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 recurrent 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 non-lethal 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
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
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

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**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.
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 60m² 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
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).

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 Hilszczanski (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 homogenity 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.

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Scott L. Stephens (sstephens@berkeley.edu) is affiliated with the Department of Environmental Science, Policy, and Management at the University of California, in Berkeley. Brandon M. Collins is with the Center for Fire Research and Outreach at the University of California, in Berkeley. Christopher J. Fettig and Malcolm P. North are affiliated with the US Department of Agriculture (USDA) Forest Service, Pacific Southwest Research Station, in Davis, California. Mark A. Finney is with the USDA Forest Service, Rocky Mountain Research Station, in Missoula, Montana. Chad M. Hoffman is affiliated with the Department of Forest and Range Stewardship at Colorado State University, in Fort Collins. Eric E. Knapp is with the USDA Forest Service, Pacific Southwest Research Station, in Redding, California. Hugh Safford and Rebecca B. Wayman are affiliated with the Department of Environmental Science and Policy at the University of California, in Davis; HS is also with the USDA Forest Service, Pacific Southwest Region, in Vallejo, California.