Drought, Tree Mortality, and Wildfire in Forests Adapted to Frequent Fire

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Massive tree mortality has occurred rapidly in frequent-fire-adapted forests of the Sierra Nevada, California. This mortality is a product of acute drought compounded by the long-established removal of a key ecosystem process: frequent, low- to moderate-intensity fire. The recent tree mortality has many implications for the future of these forests and the ecological goods and services they provide to society. Future wildfire hazard following this mortality can be generally characterized by decreased crown fire potential and increased surface fire intensity in the short to intermediate term. The scale of present tree mortality is so large that greater potential for "mass fire" exists in the coming decades, driven by the amount and continuity of dry, combustible, large woody material that could produce large, severe fires. For long-term adaptation to climate change, we highlight the importance of moving beyond triage of dead and dying trees to making "green" (live) forests more resilient.

Keywords: bark beetle, resilience, mixed conifer, adaptation

According to recent estimates, more than 100 million trees have died in California primarily in the southern and central Sierra Nevada (USDA–FS 2016a) prompting the Governor to declare a state of emergency. Why there, and why now? The answer lies in the management of fire-dependent ecosystems exacerbated by the recent episode of acute drought. Most western US ecosystems are fire dependent, meaning that for millennia, the flora and fauna depended on periodic fire to maintain ecosystem integrity. The distribution and structure of these ecosystems were sustained by fire up until Euro-American settlement in the late nineteenth century, particularly in the low- to mid-elevation yellow pine and mixed-conifer forests where fires recurred at intervals of a few years to several decades (Safford and Stevens 2017). Frequent-fire (FF) in these forests selected for, and protected the majority of large, old trees by limiting biomass accumulation and thinning competitors in the understory.

Historical FF forests were highly variable with a mixture of tree densities and size classes, but as a whole, were much more open than they are today (Taylor and Skinner 2003, Knapp et al. 2013, Collins et al. 2015, Stephens et al. 2015, Levine et al. 2017). As a result of aggressive fire suppression promulgated by land managers in the early 1900s, FF forests soon experienced prolific tree regeneration (Show and Kotok 1924, Covington et al. 1997). This was welcomed for timber-production purposes, because foresters believed that fire had kept historical FF forests at only a fraction of their stocking capacity (Show and Kotok 1924). However, for over a century, fires have been excluded under almost all practical circumstances, with the limited hectares burning in wildfires mostly relegated to extreme weather when suppression efforts are largely ineffective (North et al. 2015).

Paradoxically, aggressive and largely successful fire suppression has left FF forests increasingly vulnerable to the negative effects of fire and other tree mortality agents (Young et al. 2017). Removal of frequent, generally nonlethal fires effectively stores fuel for those dry and windy conditions when fires exhibit extreme behaviors. The result is often extensive tree mortality, occurring in large contiguous patches (Lydersen et al. 2014, Jones et al. 2016). In many wildfires burning in FF forests, tree mortality patches are an order of magnitude or two larger than those that occurred historically (Mallek et al. 2013, Stevens et al. 2017). In areas that have not yet burned at uncharacteristic severity, fire suppression-caused forest densification has increased competition among trees for water and other resources, destabilizing many FF forests by making them prone to mortality from other agents such as bark beetles (*Dendroctonus*, *Ips*, *Scolytus* spp.; Kolb et al. 2016). The recent Sierra Nevada tree mortality associated with these agents is unprecedented and far more extensive than fire-caused mortality in individual wildfires (Asner et al. 2016). In dense FF forests, tree vigor is reduced as a result of competitive stress, and the potential for native bark beetles to mass attack is greater because of the closer proximity to host trees and other factors (Fettig et al. 2007). These combined effects increase susceptibility to bark-beetle-caused tree mortality, but the trigger that leads

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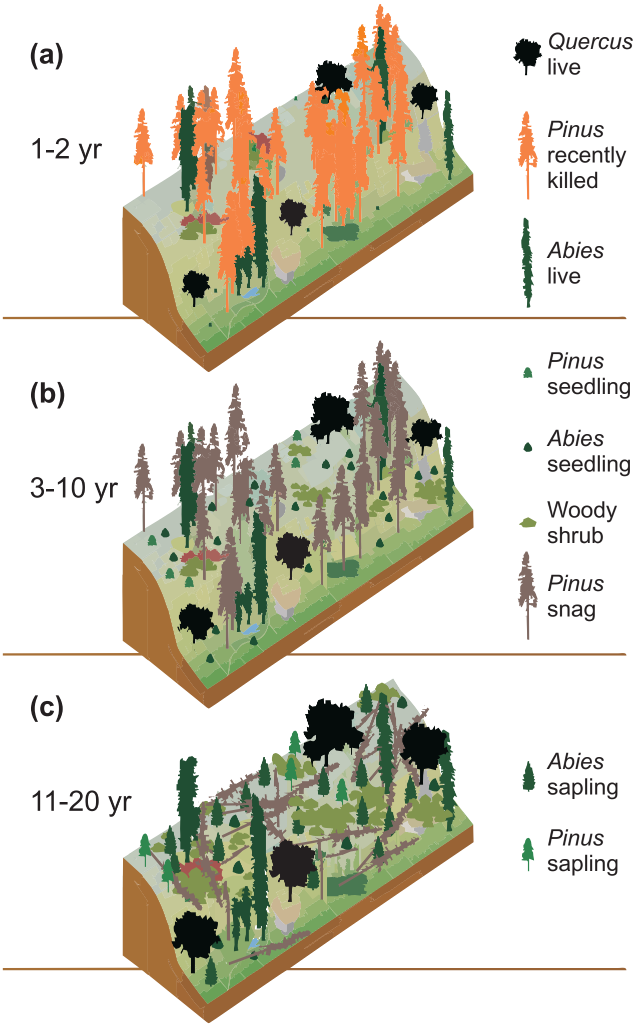

Figure 1. A theoretical depiction of vegetation and fuel dynamics following severe pine mortality due to bark-beetle attack in a mixed-conifer forest. Initially (1–2 years following mortality), the primary change would be reduced moisture content of canopy fuels (a). In the intermediate time period (3–10 years), there would be an overall loss of canopy fuels as dead foliage and branches are deposited on the forest floor, and there would be a corresponding increase in dead and live surface fuels as tree seedlings and shrubs establish (b). The longer-term changes (11–20 years) would include continued low canopy fuels—although this could be offset by the growth of residual overstory trees taking advantage of the available growing space—and considerable increases in large surface fuel (c). Increased surface fuels would be in both the dead (primarily fallen snags) and live (regenerating trees and shrubs) pools (c).

to actual widespread mortality is often a multiyear drought (Young et al. 2017).

The recent massive tree mortality has many implications for the future of FF forests and the ecological goods and services they provide to society (recreation, wildlife habitat, water storage, timber, aesthetics, carbon storage, etc.). It could be surmised that because FF forests have seen such dramatic increases in tree density relative to historical conditions, the bark-beetle-caused tree mortality could be helping to produce more resilient forest conditions (we define *resilience* as the ability of a forest to maintain characteristic structural components, such as large trees, and broad functionality following disturbance and/or chronic stressors). The actual outcome, however, will likely be forests that are very different from their historically resilient condition. For one, many of the trees killed by bark beetles are the largest trees (van Mantgem et al. 2009) and not the trees that would be preferentially killed by low- to moderate-severity wildfires or targeted for removal in restoration projects (i.e., small- to moderate-sized trees). Second, bark-beetle-killed trees are often not removed, as is commonly the case in restoration projects involving mechanical thinning or in forests subject to centuries of frequent fires. Tree biomass therefore remains on site, just shifted from the live “pool” with high moisture content to the dead “pool” with low moisture content (figure 1). This shift has the potential to significantly alter fire behavior and forest succession in FF-adapted forests.

In this article, we summarize research that may improve the understanding of the near- and longer-term effects of the massive tree mortality event in FF forests in California. It presents data and results from a recent wildfire illustrating how drought-induced tree mortality affected fire behavior and suggests management practices that might reduce future mortality and increase forest resilience and adaptation to climate change. The rapid and extensive tree mortality in the Sierra Nevada has surprised many observers and challenges management to proactively respond to what will likely become a more common occurrence under changing climate conditions (Fettig et al. 2013).

The impacts of tree mortality on wildfire

Tree mortality has long been known to play an important role in altering fuel dynamics within forests. The process of reducing live canopy fuels and subsequently increasing dead fuels alters the arrangement, composition, and quantity of fuel available for combustion. These fuel changes directly influence the spread and intensity of wildland fires, and indirectly influence micrometeorological conditions that can drive fire behavior and effects. Although a number of studies have directly evaluated alterations in forest fuel beds following bark-beetle-caused tree mortality (e.g., Hicke et al. 2012), empirical investigations of the effects of mortality on fire behavior remain limited. Instead, studies have mostly relied on the use of fire behavior modeling. Furthermore, most of the published literature has focused on investigations in more mesic forest types, such as lodgepole-pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and spruce-fir (*Picea-Abies*) forests (Agne et al. 2016), rather than in more seasonally xeric FF forest types, such as Ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus*

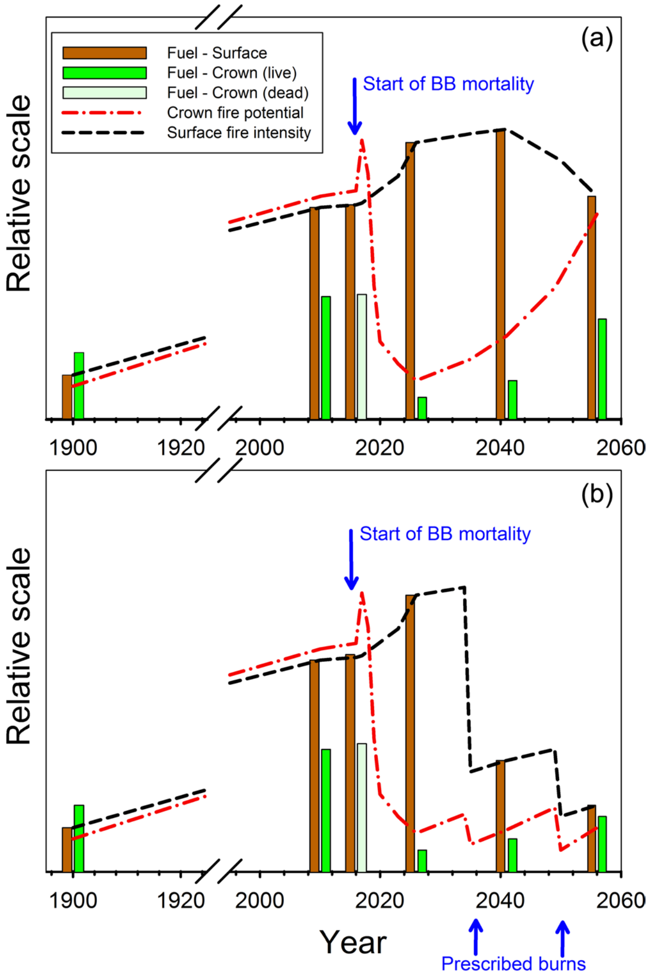

Figure 2. A conceptual diagram showing fuel load and expected fire behavior in a mixed-conifer forest prior to and following a major bark-beetle-caused tree-mortality episode, with either (a) no follow-up-fuels treatment or (b) periodic prescribed fire to consume fuels. Surface-fire intensity is expected to roughly follow surface fuel load, whereas crown-fire potential is regulated by the amount of surface fuel (necessary to heat and dry live fuels to the point of combustion), as well as crown bulk density.

jeffreyi), and mixed conifer. Outcomes from the mesic forest types, which historically experienced infrequent (75–300 years), generally more intense fires are, in many cases, not directly applicable to the xeric forest types that historically experienced frequent (every 5–25 years), generally low- to moderate-intensity fire, and where the effects of fire exclusion on stand density are most pronounced.

Short-term effects. Following the conceptual framework of Hicke and colleagues (2012), the impacts of bark-beetle-caused tree mortality on forest fuels are best understood by using broad temporal categories, or phases, to characterize changes to the fuels complex. During the initial phase, often termed the red phase, the conversion of live to dead canopy fuels reduces foliar moisture content and alters foliar chemistry. Both of these contribute to increased flammability within the tree by decreasing the heat requirements for ignition (Jolly et al. 2012, Page et al. 2012). The magnitude of this effect depends on the proportion and timing of tree mortality. If mortality is acute and extensive, increases in flammability would be expected. If mortality is more gradual, however, the increased flammability from recently killed trees can be somewhat mitigated by the loss of crown fuels from neighboring trees that died earlier, because most dead needles fall to the forest floor within 1 or 2 years following tree mortality.

In general, it is believed that the rate of fire spread and fire line intensity are increased during the red phase, at least under more severe burning conditions (figure 2); however, there is uncertainty surrounding this generality. A number of simulation studies have suggested that the decreased mean foliar moisture content of the canopy during this time period results in increased fire rates of spread and fireline intensities (Hicke et al. 2012, Hoffman et al. 2013, Linn et al. 2013). Other studies have revealed that there may be a decrease in these metrics during this time period especially in cases in which tree mortality was gradual and resulted in reduced canopy fuel loads (Simard et al. 2011). The discrepancy between studies may also in part be due to the use of simplified fire behavior models that do not account for the increased ignition characteristics of dead canopy fuels. Hoffman and colleagues (2015) used a physics-based model to compare the effects of a rapid and gradual tree-mortality event on simulated fire behavior and found that during the near term (1–3 years following mortality), the gradual and rapid scenarios increased fire rates of spread by 1.2- to 2.7-fold, suggesting that conversion of live needles to dead is an important characteristic driving near-term fire behavior. To our knowledge, the only study that has directly quantified the impacts of recent mortality (red phase) on fire spread is that by Perrakis and colleagues (2014), who in forests dominated by lodgepole pine found a rate of fire spread 2.7 times greater than that expected pre-outbreak.

Longer-term effects. The gray phase, when deposition of foliage and small-diameter branch material occurs, is associated with a shift from the canopy fuel pool to the surface fuel pool (figure 1). The old phase refers to subsequent changes to the fuel complexes involving the deposition of large-diameter branches and bole material, and the development of a live surface fuel layer as new plants establish and grow. These fuel shifts generally correspond with decreased crown fire potential and increased surface fire intensity (figure 2a). Over time, live fuels may increasingly influence fire behavior as regenerating saplings and small trees increase canopy bulk density and reduce average canopy base heights (e.g., Simard et al. 2011).

Although decade-length impacts of dead tree biomass on fire behavior at any scale have not been investigated, the potential for crown fire (passive and active) in the short-stature regenerating forest would be expected to increase during this time period (figure 2a). One thing is certain: converting live trees into dead trees increases the amount and continuity of dry, combustible large-woody material. As living trees, the boles and branches larger than a few centimeters in diameter will not be consumed even by the most extreme wildfires, but dead and dry trees are available for combustion. Unless some of this dead biomass is removed, either mechanically or by fire, recent and current bark-beetle-caused tree mortality in the Sierra Nevada could add tens to hundreds of Mg per hectare (ha) of dry woody fuel to the wildland fuel complex (John J. Battles, Department of Environmental Science, Policy and Management, University of California, Berkeley, personal communication, 20 March 2017). Unfortunately, the consequences of this increase in total energy to wildfire behavior cannot be determined by today's operational fire behavior models, which were designed to predict the forward spread rate of thin linear flame zones. The semiempirical formulation of the fire models considers only the effect of fine fuel (grasses, foliage, shrubs, and downed wood fuels less than 7.5 centimeters in diameter) on the rapid burning, flaming region (Rothermel 1983). The models do not reflect contributions by large woody material or deep forest floor layers to hours-long energy release behind the flame edge or large-scale effects on atmospheric circulations. In fact, a different and dangerous class of fire behaviors emerges at large scales and depends on the combination of high dead surface fuel loads and long burning times extended across a large area (mass fire; see below).

Landscape-level effects. Although there is little landscape-level fire behavior research to draw on, increased connectivity of heavy dead fuels over hundreds to thousands of hectares associated with rapid and extensive tree mortality events likely will increase future fire spread rates in FF forests. Large-scale tree mortality would be expected to increase fire growth through its influence on both the production of burning embers (because recently dead trees are more likely to torch; Hicke et al. 2012) and through an increase in the efficiency with which burning embers ignite and start "spot" fires in advance of the main fire front (because of overall greater proportions of fine and/or rotten, dry fuels). Similarly, exacerbated fire effects on live trees would be expected following large-scale tree mortality because of the "neighborhood" effects of torching dead trees. This effect is based on the expectation that the heat released and embers produced by torching dead trees and downed logs would allow for preheating of adjacent live trees, causing scorch-related mortality or possibly local spreading crown fire.

However, observations of total burned area and remotely sensed fire severity from fires across the western US do not universally support the assertion that bark beetle outbreaks lead to increased fire severity (e.g., Meigs et al. 2016). Such discrepancies are likely due to differences in the timing and intensity of tree mortality, forest type, and the very different spatial scales at which studies were conducted. Prichard and Kennedy (2014) analyzed fire severity patterns within an individual landscape, whereas other studies analyzed fire patterns at a regional scale, spanning several ecoregions, and mostly assessing burned areas more than 5 years after mortality had occurred (the gray phase). It is possible that at the regional scale the broad range in forest types, which includes large gradients in tree species composition and vegetation structures, masks the specific mechanisms by which tree mortality influences landscape-level fire behavior and severity. This is particularly the case when analyses combine forest types in which fire behavior is predominantly driven by surface fuels (i.e., historically FF forests) with those driven more by canopy fuels (i.e., historically infrequent, high-severity adapted forests). In the former forest types, large-scale tree mortality would be expected to increase fire behavior characteristics such as rate of fire spread and fireline intensity in the short term through increased torching, as well as over the long term, via increased surface fire intensity resulting from greater amounts of dry woody fuels deposited on the forest floor (figure 2a). In the latter forest types, it is likely that beyond early stages of mortality, fire behavior could be reduced because of the "thinning" of the canopy and associated reduction and continuity of canopy fuels (Hicke et al. 2012, Meigs et al. 2016).

Another important consideration with large-scale tree mortality is the potential to add long-burning high fuel loads over extensive areas—fuel characteristics that match the criteria for mass fires. *Mass fires*, firestorms, or conflagrations (Pitts 1991, Finney and McAllister 2011) can occur when large areas are burning simultaneously. This can happen following ignition saturation over a large area from long-distance spotting in wildfires, multiple earthquake-related ignitions in urban areas, and by incendiary bombing in war (Pitts 1991). Fuel beds need not be continuous so long as the airflow merges to a plume near the ground (Countryman 1965, Pitts 1991).

The limited science of mass fires comes from studies of urban fires (Carrier et al. 1984, 1985), a few large-scale experimental burns (Chandler 1963, Countryman 1965, Quintiere 1993), and computer simulations (Small et al. 1983, Trelles and Pagni 1997). Mass fire behaviors result from the strong coupling between the fire and induced atmospheric circulations. The system requires a large active burning zone (minimum 3–4 square kilometers) and long burning times (2–3 hours) to allow "spin-up" of in-drafts from strong surface winds (approximately 30–50 meters per second) induced by the buoyancy-caused low hydrostatic air pressure over the middle of the fire (Carrier et al. 1981). With winds drawn toward the interior, mass fires exhibit little outward spread unless the plume begins to swirl or twist (Carrier et al. 1985) or unless ambient winds produce a conflagration through spotting and downbursts from the plume (Chandler 1963, Pitts 1991). The implication is that mass fire behavior and firestorm conditions are strongly dependent on high loads of long-burning fuels—similar, but not restricted, to those observed now in FF adapted forests that have experienced severe mortality from drought and bark beetles. Strong fire-induced winds can cause tremendous damage alone, but flow interactions with topography can yield complicated fire growth patterns and extreme spread especially in complex topography (Raposo et al. 2015). The fuel impacts of large-scale forest mortality suggest this could lead to a greater incidence of mass fire behavior. Mass fires strongly contrast with historical fire regimes in FF forests, are not predictable by fire models, and risks are poorly understood. Thus, fire departments, communities, and forest managers likely will underestimate the wildfire threat posed to people, homes, and natural resources following severe tree mortality in forests adapted to FF.

Wildfire in areas of high tree mortality. Few field-based empirical studies have documented the effects of recent tree mortality on wildfire severity, and those that have focused on forest types historically associated with more infrequent, generally higher severity fire regimes (e.g., Harvey et al. 2014, Agne et al. 2016). To our knowledge, no studies using field or remote data have documented the relationship between high levels of tree mortality and wildfire severity in the Sierra Nevada. This is at least in part due to tree mortality of the scale now occurring being unprecedented, at least in the historic record (Asner et al. 2016). These forests may have a unique tree mortality–wildfire relationship relative to previously studied forest types because they were historically associated with FF but have fairly high primary productivity (North et al. 2016). Here, we report the results from analyses demonstrating this relationship using empirical data. Specifically, we collected field data within areas that experienced recent tree mortality from drought and bark beetles (red phase), which subsequently burned in a large wildfire. The goal of the study was to determine whether, and under what conditions, wildfire severity was related to the severity of prefire tree mortality in FF adapted forests. Further details are included in the supplemental material.

In 2016, we collected data on the forest stand structure, fire severity, and pre- and postfire tree mortality on 50 0.04-ha plots within the approximately 60,000 ha 2015 Rough Fire in the southern Sierra Nevada. Plots were located in Sierran mixed-conifer vegetation, a historically FF adapted forest, at elevations ranging from 1138 to 2180 meters. Plots were within 400 meters of areas of conifer mortality (minimum 25 dead trees per ha) documented within 2 years prior to the Rough Fire by US Forest Service Aerial Detection Surveys (USDA–FS 2016b). Plot-level prefire red phase mortality ranged from 0% to 100% of trees and averaged 39.6%. Dominant trees within plots were Ponderosa pine, Jeffrey pine, incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*). In addition, we obtained hourly weather data from a portable Remote Automated Weather Station established in the fire. These data, in conjunction with a detailed fire progression map, were used to assign critical fire weather variables to field plots. A remotely sensed fire severity metric, relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007), was also obtained for each plot.

We used random forest analysis to identify influential topographic, weather, vegetation, and prefire tree mortality variables on three fire severity metrics: RdNBR, torch percentage (the proportion of tree needles consumed by fire), and the percentage of live tree basal area killed by fire. The variables of potential influence on these fire severity metrics included in the analysis were elevation, Beers transformed aspect (Beers et al. 1966), slope, topographic relative moisture index (TRMI, an index ranging from 0, xeric, to 60, mesic; Parker 1982), temperature, relative humidity, wind speed, maximum wind gust speed, estimated prefire shrub cover, plot-level tree density, stand basal area (live and dead), dominant tree genus (*Pinus*, *Abies*, or *Calocedrus*), percentage of plot basal area in the red phase immediately prefire, and the percentage of plot trees in the red phase immediately prefire. We conducted partial dependence analyses to characterize the dependence of model predictions on important predictor variables. Analyses were conducted in R version 3.3.3 using the "party" package for random forest and the "edarf" package for partial dependence.

Topographic, weather, vegetation, and prefire tree mortality variables were identified as influential to our measures of fire severity. The percentage of live tree basal area killed by fire was associated most strongly with the percentage of basal area in the red phase prefire, followed by stand basal area, percentage of trees in red phase prefire, and prefire shrub cover. The most important predictors for RdNBR were temperature, percentage of trees in the red phase prefire, percentage of tree basal area in the red phase prefire, elevation, and dominant tree genus. Torch percentage was best predicted by TRMI.

Partial dependence analysis revealed that the percentage of basal area killed by fire increased as prefire mortality increased, but only up to prefire mortality levels of approximately 30% of plot-level trees or basal area (figure 3). Further increases in prefire mortality did not result in greater fire severity. A similar relationship between prefire mortality measures and RdNBR, the remotely sensed fire severity metric, was observed. Increases in fire-caused mortality corresponded to increases in total stand basal area up to approximately 60m^2 per ha. Fire caused mortality was mildly negatively associated with estimated prefire shrub cover at low shrub cover levels. Torch percentage decreased with increases in TRMI up to an index value of approximately 30, which is midway between xeric and mesic.

No single variable was identified as influential to all three measures of fire severity. Our fire severity measures fall into two categories: a physical measure of direct fire effects on trees (the torch percentage) and measures of change from live to dead fuels (the percentage of basal area killed by fire and the RdNBR, which is largely based on the proportional amount of change from green to non-green biomass). Although the physical measure (torch percentage) was most

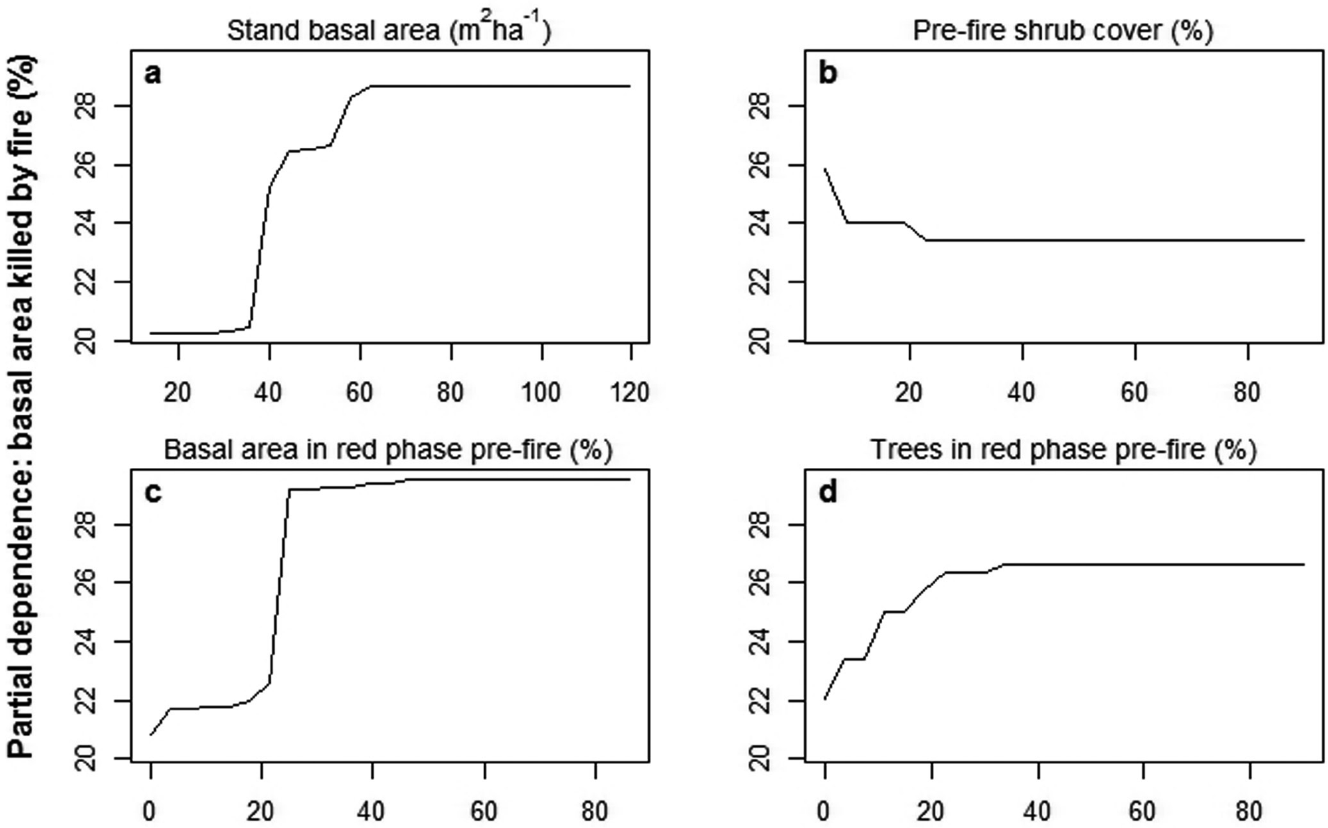

Figure 3. Partial dependence plots characterizing the dependence of model predictions on the four variables identified by random forest analysis as influential on the percentage of plot basal area killed by the Rough Fire: (a) stand-level basal area, (b) plot-level estimated prefire shrub cover, (c) plot-level percentage of basal area in the red phase prefire, and (d) plot-level percentage of trees in the red phase prefire.

strongly associated with site soil moisture (TRMI), measures of change from live to dead fuels were most strongly associated with variables related to levels of prefire tree mortality. This difference may partly reflect the fact that torching was measured on all trees (live and recently dead) in the plot, whereas changes from live to dead fuel were based only on trees that were live at the time of fire. Our analyses do not reveal the actual mechanisms by which prefire tree mortality relates to increased fire-caused tree mortality, and our data do not indicate that increased torching drives the relationship. Sampling additional fires over a wider range of weather and topographical conditions may be necessary to better understand this relationship (see box 1).

Management after severe tree mortality

Managers of western US conifer forests have relied on the definition of historic or "natural" ranges of variation to help define restoration goals (Safford and Stevens 2017). As temperatures warm, droughts worsen, forest density rises, and transformational disturbances increase in size and frequency, the ability to recreate and maintain historic conditions on western US landscapes becomes increasingly tenuous (Schoennagel et al. 2017). Another concept that could assist in developing future conditions is realignment (Stephens et al. 2010). Realigning forests implies modifying forests to present and/or future conditions, which can be quite different from those of the past. In many areas, the coupling of climatic warming and more extensive droughts may shift the conifer zone up in elevation, with severe fire and bark-beetle-caused tree mortality being a major driver of this shift (Fellows and Gouldin 2012, Clark et al. 2016). Where current conditions remain suitable for conifers, restoration of drought-affected forests could be challenging because the resulting composition, structure, and successional patterns will differ depending on whether relatively frequent fire, the dominant historic disturbance, is also returned at meaningful scales.

Proportionally, tree mortality attributed to bark beetles is higher for larger, overstory trees in FF forests (Fettig 2016), generally leaving surviving smaller trees in the understory, which in the long-term absence of fire are more likely to be of shade-tolerant species that are less drought and fire resistant (figure 1). This structural and compositional shift is also likely to be reinforced in natural recruitment as the resultant

Box 1. The contrasting impacts of drought: Frequent fire forests in the western United States versus northwest Mexico.

From 1999 to 2002, forests in the southern California mountains experienced a mortality event similar to that observed in the central and southern Sierra Nevada today (Preisler et al. 2017). The issues underlying the southern California tree mortality episode were the same as in the Sierra Nevada: fire suppression increased tree densities (Minnich et al. 1995), followed by a severe drought (Walker et al. 2006). Was this a "natural" event? We can travel about 320 kilometers south to northern Baja California (Baja), Mexico, to find an answer.

Mountain vegetation is very similar between northern Baja and southern California, and there are strong parallels with frequent-fire (FF) forests in the eastern Sierra Nevada as well (Dunbar-Irwin and Safford 2016). The largest area of Baja conifer forest is in the Sierra de San Pedro Mártir (SSPM), which is dominated by Jeffrey pine, white fir, sugar pine (*Pinus lambertiana*), lodgepole pine (*Pinus contorta* var. *murrayana*), and limited amounts of incense cedar and quaking aspen (*Populus tremuloides*; SSPM location in Fry et al. 2014). The SSPM has not been logged, and fire suppression did not begin until approximately 1970 (Stephens et al. 2003). Therefore, SSPM forests have not seen the dramatic tree densification as occurred in California FF forests from fire suppression and logging (Dunbar-Irwin and Safford 2016).

The SSPM experienced a similar drought as the forests in southern California, but the impact was different. Whereas an average of 30.5 trees per ha died on the California side of this mountain range (data in Walker et al. 2006), dead trees increased by only 1.2 per hectare (ha) in the SSPM (figure 4; Stephens 2004). Both forest regions are home to mountain pine beetle (*D. ponderosae*), fir engraver (*Scolytus ventralis*), and several species of *Ips* that can all respond quickly to drought (Kolb et al. 2016). However, western pine beetle (*Dendroctonus brevicomis*), the insect associated with high amounts of bark-beetle caused tree mortality in California FF forests, is not found in the SSPM, and its primary host, Ponderosa pine, is also absent. Western-pine-beetle populations can increase quickly during severe drought, faster than those of the Jeffrey pine beetle (*D. jeffreyi*), which is more common in Baja forests (Minnich et al. 2016).

Figure 4. Forest responses following a severe drought (1999–2002) in the Sierra de San Pedro Mártir (SSPM), Baja California, Mexico (a, drought and bark-beetle-caused tree mortality followed by wildfire; b, drought- and bark-beetle-caused tree mortality only) and in the southern California mountains (SCM), California, United States (c, drought- and bark-beetle-caused tree mortality at larger scales; d, drought and bark-beetle-caused tree mortality at stand scale. Note no wildfire in either SCM area). The SSPM and SCM photos were taken in 2004 and 2003, respectively. The SSPM site experienced a wildfire immediately following the multiyear drought (picture from 2003), with the photos capturing effects of both drought- and wildfire-related tree mortality. Pictures (a), (b), and (d) from SLS, (c) from G. Barley.

After the drought ended, a wildfire burned in the northern SSPM in 2003, but only 20% of the trees in this forest died from the combined effects of a severe 4-year drought followed by a wildfire (figure 4; Stephens et al. 2008), demonstrating considerable resilience to drought, tree-killing insects, and wildfire. FF-adapted forests in California and elsewhere once likely possessed similar resilience, which has been lost in the last 100 years. This resilience suggests that treatments producing structures similar to SSPM forests at sufficient spatial scales might also lead to resilient conditions, as has been seen in the mixed-conifer forests in Yosemite National Park that have been subjected to restored fire regimes for several decades (Boisramé et al. 2017). Treatments would also enhance adaptation to climate change by increasing the vigor, resistance, or resilience of the remaining trees to multiple stressors, buying time for forest ecosystems to respond more incrementally to changing environmental drivers.

litter fall and associated litter and duff accumulations favor non-pine seedling establishment. The higher light environment may kill some of the advanced regeneration that has mostly shade foliage (Boardman 1977), but survivors are likely to have favorable growing conditions because of greater light and soil-moisture availability. In areas having a mixture of tree species differing in susceptibility to bark beetles, an outbreak might substantially shift forest composition, favoring, for example, incense cedar or hardwoods such as oaks (*Quercus* spp.), which would have better access to light (Millar and Stephenson 2015).

Tree mortality from bark beetles rather than from fire will have a notably different effect on competing vegetation, particularly the dominant shrub species in California's pine and mixed-conifer forest types (i.e., *Ceanothus* spp., *Arctostaphylos* spp., *Chamaebatia foliolosa*). Historically competition with these shrub species strongly influenced seral development because of their vigorous postfire response that is positively associated with fire severity (Zald et al. 2008). Bark-beetle-caused tree mortality is unlikely to stimulate as much shrub cover in the earlier years (i.e., 1–5 years following overstory mortality) because response will mainly be limited to the expansion of existing shrubs (figure 1). This difference following bark-beetle-caused mortality of the overstory, relative to what might be expected after a fire, may significantly limit habitat for many small mammals and bird species that benefit from patchy distribution of shrubs (Coppeto et al. 2006, White et al. 2015). On the other hand, hardwoods such as California black oak (*Quercus kelloggii*) may achieve a larger size and more quickly dominate the overstory following bark-beetle caused tree mortality because they are not killed (figure 1). Oak seedlings, which survive relatively well but grow slowly under the shade of a dense overstory, may also benefit from the increase in light at ground level and the absence of enhanced shrub cover that usually occurs after fire.

Managers working in areas affected by bark beetles in FF forests will need to consider a sequence of decisions depending on an area's condition and location. For small patches of tree mortality, little intervention may be needed, or may be limited to planting seedlings of the affected species if favorable seed sources are lacking or the species is absent or underrepresented in the surviving seedling/sapling cohort. Reintroducing fire could be an effective approach for managing fuels and tree density in these areas (figure 2b). Using fire in more extensive patches of tree mortality in FF forests will be more challenging due the potential impact to smaller trees combined with limited tree regeneration resulting from large distances to tree seed sources. In much of the forest, commercial salvage harvesting of bark-beetle-killed trees may be limited because of reduced wood value, high operational costs when roads are distant, and the lack of mill capacity for processing logs. Where salvage does occur, priority could be placed on whole tree removal in strategic locations where fire-management options depend on lower surface fuel loads (North et al. 2009).

In areas not salvaged, safety concerns will limit silvicultural treatments such as planting and shrub removal until most snags have fallen over (about 10 years). In these areas, prescribed fire or managed fire may be the most cost effective means of reducing accumulated biomass and will likely be a vital component of long-term management (figure 2b); otherwise, the accumulated dead fuels will place any naturally recruited or planted trees at risk of complete loss in the event of a wildfire (McGinnis et al. 2010). Areas that do burn under wildfire conditions (as opposed to prescribed fire) within 15–25 years after extensive mortality are prone to long-term conversion to shrub fields because of the potential loss of both established tree regeneration and seed source for postfire conifer regeneration (Coppoletta et al. 2016).

Effective use of prescribed or managed fire without killing the young regenerated or planted trees can be difficult in FF forests (Bellows et al. 2016), in part because surface fuels have become so heavy and continuous in the long-term absence of fire. However, an advantage of prescribed burning is that it can be conducted during times of higher live and woody fuel moistures. Such burns are often patchy, leaving at least some conifer regeneration intact. In addition, when soil and live fuel moisture is high, young shrubs tend to be heat sinks that are difficult to combust, limiting fire extent and reducing intensity. If trees are replanted, one option would be to wait until at least one burn has been completed or to scrape away litter, duff, and competing shrubs around seedlings to act as a buffer to fire spread. If prescribed fire is used, managers might wish to burn shortly after the needles of the recently killed trees have fallen so that the fire consumes fuels accumulated with fire exclusion and past logging plus recent inputs, thereby breaking up surface fuel continuity. A second fire could follow this initial burn in 10–15 years to consume some of the fallen large logs and branches. The reduced fuel continuity from the first burn would further increase patchiness and likely maintain more tree regeneration.

Most climate projections for the southwestern US suggest an increase in the severity and extent of future wildfire and drought events. If these projections are realized, it will be more important than ever to develop resilient forest conditions (i.e., a sufficiently low density of fire- and drought-tolerant trees in a heterogeneous mixture of size and age classes) and stable refugia that can serve as source populations when large-scale tree mortality events occur in FF forests, whether they are due to fire, drought, insects, or other disturbances. Practices that align forest conditions with topographic drivers of moisture availability will be important to the long-term persistence of forested landscapes (North et al. 2009). Making and varying restoration decisions on a fine scale will help to break up areas of homogeneity created by large, contiguous areas of high tree mortality (North et al. 2009). Managing for heterogeneity in forest structure, in both live and dead components, may become an essential bet-hedging strategy as interannual climate variability and the accompanying threat of transformational disturbances increases. One advantage of including fire in management plans, besides the obvious fuel reduction to mitigate the intensity of subsequent wildfires, is that fire under more moderate fire weather conditions can create considerable heterogeneity in vegetation composition and structure (Collins et al. 2016). For landscapes with large contiguous patches of tree mortality, this will help diversify the developing forest and increase resilience and adaption to future fire and drought events.

Managing for resilience and adaptation: Green forests as a priority

Although dealing with dead trees has become a focus of forest management on many lands in the western US (and a priority where human safety is compromised), for long-term resilience and adaptation to climate change, we need to move beyond triage (e.g., removal of dead and dying trees) to making "green" (live) FF forests more resilient to disturbances. Unfortunately, proactively treating forests to reduce density prior to wildfires, droughts, and bark beetle outbreaks is increasingly constrained. In fiscal year 2015, the USDA Forest Service spent 52% of its appropriated budget on wildfire suppression, up from 16% just two decades earlier (Stephens et al. 2016). Without significant changes, the share of the budget devoted to wildfire suppression could exceed 67% by 2025, equating to reductions of ~$700 million from other (nonfire) programs within the agency including funding for treatments that increase forest resilience and adaptation (USFS 2015). With declining budgets, public land agencies such as the USDA Forest Service have focused considerable staff time toward managing FF forest areas affected by large, high-severity wildfires—essentially chasing undesirable outcomes. Bark-beetle-caused tree mortality has only increased this focus. With disturbance frequency and severity increasing in many western US forests, the need for proactive management of FF adapted green forests has never been greater (Stephens et al. 2016).

Well-recognized tools and tactics are available for increasing the resilience of FF forests to disturbances (Stephens et al. 2012, Collins et al. 2014). For bark beetles, Fettig and Hilszczański (2015) defined direct control as short-term tactics designed to address current infestations by manipulating beetle populations (e.g., involving the use of insecticides, semiochemicals, and/or the harvest of currently infested trees). Indirect control is preventive in nature, and designed to reduce the probability and severity of future infestations by reducing the number of susceptible hosts through manipulating stand, forest, and landscape conditions with thinning, managed fire, prescribed burning, and/or altering age classes and tree species composition. Thinning to reduce stand density increases host tree vigor and reduces the vulnerability of forests to mortality from bark beetles (Fettig et al. 2007, Bradford and Bell 2017). It is unclear how the recent emphasis on variable density thinning (i.e., creating patterns of individual trees, clumps of trees, and canopy openings; Larson and Churchill 2012, Fry et al. 2014) may affect vulnerability to mortality. Future research is needed to elucidate potential differences in thinning approaches.

A recent summary of tree mortality patterns in the Sierra Nevada showed that high climatic water deficit was associated with mortality (Young et al. 2017). This suggests managers can identify such locations and if green forests are present, proactively target treatments to reduce forest density and increase drought resilience on these most at risk sites. Treatments such as prescribed fire and mechanical thinning of small–medium diameter trees are well documented to increase resilience in FF forests (Collins et al. 2014). Such treatments would reduce density-dependent tree mortality and increase spatial heterogeneity, prudent approaches for reducing vulnerability to many disturbances exacerbated by climate change (Fettig et al. 2013).

With limited resources and large areas of dead trees with little economic value, creating more resilient future forests may also hinge on co-opting disturbance opportunities and targeting treatments to reduce density and increase heterogeneity. Much of the "work" creating more resilient FF forests might come from leveraging disturbance and successional processes. For example, managers could capitalize on existing thinned or fuel-reduced areas as "anchor points" to facilitate the expanded use of prescribed fire or managed wildfire (North et al. 2015). Wildfires burning under less-than-extreme-fire weather conditions often have extensive areas of low- to moderate-severity fire effects that will help move stands toward more resilient conditions. In patchy areas of bark-beetle-caused tree mortality, thinning and reducing surface fuels in the adjacent green FF forest might minimize damage in the event of a wildfire. In larger dead-tree patches, creating a mosaic of different silvicultural treatments (i.e., partial salvage, experimental cluster tree planting, and reduction of shrub competition) would produce greater heterogeneity, and therefore likely greater resilience in the developing forest.

Conclusions

Unprecedented Sierra Nevada tree mortality has rapidly occurred after a severe drought with effects compounded by forest densification from decades of fire suppression. In the central and southern Sierra Nevada some areas have experienced more than 90% tree mortality, producing extensive landscapes of standing dead trees. This differs from mortality resulting from stand-replacing wildfire because bark beetles do not reduce surface fuels or jumpstart succession of shade-intolerant, fire-resistant pines. Forest managers have been struggling to determine whether these new post-mortality conditions will increase wildfire intensity and/or severity, what the near- and long-term effects on forest communities will be, and what the appropriate intervention measures are.

In the first decade, wildfire severity in bark beetle killed FF forests may be little affected over current conditions. Other than a brief increase during the "red phase" when most dead needles are still on recently killed trees, the reduction in canopy fuels is counterbalanced by an increase in surface fuels (figure 2). However, these are no grounds for complacency because current conditions in the majority of mixed-conifer and yellow pine forests in California already consist of unnaturally high surface fuel loads and corresponding elevated fire hazards (figure 2; Lydersen et al. 2014, Stephens et al. 2015). The more troubling projection is how extensive loading of large-sized woody fuels in future decades may contribute to dangerous mass fires beyond the predictive capacity of current fire models. These fires can generate their own wind and weather conditions and create extensive spotting, making fire behavior and its impact on structures and public safety difficult to manage and predict. In addition, such intense fires could prevent forests from becoming re-established. Lacking the legacy of live trees that historic FF would have left (Stephens et al. 2008), large unburned areas of dead trees may also produce unusual forest succession patterns. These patterns will likely favor shade-tolerant and hardwood tree regeneration, limited shrub growth, and accumulating large woody fuels that would likely kill regenerating forests when wildfire inevitably occurs. The scale of contiguous tree mortality entrenches the homogeneity produced by fire suppression, reducing the fine-scale heterogeneity of forest conditions that contributes to resilience and biodiversity. Management could enhance adaptation to climate-change-induced stress if it focused more of its resources on creating spatially and temporally variable patterns in green FF forests that are better aligned with local moisture availability and fire patterns (North et al. 2009).

Many of our FF forests have failed to receive the very management that could increase resilience to disturbances exacerbated by climate change, such as the application of prescribed fire and mechanical restoration treatments (Stephens et al. 2016). Recent tree mortality raises serious questions about our willingness to address the underlying causes. If our society doesn't like the outcomes from recent fires and extensive drought-induced tree mortality in FF forests, then we collectively need to move beyond the status quo. Working to increase the pace and scale of beneficial fire and mechanical treatments rather than focusing on continued fire suppression would be an important step forward.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

References cited

Agne MC, Woolley T, Fitzgerald S. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. Forest Ecology and Management 366: 73–86.

Asner GP, Brodrick PG, Anderson CB, Vaughn N, Knapp DE, Martin RE. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proceedings of the National Academy of Sciences 113: E249–E255.

Beers TW, Dress PE, Wensel LC. 1966. Aspect transformation in site productivity research. Journal of Forestry 64: 691–692.

Bellows RS, Thomson AC, Helmstedt KJ, York RA, Potts MD. 2016. Damage and mortality patterns in young mixed conifer plantations following prescribed fires in the Sierra Nevada, California. Forest Ecology and Management 376: 193–204.

Boardman N. 1977. Comparative photosynthesis of sun and shade plants. Annual Review of Plant Physiology 28: 355–377.

Boisramé G, Thompson S, Collins B, Stephens S. 2017. Managed wildfire effects on forest resilience and water in the Sierra Nevada. Ecosystems 20: 717–732.

Bradford JB, Bell DM. 2017. A window of opportunity for climate-change adaptation: Easing tree mortality by reducing forest basal area. Frontiers in Ecology and Environment 15: 11–17.

Carrier GF. 1984. Big fires. Combustion Science and Technology 39: 135–162.

Carrier GF, Fendell FE, Feldman PS. 1981. Criteria for Onset of Firestorms. Defense Technical Information Center. Report no. ADP001804.

———. 1985. Firestorms. Journal of Heat Transfer 107: 19–27.

Chandler CC. 1963. A Study of Mass Fires and Conflagrations. US Forest Service Pacific Southwest Research Station. Research Note no. PSW-N22.

Clark JS, et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22: 2329–2352.

Collins BM, Das AJ, Battles JJ, Fry DL, Krasnow KD, Stephens SL. 2014. Beyond reducing fire hazard: Fuel treatment impacts on overstory tree survival. Ecological Applications 24: 1879–1886.

Collins BM, Lydersen JM, Everett RG, Fry DL, Stephens SL. 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecological Applications 25: 1167–1174.

Collins BM, Lydersen JM, Fry DL, Wilkin K, Moody T, Stephens SL. 2016. Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire. Forest Ecology and Management 381: 74–83.

Coppeto SA, Kelt DA, Van Vuren DH, Wilson JA, Bigelow S. 2006. Habitat associations of small mammals at two spatial scales in the Northern Sierra Nevada. Journal of Mammalogy 87: 402–413.

Coppoletta M, Merriam KE, Collins BM. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26: 686–699.

Countryman CM. 1965. Mass fire characteristics in large-scale tests. Fire Technology 1: 303–317.

Covington WW, Fulé PZ, Moore MM, Hart SC, Kolb TE, Mast JN, Sackett SS, Wagner MR. 1997. Restoring ecosystem health in Ponderosa pine forests of the southwest. Journal of Forestry 95: 23–29.

Donato DC, Harvey BJ, Romme WH, Simard M, Turner MG. 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecological Applications 23: 3–20.

Dunbar-Irwin M, Safford HD. 2016. Climatic and structural comparison of yellow pine and mixed-conifer forests in northern Baja California (Mexico) and the eastern Sierra Nevada (California, USA). Forest Ecology and Management 363: 252–266.

Fellows AW, Goulden ML. 2012. Rapid vegetation redistribution in Southern California during the early 2000s drought. Journal of Geophysical Research 117 (art. G03025). doi:10.1029/2012JG002044

Fettig CJ. 2016. Native bark beetles and wood borers in Mediterranean forests of California. Pages 499–528 in Lieutier F, Paine TD, eds. Insects and Diseases of Mediterranean Forest Systems. Springer.

Fettig CJ, Hilszczański J. 2015. Management strategies for bark beetles in conifer forests. Pages 555–584 in Vega FE, Hofstetter RW, eds. Bark Beetles: Biology and Ecology of Native and Invasive Species. Springer.

Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, Nowak JT. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238: 24–53.

Fettig CJ, Reid ML, Bentz BJ, Sevanto S, Spittlehouse DL, Wang T. 2013. Changing climates, changing forests: A western North American perspective. Journal of Forestry 111: 214–228.

Finney MA, McAllister SS. 2011. A review of fire interactions and mass fires. Journal of Combustion 4 (art. 548328).

Fry DL, Stephens SL, Collins BM, North MP, Franco-Vizcaino E, Gill SJ. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. PLOS ONE 9 (art. e88985).

Hart SJ, Schoennagel T, Veblen TT, Chapman TB. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences 112: 4375–4380.

Harvey BJ, Donato DC, Romme WH, Turner MG. 2014. Fire severity and tree regeneration following bark beetle outbreaks: The role of outbreak stage and burning conditions. Ecological Applications 24: 1608–1625.

Hicke JA, Johnson MC, Hayes JL, Preisler HK. 2012. Effects of bark beetle–caused tree mortality on wildfire. Forest Ecology and Management 271: 81–90.

Hoffman CM, Morgan P, Mell W, Parsons R, Strand E. Cook S. 2013. Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. Forest Science 59: 390–399.

Hoffman CM, Linn R, Parsons R, Sieg C, Winterkamp J. 2015. Modeling spatial and temporal dynamics of wind flow and potential fire behavior following a mountain pine beetle outbreak in a lodgepole pine forest. Agricultural and Forest Meteorology 204: 79–93.

Jolly WM, Parsons RA, Hadlow AM, Cohn GM, McAllister SS, Popp JB, Hubbard RM, Negron JF. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. Forest Ecology and Management 269: 52–59.

Jones GM, Gutiérrez RJ, Tempel DJ, Whitmore SA, Berigan WJ, Peery MZ. 2016. Megafires: An emerging threat to old-forest species. Frontiers in Ecology and the Environment 14: 300–306.

Knapp EE, Skinner CN, North MP, Estes BL. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 310: 903–914.

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS. 2016. Observed and anticipated impacts of drought on forests insects and diseases in the United States. Forest Ecology and Management 380: 321–334.

Larson AJ, Churchill D. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267: 74–92.

Levine CR, Cogbill CV, Collins BM, Larson AJ, Lutz JA, North MP, Restaino CM, Safford HD, Stephens SL, Battles JJ. 2017. Evaluating a new method for reconstructing forest conditions from General Land Office survey records. Ecological Applications 27: 1498–1513. doi:10.1002/eap.1543

Linn RR, Sieg CH, Hoffman CM, Winterkamp JL, McMillin JD. 2013. Modeling wind fields and fire propagation following bark beetle outbreaks in spatially-heterogeneous pinyon-juniper woodland fuel complexes. Agricultural and Forest Meteorology 173: 139–153.

Lydersen JM, North MP, Collins BM. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. Forest Ecology and Management 328: 326–334.

Mallek C, Safford H, Viers J, Miller J. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4 (art. 153).

McGinnis TW, Keeley JE, Stephens SL, Roller GB. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. Forest Ecology and Management 260: 22–35.

Meigs GW, Zald HSJ, Campbell JL, Keeton WS, Kennedy RE. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11 (art.045008).

Minnich RA, Barbour MG, Burk JH, Fernau RF. 1995. Sixty years of change in California conifer forests of the San Bernardino Mountains. Conservation Biology 9: 902–914.

Minnich RA, Goforth BR, Paine TD. 2016. Follow the water: Extreme drought and the conifer forest pandemic of 2002–2003 along the California borderland. Pages 859–890 in Lieutier F, Paine TD, eds. Insects and Diseases of Mediterranean Forest Systems. Springer.

Millar CI, Stephenson NL. 2015. Temperate forest health in an era of emerging mega disturbance. Science 349: 823–826.

Miller JD, Thode AE. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). Remote Sensing of Environment 109: 66–80.

North M, Stine P, O'Hara K, Zielinski W, Stephens S. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. US Department of Agriculture, Forest Service, Pacific Southwest Research Station. General Technical Report no. PSW-GTR-220.

North MP, Stephens SL, Collins BM, Agee JK, Aplet GH, Franklin JF, Fule PZ. 2015. Reform forest fire management. Science 349: 1280–1281.

North MP, Collins BM, Safford HD, Stephenson NL. 2016. Montane forests. Pages 553–577 in Mooney H, Zavaleta E, eds. Ecosystems of California. University of California Press.

Page WG, Jenkins MJ, Runyon JB. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Canadian Journal of Forest Research 42: 1631–1647.

Parker AJ. 1982. The topographic relative moisture index: An approach to soil-moisture assessment in mountain terrain. Physical Geography 3: 160–168.

Perrakis DDB, Lanoville RA, Taylor SW, Hicks D. 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands British Columbia, Canada. Fire Ecology 10: 10–35. doi:10.4996/fireecology.1002010

Pitts WM. 1991. Wind effects on fires. Progress in Energy and Combustion Science 17: 83–134.

Preisler HK, Grulke NE, Heath Z, Smith SL. 2017. Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. Forest Ecology and Management 399: 166–178.

Prichard SJ, Kennedy MC. 2014. Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. Ecological Applications 24: 571–590.

Quintiere JG. 1993. Canadian mass fire experiment. Journal of Fire Protection Engineering 5: 67–78.

Raposo JR, Cabiddu S, Viegas DX, Salis M, Sharples J. 2015. Experimental analysis of fire spread across a two-dimensional ridge under wind conditions. International Journal of Wildland Fire 24: 1008–1022.

Rothermel RC. 1983. How to Predict the Spread and Intensity of Forest and Range Fires. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. General Technical Report no. INT-143.

Safford HD, Stevens JT. 2017. Natural range of variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. US Department of Agriculture, Forest Service, Pacific Southwest Research Station. General Technical Report no. PSW-GTR-256.

Schoennagel T, et al. 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences 114: 4582–4590. doi:10.1073/pnas.1617464114

Show SB, Kotok EI. 1924. The Role of Fire in the California Pine Forests. US Department of Agriculture. Bulletin no. 1294.

Simard S, Romme WH, Griffin JM, Turner MG. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81: 3–24.

Small RD, Larson DA, Brode HL, 1983. Fluid dynamics of large area fires. Pages 47–54 in Quintiere JG, Alpert RL, Altenkirch RA, eds. Proceedings of the Twenty-First National Heat Transfer Conference. Society of Mechanical Engineers.

Stephens SL. 2004. Fuel loads, snag density, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in northwestern Mexico. Forest Ecology and Management 199: 103–113.

Stephens SL, Skinner CN, Gill SJ. 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. Canadian Journal of Forest Research 33: 1090–1101.

Stephens SL, Fry D, Franco-Vizcano E. 2008. Wildfire and forests in Northwestern Mexico: The United States wishes it had similar fire “problems.” Ecology and Society 13 (art. 10).

Stephens SL, Millar CI, Collins BM. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. Environmental Research Letters 5 (art. 024003).

Stephens SL, McIver JD, Boerner REJ, Fettig CJ, Fontaine JB, Hartsough BR, Kennedy P, Schwilk DW. 2012. Effects of forest fuel-reduction treatments in the United States. BioScience 62: 549–560.

Stephens SL, Lydersen JM, Collins BM, Fry DL, Meyer MD. 2015. Historical and current landscape-scale Ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6 (art. 79).

Stephens SL, Collins BM, Biber E, Fulé PZ. 2016. US federal fire and forest policy: Emphasizing resilience in dry forests. Ecosphere 7 (art. e01584).

Stevens JT, Collins BM, Miller JD, North MP, Stephens SL. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management 406: 28–36.

Taylor AH, Skinner CN. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13: 704–719.

Trelles J, Pagni PJ. 1997. Fire-induced winds in the 20 October 1991 Oakland Hills fire. Fire Safety Science 5: 911–922.

[USDA–FS] US Department of Agriculture–Forest Service. 2016a. New Aerial Survey Identifies More than 100 Million Dead Trees in California. News Release no. 0246.16, 18-November-2016, USDA–FS.

———. 2016b. Aerial Detection Survey GIS Data. Forest Health Protection, US Forest Service Pacific Southwest Region. (29 November 2017; *www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696*).

[USFS] US Forest Service. 2015. The rising cost of fire operations: Effects on the US Forest Service’s non-fire work. USFS. (29 November 2017; *www.fs.fed.us/sites/default/files/2015-Fire-Budget-Report.pdf*)

Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH. 2009. Widespread increase of tree mortality rates in the western United States. Science 323: 521–524.

Walker R, Rosenberg M, Warbington R, Schwind B, Beardsley D, Ramirez C, Fischer L, Frerichs B. 2006. Inventory of Tree Mortality in Southern California Mountains (2001–2004) Due to Bark Beetle Impacts. Fire and Resource Assessment Program, California Department of Forestry and Fire Protection.

White AN, Manley PN, Tarbill GL, Richardson TW, Russell RE, Safford HD, Dobrowski SD. 2015. Avian community responses to post-fire forest structure: Implications of fire management in mixed conifer forests. Animal Conservation 19: 256–264.

Young DJN, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecology Letters 20: 78–86.

Zald H, Gray A, North M, Kern R. 2008. Initial regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. Forest Ecology and Management 256: 168–179.

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