forest ecology

Patterns and Drivers of Recent Tree Mortality in Diverse Conifer Forests of the Klamath Mountains, California

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Tree mortality rates are increasing in North America, yet our understanding of the processes affecting mortality across different tree species is limited. We assessed drivers of recent mortality in the Russian Wilderness, an area in the Klamath Mountains (California, USA) with the highest conifer diversity on record. We surveyed 3446 trees across 142 plots and document widespread die-off of Shasta red fir (*Abies magnifica* var. *shastensis*), a common species across this area, and notably high levels of mortality for subalpine fir (*A. lasiocarpa*) and lodgepole pine (*Pinus contorta* var. *murrayana*). Both fir species were susceptible to Wien's dwarf mistletoe (*Arceuthobium abietinum* subsp. *wiensii*), and for Shasta red fir, mistletoe rating was positively correlated with the proportion of trees with fir engraver beetle (*Scolytus ventralis*). Shasta red fir mortality increased with stand density, and in plots with larger recent increases in minimum winter temperature. We also document mortality and levels of pests and pathogens for nine additional conifer taxa, including several species with limited distributions. Our study highlights the complexity of climate, stand density, pathogens, and insects as they relate to tree mortality across different taxa, and is the first to investigate the current die-off of Shasta red fir.

Keywords: bark beetles; dwarf mistletoe; fir engraver; red fir; tree mortality

Tree mortality in western North America has increased steadily throughout the past century and is predicted to continue at an elevated rate with climate projections of rising temperatures and prolonged droughts (Allen et al. 2015). Recent tree mortality has been especially notable in California; for example, an aerial survey in May 2016 estimated that 36 million trees died in 2016, bringing the total to 102 million dead trees within the past 10 years (Moore and Heath 2016). As a natural process in forests, tree mortality occurs at both background levels and in regional die-off events, in the latter case where >10% of the dominant canopy trees die in a pulse of mortality (Anderegg et al. 2013). Examples of tree taxa that have experienced recent die-offs include whitebark pine (*Pinus albicaulis* Engelm.) in the eastern Sierra Nevada due to outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Millar et al. 2012) and Port Orford cedar (*Chamaecyparis lawsoniana* [A.

Murray bis] Parl.) in northern California and southern Oregon due to the spread of a non-native fungal pathogen, *Phytophthora lateralis* Tucker & Milbrath (Jules et al. 2014). Determining where and why these sudden mortality events take place, and how they disproportionately affect certain tree taxa, are central questions in the study of forest processes.

Tree mortality is a complicated process that typically involves a suite of endogenous and exogenous factors (Franklin et al. 1987). Manion's (1991) "decline disease spiral" is one framework that describes the interaction of predisposing, inciting, and contributing factors that can lead to the progressive deterioration and death of trees within a stand. For example, predisposing factors such as poor site conditions or high competition may make trees more vulnerable to inciting factors such as regional drought, which make trees highly vulnerable to wood-boring insects or fungal pathogens as the

proximal agent of mortality (Franklin et al. 1987). In recent years, climatic stress from warmer temperatures and prolonged periods of drought have been linked to increases in both background mortality and episodic die-offs (van Mantgem and Stephenson 2007; Allen et al. 2010, 2015). In extreme cases, tree death can occur from carbon starvation and/or hydraulic failure (McDowell et al. 2011). Recent episodic tree mortality has also been linked to the indirect effect of climate on bark beetles (Coleoptera: Scolytinae), a large sub-family that includes several important pests on conifers of North America (Bentz et al. 2010). Since the life histories of bark beetles are tightly linked with temperature, slight changes in temperature can have profound effects on survival, reproduction, timing of emergence, and length of the life cycle (Bentz et al. 2010). Moreover, many bark beetles, especially those that specialize on dying trees, are more attracted to drought-stressed trees because of physiological changes that make them less resistant to bark beetle attack (Kolb et al. 2016). Bark beetle populations are typically maintained at low (endemic) levels in forested stands, but population outbreaks can occur when conditions favor beetle survival and reproduction and/or decrease tree vigor (Christiansen et al. 1987).

Our study was motivated by a recent observation of widespread die-off of Shasta red fir (*Abies magnifica* var. *shastensis* Lemmon) in the Klamath Mountains of northern California (USA). The Shasta red fir variety of the red fir complex (*A. magnifica* A. Murray) is a hybrid between California red fir (*A. magnifica* var. *magnifica* A. Murray) and a more northern species, noble fir (*A. procera* Rehder) (Oline 2008). Throughout their range, red fir typically inhabits upper-elevation (>2000 m) mesic slopes with substantial winter snow (Meyer 2013). Red fir forests provide several ecosystem services, including carbon storage, erosion control, and habitat for many animal species, including American marten (*Martes caurina*). Mortality in the red fir complex (i.e., *A. magnifica*) has received some attention in the past decade, but only one published study (Mortenson et al. 2015) has assessed recent (up to 2010) levels of mortality. Bulaon and Mackenzie (2007) first reported declines in California red fir health in the central Sierra Nevada in 2005, and subsequent USDA Forest Service Region 5 Forest Health Protection aerial detection surveys have detected increases in mortality in 2009, 2010, and 2014 (Heath et al. 2009, 2010, 2014). Similarly, forest health entomologists and pathologists have described a disease complex primarily affecting Shasta red fir in the Shasta-Trinity National Forest in northern California since 1982 (Kliejunas and Wenz 1982, Angwin 2010). Proposed mechanisms for the decline in red fir health include decreased snowpack, warmer temperatures, stand density and age (related to fire exclusion), and increased pests and pathogens, including dwarf mistletoe, canker-forming fungi (*Cytospora* spp.), root diseases (*Heterobasidion occidentale* Otrosina & Garbel*., Armillaria ostoyae* [Romagn.] Henrik), and fir engraver (*Scolytus ventralis* LeConte) (Meyer 2013). Shasta red fir has a much smaller and isolated range than either California red fir or noble fir, and has always been less studied. To date, very little is known about the extent or cause of recent mortality of Shasta red fir in the Klamath Mountains.

The Klamath Mountains, which extend from southern Oregon into northwestern California, are composed of steep and complex terrain that harbor exceptional floristic diversity (Skinner et al. 2006), including the highest diversity of conifer taxa in the world (Sawyer and Thornburgh 1974, Kauffmann 2012). Similar to other regions in California, recent aerial surveys have detected increasing trends in tree mortality in the Klamath Mountains attributed to several years of exceptional drought (Heath et al. 2014, Moore et al. 2015); however, unlike other large mountain ranges, including the Sierra Nevada and the Coast Ranges, there have been far fewer empirical investigations of large-scale die-offs in the Klamath. We investigated patterns of recent tree mortality in the Klamath region by revisiting a series of plots first established by John Sawyer and Dale Thornburgh (Humboldt State University) in 1969 in a study designed to describe the region's vegetation and document the exceptional conifer diversity of this region (Sawyer and Thornburgh 1974). Our study had two primary objectives. First, we sought to characterize the current status of recent tree mortality and mortality agents across a wide range of conifer species in the Klamath Mountains to determine if recent mortality events observed in western North America are occurring in this understudied area, and to better understand how tree taxa are differentially affected by recent drought and other regional conditions. The second main objective was to quantify the level of Shasta red fir mortality and to better understand what endogenous and exogenous processes are contributing to recent mortality.

We hypothesized that if mortality was related to host-specific pests or pathogens, we would see evidence of increased mortality and biotic infestation in the three species of fir that co-occur in this

Management and Policy Implications

Our study identifies a mortality event for Shasta red fir (*Abies magnifica* var. *shastensis*) caused by Wien's dwarf mistletoe (*Arceuthobium abietinum* subsp. *wiensii*), a canker forming fungi (*Cytospora*) and fir engraver beetle (*Scolytus ventralis*). Notably, these mortality agents are not affecting white fir (*Abies concolor*), a lower elevation, more drought-tolerant fir species in this region. We document high recent mortality for a rare conifer species, subalpine fir (*Abies lasiocarpa*), a species occasionally susceptible to Wien's dwarf mistletoe and fir engraver, and we found possible evidence of balsam wooly adelgid (*Adelges piceae*), an invasive sap-feeding insect. Further investigation and close monitoring is needed to better understand the population dynamics and health of subalpine fir. We found white pine blister rust (*Cronartium ribicola*), an invasive fungal pathogen, on a few scattered whitebark pine (*Pinus albicaulis*) and western white pine (*Pinus monticola*) in our study area. We recommend continued monitoring of all 5-needle pines in this region. Our study area falls within a remote wilderness area where silvicultural treatments to improve the health of Shasta red fir stands would be challenging to implement. In heavily infested stands, the majority of standing Shasta red fir trees will almost certainly die within a few years, and the saplings in the understory are so severely infested with mistletoe that they will not survive to maturity. Allowing wildfire in these stands may be the only way to reduce the disease complex from spreading; however, early seral, shade-intolerant species are likely to in-fill gaps and we can expect mixed species stands in some places previously dominated by Shasta red fir. In the few places where there is road access and mistletoe is not yet prolific in the understory, overstocked stands could benefit from selective thinning, targeting trees that are weakened by dwarf mistletoe and *Cytospora* infestation. If silviculture treatments are applied, managers should carefully monitor stumps for fungal root rot. If no action is taken and wildfire does not burn in this area, the health and vigor of the Shasta red fir stands will continue to deteriorate, and we can expect to see a change in community composition in these forest types.

region (Shasta red fir, white fir [*Abies concolor* (Gord & Glend.) Lindl], and subalpine fir [*A. lasiocarpa* (Hook.) Nutt.]). On the other hand, if mortality was primarily related to recent drought conditions, we would observe high levels of mortality and evidence of drought stress in a wide array of conspecifics that occupy the upper montane zone (for example, lodgepole pine [*Pinus contorta* var. *murrayana*, Loudan], western white pine [*Pinus monticola* ex D. Don.], and mountain hemlock [*Tsuga mertensiana* (Bond. Carrière]). To determine what biotic and abiotic factors are important predictors of tree mortality in this region, we compared tree- and stand-level characteristics of live versus dying and recently dead trees. We also comment on recent mortality levels and mortality agents across several species with limited or endemic distributions, and draw some general conclusions about forest health and tree mortality in this region. By examining patterns of recent tree mortality and mortality agents across a wide array of conifer taxa in this region with exceptional floristic diversity, our study contributes to a greater understanding of the complex array of factors involved in increased mortality in the western United States, and how mortality is disproportionally affecting certain tree taxa.

Materials and Methods
Study Area
Our study area included a 5000 ha area of the Klamath Mountains in northern California known as the Russian Wilderness (41°17′N, 122°57′W) (Figure 1). Elevations within the region range from 760 m to 2498 m, and the geology of the region is almost exclusively granodiorite, an intrusive igneous rock type similar to granite, but with higher concentrations of calcium and sodium. In 2014, 1180 ha of the Russian Wilderness burned in the Whites Fire; however, the rest of the study area has not experienced a wildfire in at least 100 years (Safford et al. 2011). We excluded sampling in any recently burned portions within our study area (Figure 1).

The Russian Wilderness contains the highest density of conifer taxa on record; the wilderness harbors 18 species in a 2.6 km^2 area (1.0 mi^2), an area that has come to be known as the "miracle mile" among regional botanists (Kauffmann 2012). In this study, we focus on eleven of these species for which we have adequate data to assess patterns of mortality (>60 trees) (Table 1). Three of these eleven conifer species (Engelmann spruce [*Picea engelmannii* Parry ex. Engelm.], subalpine fir, and whitebark pine) are considered rare in the Klamath Mountains, and three other species (Brewer spruce [*Picea breweriana* S. Watson], lodgepole pine, and western white pine) are considered relatively uncommon in this region (Table 1) (Kauffmann 2012).

Field Sampling and Data Collection
In summer 2015 we established 142 11.37 m radius (0.04 ha) circular plots within the study area. Plot locations were originally selected in 1969 as part of a study designed to describe the region's vegetation by Sawyer and Thornburgh (1974), and the size of our plots approximate the size of the Sawyer-Thornburgh relevé plots. Sawyer and Thornburgh (1974) collected data in broad cover class values and did not measure or count individual trees; therefore, we do not compare our own data to their 1969 data. Our rationale for using their locations was to capture a wide array of conifer taxa that could not be accomplished using a randomized approach. Fortunately, for the purposes of our study, they selected

plots in what they considered "representative stands," recording detailed notes about disturbance history that typically included fire, flooding, and occasionally insect activity. They often made notes about large dead trees that assisted with relocating plots, but they did not speculate about causal agents of mortality. Although we lack quantitative data about tree mortality from their surveys, we can reasonably assume the stands they sampled in 1969 were relatively healthy, as any widespread die-off or unusually high levels of infestation would have been recorded in their written notes.

At each plot we recorded site characteristics including elevation, slope, aspect, topographic position, and slope configuration. The latter four were used to calculate a Topographic Relative Moisture Index (TRMI) at each plot (Parker 1982), ranging from 0 to 60, with larger values indicating mesic sites. Within each plot, we measured all canopy trees and snags that were ≥7.6 cm diameter at breast height (dbh) and >1.37 m tall and recorded species, status (live, sick, and dead), dbh, and noted all identifiable forest insects and pathogens (see below). We made visual percent cover estimates of crown dieback, defined as recent and abnormal senescence of twigs and branches within the crown. The designation of "sick" was assigned to trees with substantial mechanical and/or biotic damage and poor or very poor crown vigor (Keen 1943), where we believed the tree was very likely to die in the next few years (see Figure 2, for example). All standing dead trees were given a decay rating between 1 and 5 using the classification system of Cline et al. (1980). Recently dead trees were given a rating of 1–2, indicating approximately 18 years or less of decay (recent mortality), while snags given a rating of ≥3 had estimated more than 18 years or decay (older mortality).

All trees (live and dead) were examined for external symptoms of bark beetle infestation and bark beetle–induced mortality by inspecting the lower 2 m of the bole for pitch streams, exit holes of adult beetles, boring dust, and beetle galleries (removing bark when necessary). We identified bark beetle galleries whenever possible. We examined trees for dwarf mistletoe by noting branch tumefactions (swelling), brooming, and aerial shoots. When dwarf mistletoe was present on the tree, the severity of infection was estimated using the dwarf mistletoe rating (DMR) system (Hawksworth 1977). Using this rating system, the tree crown was divided into thirds (top, middle, and bottom) and each third was visually rated for mistletoe infection as a 0 (no infected branches), 1 (<50% of branches infested), or 2 (>50% of branches infested). Ratings were then added together for a final DMR assessment for each tree rating from 1 (light infestation) to 6 (heavy infestation). We also recorded any visible fungal cankers, conks, rusts, or root disease, and identified them to species whenever possible.

Climate
For each plot, we derived climate data from 1951 to 2014 using the California Basin Characterization Model (BCM), a spatially explicit hydrologic response model that downscales climate parameters to a 270-m grid resolution (Flint and Flint 2007, 2012). To generate these fine-scale data, the BCM uses topography, elevation, soils, bedrock geology, and climate data derived from PRISM (Parameter-Elevation Regressions on Independent Slopes Model [Daly et al. 2002]). The climate parameters that we considered in this analysis included cumulative snowpack depth (mm), annual cumulative precipitation (mm), annual climatic water deficit
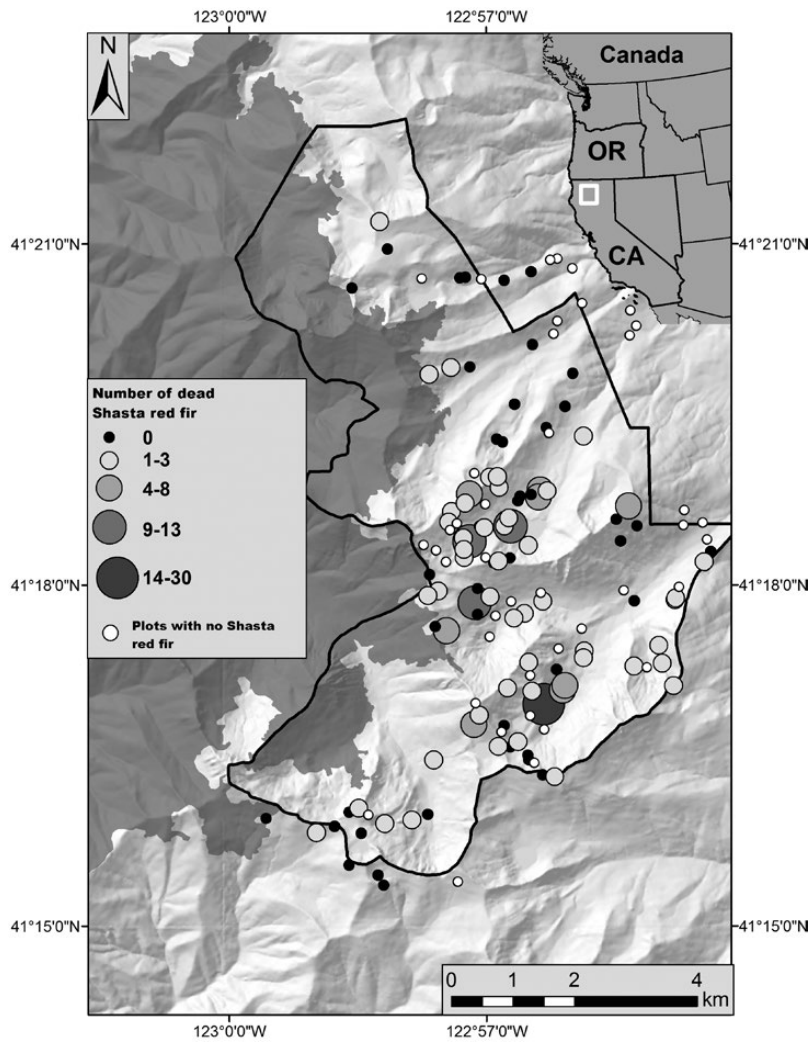
Figure 1. Map of the study area, including the location of the 142 circular survey plots. Size and shading indicate the number of dead Shasta red fir (*Abies magnifica* var. *shastensis*) trees within 0.04 ha plots. The black line denotes the boundary of the Russian Wilderness and the shaded gray area of the left represents the extent of the Whites Fire, which burned in summer 2014.

(CWD, mm H_2O), annual actual evapotranspiration (AET, mm H_2O), annual potential evapotranspiration (PET, mm H_2O), and average annual maximum and minimum temperature (°C). CWD was calculated as the difference between PET and AET. The calculation for PET is derived from solar radiation, air temperature, and the Priestly-Taylor equation incorporating a cloud cover correction,

and the calculation for AET is derived from excess water as determined by a combination of precipitation and air temperature variables (Flint and Flint 2012).

To assess climatic changes over time, we developed linear models for each of the seven climate parameters for two time periods, 1951 to 1980 (hereon called the "reference" period) and the 2004 to

Table 1. Depicts conifer species with > 60 individuals[†] sampled, their elevation ranges, location in the Klamath Mountains relative to their overall range, relative frequency within the Klamath Mountains (adapted from Kauffmann 2012), number of plots containing each species, and total number of individuals sampled.

Common name	Scientific name	Elevation (m)	Relative distribution	Relative frequency	No. trees	No. plots
White fir	*Abies concolor*	1300–2330	Widespread	Common	932	71
Subalpine fir	*Abies lasiocarpa*	1800–2190	Southern range	Rare	68	9
Shasta red fir	*Abies magnifica* var. *shastensis*	1600–2390	Widespread	Common	857	103
Brewer spruce	*Picea breweriana*	1300–2154	Endemic	Uncommon	73	24
Engelmann spruce	*Picea engelmanii*	1540–2028	Southern range	Rare	102	20
Whitebark pine	*Pinus albicaulis*	2154–2450	Widespread	Rare	75	12
Lodgepole pine	*Pinus contorta* var. *murrayana*	1600–2200	Widespread	Uncommon	245	35
Western white pine	*Pinus monticola*	1645–2300	Widespread	Uncommon	147	61
Ponderosa pine	*Pinus ponderosa*	1304–1802	Western range	Common	61	14
Douglas-fir	*Pseudotsuga menziesii* var. *menziesii*	1300–2020	Widespread	Common	130	33
Mountain hemlock	*Tsuga mertensiana*	1637–2450	Widespread	Common	650	68

[†] A total of 3446 trees were surveyed (including seven additional taxa not listed here).

Figure 2. A typical Shasta red fir (*Abies magnifica* var. *shastensis*) stand within the study area with substantial damage from dwarf mistletoe (*Arceuthobium* spp.), *Cytospora*, and fir engraver (*Scolytus ventralis*).

2014 (the "recent" period). We chose 1951 to 1980 as the reference time period because we wanted modeled climate data that overlaps with the modern instrumental record, and 30 years is a standard for calculating a climate normal. We used the past ten years as our recent time period because of estimations based on aerial imagery and local knowledge that the die-off of Shasta red fir in our study area has been noticeable for at least five to seven years, and these disease complexes often develop and worsen over at least a decade-long period (Kliejunas and Wenz 1982). For each climate parameter across each time period, we assessed normality and homoscedasticity of residuals visually, and tested for autocorrelation using the Durbin-Watson test. We then compared each climate parameter between the reference and the recent time period using *t*-tests, adjusted for multiple comparisons. We assessed monthly trends for temperature and precipitation over the entire time period (1951 to 2015) using linear regression models.

Mortality Analyses

To test if tree mortality and levels of biotic infestation (mistletoe and bark beetles) differed significantly among the eleven conifer species for which we had adequate data (>60 trees), we used generalized linear mixed effects models (GLMM) with a binomial distribution, with plot incorporated as a random effect. For all logistic regression analyses, "sick" and recently dead trees were categorized together (see section above). The effect of the fixed factor (species) was evaluated using the Wald Z-statistic test. For each species with significantly higher levels of mortality relative to the other species (subalpine fir, Shasta red fir, and lodgepole pine), we investigated the probability of mortality for each species separately using binomial GLMMs with tree- and plot-level parameters. Tree-level parameters included presence of bark beetles (0/1), presence of mistletoe (0/1), and size (dbh), and plot-level parameters included elevation (m), TRMI, the basal area of the conspecific tree in the plot, the basal area of all other trees in the plot, and the quadratic mean diameter (QMD) of the conspecific tree in the plot. For the climate parameters that changed significantly between the reference and recent

period (minimum and maximum temperature), we calculated the difference in averages for each plot as a variable representing plot-level change in climate. We first eliminated model parameters with low explanatory power by comparing candidate models with different combinations of predictors using Akaike Information Criteria (AIC). To validate the parameterized logistic regression models of tree mortality for each species, we used the area under the receiver operator characteristic (ROC) curve (AUC) values according to Hosmer and Lemeshow (2013) such that AUC < 0.7 represent poor discrimination between live and dead trees, 0.7 < AUC < 0.8 represent acceptable discrimination, 0.8 < AUC < 0.9 represent excellent discrimination, and AUC < 0.9 represent outstanding discrimination. For Shasta red fir, we compared characteristics of stands with and without bark beetles using Wilcoxon-signed rank tests, adjusted for multiple comparisons. All analyses were performed in R version 3.2.2 (R Core Development Team 2016).

Results
Summary of Mortality

We censused a total of 3446 canopy trees >7.6 cm dbh and >1.37 m tall across 142 plots (Table 1, Figure 1), of which 22% were recently dead (snag rating < 2). The average density of trees across all plots was approximately 512 live trees/ha and 74 standing dead trees/ha. Recently fallen dead trees were not included in our census, therefore the actual number of recently dead trees is higher than reported. White fir was the most common tree in our survey, followed by Shasta red fir and mountain hemlock (Table 1). Across all taxa, the proportion of sick and recently dead trees was approximately 12%. Mortality varied significantly by species, with the highest proportion of recently dead and sick trees for subalpine fir (28.3%), Shasta red fir (20.7%), and lodgepole pine (18.0%) (Figure 3, Table S1). Engelmann spruce, ponderosa pine (*P. ponderosa* Lawson & C. Lawson var. *ponderosa* C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) had the lowest levels of recent mortality (Figure 3, Table S1).

We detected signs of bark beetle activity on 13.1% of all trees (live and dead), with significant variation across species. Signs of bark beetle activity were highest for Shasta red fir (34.7%) and whitebark pine (21.3%) (Figure 3, Table S1), and almost all bark beetle galleries on Shasta red fir standing dead trees and recently fallen trees were identified as fir engraver. The proportion of Shasta red fir individuals with signs of bark beetle activity was greatest in size classes >20 cm dbh (Figure S1). We also observed fir engraver galleries on several dead subalpine fir and at least two white fir. We identified mountain pine beetle galleries on approximately ten recently dead lodgepole pine distributed across several plots and western pine beetle (*Dendroctonus brevicomis* LeC.) galleries on a few ponderosa pine. We did not see any evidence of mountain pine beetle infestation on whitebark pine, but we did observe *Ips* spp. galleries on a few individual trees. It should be noted that the majority of trees with signs of bark beetles appeared to have died more than 20 years ago, and we do not see surmounting evidence for a mountain pine beetle outbreak as we see with fir engraver. On a subsequent visit to the study area in July 2017, we found a few subalpine fir individuals (both live and dead) with heavy swelling at the twigs of the nodes ("gouting") that could be indicative of balsam wooly adelgid (*Adelges piceae* [Ratz.]) infestation; however, we did not observe white wooly patches on the tree bole (personal communication, Cynthia Snyder USFS). Balsam wooly adelgid is an invasive, sap-feeding insect that has caused declines within some

subalpine and Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) stands in Oregon and Washington (Overhulser et al. 2004), and has recently been reported in grand fir along the coast in northern California.

Across all species, 14.4% of all live trees contained dwarf mistletoe with significant variation between species. Mistletoe was most abundant for ponderosa pine (24.6% of all trees, Table S1); however, 87% of these individuals came from one plot with a heavy infestation. Mistletoe was prolific on mountain hemlock (21.7% of all trees, Table S1) and Shasta red fir (20.4%) and was widely distributed across plots for both species. For example, over 70% of sick Shasta red fir trees contained dwarf mistletoe. We detected dwarf mistletoe on Shasta red fir individuals in all size classes, but mistletoe infestation was highest in the smallest size class (<20 cm dbh) (Figure S1). Based on field collections and comparisons of dwarf mistletoe from red, white, and subalpine fir in our study area, we believe that all three species are parasitized by Wien's dwarf mistletoe (*Arceuthobium abietinum* subsp. *wiensii* Mathiasen & Daugherty), a locally abundant subspecies of dwarf mistletoe that is morphologically distinct based primarily on its reddish-brown to orange coloration (Mathiasen and Daugherty 2009). Wien's dwarf mistletoe is primarily known to infest red fir, but is occasionally parasitic on white and subalpine fir (Mathiasen and Daugherty 2009). We did not find a high abundance of fungal pathogens or root diseases (such as *Heterobasidion*) across our study area,
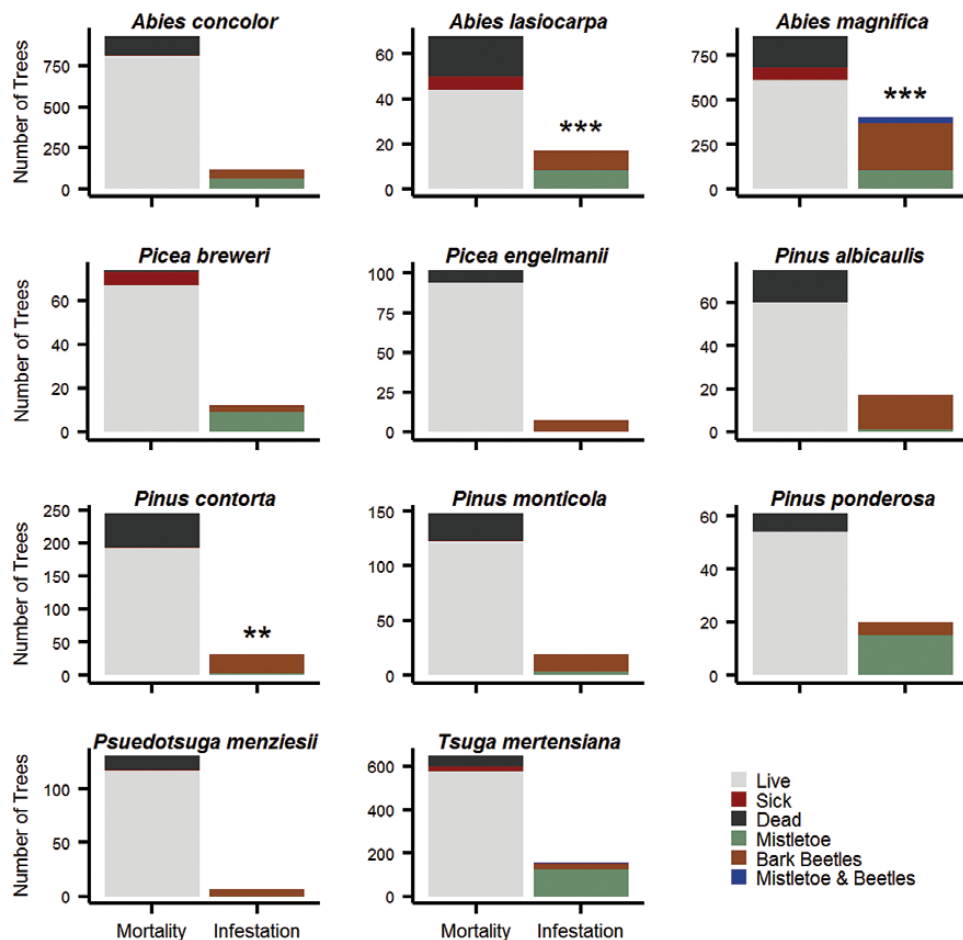

Figure 3. Mortality and biotic infestation for eleven conifer species represented by > 60 individuals. Note that the axis is scaled for each species. Asterisks denote species with significantly high levels of recent mortality relative to other species (Table S1). See methods for description of tree health status and mistletoe and bark beetle infestation.

although we found evidence of white pine blister rust infection on at least two western white pine and two whitebark pine individuals in our study plots.

Of the 142 plots in this study, 103 plots contained at least one Shasta red fir individual (Table 1, Figure 1), 96 plots contained at least five individuals, and 13 plots consisted of old-growth Shasta-red fir forest (Table 3). In the old-growth red fir stands, there was an average of 42 large dead trees per hectare (>30 cm dbh). In plots with at least five Shasta red fir individuals, a total of 10 plots had very high levels of fir engraver beetle infestation (>66% of Shasta red fir individuals with signs of bark beetles), 16 plots had medium levels of infestation (33–65%), and 11 stands had lower levels of infestation (<33%). Plots with bark beetles had a higher average QMD and greater proportion of Shasta red fir individuals (compared to other species) (Table 3). Among the plots with bark beetle infestation, the proportion of trees with bark beetles increased significantly with the average DMR (Figure S3, R^2 = 0.35, P < .001). Notably, in the 59 surveyed stands containing Shasta red fir with no bark beetle infestation, we also found no evidence of dwarf mistletoe, suggesting a very tight correlation between these mortality agents (Table 3).

Climate

We observed no significant difference in annual snowpack, annual precipitation, or climatic water deficit between the reference (1951–1980) and recent time periods (2004–2014) using the BCM modeled climate data (Figure 4, Table S2). Minimum annual temperature increased significantly by approximately 1.6° C between the two time periods, and the increase in maximum annual temperature (0.83° C) was marginally significant (Figure 4, Table S2). Both minimum and maximum temperature increased the most rapidly in January (Figure S4). Despite no trend with precipitation or snowpack, AET increased significantly because of the positive correlation between AET and minimum temperature, and PET also increased due to a positive correlation with maximum temperature (Figure S5). Annual precipitation was at an extreme low of 501 mm in 2013, and annual snowpack was more than 200 mm below average from 2012 to 2014. This is corroborated by evidence from the Klamath snow surveys, indicating that April 1 snow depth has been at historically abnormal lows for the past five years at least (USDA Forest Service 2015).

Mortality Predictors

For all three species with high levels of recent mortality (Shasta red fir, subalpine fir, and lodgepole pine), bark beetles were a significant predictor of mortality (Table 2). Because we did not track trees over time, we cannot distinguish between bark beetles that infested live trees versus those that colonized when the tree was recently dead. Endogenous factors including stand maturity and homogeneity mediated recent Shasta red fir mortality. Bark beetle infestations occurred in more mono-dominant stands with larger, more mature trees (Table 3). Mortality occurred in all size classes (Figure S1); however, the probability of mortality increased with smaller-diameter trees (Table 3). Lodgepole pine mortality was greater in stands with higher basal area (both of lodgepole and other species) and in stands with higher QMD (of lodgepole pine) (Table 2). Although lodgepole pine mortality occurred more often in plots with larger trees (i.e., higher QMD), mortality was more common in small

trees (Table 2, Figure S2). Although bark beetles were a significant predictor of mortality for lodgepole pine (Table 2), we did not observe stands with widespread beetle infestation as seen in Shasta red fir. Shasta red fir mortality was significantly greater in plots with a greater average change in minimum temperature between historical and reference time periods (Table 2). The AUC values indicate that the logistic regression model for subalpine fir showed poor discrimination between live and dead trees, and the models for Shasta red fir and lodgepole pine had excellent discrimination between live and dead trees.

Discussion

Our results indicate relatively high levels of recent mortality for three tree species in our study site in the Klamath Mountains: Shasta red fir, subalpine fir, and lodgepole pine. Because there is no baseline information about tree mortality in our study region, we compare our findings to other studies that examine levels of mortality across similar forest types in California. In old-growth Shasta red fir stands in our study area, we documented approximately 42 large snags/hectare (>30 cm dbh), which is substantially higher than the snag density reported by Potter et al. (1992), who found a mean density of 7.4 large conifer snags/hectare in a census of 340 old-growth California red fir stands across California. Our estimate is also substantially higher than the snag density reported from California red fir stands in the central and northern Sierra Nevada by Sudworth in 1899 (17 large dead trees/hectare) (Stephens 2000). In a relatively recent study that examined patterns of mortality in upper montane species across several hundred Forest Inventory and Analysis (FIA) plots in California (including some plots in the Klamath region), Mortenson (2011) reported that the mean proportion of standing dead red fir was 11.5%, and lodgepole pine was 7.9%. Our proportions of recent mortality (20% for Shasta red fir, and 18% for lodgepole pine) are about double the evaluations of Mortenson (2011). Based on these estimates from previous studies, we feel confident in characterizing the mortality of Shasta red fir in this region as a die-off event, and the mortality of lodgepole pine and subalpine fir as notably high. Below, we describe the endogenous and exogenous drivers of mortality for all three species, focusing primarily on Shasta red fir.

Our results confirm that there is an ongoing outbreak of fir engraver, a native bark beetle species, which is disproportionally infesting Shasta red fir versus the other two species of fir in this region (white fir and subalpine fir). Fir engraver beetles typically only successfully infest trees that are recently dead, or stressed by other factors, and population outbreaks can occur when resources (host trees) are abundant (Christiansen et al. 1987). Fir engraver outbreaks have typically been documented in white fir and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl) stands in the western United States. Berryman and Ferrell (1988) note that fir engraver outbreaks have occurred in nearly every decade from 1900 to 1980, typically following periods of drought and/or epidemics of fir-defoliating insects. Ferrell et al. (1994) found that white fir trees killed by fir engraver had more damaged crowns and decreased growth efficiency (vigor) versus those that were not attacked, and another study found a strong relationship between fir engraver attacks and *Phoradendron* mistletoe infection (Felix et al. 1971). Other authors have suggested that fir engraver is an important player in ongoing Shasta red fir mortality since 1982 in the Shasta-Trinity National
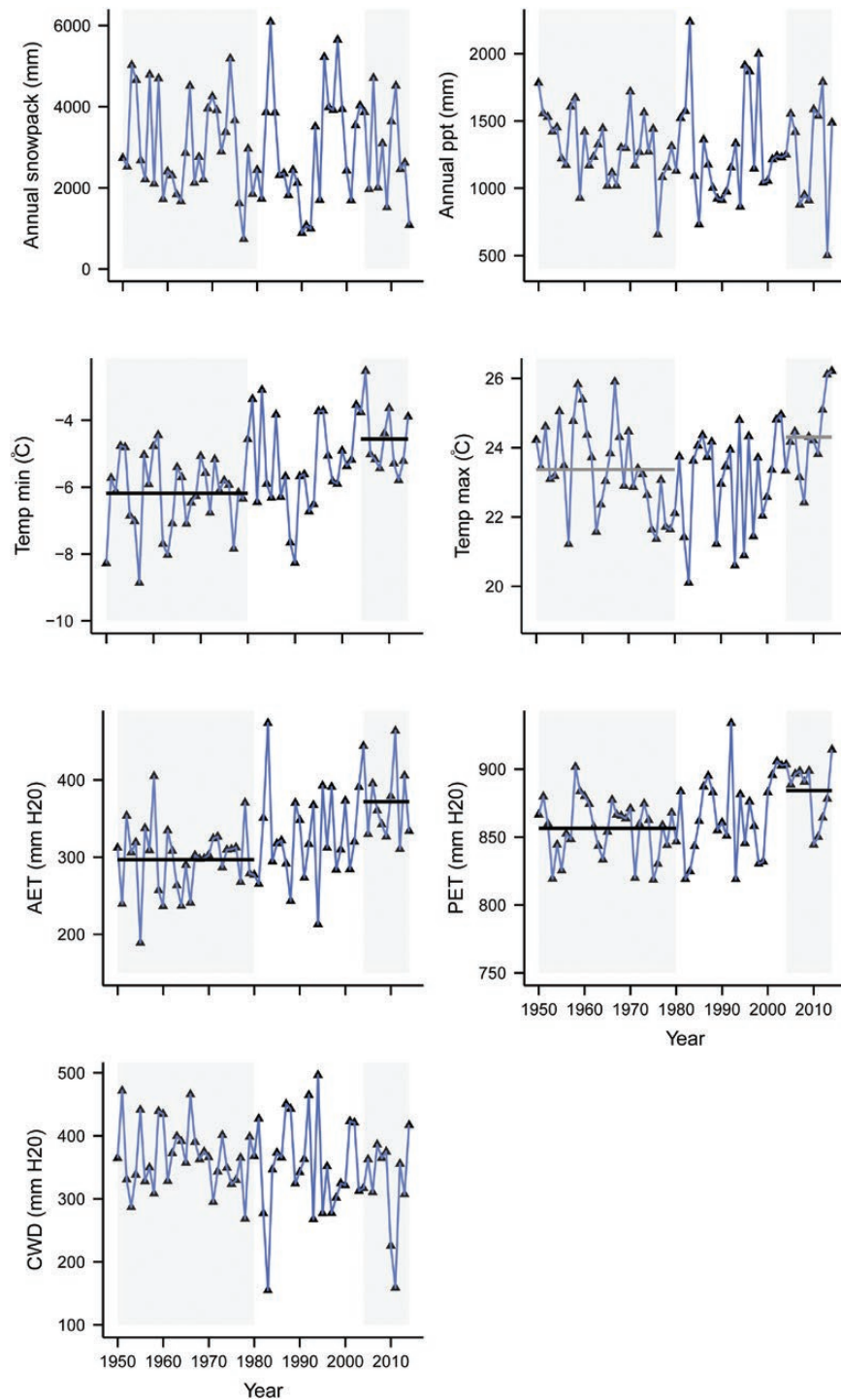
Figure 4. Climate data derived from the Basin Characterization Model (BCM) (see methods) for 132 plots from 1950 to 2014. Triangles denote averages across plots by year. Shaded areas represent the time periods (reference vs. current) compared in statistical analyses. Solid black lines represent the average values that are significantly different between the two time periods and solid gray lines represent differences that are marginally significant (Table S2).

Forest in northern California (Kliejunas and Wenz 1982, Angwin 2010) and more recently in California red fir decline in the Sierra Nevada (Bulaon and Mackenzie 2007, Mortenson et al. 2015).

We suggest two possible mechanisms for the recent population outbreak of fir engraver in Shasta red fir stands: increased availability of host trees, and more favorable environmental conditions for beetles at higher elevations. Based on a detailed 5-year life-table study, Berryman (1973) suggests that the primary factor

affecting outbreaks of fir engraver populations is food availability (the density of susceptible trees). Our data suggest that Shasta red fir are at high risk for fir engraver infestation due to damage from an important and persistent forest pathogen, dwarf mistletoe. The effects of dwarf mistletoes on host tree physiology and morphology are well documented (see Geils and Hawksworth 2002), and they are primarily known for reducing water use efficiency, slowing growth, and increasing susceptibility to other pests and pathogens.

Table 2. Logistic regression models predicting mortality for three tree species. Coefficient estimates are listed with standard error in parentheses; significance is indicated by *.01 < *P* < .05; **.001 < *P* < .01; ***P* < .001. Mortality was coded as 0 = live, 1 = dead, therefore positive coefficient estimates indicate that higher values of the predictor variable correspond to increased mortality. Diameter at breast height and bark beetles are at the individual tree level, while the other variables are at the plot level (0.04 ha). Non-significant predictors were removed from models using AIC (see methods). Model AUC (area under curve) values correspond to model validation (see methods).

Predictor	Shasta red fir	Subalpine fir	Lodgepole pine
Intercept	–2.60	–0.76	–3.27
Diameter at breast height	–0.83 (0.16)***		–2.09 (0.44)***
Bark beetles (0/1)	1.82 (0.25)***	2.19 (0.88)*	4.00 (0.86) ***
Elevation	–0.35 (0.22)*		
Quadratic mean diameter	0.92 (0.20)***		1.48 (0.52)**
Basal area (conspecific)			1.91 (0.58)**
Basal area (other)			1.32 (0.46) **
Δ Minimum temperature†	0.58 (0.23)*		
Model AUC	0.86	0.63	0.93

†Δ Minimum temperature is the difference in average minimum temperature between historical (1951–1980) and reference (2004–2014) time periods for each plot.

Several studies have shown a positive relationship between dwarf mistletoe infestation and bark beetle attack (Kenaley et al. 2006, Klutsch et al. 2014). Dwarf mistletoe infestation can also exacerbate climatic stress by further reducing host tree water use efficiency (Kane et al. 2014).

Our study was unable to quantify *Cytospora* infection as a potential contributing factor in Shasta red fir mortality. *Cytospora* is considered a weak, yet ubiquitous, parasitic fungus that is commonly found in association with dwarf mistletoe in fir species (Scharpf and Bynum 1975). *Cytospora* cankers are typically found on the same branches as dwarf mistletoe, and one study (Scharpf and Bynum 1975) estimated that about 20% of true fir branches infected with dwarf mistletoe are invaded and killed by *Cytospora*. The bole swellings that result from dwarf mistletoe infestation provide an opening in the bark for the fungus and can make the branches more prone to wind breakage (Kliejunas and Wenz 1982). We suggest that many of the Shasta red fir trees in our study area with heavy dwarf mistletoe infestation almost certainly have branches with *Cytospora* infection, and that these two pathogens in combination greatly increase the risk of fir engraver infestation.

The combination of dwarf mistletoe, *Cytospora*, and fir engraver attack in Shasta red fir has been documented for the past 33 years by forest entomologists and pathologists at a site about 40 miles south of our study area (Kliejunas and Wenz 1982, Angwin 2010). The progression of dwarf mistletoe (and *Cytospora*) building up within a stand is slow, since dwarf mistletoe takes about 4 to 6 years to produce seeds after initial infection, and lateral spread between trees in an even-aged stand is about 0.5 m per year (Kliejunas and Wenz 1982). Although pulses of mortality may occur after a few years of drought, stands are typically deteriorating for at least a decade. Since this disease complex was first described in 1984,

several management recommendations were made to increase the health and vigor of Shasta red fir stands, including selective removal of severely infested trees, and clearcutting and regenerating in heavily infested stands (Kliejunas and Wenz 1982). As of 2010, these silvicultural treatments were not yet prescribed and forest health continued to decline at this site (Angwin 2010), and in 2015, many of the severely infested stands burned in a wildfire (personal communication, Keli McElroy, USFS). Fire may be the best management strategy for slowing the spread of the disease complex, particularly in wilderness regions where silvicultural treatments are not feasible.

Another mechanism for the recent population growth of fir engraver in Shasta red fir stands could be the steady rise in minimum temperature in our study area (Figure 3) that may be creating more hospitable conditions for beetles at higher elevations. Fir engraver typically has a one-year life cycle, with overwintering occurring in the larval stage and maturation mostly between the summer months of July and August (Berryman 1973). Although there has been little work done on the cold-tolerance of fir engraver specifically, bark beetle responses to climate change are well studied. For example, outbreaks of spruce beetle (*Dendroctonus rufipennis* Kirby) in Alaska and the Yukon territory have been linked to periods of 5–6 years of warmer than average summer temperatures (Berg et al. 2006). A minimum temperature increase of 3.3° C (about double what we observed) has been suggested as a mechanism contributing to recent population outbreaks of southern pine beetle in northern forests in the eastern United States (Trân et al. 2007). More work on the physiological mechanisms affecting population dynamics of fir engraver would be necessary to confirm an indirect effect of climate warming on recent mortality via increased bark beetle survival.

Table 3. Plots (0.04 ha) with at least five Shasta red fir (*Abies magnifica* var. *shastensis*) individuals compared by level of bark beetle infestation. Values represent means with standard deviation in parentheses. * denotes significant *P*-values as determined from Kruskal-Wallace rank sum tests with a Bonferroni adjustment for multiple comparisons.

Variable	No beetles (*n* = 59)	Beetles (*n* = 37)	*P*
Elevation (m)	2022 (206.9)	2022 (170.0)	.76
Topographic moisture index (TRMI)	35.1 (11.8)	32.89 (10.2)	.39
Total plot basal area (m²)	2.12 (1.44)	2.45 (1.52)	.25
Proportion conspecific†	0.28 (0.30)	0.48 (0.36)	.006*
Quadratic mean diameter (QMD)	27.62 (17.36)	40.0 (17.8)	.003*
Average dwarf mistletoe rating (DMR)	0 (0)	1.03 (1.02)	<.001*

†The total proportion of Shasta red fir relative to other species in the plot.

Several authors attribute recent die-off events to initial abiotic stress that predisposes trees to other agents of mortality, such as pests and pathogens. The region-wide dieback of piñon pine (*Pinus edulis* Engelm.) in the southwestern United States, for example, was attributed to the 2000–2003 drought accompanied by unusually high temperatures, which predisposed trees to attack by a secondary bark beetle species, *Ips confusus* LeConte (Breshears et al. 2005). Similarly, Millar et al. (2007) found that limber pine mortality in the Sierra Nevada was linked to increased temperature and decreased precipitation, followed by dwarf mistletoe, and finally by mountain pine beetle. We do not see surmounting evidence that recent tree mortality in our study area is linked to unusually high summer temperatures, as the rising temperature trend we observe is driven by minimum temperatures and is most pronounced in winter months (Figure S4, Figure 3). Our study is consistent with literature suggesting that fir engraver outbreaks are associated with increased evapotranspiration (Wright and Berryman 1978, Berryman and Ferrell 1988); however, similar to Rapacciuolo et al. 2014, we did not see an increase in CWD. This distinguishes our study from many other tree mortality studies in the Sierra Nevada, for example, where die-offs have been attributed to large increases in CWD in recent years (Millar et al. 2012, Mcintyre et al. 2015). Finally, we used a ten-year window (2004–2014) for calculating recent changes in climate parameters, but it is possible that a few years of extreme drought within this period could have accelerated mortality, as has been shown in other systems (Breshears et al. 2005). For example, the 2011–2014 regional drought almost certainly created physiological challenges for Shasta red fir trees that exacerbated drought stress from dwarf mistletoe, and increased susceptibility to fir engraver infestation, but further investigation is needed to tease apart the abiotic vs. biotic causal agents of mortality.

Changes in the historical disturbance regime of these forest types, particularly the effects of fire exclusion, may be partially responsible for the elevated levels of recent mortality in high density and/or more mature stands throughout our study area. Similar to other parts of California, forests in the Klamath region have notable signs of fire exclusion, including in-filling of small, shade-tolerant trees (typically white fir), and dense accumulations of litter and duff around older trees. Historically, this region is characterized by a mixed-severity fire regime, with a high frequency of fires prior to the twentieth century producing mostly low and moderate fire effects in most conifer vegetation types (Skinner et al. 2006). In the upper montane zone (where we observed the highest mortality), the estimated fire return interval based on studies done in nearby forests ranges from about 15 to 41 years (Taylor and Halpern 1991, Taylor 2000) According to Forest Service records, our study area has not burned in the past 100 years (Safford et al. 2011), and based on the aforementioned estimates, we determine that the upper montane zone in our study area has missed somewhere between two and six fire cycles. Our finding of higher mortality among smaller diameter trees is consistent with a growing body of literature suggesting that increased stand density and competition from fire exclusion are major contributing factors to the increasing mortality trend in western coniferous forests (Guarin and Taylor 2005, Maloney 2011, Millar et al. 2012). Furthermore, high stand density has been shown to amplify drought stress (Gleason et al. 2017) and increase the spread of pests and pathogens. While some of the mortality observed in this study is undoubtedly related to self-thinning in high density stands, the usually high numbers of recently dead and

dying Shasta red fir trees (28%) coupled with the high levels of pathogens and forest insects is more indicative of a die-off event versus a slower change in community composition. In this case, the die-off was almost certainly precipitated by at least a decade of damage from dwarf mistletoe and *Cytospora* infestation.

Our study was motivated by the widespread decline in Shasta red fir; however, we unexpectedly found the highest levels of recent mortality for subalpine fir (28%, Table 2). Unlike white and Shasta red fir, subalpine fir is never a dominant species in our study area, and shows a very patchy distribution, occurring only in mesic sites. Found in only eight separate locations in northern California in close proximity to each other, subalpine fir becomes more common northward in the northern Cascades and coastal mountain of British Columbia (Kauffmann 2012). To our knowledge, no studies have investigated subalpine fir mortality or forest health in California; however, Bigler et al. (2007) demonstrated a relationship between subalpine fir mortality and drought (increased CWD) in the Rocky Mountains. We suggest that recent subalpine fir mortality in our study area is primarily driven by elevated levels of Wien's dwarf mistletoe and fir engraver, which is known to occasionally attack this species (Table S3). However, our limited sample size (68 trees across 9 sites) makes it difficult to draw strong conclusions. We also observed possible signs of balsam wooly adelgid infestation within a few subalpine fir stands in our study area (heavy swelling at branch nodes); however, further investigation is necessary to confirm this insect and its role as a mortality agent. Regardless of the cause, our study demonstrates levels of mortality that are notably high for a species that is presumably found on marginal habitats more akin to conditions to the north, and that close tracking of this species in this region is warranted.

Our study provides insight about recent tree mortality for an extremely diverse group of conifer taxa, spanning eleven species across five genera. We documented high levels of mortality for three taxa (Shasta red fir, subalpine fir, and lodgepole pine); however, the duration of these mortality events, and whether or not the events are a normal and periodic event for any of these taxa, remains unknown. Our study highlights the need for future work relying on dendrochronological and/or remote sensing techniques to place patterns and trends of recent mortality into a historical ecological context, particularly with regard to fir engraver outbreaks. Because our study cannot be used to infer mortality rates *per se*, repeated sampling of our plots will be essential for future work in this system. We especially recommend close monitoring of two important and rare species, whitebark pine and subalpine fir. Nonetheless, by itself, our study demonstrates the extent of Shasta red fir mortality in the Russian Wilderness, and identifies a combination of dwarf mistletoe, *Cytospora,* and fir engraver beetle as contributing factors in the recent pulse of mortality.

Supplementary Materials

Supplementary data are available with this article at http://dx.doi.org/10.1093/forsci/fxx022.

Literature Cited

ALLEN, C. D., D. D. BRESHEARS, and N. G. McDOWELL. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*. 8(6): 1–55.

Allen, C. D., A. K. Macalady, H. Chenchouni, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259(4):660–684.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* 3(1):30–36.

Angwin, P. 2010. *Biological evaluation of red fir restoration project at South Fork Mountain, South Fork Management Unit.* Shasta-Trinity National Forest. USDA Forest Service, Pacific Southwest Region, Forest Health Protection Report No. N11-01. 6 p.

Bentz, B. J., J. Regniere, C. J. Fettig, et al. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience.* 60(8):602–613.

Berg, E. E., J. David Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manage.* 227(3):219–232.

Berryman, A. A. 1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* 105(11):1465–1488.

Berryman, A. A., and G. T. Ferrell. 1988. The fir engraver beetle in western states. P. 556–578 in *Dynamics of forest insect populations: Patterns, causes, and implications*, Berryman, A.A (ed.). Plenum Press, New York.

Bigler, C., D. G. Gavin, C. Gunning, and T. T. Veblen. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos.* 116(12):1983–1994.

Breshears, D. D., N. S. Cobb, P. M. Rich, et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci.* 102(42):15144–15148.

Bulaon, B., and M. Mackenzie. 2007. *Red fir decline and mortality on the Stanislaus National Forest.* USDA For. Serv. FHP Rep. SS07-01.16 p.

Christiansen, E., R. H. Waring, and A. A. Berryman. 1987. Resistance of conifers to bark beetle attack: Searching for general relationships. *For. Ecol. Manage.* 22(1–2):89–106.

Cline, S. P., A. B. Berg, H. M. Wight, and S. P. Cline. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44(4):773–786.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *J. Appl. Meteorol.* 33(2):140–158.

Felix, L. S., B. Uhrenholdt, and J. R. Parmeter. 1971. Association of *Scolytus ventralis* (Coleoptera: Scolytidae) and *Phoradendron bolleanum* subspecies *pauciflorum* on *Abies concolor. Can. Entomol.* 103(12):1697–1703.

Ferrell, G. T., W. J. Otrosina, and C. J. Demars. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. *Can. J. For. Res.* 24(2):302–305.

Flint, A., and L. Flint. 2007. *Application of the basin characterization model to estimate in-place recharge and runoff potential in the Basin and Range carbonate-rock aquifer system, White Pine County, Nevada, and adjacent areas in Nevada and Utah.* US Geol. Surv. Sci. Investig. Rep. 2007–5099. 20 p.

Flint, L. E., and A. L. Flint. 2012. *Simulation of climate change in San Francisco Bay Basins, California: Case studies in the Russian River Valley and Santa Cruz Mountains.* US Geol. Surv. Sci. Investig. Rep. 2012–5132. 55 p.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. *Bioscience.* 37(8):550–556.

Geils, B.W., and F.G. Hawksworth. 2002. *Damage, effects and importance of dwarf mistletoes.* USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-98. 12 p.

Gleason, K. E., J. B. Bradford, A. Bottero, et al. 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere.* 8(7):1–16.

Guarin, A., and A. H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *For. Ecol. Manage.* 218(1):229–244.

Hawksworth, F. G. 1977. *The 6-class dwarf mistletoe rating system.* USDA For. Serv. Gen. Tech. Rep. RM-48. 7 p.

Heath, Z., B. Bulaon, T. F. Smith, D. Bakke, and L. Liu. 2014. *2014 California forest health highlights.* Davis, CA. Available online at http://www.fs.fed.us/foresthealth/fhm/fhh/fhh_14/CA_FHH_2014.pdf; accessed on February 24, 2018.

Heath, Z., K. Camilli, L. Fischer, D. Huerta, J. Moore, and W. Woodruff. 2009. *2009 Aerial survey highlights for California.* Davis, CA. Available online at http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_045169.pdf; accessed on February 24, 2018.

Heath, Z., L. Fischer, J. Moore, B. Oblinger, and W. Woodruff. 2010. *2010 Aerial survey highlights for California.* Davis, CA. Available online at http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5331725.pdf; accessed on February 24, 2018.

Hosmer, D. W., and S. Lemeshow. 2013. *Applied logistic regression.* John Wiley & Sons, Hoboken, NJ, USA. 475 p.

Jules, E. S., A. L. Carroll, A. M. Garcia, C. M. Steenbock, and M. J. Kauffman. 2014. Host heterogeneity influences the impact of a non-native disease invasion on populations of a foundation tree species. *Ecosphere.* 5(9):1–17.

Kane, J. M., T. E. Kolb, and J. D. McMillin. 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests. *For. Ecol. Manage.* 330:171–182.

Kauffmann, M. E. 2012. *Conifer country: A natural history and hiking guide to 35 conifers of the Klamath mountain region.* Backcountry Press, Kneeland, CA, USA. 206 p.

Keen, F. P. 1943. Ponderosa pine tree classes redefined. *J. For.* 41(4):249–253.

Kenaley, S. C., R. L. Mathiasen, and C. M. Daugherty. 2006. Selection of dwarf mistletoe—infected ponderosa pines by *Ips* species (Coleoptera: Scolytidae) in Northern Arizona. *West. North Am. Nat.* 66(3):279–284.

Kliejunas, J., and J. Wenz. 1982. *A biological evaluation of red fir restoration project at South Fork Mountain, South Fork Management Unit.* Shasta-Trinity National Forest. USDA Forest Service, Pacific Southwest Region, Forest Health Protection Report No. 82-28. 7 p.

Klutsch, J. G., R. D. Beam, W. R. Jacobi, and J. F. Negrón. 2014. Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. *For. Ecol. Manage.* 315:63–71.

Kolb, T. E., C. J. Fettig, M. P. Ayres, et al. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *For. Ecol. Manage.* 380:321–334.

Maloney, P. E. 2011. Incidence and distribution of white pine blister rust in the high-elevation forests of California. *For. Pathol.* 41(4):308–316.

Manion, P. D. 1991. *Tree Disease Concepts.* 2nd ed. Prentice-Hall, Englewood Cliffs, NJ, USA. 416 p.

Mathiasen, R. L. 2011. Morphological comparisons of white fir and red fir dwarf mistletoes in the Sierra Nevada and Southern Cascade Mountains. *Madroño.* 58(2):101–105.

Mathiasen, R. L., and C. M. Daugherty. 2009. *Arceuthobium abietinum* subspecies *wiensii*, a new subspecies of fir dwarf mistletoe (Viscaeae) from northern California and southern Oregon. *Madroño.* 56(2):118–126.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol Evol.* 26(10):523–532.

McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly. 2015. Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proc. Natl. Acad. Sci. U. S. A.* 112(5):1458–1463.

Meyer, M. D. 2013. *Natural range of variation of red fir forests in the bioregional assessment area*. USDA For. Serv. Unpubl. Rep., Pacific Southwest Region, Albany, CA. 82 p. Available online at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5434332.pdf; accessed on February 24, 2018.

Millar, C. I., R. D. Westfall, and D. L. Delany. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. *Can. J. For. Res.* 37:2508–2520.

Millar, C. I., R. D. Westfall, D. L. Delany, et al. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Can. J. For. Res.* 42:749–765.

Moore, J., and Z. Heath. 2016. *Forest health protection special aerial detection survey*. Available online at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd509278.pdf; accessed on February 24, 2018.

Moore, J., A. Jirka, and L. McAffe. 2015. *Forest health protection aerial detection survey*. Available online at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd491964.pdf; accessed on February 24, 2018.

Mortenson, L. A. 2011. *Spatial and ecological analysis of red fir decline in California using FIA data*. M.Sc. thesis, Oregon State University, Oregon, USA. 109 p. Available online at http://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/v979v6239; accessed on February 24, 2018.

Mortenson, L. A., A. N. Gray, and D. C. Shaw. 2015. A forest health inventory assessment of red fir (*Abies magnifica*) in upper montane California. *Ecoscience*. 22(1):47–58.

Oline, D. K. 2008. Geographic variation in chloroplast haplotypes in the California red fir-noble fir species complex and the status of Shasta red fir. *Can. J. For. Res.* 38(10):2705–2710.

Overhulser, D. L., I. R. Ragenovich, M. McWilliams, and E. A. Willhite. 2004. *Balsam woolly adelgid occurrence on true fir in Oregon*. Oregon Department of Forestry, Pest Management Report, Salem, OR. 7 p.

Parker, A. J. 1982. The topographic relative moisture index: An approach to soil-moisture assessment in mountain terrain. *Phys. Geogr.* 3(2):160–168.

Potter, D., M. Smith, B. Kermeen, W. Hance, and S. Robertson. 1992. *Ecological characteristics of old growth red fir in California*. San Francisco, CA.

R Core Development Team. 2016. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, et al. 2014. Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. *Glob. Chang. Biol.* 20(9):2841–2855.

Safford, H. D., K. van de Water, and D. Schmidt. 2011. *California fire return interval departure (FRID) map, 2010 version*. USDA Forest Service, Pacific Southwest Region and the Nature Conservancy, Davis, California, USA. 32 p.

Sawyer, J. O., and D. A. Thornburgh. 1974. *Subalpine and montane forests of granodiorite in the central Klamath mountains of California*. Humboldt State University, Arcata, California, USA. 87 p.

Scharpf, R.F., and Bynum, H.H. 1975. *Cytospora canker of true firs*. USDA For. Serv. Forest Pest Leaflet 146. 5 p.

Skinner, C. N., A. H. Taylor, and J. K. Agee. 2006. Klamath Mountains Bioregion. P. 170–195 in *Fire in California ecosystems*, Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (eds.). Berkeley, CA, USA.

Stephens, S. L. 2000. Mixed conifer and red fir forest structure and uses in 1899 from the Central and Northern Sierra Nevada, California. *Madroño*. 47(1):43–52.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. *J. Biogeogr.* 27(1):87–104.

Taylor, A. H., and C. B. Halpern. 1991. The structure and dynamics of Abies-Magnifica forests in the southern Cascade range, USA. *J. Veg. Sci.* 2:189–200.

Trân, J. K., T. Ylioja, R. F. Billings, J. Régnière, and M. P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of Dendroctonus frontalis. *Ecol. Appl.* 17(3):882–899.

USDA Forest Service. 2015. April 1st snow survey results. Available online at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3834244.pdf; last accessed Nov. 16, 2017.

van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol. Lett.* 10:909–916.

Wood, D. L., T. W. Koerber, and R. F. Scharpf. 2003. *Pests of the native California conifers*. University of California Press, Berkeley, CA, USA.

Wright, L. C., and A. A. Berryman. 1978. *Effect of defoliation by the Douglas-fir tussock moth on moisture stress in grand fir and subsequent attack by the fir engraver beetle (Coleoptera: Scolytidae)*. U.S. Dep. Agric. Forest Serv. Res. Note PNW-323. 14 p.