Forest responses to increasing aridity and warmth in the southwestern United States

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In recent decades, intense droughts, insect outbreaks, and wildfires have led to decreasing tree growth and increasing mortality in many temperate forests. We compared annual tree-ring width data from 1,097 populations in the coterminous United States to climate data and evaluated site-specific tree responses to climate variations throughout the 20th century. For each population, we developed a climate-driven growth equation by using climate records to predict annual ring widths. Forests within the southwestern United States appear particularly sensitive to drought and warmth. We input 21st century climate projections to the equations to predict growth responses. Our results suggest that if temperature and aridity rise as they are projected to, southwestern trees will experience substantially reduced growth during this century. As tree growth declines, mortality rates may increase at many sites. Increases in wildfires and bark-beetle outbreaks in the most recent decade are likely related to extreme drought and high temperatures during this period. Using satellite imagery and aerial survey data, we conservatively calculate that ≈2.7% of southwestern forest and woodland area experienced substantial mortality due to wildfires from 1984 to 2006, and ≈7.6% experienced mortality associated with bark beetles from 1997 to 2008. We estimate that up to ≈18% of southwestern forest area (excluding woodlands) experienced mortality due to bark beetles or wildfire during this period. Expected climatic changes will alter future forest productivity, disturbance regimes, and species ranges throughout the Southwest. Emerging knowledge of these impending transitions informs efforts to adaptively manage southwestern forests.

forest mortality | climate change | drought | fire | tree rings

Intense droughts in recent decades have been linked with extensive tree mortality in many temperate regions globally (1). Attribution of the causes of such mortality within forest ecosystems is challenging because wildfire, insect pests and diseases, invasive species, and land-use effects (e.g., grazing, fire suppression) all interact with climatic effects, confounding interpretation of mortality drivers. Forest vegetation is particularly sensitive to changes in moisture availability in semiarid landscapes (2). Within the southwestern (SW) United States (US), rapid and extensive changes in forests and woodlands recently have been associated with drought-related tree mortality, including attacks by cambium-feeding beetles and severe wildfires (1, 3–5). Land-use effects, however, probably also have contributed to changing wildfire regimes, particularly in SW ponderosa pine forests (6). High severity wildfires in SW forests can result in a multidecadal (or longer) failure of some forest stands to regenerate, converting large patches to grassland or shrubland (7). If warming continues and further amplifies severities and extent of climate-related disturbances in the SW US, the ability of forests to recover to previous species composition may be limited.

Here, we develop statistical models of SW tree-ring growth responses to variability in precipitation, temperature, and relative humidity during the 20th century. We apply these models to four scenarios of 21st century climate to evaluate anticipated changes in stem growth of three widespread conifers in the SW US. Projected changes in SW tree growth are compared with trends across the coterminous US. We also compile mapped polygons of severe wildfires and tree mortality attributed to bark beetles in SW forests over the past two decades to evaluate trends and magnitudes of these disturbances. We place our observations and syntheses in the context of long-term knowledge of climate variability and disturbance history in this region. Finally, we discuss implications for concepts of sustainability and management of forests and woodlands in the face of probable increasing temperature and drought in coming decades.

Recent Climate Change and Vegetation Responses

Within the continental US, average annual temperature increased during the 20th century by ≈0.65 °C (PRISM Climate Group, www.prismclimate.org, created February 2004), comparable with the global mean temperature trend (8). The most extreme warming of the century occurred throughout the northern and western US, whereas cooling occurred throughout much of the Southeast. Since the mid-1970s, temperature trends throughout the coterminous US have been typically positive, and the SW US has warmed particularly rapidly (Fig. S1). SW precipitation decreased and droughts intensified during this period (9, 10), stressing plant species (e.g., refs. 2 and 5). Moreover, as expected from physical models, higher elevations have experienced relatively greater warming than low elevations (11), likely contributing to reduced snowpack and earlier arrival of spring (12). Warmer winters and earlier springtime drying of soils and forest fuels are probably linked to increasing numbers of large wildfires and total area burned in western US forests (4, 13). Recent warming and drought probably also have altered bark-beetle distributions and population dynamics, partly driving unusually extensive bark beetle outbreaks in western North America (14).

Although there is high variability among global circulation model projections of precipitation patterns, a broad consensus exists among climate models that warming and associated increased potential evapotranspiration will cause more negative water balances in the SW US by the mid-21st century (8, 15), regardless of precipitation trends. Considerable uncertainty remains, however, about short-term (annual to decadal) future changes because a high degree of spatial and temporal heterogeneity in climate has occurred naturally and historically in this region (16). The mechanisms driving variability are only partly

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understood, but it is evident that seasonal to decadal climate variations in the SW US are related to atmospheric circulation patterns affected by ocean-atmosphere oscillations (e.g., ENSO, PDO, and AMO) (15).

Among broad vegetation types affected by climate change, forests and woodlands are of particular concern because changes in their growth, demography, species composition, and proportion of land cover can substantially affect biogeochemistry and hydrological processes. Affected processes include water and carbon cycling, and surface properties such as erosivity, albedo, and snowmelt dynamics (8, 17). Within tree populations, climate-driven changes in productivity and demography commonly occur first and most apparently near species-specific range boundaries (18, 19), although high levels of tree mortality also are observed at historically favorable, non-ecotone sites (1). Overall, novel species assemblages are anticipated because of changed climates (20), resulting in pervasive and complex forest ecosystem responses (8).

Continental-Scale Tree-Ring Analyses and Southwestern Patterns

Drought-driven alterations in forest and woodland demography, such as tree natality and mortality, have been primarily observed in case studies focusing on relatively small regions and short time periods (1, 3) because the temporal and spatial coverages of forest demography and growth data are insufficient for broader studies. Conveniently, many species of long-lived trees leave records of their growth over centuries by forming annual rings, offering a means to reconstruct past climate effects over broad regions. In locations where tree growth is limited by moisture availability and/or temperature, wide rings are generally formed during seasons or years of optimal climatic conditions. Thin rings develop in response to poor conditions (21, 22).

Here, we use 1,097 standardized ring-width index (RWI) records from the continental US, archived in the International Tree-Ring Databank (ITRDB), maintained by the National Climate Data Center. The SW part of the US is represented by 235 RWI chronologies. All chronologies overlap for at least 60 y (rings) with the modern climate record [1895 common era (CE) onward]. Each chronology is an average annual time series of standardized ring-width measurements from 10 to 30 trees (typically) of the same species within a local population. Raw ring-width measurements were standardized to remove long-term biological growth trends associated with tree age and trunk diameter, but still preserve interannual and interdecadal variability, often associated with climate variability (23). All standardization was carried out by the original scientists who contributed the chronologies to the ITRDB. See Fig. S2 and *SI Text* for additional discussion of the RWI datasets.

The SW RWI records are well-correlated with drought-related climate variables relative to the entire dataset. SW tree-ring growth responses typically had a highly positive correlation with interannual variability in total precipitation and a highly negative correlation with daily maximum temperature during spring through summer (Fig. 1; see Fig. 2 for delineation of the SW region used in this analysis).

To evaluate past (20th century, instrumental) and projected (21st century, simulated) tree-ring growth responses to climate, we used step-wise multiple linear regression of instrumental seasonal climate data on RWI records. We calculated an equation that uses annual climate data to predict RWI values for each of the 1,097 RWI records. Variables used as RWI predictors were precipitation, mean daily maximum temperature, mean daily minimum temperature, and mean relative humidity. We considered seasonal climate data (October–December, January–March, April–June, and July–September) because growth response to meteorological conditions varies before and throughout the growing season.

We applied the growth equations to projected future climate data to estimate the directions and relative magnitudes of climate-induced changes in tree growth throughout the continental United States (see *SI Text* for more on the growth models). In a cross-validation analysis, 78% (853) of the 1,097 growth equations produced modeled RWI values that correlated very significantly (cross-validated $P < 0.001$) with the original corresponding record. Of the modeled RWI records from the SW US, 97% (228) correlated very significantly with their corresponding original records while 72.5% (625) of non-SW modeled records correlated very significantly.

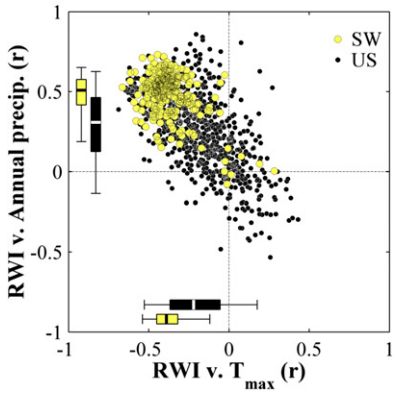

Fig. 1. Each RWI record's correlation with (*x* axis) April–September mean daily maximum temperature (T_{max}) and (*y* axis) annual precipitation. Yellow points represent the 235 RWI records within the SW US. Black points represent the 862 records from the rest of the continental US. See Fig. 2 for outlines of these regions. Box plots parallel to the axes represent the regional distributions of correlation coefficients and follow the same color scheme as the scatter plot. Boxes bound the inner quartiles. Whiskers bound the inner 90%. Thick lines within boxes represent the median.

We applied the 853 well-performing growth equations to four distinct scenarios of future climate to calculate predicted 2050–2099 RWI values and compare them to those modeled using climate data from 1950 to 1999. The climate scenarios assumed business-as-usual emission practices throughout the 21st century (A2); a gradual decrease in annual emissions after 2050 (A1B); and linear climate trends established during the past 114 and 30 y. Projected changes in RWI for these four climate scenarios demonstrate that the SW region and Colorado Rockies particularly stand out as likely to experience the largest and most widespread decreases in growth among the continental US tree populations represented in the ITRDB (Fig. 2).

Direct extrapolation of these results to all coterminous US forests is not valid because the ITRDB does not represent a random sampling of tree populations. Many sites (and individual trees) were sampled because they were in topographic and ecological conditions likely to promote climatic responsiveness (particularly drought). Therefore the tree-ring width dataset may overrepresent drought sensitivity. Alternatively, these data may underrepresent drought sensitivity because long-lived trees were commonly sampled for tree-ring studies. On dry sites, long-lived trees have typically survived chronic water stress and many previous droughts, so they may be more drought resilient than unsampled, drought-killed trees that died relatively young in these locations (24). It is unknown how regional tree-ring chronology estimates of growth variations and trends may correlate with potentially more representative forest growth estimates (e.g., Forest Inventory and Analysis data). In any case, it is evident that the majority of the broadly distributed SW tree populations represented in the ITRDB are sensitive to drought. Trees within these populations are likely to suffer decreases in annual growth rates if plant water stress increases because of rising temperatures and/or decreased precipitation.

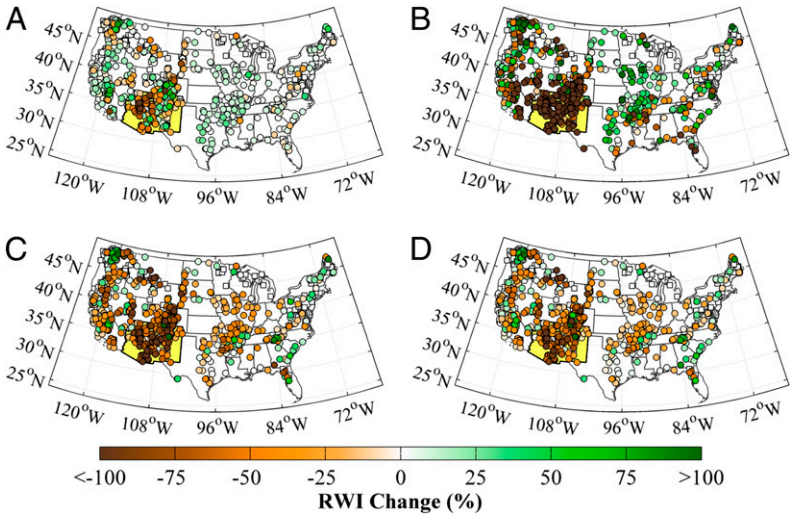

Fig. 2. Modeled percent change in mean RWI between the periods of 2050–2099 and 1950–1999. Climate scenarios were the linear continuations of climate trends established from 1896 to 2008 and 1979 to 2008 (*A* and *B*), respectively, and the A2 and A1B scenario from the NCAR CCSM3 model (*C* and *D*), respectively. Circles represent locations of the 853 tree-ring RWI records from the ITRDB used in analyses. White squares indicate the other 244 sites where the growth predictors did not accurately model RWI values. The yellow area is the zone considered to be the SW US. (Reprinted with permission from ref. 49.)

Of the SW RWI records, >90% represent one of three common tree species in these forests: piñon pine (*Pinus edulis*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*). These species are dominants in mixed species stands arrayed along elevation and moisture gradients, from piñon at semiarid lower elevations through ponderosa pine forests at middle elevations, up into relatively mesic, montane forests including Douglas-fir. There are no statistical differences among our projections of growth changes among these species, regardless of the climate scenario considered; each species is projected to experience broad declines in growth as temperatures rise and water availability decreases (Table S1). At least three-quarters of the SW populations sampled for each species are projected to experience decreased growth in the IPCC A2 scenario (Fig. 3*A*). This reduction is mainly due to projected increases in temperature. Applying a hypothetical increase of 4 °C to climate records from 1950 through 1999 (all other climate variables left unchanged) generally causes more severe decreases in modeled RWI values (Fig. 3*A*).

At relatively warm sites in the SW US, ponderosa pine and Douglas-fir ring widths tend to respond more negatively to increased spring and summer daily maximum temperatures (Fig. 3*B*). Thus, populations at warmer sites are also predicted to respond more negatively to the A2 climate scenario (Fig. 3*B*). No such trend was apparent for piñon pine, potentially because there were no piñon samples from the warmest and coolest sites. Although RWI records do not explicitly indicate mortality, this analysis suggests that SW ponderosa pine and Douglas-fir trees may be at greatest risk of drought-induced mortality at warmer, lower-elevation ecotones. In at least some areas, ponderosa and Douglas-fir mortality in New Mexico was greatest at lower elevations of their respective distributions (e.g., ref. 24), whereas piñon death tended to occur more broadly across elevations and stand densities. The broad mortality across piñon populations may have occurred because drought stress was so extreme, and the associated piñon *Ips* bark beetle irruption so great, that the effects of other factors were obscured (25).

Although the growth equations used in this study only characterize linear relationships with climate, actual growth–climate relationships are typically nonlinear (see *SI Text* for more on this). This nonlinear relationship between tree growth and drought is clear when many SW RWI records are evaluated at

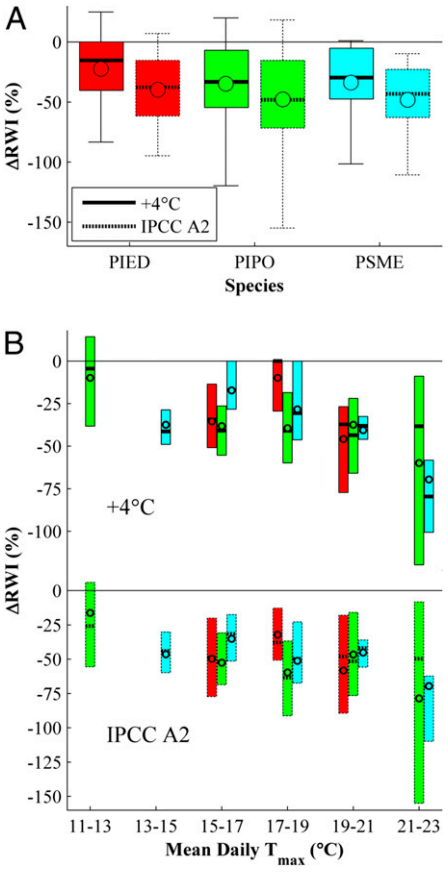

Fig. 3. Box plots of projected percent change in mean SW RWI between the periods of 2050–2099 and 1950–1999 given 4 °C warming (solid lines) and the IPCC A2 climate scenario (dashed lines). Plots are classified by species (*A*) and species and mean daily maximum temperature (*B*). Boxes bound the inner quartiles. Whiskers in *A* bound the inner 90%. Thick horizontal lines within boxes represent median values. Circles represent means. Red, piñon pine (*P. edulis*, PIED; $n = 60$); green, ponderosa pine (*P. ponderosa*, PIPO; $n = 86$); cyan, Douglas-fir (*P. menziesii*, PSME; $n = 68$). In *B*, all box plots represent at least eight populations.

once. RWI is highly responsive to winter precipitation at many dry sites and relatively unresponsive at all wetter sites (Fig. 4). This effect holds across the three main species discussed above but is particularly strong across piñon pine and Douglas-fir records. The implication is that if warming continues and effective moisture becomes increasingly less available, populations of these species may become increasingly sensitive to drought and at risk for mortality. This conclusion is supported by several recent studies. First, regional warming and consequent water deficits throughout the 20th century have been implicated as drivers of increased background (noncatastrophic) tree mortality rates across species, climate zones, size classes, and age classes throughout the western US (26). Second, recent experiments found that a 4 °C warming caused drought-stressed piñon pine to die 30% more rapidly (27).

It is not possible to directly translate tree-ring width analyses into quantified estimates of future drought-induced tree mortality because ring widths inherently represent the growth of living trees (although tree rings have been related to mortality risk; ref. 28) and the multiple mechanisms driving drought-induced mortality are still poorly understood (1, 29). Most coniferous species studied in the SW US (including the three species evaluated here) display an isohydric physiological response to water stress (29, 30), where drought induces stomatal closure to limit water loss, constraining photosynthesis and eventually causing "carbon starvation" and tree death. Carbon-starved trees are less able to fend off tree-killing bark beetles (29). Warm and dry conditions can also accelerate bark-beetle population increases, in some cases triggering major irruptions that cause or amplify mortality in already stressed tree hosts (14). In addition, for anisohydric tree species that do not regulate stomatal closure as sensitively (e.g., junipers), critically low soil-moisture levels during severe droughts can cause permanent cavitation of water columns within the stem xylem (29), resulting in partial dieback or whole plant mortality. Because increased temperatures would tend to lead to increased duration, magnitude, and frequency of SW drought (9, 15), anisohydric tree species have also been projected to experience increased direct drought-induced mortality in coming decades, such as observed for junipers in parts of the SW US during the 2000s (25). Although our growth projections are based on relatively simple statistical models of past RWI behavior, current mechanistic theories of physiological mortality processes support our predictions that increased warming and drying should cause more mortality of piñon pine, ponderosa pine, and Douglas-fir trees within the SW US.

Extensive Tree Mortality Due to Fires and Bark Beetles

Although much remains to be understood regarding mechanisms of tree mortality as a direct result of drought, there is general agreement that historical and current drought episodes and recently elevated temperatures have contributed to the recent increase in widespread fires and bark-beetle outbreaks in the SW US (3, 5, 14). Using annual aerial survey data provided by the US Forest Service (USFS) Health Technology Enterprise Team, ranges in estimates of areas affected were produced by implementing various definitions of extensive mortality, forest, woodland, and Southwest (Table S2). We conservatively estimate that 7.6–11.3% of SW forest and woodland area was affected by extensive tree mortality due to bark beetles from 1997 through 2008. Using interpreted satellite data provided by the USFS Monitoring Trends in Burn Severity (MTBS) project, we estimate that at least 2.7–3.0% of SW forest and woodland area was affected by stand-replacing fire with moderate to severe burn severity from 1984 through 2006 (Fig. 5). Fire and bark beetles combined caused high levels of mortality in 14–18% of SW forest areas (excluding woodlands).

The annual area affected by each of the two disturbances was quite episodic in nature (Figs. S3–S5), probably reflecting climate variations and their complex effects on vegetation, fire, and insect population dynamics. Within forested areas, the fraction of annual area burned by severe fires has increased substantially since 1984, with a declining fraction of area burned by relatively low severity fires (Fig. S6*B*). Interestingly, the opposite is true for woodlands (Fig. S6*C*). The cause of this pattern is unknown, but it may be related to a rising extent of highly flammable, invasive grasses in lower elevation areas. Many SW forests and woodlands have also been impacted by livestock grazing, fire suppression, fuel wood harvesting, logging, and other land uses (6, 31). Increased surface fuels and forest densities are most clearly documented for SW ponderosa pine forests. These changes have likely also contributed to wildfire and insect outbreak changes in recent decades (6).

Historical ecology studies of SW forests show extensive wildfires and bark-beetle infestations to be natural disturbance processes linked to climate variability (3, 31–34). For example, tree-ring data suggest that regionally extensive droughts in the late 1200s and late 1500s CE caused increased tree mortality throughout the SW US (3). Additionally, recent sedimentary charcoal studies identified cases of unusually severe wildfire events (but of unknown extent) in some SW forests dating to the 1200s CE period, and during warm mid-Holocene periods (32). More recently, mortality of many SW tree species occurred during the severe drought of the 1950s (3, 18). Since 1980, levels of tree mortality from bark beetle infestations and wildfires likely are the highest and most extensive in the documented record of the past ~90 y, with linkages to both drought and warmth (e.g., refs. 4, 5, 14, and 27).

The consequences of elevated rates of mortality for long-term forest and woodland sustainability are unclear. Continued warm-

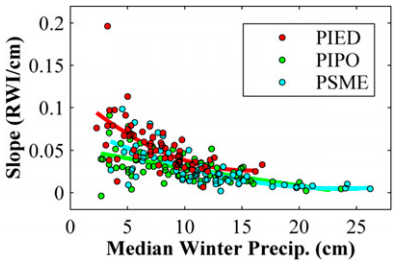

Fig. 4. SW ring-width response to winter precipitation plotted against median winter precipitation from 1896 to 2008. Response is the slope of the regression of annual RWI versus winter (January–March) precipitation in centimeters.

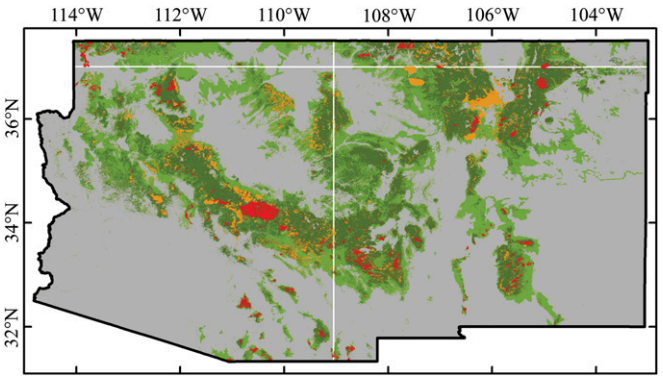

Fig. 5. Map of SW forest and woodland mortality due to bark beetles from 1997 to 2008 (orange) and wildfire (red) from 1984 to 2006. Dark green areas are conifer and mixed forest. Light green areas are piñon/juniper woodland. Gray areas are nonforest or hardwood/shrub woodland landscapes. White lines are state boundaries. Bark-beetle-induced mortality covered 18,177 km^2, and wildfire induced mortality covered 6,420 km^2.

ing and drought should result in more tree mortality, but at some point we would expect fire and insect outbreak disturbance processes to be spatially self-limiting. Severe stand-replacing fires, for example, can only occur in some forests or woodlands at intervals sufficiently long enough for continuous overstory vegetation (fuels) to re-establish. Given an estimate of 18% cumulative forest mortality during the 25-y period from 1984 to 2008, SW forest area could be reduced or converted to nonforest types by >50% with only two more recurrences of droughts and dieoffs similar or worse than the recent events. This is obviously a rough approximation, ignoring self-limiting effects, regeneration, and other complexities, so there is considerable uncertainty about how much forest and woodland may be converted in coming decades.

Managing Forests and Woodlands in the Southwest Given Climatic Change Risks

The high sensitivity of growth and mortality rates within SW forests to drought and warmth presents significant challenges in managing for sustainability. Knowledge of such historical patterns and processes informs our efforts to manage in the face of future change (3, 6, 33, 34), even while recognizing that anthropogenic land uses increasingly impose novel environmental challenges (35). In addressing these challenges, decisionmakers benefit by ranking vulnerabilities, assessing capacities to respond, and implementing short- and long-term adaptation plans (36).

Our tree-ring analyses suggest that ponderosa pine and Douglas-fir tend to be sensitive to drought and rising temperatures in warm and dry locations where forests may be most prone to fire and insect/disease effects. Piñon pine populations evaluated in this study appear to be sensitive throughout their SW distribution. For all three tree species evaluated, vulnerability to high mortality rates due to fire or drought-induced die-off is likely greatest in ecotones and dense stands where fuel build-up is high. These locations might be prioritized to receive the highest attention for active intervention. A triage or other vulnerability analysis could evaluate locations where stand-improvement treatments are likely to be successful (live trees remain, epidemic is in early stage) or if an epidemic has progressed such that trees are likely to die regardless of management. In the latter case, these locations could be further evaluated for priority of regeneration treatments, where the focus is on early eradication of invasive species and retention of forest cover rather than succession to shrub- or grasslands.

In management contexts, local assessments are critical. Regional projections such as ours begin the prioritization exercise, but because ecological trajectories and management efficacy occur at forest-stand and watershed scales, higher-resolution monitoring and trend analyses are needed to identify vulnerable targets for management (37). Once forest landscapes are assessed for risk at regional and local scales, inherent capacities to respond to treatment can inform development of specific sustainability goals. A range of policy options exists, from conservative to highly anticipatory and proactive, with the decision guided by the vulnerability assessment. For highest value resources, and in situations where capital allows significant investment, managing to resist undesired change is a defensible short-term goal (36). Tools include fuels treatment and focused fire-suppression efforts, intensive use of insect-aggregating hormones, and early detection-rapid response to eliminate aggressive invasive species. Although efforts like these might seem to deny the inevitability of change, there are local situations where such labors and expenses are warranted. These actions almost always are undertaken as short-term projects, with recognition that they are stop-gap measures in the face of projections of rapid climate change.

More appropriate at landscape scales in the SW US are treatments where the goal is to promote sustainable forests by increasing resilience to the multiple stresses exacerbated by climate change (38). Resilience goals may aim to maintain communities as forests rather than allow conversion to scrublands or grasslands, despite the likelihood of significant changes in stand structure and species composition within forests. Working with disturbances may be an effective strategy to promote landscape-scale goals widely and to move forests toward greater spatial and within-stand diversity (39, 40). For example, patch-mosaics of low to high severity burned and unburned areas caused by recent wildfires may offer timely opportunities to conduct prescribed burning and other fuel treatments more safely and effectively, because fuel amounts and continuity have been reduced. Implementing fuel-reduction treatments is commonly prescribed to promote health of stands and increase ecosystem resilience (39, 40). Recognizing and promoting genetic adaptation by enabling natural-selection processes of selective survival and mortality is another resilience strategy (41).

Assisting the transition to new ecosystem states and developing adaptation strategies for the longer term involves acknowledgment that many SW forests at vulnerable ecotones and in locations sensitive to fire and insect/disease may convert to nonforest vegetation types. In these situations, managing for adaptation means promoting efforts that sustain desired long-term ecosystem functions and services (42, 43), such as air-quality protection, soil and watershed health, promotion of native flora and fauna, and maintenance of diverse amenity functions, even in the face of eventual loss of forest cover in many or most areas. Restoration efforts in this dynamic context must move beyond frameworks where historic structure and composition are fixed targets for recovery (33, 40, 44). In special cases, however, highly valued species, ecosystems, and places might be targeted for extraordinary efforts to maintain past structures and functions (e.g., rare plant species habitats and ancient groves). A more general and effective goal is to maintain and restore ecological processes, where capacity exists, achieved by means of creative manipulation (43, 45). In moving toward novel future environments, cautious experimentation is merited. For instance, the use of new mixtures of native plant species, nontraditional diversity of native germplasm provenances, and out-plantings of native species into extranative locations merit consideration in adaptation planning (46). A fundamental requirement of all approaches to sustainability in the face of high uncertainty is the capacity to conduct and carry out long-term monitoring and adaptive-management strategies (47). Learning from change at local through national policy levels is essential for sustaining SW forests and functions in the face of climate challenges. Because these changes and ecological adaptations will play out at broad landscape scales, interdisciplinary, interagency, and long-term collaborations are key to success (47, 48).

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