product of a conservative approach towards using the historical timber inventory data. Information on smaller trees (seedlings and saplings) and dead trees was available from the historical datasheets (Appendix), however we could not be certain in both what the actual sizes were for smaller trees and that dead trees were consistently recorded across all lots. By leaving out smaller trees, hardwoods, and dead trees, the variables we constructed do not provide a complete description stand structure and composition for this forest. Rather, these variables are intended to capture the dominant forest attributes in each time period.

We tested differences in these variables among time periods (1911 against recent) and among modern fire groups (no fire, low severity, and moderate severity) using a repeated measures analysis (Proc Mixed; SAS 2009). While the point could be made that our recent plots do not represent true re-measurement due to uncertainty in exact locations and the differing sampling extents, we submit that there is likely to be more overlap in sampling efforts than disparity. Thus, we argue a repeated measures analysis is appropriate. Diagnostic plots of the residuals indicated good compliance with the normality and homogeneity of variance assumptions for all variables except the basal area proportions of both true fir and Douglas-fir. Both of these contained several zeros and were log + 1 transformed. Model covariance structure was chosen individually for each variable based on lowest Akaike information criterion (AIC). AIC provides a means for comparing among competing models by capturing the tradeoffs between model accuracy and model complexity. This predominantly resulted in unstructured covariance. Differences among time periods and modern fire groups were inferred from Tukey-Kramer adjusted P-values, with $\alpha = 0.05$. Pairwise comparisons among modern fire groups were only investigated when the modern fire group fixed effects, both overall and partitioned for the recent sampling period, were significant.

Using only data from the 2005–2007 measurement we performed an analysis of variance (ANOVA) on the density of understory trees (5.1–15.1 cm dbh) among modern fire groups (no fire, low severity, moderate severity). We did this for all conifers combined and for the four species groups individually. The 1911 data were not included due to uncertainty in the definition of seedlings and saplings (Appendix). If P-values from the ANOVA F-tests were significant ($\alpha = 0.05$) we used the Tukey-Kramer method to compare between individual modern fire groups.

Results

Tree density increased markedly between 1911 and the recent sampling effort (Fig. 2A). This increase was highly significant ($P < 0.001$) for all trees >15.2 cm dbh aggregated, as well as for the two smaller tree size classes (15.2–30.4 cm and 30.5–61.0 cm dbh). For the 61.1–91.4 cm dbh class density increased significantly, but had a higher P-value ($P = 0.04$), while for the largest size class (>91.4 cm dbh) mean densities indicated an increase, but it was marginally insignificant ($P = 0.06$). Pairwise comparisons indicated that lots with no recorded fire in the modern era (1930 to present) had significantly lower tree density in 1911 than all other period/modern fire groups, but significantly higher recent tree density than

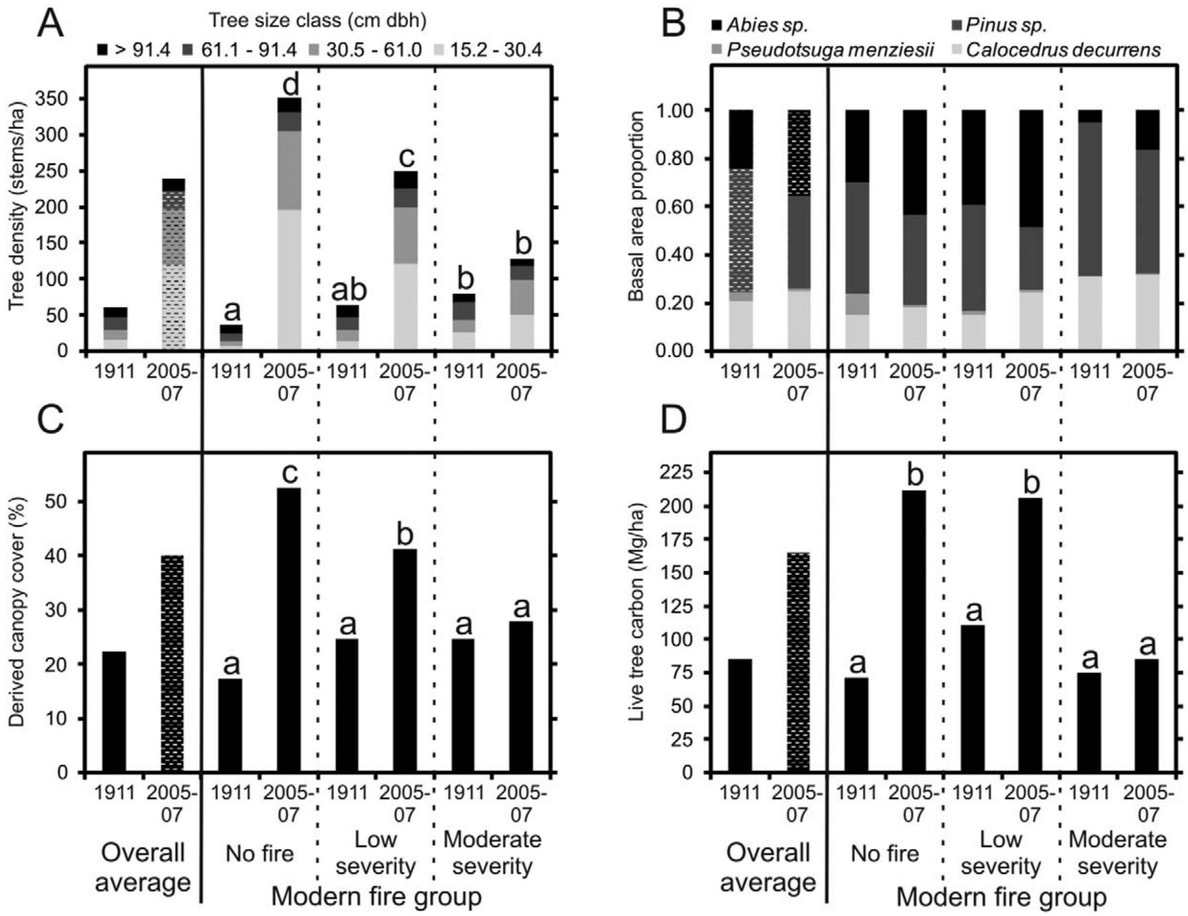

Fig. 2. Average forest structure and composition attributes by sampling period and by modern fire group. These attributes were constructed using only live conifers ≥15.2 cm diameter at breast height (dbh) and include: tree density (all species combined) by dbh class (A), proportion of basal area by species group (B), derived canopy cover (see Methods) (C), and live tree carbon (D). Dotted bars represent significantly ($P < 0.05$) higher overall period averages. Letters above bars indicate significantly different period/modern fire groups based on pairwise comparisons using Tukey-Kramer adjusted P-values. Comparisons indicated in (A) are for aggregated tree density (all trees >30.5 cm dbh).

all groups except the modern low severity (Fig. 2A). Of the modern fire groups only moderate severity had overall tree density that did not differ significantly from the same group of lots based on the 1911 inventory (Fig. 2A). The modern low severity group had significantly higher overall tree density than all three 1911 groups (Fig. 2A). When comparing among fire groups based on the recent sampling effort the moderate severity group had significantly lower overall tree density than both the low severity and no fire groups, and the low severity group was significantly lower than the no fire group (Fig. 2A).

When examining comparisons among modern fire groups for tree size classes individually (15.2–30.4, 30.5–61.0, and 61.1–91.4 cm dbh) only the two smaller tree size classes indicated significant differences among period/fire groups (not shown). For both of the smaller tree size classes only the moderate severity group densities based on the recent sampling effort did not differ significantly from densities based 1911 inventory. When comparing among fire groups based on the recent sampling effort tree densities in these two smaller size classes (15.2–30.4 and

30.5–61.0 cm dbh) for the low severity group did not differ significantly from either the moderate severity or no fire groups, while the moderate severity group did differ significantly from the no fire group.

Comparisons of understory tree (5.1–15.1 cm dbh) densities among modern fire groups, which were only performed using data from the recent sampling effort, indicated significant differences among groups when all conifers were combined (Table 1). Understory tree density in the moderate severity group was significantly lower than that for the no fire group, while the low severity group was not significantly different from either the no fire or the moderate severity group (Table 1). When analyzed by species groups significant differences among modern fire groups were only evident for the true fir group (Table 1). For true fir mean understory tree density was lowest in the moderate severity group and intermediate in the low severity group, however both were statistically indistinguishable, while the no fire group was significantly higher than both the low and the moderate (Table 1). The proportional composition of understory trees changed among fire groups demonstrating that no fire lots were dominated by true fir, low severity lot were dominated by incense-cedar, and the moderate severity lots were dominated by incense-cedar and pines (Table 1).

Significant differences in species composition, as indicated by proportion of basal area, were only evident for pine and true fir species groups, with higher proportions of pine and lower proportions of true fir in 1911 (Fig. 2B). Modern fire group fixed effects were non-significant for pine, incense-cedar, and Douglas-fir species groups; as such, no pairwise comparisons were performed. For the true fir group, modern fire group fixed effects were significant, but all pairwise comparisons were non-significant based on Tukey-Kramer adjusted P-values.

When averaged across each period both derived canopy cover and live tree carbon were significantly higher in the recent sampling compared to 1911 (Fig. 2C, D). No significant differences were evident in derived canopy cover or live tree carbon among the three groups in 1911, and the only moderate severity group based on the recent sampling was not statistically different from these 1911 groups (Fig. 2C, D). Within the recent sampling period derived canopy cover for the no modern fire group was significantly higher than that for the low severity, while the low severity group was significantly higher than the moderate severity group (Fig. 2C). For live tree carbon the no modern fire and the low severity groups were statistically indistinguishable, and both were significantly higher than the moderate severity group, in the recent period (Fig. 2D). No differences were evident among periods or modern fire groups for the density of large pines (data not shown).

For most lots in 1911 tree densities in all four size classes we analyzed ranged between 5 and 25 trees/ha (Fig. 3). Derived canopy cover in most lots was between 20 and 30% (Fig. 3). Live tree carbon varied substantially among lots, with the most lots containing 60 to 100 Mg/ha (Fig. 3). Both pine and incense-cedar were present on almost all lots; however pine most often accounted for higher proportions of stand basal area (Fig. 3). True fir was a much lesser component, or completely absent, on many lots; although there were a few lots where true fir was dominant.

Discussion

As Scholl and Taylor (2010) demonstrate fires were common in this forest, occurring frequently until ca. 1900. As such, we submit the 1911 forest inventory data describes a forest with a fairly intact fire regime, one that is a product of a range of effects from many fires over a long period of time. The changes in forest structure and composition relative to 1911 indicate substantially altered present forest conditions. The present forest in western YNP is characterized by much higher overall tree density, shifted species dominance from pine to fir, and higher canopy cover (Fig. 2A, B, C). These findings are consistent with those from previous studies in the Sierra Nevada (Parsons and Debenedetti 1979, Ansley and Battles 1998, North et al. 2007, Scholl and Taylor 2010) and in the Rocky Mountains (Fulé et al. 1997, Brown et al. 2008, Naficy et al. 2010). Given that the forest of western YNP has not been extensively harvested and that livestock grazing has not taken place for 70 to 110 years, the changes in forest structure can largely be attributed to the disruption of the key ecosystem process for these forests, fire, which occurred

Table 1. Mean understory tree (5.1–15.1 cm dbh) density for each modern fire group summarized by species group and for all conifers combined. These means are based on the 2005–2007 plot measurements only. Means for each modern fire group were compared using an ANOVA F-test, which if significant ($P > 0.05$) was followed by a multiple comparison test using the Tukey-Kramer method. Means with the same superscript letter were not significantly different for that particular species group or total (columns).

		Trees/ha (standard error) and proportion of total				
Modern fire group	Number of lots	Abies sp.	*Calocedrus decurrens*	Pinus sp.	*Pseudotsuga menziesii*	All conifers
No fire	9	286.9^a (12.8) 0.63	138.6 (16.1) 0.30	26.1 (3.6) 0.06	2.5 (0.6) 0.01	454.2^a (27.4)
Low severity	9	53.6^b (7.8) 0.24	148.6 (23.1) 0.68	16.6 (2.1) 0.08	0.3 (0.1) <0.01	217.2^{ab} (30.2)
Moderate severity	10	1.5^b (0.3) 0.04	22.7 (1.9) 0.55	16.6 (2.1) 0.40	0.3 (0.1) 0.01	41.0^b (3.6)
F-test *P*-value		<0.01	0.12	0.64	0.18	<0.01

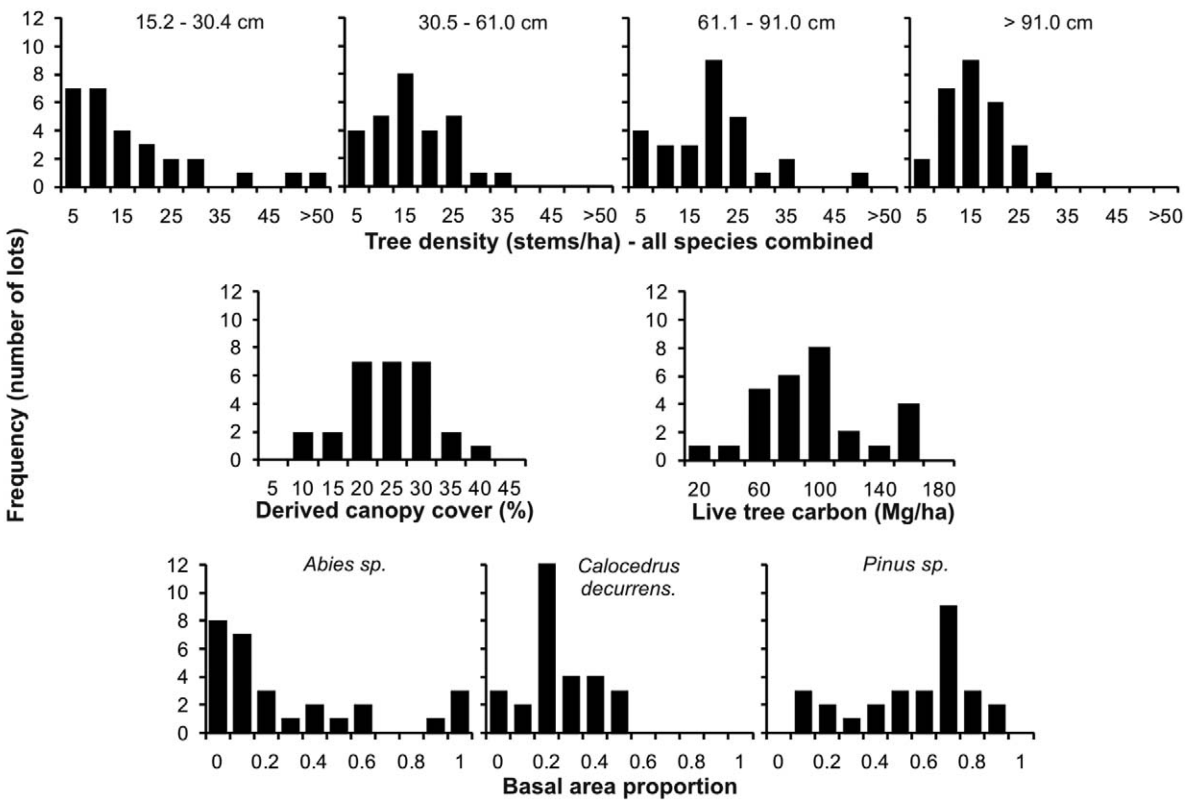

Fig. 3. Frequency distributions of forest structure and composition attributes based on 1911 timber inventories. These attributes were constructed using only live conifers ≥15.2 cm diameter at breast height (dbh). The size ranges in the upper graphs are for four dbh classes.

frequently within our study area until 1899 (Scholl and Taylor 2010).

The assumption that forest conditions in 1911 are a product of numerous low- to moderate-intensity fires that occurred frequently over a long period of time can be called into question. An alternative explanation is that the forest conditions in 1911 reflect the most recent late 19th century fires. It is possible that one of these late 19th century fires, for example 1899, which is the last extensive fire that Scholl and Taylor (2010) report in our study area, was particularly severe. If this was the case the forest conditions captured in the 1911 timber inventories may have lesser relevance with respect to forest restoration following long-established fire exclusion. While this alternative explanation cannot be disproved we submit that it is unlikely. For an area that overlapped our study area Scholl and Taylor (2010) demonstrate that there were on average over 100 trees/ha that pre-date the 1899 fire, and that these trees represented multiple age classes, up to 6–10 distinct age classes in many stands. Furthermore, spatial analysis of similar aged trees indicated clustering at very small spatial scales (2–10 and 20–25m), suggesting that openings created by fire-induced tree mortality were small (Scholl and Taylor 2010). As such, there was very little evidence of larger-scale moderate- to high-severity fires occurring prior to 1899, leaving little reason to believe that the 1899 fire was dissimilar to those occurring previously.

The findings indicating no significant differences between current forest structure in areas that burned recently with moderate severity and forest structure in 1911, while areas that burned with low severity were consistently different from 1911 structure, emphasize an important distinction with regard to using fire to restore forests (Fig. 2). This distinction is based on whether or not fires can kill trees in both the 15.2–30.4 and the 30.5–60.1 cm dbh classes, and is tied to fire intensity. Based on our results it appears that if restoration of historical forest structure is an objective and fire alone is the tool then initial fires need to be intense enough to kill trees in the lower and intermediate canopy strata. While fires of lesser intensity likely will reduce surface fuels and understory trees which is important in reducing potential tree mortality from fire (Agee and Skinner 2005, Stephens et al. 2009*a*) and possibly maintaining desired forest conditions once achieved initially, they may not be sufficient alone to achieve historical forest structure given the substantial tree establishment that occurred during the fire exclusion period (Collins and Stephens 2007). This is particularly the case for trees that established early in the fire exclusion period and have grown to a size now that they can resist low-intensity fire (Miller and Urban 2000). The fact that understory tree (5.1–15.1 cm dbh) density, particularly for the true fir species, was lower in the modern low severity fire group than in the no fire group suggests that fires of lesser intensity can meet some structural restoration objectives (Table 1). The finding indicating significantly lower derived canopy cover for the low severity group relative to the no fire group based on the recent sampling further supports this point (Fig. 2C). However, it should be noted that only the moderate severity group appeared to substantially alter the fir : pine ratio for understory trees, which is another common restoration objective (Table 1).

Our findings indicating similarity or slight increases in the density of large trees in the present forest contradicts the findings by Lutz et al. (2009). Lutz et al. (2009) demonstrate an overall decline in large diameter trees (>92 cm) throughout YNP, as well as species specific declines for several species examined in this study. The declines Lutz et al. report were based on a historical set of plots sampled between 1932 and 1936, and a more recent, but different set of plots sampled between 1988 and 1999. While the timing of historical and recent sampling efforts captures a lesser temporal extent than that analyzed in our study it does not seem that timing alone can explain the opposite findings with respect to large diameter trees. Perhaps because the Lutz et al. comparison of historical to recent forest stand conditions involves distinct sampling plots for each period, as opposed to re-sampling the same area, more confidence can be placed in the present work. Furthermore, the 1911 timber inventories were established systematically (based on the PLSS grid), which suggests a more unbiased sample of historical forest conditions relative to the more subjective plot establishment methodology used in Lutz et al. (2009).

The considerable increase in the density of trees in the 30.5–61.0 cm dbh class (12–24 in.) draws attention to an important forest management issue throughout the Sierra Nevada and elsewhere. Currently, in the Sierra Nevada there is strong debate over upper-diameter limits for fuels reduction and restoration projects (USDA 2001, 2004, Collins et al. 2011). Fire modeling and empirical studies of actual wildfires demonstrate that removing trees greater than 30.5 to 40.6 cm (12 to 16 in) dbh has little impact on fire behavior

(Agee and Skinner 2005, Stephens et al. 2009*a*). As such, arguments can be made to set upper diameter limits for fuels reduction projects somewhere between 30.5 and 40.6 cm. However, when restoration of historical forest conditions, which is often associated with increased resilience (Fulé 2008), is an objective our results demonstrate that removal of moderately sized trees may be appropriate. It should be noted, however, that our results are based on forests that have not undergone the extensive harvesting that has occurred throughout much of the Sierra Nevada. Given that the increases in density of 30.5 to 61.0 cm dbh trees far outweighs that for the larger size classes (Fig. 2A), and that there are concerns over the numbers of large trees where extensive harvesting has taken place, restoration-based projects in mixed conifer forests similar to those studied here are likely justified in focusing on retaining trees >61.0 cm dbh.

Our results indicating nearly a doubling of live tree C stocks in the present forest compared to historical conditions are consistent with those reported for an old growth ponderosa pine forest in the southwestern U.S. (Fig. 2D) (Hurteau et al. 2010). Logically, this makes sense, in that if tree density increases substantially due to fire exclusion and larger trees have not declined or been removed, C stocks would increase as well. However, results from another study in a southern Sierra Nevada mixed conifer forest demonstrate the opposite, i.e., higher live tree C stocks historically (North et al. 2009*a*). North et al. (2009*a*) estimated historical live tree C stocks to be 345 Mg/ha, which is four times our 1911 overall average (Fig. 2D). They attributed the elevated historical live tree C stocks to the presence of many very large trees (>150 cm dbh), which they argue are lacking in the current fire-excluded forest. Differences in study sites may explain some part of the discrepancy in historical estimates for live tree C stocks: (1) elevation—the southern Sierra Nevada site is approximately 500 m higher; (2) dominant tree species—our YNP study site historically was dominated by ponderosa and sugar pines (Fig. 2B) while the southern Sierra Nevada site historically was dominated by white fir; and (3) historical fire frequency—based on reconstructed point fire return intervals, our YNP site had more frequent fire, 12.4 versus 17.3 years (North et al. 2005, Scholl and Taylor 2010). Another factor that may contribute to the large discrepancy in live tree C stocks may be the methodology used by North et al. (2009*a*) to reconstruct forest conditions. Their reconstruction used the current complete inventory of trees, snags and logs, and calculated approximate historical diameters using a series of species-specific growth and decay rates. This is particularly challenging for decayed stumps and logs because without intact sapwood it is difficult to assign accurate death dates.

The frequency distributions for forest structure and composition attributes in 1911 (Fig. 3) combined with the marked changes in current forest stand structure and composition (Fig. 2) emphasize a few important points pertaining to forest restoration, resilience, and forest change. The first is that over our 4000 ha study area historical forest structure and composition varied considerably (Fig. 3), suggesting that average conditions alone are very much an oversimplification of historical forest conditions (Stephens and Gill 2005). As such, the historical data we present do not support the idea of basing management targets for restoration and forest resilience treatments on mean values (North et al. 2009*b*). Perhaps the ranges in canopy cover, tree densities by size classes, and live tree carbon can serve as quantitative justification for implementing variable targets for restoration and forest resilience treatments. The second point related to the historical distributions is that common restoration goals for stand structure attributes, particularly canopy cover, tree density, and live tree carbon, in similar forest types are on the upper end of or entirely exceed the values we report in distributions based on the 1911 data (Fig. 3) (Stephens and Moghaddas 2005, North et al. 2007, North et al. 2009*a*, Stephens et al. 2009*b*). If the treatments carried out in these studies are representative of restoration treatments throughout the Sierra Nevada region and restoration of historical forest conditions is a goal, this suggests that contemporary treatment prescriptions may be too conservative with respect to residual stand structure. The third point relates to the impact of forest structural and compositional changes from historical conditions on wildlife species. Moritz et al. (2008) documented substantial upward changes in elevation limits for many small mammal species in YNP from 1914 to the present and attributed this primarily to an increase in minimum temperatures. While changing temperatures over the last century were undoubtedly an important factor in species' shifts, these temperature changes coincide with substantial changes in mixed conifer forest structure, which are primarily driven by fire exclusion. Disentangling the impacts of these two processes, temperature increases and forest structural shifts, would be very difficult, but nonetheless it is important to consider both processes in managing contemporary forests.

Changing climates are already modifying forests in the Sierra Nevada so a specific goal to recreate past conditions may not be advisable (Stephens et al. 2010). However, the information from this work could inform the production of desired conditions because the forests sampled in 1911 were highly resilient and this is the most common characteristic that forest mangers desire in a world of changing climates (Fulé 2008, Stephens et al. 2010).

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Appendix A

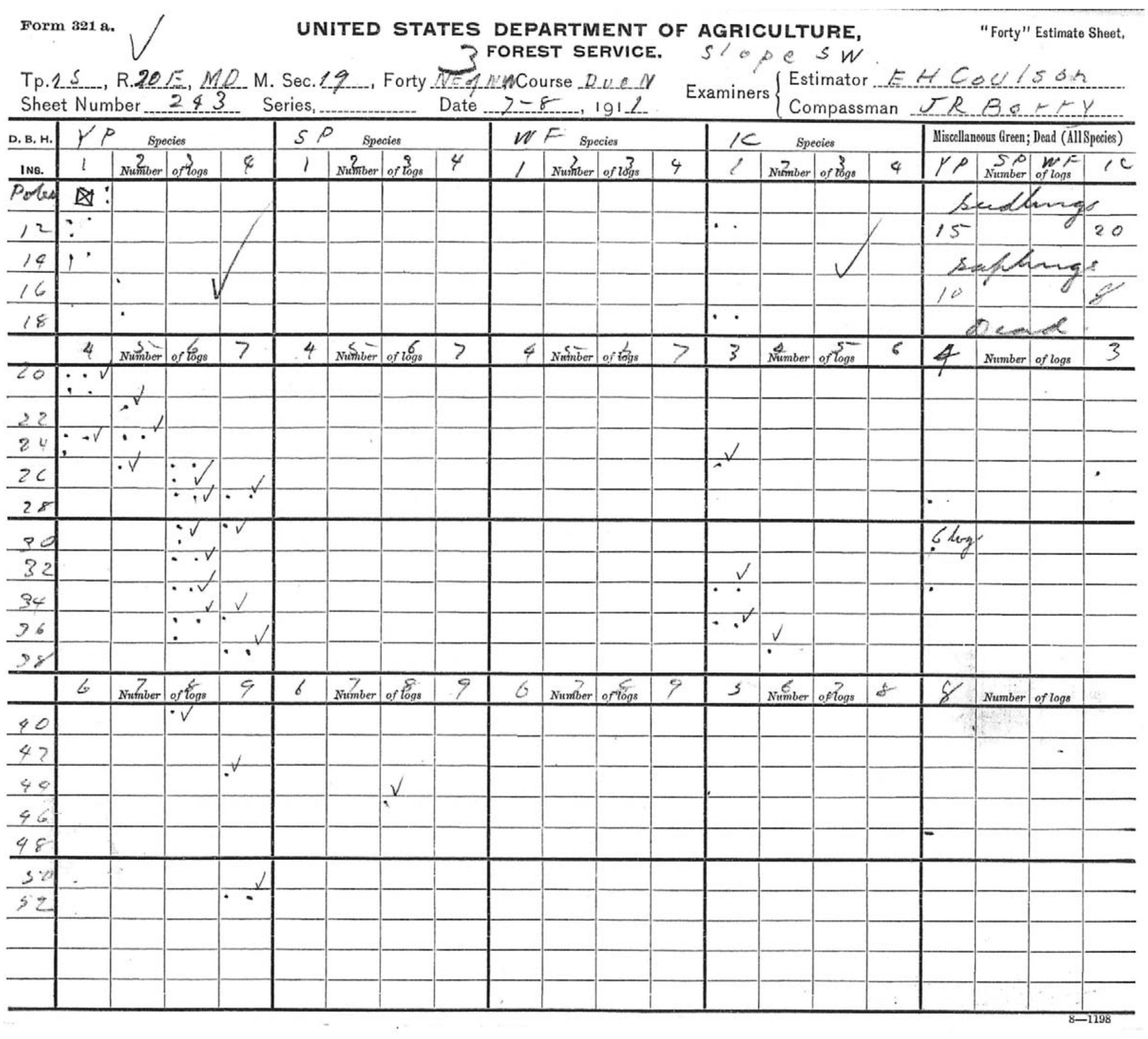
Form 321 a.
UNITED STATES DEPARTMENT OF AGRICULTURE,
FOREST SERVICE.
"Forty" Estimate Sheet.
Slope SW
Tp. 1 S, R. 20 E, MD M. Sec. 19, Forty NE4 NW Course Due N
Sheet Number 243 Series, Date 7-8, 1911
Examiners: Estimator E H Coulson; Compassman J R Berry
D. B. H. Ins. — Species: YP, SP, WF, IC; Miscellaneous Green; Dead (All Species) — Number of logs
Poles, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 36, 38, 40, 42, 44, 46, 48, 50, 52
Seedlings 15 20; Saplings 10 8; Dead; 6 logs
8—1198

Fig. A1. Data sheet from a timber inventory conducted in 1911 by USDA Forest Service in what is now Yosemite National Park, USA.