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Tree mortality in a warming world: causes, patterns, and implications

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Abstract

This ERL focus collection has published 17 papers that have advanced our understanding of different dimensions of warming-induced tree mortality. Here we summarize these focus collection papers, organized by four topics related to tree mortality: pathogens, droughts/heat waves, fire/bark beetles, and teleconnections/air pollution. This focus collection illustrates a variety of methods in measuring and modeling tree-mortality, and adds significant new research findings into the scientific literature on tree mortality from hotter droughts. Some of these results also are useful for policymakers and forest managers in addressing amplified forest stress and tree mortality as a result of increasingly severe warming-induced climate and weather extremes.

1. Introduction

This collection of research reports focuses on how warming-induced climate extremes are killing trees. Since the second half of the 19th century our global climate has warmed by over 1 °C and this warming trend is expected to continue. Furthermore, the frequency of warming-induced climate extremes in the recent decades has been increasing (IPCC 2021) so that what in the past was considered extreme climate has become normal today (Hansen and Sato 2016), and today's climate extremes are expected to become normal in the future. Both social and environmental-ecosystems are vulnerable in the face of these extreme changes in climate condition; extreme droughts have contributed to extensive wildfires and the fact that warm air can hold more water vapor, as predicted by Clausius–Clapeyron equation 150 years ago, has contributed greatly to extreme flooding (Yi *et al* 2015). Catastrophic damages caused by these temperature-induced climate extremes have become a growing global concern. Spatially aggregated climate data indicate a global expansion of areas

subject to warmer climate and prolonged drought. Recently, tree and forest pathologists and other scientists have been studying connections between forest decline and the extremes in our climate system. In these drought-prone areas tree mortality and forest die-off have increased markedly in recent decades and climate warming appears to be the main driver for widespread tree mortality acting through various mechanisms including drought, fire, weakened resistance to pest attack, and changing community competition. As summarized in table 1, 11 of the 17 published papers in this collection discuss tree-mortality caused by drought or heat waves, three by pathogens, two by fire and bark beetles, and one each by aerosol pollutants and an ecoclimate teleconnection effect.

The methods developed by the authors in this collection are quite diverse, as can be seen in table 1: (a) spatial scale from leaf-level to regional; (b) temporal scale from hourly sampling to multi-decadal tree-ring derivation; (c) field experiments including manipulated heat waves and drought condition, data sources including eddy-covariance fluxes, forest inventory databases, remote sensing images

Table 1. The essential points of 17 published papers in methods, advanced knowledge, and future research questions.

Category	Authors	Methods and data	Key contributions	Future research suggestions
Pathogens	Griebel <i>et al</i> (2017)	Synthetic analysis. A conceptual framework.	With an interdisciplinary ecosystem view, authors identified knowledge gaps in the positive and negative impacts of mistletoe presence on tree physiology, stand health and successional dynamics, soil nutrient cycling, carbon, water and energy cycling as well as plant–animal interactions and biodiversity.	Quantification of physiological mechanisms by which mistletoe infection contributes to tree mortality, identification of infection thresholds that compromise tree health, utilization of remote sensing techniques for spatial mapping and ongoing monitoring of mistletoe distributions on the landscape level.
	Wood <i>et al</i> (2018)	Data driven analysis: synthesis of eddy flux, forest inventory, and tree ring data.	Documenting key interactions between abiotic and biotic stress and influences on oak and stand mortality, and how pathogens play important roles in how drought impacts on tree mortality.	Modeling drought–pathogen interactions.
	Hood <i>et al</i> (2018)	Conceptual model development based upon reviewing many post-fire tree mortality models.	Address fire–pathogen interactions.	Model development of the fundamental processes of post-fire tree mortality coupled with the development of better management tools.
Drought	McDowell <i>et al</i> (2019)	Field experiments. Modeling by terrestrial regional ecosystem exchange simulator (TREES).	Accessing to a quasi-permanent source of soil water will increase trees' resistant to drought.	Additional research needed on the role of deep soil and bedrock water in buffering trees from severe drought stress.
Heat waves	Buras <i>et al</i> (2018)	Dendroecology in combination with remote sensing data.	Verified their hypothesis that Scots pine vulnerability to drought and mortality rates after the 2015 drought are more pronounced at the forest edge.	More research is needed assessing forest-edge effects across larger geographical gradients and including other widely distributed tree species.
	Wood <i>et al</i> (2018)	Data driven analysis: synthesis of eddy flux, forest inventory, and tree ring data.	Documenting key interactions between abiotic and biotic stresses and influences on oak tree and stand mortality, and how pathogens play important roles in how drought impacts tree mortality.	Modeling drought–pathogen interactions.
	Matusick <i>et al</i> (2018)	Field sampling survey and use of logistic regression modeling to identify short-term trigger effect and long-term legacy effect.	How drought and warming together trigger broad-scale tree mortality and crown dieback events and what are drought legacy effect.	Need development of process and empirical models on how drought and warming together trigger broad-scale tree mortality and crown dieback events.

(Continued.)

Table 1. (Continued.)

Category	Authors	Methods and data	Key contributions	Future research suggestions
	Xu et al (2018)	Tree-ring data. NDVI data. Regression analysis.	Trunk and leaf growth under drought conditions increased with canopy height for trees shorter than 18 m but decreased with height for trees taller than 18 m. Forest drought resistance depends on canopy height. The study showed clear difference in heat resilience among the studied tree species with differential damage to photosynthetic capacity. Loss in photosynthetic capacity was supported by the losses in PSII maximal efficiency and electron transport rate.	More attention needs to be given to canopy structure in forest management and risk assessments in the future.
	Guha et al (2018)	Temperate tree species of the southeastern United States were exposed to manipulative heat wave events to investigate ecophysiological responses and physiological recovery.		Effects of extreme events will not be uniform across the co-occurring temperate tree species of the southeastern United States. Heat-induced damages to PSII may be a mechanistic trait that can be used to project how different species respond to extreme weather events.
	Salazar-Tortosa et al (2018)	Measure physiological variables (assimilation rate An, stomatal conductance gs, water use efficiency WUE, transpiration E etc) at leaf-level and whole-plant level.	Analyze consequences of stomatal control under dry conditions for <i>Pinus halepensis</i> , <i>P. nigra</i> , and <i>P. sylvestris</i> . Under a hotter drought scenario: <ul style="list-style-type: none"> • <i>P. nigra</i> and <i>P. sylvestris</i> would very likely suffer reduced gas exchange and increased mortality. • <i>P. halepensis</i> could maintain gas exchange and avoid water-induced growth limitation. 	Analyze additional consequences of differential stomatal control under hotter drought conditions. Particularly, the impact of tight stomatal control in nutrient uptake and plant stoichiometry. To test the 'isohydric trap' hypothesis.
	Hopkins et al (2018)	Within die-off plots, using forest variables collected above-ground to define a gradient of drought impact, collected dead versus live tree rhizosphere samples along the gradient. Analysis approaches included informatics, molecular analysis, and statistics.	Fungal richness was not significantly different between trees in drought-affected plots compared with minimally-affected and unaffected plots. However, soil beneath trees affected by drought had different fungal community composition and changes in the abundance of key functional groups. Fungal communities were also different beneath living and dead plants within the drought-affected sites.	Future studies should focus on the potential feedbacks of drought-induced tree mortality with altered microbial communities on plant community composition, ecosystem processes, and interactions with disturbance events such as fire.

(Continued.)

Table 1. (Continued.)

Category	Authors	Methods and data	Key contributions	Future research suggestions
	Trowbridge <i>et al</i> (2019)	Used a field transplant experiment to quantify monoterpene foliar concentrations and emission rates under temperature and moisture conditions that are consistent with global change projections across the vegetative growing season. Alberta, Canada (1960–2009). 539 permanent sample plots.	Failed to find the expected positive temperature-monoterpene-emissions relationship in this study.	Drought may override the effects of temperature on monoterpene emissions and tissue concentrations, and the influence of drought may occur through processes sensitive to overall needle carbon balance. Consequently, added warming does not worsen drought-induced suppression of defensive pine emissions—findings that need to be incorporated into global biogeochemical and biogeographic models.
	Searle and Chen (2018)		Data analyses support hypotheses: (a) the probability of ageing-driven tree mortality increases with global change and (b) the mortality probability associated with global change is higher for faster-growing trees. The major drivers of declining longevity are increasing atmospheric CO ₂ and temperature, and decreases in water availability.	Tree longevity may further decline with expected increases of atmospheric carbon dioxide and warming-related decreasing water availability in the region.
	Brodrick and Asner (2017)	Annual tree-mortality probability model. <ul style="list-style-type: none"> The airborne canopy water content (CWC) derived from the HiFIS data, and the LIDAR data, used Lidar images to map out live and dead trees, and then saw how this overlapped with the NDVI values, built relationship of NDVI with tree-mortality. 	Developed remotely sensed CWC model to predict coniferous forest drought-induced mortality.	Future work could also explore the link between species traits and the community-specific relationships between CWC change and tree mortality. Finally, further investigation into fundamental, remotely-sensed limits of CWC could make these findings more concrete and universal.
	Adams <i>et al</i> (2017)	Planted pine seedlings in growth chambers, <ul style="list-style-type: none"> transplanted into tree pots, manipulated increasing temperature until all seedlings die, determined the time to mortality. 	Collected evidence that the time to mortality declines linearly with increasing temperature.	That tree mortality can be expected to accelerate across a range of increased temperatures should be represented in models, and motivate policy to reduce the anthropogenic drivers of climate warming.

(Continued.)

Table 1. (Continued.)

Category	Authors	Methods and data	Key contributions	Future research suggestions
Fire	Berner <i>et al</i> (2017)	Geospatial tree mortality data (fire, bark beetles, timber harvest) in the western US (2003–2012). Used machine learning algorithms to assess regional tree-mortality from satellite maps and US Forest Service reports.	Regional mean annual tree mortality from fires, bark beetles, and timber harvest from 2003 to 2012 on forestland in W US are 18%, 32%, and 50%, respectively.	Rising temperatures and greater risk of drought will likely increase tree mortality from fires and bark beetles during coming decades in this region. Thus, sustained monitoring and mapping of tree mortality is necessary to inform forest and greenhouse-gas management.
Bark beetles	Hood <i>et al</i> (2018)	Conceptual model development based upon reviewing many post-fire tree mortality models.	Address fire–pathogens interaction.	Model development of the fundamental processes of post-fire tree mortality coupled with the development of better management tools.
The others	Swann <i>et al</i> (2018)	<ul style="list-style-type: none"> Used Community Land Model to simulate forest loss with C-3 grass replacement, and using NCAR Community Earth System Model to simulate propagating forest loss influence; conducted 13 experiments within 13 ecoregions, each of them included one of the domains of the US NEON. 	Provided strong model-based evidence that forest loss in one region can create significant ecoclimate teleconnections to other regions.	Further consider ecoclimate teleconnections as macrosystems biology develops to address continental-scale ecology for tree-mortality and climate feedback mechanisms.
	Burkhardt <i>et al</i> (2018)	One greenhouse was ventilated with AA and the other with EA. Sampled particle numbers and epidermal minimum conductance (g_{\min}) for three species of tree-seedlings. Scanning electron microscopy.	Observed lower g_{\min} with EA plants than with AA plants, suggesting that aerosol pollution would cause reduced drought tolerance by making stomata leaky. Deliquescent aerosols make waxes appear 'degraded'.	The observation of substantial biological effects under these moderate levels of aerosol pollution suggests that potentially stronger effects and greater biological risk may be observed in areas of high concentrations and deposition rates of hygroscopic aerosols.

and maps; and (d) modeling approaches including conceptual framework and synthetic analysis, statistical models; machine learning algorithms; and Community Land Models and Community Earth System Models.

2. Droughts and heat waves

Warming-induced tree-mortality is currently driven by drought in combination with increasing temperature called ‘hotter drought’ by Allen *et al* (2010), (2015). Increasing temperature and drying usually occur together. Climate data show that land temperature has been rising significantly since at least 1980s, with the warm zone annual $T > 16$ °C, expanding and becoming dryer (Yi *et al* 2014) and tree-mortality caused by the combination of warming and drought is expected to become more extensive (Allen *et al* 2015). Eleven of seventeen studies published in this collection have explored tree-mortality caused mainly by droughts but including other aspects of mortality as well.

Four of the eleven papers (Adams *et al* 2017, Guha *et al* 2018, Hopkins *et al* 2018, McDowell *et al* 2019) have manipulated increasing hotter-dry condition to answer their specific core questions.

- Are trees dying faster with increasing warm-dry condition? To test this hypothesis, Adams *et al* (2017) planted pine seedlings in growth chambers in March 2010 and transplanted them into tree pots in September 2010. They observed these seedlings to determine changes in time-to-death under different manipulated warm-dry scenarios. They found that the time to mortality declined linearly with increasing temperature.
- Can plants’ resistance to warm-dry conditions be increased by access to bedrock water? To answer this question, McDowell *et al* (2019) used a 5 year manipulated precipitation reduction (~45% removal) and heat (+4 °C above ambient) experiment. Despite severe experimental drought and heating, no trees died. Estimates of the sources of water taken up by the trees based on isotopic measurements and a process model (TREES; MacKay *et al* 2015) both suggested that these trees survived through access to bedrock water, and that relatively small amounts of water uptake from this deeper source was sufficient to sustain trees through extreme drought and warming conditions.
- Can heat waves cause photo-system damage or reduce photosynthetic capacity? To test this hypothesis, Guha *et al* (2018) manipulated temperature conditions for different species of trees and measured many parameters of the plants eco-physiological responses. They concluded that clear difference in heat resilience occurred among the studied tree species with differential damage to photosynthetic capacity. This was supported by losses in photosystem II (PSII) maximal efficiency and electron transport rate. In addition, Salazar-Tortosa *et al* (2018) studied gas-exchange, growth and survival in saplings of three widely distributed European pine species in a common garden environment resembling rainfall and temperature conditions. They demonstrated that physiological stomatal control under warmer-dry conditions differs across species.
- Do rhizosphere fungi differ between live and dead trees along a drought gradient? To test this hypothesis, Hopkins *et al* (2018) collected dead versus live tree rhizosphere samples and above-ground forest variables within die-off plots to define a gradient of drought impact. Along the gradient they found that fungal richness was not significantly different between trees in drought-affected plots compared with minimally drought-affected and unaffected plots. However, soil beneath trees affected by drought had different fungal community composition and changes in the abundance of key functional groups. Fungal communities were also different beneath living and dead plants within the drought-affected sites.
 - * Two papers (Buras *et al* 2018, Xu *et al* 2018) of value for forest management explored the dependence of drought-induced tree-mortality on forest structure. Their contributions addressed the following key questions:
 - what is the difference in tree productivity between forest edge and interior? To address this question, Buras *et al* (2018) focused on examining forest growth performance between forest edge and interior in Germany following the 2015 European heatwave event. They investigated five different Scots pine stands and sampled 152 trees including tree-ring widths (RWs) and related variables in earlywood and latewood. Five study sites were paired between forest edge and interior, and tree-ring properties, individual growth patterns, and climate-growth relationships were analyzed. They also used close-range remote sensing data (tree height, canopy area, distance to nearest neighbor, and normalized difference vegetation index (NDVI)) to analyze tree vitality along a forest-edge distance gradient. They concluded that tree-rings showed a stronger response to drought at the forest-edge, while NDVI also revealed lower vitality towards the forest edge.
 - Will forests with shorter or taller canopies be more likely to die during extreme drought? Xu *et al* (2018) focused on the drought event that occurred in the southwestern United States in 2002 and obtained tree-mortality data associated with the drought event from previous publications. They obtained location-matched canopy data from Lidar measurement and used location-matched MODIS

NDVI (MOD13A3) to compare leaf growth. Additionally, they used the standardized precipitation evapotranspiration index (SPEI) as a drought indicator and the tree-RW index (RWI) to perform tree growth analyses. RWI data were derived from the International Tree-Ring Data Bank. They used the $\text{SPEI} \leq -1.67$, a forest drought tipping point previously identified by Huang *et al* (2015), as a severe-drought threshold condition to screen all the data. They found that for trees shorter than 18 m, trunk and leaf growth under drought conditions increased with canopy height but decreased with height for trees taller than 18 m. They concluded that medium-height trees survive drought best.

Heat waves and droughts are usually linked together because when the land surface is dry then evapotranspiration E is low, so most of the land-available energy from net radiation $R_n \approx LE + H$ (L is latent heat coefficient) is used increasing temperature by sensible heat H . However, heat and water stress can play different roles in killing trees. Guha *et al* (2018) demonstrated that heat can cause photo-system damage and reduced photosynthetic capacity, but the specific tree-mortality roles of heat and drought from a long-term perspective remained poorly defined.

To fill this knowledge gap, Matusick *et al* (2018) focused on a typical Mediterranean Jarrah forest in Southwestern Australia that experienced severe heat-compounded drought damage. There was a steady decline in SPEI from 1950 to present, with increased VPD after 2009 peaking during the heat wave of 2011. They selected 20 study sites and made a first survey during May–June 2011. They used standard forestry methods to sample tree properties for each of 20 sites and classified them into four groups: healthy, dying, recently killed, and long dead. Then they re-measured everything in April 2015 during a second survey. Then they used statistical models to link these survey samples to climatic data—using binary logistic regression modeling to determine the influence of short- or long-term changes at tree-level, and using beta regression analyses at stand-level. They found that while chronic historical drought had legacy effects on tree-mortality processes, heat waves acted as an acute stress playing a role in triggering mortality,

Tree-mortality driven by hotter-drought has been clearly evidenced globally (Allen *et al* 2010, 2015). It remains unclear if forest longevity becomes shorter with increasing temperature. Searle and Chen (2018) addressed this knowledge gap using an annual tree-mortality probability model based on 539 permanent sample plots located in Alberta, Canada from 1960 to 2009. They found that tree longevity was declining with increasing temperature, and suggested a warm-induced tree aging factor.

Theoretically, plants' monoterpene emissions will increase with increasing temperature in hotter-drier sites and consequently lower needle monoterpene concentrations, and this temperature effect would dominate the seasonal pattern of monoterpene concentrations regardless of drought. Trowbridge *et al* (2019) used a field transplant experiment to quantify monoterpene foliar concentrations and emission rates under temperature and moisture conditions that are consistent with global change projections across the vegetative growing season. However, they failed to find the expected positive temperature-monoterpene-emissions relationship in this study. They speculated that an increase in emissions at the hotter-drier site from a 1.5 °C average temperature increase was offset by decreased emissions from greater plant water stress. Thus, there is an open question to clarify in the future.

3. Pathogens

Drought clearly is a leading factor for tree-mortality in part because it acts persistently like 'gravity' as a chronic stress on tree-growth, weakening plants' resilience by photo-system damage or reduction in photosynthetic capacity as evidenced by Guha *et al* (2018). Plants with the weakened resilience are more prone to attack by insects or infection by diseases, accelerating tree death.

Mistletoes are common and widely distributed tree parasites, considered by forest pathologists to be detrimental pathogens in both angiosperm and conifer forests as their commandeering of water and nutrients from host trees can contribute to tree stress and mortality. In principle, hotter-drier climate conditions will increase ecophysiological stress on tree growth, potentially making trees more susceptible to mistletoe infection, which in turn can lead to reduced tree growth and higher tree mortality rates. Mistletoe infection generally does not directly cause tree mortality, but infection can affect a broad range of forest ecosystem processes including tree productivity, stand dynamics, physiological processes, water budgets, energy budgets, nutrient cycling, and biodiversity.

Can mistletoe parasitism amplify tree mortality? To address this knowledge gap, Griebel *et al* (2017) conducted a synthetic analytical review and formulated a conceptual framework with an interdisciplinary ecosystem perspective. Authors summarized both positive and negative impacts of mistletoe presence on tree physiology, stand health and successional dynamics, soil nutrient cycling, carbon, water and energy cycling as well as plant–animal interactions and biodiversity. The authors not only identify the knowledge gap of mistletoes infection interacting as a factor in tree-mortality but also highlight priorities for future research on this widespread agent

of biotic disturbance, determining critical thresholds that cause large-scale tree mortality events.

Wood *et al* (2018), conducted a data-driven analysis to answer the question: do drought–pathogen interactions affect tree-mortality? They focused on a recent drought-induced tree mortality event that occurred in 2013 around the Missouri Ozarks AmeriFlux site. They used many different data sources, including (a) forest inventory data spanning 24 years, (b) 12 years (2005–2016) of ecosystem-scale carbon and water fluxes, and biological data including predawn leaf water potential (ψ_{pd}) and annual plot inventories, (c) tree-ring analyses of individual white oaks that were alive and ones that died in 2013, and (d) documentation of pathogen infection. Their data-driven analysis indicates that these drought–pathogen interactions could amplify mortality under future climate conditions and thus warrant further investigation.

4. Fire and bark beetles

Climate change has contributed to alterations in fire regimes globally in recent decades (Bowman *et al* 2020), including longer and more severe wildfire seasons in many geographic regions (Pausas and Keeley 2021). Fire directly kills trees and converts organic matter into atmospheric CO₂, thereby contributing to global warming. Heat is transferred to diverse living tissues of trees during fire, resulting in injuries to different parts of trees after fire. Fire-caused tree mortality results from injuries to the crown, bole, and roots, and their fire resistance and post-fire recovery can strongly differ, strongly affecting resilience (see Yi and Jackson 2021). Changes in fire regime can dramatically change forest structures, stand dynamics, and functions of forest water and carbon cycling. Post-fire resilience of burned trees can be substantially reduced, with lower capacity to deal with further disturbances.

What are the causes and mechanisms of post-fire tree mortality? Hood *et al* (2018) conducted a literature review on this topic. Authors have given more attention to how fire affects tree defenses and ultimately influences the susceptibility of host trees to bark beetle attack and pathogen infection. Many post-fire models were reviewed, assessing their advantages and disadvantages, and two future research directions in post-fire modeling were suggested: (a) continued improvement and evaluation of empirical models to quantify uncertainty and incorporate new regions and species, and (b) acceleration of basic, physiological research on the proximate and ultimate causes of fire-induced tree mortality to incorporate processes of tree death into models.

Berner *et al* (2017) have advanced an empirical modeling approach to tree-mortality at regional scale. The authors used all potential data sources including maps, remote sensing images, to estimate the

magnitude and relative contribution to mean annual tree mortality from fires, bark beetles, and timber harvest from 2003 to 2012, both regionally and among the 11 western US states. They quantified annual tree mortality from fires and bark beetles across regions using remote sensing estimates of tree aboveground biomass (AGB) together with information on the carbon content of AGB. Also included were disturbance extent and severity, and mean annual tree mortality from timber harvest for each state using harvest statistics from the US Forest Service. They integrated these different data sources by machine learning algorithms and used Monte Carlo analyses to track uncertainty associated with parameter error and temporal variability. Their results provide an empirical path to estimate annual tree mortality at regional scales in this big-data era.

5. Ecoclimatic teleconnection and air pollution effect

Tree-mortality will substantially change land cover properties and the functions of water, carbon, and energy exchanges with the atmosphere locally or regionally. The influence of land-cover change induced by tree-mortality will be transported to anywhere on earth's surface through atmospheric circulations. The question remains: will forest loss have climate impacts sufficient to affect ecosystem functioning elsewhere? Swann *et al* (2017) used the Community Land Model to simulate forest loss with C-3 grass replacement, and using the NCAR Community Earth System Model to simulate the long-distance climatic teleconnections of regional forest loss, they conducted experiments within 13 ecoregions, each of which included one of the domains of the US National Ecological Observatory Network (NEON). They found that for the US as a whole, loss of trees in the Pacific Southwest region, an area undergoing rapid forest die-off, had the largest negative remote impact on US GPP; in contrast, the loss of trees in the Mid-Atlantic region had the largest positive impact. They provided strong model-based evidence that forest loss in one region can alter climate far away as a result of significant ecoclimatic teleconnections to other regions. As macrosystems biology develops to address continental-scale ecology, future research should consider long-distance ecoclimate teleconnections from broad-scale tree mortality and associated climate feedback mechanisms.

While we know that heat waves, drought, fire, bark beetles and pathogens cause tree-mortality and forest decline, air pollution may be another factor. Foliar accumulation of hygroscopic aerosols can cause leaf wax degradation and hence affect stomatal conductance (g_{min}). Can aerosol deposition on tree leaves cause forest decline? To tackle this question, Burkhardt *et al* (2018) used laboratory experiments to identify the impact of hygroscopic aerosol on plant's

function step-by-step. One greenhouse was ventilated with ambient air (AA) and the other with filtered air (FA). Sampled particle numbers and epidermal minimum conductance (g_{\min}) for three species of tree seedlings were determined. They observed lower g_{\min} with FA plants than with AA plants. They concluded that aerosol pollution would cause reduced drought tolerance by making stomata leaky. Deliquescent aerosols make waxes appear 'degraded'. The observation of substantial biological effects under these moderate levels of aerosol pollution suggests that potentially stronger effects and greater biological risk may be observed in areas of high concentrations and deposition rates of hygroscopic aerosol.

6. Concluding remarks

Tree-mortality science has been a subject of inquiry for many decades, and although interdisciplinary research on this topic has intensified markedly in the past 20 years, quantitative understanding of causes, patterns, and mechanisms of tree mortality remains insufficient to securely project the fate of Earth's forests this century in response to diverse global change stressors (Allen *et al* 2015, Hartmann *et al* 2018, McDowell *et al* 2020). Still, with the development of long-term forest monitoring observations from both remote-sensing (Hansen *et al* 2013) and ground-based plots (Crowther *et al* 2015) around the world—and the systematic aggregation of data from these plots into 'big-data' through national and global databases, combined with advances in computational hardware, software, and process-modeling—our ability to document, analyze, and realistically project the complexities and dynamics of forest ecosystems at broad spatial scales is rapidly improving. Authors in this collection have developed and implemented diverse methodologies to observe and diagnose how warming climate causes trees to sicken and die or recover, ranging from laboratory manipulations of seedlings to field studies of mature trees in large plots and broad-scale climate-vegetation models to remote-sensing across large regions. The 17 papers in this collection demonstrate advances in measuring and modeling tree-mortality from local to global scales. Some of these papers have taken advantage of new databases available to develop empirical models to estimate tree and forest resilience, resistance, recovery, or mortality from local to regional scales. Other articles in this special issue formulated conceptual models and frameworks through synthetic analyses of broad literature reviews that identified knowledge gaps for further exploration, and one paper used popular global models to test how tree-mortality in one region affects ecological functions in far-distant regions. Overall, these wide-ranging examples of new research and observation capabilities illustrate ongoing advances in tree mortality research, with future research directions identified by our authors outlined

in summary table 1. Despite these examples of progress, ongoing global climate change proceeds apace, and clearly large challenges remain in monitoring, measuring, and modeling tree mortality on Earth—further addressing these research challenges remains an urgent need and opportunity for Earth System science.

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References

- Adams H D, Barron-Gafford G A, Minor R L, Gardea A A, Bentley L P, Law D J, Breshears D D, McDowell N G and Huxman T E 2017 Temperature response surfaces for mortality risk of tree species with future drought *Environ. Res. Lett.* **12** 115014
- Allen C D *et al* 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *For. Ecol. Manage.* **259** 660–84
- Allen C D, Breshears D D and McDowell N G 2015 On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene *Ecosphere* **6** 1–55
- Berner L T, Law B E, Meddens A J and Hicke J A 2017 Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States 2003–2012 *Environ. Res. Lett.* **12** 065005
- Bowman D M J S, Kolden C A, Abatzoglou J T, Johnston F H, van der Werf G R and Flannigan M 2020 Vegetation fires in the Anthropocene *Nat. Rev. Earth Environ.* **1** 500–15
- Brodrick P G and Asner G P 2017 Remotely sensed predictors of conifer tree mortality during severe drought *Environ. Res. Lett.* **12** 115013
- Buras A *et al* 2018 Are scots pine forest edges particularly prone to drought-induced mortality? *Environ. Res. Lett.* **13** 025001
- Burkhardt J, Zinsmeister D, Grantz D, Vidic S, Sutton M A, Hunsche M and Pariyar S 2018 Camouflaged as 'degraded wax': hygroscopic aerosols contribute to leaf desiccation, tree mortality, and forest decline *Environ. Res. Lett.* **13** 085001
- Crowther T W *et al* 2015 Mapping tree density at a global scale *Nature* **525** 201–5

- Griebel A, Watson D and Pendall E 2017 Mistletoe, friend and foe: synthesizing ecosystem implications of mistletoe infection *Environ. Res. Lett.* **12** 115012
- Guha A, Han J, Cummings C, McLennan D and Warren J 2018 Differential ecophysiological responses and resilience to heat events in four co-occurring temperate tree species *Environ. Res. Lett.* **13** 65008
- Hansen J and Sato M 2016 Regional climate change and national responsibilities *Environ. Res. Lett.* **11** 034009
- Hansen M C et al 2013 High-resolution global maps of 21st-century forest cover change *Science* **342** 850–3
- Hartmann H et al 2018 Research frontiers for improving our understanding of drought-induced tree and forest mortality *New Phytol.* **218** 15–28
- Hood S M, Varner J M, van Mantgem P and Cansler A C 2018 Fire and tree death: understanding and improving modeling of fire-induced tree mortality *Environ. Res. Lett.* **13** 113004
- Hopkins A J M, Ruthrof K X, Fontaine J B, Matusick G, Dundas S J and Hardy G E 2018 Forest die-off following global-change-type drought alters rhizosphere fungal communities *Environ. Res. Lett.* **13** 095006
- Huang K, Yi C, Wu D, Zhou T, Zhao X, Blanford W J, Wei S, Wu H, Ling D and Li Z 2015 Tipping point of a conifer forest ecosystem under severe drought *Environ. Res. Lett.* **10** 024011
- IPCC 2021 *AR6 Climate Change 2021: The Physical Science Basis* (Geneva: IPCC)
- MacKay D S, Roberts D E, Ewers B E, Sperry J S, McDowell N G and Pockman W T 2015 Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models of tree response to drought *Water Resour. Res.* **51** 6156–76
- Matusick G, Ruthrof K X, Kala J, Brouwers N C, Breshears D D and Hardy G E S 2018 Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought *Environ. Res. Lett.* **13** 095002
- McDowell N G et al 2019 Mechanisms of a coniferous woodland persistence under drought and heat *Environ. Res. Lett.* **14** 045014
- McDowell N G et al 2020 Pervasive shifts in forest dynamics in a changing world *Science* **368** eaaz9463
- Pausus J and Keeley J 2021 Wildfires and global change *Front. Ecol. Environ.* **19** 387–95
- Salazar-Tortosa D, Castro J, de Casas R R, Viñepla B, Sánchez-Cañete E P and Villar-Salvador P 2018 Gas exchange at whole plant level shows that a less conservative water use is linked to a higher performance in three ecologically distinct pine species *Environ. Res. Lett.* **13** 045004
- Searle E B and Chen H Y H 2018 Temporal declines in tree longevity associated with faster lifetime growth rates in boreal forests *Environ. Res. Lett.* **13** 125003
- Swann A L S et al 2018 Continental-scale consequences of tree die-offs in North America: identifying where forest loss matters most *Environ. Res. Lett.* **13** 055014
- Trowbridge A M, Stoy P C, Adams H D, Law D J, Breshears D D, Helmig D and Monson R K 2019 Drought supersedes warming in determining volatile and tissue defenses of piñon pine (*Pinus edulis*) *Environ. Res. Lett.* **14** 065006
- Wood J D, Knapp B O, Muzika R M, Stambaugh M C and Gu L 2018 The importance of drought–pathogen interactions in driving oak mortality events in the Ozark Border region *Environ. Res. Lett.* **13** 015004
- Xu P, Zhou T, Yi C, Fang W, Hendrey G and Zhao X 2018 Forest drought resistance distinguished by canopy height *Environ. Res. Lett.* **13** 075003
- Yi C and Jackson N 2021 A review of measuring ecosystem resilience to disturbance *Environ. Res. Lett.* **16** 53008
- Yi C, Pendall E and Ciais P 2015 Focus on extreme events and the carbon cycle *Environ. Res. Lett.* **10** 70201–8
- Yi C, Wei S and Hendrey G 2014 Warming climate extends dryness-controlled areas of terrestrial carbon sequestration *Sci. Rep.* **4** 5472