NOTE

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

Carrie R. Levine, Flora Krivak-Tetley, Natalie S. van Doorn, Jolie-Anne S. Ansley, and John J. Battles

Abstract: In the western United States, forests are experiencing novel environmental conditions related to a 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, whereas pine recruitment and growth was significantly lower than the community-level median rates. 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.

Key words: California, mixed conifer, fire, suppression, climate change, Bayesian.

Résumé : Dans l'ouest des États-Unis, les forêts sont confrontées à de nouvelles conditions environnementales reliées au changement climatique et à la suppression des feux. Les forêts mélangées de conifères, résilientes aux perturbations à cause de leur structure et de leur composition hétérogènes semblent évoluer vers une plus grande homogénéité mais l'échelle de temps à laquelle ces changements s'opèrent est incertaine. Notre objectif consistait à évaluer les effets du climat et de la suppression des feux sur la dynamique du peuplement et les taux démographiques d'une vieille forêt mélangée de conifères située dans la Sierra Nevada. Nous avons utilisé une analyse hiérarchique bayésienne pour quantifier les taux de recrutement, de croissance et de mortalité des espèces et de la communauté. Malgré le réchauffement du climat, nous avons trouvé que la densité, la surface terrière et le contenu en carbone du peuplement ont augmenté sur une période de 56 ans. Le recrutement et la croissance du sapin étaient significativement plus élevés que les taux médians à l'échelle de la communauté tandis que c'était le contraire dans le cas du pin. L'évolution de la composition en espèces, d'un peuplement mélangé plutôt hétérogène vers un peuplement plus dense dominé par le sapin semble être le résultat des faibles taux de recrutement et de croissance des pins comparativement aux sapins. Dans de telles forêts, où le taux de mortalité des pins est constant et relativement faible, nous recommandons que les activités d'aménagement et de restauration visent avant tout à favoriser le recrutement et la croissance des pins. [Traduit par la Rédaction]

Mots-clés : Californie, mélange de conifères, feu, suppression, changement climatique, Bayésien.

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 presettlement 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 in 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* (Gordon & Glend.) Lindl. ex Hildebr. (white fir), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), and *Calocedrus decurrens* (Torr.) Florin (incense-cedar) have increased at the expense of the relatively shade-intolerant, fire-resistant species *Pinus ponderosa* Douglas ex P. Lawson & C. Lawson (ponderosa pine) and *Pinus lambertiana* Douglas (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 megafires (Stephens et al. 2014).

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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 re-ordering of fire-adapted California forests. This re-ordering 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 with 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 the following questions: (i) What are the trends in forest composition and structure in this old-growth stand? (i) Are differences in demographic rates among species contributing to a shift in forest composition? (iii) What are the relative contributions of fire suppression and climate trends as potential drivers of species re-ordering 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, California. 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 ranging from 1 to 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* Newberry) and Pacific dogwood (*Cornus nuttallii* Audubon)). 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 a professor at the University of California Berkeley, Frederick S. Baker (the Baker stand). In this first inventory, all trees >24 cm DBH (diameter at breast height; 1.37 m) were measured. Baker conducted the original inventory over a 7 year period (1954–1961). For simplicity, we refer to the timing of initial measurement by the median of the interval, i.e.,

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 mean 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 mean 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 carbon (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 C density (Mg C·ha^{-1}) of aboveground biomass to maintain consistency with national forest inventory procedures (Zhou and Hemstrom 2009). As 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 (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

$$(1) \qquad m = \frac{\ln(N_0) - \ln(N_1)}{t}$$

where N_0 and N_1 are the population size at time 0 and time 1, respectively, and t is the number of years between inventories. Mortality rates were calculated for each species and for the overall community.

Mean 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 IQRs were determined. Observations below Q1 − (1.5IQR) and above Q3 + (1.5IQR) 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 mean annual growth rate of survivors (G) was calculated as:

$$(2) \qquad G_k = \frac{\ln(\mathrm{dbh}_{k,j+1}) - \ln(\mathrm{dbh}_{k,j})}{t}$$

where dbh is the tree diameter at breast height (cm) and subscripts k and j refer to individual trees and inventories, respectively. The time interval t between inventories j and $j+1$ is calculated for each individual tree. Growth rates were calculated for individual trees, for each species, and for the overall community.

The mean annual rate of recruitment was calculated as the number of trees per hectare per year that recruited into the >9.5 cm DBH size class between inventories. Demographic rates were calculated for the three modern inventory intervals (1995–2001, 2001–2008, and 2008–2013). The number of years between inventories varied slightly (6, 7, and 5 years, respectively, for the three inventory intervals). The variation in the length of the census interval introduces some census-period dependence bias that we did not account for in the model; however, we assume this error to be minimal (Sheil and May 1996).

We used a hierarchical Bayesian model to estimate recruitment, growth, and mortality of the overall community and seven individual tree species (white fir, Douglas-fir, incense-cedar, sugar pine, ponderosa pine, California black oak, and Pacific dogwood). Bayes theorem is used to define the joint probability distribution for the overall community as the product of the species-level and the community-level probabilities. For each of the three demographic processes, we selected probability distributions that best fit the observed data. For annual mortality rates, the community-level distribution we observed was an exponential distribution among the seven species, and at the species level, mortality was distributed as a binomial distribution (dead or alive). For growth, both the community-level and species-level distributions followed a log-normal distribution. For recruitment, we observed an exponential distribution at the community level and a normal distribution at the species level.
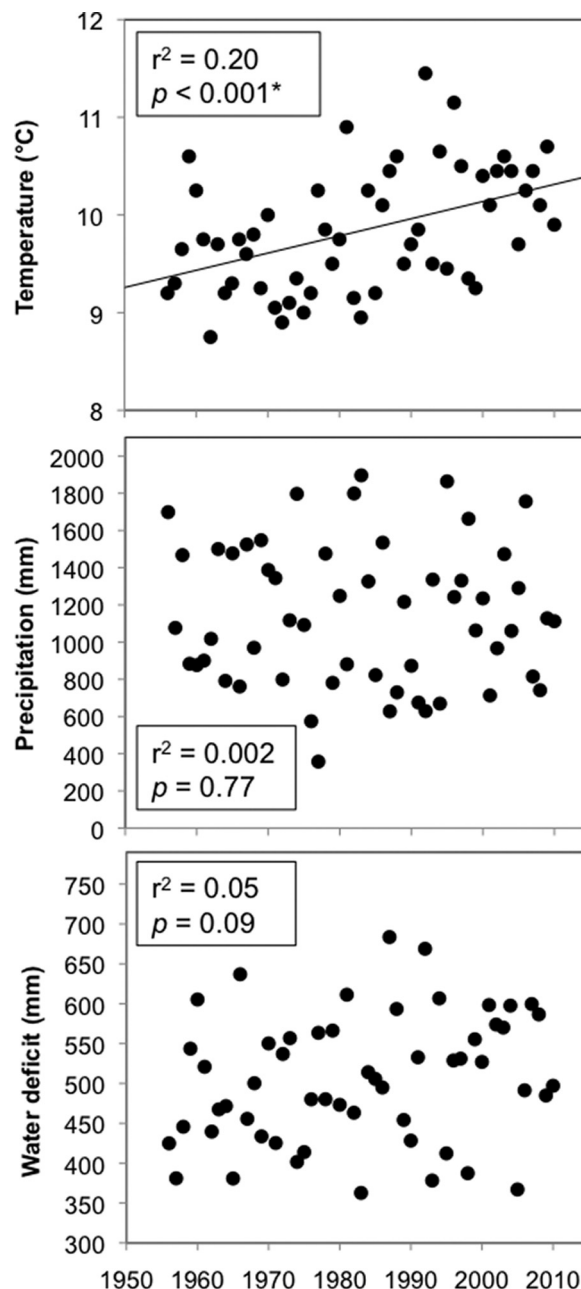
The Markov chain Monte Carlo technique with the Gibbs sampler (10 000 runs with a 1 000 run burn-in) was used to solve the integration and fit the parameters using uninformed priors. We report the median value of the runs, as well as the 2.5th and 97.5th percentiles (the Bayesian 95% credible intervals (CI)). We define a significant difference between species or inventory intervals to be nonoverlapping 95% Bayesian CI. Calculations were carried out using the software packages R (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 mean annual temperature (mean ± standard devation = 9.8 ± 0.6 °C; $p < 0.001$, $r^2 = 0.19$) but did not detect a significant trend in total annual precipitation (1144 ± 380 mm; $p = 0.77$; Fig. 1). Although there appears to be a weak trend of increasing water

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

deficit at this site due to increasing temperatures, we did not find a significant long-term increase in the annual water deficit from 1957 to 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 to 2013 ($p = 0.009$, $r^2 = 0.98$) and by 81% for trees >24 cm DBH over the 56 year period from 1957 to 2013 ($p = 0.003$, $r^2 = 0.99$; Table 1; Fig. 2). There was a notable increase in white fir dominance over the 56 year period from 1957 to 2013 (Fig. 2). Stem density increased by 8% for trees >9.5 cm DBH over the 18 year period from 1995 to 2013, although this trend was not significant ($p = 0.13$, $r^2 = 0.75$), and by 116% for trees >24 cm DBH

Table 1. Stem density, basal area, and forest carbon in the Baker stand from 1957 to 2013.

DBH	1957	1995	2001	2008	2013
Density (no. of stems·ha⁻¹)					
>9.5 cm	—	727	774	773	789
>24 cm	119	230	240	249	257
Basal area (m²·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

Note: Only trees >24 cm DBH were measured in the 1957 inventory. Because this is a complete inventory, there is no error around the estimate. DBH, diameter at breast height.

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

When the stand was first measured in 1957, Douglas-fir accounted for 43% of the total BA, whereas the four other major species (white fir, incense-cedar, ponderosa pine, and sugar pine) had relative dominance values similar to one another, ranging from 9% (ponderosa pine) to 20% (sugar pine; Fig. 2). Between 1957 and 2013, ponderosa pine decreased in relative dominance by 41% (from 9% in 1957 to 5% in 2013) and sugar pine relative dominance decreased by 27% (from 20% in 1957 to 15% in 2013). White fir increased in relative dominance by 94% (from 15% in 1957 to 28% in 2013). The relative dominance of Douglas-fir changed little from 1957 to 2013, decreasing from 43% in 1957 to 40% in 2013.

Mortality (1995–2013)

Community-wide mortality rates varied among inventory intervals. Mortality was significantly lower (0.14% year⁻¹, 5% CI = 0.10, 95% CI = 0.34) in 1995–2001 than in the later inventories (2001–2008: 1.37% year⁻¹, 5% CI = 0.67, 95% CI = 3.60; 2008–2013: 0.84% year⁻¹, 5% CI = 0.38, 95% CI = 2.47; Fig. 3). Species mortality rates did not differ systemically from one another throughout the study, but some species differed significantly among individual inventory intervals. Douglas-fir and white fir had significantly lower mortality rates in 1995–2001 compared with 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 (Supplementary Table S1[1]).

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 (Fig. 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% to 0.67% ha⁻¹·year⁻¹ (Supplementary Table S2[1]). 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 (Supplementary Table S2[1]).

Recruitment (1995–2013)

Recruitment rates of white fir and Douglas-fir into the potential canopy tree size class (>9.5 cm DBH) were significantly higher than the recruitment rates of the pines (Fig. 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, whereas 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 (Supplementary Table S3[1]).

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 re-ordering is underway in this old-growth mixed-conifer forest. White fir relative dominance increased by 94% in 1957–2013. In contrast, the relative dominance of both sugar pine and ponderosa pine declined over the 56 year study period (Fig. 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 to 2013, we observed a linear increase in BA, stem density, and forest C of trees >24 cm DBH (Fig. 2). Similar trends were observed for all trees >9.5 cm 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 C sink to a C 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).
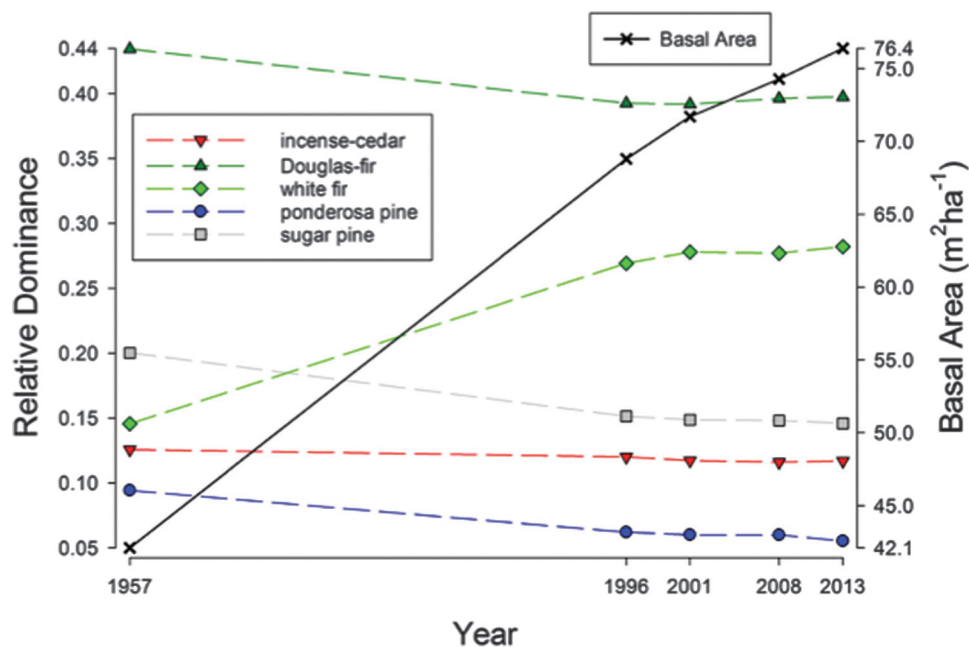
Evidence from our study suggests that differences in growth and recruitment rather than mortality appear to be responsible for the observed trend towards a species re-ordering. Mortality did not systematically differ among the major constituent species (Fig. 3). The mortality rates we observed in the Baker stand (a mean median community mortality rate of 0.78% year⁻¹ for the three inventory periods, with a 95% Baysian CI of 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% year⁻¹ 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.
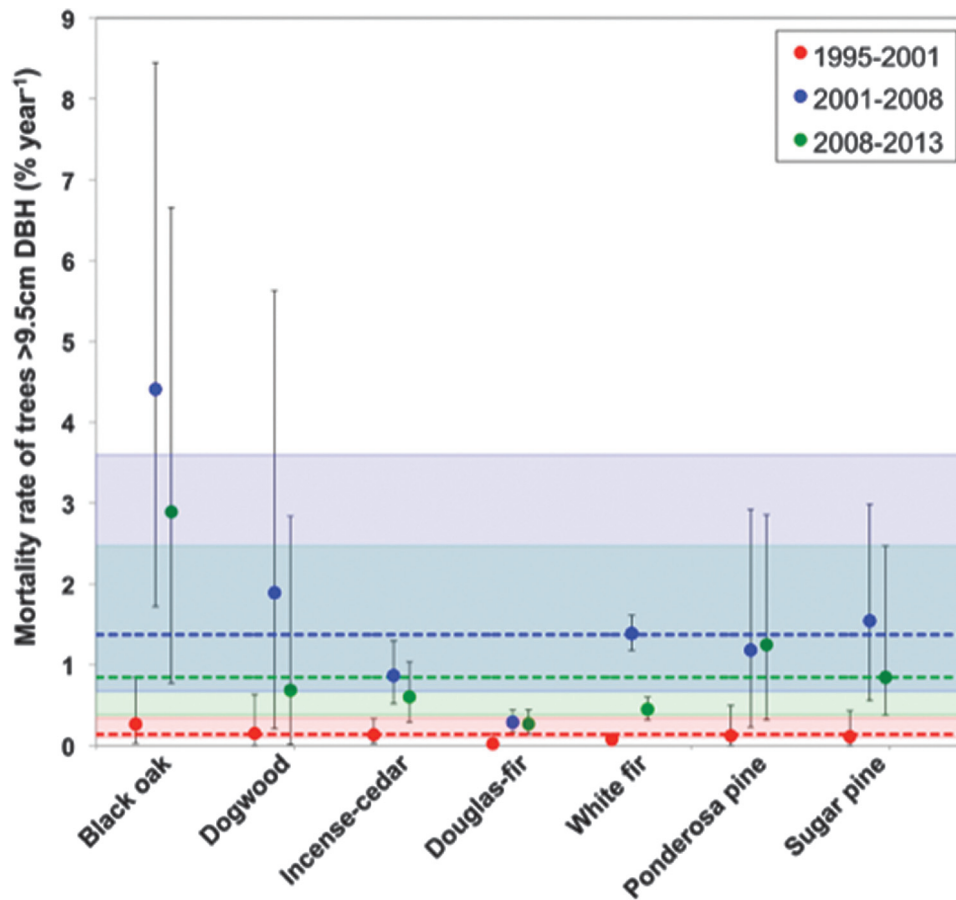
Potential drivers of forest re-ordering

We were interested not only in quantifying trends over time in an old-growth mixed conifer stand, but also in 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 United States (Allen et al. 2010; van Mantgem and Stephenson 2007; Anderegg et al. 2015). Although the mean annual temperature increased over the study period (1957–2010), neither annual
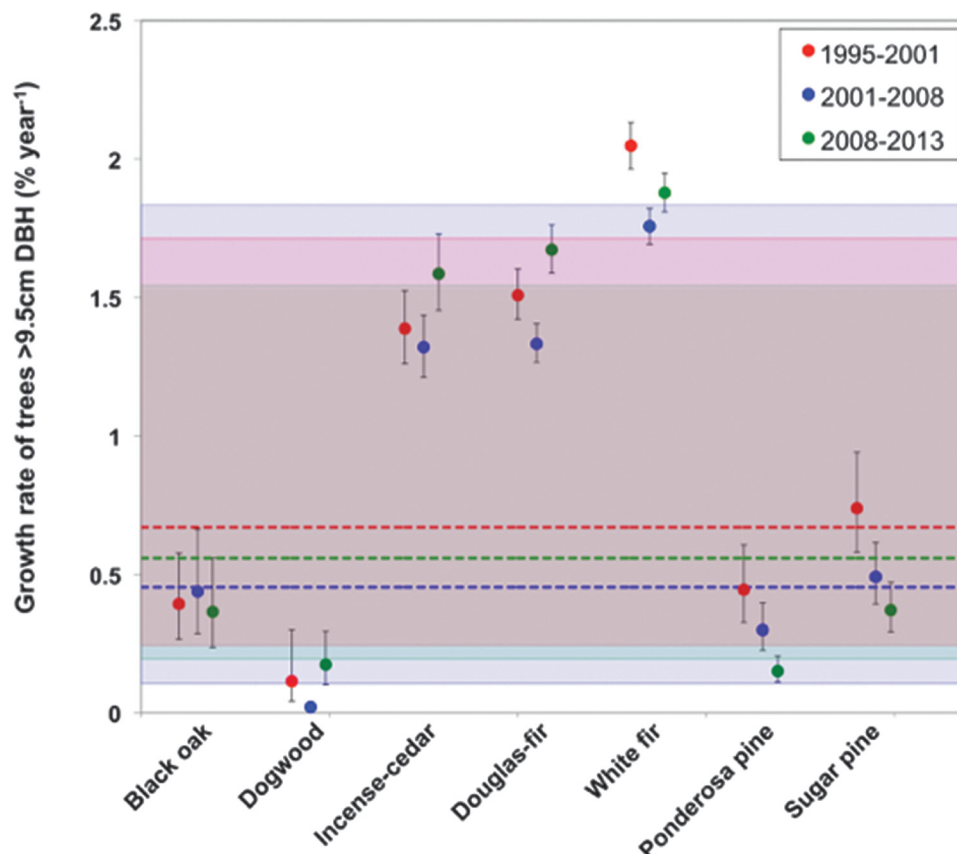

Fig. 2. Changes in relative dominance of trees >24 cm DBH by species (1957–2013) and the total basal area increase over the 56 year study period. Relative dominance is defined as the proportion of total basal area for that species. Figure is provided in colour online.

Fig. 3. Mortality rate (%·year⁻¹; median and 95% credible interval (CI)) from 1995 to 2013 of the community and of individual species. The mortality rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Baysian CI. The species rates are shown as points with error bars indicating the 95% Baysian CI. Figure is provided in colour online.

Fig. 4. Growth rate (%·year⁻¹; median and 95% credible interval (CI)) from 1995 to 2013 of the community and of individual species. The growth rate of the overall community for each inventory period is shown as a dashed line with a shaded 95% Baysian CI. The species rates are shown as points with error bars indicating the 95% Baysian CI. Figure is provided in colour online.

precipitation nor water deficit showed a significant trend. Although climatic correlates with tree mortality have been documented extensively in the southern Sierra Nevada (Das et al. 2013), no trends over time in annual water deficit or tree mortality were 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 (senus 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 (Barbo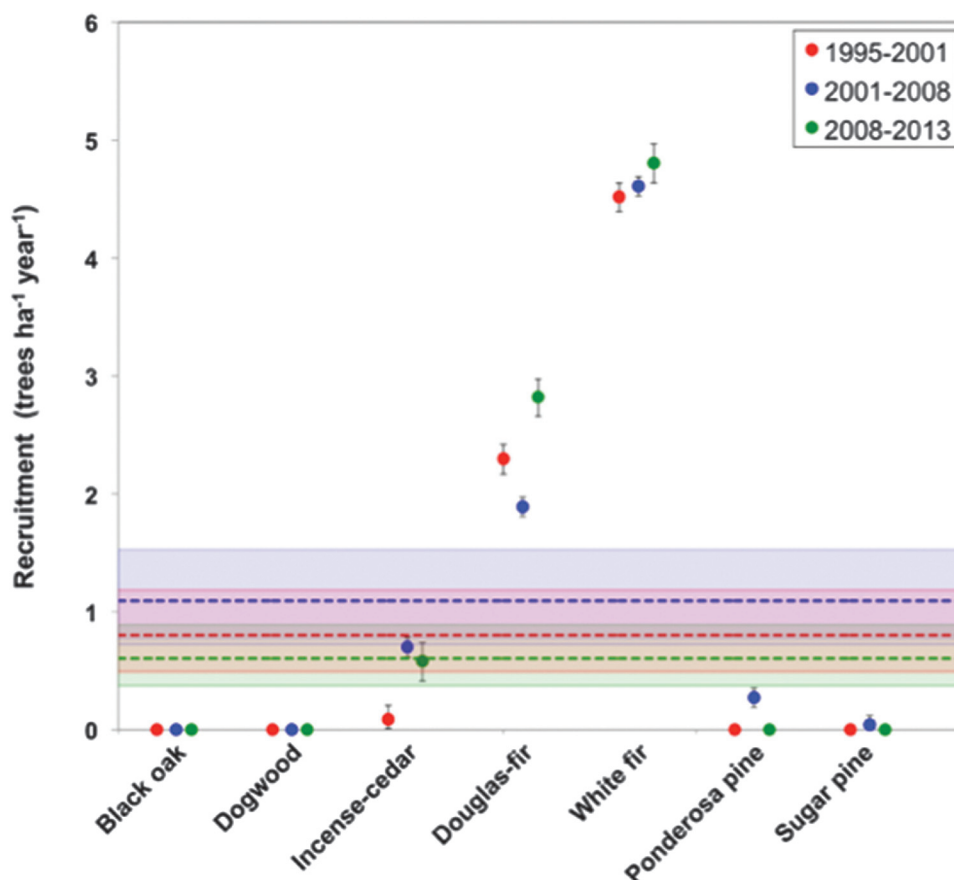ur et al. 2002). Thus, our work complements observations from the more extensive old-growth forests in the Central (Yosemite National Park) and Southern (Sequoia and Kings Canyon National Park) Sierra Nevada.

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 C sink, with a large amount of atmospheric C removed annually by large trees (Stephenson et al. 2014). It is important to understand the demographic drivers of forest change 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 presettlement Sierra Nevada forests regenerated in canopy gaps created by hotspots in otherwise low-intensity fires (White 1985). For regeneration, ponderosa pine requires disturbances 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 the shade intolerance of sugar pine 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

Fig. 5. Recruitment rate to the >9.5 cm DBH class (no. of trees·ha^{-1}·year^{-1}; median and 95% credible interval (CI)) from 1995 to 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% Baysian CI. The species rates are shown as points with error bars indicating the 95% Baysian CI. 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 and 2008–2013 intervals. Figure is provided in colour online.

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

Acknowledgements

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