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## A forest health inventory assessment of red fir (*Abies magnifica*) in upper montane California

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### ABSTRACT

We investigated the forest health of red fir (*Abies magnifica*) and how it compared with commonly-associated species Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*) and white fir (*Abies concolor*) in the upper montane forests of California. We evaluated tree mortality rates, changes in the density of recently-dead trees and the amount of insect and disease damage on live trees from comprehensive forest inventories. The annual mortality rate for red fir was 1.8%, while the rates for Jeffrey pine, lodgepole pine and white fir were 1.9, 1.1 and 3.0%, respectively. The proportion of recently-dead red fir trees increased over time, suggesting an increase in mortality; however, stage-transition models suggested the current population structure of red fir is stable. Dwarf mistletoe and drought-stressed sites were significant predictors of red fir mortality. Trees with substantial damage had a higher probability of experiencing mortality in five years. Our results are consistent with others, but the timeframe is too short to make conclusions about long-term declines. Our results suggest that the most significant of multiple biotic factors involved in red fir mortality processes is dwarf mistletoe, while tree age and the proportion of forest in old-growth may also influence mortality rates.

### RÉSUMÉ

Nous avons étudié la santé forestière du sapin rouge (*Abies magnifica*) et comment elle se compare à celle des espèces qui lui sont communément associées, telles que le pin de Jeffrey (*Pinus jeffreyi*), le pin tordu (*Pinus contorta*) et le sapin du Colorado (*Abies concolor*), dans les forêts de haute montagne de la Californie. Nous avons évalué les taux de mortalité des arbres, les changements dans la densité des arbres morts récemment, et dans la quantité de dommages causés aux arbres vivants par les insectes et les maladies avec inventaires forestiers complets. Le taux de mortalité annuel était de 1,8% pour le sapin rouge, alors que les taux pour le pin de Jeffrey, le pin tordu et le sapin du Colorado étaient respectivement de 1,9, 1,1 et 3,0%. La proportion de sapins rouges morts récemment a augmenté avec le temps, suggérant une augmentation de la mortalité. Toutefois, les modèles de transition d'état suggèrent que la structure de population actuelle du sapin rouge est stable. Les stress dus au petit gui et à la sécheresse sont des variables prédictives significatives de mortalité du sapin rouge. Les arbres présentant des dommages substantiels avaient une plus forte probabilité de subir une mortalité en 5 ans. Notre résultats sont concordent avec ceux d'autres études, mais la période étudiée est trop courte pour permettre de tirer des conclusions au sujet de déclin à plus long terme. Les résultats suggèrent que le petit gui est le plus significatif parmi plusieurs facteurs biotiques impliqués dans les processus causant la mortalité du sapin rouge, tandis que l'âge des arbres et la proportion de vieilles forêts pourraient également influencer les taux de mortalité.

### KEYWORDS

*Abies magnifica*; tree mortality; forest inventory and analysis; forest pathology

### MOTS-CLÉS

*Abies magnifica* ; analyses d'inventaires forestiers ; mortalité des arbres ; pathologie forestière

### NOMENCLATURE

Little (1979) for trees; Wood et al. (2003) for insects and pathogens

### Introduction

Decline in the health of red fir (*Abies magnifica*) in the central Sierra Nevada was hypothesized after observations by US Forest Service Forest Health and Protection aerial and ground surveys in 2005

(B. Bulaon & M. MacKenzie, unpublished observations, 2007). In 2009 and 2010 the Forest Health and Protection aerial survey found significant increases in both red and white fir (*Abies concolor*) mortality (Z. Heath et al., unpublished observations,

2010), while van Mantgem et al. (2009) noted increases in the rates of mortality in older forests across California. The observed mortality and hypothesized decline in red fir is assumed to be caused by an interaction of biotic, abiotic and anthropogenic factors including climate change.

The factors contributing to red fir decline may include air pollution, forest management practices, drought (especially decreased snowpack) and changing fire regimes (especially increased severity); the latter two have been associated with climate change (Sugihara et al. 2006). Additional biotic factors, which vary more on a stand by stand basis, include Heterobasidion root disease (*Heterobasidion occidentale*), red fir dwarf mistletoe (*Arceuthobium abietinum* f. sp. *Magnificae*), Cytospora canker (*Cytospora abietis*), fir engraver beetle (*Scotylus ventralis*; Coleoptera: Scolytidae) and occasionally Armillaria root disease (*Armillaria ostoyae*) (US Forest Service Forest Health and Protection personnel; B. Bulaon, M. MacKenzie, J. Pronos & P. Cannon, personal communications, 2009). The biotic factors are often assumed to be more prevalent in older stands and stands that have experienced tree cutting, where exposed stumps can be an infection pathway.

Fire is an important cause of tree mortality in this region, although fire frequency in the red fir zone began decreasing around 1850 and decreased dramatically since the policy of fire suppression became the norm (Sugihara et al. 2006). However, the annual burned area by wildfire increased significantly in Sierra Nevada high-elevation forests between 1984 and 2004 (Miller et al. 2008). Although highly variable throughout the red fir zone, small (<500 ha) fires of moderate to low severity are more common than large or intense fires, with median fire-return intervals ranging between 12 and 69 years (Sugihara et al. 2006; Newburn, unpublished observations, 2007). The upper montane red fir forest of northern California experiences the highest amount of snowpack of any vegetation type in California (Barbour et al. 1991; Potter 1998), but the snowpack is forecast to diminish in this century (e.g., Dettinger et al. 2004; Stewart et al. 2004). Approximately 80% of precipitation in the red fir range falls as snow and the majority occurs in winter (December–March), with summers being dry (Burns & Honkala 1990). The average elevation of freezing level during winter storms is correlated with the transition from white fir at lower elevations to red fir at higher elevations (Barbour et al. 1991). This association with snowpack, and the (probably changing) elevation where rain historically has turned to snow during the winter, makes red fir an ideal

species for examining ecological change resulting from climate change.

The rate of tree mortality is an obvious attribute of forest health (Castello & Teale 2011; Edmonds et al. 2011) but it is difficult to measure and assessing change requires long-term datasets. A recent analysis of selected old forests based on long-term datasets in the western United States reported that tree mortality rates are increasing across the region and in California they have nearly doubled from ~1% to ~2% from the 1980s to the 2000s (van Mantgem et al. 2009). Mortality rates for *Abies* species across the west more than doubled from <0.5% to nearly 2%. van Mantgem et al. (2009) consider climate change, especially warming temperatures, to be the most important factor influencing mortality in old forests of the western United States.

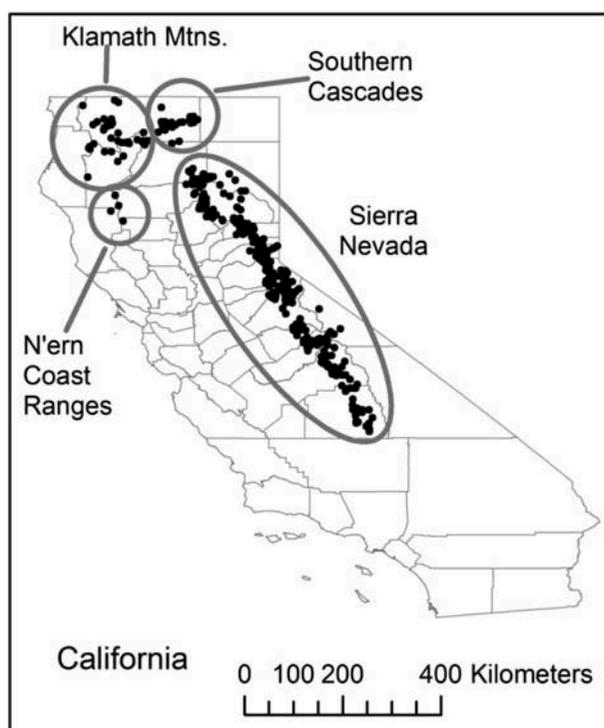
In addition to reporting change in mortality rates, stage-transition models (Lefkovich 1965) can be useful for estimating the current rate of population increase or decline (e.g., van Mantgem et al. 2004). Forest inventory and analysis (FIA) plots provide an extensive, systematic dataset for analysis of tree mortality and condition trends (Bechtold & Patterson 2005). Owing to recent changes in FIA to sampling all ownerships and to a nationally-consistent design, data on tree survival from remeasurement data are still incomplete in the west. However, analyses of the abundance of recently-dead trees as an index of mortality have been fruitful (e.g., Shaw et al. 2005; Bell et al. 2014). We used FIA data in California to investigate the rate of mortality and changes in tree condition of red fir, and the associated species white fir, lodgepole pine (*Pinus contorta*) and Jeffrey pine (*Pinus jeffreyi*) in order to better understand the causal mechanisms of red fir mortality and determine whether forest health was declining.

The questions asked in this study were as follows: what are the current forest health conditions and characteristics of red fir forests in California; is mortality increasing in red fir and at what rate; and what are the statistical and spatial patterns of red fir mortality and potential causal factors?

## Methods

### Study area

The study area is the range of red fir in California, which includes the Sierra Nevada, the Klamath Mountains, the southern Cascades and the higher reaches of the northern Californian Coast Ranges (Figure 1). The mean elevation of red fir follows a



**Figure 1.** Distribution of red fir plots in California.

latitudinal gradient with a significantly higher mean elevation at the southern end of the range than along the Oregon border, with a California-wide mean of 2206 m. In much of northern California, red fir exhibits a slight morphological difference (longer cone bract scales that are visible on closed cones) and is known as Shasta red fir (*Abies magnifica* var. *shastensis*) (Burns & Honkala 1990). Red fir in the southern Sierra has been shown to share some traits with Shasta red fir, and is now classified as *Abies magnifica* var. *critchfieldii* (Lanner 2010). In this study, red fir, the southern Sierra population of red fir and Shasta red fir were treated as one (referred to as “red fir”) because differentiating between the varieties in the field is difficult if no cones are easily visible for close examination (which is common), and because the morphologic differences are slight. Red fir (var. *shastensis*) grows in southern Oregon, but this study only examined red fir in California where the majority of its range lies. Red fir can grow in mixed-conifer stands as well as monodominant stands, and is most commonly found in association with Jeffrey pine, white fir and lodgepole pine. These three tree species’ ranges differ from red fir in some locations, and thus the comparison of red fir conditions with these species expanded the study area for some portions of the study.

### Sample design

Data on tree and forest stand conditions were used from different forest inventories conducted in California since the 1990s. Field-collected data used in this analysis were collected using standard USDA Forest Service inventory field protocols. FIA plot locations are systematically randomized (hexagonal grid over entire study area with 1 random plot location in each 2430 ha hexagon), averaging one plot every 5.2 km (Bechtold & Patterson 2005; Christensen et al. 2008). This nationally standardized inventory was implemented in 2001 in California and samples all land ownerships including private, National Park Service and wilderness areas, and is referred to in this paper as the “annual” inventory. The standard FIA measurement cycle in the western United States is 10 years, with one-tenth of the plots in a region measured every year in a spatially-balanced design. We used a complete cycle of measurements (2001–2010) that allowed for a complete “snapshot” dataset of current statewide forest stand conditions and gave us optimal coverage for spatial interpretation ( $n = 304$  red fir plots).

In California, Pacific Southwest Region (Region 5) national forests accelerated the cycle to install all plots on their lands in the first five years of annual inventory (i.e. measuring half the plots “early”) which gave us a “remeasured once” change dataset at the tree-to-tree scale on this subset of National Forest System (NFS) plots ( $n = 114$  red fir plots). A further subset of the remeasured plots had also been measured by an earlier NFS inventory in the 1990s (referred to here as the “periodic” inventory), which provided a “remeasured twice” dataset to estimate change over a longer time period ( $n = 86$  red fir plots), even though the plot design differed from that used in the subsequent inventory. Although the remeasured data only cover NFS lands, most (92%) of the red fir plots in the all-owner snapshot dataset were on NFS land.

### Plot measurements

Lands within the FIA plot footprint were classified as accessible forest land, non-forest land, water or non-sampled (due to lack of landowner permission to gain access or hazardous conditions). Many plots contained multiple conditions, in which case boundaries were defined. Accessible forest areas could be further sub-divided by protected status, owner group, forest type, stand size class, regeneration status or stand density. Information on stand structure and age, soil

depth, the presence of stumps and the disturbance and management history was recorded. To ensure a sufficient sample on each plot for examining condition variables such as stand density and stand age, analyses were restricted to plots where one forested condition class made up 60% or greater of the total plot area.

The current annual inventory sample consists of nested plot sizes of 0.10, 0.02 and 0.001 ha around four points within a 1 ha area, on which live and dead trees >61, 12.7–61 and 2.54–12.7 cm diameter at breast height (DBH) were measured, respectively. In the periodic inventories of the 1990s, the national forests used variable radius sampling on five points in a diamond around the center point, which coincided with the center of the annual plot. The differences in plot design precluded analyses of growth and mortality on individual trees from this time period. However, plot-level sums of recently-dead mortality from this time period were used.

In the annual inventory, individual damages were recorded on each tree. Root disease, bark beetles and branch flagging were recorded with severity ratings. Mistletoe presence was recorded using the standard dwarf mistletoe rating system (Hawksworth & Weins 1996). Presence of fire scars or other physical damage (e.g. broken tops) was recorded. Destructive sampling was not permitted on FIA plots and although most pests and pathogens could usually be identified without destructive sampling, there were times when identification was hindered by this restriction. Although field crews received some training by pathologists, errors of omission occurred and repeatability based on independent remeasurement of a subset of plots was low, particularly for root diseases.

Climate data for each inventory plot were generated by intersecting plot locations with estimates of 18-year climate means from Daymet (Thornton et al. 1997). The primary variables used in our analyses were mean annual temperature, August maximum temperature and mean annual precipitation, and SMRTP, a summer moisture stress index that is the ratio of mean summer (May–September) temperature (°C) to mean summer precipitation (Ohmann & Gregory 2002).

### Analysis

Plots were selected for analyses of each species of interest if 20% or more of the standing live and dead tree basal area was comprised of that species (e.g. for red fir these were referred to as “red fir plots”). The aim was to focus on plots where red fir (or other species of interest) was a significant part of the stand

composition and to avoid plots where its presence was insufficient to draw inference. To assess the impact of fire, analyses were conducted with and without plots burned within 30 years of the most recent measurement, referred to as “burned.”

One index of mortality and forest change used in this study was “recently dead.” For each of the focal species on selected plots, the proportion of standing tree basal area that consisted of recently-dead trees (decay class 1 and 2) was calculated for each time period. The quadratic mean diameter (QMD) was calculated from the DBH of trees in dominant and co-dominant crown classes. All analyses weighted trees by the sample area on the plot for the respective tree size classes (expressed as trees per hectare). Plot-level measured and calculated variables used in one or more analyses are presented in Appendix Table A1.

A damage index of insect and disease impacts was created for red fir and white fir by assigning points to the different damages known to affect the species (Appendix Table A2), which were summed by tree. For example, a tree with a dead top (1 point) and a dwarf mistletoe rating of 3 (1 point) would have a damage index score of 2. Although the frequency of the damages differed, the same damages occur on white fir, making this rating system appropriate for use on white fir for comparison. The damage index could not be used on Jeffrey pine or lodgepole pine because the damage types they routinely experience differ from those of red and white fir. The index was designed to capture the overall health of a tree even if the specific damaging agent coded was not reliable.

Associations between proportions of red fir that were recently dead and the explanatory variables (Appendix Table A1) in the complete cycle of measurements (2001–2010) snapshot dataset were estimated with generalized linear models:  $\hat{Y}_j = \alpha + \beta_1 X_{1j} + \beta_2 X_{2j} + \dots + \beta_k X_{kj}$  (where  $j$  is the plot number and  $k$  is the number of explanatory variables), with a logit transformation of recently dead proportion  $\hat{Y}_j = \{\ln[p_j(1-p_j)^{-1}]\}$  for the response variable (S-Plus 8.1; TIBCO Spotfire S+, Palo Alto, CA, USA). Model fit was assessed with stepwise selection (producing an Akaike’s Information Criterion (AIC) value for each potential model) (Ramsey & Schafer 2002). All variables were plotted, transformed, displayed spatially and checked in order to build the optimal model. Simple tests comparing plot-level recently dead among species, and changes in recently dead between measurements, were conducted with Welch’s  $t$  statistic on overall means and standard errors, using Bonferroni correction to maintain a type I experiment-wise error rate of  $\alpha = 0.05$ . Moran’s  $I$  test was used to test for spatial autocorrelation.

Mortality and basal area growth by species were calculated from the remeasured-once plots. Mortality was calculated using the density of trees that died during the remeasurement interval, standardized with a compound interest formula to enable comparison of rates among studies with different remeasurement intervals (Sheil et al. 1995). Mortality rates for the species of interest were assessed by tree size class for the population as a whole using the ratio estimator (estimated density of mortality trees/trees alive at time 1) for a post-stratified inventory (equations 4.16 and 4.17 in Bechtold & Patterson 2005); plots were classified into inventory strata defined by ownership and vegetation classes derived from satellite imagery (Dunham et al. 2002) (as opposed to a pre-stratified inventory where the strata determine the sample intensity). Comparisons of mean mortality rates and standard errors among species were carried out with the Bonferroni method. An analysis of variables associated with individual red fir tree mortality was also performed ( $n = 2387$ ). This analysis used non-linear mixed models with a logit response for mortality, while accounting for the lack of independence of trees measured on the same plot with a random-effects statement, in matrix notation:  $\hat{Y} = \beta^*X + \mu^*Z + \epsilon$  (where  $\beta$  is the vector of fixed effects,  $\mu$  is the vector of random (plot) effects with  $E(\mu) = 0$ , and  $\epsilon$  is the vector of random errors). The number of years between measurements was included as a factor in the model (median = 5 years; mean = 4.4), and the best model selected using AIC (SAS Institute Inc., Cary, NC, USA). The finite rate of population increase ( $\lambda$ ) was calculated from a Lefkovich matrix of transitions between tree size classes (i.e. the proportion of individuals in a size class that remained in the same class or grew into the next class during the five-year measurement interval for the remeasured-once dataset). Tree size classes were 2.5–6.4, 6.4–12.7, 12.7–20, 20–40 and >40 cm DBH to approximate those used by van Mantgem et al. (2004). The largest size class was assumed to represent the reproductive adults that were responsible for new recruits into the smallest size class. Five hundred bootstrap samples (unrestricted random sampling with replacement using the SURVEYSELECT procedure in SAS; SAS Institute 2008) from all of the

trees (with their transitions between classes) for each species were created,  $\lambda$  was calculated for each sample using matrix algebra of the transition table (IML procedure in SAS), and the 2.5 and 97.5 percentile values were selected to define the confidence intervals for the estimate of  $\lambda$ .

## Results

### Species comparisons

In the 30 years prior to each plot's most recent measurement, 21% of red fir plots, 24% of Jeffrey pine plots, 37% of white fir plots and 9% of lodgepole pine plots experienced at least one harvest treatment. The mean stand age by species reflected these trends, with lodgepole pine having the oldest mean stand age and white fir the youngest (Table 1). The percentage of plots with stumps roughly captured the presence of past treatments (some stumps may be a result of incidental cutting). Jeffrey pine plots had the highest fire occurrence followed by white fir, red fir and lodgepole pine. A key difference between red fir and the three other species was that 44% of red fir stands were made up of predominantly large, old ( $\geq 150$  years) dominant and co-dominant trees where the average QMD exceeded 61 cm. Only 19% of lodgepole pine plots fell into this category, compared with 24% of Jeffrey pine and 27% of white fir plots. This contributed to red fir plots having significantly higher mean live basal area than the other species (Table 1). Nineteen percent of the red fir trees contained dwarf mistletoe. Jeffrey pine, white fir and lodgepole pine all had dwarf mistletoe infection totals under 10%.

During the 15 years covered by the remeasured-twice plots in the study, all species showed a trend of increasing mean recently dead proportions (Table 2). Jeffrey pine showed the greatest increase. With the exception of lodgepole pine, these increases were significantly different from zero ( $p < 0.05$ ). Removing burned plots decreased recently-dead proportions for all species noticeably, and resulted in smaller increases over time for red fir and Jeffrey pine, and no increases for white fir and lodgepole pine.

**Table 1.** Characteristics of plots dominated by key species of interest (and number of plots in snapshot dataset).

Species	Elevation (m)	Mean stand age (years)	Plots containing stumps (%)	Mean live basal area of species ( $\text{m}^2 \text{ha}^{-1}$ )	Trees with dwarf mistletoe (%)	Plots burned in prior 30 years (%)
Red fir ( $n = 304$ )	2206	145	37%	93.21	19	22
Jeffrey pine ( $n = 415$ )	1944	113	50%	46.17	8	37
White fir ( $n = 833$ )	1773	111	61%	69.37	7	32
Lodgepole pine ( $n = 242$ )	2544	157	21%	73.58	5	17

**Table 2.** Changes in mean proportion of tree basal area in recently-dead trees by species for the remeasured-twice subset of plots, with and without plots that burned in the 30 years prior to annual measurement 2.

Species plot type	Periodic measure (1990s)	SE	Annual measurement 1 (2001–2005)	SE	Annual measurement 2 (2006–2010)	SE
<b>All plots</b>						
Red fir ( <i>n</i> = 86)	0.079	0.013	0.094	0.017	0.130	0.022
Jeffrey pine ( <i>n</i> = 97)	0.013	0.005	0.059	0.019	0.108	0.026
White fir ( <i>n</i> = 201)	0.101	0.010	0.106	0.013	0.155	0.018
Lodgepole pine ( <i>n</i> = 61)	0.077	0.012	0.083	0.019	0.102	0.023
<b>Unburned plots</b>						
Red fir ( <i>n</i> = 78)	0.077	0.014	0.084	0.014	0.095	0.013
Jeffrey pine ( <i>n</i> = 71)	0.006	0.002	0.024	0.013	0.040	0.015
White fir ( <i>n</i> = 173)	0.101	0.011	0.092	0.011	0.113	0.014
Lodgepole pine ( <i>n</i> = 58)	0.077	0.013	0.087	0.020	0.073	0.016

Note: SE, standard error.

Other than a cluster of low values in the dwarf-mistletoe-free Mt Shasta area, there was little spatial pattern in red fir recently-dead proportions other than the area burned by the 2008 lightning-ignited Trinity Alps Complex fires in northwestern California. The data were found to be not spatially autocorrelated using Moran's *I* test ( $I = 0.01$ ,  $p = 0.05$ ). There were also no spatial patterns in stand condition or stage of development, treatment history, percent red fir (of each plot), south-facing plots, fire history, basal area density, QMD and soil rooting depth. Mean dwarf mistletoe rating by plot was spatially variable, other than in the Mt Shasta area where it was virtually non-existent.

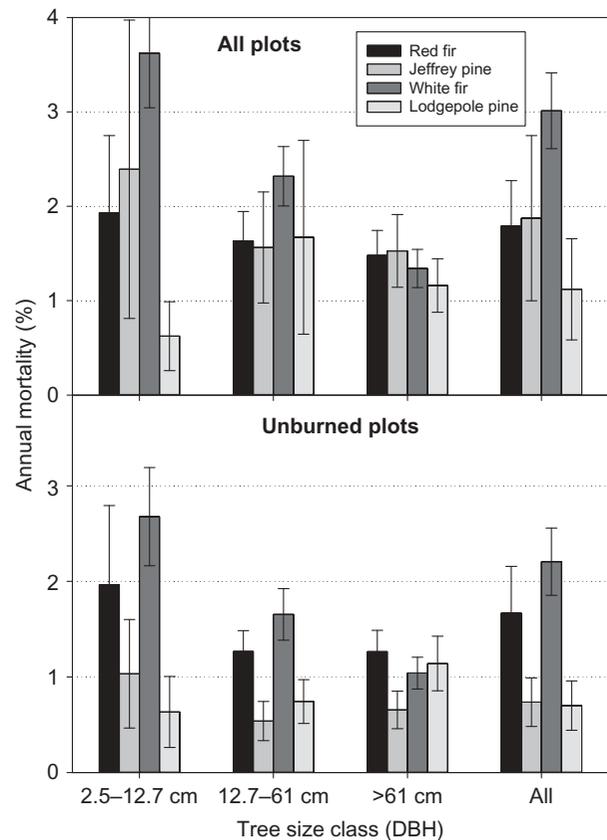
### Mortality

Annual basal area mortality was greater than growth for all species (Table 3). Because mortality did not occur on many plots, the differences in basal area mortality among species were not statistically significant ( $p < 0.05$ ) while differences in growth were. Mortality was lower when burned plots were excluded, with basal area growth exceeding mortality for white fir and Jeffrey pine, but not for red fir and lodgepole pine. Annual individual-tree mortality rates also varied by species and burn history, with mortality of white fir

**Table 3.** Mean annual basal area growth and mortality ( $\text{m}^2 \text{ha}^{-1}$ ) for remeasured-once plots with and without plots experiencing significant fire in the 30 years prior to measurement.

Species plot type	Mean growth	SE	Mean mortality	SE	Net change
<b>All plots</b>					
Red fir ( <i>n</i> = 114)	1.09	0.08	-1.53	0.29	-0.44
Jeffrey pine ( <i>n</i> = 134)	0.71	0.08	-0.85	0.31	-0.14
White fir ( <i>n</i> = 281)	1.24	0.06	-1.34	0.16	-0.11
Lodgepole pine ( <i>n</i> = 84)	0.47	0.04	-0.98	0.42	-0.52
<b>Unburned plots</b>					
Red fir ( <i>n</i> = 105)	1.11	0.08	-1.14	0.16	-0.03
Jeffrey pine ( <i>n</i> = 101)	0.77	0.09	-0.29	0.09	+0.47
White fir ( <i>n</i> = 239)	1.33	0.06	-1.09	0.15	+0.25
Lodgepole pine ( <i>n</i> = 80)	0.48	0.04	-0.54	0.17	-0.07

Note: SE, standard error.

**Figure 2.** Mean annual mortality rates (and standard errors) on remeasured annual plots for montane species in California, by tree diameter class and for all and unburned plots.

significantly greater ( $p < 0.05$ ) than mortality of the two pines on unburned plots (Figure 2). Mortality rates of red fir were somewhat lower than those of white fir, with a rate of 1.79% on all plots and 1.67% on unburned plots. Mortality rates generally decreased with increasing tree size, but on unburned plots the mortality rates of the intermediate and largest size classes were similar for red fir, Jeffrey pine and lodgepole pine. As expected, the transition rates of trees to larger size classes declined as size class increased, but survival in the largest size class (assumed to represent

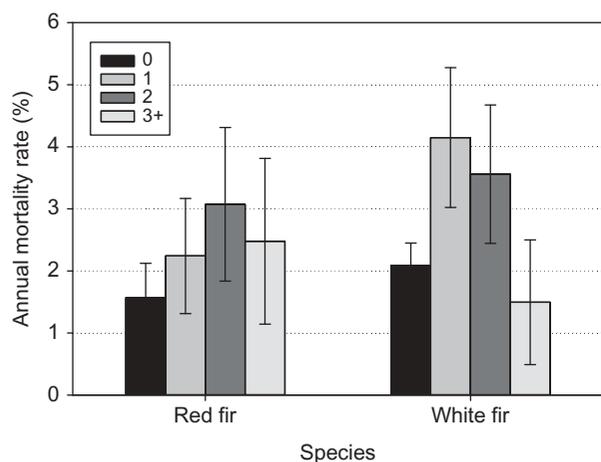
**Table 4.** Five-year transition rates between size classes and finite rate of population increase ( $\lambda$ ) by species for remeasured-once plots, estimated with stage-transition (Lefkovich) matrix models.

Tree size class transitions	All plots				Unburned plots			
	RF	JP	LP	WF	RF	JP	LP	WF
A → A	0.750	0.742	0.889	0.709	0.747	0.742	0.889	0.752
A → B	0.158	0.161	0.074	0.140	0.160	0.161	0.074	0.134
B → B	0.768	0.735	0.951	0.755	0.765	0.800	0.950	0.789
B → C	0.116	0.176	0.024	0.078	0.118	0.200	0.025	0.086
C → C	0.795	0.792	0.846	0.767	0.814	0.835	0.902	0.798
C → D	0.110	0.126	0.043	0.115	0.111	0.131	0.046	0.116
D → D	0.887	0.905	0.868	0.859	0.894	0.939	0.947	0.886
D → E	0.051	0.045	0.022	0.048	0.053	0.043	0.024	0.048
E → E	0.917	0.940	0.962	0.918	0.949	0.973	0.978	0.933
E → A	1.018	0.309	0.506	0.853	1.083	0.360	0.524	0.895
$\lambda$	1.00	0.99	0.98	0.96	1.02	1.03	1.01	0.99
2.5% CI	0.97	0.96	0.96	0.95	0.99	1.00	0.97	0.97
97.5% CI	1.02	1.01	1.00	0.98	1.04	1.05	1.02	1.01

Note: Tree size classes: A, 2.5–6.4 cm; B, 6.4–12.7 cm; C, 12.7–20 cm; D, 20–40 cm; and E, >40 cm DBH. Tree species: RF, red fir; JP, Jeffrey pine; LP, lodgepole pine; WF, white fir. CI, confidence interval.

reproducing trees) and ingrowth into the smallest size class were robust (Table 4). These transition rates resulted in estimated finite rates of population increase ( $\lambda$ ) that were close to 1.0, suggesting that current rates of growth and mortality will result in a stable population. The only exception was for white fir on all plots (i.e. including burns), where the estimated  $\lambda$  of 0.96 was significantly different from 1.0.

Mortality rates on plots that did not experience fire during the remeasured-once period were generally higher for trees with damages recorded at the first measurement than for trees without (Figure 3). The rates were almost double and were significantly different ( $p < 0.05$ ) for red fir trees with a damage index of 2 and for white fir trees with damages indices of 1 or 2. Mortality rates tended to decline at the higher damage



**Figure 3.** Mean annual mortality rates by damage score (0–3+) for red and white fir in stands unburned during the remeasurement period.

index scores; although the sample size was lower, this does suggest that fir trees with many types of damage take longer than five years to die. Tree damage index scores were twice as high for red fir than for white fir, and increased during the remeasurement period from means of 0.22 to 0.37 for red fir, and from 0.13 to 0.19 for white fir. Some of the increase in damage scores may have been due to improved identification of damage agents and effects in the field, as field crew experience and retention increased during this period.

### Causal factors of red fir mortality

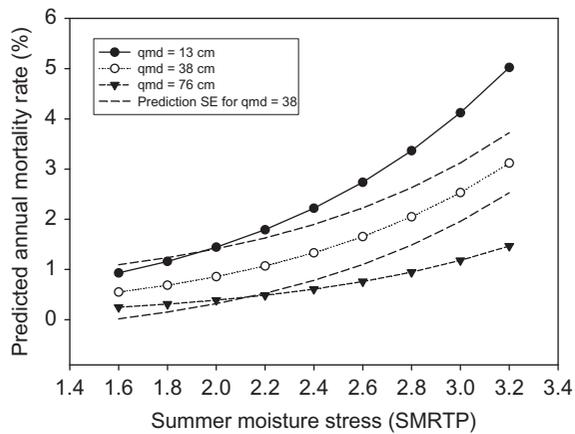
Few of the variables tested for relationships with red fir recently-dead basal area in the annual snapshot dataset were statistically significant. In the best model (i.e. with the lowest AIC value) the dwarf mistletoe rating was positively correlated with the red fir recently-dead proportion (Table 5). Stand basal area was negatively associated with red fir recently dead, probably reflecting that stands experiencing recently high mortality were less dense stands and had a higher proportion of recently-dead red fir trees. The results did not change substantially when the burned plots were removed from the analysis. Dwarf mistletoe was no longer significant when red fir plots in the dwarf-mistletoe-free Mt Shasta area were removed from the analysis. For this latter subset of the data, basal area was negatively associated with the recently-dead variable, as was QMD.

The individual tree logistic mortality analysis of the remeasured-once data found that mortality on unburned plots increased with SMRTP. The most important significant variable in the model was the damage index (positive relationship with mortality), followed by SMRTP (positive) and QMD (negative). Predicted mortality rates increased with SMRTP more rapidly for small-QMD stands than for high-QMD stands (Figure 4). An alternate model using individual damages instead of the damage index found that stem rot, dead tops and foliar damage were also significant predictors of individual tree mortality. It is important to note that these three factors were not causes of

**Table 5.** Causal factors associated with red fir recent dead in the annual snapshot database ( $n = 304$ ), for the best linear regression model (stepwise selection on AIC value).

Coefficient	Value	Standard error
(Intercept)	-0.9483	0.1217
Red fir dwarf mistletoe	0.0992	0.0454
Basal area density	-0.1004	0.0503
QMD	-0.0085	0.0063

Note: Residual standard error: 0.7308 on 300 degrees of freedom. Multiple  $R^2$ : 0.051. Adjusted  $R^2$ : 0.041.



**Figure 4.** Predicted red fir mortality rates by summer moisture stress (SMRTP) for different levels of mean stand diameter (QMD).

mortality but rather reflect effects of biotic and abiotic damage agents as well as symptoms of a declining tree.

## Discussion

### Mortality in the red fir zone

Data to compare the current mortality rates of 1.7 and 2.2% for red and white fir in unburned stands are rare. These mortality rates appear high compared with those reported by Larson and Franklin (2010) for old-growth forests of Mt Rainier National Park, Washington (~1% or less), by Shaw et al. (2005) for pinyon-juniper forests in a severe drought (1.2%), by van Mantgem et al. (2009) for California old growth stands (1.5%) and by Ansley and Battles (1998) for fire-suppressed and unsuppressed Sierran old growth (0.6 and 0.16% respectively). Silver et al. (2013) suggest that studies of mortality must be based on long-term data, and that forest mortality rates fluctuate through time, while van Mantgem et al. (2009) have suggested consistently increasing mortality rates for old-growth forests in western North America. However, mortality of red fir in stands >200 years old was 1.0% in this study (data not shown) and mortality of trees >61 cm DBH in unburned stands was 1.3%, indicating that older trees in the near term are dying at a rate within the bounds of reported studies (Silver et al. 2013).

The net change in basal area and estimates of  $\lambda$  on unburned plots suggest that current populations of all species studied here are stable when recruitment and growth are considered with mortality. Our results complement recent studies that report increased tree mortality in unmanaged old-growth forests in California (van Mantgem & Stephenson 2007; van Mantgem et al. 2009) but our study covered a shorter timeframe.

However, our study was based on a sample across the range of each species, and stands in all stages of development. The interpretation of  $\lambda$  assumes a population in equilibrium and ignores time lags between adults assumed to be currently reproductive and trees growing into the minimum 2.5 cm DBH size class. Changes in basal area of recently-dead trees are affected by mortality rates as well as snag fall rates, and fall rates are affected by tree size and condition. Changes in management, which reduce tree density, can also affect mortality rates and the abundance of recently-dead trees. Caveats therefore exist for all current published studies, and only long-term monitoring using FIA and other long-term datasets will reveal the true patterns in species mortality rates. The different types of evidence presented here suggest that recent mortality in unburned red fir stands may be elevated (mortality rates, increasing recently-dead basal area), but in the short term the mortality has been balanced by growth (basal area change, estimates of  $\lambda$ ). Wildfire has had an impact in these forests, however, and appears to have contributed to a small net decline in tree basal area for all of the species studied.

The initial focus of our work was on the health of red fir trees, but white fir mortality rates were higher (2.2%) than all other species investigated: red fir (1.7%) and Jeffrey and lodgepole pines (0.7% each). The mortality rate appeared to be increasing and is reflected in the increase of recently-dead trees (e.g., Fan et al. 2012). White fir is known to experience significant mortality during drought events associated with fir engraver bark beetles, so that mortality rates would be expected to fluctuate widely. White fir also experienced substantially more fire-related mortality than red fir.

### Factors associated with red fir mortality

The major factors associated with red fir mortality include the red fir dwarf mistletoe – *Cytospora* canker complex, fire, drought, *Heterobasidion* root disease and fir engraver. Red fir dwarf mistletoe was the most significant factor in red fir mortality and decline based on our field observations and statistical analysis. The dwarf mistletoe rating was positively associated with recently-dead red fir. The frequency with which dwarf mistletoe occurred in red fir (19%) was significantly higher than in other species in this study. A major reason red fir dwarf mistletoe is detrimental to red fir health is that it is almost always accompanied by *Cytospora* canker. Although *Cytospora* canker is considered a weak pathogen (Scharpf & Bynum 1975; Goheen & Willhite 2006), our observations indicated that *Cytospora* canker was almost always present (and

often widespread) in trees infected with red fir dwarf mistletoe and was associated with branch flagging and dieback. Cytospora canker is known to enter red fir branches through small wounds in the bark left by dwarf mistletoe shoots and/or insects (Wood et al. 2003), but it is unknown whether it is present in red fir trees that do not contain dwarf mistletoe. Signs or symptoms of Cytospora canker were not observed in red fir trees that did not contain dwarf mistletoe.

van Mantgem et al. (2009) concluded that increased mortality was driven by changes in climate after accounting for non-climatic variables that could potentially cause mortality. While our results do not explicitly support this conclusion, we did show a trend of increasing fire occurrence (and the associated mortality) in red fir as suggested by Westerling et al. (2006) and Miller et al. (2008). This increase in fire occurrence may be associated with climate change. In addition, drought stress was a significant predictor of red fir mortality in this study. Other estimates of moisture stress (e.g., Stephenson 1990) may provide more easily interpretable metrics than the SMRTP index that proved significant in this study and others (e.g., Ohmann & Gregory 2002); although based on more assumptions and calculations than SMRTP, their utility could be evaluated in future studies. The importance of drought stress is consistent with other studies (van Mantgem et al. 2009; Allen et al. 2010) that suggest drought is increasing with climate change. Moisture stress is usually thought to contribute heavily to the mortality of trees and mortality has been shown to be correlated with consecutive years of drought conditions in California (Gaurin & Taylor 2005; Oblinger et al. 2011). Ferrell (1996) explicitly shows that many forest pathogens and insect damage agents are exacerbated by drought stress in California.

Field observations as well as literature (Potter 1998) indicated that *Heterobasidion* root disease was widespread in red fir and white fir forests in California, yet this was not reflected in the 2001–2005 FIA data (Christensen et al. 2008). As a result, FIA root disease data are not currently reliable enough to draw conclusions, although they are improving over time. The presence of *Heterobasidion* root disease in red fir stands is not a new occurrence (Slaughter & Parmeter 1989), but our field observations suggest that it is now becoming more common than the 4% of total live fir trees reported from 1979 to 1980 (Slaughter & Parmeter 1989).

*Heterobasidion occidentale* was found in all but one of the 40 stands we personally visited where there was evidence of past cutting (i.e. stumps), as the disease spreads by spores infecting basal wounds

or recently cut stumps (Woodward et al. 1998). *Heterobasidion occidentale* was found in stumps throughout the Mt Shasta area (where dwarf mistletoe does not occur on red fir) and yet there was very seldom mortality in adjacent trees, as is the norm in most of the red fir distribution range. We did not find a strong statistical association between red fir mortality and the presence of stumps in our study area. This observation suggests that other tree stressors (especially red fir dwarf mistletoe and its associated Cytospora canker) may need to be present in order for *Heterobasidion* root disease-related mortality to reach levels that would warrant concern. Although it seems likely that *Heterobasidion* root disease is significantly less common in red fir stands with no cutting history, the regularity with which it occurs in these stands statewide is unknown. There was little recorded evidence of *Armillaria* root disease in the California FIA plots used in this study, which could be mostly due to measurement protocols.

Fir engraver is known to successfully colonize weakened trees, and is an indicator of tree stress that is usually assumed to be associated with drought. The extensive fir engraver-caused mortality that occurred in northern California in 1977, 1978 and 1987–1992 (Wood et al. 2003) was drought related. However, fir engraver is not usually considered one of the more aggressive bark beetles (Furniss & Carolin 1977), so we do not currently consider it one of the primary causal agents of red fir mortality but, rather, a contributing factor to mortality in already stressed trees. Additional work is needed to accurately determine the amount of fir engraver activity in red fir in California.

Minimal active management is occurring in red fir. In this study only one red fir plot out of 114 had evidence of harvest activities in the preceding five years; prescribed fire in red fir forests is uncommon. Initially it was hypothesized that red fir mortality could be tied to air pollution since the west-side, southern Sierra Nevada is one of the most at-risk forested areas in the entire United States (Bytnerowicz et al. 2003; Campbell et al. 2007; Jovan 2008). Bernal-Salazar et al. (2004) reported a lessening of annual tree ring width in *Abies religiosa* (which inhabits sites with characteristics similar to where red fir occurs) in the Mexico City basin that began in the 1970s, which they suggested may have been caused by air pollution. However, red fir is not believed to be at risk from air pollution in California because true firs are not considered to be greatly affected by ozone pollution (Bytnerowicz et al. 2003), and because red fir grows at a high enough

elevation that the amount of air pollution reaching it is minimal (Jovan 2008). There is a knowledge gap concerning how air pollutants other than ozone may affect red fir. However, there was no spatial correlation between red fir mortality and the west-side southern Sierra Nevada, suggesting that air pollution is not a significant factor in red fir mortality.

### Forest health

Forest health is a values assessment associated with the outlook of the observer. Stands with old, decadent trees may be healthy in some views due to the abundance of dead wood and cavities needed for wildlife. Alternatively these forests may have large amounts of cull, and another view is that these forests are unhealthy and need to be harvested so that young, vigorous, free-to-grow trees could exhibit low individual tree defect and damage. Everyone can agree on individual tree condition, but valuing the health of the forest is complicated (Castello & Teale 2011; Edmonds et al. 2011). However, mortality, rate of mortality and changes in these factors can be used to assess general forest condition in a forest health context with an explicit statement of values. Although wildfire is not generally considered a forest health issue, it is an important agent of mortality in western forests and should be included in any assessment of changes in species abundance and condition over time.

Red fir, white fir, lodgepole pine and Jeffrey pine are clearly threatened by climate change, but current mortality indexes used in this study suggest that mortality amount and rates are not outside the bounds of reported values for other species and forest types. In addition, regeneration and growth have the potential to balance mortality; our stage-transition model (Lefkovitch 1965) and net basal area change results suggest recent changes in populations of red fir and species have been stable. In the near term, therefore, forest health based on mortality analyses seems fair in the upper montane of California. However, wildfire and the abundance of insects and diseases that are exacerbated by seemingly frequently occurring drought conditions make a future of continued stable populations appear far from certain. Long-term monitoring and the continued remeasurement of the FIA plot network is a critical need and continued long-term maintenance of these plots and other long-term datasets will be crucial to understanding changes in forest health in these mountain forests.

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## Appendix 1

**Table A1.** Plot-level variables and definitions used in model selection and description of the annual snapshot characteristics of red fir forests in California.

Response variable	
Red fir recent dead	Proportion of red fir (RF) live and decay class I + II snag basal area on plot that is dead (snags)
Explanatory variables	
Dwarf mistletoe	Mean dwarf mistletoe rating for live RF trees
Number of trees with dwarf mistletoe	Number of live RF trees with mistletoe rated
Red fir percentage	Percent of live and class I + II snag volume on plot that is RF
Basal area density	Basal area density class: <23, 23–46, 46–69 and 69+ m <sup>2</sup> ha <sup>-1</sup>
SMRTP – moisture stress during growing season	Eighteen-year mean ratio of mean temperature (°C) to mean precipitation (natural log, mm), May–September at given plot location (from Daymet)
August maximum temperature	Mean maximum temperature in August (°C) (hottest month)
Mean annual precipitation	Mean annual precipitation (natural logarithm, mm)
Mean annual temperature	Mean annual temperature (°C)
Latitude	Actual latitude
Elevation	Elevation (m)
Land ownership group	Forest service, other federal, state and local government, private
Stand age	Mean stand age of all non-overtopped trees on plot (years)
Slope	Slope (%)
South facing	Indicates whether condition is south facing (135–225°) or not
Soil rooting depth	≤50 cm or >50 cm
Stand condition/stage of development	Not applicable, grass–forb, shrub, open sapling–poletimber, closed sapling–pole–sawtimber, open sawtimber, large sawtimber, old growth. See USDA (2009) for exact definitions
Elevation group	Elevation group (<1800, 1800–2100, 2100–2400, >2400 m)
Stumps	Indicates presence or absence of stumps
Cutting history	Indicates whether logging has occurred <10, 10–30 or >30 years before most recent measurement
Fire history	Indicates whether fire has occurred <10, 10–30 or >30 years before most recent measurement
Trees with fire scars	Proportion of RF trees with fire scars coded
QMD	Quadratic mean diameter of mainstand trees (cm)
Section name	Ecoregion section name (Cleland); Klamath Mountains, Northern California Coast Ranges, Sierra Nevada, Southern Cascades

**Table A2.** Damage index points assigned for individual damages coded on red and white fir trees.

Damage agent and severity	Points
Dwarf mistletoe rating (Hawksworth & Weins 1996)	
2–4	1
5–6	2
Rotten/missing cull	
20–50% of bole volume	1
>50% of bole volume	2
Bark beetle present	1
Root disease – general, Annosus, or Armillaria	
Present but no visible crown deterioration	1
visible crown deterioration, reduced terminal growth and/or Stress cones	2
Stem decay present	1
Foliar pathogens affecting 20% or more of foliage	1
Broken or missing top	1
Dead top	1
Unknown, impacting 20% or more of tree	1