

## ESA CENTENNIAL PAPER

# On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene

CRAIG D. ALLEN,<sup>1,†</sup> DAVID D. BRESHEARS,<sup>2</sup> AND NATE G. MCDOWELL<sup>3</sup>

<sup>1</sup>*U.S. Geological Survey, Fort Collins Science Center, Jemez Mountains Field Station, Los Alamos, New Mexico 87544 USA*

<sup>2</sup>*School of Natural Resources and the Environment, joint with the Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85745 USA*

<sup>3</sup>*Earth and Environmental Science Division, MS-J495, Los Alamos National Laboratory, Los Alamos, New Mexico 87545 USA*

**Citation:** Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6(8):129. <http://dx.doi.org/10.1890/ES15-00203.1>

**Abstract.** Patterns, mechanisms, projections, and consequences of tree mortality and associated broad-scale forest die-off due to drought accompanied by warmer temperatures—“hotter drought”, an emerging characteristic of the Anthropocene—are the focus of rapidly expanding literature. Despite recent observational, experimental, and modeling studies suggesting increased vulnerability of trees to hotter drought and associated pests and pathogens, substantial debate remains among research, management and policy-making communities regarding future tree mortality risks. We summarize key mortality-relevant findings, differentiating between those implying lesser versus greater levels of vulnerability. Evidence suggesting lesser vulnerability includes forest benefits of elevated [CO<sub>2</sub>] and increased water-use efficiency; observed and modeled increases in forest growth and canopy greening; widespread increases in woody-plant biomass, density, and extent; compensatory physiological, morphological, and genetic mechanisms; dampening ecological feedbacks; and potential mitigation by forest management. In contrast, recent studies document more rapid mortality under hotter drought due to negative tree physiological responses and accelerated biotic attacks. Additional evidence suggesting greater vulnerability includes rising background mortality rates; projected increases in drought frequency, intensity, and duration; limitations of vegetation models such as inadequately represented mortality processes; warming feedbacks from die-off; and wildfire synergies. Grouping these findings we identify ten contrasting perspectives that shape the vulnerability debate but have not been discussed collectively. We also present a set of global vulnerability drivers that are known with high confidence: (1) droughts eventually occur everywhere; (2) warming produces hotter droughts; (3) atmospheric moisture demand increases nonlinearly with temperature during drought; (4) mortality can occur faster in hotter drought, consistent with fundamental physiology; (5) shorter droughts occur more frequently than longer droughts and can become lethal under warming, increasing the frequency of lethal drought nonlinearly; and (6) mortality happens rapidly relative to growth intervals needed for forest recovery. These high-confidence drivers, in concert with research supporting greater vulnerability perspectives, support an overall viewpoint of greater forest vulnerability globally. We surmise that mortality vulnerability is being discounted in part due to difficulties in predicting threshold responses to extreme climate events. Given the profound ecological and societal implications of underestimating global vulnerability to hotter drought, we highlight urgent challenges for research, management, and policy-making communities.

**Key words:** carbon starvation; climate change; CO<sub>2</sub> fertilization; drought; ESA Centennial Paper; extreme events; forest die-off; forests; hydraulic failure; insect pests; pathogens; tree mortality; woodlands.

**Received** 9 April 2015; **revised** 30 June 2015; **accepted** 1 July 2015; **published** 7 August 2015. Corresponding Editor: D. P. C. Peters.

**Copyright:** © 2015 Allen et al. This is an open-access article distributed under the terms of the Creative Commons

Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

**Editors' Note:** This paper was commissioned by the members of the Ecosphere Editorial Board to commemorate the ESA Centennial celebration.

† **E-mail:** [craig\\_allen@usgs.gov](mailto:craig_allen@usgs.gov)

## INTRODUCTION

Ecology focuses on patterns and processes for biota and the interrelated abiotic factors influencing them. As the discipline of ecology has developed, scientists as diverse as von Humboldt, Wallace, Mobius, Haeckel, Merriam, Cowles, Tansley, F. Clements, Shelford, Lotka, Gleason, Elton, Hutchinson, F. Shreve, Braun, A. Leopold, Kittredge, Patrick, Dyksterhaus, E. Leopold, the Odums, Whittaker, Carson, MacArthur, and Davis, among many others, have contributed classic foundational concepts on ecological change and management (McIntosh 1986, Langenheim 1996, Real and Brown 2012). The need to improve ecological knowledge is as relevant as ever since the Earth has arguably entered a new epoch—the Anthropocene—in which the influence of humanity permeates the biogeosphere, particularly through the pervasive impacts of anthropogenically exacerbated climate change (Steffen et al. 2011, Lewis and Maslin 2015). Under rapidly changing climate, accelerated understanding of the diverse patterns and processes driving dynamic ecosystem responses is needed to effectively address the challenges of sustainably managing and restoring affected systems (Hobbs et al. 2014, IPCC 2014, Perring et al. 2015).

One of the major potential effects of warming climate across terrestrial biomes is an increase in climate-driven tree mortality, particularly mortality triggered by a combination of drought and hotter temperatures (Allen et al. 2010; e.g., Appendix A). Such a combination of drought and warmer temperatures has been coined “global-change-type drought” (Breshears et al. 2005; later “hot drought”, Overpeck and Udall 2010)—in this paper we use the term “hotter drought”. During drought, warmer temperatures can increase stress and mortality risk for trees (McDowell et al. 2008), directly through physiological impacts (e.g., Adams et al. 2009) or indirectly through effects on pests and pathogens (e.g., Weed et al. 2013). Extreme events, such as

severe drought compounded by unusually warm temperatures, increasingly are recognized as key drivers of vegetation change (Jentsch et al. 2007, Smith 2011, IPCC 2012), including climate-induced tree mortality. Drought and heat impacts on woody plants include: reductions in leaf area and crown “dieback” where only a portion of a tree’s canopy dies (commonly referred to as “defoliation” in Europe; e.g., Carnicer et al. 2011); increases in background tree mortality rates (van Mantgem et al. 2009, Phillips et al. 2010); and broad-scale forest die-off events (Breshears et al. 2005, Allen et al. 2010, Matusick et al. 2013, Worrall et al. 2013). We consider all of these effects of hotter drought on tree stress and mortality, recognizing that these diverse effects need to be distinguished from one another in some cases.

Explicit consideration of global forest vulnerability to mortality from hotter drought has gone from being minor in early assessments of global change risks (e.g., IPCC 1995, 2001, 2007; but see IPCC [1990] for initial concerns raised regarding tree mortality) to being more directly discussed as a key risk of concern in newer assessments (IPCC 2014, National Climate Assessment 2014), reflecting the rapid recent increase in scientific literature on tree mortality (Allen et al. 2010). Future changes in the magnitude and distribution of tree mortality have diverse and profound global implications. Tree mortality is central to projections of climate-induced vegetation change. For widely projected biome-scale shifts in wooded vegetation types to occur with anticipated climate change (Gonzalez et al. 2010, IPCC 2014), the currently dominant vegetation must die. Major vegetation shifts that implicitly include widespread tree mortality usually are communicated graphically through maps of projected vegetation change (Fig. 1A, B); however, this type of presentation does not explicitly highlight the associated tree mortality (Fig. 1C, D). Even where tree mortality does not cause species range changes or biome shifts, broad-scale tree mortality fundamentally affects

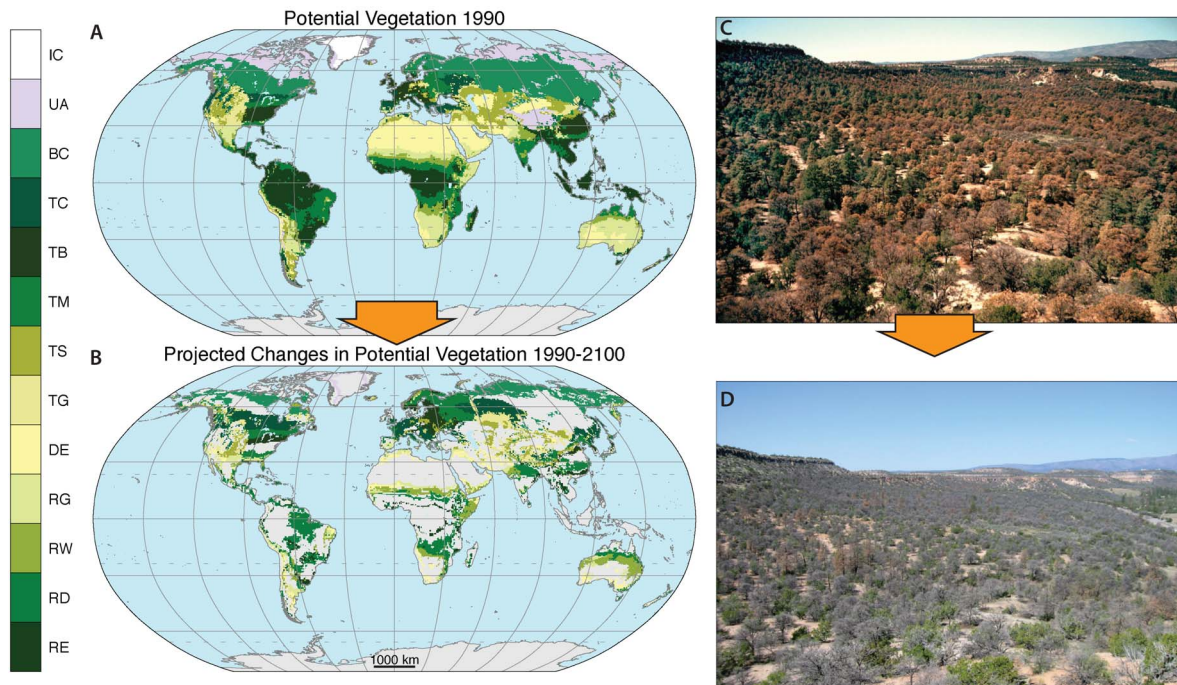


Fig. 1. Climate-driven projected changes in vegetation often are represented as maps of spatial change (A, B). Implicit and potentially overlooked in such presentations is the underlying widespread tree mortality (C, D) that necessarily would occur with many such projected changes to produce biome-level shifts in vegetation. Left panels of projected vegetation shifts are from Gonzalez et al. (2010), using the MC1 dynamic global vegetation model. (A) Modeled potential vegetation under observed 1961–1990 climate. (B) Modeled potential vegetation under projected 2071–2100 climate where any of nine climate scenario combinations of general circulation model and emissions pathway drives projected vegetation change. Displayed biomes, in panels A and B, from poles to equator: ice (IC), tundra and alpine (UA), boreal conifer forest (BC), temperate conifer forest (TC), temperate broadleaf forest (TB), temperate mixed forest (TM), temperate shrubland (TS), temperate grassland (TG), desert (DE), tropical grassland (RG), tropical woodland (RW), tropical deciduous broadleaf forest (RD), tropical evergreen broadleaf forest (RE). Right panel photographs show: (C) *Pinus edulis* mortality underway in a Southwestern USA woodland (October 2002); and (D) the same view after dead *P. edulis* trees have dropped needles but trunks remain standing (May 2004), with surviving *Juniperus monosperma* trees still green (photos by C. D. Allen from Breshears et al. [2009]).

a diverse suite of environmental processes and ecosystem services (Breshears et al. 2011), including but not limited to: forest community and ecosystem dynamics (Anderegg et al. 2013b); biodiversity (Maron et al. 2015); ecohydrology (Adams et al. 2012); biosphere-atmosphere radiation fluxes (Rotenberg and Yakir 2010, Royer et al. 2011); biogeochemical processes and associated C sequestration (Kurz et al. 2008, Pan et al. 2013); and global earth system consequences and feedbacks (Bonan 2008, Adams et al. 2010, IPCC 2013, 2014). Uncertainties related to tree mortal-

ity in response to hotter drought pose a key challenge for earth system modelers to predict future vegetation change and feedbacks to global climate with confidence (McDowell et al. 2013, Joetzjer et al. 2014, Sitch et al. 2015; see also Swann et al. 2012).

Despite the recent increase in scientific literature on tree mortality (including contributions from emerging technologies, see Appendix B), there is not broad agreement within the research community about the degree to which forests are vulnerable globally (Hartmann et al. 2015). Two

contrasting overall viewpoints on the wide range of potential future states for forests globally are: (1) *lesser vulnerability*—forests generally will be resilient to hotter drought, and many can even benefit from global change, and therefore vulnerability to future hotter drought is limited; or (2) *greater vulnerability*—forest mortality events to date represent only the beginning of an increasing phenomenon because hotter drought threatens tree survival in multiple ways, consistent with fundamental tree physiological processes. We use the terms “lesser” and “greater” because they qualitatively imply evidence in one direction or the other without being absolute, which would be inaccurate in many cases. These divergent viewpoints exist widely within the multidisciplinary research community studying tree mortality, ranging from physiology and ecology to vegetation modeling and forest management. One reason for divergent views is that across the broad spectrum of tree mortality research the results exhibit a range of sometimes contrasting findings, so there is evidence supporting both lesser and greater vulnerability viewpoints. A thorough and explicit synthesis of these contrasting viewpoints and their associated supporting evidence is needed to improve our ability to assess the future risk of amplified forest mortality due to climate change.

Here we develop a globally framed synthesis of key research findings on vulnerability to tree mortality and associated forest die-off in the Anthropocene, considering both the threats to forests under hotter drought conditions as well as the compensatory mechanisms that might mitigate those impacts or enhance forest resilience. Using these findings, we identify ten contrasting perspectives shaping the overall vulnerability debate that are not usually considered collectively. We then present a set of global drivers of mortality risk that are known with high confidence. We also identify issues that potentially affect viewpoints of global forest vulnerability. The ten perspectives and associated evidence are weighed in concert with the high confidence drivers of mortality risk to determine our overall viewpoint on forest vulnerability to tree mortality under hotter drought. Specific recommendations for dealing with forest vulnerability are outlined for sub-groups within research, management, and policy-making

communities. Overall we seek to address a broad audience, ranging from specialized researchers focused on mechanistic processes underlying tree mortality through a diverse array of ecologists, global earth system modelers, forest managers, and policy makers, including those focused on carbon emissions.

## CONTRASTING PERSPECTIVES ON TREE VULNERABILITY TO MORTALITY FROM HOTTER DROUGHT

### *Key Findings from Recent Research on Tree Mortality and Forest Die-Off Vulnerability to Hotter Drought*

Research related to many aspects of tree mortality has increased rapidly over the past decade, with multiple reviews related to particular portions of the proliferating science on drought and heat-related mortality (McDowell et al. 2008, 2011, 2013, Raffa et al. 2008, Allen et al. 2010, Choat et al. 2012, Hicke et al. 2012a, Martínez-Vilalta et al. 2012a, Anderegg et al. 2013b, Oliva et al. 2014, Teskey et al. 2014, Zeppel et al. 2014, Hartmann et al. 2015, Meir et al. 2015, Reyer et al. 2015, Sperry and Love 2015). We point readers to these reviews for more details on particular aspects of tree mortality. Here we highlight selected key findings across the spectrum of global research related to vulnerability for trees to mortality from hotter drought, addressing the full range of mortality from partial crown diebacks and increasing rates of background tree mortality to extensive forest die-off. Given the enormous increase in recent literature on tree mortality, this broad-based presentation of diverse evidence across the whole spectrum of study topics, methods, localities, tree species, and responses provides an opportunity to explicitly and more holistically consider the breadth of evidence for differing levels of forest vulnerability to future die-off events under hotter drought.

We split the spectrum of studies into two sets of relatively contrasting findings. The first set of findings (Table 1) highlights research with evidence of compensatory capacities indicating that many forests likely are able to tolerate and/or adapt to hotter droughts, providing support for concluding *lesser* levels of forest vulnerability relative to many recent studies and projections.

Table 1. Compensatory factors leading to *lesser* vulnerability to tree mortality during hotter drought. Key evidence from the scientific literature supporting perspectives that forests will be able to compensate to survive hotter droughts, along with associated references, the corresponding topical research category (C) from Appendix C, and the related perspective number from Table 3 (T3) for cross-reference. Topical categories are: CL, Climate; EF, Ecological Feedbacks; MT, Management; MC, Mechanisms; PN, Patterns; and PJ, Projections, as noted in the text and discussed in greater detail in Appendix C.

Evidence supporting <i>lesser</i> vulnerability to hotter drought	References	C	T3
Little change in global drought since 1950; most droughts are local and short duration	Sheffield et al. 2012, Trenberth et al. 2014	CL	1
Wetter climate projected for some regions	IPCC 2013	CL	1
Tree growth is robust and/or increasing in some regions:	Phillips et al. 2008, Lewis et al. 2009, McMahon et al. 2010, Fang et al. 2014	PN	1
–from tree ring studies	Salzer et al. 2009, Büntgen et al. 2013	PN	1
–from flux tower sites	Zaehle et al. 2014	PN	1
–from remote sensing	Fensholt et al. 2012, Jong et al. 2012, Liu et al. 2015a, Xia et al. 2015	PN	1
Observed tree mortality rates not unusual in many places	Dietze and Moorcroft 2011	PN	1
Drought mortality effects typically not severe at broad spatial scales	Allen et al. 2010	PN	1
Atmospheric evaporative demand observed to have declined globally	McVicar et al. 2012	CL	2
Warmer conditions promote tree growth in cold regions	Richardson et al. 2013, Juday et al. 2015	PN	2
Warmer atmosphere has increased water content and precipitation	Held and Soden 2006	CL	2
“Greening” and global forest biomass increases via CO <sub>2</sub> fertilization	Fensholt et al. 2012, Jong et al. 2012, Pan et al. 2013, Quirk et al. 2013, Poulter et al. 2014	PN	3
Increased water-use efficiency observed	Leakey 2009, Peñuelas et al. 2011, Frank et al. 2015a	PN	3
Compensatory physiological mechanisms decrease vulnerability via:			
–short-term regulation and long-term acclimation	Mencuccini 2003, Klein et al. 2013, 2014a, Rico et al. 2014, Teskey et al. 2014	MC	4
–down-regulation of respiration	Atkin and Tjoelker 2003	MC	4
–up-regulation of photosynthesis	Chaves et al. 2009	MC	4
–change in defense allocation	Herms and Mattson 1992	MC	4
–use of nonstructural carbohydrate reserves	Klein et al. 2014b, O’Brien et al. 2014	MC	4
–embolism resistance	Kolb and Sperry 1999	MC	4
–xylem refilling to reduce embolism	Klein et al. 2014a	MC	4
–acclimation to recurrent droughts	Backhaus et al. 2014, Brodribb et al. 2014	MC	4
Phenological adjustments to avoid growth in drought periods	Limousin et al. 2012, Klein et al. 2013, Richardson et al. 2013, Adams et al. 2015, Xia et al. 2015		
Morphological acclimation through:			
–shifts in allocation to foliage, sapwood, and roots	Mencuccini 2003, Lapenis et al. 2005	MC	5
–rapid short-term reductions in leaf area	Rood et al. 2000, Ciais et al. 2005, Filewod and Thomas 2014	MC	5
–post-dieback resprouting	Zeppel et al. 2014	MC	5
–changes in wood density	Britez et al. 2014	MC	5
–changes in tree morphology	Nicotra et al. 2010, Carnicer et al. 2011, Limousin et al. 2012, Liu et al. 2015b, Zanetti et al. 2015	MC	5
Genetic variability fosters tree population tolerance to drought/heat stress	Liepe 2014, Bansal et al. 2015	MC	6
Natural selection fosters adaptive acclimation	Aitken et al. 2008, Alfaro et al. 2014	MC	6
Higher genetic diversity fosters adaptive responses	Jump et al. 2009a, Mátyás et al. 2009, Sthultz et al. 2009, Harter et al. 2015	MC	6
Populations from colder portions of their species’ range have greater genetic capacity to acclimate to warming	Rehfeldt 2002, 2004, 2014	MC	6
High tree species diversity fosters forest survival and recovery	Dale et al. 2010, Fauset et al. 2012, Peters et al. 2015	EF	7
Landscape-scale microsite diversity allows for local survival and recovery	Hampe and Jump 2011, Adams et al. 2014, Peterman and Waring 2014, Dorman et al. 2015a, Silvertown et al. 2015	EF	7
Forest ecosystems have reorganized in the past, are functionally resilient	Corlett and Westcott 2013	EF	8

Table 1. Continued.

Evidence supporting <i>lesser</i> vulnerability to hotter drought	References	C	T3
Mortality events are self-limiting by reducing competition	Lloret et al. 2012	EF	8
CO <sub>2</sub> -enhanced tree growth is:			
–modeled to outpace mortality globally	Huntingford et al. 2013, Sitch et al. 2015	PJ	9
–supported by empirical, experimental, and modeled evidence	Lloyd and Farquhar 2008, Keenan et al. 2013	PJ	9
Continued growth modeled through CO <sub>2</sub> fertilization and increased water-use efficiency	Cox et al. 2013, Huntingford et al. 2013, Zscheischler et al. 2014, Sitch et al. 2015	PJ	9
Increasing background mortality may be a result of greater competition from CO <sub>2</sub> -enhanced tree growth	Phillips 2008, Doughty et al. 2015, Zhang et al. 2015	PJ	9
Forest thinning can reduce drought risk	D'Amato et al. 2013, Giuggiola et al. 2013, Tarancón et al. 2014	MT	10
Direct alteration of species composition and genetics	Aitken and Whitlock 2013, Fares et al. 2015	MT	10
Strategies to increase forest water availability	Grant et al. 2013	MT	10
Well-managed forests can continue to provide vital ecosystem services	Pinkard et al. 2014, Keenan 2015, Lugo 2015, Schelhaas et al. 2015	MT	10

In contrast, the second set of findings (Table 2) highlights recent evidence that forests likely are subject to *greater* vulnerability to tree mortality with hotter drought. In Tables 1 and 2 the listed representative research findings and associated references are cross-referenced by six topical categories: *Climate* (abbreviated in Tables 1 and 2 as CL)—observed and projected climate changes of relevance to tree mortality from drought and heat; *Patterns* (PN)—observed spatial patterns of tree growth, forest stress and productivity, and drought- and heat-induced tree mortality and forest die-off; *Mechanisms* (MC)—physiological, morphological, and genetic mechanisms and processes that affect tree vulnerability to drought- and heat-induced mortality; *Ecological Feedbacks* (EF)—ecological factors and feedbacks at forest, landscape, and earth system scales that affect forest vulnerability to drought- and heat-induced tree mortality; *Projections* (PJ)—broad-scale modeled projections of forest growth, productivity, and vulnerability to drought- and heat-induced tree mortality with climate change; and *Management* (MT)—management actions relative to forest vulnerability to drought- and heat-induced tree mortality. Appendix C integrates information within each topical category, and presents additional studies not covered in the main text (some points presented in the main text also are covered in Appendix C for context).

### *Ten Contrasting Perspectives on Tree Vulnerability to Mortality from Hotter Drought*

We identify ten contrasting perspectives shaping the vulnerability debate that arise individually but that previously have not been discussed in concert (Table 3). The vulnerability debate could be categorized other ways as well, but we think this framing of the debate highlights its most critical attributes. These ten contrasting perspectives are not mutually exclusive, and some studies are relevant to more than one perspective. We present each of the ten contrasting perspectives by iterating through evidence associated with each—first for those findings implying lesser vulnerability (from Table 1), and then for those implying greater vulnerability (from Table 2). While we recognize that a gradient of perspectives exists, categorizing the perspectives as dichotomies illuminates core issues of the vulnerability debate. Although numerous research or synthesis papers cover one or more aspects associated with these ten contrasting perspectives, we are not aware of any presentation spanning the breadth of them collectively. These ten contrasting perspectives, framed relative to lesser versus greater vulnerability of tree mortality to hotter drought, are presented below; a summary version of each is presented in Table 3.

#### *1. Observations*

*“Are the impacts of hotter drought on tree mortality and growth observed to date modest and*

Table 2. Risk factors leading to *greater* vulnerability to tree mortality during hotter drought. Key evidence from the scientific literature supporting perspectives that forests will become increasingly vulnerable to mortality from hotter droughts, along with associated references, the corresponding topical research category (C) from Appendix C, and the related perspective number from Table 3 (T3) for cross-reference. Topical categories are: CL, Climate; EF, Ecological Feedbacks; MT, Management; MC, Mechanisms; PN, Patterns; and PJ, Projections, as noted in the text and discussed in greater detail in Appendix C.

Evidence supporting <i>greater</i> vulnerability to hotter drought	References	C	T3
Global warming, hotter droughts, and more severe droughts observed and projected	IPCC 2012, 2013, Dai 2013, Trenberth et al. 2014, Diffenbaugh et al. 2015	CL	1
Plots and tree rings show growth declines in diverse regions with warm drought	Ma et al. 2012, Liu et al. 2013, Silva and Anand 2013, Girardin et al. 2014, Lévesque et al. 2014, Brien et al. 2015, Chen and Luo 2015, Walker et al. 2015	PN	1
Drought-related tree mortality observed in all main forest types globally, especially with hot drought; unprecedented forest die-offs in some regions	Breshears et al. 2005, Raffa et al. 2008, Allen et al. 2010, Matusick et al. 2013, IPCC 2014, Brien et al. 2015	PN	1
Tree rings in some regions show recent drought stress as most severe in the last 800–1200 years, linked to recent warming	Touchan et al. 2011a, b, Williams et al. 2013, Griffin and Anchukaitis 2014	PN	1
Increased background mortality rates are linked to warming and greater water stress	van Mantgem et al. 2009, Carnicer et al. 2011, Peng et al. 2011	PN	1
Hotter drought can increase mortality from insects	Raffa et al. 2008, Logan et al. 2010, Das et al. 2013	PN	1
Remote sensing shows rising forest drought and heat stress, and declining NPP, in some areas	Zhao and Running 2010, Beck et al. 2011, Hilker et al. 2014, Yi et al. 2014, Zhou et al. 2014a	PN	1
Large trees at greater risk from hotter drought	Nepstad et al. 2007, Phillips et al. 2010, Zhou et al. 2013, McDowell and Allen 2015, McIntyre et al. 2015	PN	1
Global forest health and mortality trends are uncertain because global monitoring is lacking although technically possible	Allen et al. 2010, Hansen et al. 2013, Mascaro et al. 2014, Asner 2015, McDowell et al. 2015	PN	1
In forests globally, dominant trees routinely function close to hydraulic safety margins; likely selected by historical climate conditions	Choat et al. 2012	MC	2
Hotter drought impairs key physiological processes, increases mortality risks from carbon starvation and hydraulic failure	Atkin et al. 2007, McDowell et al. 2008, 2011	MC	2
Nonlinear increase in atmospheric water demand drives greater tree drought stress and mortality	Breshears et al. 2013, Eamus et al. 2013, Williams et al. 2014	MC	2
Shorter droughts become lethal	Adams et al. 2009, Will et al. 2013, Duan et al. 2014, 2015	MC	2
Strong climate warming consensus, increasing climate extremes expected, including increased frequency of rapid swings between opposite precipitation extremes	IPCC 2012, 2014, Cai et al. 2015	CL	2
Forest “browning” observed in some regions in some years	Jong et al. 2012, Yi et al. 2014	PN	3
Hotter drought can cancel out CO <sub>2</sub> fertilization and increased water-use efficiency, as can insect herbivory	Jentsch et al. 2007, Peñuelas et al. 2011, Warren et al. 2011, Franks et al. 2013, Duan et al. 2014, 2015, Lévesque et al. 2014, Couture et al. 2015	MC	3
Nutrient limitations (N, P) can constrain CO <sub>2</sub> fertilization	Norby et al. 2010, Fernández-Martínez et al. 2014, Zhang et al. 2014a	MC	3
Increased “greening” is partly from land use changes	Lloret et al. 2012, Andela et al. 2013	PN	3
Most natural forests are still water limited	Gedalof and Berg 2010, Jenerette et al. 2012, Bernacchi and VanLoocke 2014	PN	3
Hotter drought has numerous negative physiological effects	Martínez-Vilalta et al. 2002, Atkin and Tjoelker 2003, Adams et al. 2009, Breshears et al. 2009, McDowell et al. 2011, Zhao et al. 2013, Teskey et al. 2014, Adams et al. 2015	MC	4
Rapid rate and magnitude of warming may outpace acclimation and adaptation	Aitken et al. 2008, Liu et al. 2015b	MC	4
Rapid climate shifts and extreme drought/heat events may be especially harmful	Mencuccini 2003, Frank et al. 2015b	MC	5
Reductions in leaf area reduce future carbohydrate availability and tree viability	Galiano et al. 2011, Girard et al. 2012	MC	5
Trees from warmest range areas are most vulnerable to drought and heat stress	Rehfeldt et al. 2002, 2004, 2014	MC	6
Rapid changes can exceed evolutionary tipping points	Alfaro et al. 2014, Botero et al. 2015	MC	6

Table 2. Continued.

Evidence supporting <i>greater</i> vulnerability to hotter drought	References	C	T3
Genetic variability is probably insufficient to handle the projected changes	Aitken et al. 2008, Franks et al. 2014	MC	6
Landscape diversity buffers can be overwhelmed by extreme drought	Breshears et al. 2005, Hylander et al. 2015	EF	7
Tree diversity only buffers systems in a relative sense; some species still subject to die-off	Fauset et al. 2012, Feeley et al. 2012, Brienens et al. 2015	EF	7
Past climate changes and drought have driven major turnover of forest species compositions, so tree species range shifts expected with much hotter droughts	Corlett and Wescott 2013, Iverson and McKenzie 2013, Pederson et al. 2014b, Clifford and Booth 2015	EF	8
Hotter drought favors:			
–increased fire, insect outbreaks, and pathogens	Desprez-Loustau et al. 2006, Raffa et al. 2008, Flannigan et al. 2013, Weed et al. 2013, Williams et al. 2013, IPCC 2014	EF	8
–shorter tree lifespans	Adams et al. 2009, Will et al. 2013	EF	8
–smaller trees and non-tree life forms	Zeppel et al. 2014, McDowell and Allen 2015	EF	8
Novel and no-analogue ecosystems, as well as biome shifts, expected	Williams and Jackson 2007, Gonzalez et al. 2010, Hobbs et al. 2014	EF	8
Hotter drought threatens irreplaceable old-growth trees with largest C stores	Lindenmayer et al. 2012, Stephenson et al. 2014, McDowell and Allen 2015	EF	8
Most broad-scale models lack mechanistic mortality functions and are not based on measured mortality responses	McDowell et al. 2013, Joetzier et al. 2014, Betts et al. 2015	PJ	9
Forest stress from hotter drought is already evident in many regions	Gedalof and Berg 2010, Peñuelas et al. 2011, Lévesque et al. 2014, Brienens et al. 2015	PJ	9
Lack of realistic tree mortality processes in earth system models is a key limitation	Friend et al. 2014, Betts et al. 2015, Doughty et al. 2015, Frank et al. 2015b, Sitch et al. 2015	PJ	9
Tested models poorly replicate observed die-offs	Steinkamp and Hickler 2015	PJ	9
Thinned forests can still die during hotter drought	Tarancón et al. 2014, Elkin et al. 2015	MT	10
The scale of forest management is limited and projected warming rates and magnitudes of hotter drought extremes could overwhelm the effects of management actions	Bonan 2008, Kurz et al. 2008, Phillips et al. 2009, Reichstein et al. 2013, IPCC 2014, Lindner et al. 2014	MT	10

*spatially-limited?”*

OR

*“Are hotter droughts causing global increases in rates of background tree mortality and of broad-scale forest die-off events, along with increasingly substantial and widespread forest growth declines from many regions?”*

*Lesser vulnerability evidence* (Table 1). Globally, the impacts of drought or heat-related tree mortality are inherently limited because, overall, drought is relatively infrequent and localized, and there is evidence of little change in global drought since 1950 (Sheffield et al. 2012). Furthermore, total global precipitation is increasing, with wetter conditions observed and projected for many regions (IPCC 2013), which could ameliorate future tree mortality in those locations. Tree growth and accumulating forest carbon storage across diverse regions have been robust or accelerating as determined by plots

(Phillips et al. 2008, Lewis et al. 2009, McMahon et al. 2010, Fang et al. 2014, Báez et al. 2015), tree-ring studies (Martínez-Vilalta et al. 2008, Salzer et al. 2009, Büntgen et al. 2013, Juday et al. 2015), biogeochemistry flux tower sites (Zaehle et al. 2014), and remote-sensing (Fensholt et al. 2012, Jong et al. 2012, Liu et al. 2015a, Xia et al. 2015). Indeed, global terrestrial biomass has increased recently, driven by additional woody biomass in shrublands, savannas, and some forests (Barger et al. 2011, Pan et al. 2013, Liu et al. 2015a). Even though substantial tree mortality has been documented recently, tree mortality is a natural demographic process (Franklin et al. 1987), with mortality occurring normally in association with aging and successional thinning (Clark et al. 2014). Indeed, in many areas higher rates of background tree mortality are a result of successional thinning and greater within-stand competition (Luo and Chen 2011) due to widespread increases in forest densities and biomass from



Table 3. Ten contrasting perspectives on the relative vulnerability of forests to tree mortality from hotter drought, summarizing the broad spectrum of evidence associated with perspectives of both lesser and greater vulnerability presented in the main text and Tables 1 and 2, which also provide supporting references.

Perspectives supporting <i>LESSER</i> vulnerability	Counterpoint perspectives supporting <i>GREATER</i> vulnerability
<b>1. Observations</b>	
<b>Robust growth &amp; limited mortality common.</b> Only modest, spatially limited forest stress and drought mortality impacts are observed to date, as in many regions tree growth is robust or even increasing, observed tree mortality rates and episodes are not unusual, and drought-induced tree mortality has not caused significant biome transitions anywhere yet.	<b>Growth stress, background mortality &amp; die-off increasing.</b> Significant forest growth declines are documented from many regions, background tree mortality rates are rising worldwide, and broad-scale forest die-off events are emerging in all major forest biomes—all linked to warming and drought.
<b>2. Temperature</b>	
<b>Effects small; more atmospheric water.</b> Temperature effects on tree mortality are relatively small, and global warming drives increased atmospheric water content and precipitation overall while benefiting tree growth in many colder and wetter regions.	<b>Effects big during drought.</b> Warmer temperatures greatly amplify tree stress and mortality—a significant concern given warming is anticipated globally—because warming directly impairs multiple essential tree physiological processes; trees die faster under drought conditions that are warmer; and shorter drought events will become increasingly lethal with climate warming, resulting in increasing frequency of lethal events.
<b>3. CO<sub>2</sub> Fertilization &amp; WUE</b>	
<b>Sufficient to compensate.</b> CO <sub>2</sub> fertilization and water-use efficiency effects generally compensate for drought and heat stress, fostering increased tree growth and NPP, widespread woody plant expansion in dryland ecosystems, and an overall “greening” observed in many regions.	<b>Effects limited; no benefit during severe drought.</b> Mortality processes associated with growing drought and heat stress already are overcoming CO <sub>2</sub> fertilization and water-use efficiency buffering at times and across extensive regions, with forest “browning” and NPP declines, reductions in forest growth, and markedly greater tree mortality observed in multiple regions of growing water stress in recent decades despite concurrent rising [CO <sub>2</sub> ].
<b>4. Physiological Acclimation &amp; Adaptation</b>	
<b>Diverse processes buffer stress.</b> Physiological acclimation and adaptation capacities are large, as trees routinely respond rapidly and adaptively to drought and heat stress with diverse, interactive, compensatory physiological processes and mechanisms.	<b>Threshold limitations exist.</b> Physiological adaptive capacities are small relative to the projected large and rapid increase in hotter droughts, and these adaptive processes are subject to water- and temperature-limited thresholds linked to amplified tree mortality that are likely to be exceeded by future climate.
<b>5. Phenotypic Plasticity</b>	
<b>Large compensation.</b> Phenotypic plasticity and morphological adjustments strongly buffer drought and heat stress at both individual tree and forest levels.	<b>Adjustments inadequate.</b> Phenotypic plasticity and tree morphological adjustments are too small to compensate for increased drought and heat extremes, and too slow to adapt to rapid fluctuations in growth conditions.
<b>6. Genetic Variation &amp; Selection</b>	
<b>Local populations survive &amp; evolve.</b> Genetic variability and selection will buffer drought and heat impacts at stand and population levels.	<b>Variation insufficient; evolution too slow.</b> Within-species genetic variability provides limited survival opportunities relative to the magnitude and rapidity of projected increases in drought and heat extremes.
<b>7. Biological &amp; Landscape Diversity</b>	
<b>Species richness &amp; microsites buffer.</b> Tree species diversity and microsite variation associated with landscape heterogeneity buffer tree mortality impacts.	<b>Diversity overwhelmed.</b> Biodiversity and landscape heterogeneity can ameliorate but not prevent increasing tree mortality impacts from much hotter droughts, because fundamental thresholds of physiological stress and mortality exist for all species.
<b>8. Future Dynamics</b>	
<b>Will resemble historical variability.</b> Future forest dynamics will resemble the recent historical range of variability, with robust forest recovery after mortality episodes.	<b>Novel less-forested ecosystems emerge.</b> Forests will respond to increasingly novel and extreme climate conditions with greater tree mortality and novel ecosystems, with lower tree stature and/or cover and species composition changes.
<b>9. Models</b>	
<b>Greater growth than mortality projected.</b> Current regional- to global-scale vegetation and earth system models generally project greater increases in growth than mortality.	<b>Mortality not well represented.</b> Current regional- to global-scale vegetation and earth systems models are over-optimistic because CO <sub>2</sub> fertilization and temperature benefits to growth are included in the models but realistic mortality processes are insufficiently represented.
<b>10. Management</b>	
<b>Thinning &amp; genetics options.</b> Management can effectively mitigate the impacts of hotter drought relative to excessive tree mortality.	<b>Overwhelmed by extent, magnitude &amp; frequency.</b> Management actions are far too limited spatially and in intensity to prevent widespread and chronic tree mortality impacts of hotter droughts on historical native forests.

harvest and land use histories (e.g., Nowacki and Abrams 2014), as well as from CO<sub>2</sub>-enhanced tree growth rates (Doughty et al. 2015, Zhang et al. 2015). In addition, recently observed rates and episodes of tree mortality are not unusual in some regions (Dietze and Moorcroft 2011). Overall, recent drought-induced tree mortality events often are not severe at broad spatial scales (Allen et al. 2010), and drought-induced tree mortality has not yet caused global-scale biome transitions.

*Greater vulnerability evidence* (Table 2). There is observational evidence of the ongoing global emergence of historically unprecedented large and rapid increases in global temperature this century (Diffenbaugh and Scherer 2011, IPCC 2013), linked to and consistent with predicted increases in drought frequency and duration for much of the globe as climate change progresses (IPCC 2013). Additionally, the area impacted by drought is both observed and projected to expand globally (Dai 2013). Even in locations where the frequency of drought in terms of precipitation deficits does not increase, the frequency of drought in terms of moisture deficits increases with a warmer climate (Agha-Kouchak et al. 2014, Diffenbaugh et al. 2015) and droughts become more intense—the essence of “hotter drought” (Trenberth et al. 2014).

Studies from diverse forest biomes show increased background tree mortality rates that have been associated with warmer temperatures that: (1) increase plant water stress (van Mantgem et al. 2009, Carnicer et al. 2011, Peng et al. 2011, Feeley et al. 2013, Luo and Chen 2013); (2) can amplify tree mortality from biotic agents (Logan et al. 2010, Das et al. 2013, Anderegg et al. 2015a); and (3) support greater net primary productivity in wet regions and drive higher forest turnover rates (Stephenson and van Mantgem 2005, Zhu et al. 2014). Upslope elevational shifts in tree species distributions are being observed with recent warming in tropical (e.g., Feeley et al. 2011, 2013) and temperate (e.g., Peñuelas et al. 2007, Kelly and Goulden 2008) mountain forests, involving greater tree mortality at lower-elevation range limits (e.g., McDowell et al. 2010, Fellows and Goulden 2012). In addition, recent forest die-off events within all major global forest types and on every wooded continent (Fig. 2; Allen et al. 2010, IPCC 2014)

highlight the potential impacts of hotter drought; in some forests, the extent and severity of documented mortality events already has achieved record levels (Raffa et al. 2008, Matusick et al. 2013, Brien et al. 2015). Plots show declines in growth and productivity emerging with warm droughts in forests from boreal (Ma et al. 2012, Chen and Luo 2015) to tropical (Brien et al. 2015) regions. Tree-ring growth studies document growth declines linked to warmer temperatures in many regions, from interior Asia (Liu et al. 2013) and Europe (Jump et al. 2006, Lévesque et al. 2014) to North America (Williams et al. 2010, Girardin et al. 2014, Juday et al. 2015, Walker et al. 2015). Recent hot droughts are the most severe in tree-ring records extending back 800 years in North Africa (Touchan et al. 2011a), 1000 years in the Southwest US (Touchan et al. 2011b, Williams et al. 2013), and 1200 years in California (Griffin and Anchukaitis 2014). Remote-sensing research suggests CO<sub>2</sub> fertilization effects are starting to be limited or compensated by increasing drought and heat, at forest locations ranging from boreal (Beck and Goetz 2011), temperate (Ciais et al. 2005, Potter et al. 2012), and tropical (Hilker et al. 2014, Zhou et al. 2014a) regions. More broadly there are globally widespread indications of slowing or declining forest growth in response to episodic hot drought (Zhao and Running 2010), as well as chronic rises in heat-related drought stress with extensive zones of reduced net primary productivity (NPP; Yi et al. 2014). Warming is documented to drive higher levels of forest drought stress (Liu et al. 2013, Williams et al. 2013; Appendix A), and the most significant forest die-off events commonly are associated with hotter droughts (Breshears et al. 2005, Allen et al. 2010, Matusick et al. 2013). Larger trees seem to be at greater risk of mortality from hotter drought (Phillips et al. 2010, Zhou et al. 2013, McDowell and Allen 2015, McIntyre et al. 2015). However, comprehensive determination of global forest health and tree mortality trends currently is lacking due to the absence of an adequate global monitoring system (Allen et al. 2010), although the technical capability now exists to track forest health relative to tree mortality across broad scales with remote sensing (Hansen et al. 2013, Mascaró et al. 2014, Asner 2015, McDowell et al. 2015). Expanded

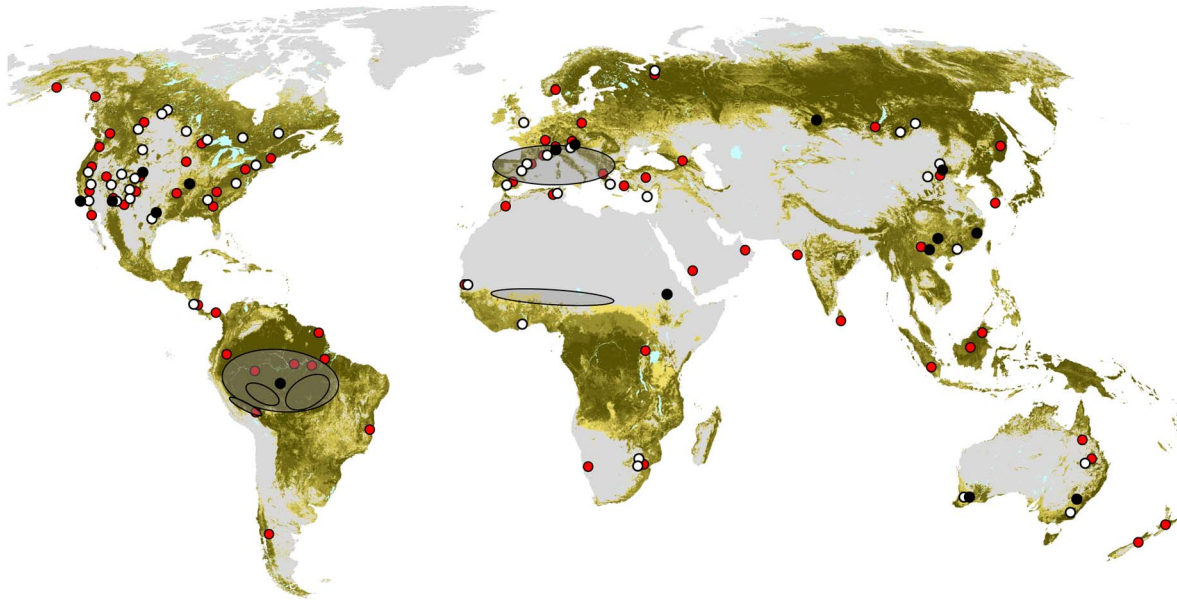


Fig. 2. Locations of substantial drought- and heat-induced tree mortality around the globe since 1970, documented by peer-reviewed studies. Global forest cover (dark green) and other wooded regions (light green) based on FAO (2005). Studies compiled through 2009 (red dots) are summarized and listed in Allen et al. (2010). Additional localities, documented by mostly post-2009 studies, include: the white dots and oval shapes derived from Fig. 4-7 and its associated caption in IPCC (2014); and the black dots reported from other recent publications, listed below. References documenting the most recent localities (black dots), by region: *Africa*, Mokia et al. 2015; *Asia*, Xiong et al. 2011, Zhang et al. 2012, Kharuk et al. 2013, Zhang et al. 2014b, Zhou et al. 2013, 2014b; *Australasia*, Semple et al. 2010, Brouwers et al. 2013; *Europe*, Čater 2015; *North America*, Vogelmann et al. 2009, Zegler et al. 2012, Baguskas et al. 2014, Hart et al. 2014, Kane et al. 2014, Twidwell et al. 2014, Gu et al. 2015, Smith et al. 2015; *South America*, Brienen et al. 2015.

discussion of these studies and additional research findings regarding observed global patterns of tree mortality and growth are presented under the *Patterns* category in Appendix C.

## 2. Temperature

*“Are the effects of warmer temperatures on tree stress and mortality relatively small?”*

OR

*“Do warmer temperatures greatly amplify tree stress and mortality?”*

*Lesser vulnerability evidence* (Table 1). Warmer conditions benefit tree growth in many colder and wetter regions (Richardson et al. 2013, Juday et al. 2015). In addition, global warming drives increased atmospheric water content and greater precipitation in some extensive regions and overall globally (Held and Soden 2006, IPCC

2013, Yi et al. 2015), which should improve moisture conditions for trees in some regions. Also, despite warming temperatures in recent decades, pan evaporation measurements indicate a global trend of declining atmospheric evaporative demand, largely attributed to declines in near-surface wind speeds (McVicar et al. 2012); such a trend suggests potential for amelioration of anticipated forest drought stress from projected warming-driven increases in atmospheric moisture demand. Further, warmer temperatures in the absence of significant drought have been shown to increase tree growth rates, particularly in deciduous species (Way and Oren 2010). Overall, the direct mortality consequences of warming could be relatively small and limited when considered globally, as earth system feedbacks (e.g., greater atmospheric moisture and precipitation) combined with multiple tree-level compensatory processes can buffer future

tree mortality relative to hotter droughts (e.g., Klein et al. 2014a).

*Greater vulnerability evidence* (Table 2). Warming directly impairs multiple essential tree physiological processes (Fig. 3), thereby driving increased vulnerability to mortality (McDowell et al. 2008, 2011, Teskey et al. 2014). Hotter temperatures increase respiration carbon costs, affecting the ratio of carbon assimilation to respiration such that warming could lead to faster carbon starvation (Atkin et al. 2007). All else being equal, warming also increases tree water stress and mortality risk by driving nonlinear increases in atmospheric moisture demand (or vapor pressure deficit, VPD), which amplifies evapotranspiration demand and dries soils (Jung et al. 2010), increasing drought stress on trees (Breshears et al. 2013, Eamus et al. 2013). In some regions recent VPD levels with hotter drought already are large relative to historical conditions (e.g., Williams et al. 2014), and are projected to become unprecedentedly extreme in coming decades, exacerbating forest drought stress and associated tree mortality risk (Fig. 4; Williams et al. 2013). Warmer temperature, with or without drought, can delay spring leaf emergence and reduce leaf and shoot growth (Adams et al. 2015). The combination of low water availability and warmer temperature can have negative impacts on whole-plant carbon balance (Zhao et al. 2013), and also on tree water use regardless of the species' stomatal and hydraulic responses to drought (Garcia-Forner et al. 2015). Failure of phloem translocation of carbon within trees could accelerate carbon starvation by limiting carbon transport to tissues (McDowell and Sevanto 2010, Sala et al. 2010, Mencuccini et al. 2015). Rising temperature has a small benefit on phloem flow through reductions in viscosity, but far more important to phloem flow is the availability of carbohydrates in the foliage to provide a concentration gradient for flow, and the availability of water from the xylem to maintain a tolerable water potential gradient. Thus the effects of hotter drought in reducing photosynthesis and plant water availability may have much larger negative impacts on phloem transport than the benefits of lowered viscosity (e.g., Hölttä et al. 2009, McDowell et al. 2011). Experimental data indicate trees can die faster

under drought conditions that are warmer, as exhibited in 13 of 14 species from 11 different genera recently studied (Adams et al. 2009, Will et al. 2013, Duan et al. 2014, 2015; see also earlier related research by Daubenmire 1943). Consequently, shorter drought events that previously were non-lethal can become lethal with climate warming, producing more frequent tree mortality events (Fig. 5; Adams et al. 2009). Droughts essentially happen everywhere eventually due the combination of inherent climate variability and the site-specific relative nature of drought (Palmer 1965, Vicente-Serrano et al. 2010, Jenerette et al. 2012), and substantial global warming is a consensus climate projection (IPCC 2013). As a result, future droughts are projected to become increasingly severe due to warming (AghaKouchak et al. 2014, Trenberth et al. 2014), driving greater drought stress and mortality effects on current overstory forest trees (Williams et al. 2013) that were selected for dominance under historical conditions with cooler climate (Choat et al. 2012). An increasing literature that spans theory, observations, experiments, and models suggests that tree mortality is highly likely to increase globally as hotter drought intensifies (Table 2), by effects from both incremental chronic warming and episodically through more extreme heat waves during droughts (Fig. 4; IPCC 2012, 2014). Additional notable findings related to this pair of contrasting perspectives can be found in each of the *Climate*, *Patterns*, and *Mechanisms* categories of Appendix C.

### 3. CO<sub>2</sub> Fertilization & WUE

*“Will CO<sub>2</sub> fertilization and associated increased water-use efficiency (WUE) generally compensate for drought and heat stress?”*

OR

*“Are mortality processes associated with increasing drought and heat stress likely to overwhelm the compensatory effects of CO<sub>2</sub> fertilization and any buffering associated with increased water-use efficiency?”*

*Lesser vulnerability evidence* (Table 1). There is abundant and strong evidence demonstrating that CO<sub>2</sub> fertilization and associated effects on water-use efficiency are large globally, including

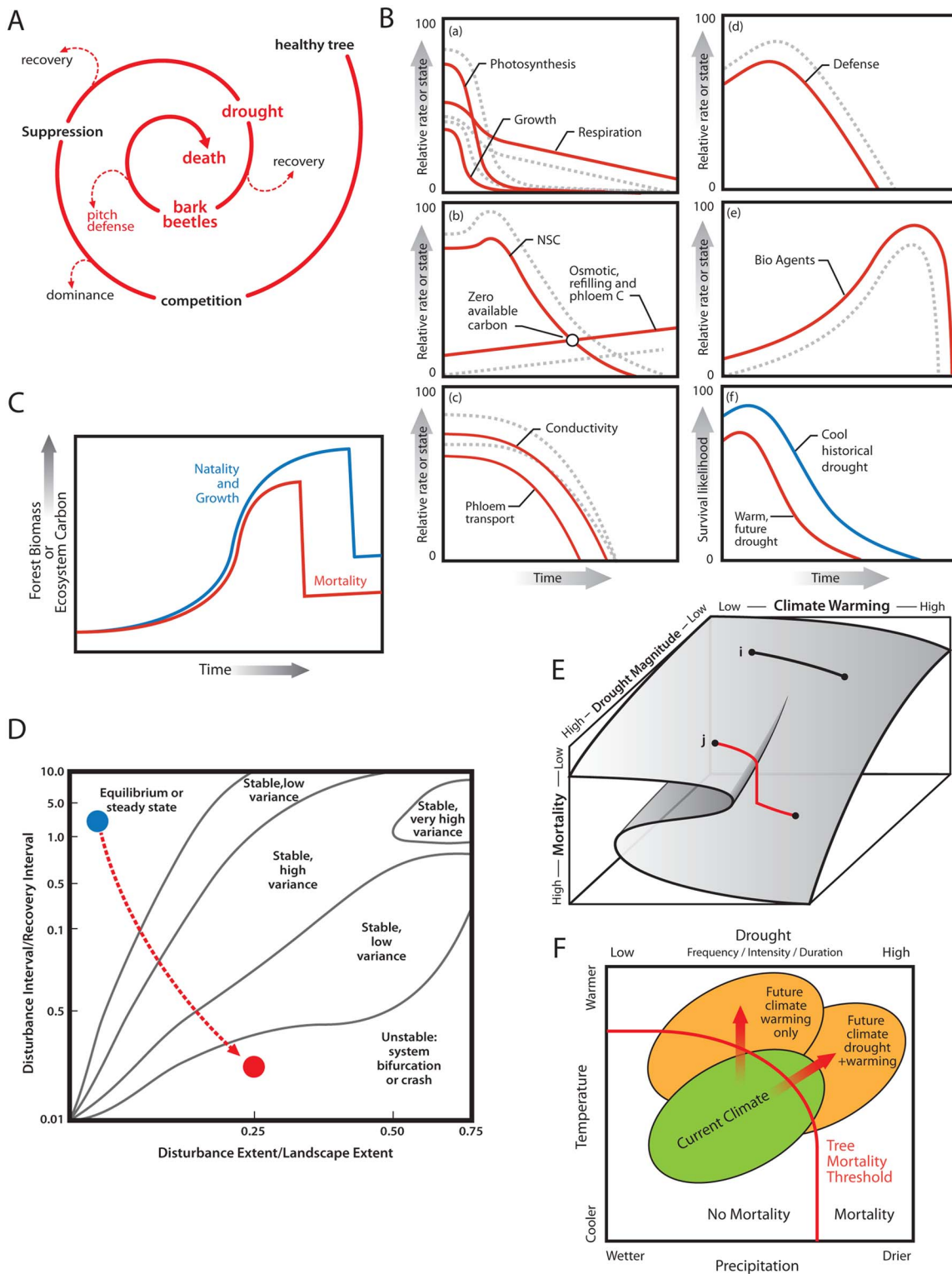


Fig. 3. Examples of conceptual frameworks highlighting some of the many ways that hotter temperatures accompanying drought can exacerbate tree mortality processes (shown with red lines, arrows, and text), (Fig. 3 legend continues on next page)

(continuation of Fig. 3 legend)

particularly relative to thresholds. (A) Tree mortality as a “death spiral” (modified from Franklin et al. [1987]), showing that drought, bark beetles, pitch defense, and death are responsive to hotter temperatures. (B) Components (a)–(e) illustrate the responses to warming (the red lines) of diverse physiological processes and other factors linked to mechanisms of tree mortality (NSC is nonstructural carbohydrates, C is carbohydrates); component (f) summarizes overall likelihood of tree survival with drought duration, depending on temperature (all components in B modified from McDowell et al. [2011]). There are many interrelated temperature-sensitive feedbacks among these processes that exacerbate tree mortality under drought. (C) Trees take a long time to grow to maturity, but can die rapidly; mortality will occur sooner and be more severe under hotter drought (red line), and biomass recovery could be delayed and reduced (modified from Allen et al. [2010]). (D) Stability parameter space for ecosystems relative to the spatial scale of [(disturbance extent)/(landscape event)] and the temporal scale of [(disturbance interval)/(recovery interval)]; modified from Turner et al. (1993). The parameter space indicates whether or not an ecosystem response is stable and its level of variability. The red arrow represents how under rapid global warming, tree mortality events from hotter drought could become so frequent and severe that ecosystems shift to unstable configurations. (E) A catastrophe cusp surface, expressed in terms of mortality or forest cover, relative to drought magnitude and future climate warming (modified from Davenport et al. [1998]). This example illustrates the exacerbating effects of climate warming on tree mortality across a range of drought magnitudes (e.g., pathways i and j), highlighting that for larger magnitude droughts (j) the effects of hotter temperatures can become particularly pronounced and especially difficult to reverse. (F) A conceptual diagram (modified from Allen et al. [2010]) showing the range of variability of “Current Climate” parameters for temperature and precipitation or drought, with only a small portion of the current climate envelope currently exceeding a species-specific tree mortality threshold (the red line). The two future climate envelopes show shifts to more extreme temperature and drought conditions associated with projected climate changes, indicating greater risks of drought-induced die-off for current tree populations. Note that warming alone, without declines in precipitation, can drive climate to exceed tree mortality thresholds.

substantial increases in water-use efficiency (Leakey 2009, Peñuelas et al. 2011, Frank et al. 2015a), increased tree growth and NPP (Martinez-Vilalta et al. 2008, Pan et al. 2013), widespread woody plant expansion in dryland ecosystems (Buitenwerf et al. 2012, Fensholt et al. 2012, Poulter et al. 2014), and an overall “greening” observed in many regions (Jong et al. 2012, Donohue et al. 2013, Ahlström et al. 2015). Thus, with further enrichment of atmospheric CO<sub>2</sub> concentrations at a global scale, forests are projected to continue to grow with enhanced water-use efficiency into the future (Cox et al. 2013, Huntingford et al. 2013, Zscheischler et al. 2014, Sitch et al. 2015), which will constrain the overall importance of tree mortality from hotter drought.

*Greater vulnerability evidence* (Table 2). Forest “browning” (Jong et al. 2012), NPP declines (Yi et al. 2014), reductions in forest growth (Williams et al. 2010, Brienen et al. 2015), and markedly greater tree mortality (Matusick et al. 2013, Williams et al. 2013, Zhou et al. 2013) have been observed despite rising [CO<sub>2</sub>]. Some

“greening” globally is primarily due to tree recovery into previously cleared and grazed land (Lloret et al. 2012) and increased woody plant encroachment due to fire suppression (Andela et al. 2013). In some regions forests show no increases in tree growth despite documented increases in water-use efficiencies, attributed to drought and warmth effects (Peñuelas et al. 2011, Lévesque et al. 2014). Consistent with these observations, an analysis of a tree-ring database of over 2300 forest sites globally found that only 20% of the sites exhibited increased growth potentially due to CO<sub>2</sub> fertilization, with the ring-width growth at other sites constrained primarily by water limitation (Gedalof and Berg 2010). During drought stomata are closed, hence benefits of greater [CO<sub>2</sub>] could be minimal if drought severities, frequencies, and durations increase as projected (Franks et al. 2013). While greater water-use efficiencies from elevated [CO<sub>2</sub>] may support increases in leaf area at tree and stand levels and benefit trees during moderate droughts, more extreme drought and heat stress

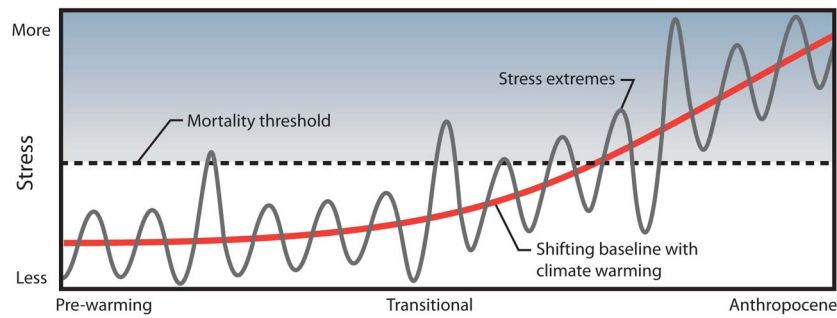


Fig. 4. Stress is the result of both trends and events in climate (Jentsch et al. 2007). The red line indicates a shifting baseline level of forest stress through time due to an increasing trend in temperature; the grey line represents stress changes due to multi-year oscillations in precipitation and temperature that are inherent in the climate system, producing stress events like extreme droughts and heat waves. Atmospheric warming increases both baseline and extreme drought stresses through time, thereby driving elevated tree mortality vulnerability. Increasing temperature alone drives greater forest drought stress (Adams et al. 2009, Williams et al. 2013), and because temperature is increasing chronically, so is forest stress. Swings in forest drought stress push forests closer (or further) from the historical mortality threshold (dashed black line), but given the chronic increase in forest stress associated with ongoing anthropogenic warming, the frequency, magnitude, and duration of these swings above the mortality threshold increase through time. If unabated, chronic warming eventually will cause even relatively wet periods to exceed the mortality stress threshold for present-day forests.

can drive excessive stomatal closure and reduced photosynthesis—resulting in negative carbon balances, risk of hydraulic failure, and associated leaf senescence and abscission (Warren et al. 2011, Dickman et al. 2014). Most studies of CO<sub>2</sub> fertilization are not focused on tree mortality and have not been concurrent with drought (Jentsch et al. 2007), limiting their value for understanding interactions between [CO<sub>2</sub>] and drought (Duan et al. 2015). In two particularly relevant [CO<sub>2</sub>]-by-drought experiments, elevated [CO<sub>2</sub>] did not ameliorate drought stress nor delay tree seedling mortality during combined heat and drought treatments in *Eucalyptus* (Duan et al. 2014), nor did it delay mortality in two gymnosperms (*Pinus radiata* and *Callitris rhomboidea*; Duan et al. 2015). There also is substantial evidence that CO<sub>2</sub> fertilization effects are limited by nutrient availability, especially nitrogen and phosphorus (Norby et al. 2010, Fernández-Martínez et al. 2014, Zhang et al. 2014a). Also, greater insect herbivory of forest foliage could affect forest health and limit the net primary production of some forests under elevated [CO<sub>2</sub>] conditions (Couture et al. 2015). Additional notable findings related to this pair of contrasting perspectives can be found in each of the *Patterns*, *Mechanisms*, and *Projections*

categories of the Appendix C.

#### 4. Physiological Acclimation & Adaptation

*“Are physiological acclimation and adaptation capacities large?”*

OR

*“Are physiological adaptive capacities small relative to the projected large and rapid increase in hotter droughts?”*

*Lesser vulnerability evidence* (Table 1). Trees have many adaptive mechanisms to survive stress from droughts (Klein et al. 2014a) and associated heat waves (Teskey et al. 2014), at scales ranging from intracellular to whole-tree. Trees routinely respond rapidly to drought and heat stress with diverse, interactive, compensatory physiological processes and mechanisms ranging from stomatal closure to investments in chemical defenses (Klein et al. 2014a, Teskey et al. 2014). At the plant scale, acclimation and adaptation of a wide range of physiological processes are known to occur, including: down-regulation of respiration (e.g., Atkin and Tjoelker 2003); up-regulation of photosynthesis (e.g., Chaves et al. 2009); changes in carbon allocation to plant chemical defenses (Herms and Mattson

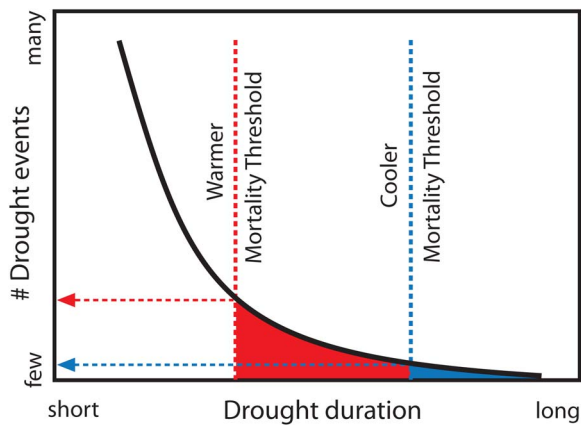


Fig. 5. Drought frequency (black line) increases nonlinearly as drought duration decreases, as there are many more short-duration droughts than long ones (Lauenroth and Bradford 2009). With warmer drought (red dashed vertical line, warmer mortality duration threshold) trees die faster than with cooler drought (blue dashed vertical line, cooler mortality duration threshold), resulting in more tree-killing drought events at the minimum duration mortality threshold for hotter drought (red arrow line) than for cooler drought (blue arrow line). This cumulatively translates into more total tree-killing droughts under hotter drought conditions (filled red + blue areas) than under cooler drought conditions (filled blue area only) because many additional shorter duration droughts become lethal with warming (Adams et al. 2009).

1992); shifts in metabolism to maintain positive carbon balances (Klein et al. 2014b); use of nonstructural carbohydrates to retain or acquire water (O'Brien et al. 2014); shifts in embolism resistance (e.g., Kolb and Sperry 1999); xylem refilling to reverse embolism (Klein et al. 2014a); shifts in hydraulic anatomy (Mencuccini 2003); adjusting growth phenology to avoid drought periods (Limousin et al. 2012, Klein et al. 2013, Richardson et al. 2013, Xia et al. 2015); molecular-level epigenetic changes in gene expression (Rico et al. 2014, Hu et al. 2015); and acclimation to recurrent mild droughts (Backhaus et al. 2014, Brodribb et al. 2014). Some of these physiological responses are closely interrelated with morphological adjustments discussed in the next pair of contrasting perspectives (“5. Phenotypic Plasticity”).

*Greater vulnerability evidence* (Table 2). There

are many ways in which hotter temperatures, particularly if they accompany drought, have negative biological effects that can increase vulnerability of trees to mortality (McDowell et al. 2011, Teskey et al. 2014). Many of the compensatory processes discussed above are subject to water- and temperature-limited thresholds linked to amplified tree mortality that could be exceeded by anticipated climate changes (e.g., Fig. 3). One of the most important effects of rising temperature is to elevate atmospheric VPD, with associated subsequent impacts on transpiration and photosynthesis. VPD is nonlinearly dependent upon temperature such that a small rise in temperature causes a relatively larger rise in VPD (discussed in the context of tree mortality by Breshears et al. [2013], Eamus et al. [2013], and Williams et al. [2013]). Elevated VPD induces greater water loss through plant stomata and from the soil surface, typically increasing plant water stress. The risk of hydraulic failure, or the loss of water transport capacity, is thus enhanced by rising VPD (McDowell et al. 2008). To compensate for this greater risk of hydraulic failure, plants typically close their stomata to limit water loss; however, this comes at the cost of reduced photosynthesis (Martínez-Vilalta et al. 2002) and increased risk of carbon starvation (the process of failure to maintain metabolism or defend against biotic agent attacks; McDowell et al. 2011). Thus, rising temperature increases the risks of both hydraulic failure and carbon starvation, resulting in limited tree growth (e.g., Adams et al. 2015). Additionally, warmer droughts increase the risk of mortality through a myriad of additional mechanisms that can accelerate the processes of hydraulic failure and carbon starvation, or even bypass these mechanisms. Respiration is nonlinearly (positively) related to temperature (Atkin and Tjoelker 2003), potentially resulting in greater consumption of energy stores at higher temperatures in the absence of adequate down-regulation (acclimation) of respiratory biochemistry (Atkin et al. 2007). This should accelerate the carbon starvation process, and indeed it has been shown that respiration rates are higher, and death can occur more rapidly, in experimental warm-drought scenarios (Adams et al. 2009). Physiological acclimation and adaptation may be inadequate to compensate for large projected changes in



drought and heat ranges due to limits on the absolute magnitude of acclimation and adaptation achievable, and because the emergence of more severe drought stress with climate warming may occur faster than acclimation and adaptation can occur (Aitken et al. 2008). Although the dominant trees in current forests were successful in the historical climate conditions in which they grew up, these rooted individuals will have to acclimate and adapt in situ to survive major anticipated climate changes. Other studies relevant to this contrasting perspective pair are discussed in the *Mechanisms* category of the Appendix C.

### 5. Phenotypic Plasticity

*“Will phenotypic plasticity and tree morphological adjustments strongly buffer drought and heat stress at both individual tree and forest levels?”*

OR

*“Are morphological adjustments too small to compensate for increased drought and heat extremes, and too slow to adapt to rapid fluctuations in growth conditions?”*

*Lesser vulnerability evidence* (Table 1). Individual trees and forest communities can adaptively respond morphologically to hotter droughts at multiple time scales through shifts in allocation to foliage, sapwood, and roots to enable greater hydraulic efficiency (i.e., a greater capacity to supply water per unit of leaf area; Mencuccini 2003, Lapenis et al. 2005). These adaptive morphological responses can include rapid short-term reductions in leaf area through early senescence or partial canopy/stem dieback (Rood et al. 2000, Ciais et al. 2005, Filewod and Thomas 2014); post-dieback resprouting from stems or roots (Zeppel et al. 2014); longer-term growth-mediated transformations of hydraulic architecture and wood density (Britez et al. 2014); and overall tree morphological and architectural changes (e.g., altered relative growth investments in the size, number, and longevity of leaves, stems, roots, and mycorrhizal symbionts; Nicotra et al. 2010, Carnicer et al. 2011, Limousin et al. 2012, Liu et al. 2015b, Zanetti et al. 2015). In addition, forest-scale canopy defoliation, dieback, and elevated whole-tree mortality rates

reduce competition between surviving trees for resources (water, light, nutrients), thereby reducing stress and facilitating forest survival, albeit at lower levels of live biomass (Lloret et al. 2012, Liu et al. 2015b).

*Greater vulnerability evidence* (Table 2). Buildup of above-ground biomass from growth during favorable climate conditions can increase tree vulnerability under subsequent drought and heat stress, because these morphological commitments to leaf and stem tissues require substantial water and carbohydrate maintenance costs during later drought conditions, driving mortality risks from both carbon starvation and embolism (McDowell et al. 2011, Peterman and Waring 2014, McDowell and Allen 2015). Similarly, trees at warmer temperatures generally grow more stem tissue, leaf biomass, and leaf area, with unchanged or even lower growth of roots, resulting in reduced root-to-leaf-area ratios; these allometric changes increase the difficulty of water transport and can predispose trees to greater vulnerability to episodic drought (Way and Oren 2010). Because it takes time for trees to respond to drought stress through plastic growth-mediated responses or morphological tissue-shedding adjustments like canopy dieback (Mencuccini 2003), tree mortality risk can be especially high under rapid shifts to an unfavorable climate; thus indications of future increases in the frequency of rapid swings between opposite precipitation extremes from one year to the next (Cai et al. 2015) imply greater forest vulnerability. Further, while morphological adjustments can help trees adapt to drought stress, projected increases in drought and heat stresses eventually may become too chronic or extreme (Fig. 4), resulting in whole-tree death (e.g., Liu et al. 2015b). Note that even short-term morphological adjustments that enable survival (e.g., canopy dieback) may substantially draw down tree carbohydrate reserves (Filewod and Thomas 2014) and can architecturally constrain the ability to quickly recover canopy position and leaf area (Girard et al. 2012), thereby further reducing tree vigor and defenses and increasing future tree mortality risk (Galiano et al. 2011). Additional notable findings related to this pair of contrasting perspectives are found in the *Mechanisms* category of Appendix C.

## 6. Genetic Variation & Selection

*“Will genetic variability and selection buffer drought and heat impacts at stand and population levels?”*

OR

*“Does within-species genetic variability provide only limited survival opportunities relative to the magnitude and rate of projected increases in drought and heat extremes?”*

*Lesser vulnerability evidence* (Table 1). Tree populations contain substantial genetic variability in tolerance to drought and heat stress (Liepe 2014, Bansal et al. 2015), so survival of better-adapted genotypes promotes forest persistence in the short run, and fosters natural selection of more adaptive genotypes for future survival (Aitken et al. 2008, Grady et al. 2011, Alfaro et al. 2014). For example, tree species have optimal climate zones, with populations in colder portions of their distributions expected to have significant genetic capacity for acclimation to warmer temperatures, whereas populations from warmer range-limit portions of the species' distribution are expected to be more vulnerable to stress from warming climate (Rehfeldt et al. 2002, 2004, 2014). Overall, higher levels of genetic diversity foster adaptive responses to climate change stresses (Jump et al. 2009a, Harter et al. 2015), including drought and heat stress (Mátyás et al. 2009, Sthultz et al. 2009).

*Greater vulnerability evidence* (Table 2). Existing genetic variability and adaptation at a forest stand level likely is inadequate to compensate for the large magnitude of projected local changes in drought and heat (Aitken et al. 2008, Franks et al. 2014). Furthermore, both in situ natural selection for greater adaptation and migration of drought-adapted genotypes may be too slow relative to anticipated rapid rates of climate change (Alfaro et al. 2014). Overall, greater vulnerability is expected where large and rapid climate changes exceed evolutionary thresholds (Botero et al. 2015). Related findings on genetics applicable to this pair of contrasting perspectives also are found in the *Mechanisms* category of Appendix C.

## 7. Biological & Landscape Diversity

*“Will biodiversity and landscape heterogeneity buffer tree mortality impacts?”*

OR

*“Are the buffering effects of biodiversity and landscape heterogeneity insufficient to prevent increasing tree mortality impacts from hotter droughts, given the fundamental thresholds of physiological stress and mortality that exist for all species?”*

*Lesser vulnerability evidence* (Table 1). Tree species vary dramatically in their physiological tolerances, acclimation capacities, and autecology, and some will be much more resistant to hotter drought than others (Anderson-Teixeira et al. 2013). Productive forests with high tree species diversity could be at less risk because rich species pools with rapid growth potential allow surviving tree species to quickly fill gaps and compensate for tree mortality losses; examples include both temperate (Dale et al. 2010) and tropical (Fauset et al. 2012, Peters et al. 2015) forests. In places where global warming is better buffered by favorable geographic circumstances (e.g., coastal regions adjoining and downwind of cold oceans), forests may experience less warming, lower drought stress, and thus less tree mortality from hotter drought. At landscape scales the diversity of topographic (Adams et al. 2014), soil (Peterman and Waring 2014, Twidwell et al. 2014, Dorman et al. 2015a), and hydrological (Fellows and Goulden 2013, Silvertown et al. 2015) settings and microsites provides relatively buffered refugia where trees have cooler-moister conditions to survive hot drought stresses, as well as favorable sites to recover more readily after mortality events. Such landscape diversity can allow “climate relict” populations of trees to persist as climate conditions become less favorable (Hampe and Jump 2011).

*Greater vulnerability evidence* (Table 2). Although higher levels of tree species diversity provide a larger onsite pool of potential tolerances to drought stress, the basic ways in which warmer temperatures affect physiology ultimately put all species at some level of risk from hotter drought (McDowell et al. 2011, Teskey et al. 2014). Drought has been shown to increase tree mortality and reduce standing biomass even in systems of high tree diversity such as tropical moist forests (van Nieuwstadt and Sheil 2005, Phillips et al. 2010, Brienen et al. 2015), and drought-induced mortality can preferentially

affect the dominant tree species (Fensham et al. 2015). In the Amazon, forest function is concentrated in ~1% of tree species that account for 50% of carbon storage and productivity (Fauset et al. 2015), so hotter drought effects on these relatively few hyperdominant species would have relatively large ecosystem effects. Greater tree species richness sometimes can exacerbate drought stress through interspecific competition (Martínez-Vilalta et al. 2012b). In general, high-diversity forest communities already are observed to exhibit heightened mortality rates in response to historical drought stresses (see examples in Allen et al. [2010] and Fig. 2). Similarly, while at-risk trees will survive longer in relatively mesic geographic regions and in localized topographic refuges in diverse landscape settings, the buffering capacity due to landscape diversity is limited and subject to being overwhelmed eventually by more extreme drought and heat events (e.g., Breshears et al. 2005, Fellows and Goulden 2013, Hylander et al. 2015). Although biological or landscape diversity can provide some level of resistance to mortality, it is only in a relative sense and is limited, particularly given the rapid increase and large magnitude of hotter drought projected by climate models. Additional notable findings related to this pair of contrasting perspectives on biodiversity and landscape heterogeneity can be found in the *Ecological Feedbacks* category of Appendix C.

## 8. Future Dynamics

*“Will future forest dynamics resemble the recent historical range of variability, with robust forest recovery after mortality episodes?”*

OR

*“Will forests respond to increasingly novel and extreme drought and heat conditions with greater tree mortality and novel ecosystems?”*

*Lesser vulnerability evidence* (Table 1). Forest ecosystems naturally and necessarily respond dynamically to ongoing environmental changes, which is well-documented in paleoecological records (Corlett and Westcott 2013). Since old-growth trees and forests by definition have survived substantial centennial- and even millennial-scale climate variability, including past droughts and heat waves, and since trees will

continue to be buffered by the large array of compensatory processes reviewed above, it is possible that future forest changes generally will be incrementally adaptive in response to projected incremental climate changes. Forest expansions into newly suitable climatic zones are expected in some regions (e.g., Juday et al. 2015). In general, pulses of tree mortality have self-limiting negative feedbacks from release of resources for surviving trees and reduction in host availability for biotic agents, thereby also fostering robust post-mortality forest recovery (Lloret et al. 2012).

*Greater vulnerability evidence* (Table 2). Increasingly extreme droughts and heat waves are expected to exceed inherent thresholds in multiple tree mortality processes (e.g., Figs. 3, 4). Warmer conditions and greater drought stress can amplify additional tree-killing disturbance processes and their interactions, including increased insect pest outbreaks (Raffa et al. 2008, Weed et al. 2013) and more frequent and severe fires (Pechony and Shindell 2010, Flannigan et al. 2013, Williams et al. 2013, 2014, Brando et al. 2014, IPCC 2014). As projected hotter droughts intensify in coming decades, post-mortality forest recovery could be limited, delayed for long time periods, or impossible because hotter droughts in association with more frequent and severe disturbances will create less favorable conditions for regeneration of many currently dominant species (Suarez and Kitzberger 2010, Anderson-Teixeira et al. 2013, Tarancón et al. 2014, Fensham et al. 2015). Additionally, hotter droughts drive shorter lifespans for surviving and establishing plants (Adams et al. 2009) and can be expected to favor: smaller-statured trees; transition of resprouting tree species toward more shrub-like morphologies; and non-tree life forms such as resprouting shrubs and grasses in many areas (Zeppel et al. 2014, McDowell and Allen 2015). Drought mortality can disproportionately affect the most dominant tree species (Fensham et al. 2015) and the biggest old-growth trees (Phillips et al. 2010, McDowell and Allen 2015) that contain large biomass carbon pools (Stephenson et al. 2014, Fauset et al. 2015) and old-growth characteristics that are irreplaceable for centuries (Lindenmayer et al. 2012). Relative to rapid mortality processes, tree establishment and growth are slow due to natural regeneration

processes, dispersal limitations, or lags in migration or regeneration (Feeley et al. 2012, Frank et al. 2015b, Yi et al. 2015)—thus old sequestered carbon lost to amplified forest die-off may take significant time to fully recover, even in productive environments with rapid biomass regrowth, and particularly in dry or cold environments where growth is slower (Janisch and Harmon 2002; Fig. 3C). Forest die-off events also can potentially offset sequestered carbon increases associated with woody plant encroachment (Barger et al. 2011). The short-term dynamics of carbon released from pulses of tree mortality can be significant at regional scales (Kurz et al. 2008, Phillips et al. 2009), illustrating possible global risks of tipping-point amplification of greenhouse gas warming from broad-scale forest die-offs under hotter drought conditions (Barnosky et al. 2012, IPCC 2014). Paleoecological records clearly demonstrate that significant climate changes drive mass turnover in the composition of dominant forest species (Corlett and Westcott 2013), so extensive shifts in ranges and dominance patterns are anticipated for many tree species in response to projected warming (Feeley et al. 2012, Iverson and McKenzie 2013), including range retractions through mortality (Allen and Breshears 1998, Jump et al. 2009b, Feeley et al. 2013). Past droughts and associated fires are known to have triggered widespread shifts in the composition and structure of forests in mesic regions (e.g., Pederson et al. 2014b, Clifford and Booth 2015), as well as in more xeric forests (e.g., Swetnam and Betancourt 1998). Overall, given individualist species responses to anticipated changes in climate and altered disturbance regimes (Jackson et al. 2009), the emergence of novel no-analog ecosystems is expected (Williams and Jackson 2007, Feeley et al. 2012, Hobbs et al. 2014) along with widespread shifts in biomes (Gonzalez et al. 2010; Fig. 1). Related findings on future forest dynamics applicable to this pair of contrasting perspectives also are found in the *Ecological Feedbacks* category of Appendix C.

## 9. Models

*“Are current global vegetation models—which generally project greater increases in growth than mortality—accurate?”*

OR

*“Are current broad-scale vegetation models over-optimistic because CO<sub>2</sub> fertilization and temperature benefits to growth are included in the models but realistic mortality processes are insufficiently represented?”*

*Lesser vulnerability evidence* (Table 1). Most process-based global vegetation models simulate the combined changes in [CO<sub>2</sub>], temperature, humidity, and growing season length (among other factors) within earth system models (e.g., dynamic global vegetation models [DGVMs]), generally projecting enhanced growth of terrestrial vegetation as this century proceeds (e.g., Huntingford et al. 2013). Such model predictions of overall increasing forest growth are consistent with various observations, theory, and model experiments (e.g., Farrior et al. 2015), ranging from work in tropical moist forests (e.g., Lloyd and Farquhar 2008) and CO<sub>2</sub> fertilization experiments in non-water limited situations (e.g., Keenan et al. 2013) to evidence of recent expansions of woody plant dominance and biomass in semiarid savannas and shrublands (e.g., Buitenwerf et al. 2012, Liu et al. 2015a). Indeed, elevated water-use efficiency typically is observed under elevated [CO<sub>2</sub>], even in water-limited conditions (Leakey 2009, Peñuelas et al. 2011, Frank et al. 2015a). Findings of enhanced tree growth rates in many regions (Phillips et al. 2008, McMahon et al. 2010, Fang et al. 2014, Frank et al. 2015a, Xia et al. 2015) further support model projections of future increases in global forest growth (Zscheischler et al. 2014, Farrior et al. 2015, Sitch et al. 2015). Even widespread observations of increased background tree mortality rates could largely reflect that rising [CO<sub>2</sub>] is promoting greater vegetation productivity and thus more competition and higher mortality rates (Phillips et al. 2008, Doughty et al. 2015, Zhang et al. 2015).

*Greater vulnerability evidence* (Table 2). Most broad-scale vegetation models do not mechanistically represent tree mortality and are not based on measured mortality responses (McDowell et al. 2011, 2013, Joetzjer et al. 2014). Many current earth system model predictions of increasing forest growth may be over-optimistic because persistent future CO<sub>2</sub> fertilization and temperature benefits to growth commonly are

included in the models, despite substantial evidence from diverse forest biomes that temperature-induced drought stress already is often overriding the potential CO<sub>2</sub> fertilization benefits on tree growth even in mesic and humid forests (Gedalof and Berg 2010, Peñuelas et al. 2011, Lévesque et al. 2014, Brienen et al. 2015). The number of days with suitable climate conditions for plant growth have been projected to decrease by up to 11% globally by 2100 under “business-as-usual” emissions scenarios when temperature and other climate variables that limit growth are considered (Mora et al. 2015), with up to 200-day declines in annual growing days projected for the tropics; if realized, such significant decreases in growing days likely would have substantial implications for tree mortality. A key issue relative to confidence in model projections of future forest conditions is the general omission or inadequate representation of ecologically realistic processes of tree mortality in current DGVMs, ranging from physiological and demographic mortality processes to other important tree-killing disturbances (fire, insect outbreaks, diseases), all responsive to variability in drought and heat conditions (McDowell et al. 2011, 2013, Friend et al. 2014, Joetzjer et al. 2014, Lindner et al. 2014, Betts et al. 2015, Doughty et al. 2015, Frank et al. 2015b, Sitch et al. 2015). In addition, the general circulation models which project the future climate conditions in DGVMs currently are limited in their ability to realistically model extreme droughts and heat waves (Sillmann et al. 2013, Williams et al. 2014)—since extreme climate events are key drivers of major forest die-off episodes, this limitation likely further reduces projected levels of tree mortality to hotter droughts in current earth system models. Neither observed growth slowdowns in the Amazon nor “browning” in the boreal are projected in current models (Sitch et al. 2015), and tested models poorly replicate observed global die-off events (Steinkamp and Hickler 2015), exemplifying ongoing challenges to accurately project forest vulnerability to anticipated climate changes. Additional notable findings related to this pair of contrasting perspectives, including discussion of climate-envelope models and empirical models of drought-induced tree mortality, can be found in the *Projections*

category of Appendix C.

## 10. Management

*“Can management effectively mitigate the impacts of hotter drought relative to excessive tree mortality?”*

OR

*“Are management actions too limited spatially, and in intensity, to prevent widespread tree mortality impacts of hotter droughts on historical native forests?”*

*Lesser vulnerability evidence* (Table 1). Many options exist for adapting forest management to address climate change impacts (Millar et al. 2007, Lindner et al. 2010, Pinkard et al. 2014, Fares et al. 2015, Keenan 2015, Lugo 2015, Schelhaas et al. 2015). Forest thinning can reduce competition and increase tree growth, vigor, and defenses against insect pests (D’Amato et al. 2013, Giuggiola et al. 2013). Management can change the species composition and genetics of tree populations by selective cutting, planting (including assisted migration beyond historical ranges), and breeding (Millar et al. 2007, Aitken and Whitlock 2013, Fares et al. 2015). Managing for shorter-statured (and thus younger) forests potentially could decrease vulnerability to hotter drought (McDowell and Allen 2015), although there is evidence that younger forests can be more sensitive to regional warming and drought stress (Luo and Chen 2013). Approaches to retain or add water on forest sites could reduce tree drought stress (Grant et al. 2013). Various pest management techniques (from pheromone traps to spraying microbial or petrochemical insecticides) can reduce impacts of biotic pests such as insect defoliators or bark beetles. Well-managed forests could continue to provide diverse and essential ecosystem services (Keenan 2015, Schelhaas et al. 2015), including forests’ role as a major carbon sink, currently sequestering ~25% of annual anthropogenic CO<sub>2</sub> emissions globally (Pan et al. 2013).

*Greater vulnerability evidence* (Table 2). Thinned forests can still die from sufficiently extreme drought and heat stress (Tarancón et al. 2014, Elkin et al. 2015). On-site water retention (e.g., mulching) or enhancement (irrigation) are practical only on small selected locations. Pesticides have limited effectiveness and applicability at

broad scales. Forest management can only be applied to a small fraction of all forests due to inherent landscape constraints (e.g., rugged terrain, inaccessibility), social limitations (e.g., protected reserves), and limited funding for treatments. Tipping-point feedbacks from hotter droughts, including risks of forests becoming a net carbon source globally due to amplified forest die-off processes (Bonan 2008, Kurz et al. 2008, Phillips et al. 2009, IPCC 2014), could overwhelm management measures to sustain historical native forests. Related findings applicable to this pair of contrasting perspectives also can be found in the *Management* category of Appendix C.

#### A SET OF GLOBAL DRIVERS KNOWN WITH HIGH CONFIDENCE THAT POINT TOWARD GREATER VULNERABILITY

Considered collectively, the relative weight of the ten contrasting perspectives listed above influences our overall viewpoints about the vulnerability of the world's forests to amplified tree mortality from anticipated hotter droughts. There clearly are varying levels of support for both the lesser (Table 1) and the greater (Table 2) vulnerability side of each of the ten perspectives (Table 3). Also, many forest responses will be site- and region-specific, so it is important to be cautious about overgeneralizing. Nonetheless, a broad assessment of global forest vulnerability to increasing tree mortality under hotter drought in the Anthropocene is still needed. Overall viewpoints on vulnerability additionally should consider broad-scale drivers of tree mortality known with high confidence, and whether they point toward lesser or greater vulnerability. Here, drawing and expanding on material presented above, we identify a set of global drivers of tree mortality that are known with high confidence, defined here as having little or no uncertainty, that point toward greater vulnerability.

- ***Droughts occur everywhere.*** Essentially all locations will experience extreme drought and heat events sooner or later (Palmer 1965, Vicente-Serrano et al. 2010, IPCC 2012, Jenerette et al. 2012). Even areas projected to become wetter are expected to still experience periodic drought due to inherent

climate variability.

- ***Hotter droughts from warming.*** Widespread global warming is one of the most robust climate change projections (IPCC 2013), and consequently locations experiencing drought are much more likely to experience hotter droughts in the future (Vicente-Serrano et al. 2013, AghaKouchak et al. 2014, Trenberth et al. 2014).
- ***Nonlinear VPD increase.*** Atmospheric moisture demand (VPD) increases nonlinearly with hotter temperatures, especially when accompanying drought because during drought VPD cannot be offset by increases in humidity (Breshears et al. 2013, Eamus et al. 2013, Williams et al. 2014).
- ***Faster death from hotter drought.*** Despite debate about the relative roles of interrelated mechanisms driving tree mortality, trees can die faster under hotter temperatures during drought (Adams et al. 2009, Will et al. 2013, Duan et al. 2014, 2015), consistent with many fundamental physiological responses related to carbon starvation and hydraulics that negatively impact trees (McDowell et al. 2011).
- ***Increased frequency of lethal drought.*** The frequency of drought occurrence increases nonlinearly as drought duration decreases (Fig. 5), as there are many more short-duration droughts than long ones (Shiau 2006, Lauenroth and Bradford 2009). Consequently, because trees die faster during hotter drought, shorter droughts become lethal under warmer conditions, increasing the number of droughts (per unit time) that trigger tree mortality (Adams et al. 2009).
- ***Death faster than growth.*** Even in the most rapidly growing and diverse forests, mortality can occur much faster than associated recovery by growth to similar tree sizes and forest structure (Franklin et al. 1987, Janisch and Harmon 2002, Lindenmayer et al. 2012, Frank et al. 2015b), placing upper limits on the frequency and severity of mortality events to which a forest ecosystem can be resilient (Adams et al. 2009).

Note that these global drivers known with high confidence can be synergistic with one another, interacting to amplify tree mortality

processes. Considered collectively, this set of general vulnerability drivers *alone* provides a strong counterpoint relative to the potential for compensatory processes to protect the world's forests from projected hotter droughts. Note that these high-confidence drivers do not require full resolution of mortality mechanisms. Our weighing of the broad spectrum of evidence across the range of lesser and greater vulnerability perspectives (Table 3), especially when considering these high-confidence drivers, leads us to the overall viewpoint that most forests globally are much more vulnerable to tree mortality from hotter drought than commonly reflected in recent studies and projections (synthetically presented in Fig. 6). Although debate and important research continues regarding many of the specifics of mortality mechanisms, the enormous energy the research community has put into resolving the mechanisms of tree mortality already has provided substantial physiological findings that point toward increased vulnerability to mortality with hotter droughts. Particularly notable is that the available physiological evidence shows hotter droughts can kill trees faster, despite any benefits of greater [CO<sub>2</sub>] (Duan et al. 2014, 2015), and that most mechanisms of mortality—whether related to carbon metabolism, hydraulics, or pests and pathogens—are enhanced by warmer temperatures during drought (McDowell et al. 2011). In addition, drought- and heat-induced tree mortality events already are being observed in all major forest biomes around the world (Fig. 2; Allen et al. 2010). When these findings are specifically considered in concert with the global drivers known with high confidence, we conclude that an overall case for greater vulnerability is strong. Our view, then, is that vulnerability is high, consistent with abundant and diverse research findings that suggest growing risks of widespread tree mortality for the Earth's forests in the Anthropocene. Based on the ongoing debate within the scientific community (e.g., Hartmann et al. 2015), we think that there is much underestimation of this vulnerability.

#### ISSUES CONTRIBUTING TO UNDERESTIMATION OF VULNERABILITY

We think that the overall evidence implies

greater vulnerability of forests to hotter drought, especially when the factors with high confidence are explicitly considered. Building on our synthesis above, we highlight three general issues that may be contributing to underestimation of forest vulnerability, in addition to a focus on the various specific findings supportive of lesser vulnerability perspectives presented above (Tables 1 and 3).

First, aggregating studies that use different methods and that focus on differing aspects of tree mortality can confound the appropriate interpretations of individual studies. In particular, studies that focus on longer-term climatic trends, such as experimental manipulations of background warming alone, need to be differentiated from those that include extreme drought and heat events (Jentsch et al. 2007, Kayler et al. 2015). Similarly, studies focused on drought but which do not include a mortality response need to be differentiated from those that do include tree mortality. Although these points have been highlighted before (e.g., McDowell and Sevanto 2010, Smith 2011, McDowell et al. 2013, Reichstein et al. 2013, Reyer et al. 2013, Zscheischler et al. 2013, Kreyling et al. 2014, Frank et al. 2015b), such differentiations are not always considered. Similarly, inferences about prior and projected patterns of tree mortality, mechanisms driving mortality, and consequences of and recovery from mortality all need to appropriately weigh studies relative to their methods and evidence. Did the study occur during stressful drought or heat conditions? How extreme was the studied event relative to historical and projected climate patterns? Did the study include a mortality response (McDowell and Sevanto 2010)? For example, evidence of increased water-use efficiency or CO<sub>2</sub> fertilization benefits under conditions of wetness could be irrelevant to how those same systems may respond to more prolonged and severe droughts that are expected to occur eventually (McDowell et al. 2013). Hotter drought may not have occurred in some places yet, or not have been extreme enough yet to trigger amplified tree mortality, but that does not make those locations invulnerable to more extreme future events. Eastern USA forests, for example, recently have not experienced hotter drought events of similar magnitude to western USA forests (Pederson et al. 2014a), nor similarly

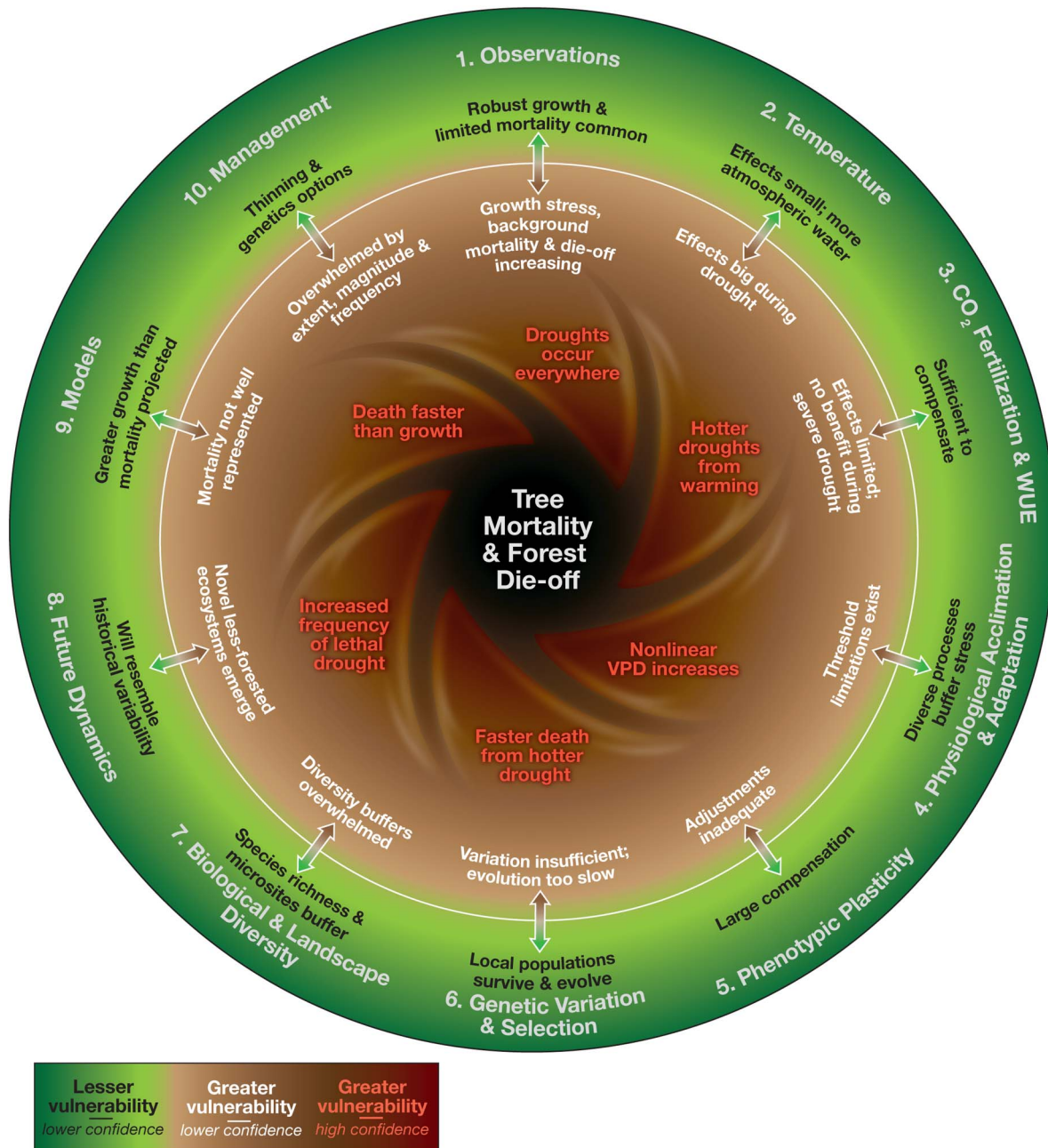


Fig. 6. A synthesis of considerations regarding global vulnerability to tree mortality and forest die-off from hotter drought, highlighting the critical role of high-confidence drivers. Circular visualization of ten contrasting perspectives on the vulnerability of forests to hotter drought (from Table 3), presented clockwise sequentially around the outside zones; black text for lesser vulnerability perspectives and white text for greater vulnerability perspectives, arrayed on opposite sides of the neutral position of the circular white line. Arrows point outward from neutral toward lesser vulnerability (green background) and inward toward greater vulnerability (brown background). Around the center are six global drivers of tree mortality (inner red text) known with high confidence (i.e., little or no uncertainty), further increasing the vulnerability toward a central zone of tree mortality and forest die-off. WUE is “water-use efficiency”; VPD is “vapor pressure deficit”. Note that there is (Fig. 6 legend continues on next page)



(continuation of Fig. 6 legend)

lower confidence in the overall vulnerability implications of the ten contrasting perspectives, both individually and collectively, relative to the set of six global drivers with high confidence that point to high vulnerability. As described in the text, we find that these high-confidence drivers, considered in concert with the cumulative weight of research pointing toward greater vulnerability perspectives, support an overall viewpoint of greater forest vulnerability globally than commonly reflected in recent studies and projections.

severe levels of associated drought-induced tree mortality, but nonetheless these eastern forests are potentially vulnerable to mortality when hotter drought extremes do occur (National Climate Assessment 2014, Pederson et al. 2014*b*, Martin-Benito and Pederson 2015; also see historical eastern USA drought mortality references in Allen et al. [2010] and Fig. 2).

Second, challenges predicting threshold-type responses of tree mortality and forest die-off to hotter drought may enable a discounting of their probability. When warmer temperatures accompany drought, risks for trees increase in a variety of tipping-point ways (Fig. 3; Scheffer et al. 2001), but the ubiquity of potential temperature-linked mortality thresholds that occur at multiple spatial and temporal scales may not be explicitly recognized. The occurrence of unforeseen threshold ecological responses to increasingly extreme drought and heat events further compounds prediction challenges (Phillips et al. 2010, Smith 2011, Kreyling et al. 2014), and can require considering multiple aspects of a given event, including drought duration, frequency, and magnitude (e.g., Figs. 4 and 5; Anderegg et al. 2013*a*). The limited range of our observations of historical forest-climate conditions and interactions can constrain our ability to recognize, appreciate, and anticipate historically-unseen threshold responses and projected novel conditions (Scheffer et al. 2012*a*, Hughes et al. 2013). Additionally, the co-occurrence of multiple stresses, inadequately understood tipping-points, and the interactions of disturbance processes across spatial scales (Peters et al. 2004) increases the difficulty of assessing cumulative risk (National Research Council 2007). Thus a more optimistic perspective of forest vulnerability may result when considering only a single risk factor in contrast to cumulative risk assessments involving multiple factors (each potentially including thresholds), such as cross-scale interactions among multiple climate and disturbance drivers of tree mortality associated with hotter

drought (e.g., Allen 2007, Anderegg et al. 2015*a*, Keane et al. 2015).

Third, there are various ongoing debates about specific aspects of the complex processes of tree mortality which span a broad range of methodological approaches, a large volume of literature, and the gradient of contrasting lesser and greater findings regarding multiple compensatory processes and vulnerability factors (including observed variability in the responses of diverse tree species through time and space). Essential as these particular debates are to advancing the science, a focus on specific aspects of these debates may be obscuring the overall evidence across the broad spectrum of global tree mortality research pointing to the fundamental high vulnerability of forests to hotter drought. Continuation of research on the details of tree mortality mechanisms remains critically needed. Equally important is recognition of the set of high confidence global drivers, none of which depend on the specifics of mortality mechanism, and of the greater level of forest vulnerability that these broad drivers imply.

#### UNDERESTIMATION OF VULNERABILITY OF TREE MORTALITY TO HOTTER DROUGHT

This global synthesis highlights the likely vulnerability of forests to mortality from hotter droughts. Our core message is that substantial and diverse evidence supports an overall viewpoint that forests are subject to growing risks of drought- and heat-induced tree mortality in a rapidly warming world. We acknowledge there is currently substantial countervailing evidence in support of lesser vulnerability, and we expect that there will continue to be some regions with increased tree growth and forest expansions. Furthermore, we are not asserting that all forests will concurrently collapse, nor that most forests today are at risk of disappearing this century. We do expect, however, major forest ecosystem reorganizations tied to increased tree mortality

Table 4. Challenges posed to diverse audiences relative to the vulnerability of forests to increasing tree mortality and forest die-off events from anticipated hotter droughts.

Audience	Challenge
Ecologists	Continue to investigate the full spectrum of interactive factors relevant to the high vulnerability of many forests; maintain and expand long-term observations; scientifically document irreplaceable forest ecosystems.
Plant physiologists	Continue to resolve mechanisms but specifically focus on killing trees in experiments with warmer temperature as a treatment, recognizing stress alone does not allow rigorous tests of how trees die.
Remote sensing scientists	Continue development of global-scale forest stress and mortality detection and attribution techniques, moving toward near real-time assessments of forest status and trends; these products also are needed as inputs to empirical models.
Vegetation and earth system modelers	Continue to improve the realism of tree mortality processes in dynamic global vegetation models; fully explore sensitivity analyses of mortality algorithms; further explore empirical modeling approaches to project climate-driven tree mortality.
Atmospheric modelers	Further assess atmospheric consequences of vegetation change; assess the potential for ecoclimatic teleconnections impacted by broad-scale forest die-off; continue improving simulations of precipitation, extreme droughts, and heat waves.
Foresters	Recognize the extent of the threat and plan accordingly; increase focus on potential for management through genetics; recognize associated risks of wildfire and insect/disease feedbacks with drought- and heat-related tree mortality.
Conservation land managers in general	Recognize how rapidly forest ecosystems can change; identify and protect local-to-regional “climate refuge” sites likely to be more resilient to drought stress; plan ahead and take mitigation measures, particularly for iconic old-growth trees and groves and for key service-supplying stands, potentially including supplemental water retention/addition where feasible.
Communities with significant direct subsistence from forest goods and services	Create broader-scale collaborative networks for accessing resources to buffer against potential for unpredicted local forest die-off events.
Teachers focused on global change and science literacy	Use examples of drought and heat-related tree mortality to illustrate the emerging large and visible effects of climate change to students.
Artists collaborating with scientists on global change communication	Work collaboratively with tree mortality researchers to develop art that records and communicates ideas, impressions, and feelings about climate change risks and forest loss.
Research funding agencies	Support research on the frontiers of vegetation mortality, including both mechanistic and empirically based approaches.
Policymakers	Advance policies reducing greenhouse gas emissions as fast as possible to mitigate the worst impacts of warmer droughts on forests.
The general public, and those engaged with them	Recognize the great value and irreplaceability of impending forest loss, including associated ecosystem services loss, and support policies to reduce global change risks to forests.

in coming decades, including declines in productivity, changes in forest species composition and dominance patterns, a shift to smaller tree sizes, and reductions in forest extent. If realized, the magnitude and rapidity of associated changes to many forest ecosystems will pose enormous challenges to managing forests for diverse benefits and ecosystem services, and will require additional rethinking of paradigms for natural resources management. The current lack of societal resolve to address ongoing global warming further amplifies the increasing vulnerability of forests.

Based on our review of contrasting perspec-

tives, it appears that the future vulnerability of forests globally is being widely underestimated, including the vulnerability of forests in wetter regions. Thus we urge the scientific community to explicitly and holistically consider the spectrum of evidence and the contrasting perspectives discussed here—including those drivers known with high confidence—to assess the cumulative potential vulnerability of forests to hotter drought. Given the weight of evidence indicating a high level of future vulnerability, and the extraordinary importance of forests locally and globally, we pose challenges for key sub-communities of tree mortality researchers, as

well as for various stakeholders, managers, and policymakers (Table 4). Consistent among these challenges is the need to recognize not only the high vulnerability of forests to hotter drought, but also the urgency with which relevant advances and actions are needed. Disconcertingly, the trends and magnitudes of changes in global forest health and tree mortality remain largely unquantified due to the absence of an adequate monitoring system, and global-scale models remain unable to accurately project the fate of the Earth's forests in response to hotter drought with confidence, despite the profound global implications of high vulnerability to tree mortality. In closing, we caution against what we perceive as current widespread underestimation of global vulnerability to broad-scale tree mortality and forest die-off from hotter drought in the Anthropocene. Recognizing and addressing the challenges ahead posed by forest vulnerability to hotter drought is a timely—and urgent—priority of immense ecological and societal importance.

#### ACKNOWLEDGMENTS

Our perspectives have benefited from countless discussions through the years with many colleagues around the world, including participants in the International Interdisciplinary Workshop on Tree Mortality (Jena, Germany, October 2014), and colleagues in the project “Assessing ecosystem recovery after extreme drought-related dieback events worldwide” (A. Jump, R. Fensham, S. Greenwood, T. Kitzberger, F. Lloret, J. Martínez-Vilalta, and P. Ruiz-Benito). For this paper we particularly acknowledge discussions with and comments from D. Eamus, C. Haffey, G. Hardy, H. Hartmann, A. Huete, J. Fontain, T. Huxman, A. Macalady, M. Perring, B. Poulter, K. Ruthrof, T. Swetnam, D. Tissue, and two anonymous reviewers. Funding support provided by the U.S. Geological Survey's Ecosystems and Climate & Land Use Change mission areas (through the USGS Western Mountain Initiative project), and International Network Support from The Leverhulme Trust (C. D. Allen); NSF EF-1340624 and EAR-1331408, Arizona Agriculture Experiment Station, and a Murdoch University Visiting Distinguished Collaborator award (D. D. Breshears); and DOE Department of Science, Office of Biological and Environmental Research and Laboratory Directed Research and Development (N. G. McDowell). Figure support by Donald Montoya; table and reference support by Collin Haffey and Alanna Jornigan. Any use of trade, firm, or product names is

for descriptive purposes only and does not imply endorsement by the U.S. Government.

#### LITERATURE CITED

- Adams, H. D., A. D. Collins, S. P. Briggs, M. Vennetier, L. T. Dickman, S. A. Sevanto, N. Garcia-Forner, and N. G. McDowell. 2015. Experimental drought and heat can delay phenological development and reduce foliar and shoot growth in semiarid trees. *Global Change Biology*. doi: 10.1111/gcb.13030
- Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Villegas, D. D. Breshears, C. B. Zou, P. A. Troch, and T. E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences USA* 106:7063–7066.
- Adams, H. D., C. H. Luce, D. D. Breshears, M. Weiler, V. C. Hale, C. D. Allen, A. M. S. Smith, and T. E. Huxman. 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology* 5:145–159.
- Adams, H. D., A. K. Macalady, D. D. Breshears, C. D. Allen, N. L. Stephenson, S. R. Saleska, T. E. Huxman, and N. G. McDowell. 2010. Climate-induced tree mortality: earth system consequences. *Eos, Transactions, American Geophysical Union* 91:153–154.
- Adams, H. D., A. P. Williams, C. Xu, S. A. Rauscher, X. Jiang, and N. G. McDowell. 2013. Empirical and process-based approaches to climate-induced forest mortality models. *Frontiers in Plant Science* 4:438.
- Adams, H. R., H. R. Barnard, and A. K. Loomis. 2014. Topography alters tree growth-climate relationships in a semi-arid forested catchment. *Ecosphere* 5(11):148. <http://dx.doi.org/10.1890/ES14-00296.1>
- AghaKouchak, A., L. Cheng, O. Mazdiyasn, and A. Farahmand. 2014. Global warming and changes in risk of concurrent climate extremes: Insights from the 2014 California drought. *Geophysical Research Letters* 41:8847–8852.
- Ahlström, A., et al. 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO<sub>2</sub> sink. *Science* 348:895–899.
- Ainsworth, E. A., and A. Rogers. 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant, Cell & Environment* 30:258–270.
- Aitken, S. N., and M. C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44:367–388.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1:95–111.

- Alberto, F. J., S. N. Aitken, R. Alía, S. C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, T. Lenormand, S. Yeaman, R. Whetten, and O. Savolainen. 2013. Potential for evolutionary responses to climate change-evidence from tree populations. *Global Change Biology* 19:1645–1661.
- Alfaro, R. I., et al. 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *Forest Ecology and Management* 333:76–87.
- Allen, C. D. 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems* 10:797–808.
- Allen, C. D. 2015. Forest ecosystem reorganization underway in the Southwestern US: A preview of widespread forest changes in the Anthropocene? *In* V. A. Sample, R. P. Bixler, and C. Miller, editors. *Forest conservation and management in the Anthropocene: adaptation of science, policy and practices*. University Press of Colorado, Boulder, Colorado, *in press*.
- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA* 95:14839–14842.
- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Andela, N., Y. Y. Liu, A. I. J. M. Van Dijk, R. A. M. De Jeu, and T. R. McVicar. 2013. Global changes in dryland vegetation dynamics (1988–2008) assessed by satellite remote sensing: Comparing a new passive microwave vegetation density record with reflective greenness data. *Biogeosciences* 10:6657–6676.
- Anderegg, L. D. L., W. R. L. Anderegg, and J. A. Berry. 2013a. Not all droughts are created equal: translating meteorological drought into woody plant mortality. *Tree Physiology* 33:672–683.
- Anderegg, W. R. L., et al. 2015a. Advancing the understanding and prediction of climate-induced tree mortality from drought, insects, and their interactions. *New Phytologist*. doi: 10.1111/nph.13477
- Anderegg, W. R. L., A. Flint, C. Huang, L. Flint, J. A. Berry, F. W. Davis, J. S. Sperry, and C. B. Field. 2015b. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* 8:367–371.
- Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013b. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* 3:30–36.
- Anderson-Teixeira, K. J., et al. 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* 21:528–549.
- Anderson-Teixeira, K. J., A. D. Miller, J. E. Mohan, T. W. Hudiburg, B. D. Duval, and E. H. Delucia. 2013. Altered dynamics of forest recovery under a changing climate. *Global Change Biology* 19:2001–2021.
- Arora, V. K., et al. 2013. Carbon-concentration and carbon-climate feedbacks in CMIP5 earth system models. *Journal of Climate* 26:5289–5314.
- Asner, G. P. 2015. Organismic remote sensing for tropical forest ecology and conservation 1, 2. *Annals of the Missouri Botanical Garden* 100:127–140.
- Atkin, O. K., I. Scheurwater, and T. L. Pons. 2007. Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytologist* 174:367–380.
- Atkin, O. K., and M. G. Tjoelker. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* 8:343–351.
- Backhaus, S., J. Kreyling, K. Grant, C. Beierkuhnlein, J. Walter, and A. Jentsch. 2014. Recurrent mild drought events increase resistance toward extreme drought stress. *Ecosystems* 17:1068–1081.
- Báez, S., et al. 2015. Large-scale patterns of turnover and basal area change in Andean forests. *PLoS One* 10(5):e0126594.
- Baguskas, S. A., S. H. Peterson, B. Bookhagen, and C. J. Still. 2014. Evaluating spatial patterns of drought-induced tree mortality in a coastal California pine forest. *Forest Ecology and Management* 315:43–53.
- Bahn, M., M. Reichstein, J. S. Dukes, M. D. Smith, and N. G. McDowell. 2014. Climate-biosphere interactions in a more extreme world. *New Phytologist* 202:356–359.
- Baker, T. R., et al. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London B* 359:353–365.
- Ballantyne, A. P., C. B. Alden, J. B. Miller, P. P. Tans, and J. W. C. White. 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488:70–72.
- Bansal, S., C. A. Harrington, P. J. Gould, and J. B. St. Clair. 2015. Climate-related genetic variation in drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). *Global Change Biology* 21:947–958.
- Barger, N. N., S. R. Archer, J. L. Campbell, C.-Y. Huang, J. A. Morton, and A. K. Knapp. 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research* 116:G00K07. doi: 10.1029/2010JG001506
- Barnosky, A. D., et al. 2012. Approaching a state shift in Earth's biosphere. *Nature* 486:52–58.

- Beck, P. S. A., and S. J. Goetz. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters* 6:45501.
- Bernacchi, C. J., and A. VanLoocke. 2014. Terrestrial ecosystems in a changing environment: a dominant role for water. *Annual Review of Plant Biology* 66:150126112146002.
- Betts, R. A., N. Golding, P. Gonzalez, J. Gornall, R. Kahana, G. Kay, L. Mitchell, and A. Wiltshire. 2015. Climate and land use change impacts on global terrestrial ecosystems, fire, and river flows in the HadGEM2-ES earth system model using the representative concentration pathways. *Biogeosciences* 10:6171–6223.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449.
- Borovics, A., and C. Mátyás. 2013. Decline of genetic diversity of sessile oak at the retracting (xeric) limits. *Annals of Forest Science* 70:835–844.
- Botero, C. A., F. J. Weissing, J. Wright, and D. R. Rubenstein. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences USA* 112:184–189.
- Brando, P. M., J. K. Balch, D. C. Nepstad, D. C. Morton, F. E. Putz, M. T. Coe, D. Silvério, M. N. Macedo, E. A. Davidson, and C. C. Nóbrega. 2014. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences USA* 111:6347–6352.
- Breshears, D. D., H. D. Adams, D. Eamus, N. G. McDowell, D. J. Law, R. E. Will, A. P. Williams, and C. B. Zou. 2013. The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Frontiers in Plant Science* 4(266):1–4.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* 102:15144–15148.
- Breshears, D. D., L. López-Hoffman, and L. J. Graumlich. 2011. When ecosystem services crash: preparing for big, fast, patchy climate change. *Ambio* 40:1–8.
- Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D. Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7:185–189.
- Brienen, R. J. W., et al. 2015. Long-term decline of the Amazon carbon sink. *Nature* 519:344–348.
- Britez, M. R. D., A. S. Sargent, A. Martinez Meier, N. Bréda, and P. Rozenberg. 2014. Wood density proxies of adaptive traits linked with resistance to drought in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Trees* 28:1289–1304.
- Brodribb, T. J., S. A. M. McAdam, G. J. Jordan, and S. C. V. Martins. 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences USA* 111:14489–14493.
- Brook, B. W., E. C. Ellis, M. P. Perring, A. W. Mackay, and L. Blomqvist. 2013. Does the terrestrial biosphere have planetary tipping points? *Trends in Ecology and Evolution* 28:396–401.
- Brouwers, N. C., J. Mercer, T. Lyons, P. Poot, E. Veneklaas, and G. Hardy. 2013. Climate and landscape drivers of tree decline in a Mediterranean ecoregion. *Ecology and Evolution* 3:67–79.
- Büntgen, U., et al. 2013. Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Frontiers in Ecology and the Environment* 12:100–106.
- Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO<sub>2</sub> as a driver. *Global Change Biology* 18:675–684.
- Bussotti, F., M. Pollastrini, V. Holland, and W. Brüggemann. 2015. Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany* 111:91–113.
- Cai, W., et al. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111–116.
- Cai, W., et al. 2015. Increased frequency of extreme La Niña events under greenhouse warming. *Nature Climate Change* 5:132–137.
- Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sánchez, and J. Peñuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences USA* 108:1474–1478.
- Carsjens, C., Q. Nguyen Ngoc, J. Guzy, F. Knutzen, I. C. Meier, M. Muller, R. Finkeldey, C. Leuschner, and A. Polle. 2014. Intra-specific variations in expression of stress-related genes in beech progenies are stronger than drought-induced responses. *Tree Physiology* 34:1348–1361.
- Čater, M. 2015. A 20-year overview of *Quercus robur* L. mortality and crown conditions in Slovenia. *Forests* 6:581–593.
- Chaves, M. M., J. Flexas, and C. Pinheiro. 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Annals of Botany* 103:551–560.
- Chen, H. Y. H., and Y. Luo. 2015. Net aboveground biomass declines of four major forest types with

- forest ageing and climate change in western Canada's boreal forests. *Global Change Biology*. doi: 10.1111/gcb.12994
- Chen, P. Y., C. Welsh, and A. Hamann. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biology* 16:3374–3385.
- Choat, B., et al. 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491:752–755.
- Chou, C., J. C. H. Chiang, C.-W. Lan, C.-H. Chung, Y.-C. Liao, and C.-J. Lee. 2013. Increase in the range between wet and dry season precipitation. *Nature Geoscience* 6:263–267.
- Ciais, P., et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533.
- Clark, J. S., D. M. Bell, M. C. Kwit, and K. Zhu. 2014. Competition-interaction landscapes for the joint response of forests to climate change. *Global Change Biology* 20:1979–1991.
- Clifford, M. J., and R. K. Booth. 2015. Late-Holocene drought and fire drove a widespread change in forest community composition in eastern North America. *Holocene* 25:1102–1110.
- Clifford, M. J., P. D. Royer, N. S. Cobb, D. D. Breshears, and P. L. Ford. 2013. Precipitation thresholds and drought-induced tree die-off: Insights from patterns of *Pinus edulis* mortality along an environmental stress gradient. *New Phytologist* 200:413–421.
- Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1:e1400082–e1400082.
- Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology and Evolution* 28:482–488.
- Couture, J. J., T. D. Meehan, E. L. Kruger, and R. L. Lindroth. 2015. Insect herbivory alters impact of atmospheric change on northern temperate forests. *Nature Plants*. doi: 10.1038/NPLANTS.2015.16
- Cox, P. M., D. Pearson, B. B. Booth, P. Friedlingstein, C. Huntingford, C. D. Jones, and C. M. Luke. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494:341–344.
- Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* 3:52–58.
- Dale, V. H., M. L. Tharp, K. O. Lannom, and D. G. Hodges. 2010. Modeling transient response of forests to climate change. *Science of the Total Environment* 408:1888–1901.
- D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications* 23:1735–1742.
- D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2008. On the 'Divergence Problem' in northern forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change* 60:289–305.
- Das, A. J., N. L. Stephenson, A. Flint, T. Das, and P. J. van Mantgem. 2013. Climatic correlates of tree mortality in water- and energy-limited forests. *PLoS One* 8 (7):e69917. doi: 10.1371/journal.pone.0069917
- Daubenmire, R. F. 1943. Soil temperature *versus* drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. *Botanical Gazette* 105:1–13.
- Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: Sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. *Journal of Range Management* 51:229–238.
- Defraeye, T., D. Derome, W. Aregawi, D. Cantré, S. Hartmann, E. Lehmann, J. Carmeliet, F. Voisard, P. Verboven, and B. Nicolai. 2014. Quantitative neutron imaging of water distribution, venation network and sap flow in leaves. *Planta* 240:423–436.
- De Frenne, P., et al. 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences USA* 110:18561–18565.
- De Kauwe, M. G., et al. 2014. Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO<sub>2</sub> enrichment sites. *New Phytologist* 203:883–899.
- de Schepper, V., J. Bühler, M. Thorpe, G. Roeb, G. Huber, D. van Dusschoten, S. Jahnke, and K. Steppe. 2013. 11C-PET imaging reveals transport dynamics and sectorial plasticity of oak phloem after girdling. *Frontiers in Plant Science* 4:200. doi: 10.3389/fpls.2013.00200
- Desprez-Loustau, M.-L., B. Marçais, L.-M. Nageleisen, D. Piou, and A. Vannini. 2006. Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science* 63:597–612.
- Dickman, L. T., N. G. McDowell, S. Sevanto, R. E. Pangle, and W. T. Pockman. 2014. Carbohydrate dynamics and mortality in a piñon-juniper woodland under three future precipitation scenarios. *Plant, Cell and Environment*. doi: 10.1111/pce.12441
- Dietze, M. C., and P. R. Moorcroft. 2011. Tree mortality in the eastern and central United States: Patterns and drivers. *Global Change Biology* 17:3312–3326.
- Diffenbaugh, N. S., and C. B. Field. 2013. Changes in

- ecologically critical terrestrial climate conditions. *Science* 341:486–492.
- Diffenbaugh, N. S., and M. Scherer. 2011. Observational and model evidence of global emergence of permanent, unprecedented heat in the 20th and 21st centuries. *Climatic Change* 107:615–624.
- Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences* 112:3931–3936.
- Donohue, R. J., M. L. Roderick, T. R. McVicar, and G. D. Farquhar. 2013. Impact of CO<sub>2</sub> fertilization on maximum foliage cover across the globe's warm, arid environments. *Geophysical Research Letters* 40:3031–3035.
- Dorman, M., A. Perevolotsky, D. Sarris, and T. Svoray. 2015a. The effect of rainfall and competition intensity on forest response to drought: lessons learned from a dry extreme. *Oecologia* 177:1025–1038.
- Dorman, M., A. Perevolotsky, D. Sarris, and T. Svoray. 2015b. Amount vs. temporal pattern: on the importance of intra-annual climatic conditions on tree growth in a dry environment. *Journal of Arid Environments* 118:65–68.
- Dorman, M., T. Svoray, A. Perevolotsky, and D. Sarris. 2013. Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. *Forest Ecology and Management* 310:1–9.
- Doughty, C. E., et al. 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* 519:78–82.
- Duan, H., R. A. Duursma, G. Huang, R. A. Smith, B. Choat, A. P. O'Grady, and D. T. Tissue. 2014. Elevated [CO<sub>2</sub>] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant, Cell & Environment* 37:1598–1613.
- Duan, H., A. P. O'Grady, R. A. Duursma, B. Choat, G. Huang, R. A. Smith, Y. Jiang, and D. T. Tissue. 2015. Drought responses of two gymnosperm species with contrasting stomatal regulation strategies under elevated [CO<sub>2</sub>] and temperature. *Tree Physiology* 00:1–15. doi: 10.1093/treephys/tpv047
- Dyer, L. A., and D. K. Letourneau. 2013. Can climate change trigger massive diversity cascades in terrestrial ecosystems? *Diversity* 5:479–504.
- Eamus, D., N. Boulain, J. Cleverly, and D. D. Breshears. 2013. Global change-type drought-induced tree mortality: Vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecology and Evolution* 3:2711–2729.
- Elkin, C., A. Giuggiola, A. Rigling, and H. Bugmann. 2015. Short-and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. *Ecological Applications* 25:1083–1098.
- Espírito-Santo, F. D. B., et al. 2014. Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nature Communications* 5:3434.
- Fang, J., T. Kato, Z. Guo, Y. Yang, H. Hu, H. Shen, X. Zhao, A. W. Kishimoto-Mo, Y. Tang, and R. A. Houghton. 2014. Evidence for environmentally enhanced forest growth. *Proceedings of the National Academy of Sciences USA* 111:9527–9532.
- FAO. 2005. *Global Forest Resources Assessment 2005*. FAO Forestry Paper Series 147. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Fares, S., G. S. Mugnozza, P. Corona, and M. Palahí. 2015. Sustainability: five steps for managing Europe's forests. *Nature* 519:407–409.
- Farrior, C. E., I. Rodriguez-Iturbe, R. Dybzinski, S. A. Levin, and S. W. Pacala. 2015. Decreased water limitation under elevated CO<sub>2</sub> amplifies potential for forest carbon sinks. *Proceedings of the National Academy of Sciences USA* 112:7213–7218.
- Fauset, S., T. R. Baker, S. L. Lewis, T. R. Feldpausch, K. Affum-Baffoe, E. G. Foli, K. C. Hamer, and M. D. Swaine. 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters* 15:1120–1129.
- Fauset, S., et al. 2015. Hyperdominance in Amazonian forest carbon cycling. *Nature Communications* 6. doi: 10.1038/ncomms7857
- Feeley, K. J. 2015. Moving forward with species distributions. *American Journal of Botany* 102:173–175.
- Feeley, K. J., J. Hurtado, S. Saatchi, M. R. Silman, and D. B. Clark. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology* 19:3472–3480.
- Feeley, K. J., E. M. Rehm, and B. Machovina. 2012. The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? *Frontiers of Biogeography* 4(2).
- Feeley, K. J., M. R. Silman, M. B. Bush, W. Farfan, K. G. Cabrera, Y. Malhi, P. Meir, N. S. Revilla, M. N. R. Quisipyanqui, and S. Saatchi. 2011. Upslope migration of Andean trees. *Journal of Biogeography* 38:783–791.
- Fellows, A. W., and M. L. Goulden. 2012. Rapid vegetation redistribution in Southern California during the early 2000s drought. *Journal of Geophysical Research: Biogeosciences* 117. doi: 10.1029/2012JG002044
- Fellows, A. W., and M. L. Goulden. 2013. Controls on gross production by a semiarid forest growing near its warm and dry ecotonal limit. *Agricultural and Forest Meteorology* 169:51–60.
- Fensham, R. J., D. L. Bouchard, C. P. Catterall, and J. M. Dwyer. 2014. Do local moisture stress

- responses across tree species reflect dry limits of their geographic ranges? *Austral Ecology* 39:612–618.
- Fensham, R. J., J. Fraser, H. J. MacDermott, and J. Firm. 2015. Dominant tree species are at risk from exaggerated drought under climate change. *Global Change Biology*. doi: 10.1111/gcb.12981
- Fensholt, R., et al. 2012. Greenness in semi-arid areas across the globe 1981–2007—an Earth Observing Satellite based analysis of trends and drivers. *Remote Sensing of Environment* 121:144–158.
- Fernández-Martínez, M., et al. 2014. Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4:471–476.
- Filewod, B., and S. C. Thomas. 2014. Impacts of a spring heat wave on canopy processes in a northern hardwood forest. *Global Change Biology* 20:360–371.
- Fisher, R. A., et al. 2015. Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes. *Geoscientific Model Development* 8:3293–3357.
- Flannigan, M., A. S. Cantin, W. J. de Groot, M. Wotton, A. Newbery, and L. M. Gowman. 2013. Global wildland fire season severity in the 21st century. *Forest Ecology and Management* 294:54–61.
- Frank, D. C., et al. 2015a. Water-use efficiency and transpiration across European forests during the Anthropocene. *Nature Climate Change* 5:579–583.
- Frank, D. C., et al. 2015b. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Global Change Biology*. doi: 10.1111/gcb.12916
- Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. *BioScience* 37:550–556.
- Franks, P. J., et al. 2013. Tansley review—Sensitivity of plants to changing atmospheric CO<sub>2</sub> concentration: from the geological past to the next century. *New Phytologist* 197:1077–1094.
- Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications* 7:123–139.
- Friend, A. D., et al. 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences USA* 111:3280–3285.
- Galbraith, D., et al. 2013. Residence times of woody biomass in tropical forests. *Plant Ecology and Diversity* 6:139–157.
- Galiano, L., J. Martínez-Vilalta, and F. Lloret. 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytologist* 190:750–759.
- García-Forner, N., H. D. Adams, S. Sevanto, A. D. Collins, L. T. Dickman, P. J. Hudson, M. Zeppel, J. Martínez-Vilalta, and N. G. McDowell. 2015. Responses of two semiarid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. *Plant, Cell & Environment*. doi: 10.1111/pce.12588
- Garrity, S. R., C. D. Allen, S. P. Brumby, C. Gangodagamage, N. G. McDowell, and D. M. Cai. 2013. Quantifying tree mortality in a mixed species woodland using multitemporal high spatial resolution satellite imagery. *Remote Sensing of Environment* 129:54–65.
- Gatti, L. V., et al. 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506:76–80.
- Gedalof, Z., and A. A. Berg. 2010. Tree ring evidence for limited direct CO<sub>2</sub> fertilization of forests over the 20th century. *Global Biogeochemical Cycles* 24(3):doi: doi: 10.1029/2009GB003699
- Girard, F., M. Vennetier, F. Guibal, C. Corona, S. Ouarmim, and A. Herrero. 2012. *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. *European Journal of Forest Research* 131:919–931.
- Girardin, M. P., X. J. Guo, R. De Jong, C. Kinnard, P. Bernier, and F. Raulier. 2014. Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Global Change Biology* 20:851–866.
- Gitlin, A. R., C. M. Sthultz, M. A. Bowker, S. Stumpf, K. L. Paxton, K. Kennedy, A. Muñoz, J. K. Bailey, and T. G. Whitham. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* 20:1477–1486.
- Giuggiola, A., H. Bugmann, A. Zingg, M. Dobbertin, and A. Rigling. 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. *Forest Ecology and Management* 310:827–835.
- Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drake. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography* 19:755–768.
- Grady, K. C., S. M. Ferrier, T. E. Kolb, S. C. Hart, G. J. Allan, and T. G. Whitham. 2011. Genetic variation in productivity of foundation riparian species at the edge of their distribution: Implications for restoration and assisted migration in a warming climate. *Global Change Biology* 17:3724–3735.
- Grant, G. E., C. L. Tague, and C. D. Allen. 2013. Watering the forest for the trees: An emerging priority for managing water in forest landscapes. *Frontiers in Ecology and the Environment* 11:314–321.
- Graven, H. D., et al. 2013. Enhanced seasonal exchange



- of CO<sub>2</sub> by northern ecosystems since 1960. *Science* 341:1085–9.
- Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? *Geophysical Research Letters* 41:9017–9023.
- Gu, L., S. G. Pallardy, K. P. Hosman, and Y. Sun. 2015. Drought-influenced mortality of tree species with different predawn leaf water dynamics in a decade-long study of a central US forest. *Biogeosciences* 12:2831–2845.
- Gutschick, V. P., and H. BassiriRad. 2003. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist* 160:21–42.
- Haddad, N. M., et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:e1500052. doi: 10.1126/sciadv.1500052
- Hampe, A., and A. S. Jump. 2011. Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics* 42:313–333.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–3.
- Hart, S. J., T. T. Veblen, and D. Kulakowski. 2014. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? *Forest Ecology and Management* 318:44–53.
- Harter, D. E. V., L. Nagy, S. Backhaus, C. Beierkuhnlein, B. Fussi, G. Huber, A. Jentsch, M. Konnert, D. Thiel, and J. Kreyling. 2015. A comparison of genetic diversity and phenotypic plasticity among European Beech (*Fagus sylvatica* L.) populations from Bulgaria and Germany under drought and temperature manipulation. *International Journal of Plant Sciences* 176:232–244.
- Hartmann, H., H. D. Adams, W. R. L. Anderegg, S. Jansen, and M. J. B. Zeppel. 2015. Research frontiers in drought-induced tree mortality: crossing scales and disciplines. *New Phytologist* 205:965–969.
- Hartmann, H., W. Ziegler, O. Kolle, and S. Trumbore. 2013. Thirst beats hunger—declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* 200:340–349.
- Held, I. M., and B. J. Soden. 2006. Robust responses of the hydrological cycle to global warming. *Journal of Climate* 19:5686–5699.
- Hember, R. A., W. A. Kurz, J. M. Metsaranta, T. A. Black, R. D. Guy, and N. C. Coops. 2012. Accelerating regrowth of temperate-maritime forests due to environmental change. *Global Change Biology* 18:2026–2040.
- Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283–335.
- Hicke, J. A., C. D. Allen, A. R. Desai, M. C. Dietze, R. J. Hall, D. M. Kashian, D. Moore, K. F. Raffa, R. N. Sturrock, and J. Vogelmann. 2012a. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* 18:7–34.
- Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012b. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271:81–90.
- Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research: Biogeosciences* 111:G2. doi: 10.1029/2005JG000101
- Hilker, T., A. I. Lyapustin, C. J. Tucker, F. G. Hall, R. B. Mynen, Y. Wang, J. Bi, and P. J. Sellers. 2014. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences USA* 111:16041–16046.
- Hlásny, T., C. Mátyás, R. Seidl, L. Kulla, K. Merganiová, J. Trombik, L. Dobor, Z. Barcza, and B. Konôpka. 2014. Climate change increases the drought risk in Central European forests: What are the options for adaptation? *Lesnícky časopis—Forestry Journal* 60:5–18.
- Hobbs, R. J., et al. 2014. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment* 12:557–564.
- Hoch, G. 2015. Carbon reserves as indicators for carbon limitation in trees. *Progress in Botany* 76:321–346.
- Hölttä, T., M. Mencuccini, and E. Nikinmaa. 2009. Linking phloem function to structure: analysis with a coupled xylem–phloem transport model. *Journal of Theoretical Biology* 259:325–337.
- Hu, R., B. Wu, H. Zheng, D. Hu, X. Wang, H. Duan, Y. Sun, J. Wang, Y. Zhang, and Y. Li. 2015. Global reprogramming of transcription in Chinese fir (*Cunninghamia lanceolata*) during progressive drought stress and after rewatering. *International Journal of Molecular Sciences* 16:15194–15219.
- Huang, K., C. Yi, D. Wu, T. Zhou, X. Zhao, W. J. Blanford, and Z. Li. 2015. Tipping point of a conifer forest ecosystem under severe drought. *Environmental Research Letters* 10(2):024011.
- Hughes, T. P., S. Carpenter, J. Rockström, M. Scheffer, and B. Walker. 2013. Multiscale regime shifts and planetary boundaries. *Trends in Ecology and Evolution* 28:389–395.
- Huntingford, C., et al. 2013. Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate change. *Nature Geoscience* 6:268–273.
- Hylander, K., J. Ehrlén, M. Luoto, and E. Meineri. 2015. Microrefugia: not for everyone. *Ambio* 44:60–68.

- IPCC. 1990. Climate change: the IPCC impacts assessment. Report prepared for Intergovernmental Panel on Climate Change by Working Group II. Intergovernmental Panel on Climate Change, Canberra, ACT, Australia.
- IPCC. 1995. Climate change 1995: impacts, adaptation and vulnerability. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press Cambridge, UK.
- IPCC. 2001. Climate change 2001: impacts, adaptation and vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- IPCC. 2007. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- IPCC. 2012. Managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- IPCC. 2013. Climate change 2013: the physical science basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- IPCC. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Iverson, L. R., and D. McKenzie. 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. *Landscape Ecology* 28:879–889.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. P. Peters. 2011. Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14:1005–1020.
- Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences USA* 106:19685–19692.
- Jamieson, M. A., A. M. Trowbridge, K. F. Raffa, and R. L. Lindroth. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology* 160:1719–1727.
- Janisch, J. E., and M. E. Harmon. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiology* 22:77–89.
- Jenerette, G. D., G. A. Barron-Gafford, A. J. Guswa, J. J. McDonnell, and J. C. Villegas. 2012. Organization of complexity in water limited ecohydrology. *Ecohydrology* 5:184–199.
- Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5:365–374.
- Jiang, X., S. A. Rauscher, T. D. Ringler, D. M. Lawrence, A. P. Williams, C. D. Allen, A. L. Steiner, D. M. Cai, and N. G. McDowell. 2013. Projected future changes in vegetation in western North America in the twenty-first century. *Journal of Climate* 26:3671–3687.
- Joetzjer, E., C. Delire, H. Douville, P. Ciais, B. Decharme, R. Fisher, B. O. Christoffersen, J. C. Calvet, A. C. L. da Costa, L. V. Ferreira, and P. Meir. 2014. Predicting the response of the Amazon rainforest to persistent drought conditions under current and future climates: a major challenge for global land surface models. *Geoscientific Model Development Discussions* 7:5295–5340.
- Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*. doi: 10.1038/ncomms8537
- Jong, R., J. Verbesselt, M. E. Schaepman, and S. Bruin. 2012. Trend changes in global greening and browning: contribution of short-term trends to longer-term change. *Global Change Biology* 18:642–655.
- Juday, G. P., C. Alix, and T. A. Grant. 2015. Spatial coherence and change of opposite white spruce temperature sensitivities on floodplains in Alaska confirms early-stage boreal biome shift. *Forest Ecology and Management* 350:46–61.
- Jump, A. S., J. M. Hunt, and J. Peñuelas. 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology* 12:2163–2174.
- Jump, A. S., R. Marchant, and J. Peñuelas. 2009a. Environmental change and the option value of genetic diversity. *Trends in Plant Science* 14:51–58.
- Jump, A. S., C. Mátyás, and J. Peñuelas. 2009b. The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution* 24:694–701.
- Jung, M., et al. 2010. Recent decline in the global land evapotranspiration trend due to limited moisture supply. *Nature* 467:951–954.
- Kane, J. M., F. L. Dugi, and T. E. Kolb. 2015. Establishment and growth of piñon pine regeneration vary by nurse type along a soil substrate age

- gradient in northern Arizona. *Journal of Arid Environments* 115:113–119.
- Kane, J. M., T. E. Kolb, and J. D. McMillin. 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests. *Forest Ecology and Management* 330:171–182.
- Kayler, Z. E., H. J. De Boeck, S. Fatichi, J. M. Grünzweig, L. Merbold, C. Beier, N. G. McDowell, and J. S. Dukes. 2015. Experiments to confront the environmental extremes of climate change. *Frontiers in Ecology and the Environment* 13:219–225.
- Keane, R. E., D. McKenzie, D. A. Falkc, E. A. H. Smithwick, C. Miller, and L.-K. B. Kellogg. 2015. Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling* 309–310:33–47.
- Keenan, R. J. 2015. Climate change impacts and adaptation in forest management: a review. *Annals of Forest Science* 72:145–167.
- Keenan, T. F., J. Gray, M. A. Friedl, M. Toomey, G. Bohrer, D. Y. Hollinger, J. W. Munger, J. O’Keefe, H. P. Schmid, and I. S. Wing. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* 4:598–604.
- Keenan, T. F., D. Y. Hollinger, G. Bohrer, D. Dragoni, J. W. Munger, H. P. Schmid, and A. D. Richardson. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499:324–327.
- Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences USA* 105:11823–11826.
- Kharuk, V. I., K. J. Ranson, P. a. Oskorbin, S. T. Im, and M. L. Dvinskaya. 2013. Climate induced birch mortality in Trans-Baikal lake region, Siberia. *Forest Ecology and Management* 289:385–392.
- Kitzberger, T. 2013. Impact of extreme and infrequent events on terrestrial ecosystems and biodiversity. Pages 209–223 in S. A. Levin, editor. *Encyclopedia of biodiversity*. Second edition. Volume 4. Academic Press, Waltham, Massachusetts, USA.
- Klein, T., G. Di Matteo, E. Rotenberg, S. Cohen, and D. Yakir. 2013. Differential ecophysiological response of a major Mediterranean pine species across a climatic gradient. *Tree Physiology* 33:26–36.
- Klein, T., D. Yakir, N. Buchmann, and J. M. Grünzweig. 2014a. Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought. *New Phytologist* 201:712–716.
- Klein, T., D. Yakir, and G. Hoch. 2014b. Drought stress, growth, and nonstructural carbohydrate dynamics of pine trees in a semi-arid forest. *Tree Physiology* 34:981–992.
- Kolb, K. J., and J. S. Sperry. 1999. Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant, Cell & Environment* 22:925–936.
- Kolström, M., M. Lindner, T. Vilén, M. Maroschek, R. Seidl, M. J. Lexer, S. Netherer, A. Kremer, S. Delzon, A. Barbati, M. Marchetti, and P. Corona. 2011. Reviewing the science and implementation of climate change adaptation measures in European forestry. *Forests* 2:961–982.
- Kreyling, J., A. Jentsch, and C. Beier. 2014. Beyond realism in climate change experiments: gradient approaches identify thresholds and tipping points. *Ecology Letters* 17:125–e1. doi: 10.1111/ele.12193
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990.
- Langenheim, J. H. 1996. Early history and progress of women ecologists: emphasis upon research contributions. *Annual Review of Ecology and Systematics* 27:1–53.
- Lapenis, A., A. Shvidenko, D. Shepaschenko, S. Nilsson, and A. Aiyer. 2005. Acclimation of Russian forests to recent changes in climate. *Global Change Biology* 11:2090–2102.
- Lau, W. K. M., and K.-M. Kim. 2015. Robust Hadley Circulation changes and increasing global dryness due to CO<sub>2</sub> warming from CMIP5 model projections. *Proceedings of the National Academy of Sciences USA* 112:3630–3635.
- Lauenroth, W. K., and J. B. Bradford. 2009. Ecohydrology of dry regions of the United States: precipitation pulses and intraseasonal drought. *Ecohydrology* 2:173–181.
- Lawrence, D., and K. Vandecar. 2014. The impact of tropical deforestation on climate and links to agricultural productivity. *Nature Climate Change* 5:27–36.
- Leakey, A. D. B. 2009. Rising atmospheric carbon dioxide concentration and the future of C4 crops for food and fuel. *Proceedings of the Royal Society B* 276:2333–2343.
- Lenton, T. M., H. Held, E. Kriegler, J. W. Hall, W. Lucht, S. Rahmstorf, and H. J. Schellnhuber. 2008. Tipping elements in the Earth’s climate system. *Proceedings of the National Academy of Sciences USA* 105:1786–1793.
- Leuzinger, S., Y. Luo, C. Beier, W. Dieleman, S. Vicca, and C. Körner. 2011. Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology and Evolution* 26:236–241.
- Lévesque, M., R. Siegwolf, M. Saurer, B. Eilmann, and A. Rigling. 2014. Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions. *New Phytologist* 203:94–109.
- Lewis, S. L. 2006. Tropical forests and the changing

- earth system. *Philosophical Transactions of the Royal Society B* 361:195–210.
- Lewis, S. L., et al. 2009. Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006.
- Lewis, S. L., and M. A. Maslin. 2015. Defining the Anthropocene. *Nature* 519:171–180.
- Li, Y., M. Zhao, S. Motesharrei, Q. Mu, E. Kalnay, and S. Li. 2015. Local cooling and warming effects of forests based on satellite observations. *Nature Communications* 6:6603.
- Liepe, K. J. 2014. Genetic variation in lodgepole pine and interior spruce: adaptation to climate and implications for seed transfer. Thesis. University of Alberta, Calgary, Alberta, Canada.
- Limousin, J. M., S. Rambal, J. M. Ourcival, J. Rodríguez-Calcerrada, I. M. Pérez-Ramos, R. Rodríguez-Cortina, L. Misson, and R. Joffre. 2012. Morphological and phenological shoot plasticity in a Mediterranean evergreen oak facing long-term increased drought. *Oecologia* 169:565–577.
- Limousin, J., E. A. Yezpez, N. G. McDowell, and W. T. Pockman. 2015. Convergence in resource use efficiency across trees with differing hydraulic strategies in response to ecosystem precipitation manipulation. *Functional Ecology*. doi: 10.1111/1365-2435.12426
- Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012. Global decline in large old trees. *Science* 338:1305–1306.
- Lindner, M., et al. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259:698–709.
- Lindner, M., et al. 2014. Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *Journal of Environmental Management* 146:69–83.
- Liu, H., A. P. Williams, C. D. Allen, D. Guo, X. Wu, O. A. Anenkhonov, E. Liang, D. V. Sandanov, Y. Yin, and Z. Qi. 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. *Global Change Biology* 19:2500–2510.
- Liu, Y. Y., A. I. J. M. van Dijk, R. A. M. de Jeu, J. G. Canadell, M. F. McCabe, J. P. Evans, and G. Wang. 2015a. Recent reversal in loss of global terrestrial biomass. *Nature Climate Change* 5:470–474.
- Liu, D., R. Ogaya, A. Barbeta, X. Yang, and J. Peñuelas. 2015b. Contrasting impacts of continuous moderate drought and episodic severe droughts on the aboveground-biomass increment and litterfall of three coexisting Mediterranean woody species. *Global Change Biology*. doi: 10.1111/gcb.13029
- Lloret, F., A. Escudero, J. M. Iriondo, J. Martínez-Vilalta, and F. Valladares. 2012. Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology* 18:797–805.
- Lloret, F., and I. Granzow-de la Cerda. 2013. Plant competition and facilitation after extreme drought episodes in Mediterranean shrubland: Does damage to vegetation cover trigger replacement by juniper woodland? *Journal of Vegetation Science* 24:1020–1032.
- Lloyd, J., and G. D. Farquhar. 2008. Effects of rising temperatures and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B* 363:1811–1817.
- Logan, J. A., W. W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications* 20:895–902.
- López-Hoffman, L., D. D. Breshears, C. D. Allen, and M. Miller. 2013. Key landscape ecology metrics for assessing climate change adaptation options: rate of change and patchiness of impacts. *Ecosphere* 4:1–18.
- Lugo, A. E. 2015. Evolving conservation paradigms for the Anthropocene. Pages 47–60 in V. A. Sample and R. P. Bixler, editors. *Forest conservation and management in the Anthropocene: Conference Proceedings*. Proceedings RMRS-P-71. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. [http://www.fs.fed.us/rm/pubs/rmrs\\_p071.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p071.pdf)
- Luo, Y., and H. Y. H. Chen. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. *Journal of Ecology* 99:1470–1480.
- Luo, Y., and H. Y. H. Chen. 2013. Observations from old forests underestimate climate change effects on tree mortality. *Nature Communications* 4:1655. doi: 10.1038/ncomms2681
- Luyssaert, S. M., et al. 2014. Land management and land-cover change have impacts of similar magnitude on surface temperature. *Nature Climate Change* 4:389–393.
- Ma, Z., C. Peng, Q. Zhu, H. Chen, G. Yu, W. Li, X. Zhou, W. Wang, and W. Zhang. 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences USA* 109:2423–2427.
- Macalady, A. K., and H. Bugmann. 2014. Growth-mortality relationships in piñon pine (*Pinus edulis*) during severe droughts of the past century: shifting processes in space and time. *PLoS One* 9:e92770.
- Malhi, Y., et al. 2015. The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology* 6:2283–2295.
- Maron, M., C. A. McAlpine, J. E. M. Watson, S. Maxwell, and P. Barnard. 2015. Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions* 21:731–

- 743.
- Martin-Benito, D., and N. Pederson. 2015. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *Journal of Biogeography* 42:925–937.
- Martínez-Vilalta, J., F. Lloret, and D. D. Breshears. 2012a. Drought-induced forest decline: causes, scope and implications. *Biology Letters* 8:689–691.
- Martínez-Vilalta, J., B. C. López, N. Adell, L. Badiella, and M. Ninyerola. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology* 14:2868–2881.
- Martínez-Vilalta, J., B. C. López, L. Loepfe, and F. Lloret. 2012b. Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168:877–888.
- Martínez-Vilalta, J., E. Prat, I. Oliveras, and J. Piñol. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* 133:19–29.
- Marvel, K., and C. Bonfils. 2013. Identifying external influences on global precipitation. *Proceedings of the National Academy of Sciences USA* 110:19301–19306.
- Mascaro, J., G. P. Asner, S. Davies, A. Dehgan, and S. Saatchi. 2014. These are the days of lasers in the jungle. *Carbon Balance and Management* 9:7. doi:10.1186/s13021-014-0007-0
- Matusick, G., K. X. Ruthrof, N. C. Brouwers, B. Dell, and G. S. J. Hardy. 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research* 132:497–510.
- Mátyás, C., B. Fady, and G. G. Vendramin. 2009. Forests at the limit: Evolutionary-genetic consequences of environmental changes at the receding (xeric) edge of distribution. *Acta Silvatica et Lignaria Hungarica* 5:201–204.
- McDowell, N. G. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155:1051–1059.
- McDowell, N. G., and C. D. Allen. 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* 5:669–672.
- McDowell, N., C. D. Allen, and L. Marshall. 2010. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. *Global Change Biology* 16:399–415.
- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* 26:523–532.
- McDowell, N. G., N. C. Coops, P. S. A. Beck, J. Q. Chambers, C. Gangodagamage, J. A. Hicke, C. Huang, R. Kennedy, D. J. Krofcheck, and M. Litvak. 2015. Global satellite monitoring of climate-induced vegetation disturbances. *Trends in Plant Science* 20:114–123.
- McDowell, N. G., et al. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* 200:304–321.
- McDowell, N. G., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yezzer. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- McDowell, N. G., and S. Sevanto. 2010. The mechanisms of carbon starvation: How, when, or does it even occur at all? *New Phytologist* 186:264–266.
- McIntosh, R. P. 1986. *The background of ecology: concept and theory*. Cambridge University Press, Cambridge, UK.
- McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly. 2015. Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences USA* 112:1458–1463.
- McKenzie, D., D. L. Peterson, and J. J. Littell. 2008. Global warming and stress complexes in forests of western North America. *Developments in Environmental Science* 8:319–337.
- McMahon, S. M., G. G. Parker, and D. R. Miller. 2010. Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences USA* 107:3611–3615.
- McVicar, T. R., et al. 2012. Global review and synthesis of trends in observed terrestrial near-surface wind speeds: implications for evaporation. *Journal of Hydrology* 416:182–205.
- Meddens, A. J. H., and J. A. Hicke. 2014. Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. *Forest Ecology and Management* 322:78–88.
- Meir, P., M. Mencuccini, and R. C. Dewar. 2015. Drought-related tree mortality: addressing the gaps in understanding and prediction. *New Phytologist* 27:28–33.
- Mencuccini, M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell & Environment* 26:163–182.
- Mencuccini, M., F. Minunno, Y. Salmon, J. Martínez-Vilalta, and T. Hölttä. 2015. Coordination of

- physiological traits involved in drought-induced mortality of woody plants. *New Phytologist*. doi: 10.1111/nph.13461
- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17:2145–51.
- Mitchell, P. J., A. P. O'Grady, K. R. Hayes, and E. A. Pinkard. 2014. Exposure of trees to drought-induced die-off is defined by a common climatic threshold across different vegetation types. *Ecology and Evolution* 4:1088–1101.
- Mokria, M., A. Gebrekirstos, E. Aynekulu, and A. Bräuning. 2015. Tree dieback affects climate change mitigation potential of a dry afro-montane forest in northern Ethiopia. *Forest Ecology and Management* 344:73–83.
- Moore, D. J. P., N. A. Trahan, P. Wilkes, T. Quaife, B. B. Stephens, K. Elder, A. R. Desai, J. Negron, and R. K. Monson. 2013. Persistent reduced ecosystem respiration after insect disturbance in high elevation forests. *Ecology Letters* 16:731–737.
- Mora, C., I. R. Caldwell, J. M. Caldwell, M. R. Fisher, B. M. Genco, and S. Q. Running. 2015. Suitable days for plant growth disappear under projected climate change: Potential human and biotic vulnerability. *PLoS Biology* 13(6):e1002167.
- National Climate Assessment. 2014. Climate change impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program. doi: 10.7930/J0Z31WJ2
- National Research Council, Committee on Earth-Atmosphere Interactions. 2007. Understanding multiple environmental stresses: report of a workshop. National Academies Press, Washington, D.C., USA.
- Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88:2259–2269.
- Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15:684–692.
- Niu, S., Y. Luo, D. Li, S. Cao, J. Xia, J. Li, and M. D. Smith. 2014. Plant growth and mortality under climatic extremes: an overview. *Environmental and Experimental Botany* 98:13–19.
- Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie. 2010. CO<sub>2</sub> enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences USA* 107:19368–19373.
- Nowacki, G. J., and M. D. Abrams. 2014. Is climate an important driver of post-European vegetation change in the Eastern United States? *Global Change Biology* 21:314–334.
- O'Brien, M. J., S. Leuzinger, C. D. Philipson, J. Tay, and A. Hector. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4:710–714.
- Oliva, J., J. Stenlid, and J. Martinez-Vilalta. 2014. The effect of fungal pathogens on the water and carbon economy of trees: implications for drought-induced mortality. *New Phytologist* 203:1028–1035.
- Orsenigo, S., A. Mondoni, G. Rossi, and T. Abeli. 2014. Some like it hot and some like it cold, but not too much: plant responses to climate extremes. *Plant Ecology* 215:677–688.
- Overpeck, J., and B. Udall. 2010. Dry times ahead. *Science* 328:1642–1643.
- Palmer, W. C. 1965. Meteorological drought. Research Paper 45. Weather Bureau, Office of Climatology, Washington, D.C., USA.
- Pan, Y., R. A. Birdsey, O. L. Phillips, and R. B. Jackson. 2013. The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics* 44:593–622.
- Pechony, O., and D. T. Shindell. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences USA* 107:19167–19170.
- Pederson, N., et al. 2014a. Climate remains an important driver of post-European vegetation change in the eastern United States. *Global Change Biology* 21:2105–2110.
- Pederson, N., J. M. Dyer, R. W. McEwan, A. E. Hessler, C. J. Mock, D. A. Orwig, H. E. Rieder, and B. I. Cook. 2014b. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs* 84:599–620.
- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* 1:467–471.
- Peng, S.-S., S. Piao, Z. Zeng, P. Ciais, L. Zhou, L. Z. X. Li, R. B. Myneni, Y. Yin, and H. Zeng. 2014. Afforestation in China cools local land surface temperature. *Proceedings of the National Academy of Sciences USA* 111:2915–2919.
- Peñuelas, J., J. G. Canadell, and R. Ogaya. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography* 20:597–608.
- Peñuelas, J., R. Ogaya, M. Boada, and A. S. Jump. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30:829–837.
- Perring, M. P., R. J. Standish, J. N. Price, M. D. Craig,

- T. E. Erickson, K. X. Ruthrof, A. S. Whiteley, L. E. Valentine, and R. J. Hobbs. 2015. Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* 6(8):131.
- Peterman, W., and R. H. Waring. 2014. Does overshoot in leaf development of ponderosa pine in wet years leads to bark beetle outbreaks on fine-textured soils in drier years? *Forest Ecosystems* 1:1–13.
- Peters, D. C., R. A. Pielke, Sr., B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA* 101:15130–15135.
- Peters, M. P., L. R. Iverson, and S. N. Matthews. 2015. Long-term droughtiness and drought tolerance of eastern US forests over five decades. *Forest Ecology and Management* 345:56–64.
- Phillips, O. L., et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323:1344–1347.
- Phillips, O. L., S. L. Lewis, T. R. Baker, K.-J. Chao, and N. Higuchi. 2008. The changing Amazon forest. *Philosophical Transactions of the Royal Society B* 363:1819–1827.
- Phillips, O. L., G. van der Heijden, S. L. Lewis, G. López González, and E. Honorio Coronado. 2010. Drought–mortality relationships for tropical forests. *New Phytologist* 187:631–646.
- Pinkard, E., et al. 2014. A history of forestry management responses to climatic variability and their current relevance for developing climate change adaptation strategies. *Forestry* 88:155–171.
- Ponce-Campos, G. E., et al. 2013. Ecosystem resilience despite large-scale altered hydroclimatic conditions. *Nature* 494:349–52.
- Potter, C., S. Li, and C. Hiatt. 2012. Declining vegetation growth rates in the eastern United States from 2000 to 2010. *Natural Resources* 3:184–190.
- Poulter, B., et al. 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509:600–603.
- Quirk, J., N. G. McDowell, J. R. Leake, P. J. Hudson, and D. J. Beerling. 2013. Increased susceptibility to drought-induced mortality in *Sequoia sempervirens* (Cupressaceae) trees under Cenozoic atmospheric carbon dioxide starvation. *American Journal of Botany* 100:582–591.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58:501–517.
- Real, L. A., and J. H. Brown, editors. 2012. *Foundations of ecology: classic papers with commentaries*. University of Chicago Press, Chicago, Illinois, USA.
- Rehfeldt, G. E., N. L. Crookston, C. Sáenz-Romero, and E. M. Campbell. 2012. North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. *Ecological Applications* 22:119–141.
- Rehfeldt, G. E., B. C. Jaquish, C. Sáenz-Romero, D. G. Joyce, L. P. Leites, J. B. St Clair, and J. López-Upton. 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. *Forest Ecology and Management* 324:147–157.
- Rehfeldt, G. E., N. M. Tchebakova, and E. I. Parfenova. 2004. Genetic responses to climate and climate change in conifers of the temperate and boreal forests. *Recent Research Developments in Genetics & Breeding* 1:113–130.
- Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wyckoff, N. A. Kuzmina, and L. I. Milyutin. 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology* 8:912–929.
- Reichstein, M., et al. 2013. Climate extremes and the carbon cycle. *Nature* 500:287–95.
- Reyer, C. P. O., et al. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology* 19:75–89.
- Reyer, C. P. O., et al. 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology* 103:5–15.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Richter, S., T. Kipfer, T. Wohlgemuth, C. C. Guerrero, J. Ghazoul, and B. Moser. 2012. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia* 169:269–279.
- Rico, L., R. Ogaya, A. Barbeta, and J. Peñuelas. 2014. Changes in DNA methylation fingerprint of *Quercus ilex* trees in response to experimental field drought simulating projected climate change. *Plant Biology* 16:419–427.
- Rood, S. B., S. Patiño, K. Coombs, and M. T. Tyree. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* 14:248–257.
- Rotenberg, E., and D. Yakir. 2010. Contribution of semi-arid forests to the climate system. *Science* 327:451–454.
- Royer, P. D., D. D. Breshears, C. B. Zou, J. C. Villegas, N. S. Cobb, and S. A. Kurc. 2012. Density-dependent ecohydrological effects of piñon-juniper woody canopy cover on soil microclimate and potential soil evaporation. *Rangeland Ecology & Management* 65:11–20.
- Royer, P. D., N. S. Cobb, M. J. Clifford, C.-H. Huang,

- D. D. Breshears, H. D. Adams, and J. C. Villegas. 2011. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. *Journal of Ecology* 99:714–723.
- Ruiz-Benito, P., E. R. Lines, L. Gómez-Aparicio, M. A. Zavala, and D. A. Coomes. 2013. Patterns and drivers of tree mortality in Iberian forests: climatic effects are modified by competition. *PLoS ONE* 8. doi: 10.1371/journal.pone.0056843
- Sala, A., F. Piper, and G. Hoch. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186:274–281.
- Salzer, M. W., M. K. Hughes, A. G. Bunn, and K. F. Kipfmüller. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences USA* 106:20348–20353.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Scheffer, M., et al. 2012a. Anticipating critical transitions. *Science* 338:344–348.
- Scheffer, M., M. Hirota, M. Holmgren, E. H. Van Nes, and F. S. Chapin. 2012b. Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences USA* 109:21384–21389.
- Scheffer, M., et al. 2015. Creating a safe operating space for iconic ecosystems. *Science* 347:1317–1319.
- Schelhaas, M. J., G. J. Nabuurs, G. M. Hengeveld, C. Reyer, M. Hanewinkel, N. E. Zimmermann, and D. Cullmann. 2015. Adaptive forest management to account for climate change-induced productivity and species suitability changes in Europe. *Regional Environmental Change*. doi: 10.1007/s10113-015-0788-z
- Simple, B., M. Rankin, T. Koen, and G. Geeves. 2010. A note on tree deaths during the current (2001–?) drought in South-eastern Australia. *Australian Geographer* 41:391–401.
- Sevanto, S., N. G. McDowell, L. T. Dickman, R. Pangle, and W. T. Pockman. 2014. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment* 37:153–161.
- Sheffield, J., E. F. Wood, and M. L. Roderick. 2012. Little change in global drought over the past 60 years. *Nature* 491:435–8.
- Shiau, J. T. 2006. Fitting drought duration and severity with two-dimensional copulas. *Water Resources Management* 20:795–815.
- Sillmann, J., V. V. Kharin, X. Zhang, F. W. Zwiers, and D. Bronaugh. 2013. Climate extremes indices in the CMIP5 multimodel ensemble: Part 1. Model evaluation in the present climate. *Journal of Geophysical Research: Atmospheres* 118:1716–1733.
- Silva, L. C. R., and M. Anand. 2013. Probing for the influence of atmospheric CO<sub>2</sub> and climate change on forest ecosystems across biomes. *Global Ecology and Biogeography* 22:83–92.
- Silvertown, J., Y. Araya, and D. Gowing. 2015. Hydrological niches in terrestrial plant communities: a review. *Journal of Ecology* 103:93–108.
- Sitch, S., P. Friedlingstein, N. Gruber, S. D. Jones, G. Murray-Tortarolo, A. Ahlström, S. C. Doney, H. Graven, C. Heinze, and C. Huntingford. 2015. Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* 12:653–679.
- Smith, J. M., J. Paritsis, T. T. Veblen, and T. B. Chapman. 2015. Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. *Forest Ecology and Management* 341:8–17.
- Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology* 99:656–663.
- Sperry, J. S., and D. M. Love. 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* 207:14–27.
- Steffen, W., Å. Persson, L. Deutsch, J. Zalasiewicz, M. Williams, K. Richardson, C. Crumley, P. Crutzen, C. Folke, and L. Gordon. 2011. The Anthropocene: from global change to planetary stewardship. *Ambio* 40:739–761.
- Steffen, W., et al. 2015. Planetary boundaries: Guiding human development on a changing planet. *Science* 347. doi: 10.1126/science.1259855
- Steinkamp, J., and T. Hickler. 2015. Is drought-induced forest dieback globally increasing? *Journal of Ecology* 103:31–43.
- Stephenson, N. L., and P. J. van Mantgem. 2005. Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters* 8:524–531.
- Stephenson, N. L., et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507:90–93.
- Stultz, C. M., C. A. Gehring, and T. G. Whitham. 2009. Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species. *Global Change Biology* 15:1949–1961.
- Suarez, M. L., and T. Kitzberger. 2010. Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *Journal of Ecology* 98:1023–1034.
- Swann, A. L. S., I. Y. Fung, and J. C. H. Chiang. 2012. Mid-latitude afforestation shifts general circulation and tropical precipitation. *Proceedings of the National Academy of Sciences USA* 109:712–716.
- Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128–3147.



- Tague, C. L., N. G. McDowell, and C. D. Allen. 2013. An integrated model of environmental effects on growth, carbohydrate balance, and mortality of *Pinus ponderosa* forests in the southern Rocky Mountains. *PLoS One* 8(11). doi: 10.1371/journal.pone.0080286
- Tang, X., et al. 2014. How is water-use efficiency of terrestrial ecosystems distributed and changing on Earth? *Scientific Reports* 4:7483.
- Tarancón, A., P. Z. Fulé, K. L. Shive, C. H. Sieg, A. Sanchez-Meador, and A. Azpeleta. 2014. Simulating post-wildfire forest trajectories under alternative climate and management scenarios. *Ecological Applications* 24:1626–1637.
- Teskey, R., T. Werten, I. Bauweraerts, M. Ameye, M. A. Mcguire, and K. Steppe. 2014. Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment*. doi: 10.1111/pce.12417
- Thomas, H. 2013. Senescence, ageing and death of the whole plant. *New Phytologist* 197:696–711.
- Tognetti, R., P. Cherubini, and J. L. Innes. 2000. Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO<sub>2</sub> concentrations. *New Phytologist* 146:59–74.
- Touchan, R., K. J. Anchukaitis, D. M. Meko, M. Sabir, S. Attalah, and A. Aloufi. 2011a. Spatiotemporal drought variability in northwestern Africa over the last nine centuries. *Climate Dynamics* 37:237–252.
- Touchan, R., C. A. Woodhouse, D. M. Meko, and C. D. Allen. 2011b. Millennial precipitation reconstruction for the Jemez Mountains, New Mexico, reveals changing drought signal. *International Journal of Climatology* 31:896–906.
- Trenberth, K. E., A. Dai, G. van der Schrier, P. D. Jones, J. Barichivich, K. R. Briffa, and J. Sheffield. 2014. Global warming and changes in drought. *Nature Climate Change* 4:17–22.
- Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* 8:213–227.
- Twidwell, D., C. L. Wonkka, C. A. Taylor, C. B. Zou, J. J. Twidwell, and W. E. Rogers. 2014. Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topographic factors and land management. *Applied Vegetation Science* 17:42–52.
- van der Sleen, P., P. Groenendijk, M. Vlam, N. P. R. Anten, A. Boom, F. Bongers, T. L. Pons, G. Terburg, and P. A. Zuidema. 2014. No growth stimulation of tropical trees by 150 years of CO<sub>2</sub> fertilization but water-use efficiency increased. *Nature Geoscience* 8:24–28.
- van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, and M. Brooks. 2013. Tree mortality patterns following prescribed fire for *Pinus* and *Abies* across the southwestern United States. *Forest Ecology and Management* 289:463–469.
- van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.
- van Nieuwstadt, M. G., and D. Sheil. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology* 93:191–201.
- Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate* 23:1696–1718.
- Vicente-Serrano, S. M., J. J. Camarero, J. Zabalza, G. Sangüesa-Barreda, J. I. López-Moreno, and C. L. Tague. 2015. Evapotranspiration deficit controls net primary production and growth of silver fir: implications for circum-Mediterranean forests under forecasted warmer and drier conditions. *Agricultural and Forest Meteorology* 206:45–54.
- Vicente-Serrano, S. M., et al. 2014. Evidence of increasing drought severity caused by temperature rise in southern Europe. *Environmental Research Letters* 9. doi: 10.1088/1748-9326/9/4/044001
- Vicente-Serrano, S. M., C. Gouveia, J. J. Camarero, S. Beguería, R. Trigo, J. I. López-Moreno, C. Azorín-Molina, E. Pasho, J. Lorenzo-Lacruz, and J. Revuelto. 2013. Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences USA* 110:52–57.
- Vogelmann, J. E., B. Tolk, and Z. Zhu. 2009. Monitoring forest changes in the southwestern United States using multitemporal Landsat data. *Remote Sensing of Environment* 113:1739–1748.
- Walker, X. J., M. C. Mack, and J. F. Johnstone. 2015. Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Global Change Biology*. doi: 10.1111/gcb.12893
- Warren, J. M., R. J. Norby, S. D. Wullschlegel, and R. Oren. 2011. Elevated CO<sub>2</sub> enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiology* 31:117–130.
- Way, D. A., and R. Oren. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* 30:669–688.
- Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83:441–470.
- Wei, S., et al. 2014. Data-based perfect-deficit approach

- to understanding climate extremes and forest carbon assimilation capacity. *Environmental Research Letters* 9. doi: 10.1088/1748-9326/9/6/065002
- Westerling, A., T. Brown, T. Schoennagel, T. Swetnam, M. Turner, and T. Veblen. 2014. Briefing: Climate and wildfire in western U.S. forests. Pages 81–102 in V. A. Sample and R. P. Bixler, editors. *Forest conservation and management in the Anthropocene: adaptation of science, policy, and practices*. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Will, R. E., S. M. Wilson, C. B. Zou, and T. C. Hennessey. 2013. Increased vapor pressure deficit due to higher temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the forest–grassland ecotone. *New Phytologist* 200:366–374.
- Williams, A. P., C. D. Allen, C. I. Millar, T. W. Swetnam, J. Michaelsen, C. J. Still, and S. W. Leavitt. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences USA* 107:21289–21294.
- Williams, A. P., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3:8–13.
- Williams, A. P., et al. 2014. Causes and implications of extreme atmospheric moisture demand during the record-breaking 2011 wildfire season in the southwestern United States. *Journal of Applied Meteorology and Climatology* 53:2671–2684.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Williams, M., and K. Dumroese. 2013. Preparing for climate change: forestry and assisted migration. *Journal of Forestry* 111:287–297.
- Worrall, J. J., G. E. Rehfeldt, A. Hamann, E. H. Hogg, B. Suzanne, S. B. Marchetti, M. Michaelian, and L. K. Gray. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management* 299:35–51.
- Wunder, J., B. Brzeziecki, H. Żybura, B. Reineking, C. Bigler, and H. Bugmann. 2008. Growth–mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. *Oikos* 117:815–828.
- Wythers, K. R., P. B. Reich, and J. B. Bradford. 2013. Incorporating temperature-sensitive Q10 and foliar respiration acclimation algorithms modifies modeled ecosystem responses to global change. *Journal of Geophysical Research: Biogeosciences* 118:77–90.
- Xia, J., et al. 2015. Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proceedings of the National Academy of Sciences USA* 112:2788–2793.
- Xiong, H.-F., S.-J. Wang, L. Rong, A.-Y. Cheng, and Y.-B. Li. 2011. Effects of extreme drought on plant species in Karst area of Guizhou Province, Southwest China. *Chinese Journal of Applied Ecology* 22:1127–1134.
- Yaussy, D. A., L. R. Iverson, and S. N. Matthews. 2013. Competition and climate affects US hardwood-forest tree mortality. *Forest Science* 59:416–430.
- Yi, C., E. Pendall, and P. Ciais. 2015. Focus on extreme events and the carbon cycle. *Environmental Research Letters* 10:70201–70208.
- Yi, C., S. Wei, and G. Hendrey. 2014. Warming climate extends dryness-controlled areas of terrestrial carbon sequestration. *Scientific Reports* 4. doi: 10.1038/srep05472
- Zaehle, S., et al. 2014. Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment studies. *New Phytologist* 202:803–822.
- Zanetti, C., M. Vennetier, P. Meriaux, and M. Provan-sal. 2015. Plasticity of tree root system structure in contrasting soil materials and environmental conditions. *Plant and Soil* 387:81–101.
- Zegler, T. J., M. M. Moore, M. L. Fairweather, K. B. Ireland, and P. Z. Fulé. 2012. *Populus tremuloides* mortality near the southwestern edge of its range. *Forest Ecology and Management* 282:196–207.
- Zeppel, M. J. B., et al. 2014. Drought and resprouting plants. *New Phytologist* 206:583–589.
- Zhang, J., S. Huang, and F. He. 2015. Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences USA* 112:4009–4014.
- Zhang, L., J. Xiao, J. Li, K. Wang, L. Lei, and H. Guo. 2012. The 2010 spring drought reduced primary productivity in southwestern China. *Environmental Research Letters* 7:045706.
- Zhang, Q., Y. P. Wang, R. J. Matear, A. J. Pitman, and Y. J. Dai. 2014a. Nitrogen and phosphorous limitations significantly reduce future allowable CO<sub>2</sub> emissions. *Geophysical Research Letters* 41:632–637.
- Zhang, X., and X. Cai. 2013. Climate change impacts on global agricultural water deficit. *Geophysical Research Letters* 40:1111–1117.
- Zhang, X., Y. Lei, and Y. Pang. 2014b. Tree mortality in response to climate change induced drought across Beijing, China. *Climatic Change* 124:179–190.
- Zhao, J., H. Hartmann, S. Trumbore, W. Ziegler, and Y. Zhang. 2013. High temperature causes negative whole-plant carbon balance under mild drought. *New Phytologist* 200:330–339.
- Zhao, M., and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329:940–943.
- Zhou, G., et al. 2014b. Substantial reorganization of

- China's tropical and subtropical forests: Based on the permanent plots. *Global Change Biology* 20:240–250.
- Zhou, G., C. Peng, Y. Li, S. Liu, Q. Zhang, X. Tang, J. Liu, J. Yan, D. Zhang, and G. Chu. 2013. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in southern China. *Global Change Biology* 19:1197–1210.
- Zhou, L., et al. 2014a. Widespread decline of Congo rainforest greenness in the past decade. *Nature* 509:86–90.
- Zhu, K., C. W. Woodall, S. Ghosh, A. E. Gelfand, and J. S. Clark. 2014. Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology* 20:251–264.
- Zimmermann, N. E., N. G. Yoccoz, T. C. Edwards, E. S. Meier, W. Thuiller, A. Guisan, D. R. Schmatz, and P. B. Pearman. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences USA* 106:19723–19728.
- Zscheischler, J., M. Reichstein, J. von Buttlar, M. Mu, J. T. Randerson, and M. D. Mahecha. 2014. Carbon cycle extremes during the 21st century in CMIP5 models: future evolution and attribution to climatic drivers. *Geophysical Research Letters* 41:8853–8861.
- Zscheischler, J., et al. 2013. A few extreme events dominate global interannual variability in gross primary production. *Environmental Research Letters* 9. doi: 10.1088/1748-9326/9/3/035001

## SUPPLEMENTAL MATERIAL

### APPENDIX A

#### *Forest vulnerability to hotter drought: observations from the Southwest USA*

Recent events in the mountainous landscapes of the Southwest USA (Arizona, New Mexico, and southern portions of Utah and Colorado) highlight the effects of hotter drought on forest stress, insect outbreaks, wildfire, and forest die-offs. Since ca. 2000 the Southwest has been subject to large increases in tree mortality in response to the combination of protracted drought and early 21st century warmth (Breshears et al. 2005, Williams et al. 2010, 2013, Allen 2015), as part of a broader sub-continental pattern of hotter drought that has been driving historically unprecedented insect outbreaks (Raffa et al. 2008) and wildfire (Westerling et al. 2014) in western North America. While past severe droughts are documented to have caused substantial tree mortality in the Southwest during the 1950s (Allen and Breshears 1998) and likely even as far back as the 1580s “megadrought” (Swetnam and Betancourt 1998), the recent hotter “global-change-type” drought (Breshears et al. 2005) has caused particularly pronounced tree mortality. High levels of tree mortality have been

observed across broad elevational and landscape gradients, from the mesic spruce-fir (*Picea-Abies*) forests above 3500 m elevation down through mixed-species forests of Douglas-fir (*Pseudotsuga*), aspen (*Populus*) and pine (*Pinus*) to the lowest woodlands of juniper (*Juniperus*) at 1500 m (Gitlin et al. 2006), with substantial dieback and mortality of still lower-elevation shrubs and grasses (C. D. Allen, *unpublished data*), and even riparian trees along some ephemeral watercourses during the peak drought stress periods of 2000–2004 and 2011–2013 (C. D. Allen, *personal observations*).

The Southwest USA has been a productive setting for a diverse range of tree mortality research that is providing insights into the linked roles of drought and heat stress in driving Southwest forest productivity and health, physiological thresholds of tree mortality, and forest disturbance processes (e.g., Breshears et al. 2005, 2009, Allen 2007, Adams et al. 2009, 2015, McDowell et al. 2011, Clifford et al. 2013, Garrity et al. 2013, Sevanto et al. 2014, Anderegg et al. 2015b, Limousin et al. 2015). Notable recent work by Williams et al. (2013) derived a forest drought-stress index (FDSI) for the Southwest region using a comprehensive tree-ring growth dataset

representing AD 1000–2007, determined by both warm-season temperature and cold-season precipitation. Substantial warming over the past 25 years has significantly amplified regional forest drought stress, likely to a large degree by increasing atmospheric vapor pressure deficits during the growing season months. Strong correspondence exists between FDSI and forest productivity, tree mortality, bark-beetle infestations, and wildfire in the Southwest (Williams et al. 2013), illustrating the powerful interactions among climate, land use history (livestock grazing, fire suppression), disturbance processes, and forest dynamics in this region (Allen 2015). After nearly a century of fire suppression, a wet period highly favorable to tree growth occurred from ca. 1978–1995 that supported maximal development of dense high-biomass forests in the Southwest, followed by the onset of warmer drought conditions that have driven historically extreme levels of drought-induced tree mortality, bark beetle outbreaks, and high-severity fires (Williams et al. 2010, 2014, Allen 2015). Tree rings document 2002 as the worst year for regional tree growth since at least AD 1000, due to hotter drought conditions (Williams et al. 2013). If regional temperatures increase as projected by climate models, the *mean* forest drought stress by the 2050s will exceed that of the most severe droughts in the past 1,000 years (Williams et al. 2013; cf. Cook et al. 2015), suggesting high vulnerability of current forests to extreme levels of tree mortality within just a few decades.

The observed emergence of extensive, ongoing, and diverse episodes of tree mortality and forest die-offs related to hotter droughts in the Southwest USA may be an early regional harbinger of broader forest vulnerability to hotter drought worldwide. Few scientists explicitly predicted the rapidity and broad extent of the forest changes that have occurred in the region over the past two decades. Indeed, note that if the only time window available with observations on Southwest forest growth and health was the favorable wetter years of the 1980s (Williams et al. 2013), the conclusion could be “what a great place to be a tree”—whereas today the continued existence of old-growth trees and historical forest ecosystems appears increasingly at risk in this region. Whether this region is particularly sensitive to tree mortality, given its climatology and

forest history, could be debated. Nonetheless, rapid recent changes in Southwest USA forests provide cautionary insights about the vulnerability of other wooded ecosystems globally, illustrating that tree mortality can escalate rapidly beyond historical levels once critical drought and heat stress thresholds are exceeded. Overall, a global perspective illustrates that similarly dramatic changes in forest growth, productivity, and mortality can (and do) occur abruptly and pervasively elsewhere in response to changes in climate drivers, as exemplified by recent tree mortality events linked to combinations of drought and heat events in all major forest biomes around the world (Fig. 2; Allen et al. 2010).

## APPENDIX B

### *The role of open access publication and emerging technologies in facilitating recent progress in tree mortality research*

Research on forest vulnerability to tree mortality from drought and heat stress has grown rapidly in recent years, aided in part by open access publication and emerging technologies; highlighting such advances is part of the general focus of this set of ESA Centennial articles. Widespread e-publication and electronic communication technologies have: (1) fostered the rapid development of regional, national, and global networks and collaborations of researchers in this topic area (e.g., DIRENet (<http://www7.nau.edu/mpcer/direnet/>), Allen et al. 2010, Choat et al. 2012, Büntgen et al. 2013, Zeppel et al. 2014, Doughty et al. 2015, Frank et al. 2015a, b, Hartmann et al. 2015, Sitch et al. 2015); (2) increased communication through new media (e.g., the interactive website corresponding with the 2014 release of the US National Climate Assessment <http://nca2014.globalchange.gov/>); (3) supported electronic archival publication of datasets, enabling subsequent extension and re-analysis of datasets (e.g., Breshears et al. 2009, McDowell 2011); and (4) led to increasing numbers of syntheses from widespread research activities and networks, ranging from tree-growth data from the International Tree-Ring Data Bank (ITBRD, <http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>) that enable broad-scale analyses of tree growth respons-

es to climate (e.g., Williams et al. 2013, van der Sleen et al. 2014, Martin-Benito and Pederson 2015) to large data syntheses from permanent forest plot demography and growth networks that address fundamental questions of relative forest growth versus mortality in an increasingly greenhouse world (Carnicer et al. 2011, Luo and Chen 2013, Brienen et al. 2015).

Emerging and improving technologies also are supporting recent progress in climate-induced tree mortality research. Many of the tools currently used to assess how trees die are decades old but still are being continuously refined, including measurements of growth via dendrometers, photosynthesis and respiration via infra-red gas analyzers, measurements of plant water potential with pressure chambers, and water use via sapflow. New techniques also are making major contributions to understanding tree mortality, such as distributed sensors that can evaluate how soil temperature changes with changes in canopy cover (Royer et al. 2012), phloem function sensors (Sevanto et al. 2014), on-line isotopic measurements (Hartmann et al. 2013), highly controlled chamber systems for experimental manipulations of both [CO<sub>2</sub>] (e.g., Quirk et al. 2013, Duan et al. 2014), and water availability (e.g., Limousin et al. 2012), and revolutionary “omics” advances that enable understanding the interplay between physiological responses and regulatory control during stress and mortality (reviewed in McDowell et al. [2011] and Thomas [2013]). Various emerging technologies have promise to provide breakthrough understanding of mortality processes, including improvements in our understanding of the roles of lipids as a storage reserve in trees (Hoch 2015) and micro-analysis of tree anatomy and physiological dynamics via imaging with nuclear magnetic resonance (NMR; Defraeye et al. 2014) and positron emission topography (PET; de Schepper et al. 2013). Observational capabilities of tree mortality are rapidly increasing as exemplified by globally-widespread forest inventory monitoring networks (e.g., Lewis et al. 2009, Anderson-Teixeira et al. 2015, Brienen et al. 2015, Malhi et al. 2015) and advances in airborne and satellite-based remote sensing techniques (e.g., Garrity et al. 2013, Hansen et al. 2013, Meddens and Hicke 2014, Asner 2015, McDowell et al. 2015). Ultimately, much of this work serves not

only to provide better fundamental understanding, but importantly, supports the predictive capability of next-generation models that are being developed to better simulate tree mortality (e.g., McDowell et al. 2013, Fisher et al. 2015).

## APPENDIX C

This appendix provides additional non-comprehensive review of diverse research findings implying lesser or greater vulnerability of trees to mortality from hotter drought, organized by six topical categories that are cross-walked to Tables 1 and 2: *Climate* (abbreviated in Tables 1 and 2 as CL), *Patterns* (PN), *Mechanisms* (MC), *Ecological Feedbacks* (EF), *Projections* (PJ), and *Management* (MT). This presentation considers a range of findings within each topical category, rather than working through the ten contrasting perspectives framework of the main text and Table 3. Additional studies are presented here that are not covered in the main text. Some points presented in the main text also are covered here for context.

### CLIMATE (CL)

#### *Observed and projected climate changes of relevance to tree mortality from drought and heat*

Observed and projected climate changes could indicate *lesser* (Table 1, “Climate” category) or *greater* (Table 2, “Climate” category) vulnerability of forests to mortality from hotter drought. Implying *lesser* vulnerability (Table 1, CL), arguably the greatest benefits of global climate change to forest growth and resilience are rising atmospheric CO<sub>2</sub> concentrations, and increases in growing season length in high-latitude and other cold regions from rising temperatures (IPCC 2014, Xia et al. 2015). Rising [CO<sub>2</sub>] benefits plants by increasing the essential C substrate available for photosynthesis, and simultaneously increases the ratio of CO<sub>2</sub> uptake to water lost (water-use efficiency; Ainsworth and Rogers 2007, Keenan et al. 2013). Additionally, increases in growing season length in high-latitude and other cold regions from rising temperatures could result in greater overall plant growth. Another factor suggesting lesser vulnerability is that increased evaporation of ocean water into a warmer

atmosphere should increase average atmospheric humidity and increase rainfall in some regions, partially buffering rising vapor pressure deficit (VPD) due to rising temperature (Held and Soden 2006), and supporting greater tree growth and resilience in water-limited regions (e.g., Liu et al. 2015a). Indeed, despite warming temperatures in recent decades, pan evaporation measurements indicate a global trend of declining atmospheric evaporative demand, largely attributed to declines in near-surface wind speeds (McVicar et al. 2012); such a trend suggests potential amelioration of forest drought stress from projected warming-driven increases in atmospheric moisture demand. Also, precipitation has been rising in some regions and globally overall (Chou et al. 2013, IPCC 2013), with continued increases projected for some regions of the world; this could promote larger on-site water stores for trees to survive droughts when they do occur. Increases in the proportion of precipitation from large events can somewhat compensate for decline in total precipitation amounts (Dorman et al. 2015b). Warming has markedly increased growing season length across extensive temperate and boreal regions (Richardson et al. 2013), promoting additional growth in many temperature-limited forests (Keenan et al. 2014, Xia et al. 2015). As a consequence of these atmospheric changes, overall forest growth and carbon storage in many locations has increased in recent decades (Baltantyne et al. 2012, Graven et al. 2013), as further documented below.

In contrast, other climatic studies (Table 2, CL) indicate *greater* levels of forest vulnerability to projected hotter drought conditions. An increase in drought frequency and duration is predicted for much of the globe as climate change progresses (IPCC 2013). There is both observational and model evidence of the ongoing global emergence of historically unprecedented large and rapid increases in global temperature this century (Diffenbaugh and Scherer 2011, IPCC 2013). Additionally, the area impacted by drought is both observed and projected to increase globally (Dai 2013). Even if the increased heating from global warming does not directly cause increases in drought frequency, hotter conditions will result in droughts intensifying more quickly once they do occur and generally

being more severe—the essence of “hotter drought” (Trenberth et al. 2014). Projected warming also is anticipated to reduce tropospheric relative humidity in the tropics and subtropics, in conjunction with a widening of the subsiding branches of the Hadley Cell, resulting in increased frequency of dry events in many geographic locations worldwide (Lau and Kim 2015)—observations show these predicted changes already emerging (Marvel and Bonfils 2013). Additionally, there is evidence of increasing drought severity caused by temperature rise and associated VPD in southern Europe and elsewhere (Vicente-Serrano et al. 2014). This is critical because nonlinear increases in atmospheric moisture demand (VPD) associated with hotter temperatures during drought are a key driver of forest physiological and ecological vulnerabilities to drought stress and increased mortality risk (e.g., Breshears et al. 2013, Eamus et al. 2013, Williams et al. 2013, Hart et al. 2014). When the effects of warmer temperature and greater VPD during drought are isolated from one another, model predictions highlight that it is the increased atmospheric moisture demand component that is most important in amplifying tree drought stress that could drive associated mortality (Eamus et al. 2013).

On longer time scales, the earth system is now moving into an altered regime of multi-decadal rates of climate warming that are unprecedented over at least the past 1,000 years (Smith et al. 2015), and perhaps over the past 65 million years (Diffenbaugh and Field 2013). Further, models project increasingly extreme precipitation (drought) and temperature (heat wave) events (IPCC 2012, 2013, Cai et al. 2014, 2015), including more frequent swings between opposite precipitation extremes from one year to the next (Cai et al. 2015), with an increased range between wet and dry season precipitation already observed (Chou et al. 2013). Recent extension of dryness-controlled areas of limited terrestrial carbon sequestration, driven by warming, already may be triggering a positive feedback that is further accelerating global warming by suppressing vegetation productivity in these areas (Wei et al. 2014). Finally, changes in tree cover can cause broad-scale ecoclimatic teleconnections, whereby vegetation change in one area affects not only regional climate but also climate and subsequent-

ly vegetation in another region or even another continent (Swann et al. 2012), including vegetation change associated with widespread forest die-off.

## PATTERNS (PN)

### *Observed spatial patterns of tree growth, forest stress and productivity, and drought- and heat-induced tree mortality and forest die-off*

Substantial research is being generated on spatial patterns of tree growth, productivity, and hotter-drought-induced tree mortality and forest die-off using diverse approaches and providing perspectives that sometimes differ markedly between study regions, methodologies, and time periods—ranging from implications of lesser (Table 1, “Patterns” category) to greater vulnerability (Table 2, “Patterns” category). Regarding lesser vulnerability, the development of spatially extensive networks of permanent forest plots, where individual trees are repeatedly measured through time for ecological or forestry purposes, provide direct field measurements on forest growth and mortality patterns that are beginning to span sufficient time (decades) to determine significant trends in tropical, temperate, and boreal regions (Pan et al. 2013). In some portions of the world, forests are observed to be growing as well as, or faster than, ever measured before (e.g., McMahon et al. 2010, Hember et al. 2012, Fang et al. 2014), particularly where water has not been limiting recently—consistent with predictions of strong CO<sub>2</sub> fertilization effects, and of the benefits of longer growing seasons in some colder regions (Pan et al. 2013, Keenan et al. 2014). For example, plot measurements have generally shown pan-tropical increases in forest growth and carbon storage in recent decades (Baker et al. 2004, Lewis 2006, Lewis et al. 2009).

In contrast, (Table 2, PN) findings of declines in forest growth and productivity are emerging in some regions due to episodic or growing drought and heat stress, particularly in historically hot or dry regions (Carnicer et al. 2011, Dorman et al. 2013), but also sometimes in wet or cool areas such as the Amazon (Brienen et al. 2015) and boreal forests (Chen and Luo 2015). Growth of most natural forests is water limited in

various ways (Gedalof and Berg 2010, Jenerette et al. 2012, Bernacchi and VanLoocke 2014). Recent work in the Amazon (Malhi et al. 2015) highlights that to accurately assess forest biomass cycling relationships with climate it is necessary to address the significant spatial and temporal variability in poorly understood processes such as carbon-use efficiency, allocation of net primary productivity (NPP), and biomass turnover times (i.e., mortality rates, rooting depths, and phenological patterns and drivers). From forests worldwide there is increasing evidence that bigger, taller trees are most vulnerable to drought stress and mortality in a warming world (Phillips et al. 2010, McDowell and Allen 2015, McIntyre et al. 2015).

Shifting focus to tree-ring data, aggregated networks allow geographically extensive syntheses of annually-resolved tree growth-climate relationships that can extend back centuries to millennia. These dendrochronological analyses confirm variability in regional growth trends and climate drivers (Gedalof and Berg 2010, Peñuelas et al. 2011, Silva and Anand 2013, Vicente-Serrano et al. 2014), ranging from observations implying lesser vulnerability (Table 1, PN) with historically-unprecedented surges in growth found in some boreal (Juday et al. 2015) and high-elevation temperate (Salzer et al. 2009) forests; to nearly stable tree growth in diverse tropical forest sites (van der Sleen et al. 2014); to observations suggesting greater vulnerability (Table 2, PN) with significant declines in tree growth attributed to greater drought/heat stress in many dry regions, including the Southwest USA (Williams et al. 2010, 2013), Mediterranean Europe (Tognetti et al. 2000) and North Africa (Touchan et al. 2011a), other parts of Europe (Lévesque et al. 2014), interior Asia (Liu et al. 2013), and boreal Canada (Girardin et al. 2014) and Alaska (Juday et al. 2015, Walker et al. 2015). A subset of global tree-ring chronologies, mostly boreal, shows a recent divergence of tree-growth responses to climate in the 20th and 21st centuries from previous historical patterns, due to a complex of changing climate/hydrological/soil/physiological drivers (D’Arrigo et al. 2008, Juday et al. 2015); this “divergence problem” further emphasizes the risk of sweeping global over-generalizations from tree-ring growth patterns. Studies of carbon isotopes from within

tree-rings also provide historical evidence regarding levels of tree water stress (e.g., McDowell et al. 2010) and widespread increases of intrinsic water-use efficiency without corresponding increased tree growth (Peñuelas et al. 2011, Silva and Anand 2013). Also implying greater vulnerability (Table 2, PN) are recent dendroclimatic studies that have increasingly linked warmer temperatures to poor tree growth and higher levels of forest drought stress (e.g., Williams et al. 2010, 2013, Girardin et al. 2014, Juday et al. 2015, Walker et al. 2015), with the most recent hot droughts appearing as the most severe relative to tree growth in some tree-ring records extending back for at least 800 years in North Africa (Touchan et al. 2011a), 1000 years in the Southwest USA (Touchan et al. 2011b, Williams et al. 2013), and 1200 years in California (Griffin and Anchukaitis 2014).

The development of networks of biogeochemistry flux tower sites (e.g., FLUXNET) and Free-Air CO<sub>2</sub> Enrichment (FACE) experiments have allowed ever-more detailed and broader-scale assessments of forest stand-scale photosynthesis, respiration, gross primary productivity, water-use efficiency, etc. in response to temperature and precipitation variability (e.g., Tang et al. 2014) in a global-change world of elevated CO<sub>2</sub> concentrations. Recent analyses highlight complicated and sometimes conflicting forest vegetation responses, including trends of alternating increasing and decreasing growth (Gatti et al. 2014), evidence for and against strong and persistent CO<sub>2</sub> fertilization effects (De Kauwe et al. 2014, Zaehle et al. 2014), and changes in water-use efficiency (Tang et al. 2014).

Rapid advancements in remote-sensing techniques (often in concert with advances in ground observations) provide increasingly high-resolution data on spatial and temporal patterns of global temperature and precipitation, drought severity (atmospheric moisture demand, soil moisture and associated plant water availability), water-use efficiency (Tang et al. 2014), forest growth and productivity (Hilker et al. 2014), and forest disturbance patterns (Espírito-Santo et al. 2014). Similar to patterns from ground observations, remote-sensing analyses show diverse responses to recent climate variability and change. Implying lesser forest vulnerability (Table 1, PN), many studies show widespread

“greening” and biomass accumulation (Jong et al. 2012, Pan et al. 2013), from uncut tropical moist forests (Liu et al. 2015a) to semiarid savanna ecosystems (Buitenwerf et al. 2012, Fensholt et al. 2012, Liu et al. 2015a), consistent with strong CO<sub>2</sub> fertilization paradigms, and perhaps in part through increases in growing season length (Keenan 2015, Xia et al. 2015). Remote-sensing (and confirming ground observations) also document substantial invasions, expansions, and densifications of woody vegetation in many regions, consistent with several hypotheses regarding the potential roles of: fire suppression (Andela et al. 2013); vegetation recovery since historical land clearing in regions from Mediterranean Europe (Lloret et al. 2012) and the eastern USA (Nowacki and Abrams 2014) to Russia and China (Liu et al. 2015a); and atmospheric drivers of greening in semi-arid landscapes from increased water-use efficiency with greater CO<sub>2</sub> concentrations (Buitenwerf et al. 2012) and wetter periods in some regions (Liu et al. 2015a).

Yet implying greater vulnerability (Table 2, PN), other remote-sensing work suggests CO<sub>2</sub> fertilization effects are starting to be limited by increasing drought and heat stresses, ranging from forests in boreal (Beck and Goetz 2011) and temperate (Ciais et al. 2005, Potter et al. 2012) regions to tropical forests in the Congo (Zhou et al. 2014a) and Amazon (Hilker et al. 2014) basins. More broadly there are globally widespread indications of slowing or declining forest growth in response to episodic drought and heat events (Zhao and Running 2010) as well as from chronic rises in heat-related drought stress with extensive zones of reduced NPP (Yi et al. 2014).

Finally, also implying greater vulnerability (Table 2, PN) growing interest in drought- and heat-related tree mortality issues has accompanied an overall increase in documentation of both increasing background tree mortality and forest die-offs in many regions globally (Fig. 2), with methods ranging from direct ground observations to synoptic remote-sensing (Allen et al. 2010, IPCC 2014). Studies from forest biomes in many areas show increased background tree mortality rates that have been linked to: (1) warmer temperatures that increase plant water stress (van Mantgem et al. 2009, Carnicer et al. 2011, Peng et al. 2011); (2) warmer temperatures that can amplify mortality from biotic agents



(Raffa et al. 2008, Logan et al. 2010, Das et al. 2013, Anderegg et al. 2015a); and (3) increased competition resulting from CO<sub>2</sub>-enhanced tree growth rates (Zhang et al. 2015, Doughty et al. 2015). Two emerging global patterns are noteworthy: (1) the most significant forest die-off events are associated with hotter droughts (i.e., “global-change-type” droughts; Breshears et al. 2005, Allen et al. 2010, Matusick et al. 2013), where the warming is thought to drive higher levels of forest drought stress (consistent with Williams et al. 2013); and (2) larger trees seem to be at greater risk of mortality from hotter drought (Nepstad et al. 2007, Phillips et al. 2010, Zhou et al. 2013, McDowell and Allen 2015, McIntyre et al. 2015). Comprehensive documentation of global forest health and definitive determination of tree mortality trends currently is lacking due to the absence of an adequate global monitoring system (Allen et al. 2010); however, the technical capability has now been demonstrated (Vogelmann et al. 2009, Hansen et al. 2013, Mascaro et al. 2014, Meddens and Hicke 2014, Asner 2015, McDowell et al. 2015)—what is lacking yet is the global vision and will to support such a worldwide monitoring system (Mascaro et al. 2014).

Overall these wide-ranging studies document highly variable patterns and trends in tree growth, forest productivity, and tree mortality. Unprecedented strong forest growth in some portions of the world implies lesser vulnerability and is consistent with predictions of strong CO<sub>2</sub> fertilization effects and of the benefits of longer growing seasons in some colder regions, particularly where water has not been limiting recently. In contrast, declines in forest growth and productivity, and also widespread increases in background tree mortality and forest dieoff, are emerging in many regions due to growing drought and heat stress—often in historically hot dry regions where warming temperatures are increasing drought stress, but also occurring in cooler and wetter areas such as boreal forests and the Amazon. These latter studies consistently imply greater forest vulnerability to hotter drought. The current broad range of observed forest responses to climate variability in the Amazon, and the associated range of interpretations about the relative vulnerability of these forests to drought and heat stress, is emblematic

of the ongoing challenges in sorting out seemingly conflicting observations using diverse methodologies.

## MECHANISMS (MC)

### *Physiological, morphological, and genetic mechanisms and processes that affect tree vulnerability to drought- and heat-induced mortality*

Research has proliferated recently on diverse physiological, morphological, and genetic mechanisms and processes that affect tree vulnerability to drought and heat mortality, yielding findings that could imply either lesser vulnerability (Table 1, “Mechanisms” category) or greater vulnerability (Table 2, “Mechanisms” category). Beginning with physiological studies that imply lesser vulnerability (Table 1, MC), there are many physiological mechanisms at the tissue and stand-scales that may partially compensate for rising temperatures, drought stress, and associated impacts on mortality. These mechanisms are generally not included in process models, which may lead to a conservative bias in regards to simulation of forest vulnerability to climate change. At the plant scale, acclimation and adaptation is known to occur for a wide range of physiological processes (Mencuccini 2003), such as: down-regulation of respiration (e.g., Atkin and Tjoelker 2003); upregulation of photosynthesis (e.g., Chaves et al. 2009); changes in carbon allocation to plant chemical defenses (Herms and Mattson 1992); maintenance of positive C balances by coordination of nonstructural carbohydrate carbon reserves to meet demand even when stress reduces photosynthate C supply (Klein et al. 2014b); shifts in embolism resistance (e.g., Kolb and Sperry 1999); and xylem refilling to reverse embolism (Klein et al. 2014a). Trees have many mechanisms to avoid drought stress (Klein et al. 2014a), ranging from leaf-scale to whole-tree level, including phenological adjustment of growth processes to avoid drought periods (Klein et al. 2013, Adams et al. 2015).

There are many ways in which hotter temperatures, particularly if they accompany drought, have negative biological effects that imply greater vulnerability of trees to mortality under hotter drought (Table 2, MC). One of the most important impacts of rising temperature is upon

VPD and subsequent impacts on transpiration and photosynthesis (Eamus et al. 2013). VPD is nonlinearly dependent upon temperature such that a small rise in temperature causes a relatively larger rise in VPD (discussed in the context of tree mortality in Breshears et al. 2013). This induces greater water loss through the stomata and from the soil surface, increasing water stress. The risk of hydraulic failure, or the loss of water transport capacity, is thus enhanced by rising VPD (McDowell et al. 2008). To compensate for this greater risk of hydraulic failure, plants typically close their stomata to limit water loss; however, this comes at the cost of reduced photosynthesis (Martínez-Vilalta et al. 2002) and increased risk of carbon starvation (the process of failure to maintain metabolism and defend against biotic agent attacks; McDowell et al. 2011). Thus, rising temperature increases the risk of both hydraulic failure and carbon starvation. Additionally, warmer droughts increase the risk of mortality through a myriad of additional mechanisms that can accelerate the processes of hydraulic failure and carbon starvation, or even bypass these mechanisms. Respiration is nonlinearly (positively) related to temperature (Atkin and Tjoelker 2003), potentially resulting in greater consumption of energy stores at higher temperatures in the absence of adequate down-regulation (acclimation) of respiratory biochemistry. This should accelerate the carbon starvation process, and indeed it has been shown that respiration rates are higher, and death occurs more rapidly, in experimental warm-drought scenarios (e.g., Adams et al. 2009).

Regarding phenotypic plasticity and morphological adjustments, a variety of studies support lesser vulnerability to mortality (Table 1, MC). Trees compete for light and growing space during favorable climate conditions when water is not limiting, investing in above-ground leaf and stem tissues and building up high levels of live biomass, but under drought and heat stress individual trees and forest communities can adapt through diverse morphological responses at multiple time scales (Nicotra et al. 2010, Richter et al. 2012, Bussotti et al. 2015). Note that these morphological adjustments are closely interrelated with the physiological responses discussed above (Mencuccini 2003). Such phenotypically plastic morphological adjustments can

include rapid short-term reductions in leaf area through early senescence or partial dieback of stems and leafy canopies (Rood et al. 2000, Mencuccini 2003, Ciais et al. 2005, Carnicer et al. 2011, Limousin et al. 2012, Filewod and Thomas 2014), which can be followed by post-dieback resprouting of woody tissues and leaves from stems or roots (Zeppel et al. 2014). Other phenotypically plastic responses include longer-term growth-mediated transformations of hydraulic architecture, wood density (Britez et al. 2014), and overall tree morphological architecture, emerging through altered relative growth investments in the size, number, and longevity of leaves, stems, roots, and mycorrhizal symbionts (Nicotra et al. 2010, Limousin et al. 2012, Zanetti et al. 2015). These morphological compensatory responses all lessen vulnerability to tree mortality, so for these compensatory responses the issue of lesser versus greater vulnerability largely hinges on whether these are sufficient to overcome the risk factors listed in other categories.

Regarding genetic variation, lesser vulnerability can also be implied (Table 1, MC) from studies documenting drought and heat resistance within tree species populations at multiple spatial scales (local, landscape, whole population), allowing survival of pre-adapted individuals in the short term, which also promotes natural selection of genotypes better adapted to survive warmer and drier future conditions (Gutschick and BassiriRad 2003, Alberto et al. 2013, Alfaro et al. 2014, Liepe 2014). Tree species have optimal climate zones, such that populations in the colder portions of their distributions are expected to have significant genetic acclimative capacity for warmer temperatures, whereas populations from warmer range-limit portions of the species' distribution are generally expected to be more vulnerable to stress from warming climate (Rehfeldt et al. 2002, 2004, 2014). Tree populations from warmer outlying localities can be better adapted genetically to handle drought conditions (Chen et al. 2010, Carsjens et al. 2014), although they may become subject to reduced genetic diversity at such "trailing edge" sites (Borovics and Mátyás 2013). Overall, higher levels of genetic diversity foster adaptive responses to climate change stresses (Jump et al. 2009a, Harter et al. 2015), including drought and heat stress (Mátyás et al. 2009, Sthultz et al. 2009).

Nonetheless, greater vulnerability (Table 2, MC) is implied for those cases where large rapid climate changes exceed evolutionary tipping points (Botero et al. 2015).

## ECOLOGICAL FEEDBACKS (EF)

### *Ecological factors and feedbacks at forest, landscape, and earth system scales that affect forest vulnerability to drought- and heat-induced tree mortality*

There also are many ecological factors and feedbacks at forest, landscape, and earth system spatial scales that affect tree vulnerability to drought and heat mortality. Again, several of these imply lesser vulnerability of forests to hotter drought (Table 1, EF). Forests with higher levels of tree diversity have more species options to respond to both climate stresses and post-disturbance opportunities, resulting in relatively incremental adjustments at the forest scale (Fauset et al. 2012, Peters et al. 2015). In addition, more diverse forests are less likely to experience mortality events driven by outbreaks of biotic agents, whereas low diversity systems (e.g., monocultures) can be far more susceptible (Dyer and Letourneau 2013). In some ecosystems, climate change may actually hurt the insect pest agents that attack trees either through direct climate impacts on population growth or through increases in the abundance of predators which control those agents (Hicke et al. 2006, Raffa et al. 2008, Jamieson et al. 2012). At landscape scales the diversity of topographic (Adams et al. 2014), soil (Peterman and Waring 2014, Twidwell et al. 2014, Dorman et al. 2015a), and hydrological (Silvertown et al. 2015) settings and microsites provides relatively buffered refuge locales where trees have cooler-moister conditions to survive hot drought stresses (e.g., Allen and Breshears 1998), as well as favorable sites to recover more readily after mortality events. Such landscape diversity can allow “climate relict” populations of trees to persist as climate conditions become less favorable (Hampe and Jump 2011). Note, however, that “micro-refugia” have limited buffering capacities (Hylland et al. 2015), implying greater vulnerability to increasingly severe hotter droughts (Table 2, EF).

Lesser vulnerability (Table 1, EF) is also

suggested by a number of forest-scale “stabilizing processes” in response to tree mortality which can support the retention and recovery of original species or of new species, thereby buffering the system from a complete loss of forest (Lloret et al. 2012). Tree mortality is often strongly enhanced by competition for growth-limiting resources (water, light, nutrients; Ruiz-Benito et al. 2013), so forest-scale canopy defoliation, dieback, and elevated whole-tree mortality rates reduce competition between surviving trees, thereby reducing stress and limiting further mortality (Lloret et al. 2012), while surviving plants can facilitate new regeneration (Lloret and Granzow-de la Cerda 2013, Kane et al. 2015). Meanwhile, forests have strong effects on local climate by modulating evapotranspiration and albedo (Peng et al. 2014), with tropical and temperate forests cooling the local climate (Li et al. 2015); reductions in forest cover in these biomes could be expected to amplify climate warming. Changes in forest densities and canopy cover can have both positive and negative feedbacks on tree mortality processes by altering understory microclimates. For example, increased forest densities and canopy cover in European and eastern USA temperate forests moderate the impacts of macroclimatic warming on understory microclimates, fostering resilience of forest understory plants, including young trees (De Frenne et al. 2013)—whereas in tropical moist forests of the Amazon, reductions in tree canopy cover from drought mortality (as well as by timber harvest or fire) causes more open, drier understory conditions that can lead to greater drought stress and increasingly flammable fuel conditions (Brando et al. 2014). Alternatively, in some temperate coniferous forest types, moderate levels of drought-related tree mortality can sometimes reduce risks of high-severity stand-replacing fire by reducing ladder fuels, increasing the height-to-live-crown and canopy spacing, and decreasing crown bulk density, similar to mechanical forest thinning treatments (e.g., Hicke et al. 2012b).

For a general review of the effects of increasing atmospheric [CO<sub>2</sub>] and changing climate on the dynamics of forest recovery after disturbances, including drought-induced tree mortality, see Anderson-Teixeira et al. (2013).

Also implying lesser vulnerability at broader

spatial scales (Table 1, EF), tree populations in the past naturally have responded to environmental changes with adjustments in their geographic distributions (Corlett and Westcott 2013). With global warming the expectations are for range retractions through mortality at the warmer “trailing edge” margins of species distributions, with range extensions through migration anticipated at the colder “leading edge” (Hampe and Jump 2011). However, implying greater vulnerability (Table 2, EF), in some regions tree populations do not appear to be tracking recent climate changes fully or at all (Feeley et al. 2011, 2013, Zu et al. 2013, Fensham et al. 2014, Nowacki and Abrams 2014; but see Pederson et al. 2014a), and overall there are questions about whether natural tree migration rates will be fast enough to keep up with projected rates and magnitudes of climate change (Feeley et al. 2012, Corlett and Westcott 2013, IPCC 2014, Zhu et al. 2014), with habitat fragmentation a growing impediment to species migration and colonization (Haddad et al. 2015).

Implying lesser vulnerability at global scales (Table 1, EF), biome-scale resilience in water-use efficiency to interannual precipitation variability has been observed (Ponce-Campos et al. 2013), which can somewhat buffer hotter drought effects. There also are reasons to doubt the existence of global tipping points related to vegetation change and atmospheric dynamics (e.g., Brook et al. 2013). Further implying greater vulnerability (Table 2, EF), however, it is likely that prolonged droughts could exceed hydroclimate thresholds and trigger considerable vegetation mortality (Ponce-Campos et al. 2013). Additionally, recent work (Vicente-Serrano et al. 2013, 2014) finds that forest growth declines occur in humid biomes in response to shorter-duration drought stress relative to forests in more semi-arid and subhumid conditions where longer-duration drought drives growth declines; these biome-level differences likely reflect the relative drought vulnerability of the dominant tree species in current forest communities that have been subject to differing durations and severities of historical drought stress.

Drought and heat also have major direct and indirect amplifying effects on multiple other tree-killing disturbance processes, including fire (Pechony and Schindell 2010, Flannigan et al.

2013, Williams et al. 2014, Jolly et al. 2015), insect outbreaks (Raffa et al. 2008, Weed et al. 2013), and pathogens (Desprez-Loustau et al. 2006). These climate-related disturbances, sometimes also including other human disturbances such as logging or fire ignitions, can interact in “disturbance complexes” (McKenzie et al. 2008), often synergistically amplifying tree mortality (Allen 2007, van Mantgem et al. 2013, Brando et al. 2014). Individually, many of these forest disturbance processes involve nonlinear threshold responses to drought and heat drivers (Williams et al. 2014, Anderegg et al. 2015a) at multiple spatial scales, from local and regional (Allen 2007, Brando et al. 2014) to global (Hughes et al. 2013, IPCC 2014). In addition, cover loss of tropical moist forest can have significant feedback effects on local and regional climate (amplifying both drought and heat; Brando et al. 2014, Lawrence and Vandecar 2014), with emerging indications of inter-hemispheric teleconnections linking forest cover change and climate between North and South America (Swann et al. 2012). Indeed, there is significant concern about the potential existence of forest-related tipping points at global scales in response to projected climate changes (Lenton et al. 2008, Barnosky et al. 2012, Scheffer et al. 2012b, Hughes et al. 2013, IPCC 2014). In particular relative to forests, if growing drought and heat stresses reduce forest productivities and cause massive forest die-offs, there are concerns that forests, which currently sequester about 25% of the human atmospheric carbon emissions annually (Pan et al. 2013), could switch to become a net source of carbon back to the atmosphere (Bonan 2008, Kurz et al. 2008, Phillips et al. 2009). However, overall ecosystem carbon dynamics also depend on post-die-off soil respiration responses that strongly affect net release of forest-sequestered carbon back to the atmosphere (e.g., Moore et al. 2013).

## PROJECTIONS (PJ)

### *Broad-scale modeled projections of forest growth, productivity, and vulnerability to drought- and heat-induced tree mortality with climate change*

Regarding broad-scale modeled projections of vegetation change, studies also vary regarding support for lesser or greater levels of vulnerabil-

ity of forests to hotter drought. Implying lesser vulnerability (Table 1, PJ), process models of vegetation responses to projected climate (e.g., DGVMs) generally project increasing future forest growth and resilient forest carbon stocks (e.g., Huntingford et al. 2013, Sitch et al. 2015). Most of the models include substantial positive effects of CO<sub>2</sub> fertilization and associated increased water-use efficiency, reflecting core physiological knowledge (e.g., Ainsworth and Rogers 2007, Arora et al. 2013, Keenan et al. 2013). For example, recent modeling work "... indicates a much lower risk of Amazon forest dieback under CO<sub>2</sub>-induced climate change if CO<sub>2</sub> fertilization effects are as large as suggested by current models" (Cox et al. 2013). Also, note that many of the compensatory physiological mechanisms reviewed above generally are not included in these process models of forest responses to climate change, which could lead to overestimating simulated forest vulnerability to projected drought and heat stresses (e.g., Wythers et al. 2013).

In contrast, without strong CO<sub>2</sub> fertilization processes, models would tend to show vegetation "browning" sooner rather than "greening" in response to future warming, implying greater vulnerability of forests (Table 2, PJ). There are many questions about the actual strength and duration of CO<sub>2</sub> fertilization effects in varying "real world" situations (e.g., Peñuelas et al. 2011). Additionally, realistic projections of future tree mortality response to anticipated climate changes likely are greatly limited currently because few DGVMs or earth system models mechanistically represent physiological tree mortality processes (McDowell et al. 2011; cf. Betts et al. 2015). Further, other important tree-killing disturbance processes (fire, insect outbreaks, diseases) currently are missing or poorly represented in DGVMs (Lindner et al. 2014, Sitch et al. 2015). Each of these forest disturbance processes involves nonlinear threshold responses to drought and heat drivers (e.g., Williams et al. 2014, Anderegg et al. 2015a) that are difficult to realistically represent individually in process models, much less collectively, despite their importance as interactive disturbance complexes in real-world forest dynamics (Allen 2007, McKenzie et al. 2008). The incomplete and uneven inclusion of realistic mortality processes

likely is one major reason that tests of diverse vegetation models result in poor performance when predicting change in vegetation carbon storage from elevated [CO<sub>2</sub>] versus FACE experimental data (De Kauwe et al. 2014, Zaehle et al. 2014). Improving the representation of mechanistically realistic tree mortality processes in DGVMs increasingly is acknowledged as an important strategy to more accurately predict the tree mortality rates (i.e., "carbon turnover times" [Brienen et al. 2015] or "woody biomass residence times" [Galbraith et al. 2013, Malhi et al. 2015]) needed to better project future changes in ecosystem biomass (e.g., Sitch et al. 2015); however, pursuing greater realism of tree mortality processes drives associated increases in model complexity and more challenging "requirements for model specification using data that are difficult to acquire" (Joetzjer et al. 2014). As models incorporate more realistic mortality functions, some are showing greater vulnerability of forests to mortality from projected future hotter droughts (e.g., Jiang et al. 2013, Tague et al. 2013, Vicente-Serrano et al. 2015). Another significant limitation of most current DGVMs is inadequate representation of the effects of extreme climatic events on vegetation (Zimmermann et al. 2009, Kitzberger 2013, Reyer et al. 2013, Zhang and Cai 2013, Bahn et al. 2014, Niu et al. 2014, Orsenigo et al. 2014), particularly including extreme droughts and heat waves which drive major pulses of forest die-off that can filter out particular and significant components of tree populations and forest species compositions via rapid mortality.

Another modeling challenge may be inherent when using localized experimental results (e.g., CO<sub>2</sub> enrichment or drought mortality experiments) to scale up from individual trees to earth system models, as there is evidence of "a general trend for the magnitude of the responses to decline with higher-order interactions, longer time periods and larger spatial scales" (Leuzinger et al. 2011); if so, DGVMs may overestimate both positive and negative impacts of climate change. Meanwhile, the current absence or inadequate representation in DGVMs of many ecologically-fundamental forest disturbance processes that generally are amplified by warmer and drier conditions (e.g., drought-induced tree mortality, fire, insect attacks), suggests that

current broad-scale model projections of forest vulnerability to hotter droughts may be too conservative.

In addition to process-based mechanistic models of climate-induced tree mortality, a variety of other modeling approaches instead are based upon empirical relationships between climate/environmental factors and tree mortality or forest biome transitions, here lumped as “empirical models” (Adams et al. 2013). Widely used examples are “climate-envelope” species-distribution models based upon observed geographic distributions of individual tree species (Jackson et al. 2009, Iverson et al. 2011, Rehfeldt et al. 2012, Iverson and McKenzie 2013) or forest biomes (Gonzalez et al. 2010); note Feeley (2015) addresses two major unresolved assumptions that underlie these climate envelope models. If solid experimental and observational data could be used to determine climate envelopes that reflect mortality in response to extreme events (rather than envelopes based on species presence as related to mean climate conditions), climate envelopes potentially could be powerful predictive tools. Other empirical models of tree mortality risk include: forest demography models (e.g., Wunder et al. 2008); climate-growth-mortality response models (Williams et al. 2010, Williams et al. 2013, Macalady and Bugmann 2014, Huang et al. 2015); various models of tree mortality as a function of climate ranging from Australia (Mitchell et al. 2014) to Arizona (Clifford et al. 2013) and California (Das et al. 2013); a hybrid empirical-process model of a climatic water deficit threshold for *Populus tremuloides* mortality in Colorado USA (Anderegg et al. 2015b); and a model based upon joint climate-competition interactions for eastern US forests (Clark et al. 2014).

## MANAGEMENT (MG)

### *Management actions relative to forest vulnerability to drought- and heat-induced tree mortality*

In general, land management has large earth system effects, including significant feedback interactions with climate (IPCC 2014, Luyssaert et al. 2014). With growing recognition of climate change risks to forests, there has been increasing interest in the potential for management actions to reduce vulnerability of trees to mortality from

drought and heat effects (Table 1, MG). At a broad level, a practical conceptual framework to manage forests in the face of climate change uncertainties includes supporting a multitude of flexible approaches utilizing incremental and reversible actions and an emphasis on adaptive learning (Millar et al. 2007). Three major categories of adaptation options include forest management adaptation actions, new approaches and tools for decision-making with stronger researcher-practitioner partnerships, and policy arrangements to support adaptation in forest management (Keenan 2015). Other recent overviews of adaptation options to address forest drought and heat stresses from climate change address similar themes (e.g., for Europe see Lindner et al. 2010, Kolström et al. 2011, Hlásny et al. 2014, Lindner et al. 2014). Five key management actions to address hotter drought stressors on forests (presented relative to European forests but potentially much more widely applicable) include: use resilient plant species; increase forest carbon storage; manage disturbance impacts; manage forests as renewable energy resources; and value and marketize forest ecosystem benefits and services to society (Fares et al. 2015). Another strategy is to start incrementally with historically proven management practices, and use adaptive management learning to gradually utilize more novel transformational practices as needed to accompany anticipated more extreme climate change progresses (Pinkard et al. 2014). Numerous studies support various historically-proven forest harvesting and thinning practices to improve the resilience of post-treatment tree mortality from drought and heat stresses by directly reducing resource competition and increasing tree growth, vigor, and defenses against pests (e.g., D’Amato et al. 2013, Giuggiola et al. 2013, Yaussy et al. 2013, Tarancón et al. 2014). Management can change species composition and genetics of tree populations to promote resistance to hotter droughts by selective cutting, planting (including assisted migration beyond historical ranges; Williams and Dumroese 2013), and breeding. To maintain valued ecosystem services (Bonan 2008), forest management can target retaining more water onsite to ameliorate forest vulnerability despite growing stress from warmer global-change-type droughts (Grant et al. 2013). There

also are opportunities to shift traditional perspectives and work with the new biotic assemblages which are necessarily emerging in response to changing environmental conditions in the Anthropocene, “applying adaptive conservation to all human activities”, including forest management (Lugo 2015). Fitting local actions into a global perspective on global change risks, Scheffer et al. (2015) suggest “positive, action-oriented framing of a safe operating space for the world’s iconic ecosystems” such as the Amazon rainforest, to muster societal support to manage local stressors to promote ecological resilience at local-to-global scales (cf. Steffen et al. 2015). Networking within a region also could buffer against impacts of forest die-off (Breshears et al. 2011), with effectiveness depending on the degree of patchiness (López-Hoffman et al. 2013). Collectively, then, many management actions have been identified that could contribute to reducing forest vulnerability to hotter drought.

The effectiveness of potential management responses, however, also depends on the relative expression of many other risk factors that drive

greater tree vulnerability (Table 2, MC, EF). As considered throughout this article, the diverse impacts of hotter drought could overwhelm the effects of forest management actions. For example, one key management strategy, forest thinning, likely becomes insufficient to buffer trees against mortality when droughts become severe enough (Williams et al. 2013), just as it may be insufficient to prevent wildfire spread under hotter drought conditions (Tarancón et al. 2014). As another example, sustaining historical forests through management of the genetics of native tree populations depends on genetic variation being sufficiently large to buffer against hotter drought events, which generally is uncertain currently. Overall, today’s forests inevitably will become more vulnerable to amplified tree mortality if climate warming proceeds to extreme enough levels to drive effects of the diverse risk factors associated with hotter drought (Table 2) to exceed the compensatory capacities of the various lesser vulnerability factors (Table 1), including the mitigating potential of management actions.