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Annual Review of Plant Biology

Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide

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Keywords

global forests, dynamic global vegetation models, forecasting, forest assessment, remote sensing, mortality mechanisms, hotter drought

Abstract

Recent observations of elevated tree mortality following climate extremes, like heat and drought, raise concerns about climate change risks to global forest health. We currently lack both sufficient data and understanding to identify whether these observations represent a global trend toward increasing tree mortality. Here, we document events of sudden and unexpected elevated tree mortality following heat and drought events in ecosystems that previously were considered tolerant or not at risk of exposure. These events underscore the fact that climate change may affect forests with unexpected force in the future. We use the events as examples to highlight current difficulties and challenges for realistically predicting such tree mortality events and the uncertainties about future forest condition. Advances in remote sensing technology and greater availably of high-resolution data, from both field assessments and from satellites, are needed to improve both understanding and prediction of forest responses to future climate change.

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1. CLIMATE CHANGE AND FORESTS

Global temperatures have been rising rapidly over recent decades, with drought and heatwaves occurring at increased frequency (83). Because the distribution of forest types on Earth is strongly

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determined by the interplay of temperature, precipitation, and radiation, shifts in climate conditions can substantially change forest ecosystems. Climatic extremes have caused elevated tree mortality on all forested continents (6, 9, 78), and, in some cases, forests have not recovered from these events (8), whereas, in others, fundamental shifts in tree species composition are occurring (55). Such observations suggest that persistent alterations of global forests may occur in response to climate change. In this article, we document instances where climate extremes had severe, sudden, and unexpected impacts on forest ecosystems and then highlight how difficult it is to predict such events, which leaves large uncertainties about the fate of forests under ongoing climate change.

Vapor pressure deficit (VPD): describes the difference (deficit) between the amount of moisture in the air and how much moisture the air can hold at a given temperature when it is saturated

2. CLIMATE CHANGE AND TREE MORTALITY

Climate change affects trees directly via its impact on physiological processes, such as photosynthesis or water transport, or by promoting indirect drivers of mortality, such as biotic attack by insects, but may also have consequences far beyond tree physiology and tree communities. Evidence is accumulating on the potential effects of climate change on the trophic chain, e.g., on the animal species that depend on plants through drought-linked changes in plant productivity, allocation to fruits and flowers (34, 163), and plant secondary chemistry and defense compounds (67). Complex interactions between the animal and plant kingdom may be disturbed by climatic change, with long-term consequences on forest regeneration and development and thus on forest persistence. In the following, we focus on direct effects of drought and heat on tree physiology and how physiological changes influence interactions with bark-boring beetles as a prominent example of biotic drivers of mortality.

2.1. Drivers and Mechanisms of Climate Change–Induced Tree Mortality

Trees can efficiently respond to water deficit by closing stomata or by reducing transpiring surfaces, e.g., leaf shedding, to tolerate drought. Yet excessive transpiration during drought can still lead to substantial increases in the tension of the water column in the conducting tissue and eventually to the formation of embolisms (154). Efficient control of transpiration, however, has negative side effects, as reduced stomatal conductance or smaller leaf area also entails reductions in carbon uptake (131). A tree's water and carbon balances are thus tightly intertwined, even more so because the maintenance of hydraulic function is in part dependent on the utilization of carbohydrates for the growth of conducting tissues, for cellular osmoregulation, and for the production of defense compounds against biotic attack (105). These water and carbon balances directly impact the susceptibility of trees to changing droughts and rising CO_2, heat waves, and elevated atmospheric water vapor pressure deficit (VPD, a measure of air dryness) (161), which describes the evaporative power of the atmosphere, seen from the plant's perspective. VPD increases exponentially with temperature, making hotter droughts even more threatening, as atmospheric water demand increases while soil moisture availability decreases.

Hydraulic failure, or the inability of a plant to transport sufficient water to its distal organs, causing dehydration and death, is a likely mechanism of mortality under warmer droughts (2). Carbon starvation, or the inability to supply enough carbon to maintain hydraulic function and other metabolic processes, might also play a role in hastening tree mortality under warming conditions (105), at least as a contributing factor. The depletion or loss of function of either carbon or water pools or fluxes may also promote the failure of defensive functions against biotic attack, which, when it occurs, feeds back upon the physiology of the trees through fungal, insect, or other damage to above- or belowground organs. Understanding these intertwined physiological mechanisms of tree responses to hotter droughts is arguably one of the largest challenges to the prediction of future tree mortality (12, 78, 108).

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The persistent rise in surface temperatures exacerbates drought impacts on trees through increasing VPD and increased evaporative demand of water from plants and soils (69). Given ongoing global warming, future droughts will occur under conditions of greater atmospheric demand and greater soil moisture limitations (164). Thus, as VPD rises chronically, so too does the potential for increasing tree mortality (161) due to hydraulic failure and/or carbon starvation (110). By contrast, elevated atmospheric CO_2 concentrations may have both positive and negative impacts on mortality under a changing climate (48, 107, 157). Rising CO_2 can allow plants to reduce stomatal conductance without negative feedbacks on photosynthetic rates and may increase photosynthesis during nondrought periods (3), although reduced evaporative cooling during heat could lead to early leaf senescence (159). The increased provision of carbon from elevated CO_2 may subsequently be allocated to produce more roots during drought or to regrow damaged conducting tissue following drought (129). Yet, greater allocation to foliage or height growth during favorable environmental conditions can lead to structural overshoot (85), with greater whole-tree transpiration and greater stand-level competition for resources such as nutrients and water, that may predispose trees to greater mortality under subsequent drought stress (but see 57). Ultimately, there are important unknowns regarding the physiological mechanisms of mortality and their potential responses to the conflicting drivers of rising CO_2 and VPD; however, the increasing rate of mortality observed in many parts of the world (107), combined with theory (106), observations (10), and model forecasts (110), suggests a risk of greater physiological vulnerability to hotter droughts and of higher tree mortality rates in the future.

2.2. Biotic Drivers of Tree Mortality

Trees in forest ecosystems are constantly interacting with both the abiotic environment and other organisms, such as con- or heterospecific neighbors, soil biota, animals, pathogens, or insects. In particular, interactions with insects have been shown to be highly dynamic under climate change and have caused tree mortality over millions of hectares of forests (e.g., 82). For example, attacks by bark beetles on conifers can become more prevalent under warming conditions with an increased abundance of stressed trees and accelerated ontogenic development of the insects (126). Decreased carbon uptake from predisposing factors, like atmospheric pollution or increasing temperatures, makes trees more susceptible to other stressors, like strong drought or heat waves, that cause a further rapid decline in survival likelihood and, often accelerated by disease, ultimately lead to tree death (97). The predisposition to death via insect attack is thought to be mediated by reduced tree defense capacity during drought: Fewer carbohydrates are produced from photosynthesis, reducing the availability of resources for the synthesis of secondary defense metabolites that can fend off attackers (91), while decreasing water potential reduces resin pressure that might otherwise smother and expel invading beetles (116). At the same time, insect growth is strongly accelerated under elevated temperatures; for example, the development time of the European spruce bark beetle from egg to adult beetle in the bark of trees is shortened from ~50 days at 15°C to ~20 days at 25°C (160). Thus, the reproductive cycles of beetle populations unfold more rapidly during hot periods, allowing generations of beetles to develop more rapidly. Under good breeding conditions, population sizes can increase 15-fold from one generation to the next (81), and, given that beetle populations can undergo three or even four generations during an exceptionally hot and dry year, the number of attacking insects can explode a thousandfold, creating an epidemic outbreak. While trees are usually well-defended against beetle attacks during endemic phases, the sheer number of attacks will also cause healthy trees to succumb and die during epidemic attacks (25, 91).

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3. SELECTED REPORTS OF SUDDEN AND UNEXPECTED TREE MORTALITY EVENTS

Episodes of sudden and unexpected tree mortality due to extreme climatic events have been reported repeatedly over the last three decades. One of the first systematic literature syntheses of peer-reviewed reports on global tree mortality following drought and heat events was published more than a decade ago (6) and has been updated regularly (9, 10, 78). While such ground-based data sets cannot provide a robust empirical basis for spatiotemporal trends in global tree mortality rates due to geographical observation bias (76), they corroborate more recent remote sensing–based systematic assessments of how climate change is driving the dynamics of tree mortality at regional scales (e.g., 14, 28, 31, 63, 140).

In this section, we focus on a few selected examples of the many mortality events observed worldwide (**Figure 1**) that were both sudden and unexpected. We report events from temperate

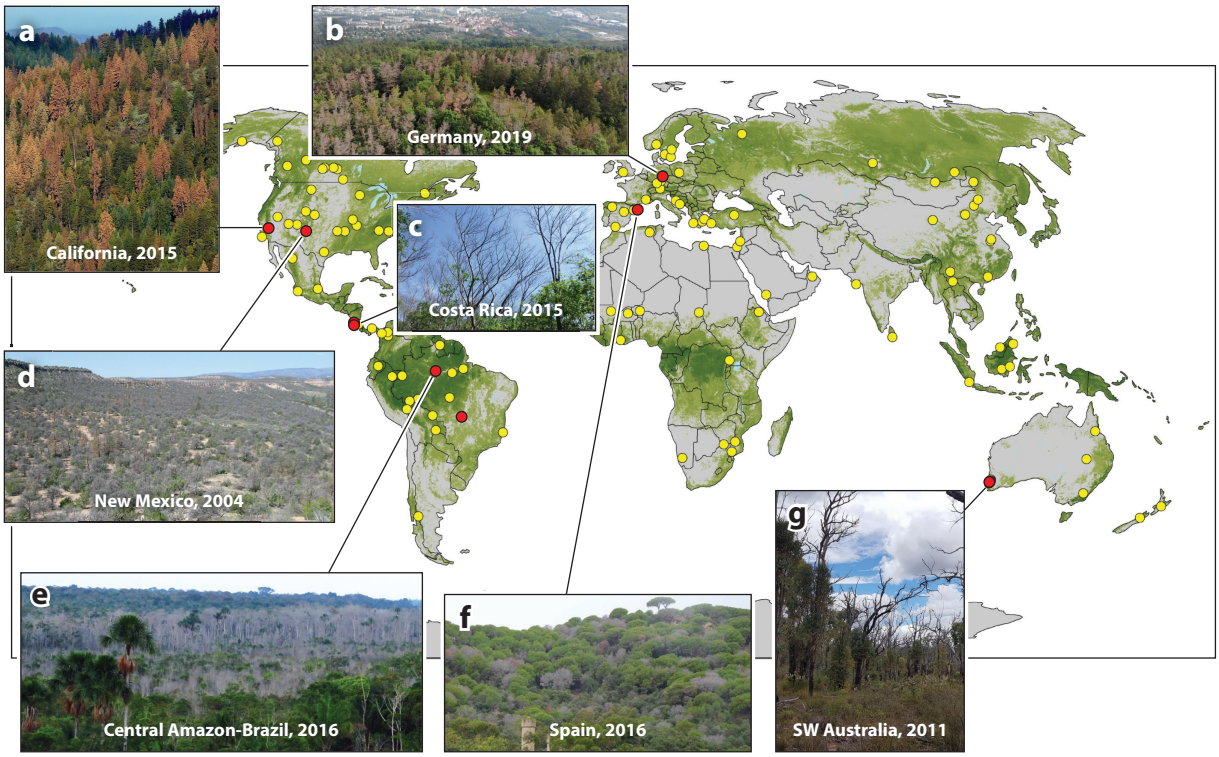

Figure 1

Published observations of elevated tree mortality in response to drought and heat. These documented observations have been presented in References 9, 10, 72, and 78. Locations of selected mortality events presented here as case studies are indicated by red dots and illustrated by inset photos. The forest cover shown here is adapted with permission from the canopy height map of Reference 142, with only canopies 5 m or taller plotted and taller canopies in increasingly darker green. (*a*) Dying *Pinus* and *Abies* in California; photo provided by Nate Stephenson. (*b*) *Pinus sylvestris* mortality in a matrix of living *Fraxinus excelsior* in Germany; photo provided by Henrik Hartmann. (*c*) Photo taken in 2017 of ongoing mortality after 2015 drought in Costa Rica; photo provided by Jennifer Powers. (*d*) Dead *Pinus edulis* after 2002 die-off in New Mexico; photo provided by Craig D. Allen. (*e*) Tree mortality from a combination of drought and fire in the Central Amazon; photo provided by Adriane Esquivel-Muelbert. (*f*) *Quercus ilex* mortality in Spain; photo provided by Mireia Banqué. (*g*) *Eucalyptus marginata* die-off in Southwest Australia; photo provided by Katinka X. Ruthrof.

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CALIFORNIA (WESTERN UNITED STATES), ADRIAN DAS

More than two decades ago, I began working in a research program meant to inform our understanding of how climatic change might affect the magnificent forests of Sequoia National Park—something that I imagined as a series of subtle alterations that would only finally play out in some amorphously distant future. During the unprecedented extreme drought in California from 2012 to 2016, the "future" began to play out dramatically in real time, killing tens of millions of trees. This event taught us that ecosystem change can come quickly and unexpectedly to forests long thought to be highly resilient. As for myself, I am left to wonder how much of the rest of my career will be spent documenting changes I had not truly expected to experience in my lifetime, witnessing transformations substantial enough to leave behind something very different from the iconic forests that drew me to this work in the first place.

forests that were long thought to be buffered from climatic extremes and the somewhat surprising occurrence of drought-induced tree mortality in wet tropical forests. We also document examples of unexpected mortality in dry forests, where these systems are adapted to rather harsh climatic conditions and are commonly assumed to be tolerant to drought. We deliberately include first-person narrative sidebars between examples here as the reporting is meant to convey not just facts but also expert perceptions of mortality events by the scientists working in these forests. This approach emphasizes that forests presently thought to be safe from climate-induced mortality may not be sheltered from future climatic threats.

3.1. Temperate Forest, California, USA

From 2012 to 2016, California experienced its most severe drought in centuries (68) and hundreds of millions of trees were simultaneously under stress, while tens of millions of them died (112, 113). In Sequoia National Park, we found over 20% tree mortality in heavily affected areas, with percentages much higher for some taxa and size classes (147) (**Supplemental Figure 1**). Such impacts were common elsewhere in the southern Sierra Nevada, and this damage was not restricted to conifer forests, with similar percentages of trees dying in oak woodlands (47). Even the iconic giant sequoias (*Sequoiadendron giganteum*), generally insensitive to drought, displayed an unprecedented loss of foliage (148), and, while the species as a whole had low mortality, a few dozen mature sequoias appear to have been killed by bark beetles—an occurrence so unusual that it sparked a new research program [see the sidebar titled California (Western United States), Adrian Das].

The consequences of this event will probably extend well beyond the drought itself, as forests can take decades or centuries to recover, and in a changing environment such events may herald the beginnings of long-term ecosystem transformations. For example, in ecosystems like blue oak woodlands, where recruitment has been failing for decades, losing a fifth of canopy trees from drought might eventually be unsustainable. For individual species like sugar pine (*Pinus lambertiana*), which lost upwards of 70% of canopy trees in heavily affected areas, the consequences could be disastrous, since this species is already experiencing dramatic declines due to fire suppression and an exotic disease (155).

In short, the drought brought a game-changing new perspective to our understanding of the vulnerability of California forests, and the nature of that vulnerability was not straightforward. The drought itself did not generally result in the loss of forested ecosystems since, despite high mortality, plenty of trees remained on the landscape. Impacts tended to increase with decreasing elevation and vary with apparent water availability (118). But, more strikingly, the vulnerability of trees within a site varied dramatically depending on tree size and species. In conifer forests, these

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differences were driven by the particular behaviors of individual bark beetle species rather than by tree characteristics alone (147). Furthermore, some biotic attackers not previously linked to mortality caused significant damage during the drought—a likely harbinger of the future as even more biotic agents respond to novel climate conditions in ways that are increasingly independent of the physiology and health of their hosts.

3.2. Temperate Forest, Thuringia, Germany

Thuringia is located in Central Germany and lies within the Western European broadleaf forest ecoregion, characterized by beech (*Fagus sylvatica*) and oak (*Quercus petraea*, *Quercus robur*) forests, but large parts of Thuringia are covered with Norway spruce and Scots pine, both commercially important species. Scots pine is considered a drought-tolerant species, with a taproot system that allows access to deeper soil horizons during drought, and is often found on poor, sandy soils or even rocky outcrops where it cannot be outcompeted by other species (50) [see the sidebar titled Thuringia (Germany), Henrik Hartmann].

In 2018–2019, a drought occurred in Central Europe that was both substantial and unusual, leaving northeastern Germany with the most extreme soil water scarcity in deep layers (0–1.8 m) that has been documented over the last 70 years (**Figure 2**). The summer of 2018 was also one of the hottest on record, followed by a similar record-breaking hot summer in 2019. The resulting very high VPD in combination with the severe soil water limitations had devastating effects, even on pine trees, despite their apparent drought tolerance. Surprisingly, Scots pines are sometimes dying in large numbers in close proximity to other, seemingly unaffected, species (**Figure 1*b***). Over the entire German forest, mortality rates of Scots pine increased tenfold, from <0.1% in 2018 to almost 1% in 2020, with the situation in Thuringia being much worse. While these numbers appear low for natural forests, they are actually very high for the intensively managed German forests. Yet, the urgency of the current forest situation is documented by not only pine mortality but also many other species that are showing strong symptoms of decline (e.g., increasing leaf loss, dead branches). European beech, until recently considered a viable option for future forest management because of its apparent drought and heat resilience (11, 27), is also dying in large numbers in many regions. Beech also suffers severe damage from increasingly frequent late frost events in montane regions, and European ash and maples (*Acer pseudoplatanus*, *Acer platanoides*) are affected by diseases that are spreading with increased speed through populations following climate

THURINGIA (GERMANY), HENRIK HARTMANN

I grew up during a time when concerns about forests were already a big issue. During the late 1970s and early 1980s, forests in Central Europe were affected by severe tree die-off and disease from acid rain (termed Waldsterben). Public pressure caused politicians to impose counteractive measures against air pollution, and by the early 2000s we thought that our forests were in good shape again. That perception quickly changed after the extreme hot, dry summers of 2018 and 2019. Mortality rates increased 20-fold in some species, and many forests do not look healthy anymore: Tree crowns are sparse and show many dead branches. Foresters are both alarmed and desperate, not knowing which species will grow and which will survive in an even drier and hotter future. The forests I marveled at as a child have almost disappeared in my home region, leaving large areas that look like huge clear cuts. I am at a loss to predict how future Central European forests will look. The 1980s forest crisis increased environmental awareness and drove better environmental policies in many European societies; I hope that this new forest crisis will also contribute to strengthening policy-making toward more concrete climate protection measures.

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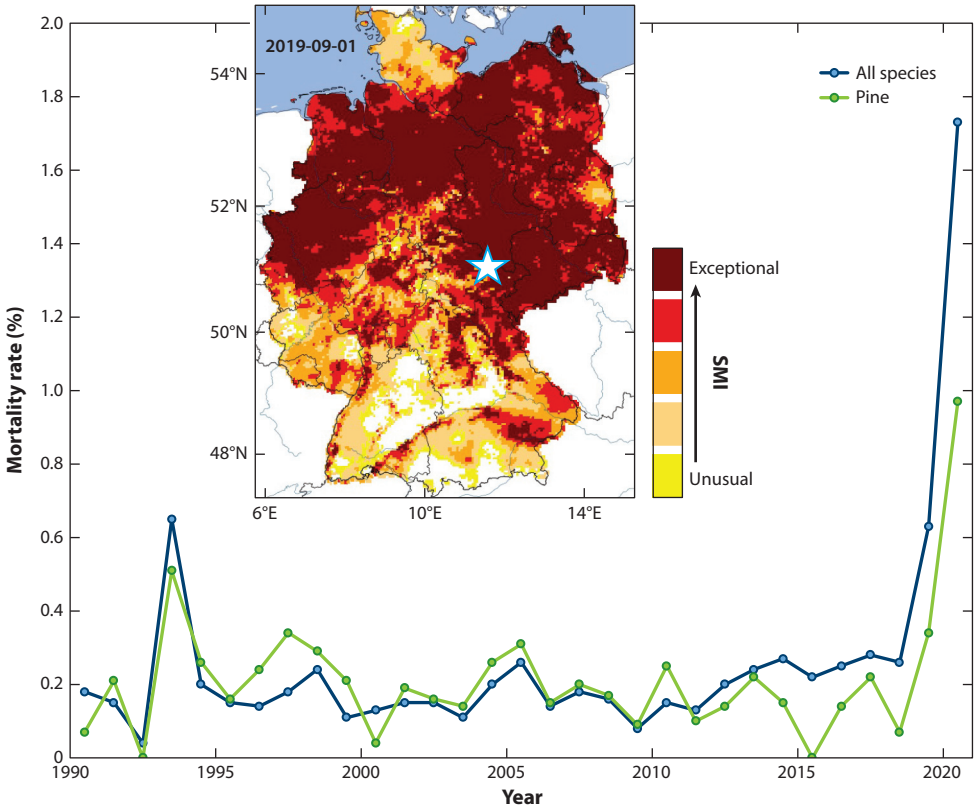

Figure 2

The 2018–2019 drought that affected most of northern and eastern Germany. Exceptional soil moisture index (SMI) values indicate extremely severe soil water depletion by September 2019, even in the deeper soil horizons (*inset*). Tree mortality following the extreme summers increased exponentially throughout Germany, with tenfold increases for *Pinus sylvestris* and sevenfold for all species combined (data from Reference 26). Location of the mortality event in Thuringia shown in **Figure 1** is indicated by the star. Drought map © UFZ-Dürremonitor/ Helmholtz-Zentrum für Umweltforschung.

extremes (75, 137, 139). In Germany, the mortality rates of all tree species combined, comprising many other conifers and deciduous species, have increased sevenfold from 0.25% in 2018 to 1.73% in 2020 (**Figure 2**), underscoring that changes in forest condition triggered by the 2018–2019 hot drought may continue to act upon the forests during the coming years, or even decades.

El Niño Southern Oscillation (ENSO): the semiperiodic variation in trade winds and sea surface temperatures over the tropical eastern Pacific Ocean, influencing the climate in the tropics and having teleconnections to the subtropics

3.3. Tropical Forest, Guanacaste, Costa Rica

The boldest cases of extreme shifts in forest composition and increases in tree death in tropical forests have occurred in the drier regions. Several cases of striking drought-induced tree mortality were observed in the tropics during the very strong El Niño Southern Oscillation (ENSO) of 2015–2016 that led to the strongest drought on record in Guanacaste (42), a region in northwestern Costa Rica that supports seasonally dry tropical forests. Rainfall is extremely seasonal in Guanacaste, with a 5–6-month dry season that typically has little to no rain. Most trees are drought-deciduous and leaf out in April to May, as if in anticipation of the rains that typically start mid-May. Delay in the onset of the rainy season (**Figure 3*a***) combined with extremely high

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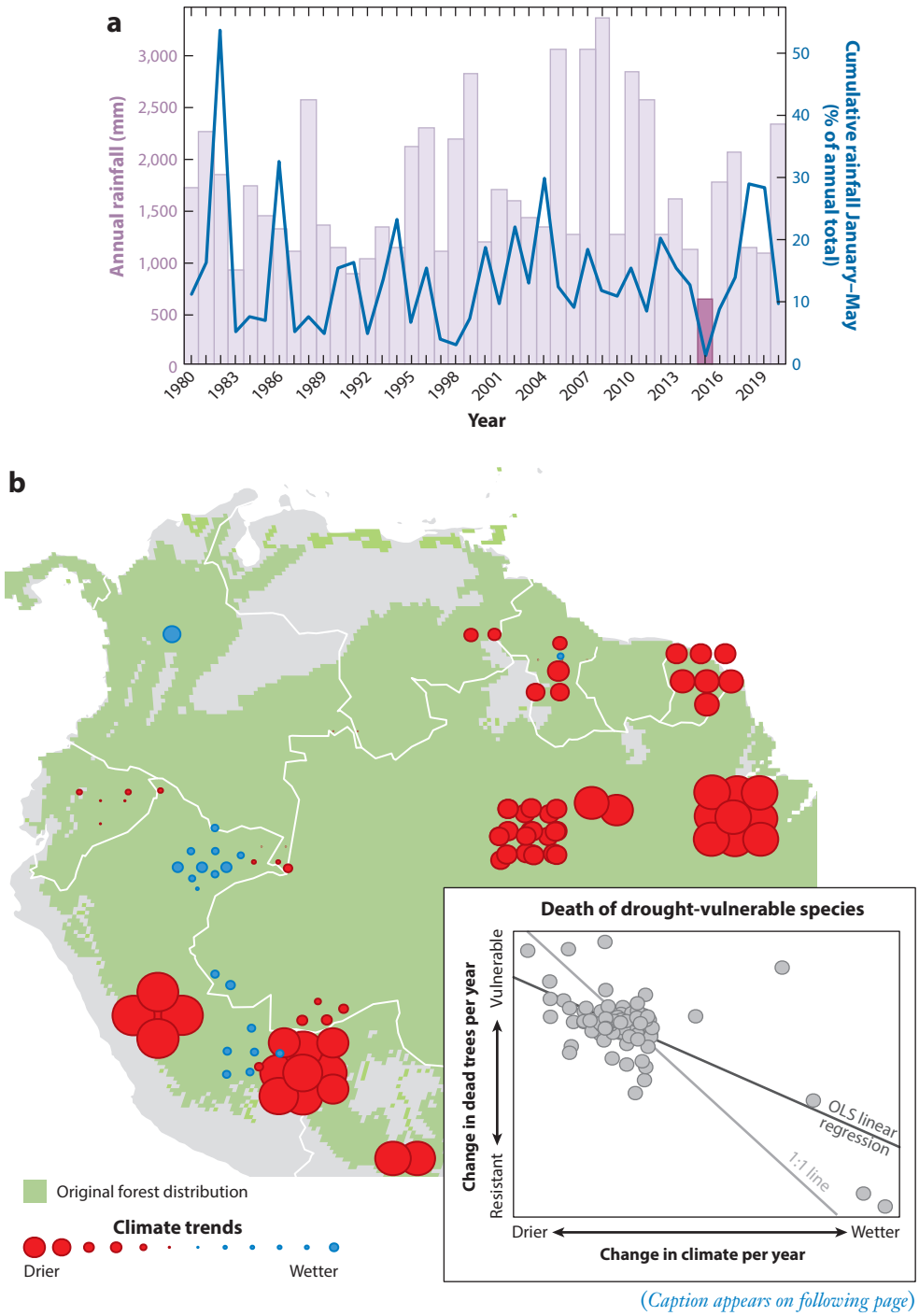

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Figure 3 (*Figure appears on preceding page*)

Drought impacts on tropical forests. (*a*) Long-term rainfall records from Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (*purple bars*). Data from Reference 23. Interannual variation in rainfall is large; however, 2015 (*dark purple*) stands out as having both low total annual rainfall and low cumulative rainfall from January–May (*blue line*). (*b*) Thirty-year trends in dry season length and intensity across RAINFOR inventory plots (96) across Amazonia, including 1,820 tree species. Dots in the map show the location of each inventory plot across neotropical forests (*green*). Colors represent the direction of the trends in dry season length, with drying, i.e., a longer dry season, shown in red and wetting, i.e., a shorter dry season, shown in blue. The intensity of climate change is represented by the size of the dots. The inset graph shows the relationship between the annual change in water availability (*x-axis*) and trends in the drought vulnerability of the tree species that died during the monitoring period (*y-axis*). Each dot in the inset represents an inventory plot. Note that greater mortality of drought-vulnerable species was observed in those regions that became drier during the monitoring period. Panel *b* is adapted from Reference 55. The dry season metric was calculated using data from the Climatic Research Unit (73) between 1985 and 2015. Abbreviation: OLS, ordinary least squares.

temperatures led to a doubling and even tripling of mortality in protected areas in Guanacaste. Yet, tree species were not equally impacted, and mortality rates ranged from 0 to ∼35% among a sample of 53 abundant species (123). This large mortality event challenged the idea that tropical dry forests will be better able to cope with acute drought because their species are adapted to seasonal drought [see the sidebar titled Guanacaste (Costa Rica), Jennifer Powers].

3.4. Tropical Forest, Amazonia, Brazil

The most diverse forests on Earth are in the tropical latitudes (86), where more tree species can be found in a single hectare than in the entire boreal biome (61). Gradients of soil fertility and water availability, as well as disturbance heterogeneity, shape the diversity and composition of species in tropical forests, thereby creating an extremely diverse landscape (56, 114). This high diversity and heterogeneity mask some of the striking drought impacts observed in other forest types, but recent observations provide alarming evidence of the increasing vulnerability of tropical forest species to changing drought regimes (55, 59, 123). Clear evidence of drought-induced tree mortality in tropical forests has started to emerge during the last two decades (121), as data from forest inventory plots have accumulated. This evidence includes the continuous increase in tree death across the Amazon forest (30) and spikes in tree mortality following drought events across several parts of Amazonia (59, 60, 123) [see the sidebar titled Amazonia (Brazil), Adriane Esquivel-Muelbert].

GUANACASTE (COSTA RICA), JENNIFER POWERS

The extreme drought of 2015 caught our research group in the seasonally dry tropical forest of Guanacaste, Costa Rica, by surprise. The 100+ tree species in this forest deploy diverse strategies to cope with the dry season that can last for five to six months without rain, which may lead to the expectation of forest resilience to drought. In 2015, the rainy season started late and precipitation was historically low, while temperatures were higher than usual. Walking through our permanent monitoring plots in the middle of the rainy season and hearing dried leaves crunch underfoot gave me the first clue that something was wrong. Trees typically do not drop leaves in the middle of the rainy season, and any leaves that do fall are too wet to crunch. While plot-level mortality rates only doubled or tripled in 2015 compared to other years (in typical years, 0.6% to 3% of trees die in the plots while the mean 2015 rate was 6.14%), several species showed mortality rates up to 35%. This drought pushed the forest to the limit, something I had never expected. Given climate predictions of increasingly shorter rainy seasons, I wonder how these beautiful forests will look in the future.

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AMAZONIA (BRAZIL), ADRIANE ESQUIVEL-MUELBERT

In 2015, I joined a team from the Brazilian Institute of Amazonian Research (INPA) on a few field expeditions in the heart of the Amazon. We visited several forests before and after the 2015–2016 El Niño that brought about a long and hot drought and even forest fires. After the drought, it was shocking to see that all of the lush green had turned into dull gray and vast amounts of trees at the margins of the forest were dead. In contrast with those in drier regions of the tropics, the incredibly resilient trees from the Central Amazon region were still flourishing after the drought in the forest interior, not reached by the fires. But how much more drought and heat can these trees tolerate before they also die? We are yet to find out, and I am worried that further climate change and more forest fires will threaten the persistence of the Amazon as we know it now.

Droughts may increase mortality rates from background levels of 1–3% to 6–7% (123), while a combination of drought and epidemic outbreaks of individual insect species that often causes die-offs in nontropical forest ecosystems (9) so far has been avoided likely because of the interplay of high tree and insect diversity that drives a strong competition within insect communities and a high specialization level in plant–insect interactions (22, 80). The lack of ensuing clustered die-offs suggests that high-diversity tropical forests, such as those in the Central Amazon, are more functionally resilient to drought than many less diverse ecosystems. However, the contribution of diversity to resilience to global change–type drought of this biome and the limits of this diversity-buffered resistance are yet to be more comprehensively investigated and understood (but see 13, 94).

As in Guanacaste, the combination of drought and extremely high temperatures (also referred to as global change–type drought; 27), seems to be pushing other dry fringes of tropical forests to their limits, while the wetter tropical forests appear to be less affected due to overall higher rainfall levels (13) or local topographic conditions (145). Throughout the tropics, spikes in drought-induced tree death were observed during the same period at the dry edges of other tropical forests (111); however, mortality has also been observed in wet forests (4, 41, 121), in particular following ENSO and in combination with wildfire (24), but often with lower increases in tree mortality during the drought period compared to dry forests (55, 123) (**Figure 3*b***). It could well be that these wet forests have not yet been pushed to their climate limit, and the consequences for tree survival when that happens are still unknown. Observations from throughfall exclusion experiments in tropical forests indicate that drier systems (128) are more vulnerable to drought mortality than wetter forests (138), although substantial increases in tree mortality, in particular of large individuals, are also observed in wet tropical forests during long-term drought (128).

3.5. Temperate Dry Forest, New Mexico, USA

In the mountainous uplands of northern New Mexico, vegetation is arrayed along a 2,400-m elevational gradient, from semiarid valleys up through diverse montane woodlands and forests of *Juniperus*, *Pinus*, *Pseudotsuga*, *Populus*, *Abies*, and *Picea* (5). An extended wet period (ca. 1978–1995) characterized by abundant winter precipitation fostered extremely robust tree growth, and fire suppression was still so effective that local land managers talked of "asbestos forests." In this wet window of the 1980s and early 1990s, Southwestern United States vegetation concerns included recognition of a century-long trend of woodification associated with fire suppression, ranging from extensive tree invasion into grasslands to widespread forest densification and hazardous woody fuel buildups (5). From abundant paleoecological evidence of recurrent regional droughts and their ecological effects (149), forest ecologists anticipated that the next multiyear drought could trigger

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NEW MEXICO (SOUTHWESTERN UNITED STATES), CRAIG D. ALLEN

I have spent the last 40 years coming to know and love the upland forests of the Southwestern United States, as my graduate fieldwork in the Jemez Mountains of northern New Mexico evolved into a job here as a place-based research ecologist, conducting long-term field studies on landscape change ever since. As the climate trended hotter and drier over the past 25 years, the Jemez landscape became an extremely dynamic place to live and work, as hundreds of thousands of hectares of forests were transformed by die-offs and severe wildfires. Although I know that change is inherent to ecosystems and life, I still have experienced a deep sense of loss over the disorienting, rapid conversion of so much old conifer forest to nonforest—over the widespread death of so many familiar and favorite beautiful trees, from magnificent overstory titans to ancient gnarled dwarves. I have met many other forest-lovers around the world and some of their favorite trees and forests. I worry about the world's remaining historical forests. I mourn the coming losses I now expect soon, what my grandchildren likely will never be able to experience and might never even know is missing. I feel an ever-greater urgency to foster conservation of Earth's remaining old-growth forests.

substantial forest die-off on the dry margins of species' distributional ranges (8), along with more severe wildfires (150). Yet, despite our substantial historical perspectives and growing awareness of emerging climate change stresses, we did not yet fully appreciate the abrupt rapidity and expanded magnitude of the forest die-offs and wildfires that were about to occur [see the sidebar titled New Mexico (Southwestern United States), Craig D. Allen].

After 1995, drier winters became common, and by 2000, the entire Southwestern United States was gripped by drought that has since deepened into a warming-amplified megadrought—one of the two most severe droughts in the past 1,200 years (162). Since the 1990s, a strong regional warming trend also has emerged, and by the 2000s, hotter global change–type droughts (29) were clearly intensifying tree-killing ecological disturbance processes such as physiological drought stress, bark beetle outbreaks, and increasingly large and severe wildfires (161). Hotter drought made 2002 by far the worst single year for tree growth in the Southwest over the previous 1,000 years of regional tree-ring records (161) (**Supplemental Figure 2**). This extreme hot drought year triggered extensive forest die-offs from 2002 through 2004, involving associated bark beetle outbreaks (>1,000,000 ha each of *Pinus edulis* and *Pinus ponderosa* mortality in the Southwest) and also huge high-severity fires (e.g., the Rodeo-Chediski Fire affecting 190,000 ha; cf. 7). Within just a few years, the Southwest transitioned from the pre-1996 period of thriving forests into an era of rapid forest ecosystem transformation through massive forest die-offs and wildfires (7). Many forest managers and society at large were caught by surprise and are still struggling to adjust.

In the eastern Jemez Mountains, over 95% of mature *P. edulis* trees died in 2002–2003 (29), completely shifting local woodlands to dominance by *Juniperus monosperma*, while combinations of forest die-off and wildfires have largely converted extensive old-growth conifer forests into early successional stands of *Populus*, shrublands of *Quercus* and *Robinia*, and grasslands (7). Warming-amplified regional drought has persisted and deepened since then (162), with further extreme drought stress in 7 of the past 11 years (2011–13, 2016, 2018, 2020, and 2021), driving additional pulses of tree mortality and constraining regional ecosystem productivity and tree regeneration (71), thereby limiting forest recovery (43).

The vigorous dense conifer forests of the early 1990s are now only faded memories from an innocent era of vanished abundance, replaced by growing public concerns about rising drought stress and massive forest losses. Looking forward, multiple climate–vegetation models project existential threats from further warming to historical Southwest conifer forests by mid-century (110,

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MEDITERRANEAN BASIN FORESTS (SPAIN), JORDI MARTINEZ-VILALTA

I started my PhD in 1997 at the Prades Mountains (on the northeastern Iberian Peninsula), three years after an extreme drought had hit the region. I was working on a throughfall simulation experiment on a south-facing forest. On the way to the study site, we noticed that some *Pinus sylvestris*, the dominant species on the wetter, north-facing slopes, were dying. The situation got worse after a second severe drought hit the region in 1998. While our throughfall simulation experiment is still ongoing, *P. sylvestris* on the north-facing slopes is largely gone, and the canopy is now dominated by *Quercus ilex*. These severe impacts from climate change make me worry that we cannot predict where and when Mediterranean forests will suffer next and that we must be prepared for further sudden changes.

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161). Meanwhile, the emergence of greater forest vulnerability to die-off from hotter droughts is increasingly documented in all major forest types worldwide (9, 10, 78, 107).

3.6. Temperate Dry Forest, Mediterranean Basin, Spain

In the Mediterranean basin, recent changes in climate have been accompanied by large-scale changes in land use and forest management, involving the abandonment of agricultural lands and traditional management practices. As a result, forest cover and stand densities have increased substantially in many areas, with strong impacts on forest dynamics and the potential to interact with drought effects (36, 93). However, even under the progressively drier climate (151), extensive tree mortality and forest decline events were not generally expected due to the drought-resistant nature of Mediterranean vegetation [see the sidebar titled Mediterranean Basin Forests (Spain), Jordi Martinez-Vilalta].

Public concerns about Mediterranean forests started to emerge when episodes of forest mortality occurred in parts of the Iberian Peninsula following the extremely dry summer of 1994 (120). At the time, temperate tree species growing there at the southern (and dry) limit of their distribution were most affected (particularly *Pinus sylvestris*; 99), but iconic Mediterranean tree species also showed severe die-off (e.g., *Quercus ilex*; 95). Similar events have occurred since throughout the Mediterranean Basin, associated with particularly dry and hot summers, such as those of 2000 and 2007 in the Eastern Mediterranean (134), 2005 in Spain (65), and 2012 in Spain again (38) and Italy (115). In many cases, episodes of drought-related tree mortality were associated with biotic agents, such as *Phytophthora*-induced decline in oak species (100). In response to these events, the Public Administration of Catalonia (northeastern Spain) established in 2012 a regional forest-monitoring network (DeBosCat) to annually identify and map decline events (characterized by >50% canopy loss or >5% tree mortality), particularly those associated with severe drought (38).

From 2012 to 2020, 43,669 ha, or 3.3% of the total forested area, had been affected by tree die-off in Catalonia, particularly in the summers of 2012 and 2016. Relative to the area each species covers, the most impacted species were *F. sylvatica* (23%), deciduous oaks (mostly *Quercus humilis* and *Quercus faginea*, which frequently hybridize in the study region; 22% in total), and the evergreen *Quercus ilex* (12%) (**Figure 4*a***). Although the percentage area affected was lower for conifers (7% for *Pinus pinea*, 6% for *Pinus pinaster*, <3% for other species), the long-term impact on ecosystem dynamics was generally greater for coniferous (e.g., 156) than for broadleaf forests because the latter can resprout after heavy canopy loss (e.g., 95). Some of the species that were most affected by drought (particularly *F. sylvatica*) grew close to their southern and dry limit in the Mediterranean region, but even typically aridity-tolerant species, like *Q. ilex* and *P. pinea*, were affected (**Figure 4*a***).

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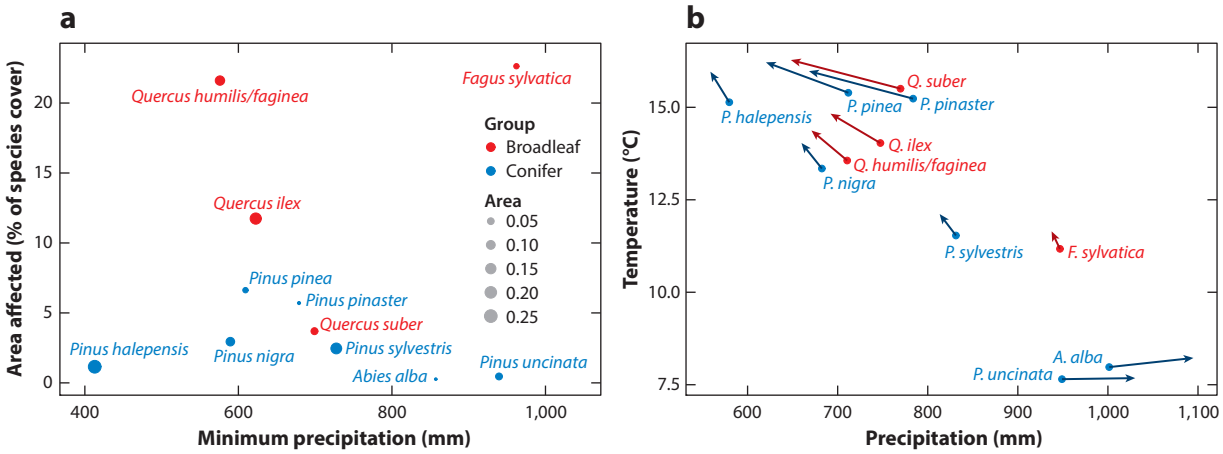

Figure 4

(*a*) The relationship between minimum precipitation (5%) of the species distribution in Catalonia, characterizing the climatic affiliation, and the percentage of its distribution affected by forest decline events (>50% canopy loss or >5% tree mortality), as recorded by the DeBosCat forest health monitoring program (2012–2020) (M. Banqué, J. Martínez-Vilalta & J. Vayreda, unpublished data). Symbol sizes are proportional to the percentage cover area of the species in Catalan forests. (*b*) Illustrates the shift (2012–2019, *arrows*) of mean annual temperature and precipitation for each species in Catalonia, with respect to the reference period 1976–1990 (*dots*). Colors identify broadleaf (*red*) versus coniferous (*blue*) species.

An important conclusion from drought-induced decline events in the Mediterranean Basin is that even typically drought-resistant species are potentially at risk. Climate-induced mortality events cannot be understood without explicitly accounting for the effect of land use and management legacies (e.g., forest densification), as well as the interaction with other drivers of regional forest dynamics such as wildfires (20, 153). Shifts in the temperature-precipitation domain that many species experienced during the last decade (**Figure 4*b***) are likely to increase under a warmer and drier climate, and this may lead to directional, large-scale change in forest composition. For those ecosystems that are currently at the dry limit of forest occurrence in the region (e.g., many *Pinus halepensis* and *Quercus ilex* forests), encroachment by shrublands is likely and may entail great changes in ecosystem structure and function (21).

3.7. Temperate Dry Forest, Northern Jarrah Forest, Southwestern Australia

Southwestern Australia has experienced chronic drying and warming for decades. Since the 1970s, annual rainfall has decreased (a 30–50% decline in winter rainfall) and the mean annual temperature increased by ∼0.15°C (19, 84). Such mean changes may not seem very dramatic, but such drying and warming have also been accompanied by acute drought and heatwaves. This was the case in 2010–2011, when rainfall was 42% below the long-term average and a series of heatwaves occurred in quick succession in early 2011 (35, 130) and resulted in pronounced biological and ecological effects. For example, net primary production for the Southwest Australia ecoregion (37,042 km^2) declined by 0.38 Mg C yr^{-1} for 2000–2011 (32), and over 16,000 km^2 showed widespread decline in forest cover between 1989–2007 (158) [see the sidebar titled Northern Jarrah Forest (Southwestern Australia), K. X. Ruthrof].

The Northern Jarrah Forest spans over 1 million hectares and has a globally unique hydrogeology with a deeply weathered lateritic profile and a large soil water storage capacity at depth. Some species, such as *Eucalyptus marginata*, which has a rooting depth of up to 50 m, rely upon this storage during the six months of summer drought (49, 136). While severe, acute drying and

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NORTHERN JARRAH FOREST (SOUTHWESTERN AUSTRALIA), K. X. RUTHROF

Growing up and living in southwestern Australia always gave me the sense that the local eucalypt forests and the associated species are incredibly resilient. After all, every year these forests withstand a drought of up to seven months, typical of our Mediterranean-type climate. Thus, the forest die-off that started in 2011 was, for me and many others, both unexpected and shocking. An estimated 16,000 ha of the Northern Jarrah Forest experienced high levels of tree die-off of dominant and midstory species, and forests have not recovered yet. Although I have no doubt that forests in this region will continue to persist, the type of die-off seen in 2011 and its long-term effects gives insight into how our forests will be different in the future under anticipated increased warming and drying for the region.

warming are thought to cause stepwise adjustments of forest and woodland ecosystems, they may also have devastating effects on forests, as was observed following the acute drought/heatwave event in 2010–2011. Massive die-off was recorded in the Northern Jarrah Forest, dominated by the resprouting jarrah (*E. marginata*) and marri (*Corymbia calophylla*) (101), but also in tuart (*Eucalyptus gomphocephala*) woodland (103), *Banksia* (*Banksia attenuata* and *Banksia menziesii*) woodland (17, 37), and diverse shrublands dominated by *Eremaea beaufortioides* and *Leptospermum spinescens*, as well as small trees, such as *Banksia hookeriana* (53, 54, 130). In 2011 alone, over 16,000 ha of the forest were impacted to varying degrees, and up to 74% (±3%) of tree crowns were dying or recently killed in affected plots (101). Greater dieback was observed at sites with rocky soils, at higher elevations, near bedrock outcrops, and on steep slopes as well as those that were more clustered in xeric areas (15, 33). The die-off in the forest included both the key overstory and midstory species, changing the stand structure and density drastically (101, 146). There was also evidence that sites with a history of chronic drought are more prone to die-off during acute climatic events, suggesting a legacy effect of historical drought stress (104). These die-off events were particularly shocking to the community and scientists because they occurred in a region dominated by what was typically thought of as very drought-tolerant species. Given that the Northern Jarrah Forest is known to be particularly resilient to disturbances, there was an expectation that recovery would occur rapidly. While some recovery did occur, the structure of the die-off sites had not recovered to predisturbance levels even 10 years after the event; they are much shorter and dominated by multistemmed individuals, and seasonal die-off of resprouts is often observed (102) (**Supplemental Figure 3**).

With its historically resilient ecosystems that have changed dramatically, a distinct and clear signal of climate change, the southwestern Australian region could be seen as one of the canaries in the climate change coal mine. We will need to better understand where and when forests are vulnerable to drought and how well they may adapt to new conditions, either by themselves or via management intervention actions that may help parts of forests transition to a drier future (40).

4. UNDERSTANDING AND PREDICTING SUDDEN CHANGES IN TREE MORTALITY FROM CLIMATE CHANGE: GAPS IN DATA AND IN UNDERSTANDING

Trees are long-lived and resilient organisms, and tree decline may take years or decades before mortality occurs (77, 119) so that even dying trees often outlive the duration of project funding or even the careers of individual tree researchers. Changes in forest attributes resulting from mortality are thus difficult to investigate comprehensively. Moreover, what constitutes a range of normal

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mortality is difficult to define, as the inherent spatiotemporal dynamics of ever-changing forest conditions always involves an interplay of regeneration, maturation, and dying at larger spatial scales, over landscapes or regions (51, 125) and creates a diversity of forest age classes, stand structures, and cover types (89). To understand such long-term dynamics, broad-scale monitoring that can characterize spatiotemporal patterns of forest attributes, including mortality rates, is needed and will eventually provide a baseline for the prediction of future forest dynamics. In this section, we give a perspective on what challenges such long-term monitoring implies, starting with the availability of ground-based high-resolution data on forests that allow inferences on changes in tree mortality. We then illustrate how information from satellite data products like the enhanced vegetation index (EVI) from MODIS (Moderate Resolution Imaging Spectroradiometer) and simulated forest attributes like gross primary productivity (GPP, as a measure of vegetation activity) relate to hindcasted tree mortality using a state-of-the-art global vegetation model. We show how these attributes varied prior to and during the hotter drought mortality events presented above. This exercise illustrates how interdisciplinary approaches can help to detect gaps in understanding mortality mechanisms and highlights the limitations of current technologies to realistically detect and predict future trends in broad-scale forest decline events.

Enhanced vegetation index (EVI): a measure of surface greenness, less prone to saturation in dense canopies and with improved decoupling of the canopy background signal compared to other vegetation indices

Gross primary production (GPP): the amount of organic mass that primary producers create via photosynthesis

4.1. From Field to Space: Spatial and Temporal Limitations in Data Availability on Tree Mortality

Much of our understanding about the trends in tree death derives from forest research monitoring plots. Unfortunately, these are still relatively rare at the global level, and their continuity often depends on funding availability and the research agendas of individual scientists. Another potential source of information to monitor tree mortality and forest health is national or state-level forest inventories. These are typically spatially defined by boundaries and objectives of the political or administrative authorities (e.g., national or state level) that carry them out. The first forest inventories may date back more than 100 years in some regions of Central Europe (58, 70); however, truly systematic and representative inventories were initiated in many European countries only in the 1960s and 1970s, taking point samples with a typical census interval of ∼10 years. In the United States, the Forest Inventory and Analysis (FIA) program started in 1930 (with the first cycle completed in the 1960s) and is now repeated at 5- to 10-year intervals (92). Yet, for many regions, particularly in countries with a large coverage of primary forests, such inventories are not available or have been initiated only recently; for example, the first National Forest Inventory of Brazil started in 2009 (46, 64). Particularly in the tropics, research-led monitoring initiatives (e.g., RAINFOR, ForestGeo) are our only gateway to track the fate of these globally important forests (62). Because it takes several decades until data series are long enough to capture dynamics in forest condition, continuing the current forest-monitoring initiatives is essential.

Inventories are a powerful tool that will become ever more valuable as their time series are extended, but they also have significant limitations when it comes to assessing tree mortality rates. They only take point samples, census intervals are often too long (∼5 to 10 years) to link tree responses to specific climatic events on shorter scales (e.g., drought), planned harvest and salvage logging are not differentiated, and many national forest inventories do not follow the fate of individual trees between censuses or have not even tracked tree mortality until recently. The pan-European International Co-operative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), carried out on a 16 km × 16 km grid since 1985 (133), is one of a few assessments to evaluate crown condition as a metric of tree health on an annual basis, although the US FIA more recently has initiated a similar assessment of forest health indicators.

Making use of these data across broad scales is challenging, as they are dispersed in many repositories, often with legislative constraints on data usage, making the merging of data a very

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complex and challenging task. Recent initiatives to create globally harmonized data depositories that combine data from scientific networks and national forest inventories have been established (e.g., **https://www.tree-mortality.net**), making an important first step toward a more comprehensive understanding of climate change risk to global forests.

Remote sensing technologies provide the advantages of recurrent observations over large areas at a higher temporal resolution than that of inventories and with much lower long-term costs compared to terrestrial surveys. Early signs of tree mortality risk associated with drought stress or other disturbances can include changes in pigment pools, canopy structure, and plant water content; these can be detected by remote sensing and linked to climate–vegetation responses using models. However, current technologies still engage in compromises between temporal and spatial resolution, as well as temporal coverage. Remote sensing products have been successfully employed to gain information on changes in forest condition from drought, storms, and fire (e.g., 140, 141) and land-use change/deforestation (45), as well as to detect forest susceptibility to insect disturbances under ongoing climate change (e.g., 63). The key challenges in such assessments remain in the linkages between field-based observations at the tree level, providing information on physiological stress and its potential causes, and the broad-scale impacts on forest cover from remote sensing approaches at moderate spatial resolution (79, 88). In Section 4.2, we illustrate these challenges and highlight uncertainties in simulating tree mortality by hindcasting vegetation responses of our showcase forests using a state-of-the-art vegetation model, LPJ-GUESS (144). Forecasts of forest dynamics such as tree cover change during the twenty-first century are still highly variable across different vegetation models (143), and woody carbon turnover, a function of input versus loss via mortality, also shows different patterns (**Figure 5**). We thus employ LPJ-GUESS as one representative of such models; the use of other models would change prediction details but not the overall conclusion.

Dynamic global vegetation models (DVGMs): numerical models of terrestrial ecosystems that simulate the states, dynamics, and processes of potential, natural, and managed vegetation and its associated biogeochemical and hydrological cycles

4.2. From Past to Future: Projecting Forest Responses to Climate Change

Projecting tree mortality and forest dynamics into the future requires synthesizing knowledge of the different components of forest function into computer simulation models. Dynamic global vegetation models (DGVMs) have been the cornerstone of assessments of continental and global-scale forest function for more than two decades (44). These models are built on a process-based framework combining representations of photosynthesis, respiration, and hydrological cycling, and additionally some models also explicitly simulate competition and mortality. They offer a broad-scale view into the overall ecological dynamics of large regions, integrating local patterns of disturbance and regrowth.

Combining observations from the field (showcases) with data from satellites and model estimates indicates that detection and forecasting of mortality during hotter droughts remains a challenge. All case studies presented in Section 3 show a consistent signal of hotter and/or drier conditions than the 1958–2019 long-term mean during the observed pulses of forest die-off (**Supplemental Figure 4**). In Manaus, New Mexico, and Thuringia, the combination of hot and dry were particularly pronounced. In four of the eight case studies (New Mexico, California, Thuringia, and southwestern Australia), the reported mortality years are associated with EVI decline (**Figure 6**), which can be seen several years before the mortality events for three of those sites (New Mexico, California, Thuringia). This highlights the importance of persistent drought (18, 66) in triggering large-scale mortality events. In the other sites, the mortality years are associated with decreases in EVI but cannot be easily separated from the interannual variability.

In two of the eight case studies (New Mexico, Southwest Australia) the reported mortality years are associated with a clear peak in drought-related mortality simulated by LPJ-GUESS, as

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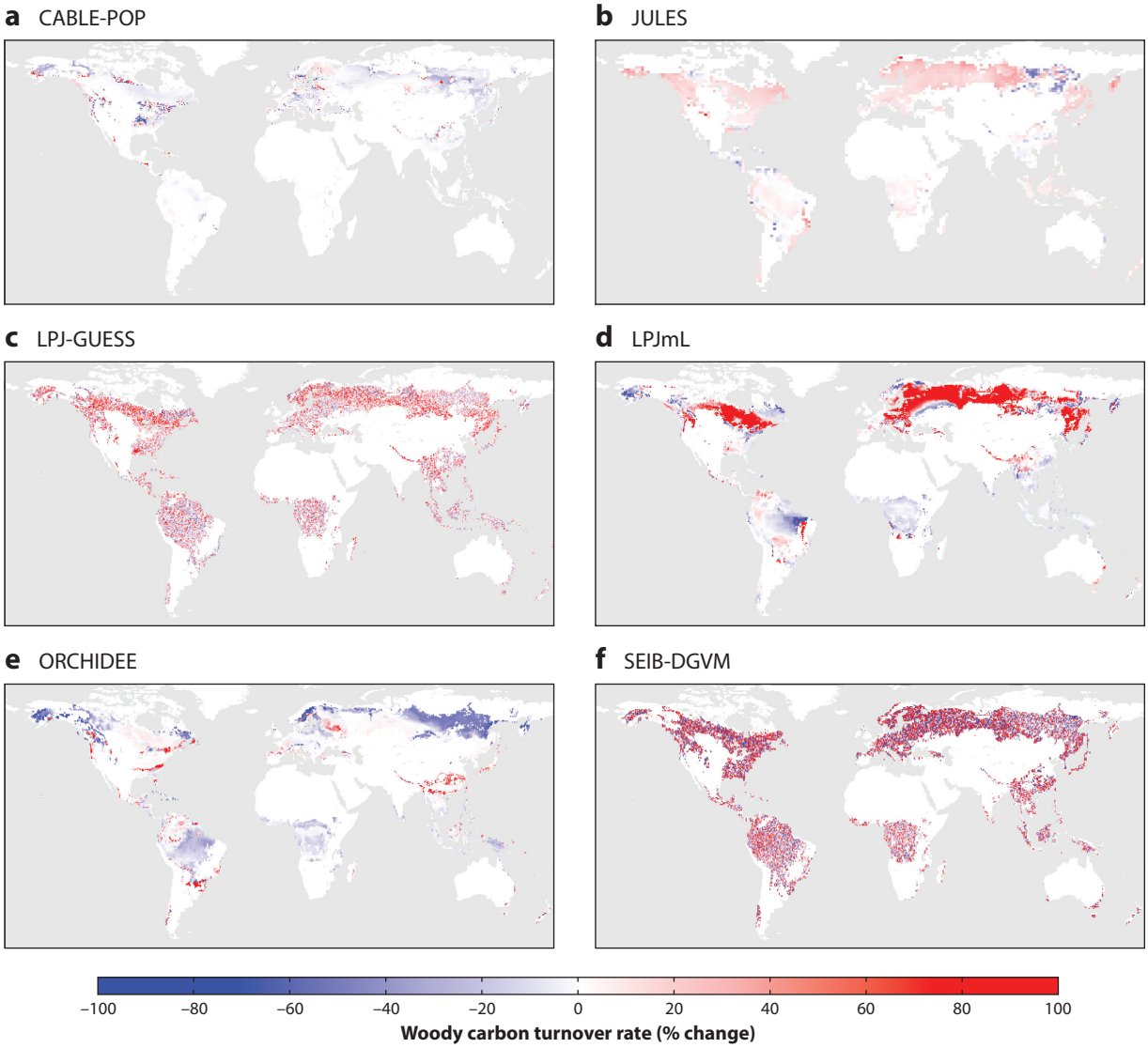

Figure 5

Percentage change in woody carbon turnover rate between 1985–2014 and 2035–2064 for six different global vegetation models using Representative Concentration Pathway (RCP) 8.5 climate data from the IPSL-CM5A-LR climate model. Red and blue colors indicate an increase or decrease, respectively, in the turnover rate in 2035–2064 versus 1985–2014. Based on model simulations described in Reference 124.

well as decreases in GPP (**Figure 6**). For a further two (California, Thuringia) there is a subtler increase in drought-related mortality associated with the event. In the other sites, no associated increases in mortality were simulated, although the mortality years are sometimes associated with a drop in GPP, indicating stress. In several cases, this GPP drop is without a concomitant decline in EVI, showing complementarity between modeling and remote sensing approaches (**Supplemental Figure 4**). Overall, however, the limited success in simulating tree mortality events is consistent with those of other studies in which DGVMs have had limited success in capturing

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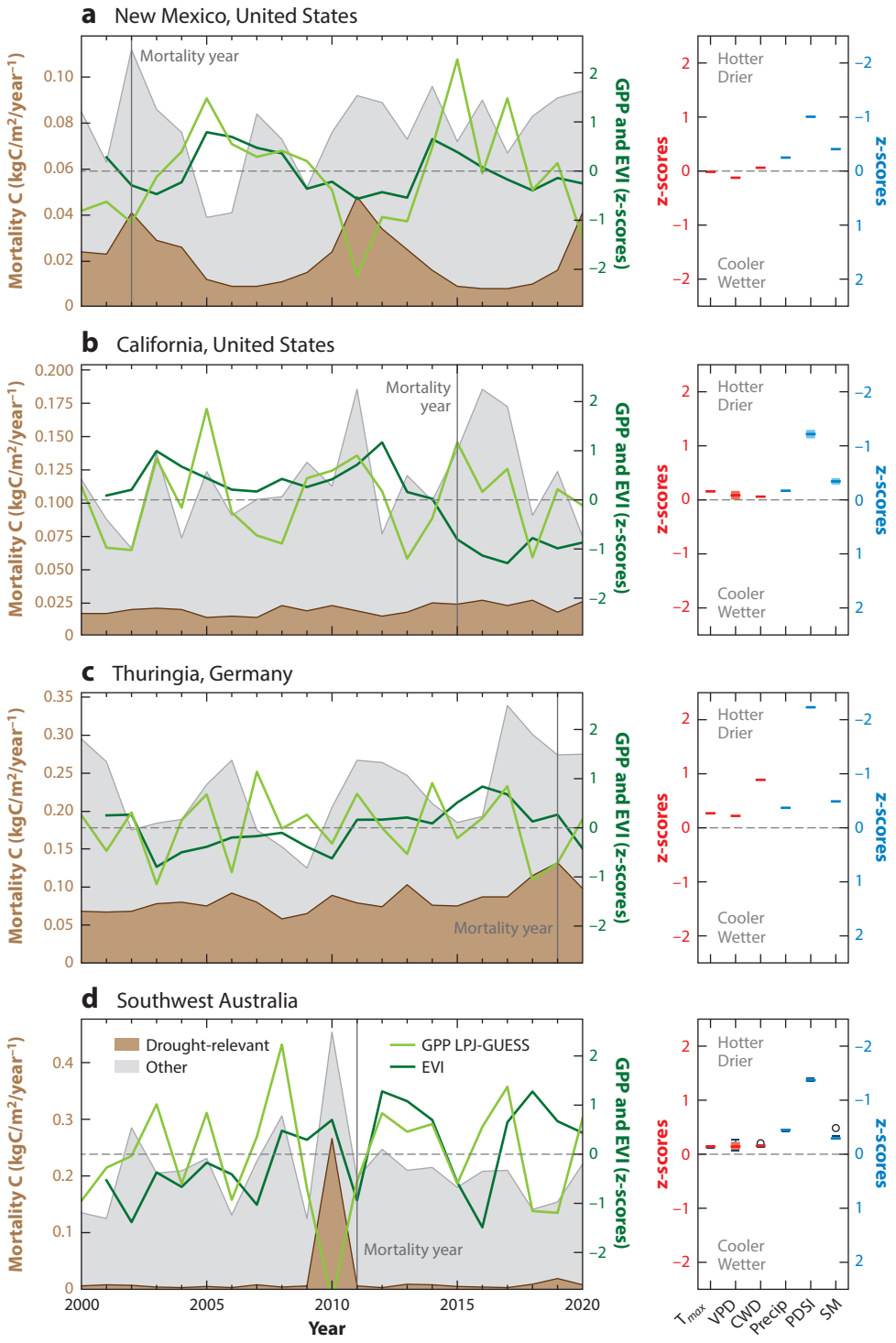

(*Caption appears on following page*)

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Figure 6 (*Figure appears on preceding page*)

Observation and modeling of tree mortality in a subset of four showcases: (*a*) New Mexico, United States; (*b*) California, United States; (*c*) Thuringia, Germany; and (*d*) Southwest Australia. (*left graphs*) For each region, we compare standardized mean annual anomalies of the enhanced vegetation index (EVI) from MODIS and of gross primary production (GPP) simulated by LPJ-GUESS (*dark green* and *light green lines*, respectively). Mortality years are indicated by vertical gray lines. The shaded areas show the annual carbon losses due to mortality processes simulated by LPJ-GUESS (144) such as wind, fire, and tree age (*gray*), as well as those due to drought-related declines of the carbon balance (*brown*). LPJ-GUESS was forced by CRU TS4.05 climate data (74). (*right graphs*) The standardized annual anomalies (z-score units) of six relevant climatic variables: the climatic water deficit (CWD), maximum average monthly temperature (T_{MAX}), Palmer Drought Severity Index (PDSI), precipitation (Precip), soil moisture (SM), and vapor pressure deficit (VPD). Climate data are from TerraClimate (1).

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drought-related mortality (122, 124). This mixed performance may reflect the diversity in environmental drivers of any particular drought. While all the events herein were associated with hotter and/or drier conditions than the 1958–2019 long-term mean, the fingerprints of the different parameter changes through which these extreme conditions were expressed varied substantially (**Supplemental Figure 4**), implying that quite different stresses were imposed on the trees and different mechanisms may have led to mortality.

Several of our case studies highlighted the importance of landscape position, tree size, and species as key factors in governing which trees died. To be applied at broad spatial extents, DGVMs necessarily generalize over these factors, which accentuates the challenge of appropriately parameterizing model mortality mechanisms so that they are broadly applicable (90). Two case studies also highlighted the importance of management legacies leading to denser stands and structural overshoot in trees. Such processes are rarely considered in DGVMs, primarily because the necessary data sets have not been assembled. Furthermore, hydraulic failure is increasingly recognized as an important mode of tree death under drought (128), but historically this mechanism has not been included in DGVMs.

Our exercise shows that severe, broad-scale tree mortality events (e.g., massive mortality of canopies over large areas) like those in New Mexico and California can be detected by remote sensing indices including early signs of forest die-off, even by moderate resolution sensors. The other events are more limited in spatial scale so that the mortality signal may not be detected in the moderate-resolution signal (109), in particular because reflectance-based remote sensing indices are less sensitive to structural or compositional changes of forests (14). In the tropical sites, for example, the signal of tree mortality may be masked by understory greening in response to canopy opening. The capacity of remote sensing products to separate the effects of multiple agents of tree mortality, for instance, heat and drought but also human and biotic agents, is still limited and poses further challenges in predicting tree mortality (152).

4.3. Outlook

Reliable projections of tree mortality are essential to allow planning for likely changes in the world's forests. Currently there is no one-size-fits-all forest monitoring or modeling approach to accurately detect or realistically simulate tree mortality events, and current DGVM projections of future tree mortality rates show large divergence (**Figure 5**). However, ongoing work on several fronts is expected to improve capabilities substantially over the coming years.

The range of remote sensing products is increasing rapidly, along with the lengths of time series, which are needed to define undisturbed baselines and to capture temporal trends. Information from very high-resolution satellite imagery (<1 m) can improve the detection of changes in forest condition by providing signals relating to structural or compositional changes of forests, and

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sensors combining high spatiotemporal resolution and spectral coverage (e.g., Sentinel-2) have the potential to detect early signs of tree decline (165). Information on vegetation water content derived from microwave data can be used as a drought-stress indicator of forest declines leading to tree mortality and also support detection of structural changes (98).

Work is ongoing globally to improve representations of plant hydraulics in DGVMs (39, 52, 87, 117) and to investigate new empirical formulations to parameterize tree mortality (16, 90). Likewise, efforts to improve the implementation of topography and tree size in models (90, 135, 144), along with grouping species into plant functional types that consider the life history strategy of trees rather than leaf type (needle, broadleaf) and habit (deciduous, evergreen) (90, 132), are likely to further improve model accuracy. Data assimilation approaches, which combine remote sensing with models, have been applied to constrain long-term mortality rates (127) and may provide exciting potential for early warning of future mortality events. Initiatives like the International Tree Mortality Network (**https://www.tree-mortality.net**) can assist these efforts by facilitating both coverage of and access to required data at the global level.

5. CONCLUSION

The complexities of tree mortality processes continue to be very challenging to model realistically, making our current projections of global tree mortality under further climate change highly uncertain (78). The coming years are likely to bring a revolution in the ability of (*a*) remote sensing to broadly monitor patterns and trends in forest health and tree mortality and thereby foster stronger empirical models of tree mortality (e.g., 161) and (*b*) process-based DGVMs to better simulate tree mortality. Such improved tools are needed for forecasting future forest dynamics and conditions over extensive spatial scales, in support of conservation and sustainable management of the world's forests.

Despite various uncertainties, it is increasingly clear that Earth's forests are vulnerable to amplified tree mortality processes driven by more extreme, hotter droughts in many regions. The recent tree mortality events reported here exemplify how vulnerable forest components of landscapes respond when and where hotter drought-stress thresholds are reached. Given the consensus in global climate projections of increasingly frequent and more severe drought and heat stress episodes (83), it appears likely that further sudden and unexpected elevated tree mortality events may be "coming soon, to a forest near you" (Craig D. Allen).

SUMMARY POINTS

1. Reports of increased tree mortality are accumulating, raising concerns about global forest health under ongoing climate change.
2. Forests experiencing unusually high tree mortality rates can experience irreversible ecosystem changes of uncertain trajectory.
3. Tree mortality occurs even in ecosystems that historically have been considered relatively resistant to hotter drought climate extremes.
4. Such observations suggest that substantial future climate change risks exist for many forest ecosystems that presently are not yet affected.
5. Predicting tree mortality remains a challenging task due to limited understanding of the complex interactions between trees and their environment.

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6. Current vegetation models still cannot realistically predict tree mortality responses to climate extremes, due to a lack of sufficient observational data for parameterization, evaluation, and process understanding.
7. Further forest monitoring and improvements in both empirical and process-based vegetation models will provide more information on potential climate change risks to global forest survival.

FUTURE ISSUES

1. Tree mortality mechanisms during drought and heat are still not well understood and require further investigations. In particular, the interactions between processes driving carbon and water budgets and their impact on secondary metabolism are major knowledge gaps to be addressed.
2. Vegetation models should implement more physiological details to better represent tree ecophysiological responses to climate extremes.
3. Biotic factors such as damaging insects play an important role in many large-scale tree mortality events, but these interactions are seldom implemented in vegetation models. Linking biotic and vegetation dynamics is a key challenge to improve predictions of future forest condition.
4. Data sharing across national boundaries and legislative entities will become increasingly important to better understand forest responses to climatic extremes when they occur.
5. Interdisciplinary approaches that link tree ecophysiology with regional forest dynamics will help to identify processes that are important for scaling to larger scales via vegetation models.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

C.D.A. and H.H. developed the concept of the paper and contributed their individual sections. H.H. wrote the general sections; A.J.D., H.H., J.S.P., A.E.-M., C.D.A., J.M.-V., and K.X.R. contributed individual sections and sidebars; N.G.M. and H.H. contributed the section on mortality mechanisms; and A.B, A.E.-M., T.A.M.P, and W.M.H. contributed the section on data availability and modeling. All authors have revised the final version.

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