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Long-term demographic trends in a fire-suppressed mixed-conifer forest

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Abstract:

In the western US, forests are experiencing novel environmental conditions related to changing climate and a suppression of the historical fire regime. Mixed-conifer forests, considered resilient to disturbance due to their heterogeneity in structure and composition, appear to be shifting to a more homogeneous state, but the timescale of these shifts is not well understood. Our objective was to assess the effects of climate and fire suppression on stand dynamics and demographic rates of an old-growth mixed-conifer forest in the Sierra Nevada. We used a Bayesian hierarchical analysis to quantify species and community rates of recruitment, growth, and mortality. Despite a warming climate, we found that stand density, basal area, and carbon have increased over 56 years. Fir recruitment and growth significantly exceeded the community-level median rates, while pine recruitment and growth was significantly lower than the community-level median. Shifts in species composition from a well-mixed stand to a more dense fir-dominated stand appear to be driven by low growth and recruitment rates of pines relative to firs. In forests such as these with consistent and relatively low mortality rates, we recommend that restoration and management activities be focused on promoting pine recruitment and growth.

Introduction

Novel environmental conditions created by human enterprise (e.g., management decisions and climate change) are contributing to shifts in the structure and function of forests worldwide (Allen et al. 2010). In California, a century of fire suppression has resulted in forest conditions that diverge greatly from pre-settlement forest structure and composition (Dolanc et al. 2014). Historically, frequent, low-intensity fires in the vast California mixed-conifer forest (approximately 3.7 million ha, LANDFIRE 2010) helped to maintain a structurally heterogeneous landscape with dominance shared among several conifer species (van Mantgem et al. 2011). Fire exclusion has resulted in a sharp decrease in the species richness of recruits in the forest understory and changes in the structure of the forest due to the loss of large trees (McIntyre et al. 2015). Abundances of relatively shade-tolerant, fire-sensitive species *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), and *Calocedrus decurrens* (incense-cedar) have increased at the expense of the relatively shade-intolerant, fire-resistant species *Pinus ponderosa* (ponderosa pine) and *Pinus lambertiana* (sugar pine; Scholl and Taylor 2010, Knapp et al. 2013). These compositional changes have been accompanied by increased fuel loads and an increase in the density of small diameter shade-tolerant trees. The resulting increased fuel loads exacerbate fire hazard (Agee and Skinner 2005) and have contributed to an altered fire regime characterized by low frequency but high intensity mega-fires (Stephens et al. 2014).

Climate-induced physiological stress due to increased temperature and drought has also contributed to forest change as a result of recent mortality events (Allen et al. 2010). Increased tree density resulting from fire suppression may interact with changing

climate variables and contribute to greater water stress and potentially increased mortality due to competition for resources in these dry forests (Das et al. 2011). In some areas of the Sierra Nevada, rising water deficits resulting from increased annual temperatures have been linked to increased tree mortality (van Mantgem and Stephenson 2007). The possible compounding effects of interacting disturbances (*sensu* Paine et al. 1998) may be substantial but are not well understood.

The differential responses by species to fire exclusion and climate change appear to be contributing to a species reordering of fire-adapted California forests. This reordering potentially represents the first phase of a transition from a well-mixed, resilient forest to a less diverse community that is more susceptible to catastrophic loss due to fire, pests, or pathogens. However most of the evidence for this trend is based on extrapolations from short-term observations (e.g. van Mantgem et al 2004), reconstructions of historical data (e.g., Scholl and Taylor 2010), or space-for-time substitutions (Minnich et al. 2000). These indirect approaches introduce considerable uncertainty compared to the direct alternative -- long-term observations on repeatedly measured plots (Harmon and Pabst 2015).

In this study, we use a 56-year record of tree mortality, growth, and recruitment to test the hypothesis that the era of fire suppression and climate warming coincides with the “homogenization” of an old-growth, Californian mixed-conifer forest. Specifically we ask: 1) What are the trends in forest composition and structure in this old-growth stand? 2) Are differences in demographic rates among species contributing to a shift in forest composition? 3) What are the relative contributions of fire suppression and climate trends as potential drivers of species reordering at this site over the last six decades?

Methods

Study Area

The study site is located on an east-facing slope of Little Schneider Ridge in the Plumas National Forest, CA. The elevation of this gently sloping stand (14%) ranges from 1158 to 1219 m (Ansley and Battles 1998). Soils are classified as Ultic Haploxeralf formed from basic igneous bedrock and have been weathered to a relatively fine loam with depths from 1-2 m (Ansley and Battles 1998). Mean annual temperature was 9.8° C and mean annual precipitation was 1144 mm for the period 1956-2010 (PRISM Climate Group 2015).

The stand is an old-growth, all-aged mixed-conifer stand with five major constituent tree species (white fir, Douglas-fir, ponderosa pine, sugar pine, and incense-cedar) and two minor species (California black oak (*Quercus kelloggii*), and Pacific dogwood (*Cornus nuttallii*)). Policies of fire exclusion were implemented in this region in the late 19th and early 20th centuries. Prior to the implementation of these policies, the mean fire interval was estimated to be 12 years (Moody et al. 2006). Since 1900, only two fires have been recorded in the vicinity of the study area (Moody et al. 2006), and there is no record of fire in this stand for the duration of the inventory record (1954-2013).

Data Collection

The measured area of the stand consists of 4.7 ha that were originally surveyed in 1954 by UC Berkeley Professor Frederick S. Baker (the Baker Stand). In this first inventory, all trees >24 cm DBH (diameter at breast height; 1.37m) were measured.

Baker conducted the original inventory over a seven year period, from 1954-1961. For simplicity, we refer to the timing of initial measurement by the median of the interval, 1957 (Ansley and Battles 1998). The inventory was repeated in summer 1995, and all trees >9.5 cm DBH were tagged and added to the inventory. All tagged, live trees were remeasured in the summers of 2001, 2008, and 2013. New recruits into the >9.5 cm DBH size class were tagged and added to the inventory at each sampling period. All tagged trees that had died since the previous inventory were recorded. The boundaries of the original Baker Stand were trimmed to a 3.9 ha area for analysis to minimize errors associated with the inclusion or exclusion of trees near the edge of the stand (Ansley and Battles 1998).

Analytical approach

To assess the possible effect of climatic conditions on demographic processes, we tested for trends in average annual temperature (°C), total annual precipitation (mm), and annual climatic water deficit (mm) for the period 1956-2010. Annual climatic water deficit is an index that represents a biologically relevant metric of climate variability by integrating temperature and precipitation (van Mantgem and Stephenson 2007). To calculate deficit, we used the Basin Characterization Model. This physically-based model includes data inputs for topography, soil composition and depth, underlying bedrock geology, and spatially-explicit values of air temperature and precipitation (Flint et al. 2013). Temperature and precipitation values were monthly average values from the empirically-based Parameter-Elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994). We evaluated trends using linear regression.

We calculated basal area (BA), stem density, and aboveground forest C for all trees >9.5 cm DBH for the four modern inventories (1995, 2001, 2008, and 2013). We calculated the same metrics for trees >24 cm DBH for all five inventories (1957, 1995, 2001, 2008, and 2013), because only trees >24 cm DBH were measured in the 1957 inventory. We used species-specific regional volume equations (Waddell and Hiserote 2005) and wood density estimates to calculate the carbon density (Mg C ha^{-1}) of aboveground biomass to maintain consistency with national forest inventory procedures (Zhou and Hemstrom 2009). Since all trees were measured in this complete inventory, there is no sampling error in these estimates. We evaluated trends using linear regression. We also calculated the relative dominance of each of the five major and two minor species present in the stand at each sampling interval. Relative dominance is defined as the proportion of total BA per species. Calculations were carried out in R ver. 3.1.1 (R Development Core Team 2014).

To estimate annual rates of mortality, growth, and recruitment, we used a hierarchical Bayesian approach to quantify community and individual species demography (Condit et al. 2006). This model accounts for variation in two levels, between-species and within-species, by defining a joint probability distribution that incorporates distributions from both the species and community levels. This method is advantageous because scant observations for rare species are informed by the overall community mean. The annual rate constant of mortality (m) was calculated as:

$$m = \frac{\ln(N_0) - \ln(N_1)}{t} \tag{Eq. 1}$$

where N_0 and N_1 are the population size at time₀ and time₁, respectively, and t is the number of years between inventories. Mortality rates were calculated for each species and for the overall community.

Average annual growth rates were calculated for surviving trees. Because negative growth rates are biologically unrealistic, Condit et al. (2006) recommend that these values be excluded from growth rate calculations. To avoid introducing bias, we also excluded an equal proportion of trees above the upper growth threshold, defined by the interquartile range (IQR). This approach is a nonparametric method that uses the distribution of the data to identify outliers (Sokal and Rohlf 1981). The diameter growth between inventory intervals were ranked from lowest to highest, and the quartiles and the difference between the quartiles (IQR) were determined. Observations below $Q1 - (1.5 \times \text{IQR})$ and above $Q3 + (1.5 \times \text{IQR})$ were excluded from the growth analysis. This process omitted an average of 3% of surviving trees for the three modern inventory intervals we evaluated: 1995-2001 (54 of 2830 trees), 2001-2008 (83 of 2803 trees), and 2008-2013 (114 of 2950 trees). After the IQR outliers were excluded, remaining negative growth rates were recalculated by adding the overall minimum growth change for each inventory interval (Condit et al. 2006) because the log component of the relative growth rate equation requires non-negative values. The average annual growth rate of survivors (G) was calculated as:

$$G_k = \frac{\ln(dbh_{k,j+1}) - \ln(dbh_{k,j})}{t} \quad (\text{Eq. 2})$$

where dbh is the tree diameter (cm), k refers to individual trees, and j refers to inventories. The time interval t between inventories j and $j+1$ is calculated for each

168 individual tree. Growth rates were calculated for individual trees, for each species, and
169 for the overall community.

170 The average annual rate of recruitment was calculated as the number of trees ha⁻¹
171 yr⁻¹ that recruited into the >9.5 cm DBH size class between inventories. These three
172 demographic rates were calculated for the three modern inventory intervals (1995-2001,
173 2001-2008, and 2008-2013). The number of years between inventories varied slightly (6,
174 7, and 5 years, respectively for the three inventory intervals). The variation in the length
175 of the census interval introduces some census-period dependence bias that we did not
176 account for in the model, but we assume this error to be minimal (Sheil and May 1996).

177 We used a hierarchical Bayesian model to estimate recruitment, growth, and
178 mortality of the overall community and seven individual tree species (white fir, Douglas-
179 fir, incense-cedar, sugar pine, ponderosa pine, black oak, and Pacific dogwood). Bayes
180 theorem is used to define the joint probability distribution for the overall community as
181 the product of the species-level and the community-level probabilities. For each of the
182 three demographic processes, we selected probability distributions that best fit the
183 observed data. For annual mortality rates, the community level distribution we observed
184 was an exponential distribution among the seven species and at the species level,
185 mortality was distributed as a binomial probability (dead or alive). For growth, both the
186 community-level and species-level distributions followed a log-normal distribution. For
187 recruitment, we observed an exponential distribution at the community-level and a
188 normal distribution at the species level.

189 The Markov Chain Monte Carlo technique with the Gibbs sampler (10,000 runs
190 with a 1,000 run burn-in) was used to solve the integration and fit the parameters using

uninformed priors. We report the median value of the runs as well as the 2.5th and 97.5th percentiles (the Bayesian 95% credible intervals.) We define a significant difference between species or inventory intervals to be non-overlapping 95% Bayesian credible intervals (CI). Calculations were carried out using the software packages R ver. 3.1.1 (R Development Core Team 2014) and OpenBUGS 3.0.2 (Lunn et al. 2009).

Results

Climate trends

Over the period 1957-2010, we detected a significant increasing trend in average annual temperature (mean±standard deviation = $9.8 \pm 0.6^{\circ}\text{C}$; $p < 0.001$, $r^2 = 0.19$) but did not detect a significant trend in total annual precipitation (mean±standard deviation = 1144 ± 380 mm; $p = 0.77$; Figure 1). While there appears to be a weak trend of increasing water deficit at this site due to increasing temperatures, we did not find a significant long-term increase in the annual water deficit from 1957-2010, which averaged 504.8 mm (standard deviation = ± 80.4 ; $p = 0.09$).

Stand dynamics (1957-2013)

Basal area increased linearly by 11% for trees >9.5 cm DBH over the 18-year period from 1995-2013 ($p = 0.009$, $r^2 = 0.98$) and by 81% for trees >24 cm DBH over the 56-year period from 1957-2013 ($p = 0.003$, $r^2 = 0.99$; Table 1; Figure 2). There was a notable increase in white fir dominance over the 56-year period from 1957-2013 (Figure 2). Stem density increased by 8% for trees >9.5 cm DBH over the 18-year period from 1995-2013 though this trend was not significant ($p = 0.13$, $r^2 = 0.75$) and by 116% for trees

214 >24 cm DBH over the 56-year period from 1957-2013 ($p=0.0007$, $r^2=0.99$; Table 1).
215 Forest carbon increased linearly by 8% for trees >9.5 cm DBH over the 18-year period
216 from 1995-2013 ($p=0.005$, $r^2=0.99$) and by 116% for trees >24 cm DBH over the 56-
217 year period from 1957-2013 ($p=0.0003$, $r^2=0.99$; Table 1).

218 When the stand was first measured 1957, Douglas-fir accounted for 43% of the
219 total BA, while the other 4 major species (white fir, incense-cedar, ponderosa pine, and
220 sugar pine) had relative dominance values similar to one another, ranging from 9%
221 (ponderosa pine) to 20% (sugar pine; Figure 2). Between 1957 and 2013, ponderosa pine
222 decreased in relative dominance by 41% (from 9% relative dominance in 1957 to 5% in
223 2013) and sugar pine relative dominance decreased by 27% (from 20% relative
224 dominance in 1957 to 15% in 2013). White fir increased in relative dominance by 94%
225 (from 15% relative dominance in 1957 to 28% in 2013). The relative dominance of
226 Douglas-fir changed little from 1957-2013, decreasing from 43% in 1957 to 40% in
227 2013.

228

229 *Mortality (1995-2013)*

230 Community-wide mortality rates varied among inventory intervals. Mortality was
231 significantly lower ($0.14\% \text{ yr}^{-1}$, 5% CI = 0.10, 95%CI = 0.34) from 1995-2001 than the
232 later inventories (2001-2008: $1.37\% \text{ yr}^{-1}$, 5% CI = 0.67, 95%CI = 3.60; 2008-2013:
233 $0.84\% \text{ yr}^{-1}$, 5% CI = 0.38, 95%CI = 2.47; Figure 3). Species mortality rates did not differ
234 systemically from one another throughout the study, but some species differed
235 significantly among individual inventory intervals. Douglas-fir and white fir had
236 significantly lower mortality rates in 1995-2001 as compared to the later inventories.

White fir had significantly higher mortality rates in the 2001-2008 inventory period relative to the other periods. There tended to be more variation in mortality rates among inventory intervals than among species within inventory periods. Douglas-fir had significantly lower mortality than the community median for the 2001-2008 inventory period, which was the only instance of a species differing significantly from the community median (Table S1).

Growth (1995-2013)

Growth rates of white fir, Douglas-fir, and incense-cedar significantly outpaced the growth rates of the pines and hardwoods in all inventory periods (Figure 4). The growth rates of white fir, Douglas-fir, and incense-cedar were significantly higher than the community median for all three inventory periods, which ranged from 0.45-0.67% ha⁻¹ yr⁻¹ (Table S2). The growth rates of ponderosa pine and sugar pine were significantly lower than the community median for those same intervals. The community median did not differ significantly among inventory periods (Table S2).

Recruitment (1995-2013)

Recruitment rates of white fir and Douglas-fir into the potential canopy tree size class (>9.5cm DBH) were significantly higher than the recruitment rates of the pines (Figure 5). There was no recruitment of hardwoods in any of the inventory periods and no recruitment of pine species in the 1995-2001 and 2008-2013 inventory periods. The recruitment rates of white fir and Douglas-fir were significantly higher than the community median for all three inventory periods, while the recruitment rates of

ponderosa and sugar pine were significantly lower than the community median for those same intervals. The community median did not differ significantly among inventory periods (Table S3).

Discussion

Long-term trends of forest composition, structure, and demography

Our longitudinal results documenting forest change over the last half-century indicate that a species reordering is underway in this old-growth mixed-conifer forest. White fir relative dominance increased by 94% from 1957-2013. In contrast, the relative dominance of both sugar pine and ponderosa pine declined over the 56-year study period (Figure 2). Throughout the study, Douglas-fir remained the largest contributor to total BA. Forest structure also changed over the 56-year study period. From 1957-2013, we observed a linear increase in BA, stem density, and forest C of trees >24cm DBH (Fig. 2). Similar trends were observed for all trees >9.5cm DBH at the shorter timeframe of 1995-2013. It does not appear that increased competition as a result of greater density has resulted in a plateau of forest growth at this site. This forest is an example of the capacity of old-growth forests to act as an important net C sink in the absence of disturbance (Luyssaert et al. 2008). However, forests can easily transition from a net carbon sink to a carbon source when wildfires re-enter the system (Gonzales et al. 2015). Densifying, fire suppressed forests such as the Baker stand are at high risk for such a transition (Stephens et al. 2014).

Evidence from our study suggests that differences in growth and recruitment rather than mortality appear to be responsible for the observed trend towards a species

reordering. Mortality did not systematically differ among the major constituent species (Fig. 3). The mortality rates we observed in the Baker stand (an average media community mortality rate of $0.78\% \text{ yr}^{-1}$ for the three inventory period with a 95% Bayesian credible interval 0.1%-3.6%) overlap with mortality rates for California forests reported by van Mantgem et al. (2009; plot-level mean mortality rates of 1.2% and 1.6% year^{-1} for two census intervals). However, recruitment and growth of firs has far outpaced that of pines (Figs.4 and 5), leading to an absence of pines in smaller diameter classes (9.5–24 cm DBH) in this stand and a decline in the relative dominance of pine species.

Potential drivers of forest reordering

We were interested not only in quantifying trends over time in an old-growth mixed conifer stand but also assessing the potential role of climate and disturbance regimes as drivers of shifts in composition and structure. Climate stress has been identified as an important factor in increased mortality rates in the Western US (Allen et al. 2010, van Mantgem and Stephenson 2007, Anderegg et al. 2015). While the average annual temperature increased over the study period (1957-2010), neither annual precipitation nor water deficit showed a significant trend. While climatic correlates with tree mortality have been documented extensively in the southern Sierra Nevada (Das et al. 2013), no trend over time in annual water deficit or tree mortality was detectable at our study site in the northern Sierra Nevada. The more mesic conditions relative to more southern sites indicates that there may be areas of the Sierra Nevada that are less

susceptible to climate-induced mortality (Dettinger et al. 1998). These sites may serve as refugia for drought-sensitive species under future climate conditions.

The lack of a strong climate signal at this site implies some other force(s) driving trends in vegetation away from the steady-state behavior expected of old-growth forests (sensu Bormann and Likens 1979). Our results are consistent with expected consequences of a disturbance regime altered by a century of fire suppression (Collins et al. 2011). Historically, mixed-severity fires would remove relatively fire-intolerant fir saplings and small trees, allowing sufficient gaps for relatively shade-intolerant pines to recruit (York et al. 2012). It is likely that the increasingly crowded Baker Stand has constrained the regeneration of the shade-intolerant pines (Table 1). The lack of pine recruitment as a legacy of fire suppression policies is well-documented throughout the Sierran mixed conifer forest (Dolanc et al. 2014, Knapp et al. 2013, North et al. 2007, Scholl and Taylor 2010, Zald et al. 2008).

Our study included only one stand, which we acknowledge limits the scope of inference of our results. Though the spatial extent of the Baker Stand is small, the insights provided by this 56-year record are valuable because in addition to being one of the few long-term inventories in the Sierra Nevada, old-growth forests in the northern reaches of the Sierra Nevada are particularly rare (Barbour et al. 2002). Thus our work complements observations from the more extensive old-growth forests in the Central (Yosemite NP) and Southern (Sequoia-Kings Canyon NP) Sierra Nevada.

Conclusion

Old-growth forests have many important ecological functions. Their heterogeneous structure and composition can confer resilience in the face of drought, pests, pathogens, and fire (Stevens et al. 2014). Additionally, they serve as an important carbon sink, with a large amount of atmospheric carbon removed annually by large trees (Stephenson et al. 2014). It is important to understand the demographic drivers of forest change in order to maintain resilient old-growth forests as mortality risks from climate change and catastrophic fire continue to accelerate. Long-term, in-depth studies of forest dynamics are a crucial source of information regarding best practices for sustaining these forests in the future.

Our results indicate that creating opportunities for pine recruitment and growth is essential to maintain the shared-dominance characteristic of the mixed conifer forest. Research suggests that pine species in pre-settlement Sierra Nevada forests regenerated in canopy gaps created by hotspots in otherwise low-intensity fires (White 1985). Ponderosa pine requires disturbances for regeneration that reduce competition, increase light availability, and create a charred seedbed (White 1985, York et al. 2012). Sugar pine regeneration has not been as closely linked to disturbance as ponderosa pine, but sugar pine's shade-intolerance leads it to regenerate where larger gaps have formed in fires (North et al. 2005). A gap-based approach to harvesting, followed by a post-harvest burning treatment within gaps has been suggested as one method to encourage pine recruitment in mixed-conifer forests (York et al. 2012). However, Zald et al. (2008) found that high seed rain of white fir and incense cedar relative to pines after experimental fire and thinning treatments negated efforts to increase pine abundance.

349 Control of competitors as well as planting may also be required for successful pine
350 recruitment in fire-suppressed forests.

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495 **Tables and Figures**

496 Table 1. Stem density (stems ha⁻¹), basal area (m² ha⁻¹), and forest carbon (Mg ha⁻¹) in the
 497 Baker stand from 1957-2013. Only trees >24cm DBH were measured in the 1957
 498 inventory. Because this is a complete inventory, there is no error around the estimate.

		1957	1995	2001	2008	2013
Density (stems ha ⁻¹)	>9.5 cm		727	774	773	789
	>24 cm	119	230	240	249	257
Basal Area (m ² ha ⁻¹)	>9.5 cm		77.7	81.2	83.7	86.1
	>24 cm	42.1	68.8	71.7	74.3	76.4
Forest Carbon (Mg ha ⁻¹)	>9.5 cm		231	241	251	256
	>24 cm	137	220	228	238	243

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500

Figure 1. Average annual temperature increased significantly from 1956-2010 ($p < 0.001$, $r^2 = 0.20$). Average annual precipitation and annual water deficit did not have significant long-term trends over the same period.

Figure 2. Changes in relative dominance of trees >24 cm DBH by species (1957-2013) and the total basal area increase over the 56-year study period. Relative dominance is defined as the proportion of total basal area for that species.

509

510 Figure 3. Mortality rate (% yr⁻¹; median and 95% CI) from 1995-2013 of the community
511 and of individual species. The mortality rate of the overall community for each inventory
512 period is shown as a dashed line with a shaded 95% Bayesian credible interval. The
513 species rates are shown as points with error bars indicating the 95% Bayesian credible
514 interval.

515

516 Figure 4. Growth rate (% yr⁻¹; median and 95% CI) from 1995-2013 of the community
 517 and of individual species. The growth rate of the overall community for each inventory
 518 period is shown as a dashed line with a shaded 95% Bayesian credible interval. The
 519 species rates are shown as points with error bars indicating the 95% Bayesian credible
 520 interval.

Figure 5. Recruitment rate to the >9.5 cm DBH class (trees ha⁻¹ yr⁻¹; median and 95% CI) from 1995-2013 of the community and of individual species. The recruitment rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Bayesian credible interval. The species rates are shown as points with error bars indicating the 95% Bayesian credible interval. There was no recruitment of black oak or dogwood in any inventory. There was no recruitment of ponderosa pine or sugar pine in the 1995-2001 or 2008-2013 intervals.

Table S1. Model estimates of median mortality rates (% yr⁻¹) and 95% credible intervals of individual species and the overall community for all trees >9.5 cm.

	1995-2001 (n=3017)			2001-2008 (n=3015)			2008-2013 (n=2839)		
	5%CI	Median	95%CI	5%CI	Median	95%CI	5%CI	Median	95%CI
Black oak	0.03	0.27	0.84	1.72	4.41	8.45	0.77	2.89	6.66
Dogwood	0.00	0.15	0.63	0.21	1.89	5.63	0.02	0.68	2.84
Incense-cedar	0.03	0.14	0.33	0.52	0.87	1.29	0.29	0.60	1.04
Douglas-fir	0.00	0.02	0.08	0.17	0.29	0.44	0.14	0.27	0.44
White fir	0.03	0.08	0.15	1.18	1.38	1.61	0.32	0.45	0.60
Ponderosa pine	0.00	0.12	0.50	0.23	1.18	2.92	0.25	1.30	3.32
Sugar pine	0.00	0.11	0.43	0.56	1.54	2.99	0.32	1.25	2.86
Community	0.10	0.14	0.34	0.67	1.37	3.60	0.38	0.84	2.47

Table S2. Model estimates of median growth rates (% yr⁻¹) and 95% credible intervals of individual species and the overall community for all trees >9.5 cm.

	1995-2001 (n=2830)			2001-2008 (n=2803)			2008-2013 (n=2950)		
	5%CI	Median	95%CI	5%CI	Median	95%CI	5%CI	Median	95%CI
Black oak	0.27	0.39	0.58	0.29	0.44	0.66	0.24	0.37	0.56
Dogwood	0.04	0.11	0.3	0.01	0.02	0.04	0.1	0.17	0.3
Incense-cedar	1.26	1.39	1.53	1.21	1.32	1.44	1.45	1.59	1.73
Douglas-fir	1.42	1.51	1.6	1.27	1.33	1.41	1.59	1.67	1.76
White fir	1.96	2.05	2.13	1.69	1.76	1.82	1.81	1.88	1.95
Ponderosa pine	0.33	0.45	0.61	0.23	0.3	0.4	0.11	0.15	0.21
Sugar pine	0.58	0.74	0.94	0.39	0.49	0.62	0.29	0.37	0.47
Community	0.25	0.67	1.71	0.11	0.45	1.84	0.19	0.56	1.54

Table S3. Model estimates of median recruitment rates (trees ha⁻¹ yr⁻¹) and 95% credible intervals of individual species and the overall community for all trees >9.5 cm.

	1995-2001 (n=2830)			2001-2008 (n=2803)			2008-2013 (n=2950)		
	5%CI	Median	95%CI	5%CI	Median	95%CI	5%CI	Median	95%CI
Black oak	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dogwood	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Incense-cedar	0.01	0.09	0.21	0.62	0.70	0.78	0.41	0.58	0.74
Douglas-fir	2.17	2.30	2.42	1.81	1.89	1.97	2.66	2.82	2.97
White fir	4.40	4.52	4.64	4.53	4.61	4.69	4.64	4.81	4.97
Ponderosa pine	0.00	0.00	0.00	0.19	0.27	0.35	0.00	0.00	0.00
Sugar pine	0.00	0.00	0.00	0.00	0.04	0.12	0.00	0.00	0.00
Community	0.50	0.80	1.18	0.73	1.09	1.52	0.38	0.61	0.89