

## Research review

# Tree mortality from drought, insects, and their interactions in a changing climate

Author for correspondence:

William R. L. Anderegg

Tel: +1 970 739 4954

Email: [anderegg@princeton.edu](mailto:anderegg@princeton.edu)

Received: 20 November 2014

Accepted: 23 April 2015

**William R. L. Anderegg<sup>1</sup>, Jeffrey A. Hicke<sup>2</sup>, Rosie A. Fisher<sup>3</sup>, Craig D. Allen<sup>4</sup>, Juliann Aukema<sup>5</sup>, Barbara Bentz<sup>6</sup>, Sharon Hood<sup>7</sup>, Jeremy W. Lichstein<sup>8</sup>, Alison K. Macalady<sup>9</sup>, Nate McDowell<sup>10</sup>, Yude Pan<sup>11</sup>, Kenneth Raffa<sup>12</sup>, Anna Sala<sup>7</sup>, John D. Shaw<sup>13</sup>, Nathan L. Stephenson<sup>14</sup>, Christina Tague<sup>15</sup> and Melanie Zeppel<sup>16</sup>**

<sup>1</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, USA; <sup>2</sup>Department of Geography, University of Idaho, Moscow, ID 83844, USA; <sup>3</sup>National Center for Atmospheric Research, Boulder, CO 80305, USA; <sup>4</sup>US Geological Survey, Fort Collins Science Center, Jemez Mountains Field Station, Los Alamos, NM 87544, USA; <sup>5</sup>National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93117, USA; <sup>6</sup>USDA Forest Service, Rocky Mountain Research Station, Logan, UT 84321, USA; <sup>7</sup>Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA; <sup>8</sup>Department of Biology, University of Florida, Gainesville, FL 32611, USA; <sup>9</sup>School of Geography and Development, University of Arizona, Tucson, AZ 85712, USA; <sup>10</sup>Earth and Environmental Sciences Division, Los Alamos National Lab, Los Alamos, NM 87545, USA; <sup>11</sup>Northern Research Station, US Forest Service, Newtown Square, PA 19073, USA; <sup>12</sup>Department of Entomology, University of Wisconsin, Madison, WI 53706, USA; <sup>13</sup>Rocky Mountain Research Station, US Forest Service, Ogden, UT 84401, USA; <sup>14</sup>US Geological Survey, Western Ecological Research Center, 47050 Generals Highway No. 4, Three Rivers, CA 93271, USA; <sup>15</sup>Bren School of Environmental Science and Management, University of California – Santa Barbara, Santa Barbara, CA 93106, USA; <sup>16</sup>Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

## Summary

Climate change is expected to drive increased tree mortality through drought, heat stress, and insect attacks, with manifold impacts on forest ecosystems. Yet, climate-induced tree mortality and biotic disturbance agents are largely absent from process-based ecosystem models. Using data sets from the western USA and associated studies, we present a framework for determining the relative contribution of drought stress, insect attack, and their interactions, which is critical for modeling mortality in future climates. We outline a simple approach that identifies the mechanisms associated with two guilds of insects – bark beetles and defoliators – which are responsible for substantial tree mortality. We then discuss cross-biome patterns of insect-driven tree mortality and draw upon available evidence contrasting the prevalence of insect outbreaks in temperate and tropical regions. We conclude with an overview of tools and promising avenues to address major challenges. Ultimately, a multitrophic approach that captures tree physiology, insect populations, and tree–insect interactions will better inform projections of forest ecosystem responses to climate change.

*New Phytologist* (2015) **208**: 674–683

doi: 10.1111/nph.13477

**Key words:** biosphere–atmosphere feedbacks, carbon cycle, disturbance, dynamic global vegetation model, trophic interactions.

## Introduction

Forests cover *c.* 30% of the globe's land surface area, provide numerous ecosystem services to human societies, and play a central role in global biogeochemical cycles (Bonan, 2008). Yet the future of forest ecosystems given expected changes in climate and other environmental drivers is uncertain. Warming and drought,

sometimes co-occurring with insect outbreaks, have been linked to tree mortality in many regions, and future changes in climate are expected to drive more extensive, severe, or frequent tree mortality events (Allen *et al.*, 2010). Forest mortality can have manifold consequences for biodiversity, ecosystem function and services, and feedbacks to climate change through biophysical effects and loss of carbon sinks (Adams *et al.*, 2010; Anderegg *et al.*, 2013). The

mechanisms that lead to forest mortality are complex and include plant physiological responses to climate, climate influences on insect pests and pathogens, and their interactions. Efforts to model climate-driven forest mortality, however, most often focus on tree physiological responses to drought (Tague *et al.*, 2013; Anderegg *et al.*, 2015) and, very rarely, on tree responses to insect attack (Dietze & Matthes, 2014), but no model exists that incorporates both drought and insects and their interaction.

Approaches to modeling drought-induced tree or forest mortality typically define drought from an ecosystem water-use perspective, using such measures as an extended period of above-average climatic water deficit, that is, unusually large or persistent excess of water demand by evaporation and transpiration relative to supply. A rapidly evolving plant physiology literature that examines tree responses to drought and how these can lead to tree mortality provides a basis to incorporate the effects of drought on trees in models. Research on tree responses focuses on failure of the hydraulic system to conduct water (Anderegg *et al.*, 2012b; Nardini *et al.*, 2013; Urlin *et al.*, 2013) and reductions in available carbohydrates (e.g. O'Brien *et al.*, 2014).

Insect outbreaks are often driven by drought, which stresses host trees (Raffa *et al.*, 2008), but also by many other factors. Temperature directly affects insects through developmental rates and survival that drive population success (Regniere & Bentz, 2007; Powell & Bentz, 2009; Weed *et al.*, 2013). Characteristics of host trees, such as abundance, density, size, and physiology, and their spatial pattern across the landscape, are known to influence the capacity for insect population growth and spread (Raffa *et al.*, 2008). Community associates (e.g. natural enemies and symbiotic associates) influence population outbreaks and subsequent tree mortality and are also affected by climate (Hajek, 1999; Régnière & Nealis, 2007; Raffa *et al.*, 2008; Six, 2013). Clearly, the interaction of drought and insects may lead to increased insect populations, with disproportionate consequences for tree mortality that may not be accounted for by drought or insects alone.

While mechanistic and conceptual models of insect population dynamics (Dietze & Matthes, 2014; Powell & Bentz, 2014) and ecosystem carbon cycling in response to climate (Fisher *et al.*, 2010; Powell *et al.*, 2013; Tague *et al.*, 2013) have been used to estimate forest mortality, a key question is: how much detail in drought-induced tree physiological responses as well as representation of insect outbreaks that respond to both climate and host (tree) condition is needed in models to predict mortality in a changing climate?

In this paper, we argue that an integrated approach that considers both drought and insects is needed to accurately predict forest dynamics in a changing climate. We first present a framework that provides conceptual models of drought, insects, and their interactions that can serve as guides for implementing a fully coupled insect–drought physiology model of tree mortality. We then briefly summarize the mechanisms by which plants respond physiologically to drought. We further illustrate the mechanisms by which two major categories of insects, bark beetles and defoliators, kill trees, and show the linkages between insects and drought. Our framework suggests a continuum of forest mortality drivers, from mortality mostly dominated by drought effects on tree physiology independent of insects, to mortality dominated by insect dynamics

independent of drought. We highlight the measurements that might contribute to identifying where on this spectrum a given mortality event occurs, and identify events where both insects and plant drought response must be considered. Finally, we review the evidence for cross-biome patterns in the relative importance of insect- and drought-triggered mortality and highlight promising avenues for future research.

## Partitioning the roles of drought, insects, and their interactions in recent tree mortality

The coupling between drought and insect outbreaks in many past events suggests that a simple approach for including the effects of insects might be based on drought metrics. However, this approach is often overly simplistic. We posit that it is critical to separate and understand the relative contribution of insects and drought tree responses when: (1) insect and tree physiology exhibit different responses to climate drivers (e.g. winter warming is likely to have a disproportionate effect on overwintering insect population dynamics (e.g. Bentz *et al.*, 2010) relative to their host trees); (2) nonlinear thresholds can be passed where drought processes can favor initial insect population increments but thereafter no longer drive tree mortality (e.g. populations of aggressive bark beetles rely on stressed trees at low beetle densities, but at high beetle densities healthy trees are killed; Raffa *et al.*, 2008); or (3) interactions between insects and tree physiology lead to nonadditive effects in tree mortality rates (e.g. moderate (but nonlethal) drought can make trees more vulnerable to dying from defoliation (often nonlethal alone) or more susceptible to subsequent lethal attack by wood borers, secondary bark beetles, and latent pathogens; Davidson *et al.*, 1999; Wallin & Raffa, 2001; Muilenburg & Herms, 2012).

We show later that one or more of these three cases are met for multiple major mortality events affecting millions of hectares of forest in western North America (e.g. *Pinus contorta* and *Pinus edulis*). Partitioning of the relative contribution of insects and host drought is useful for separating causalities from correlations and to understand and predict these large-scale mortality events in a changing climate.

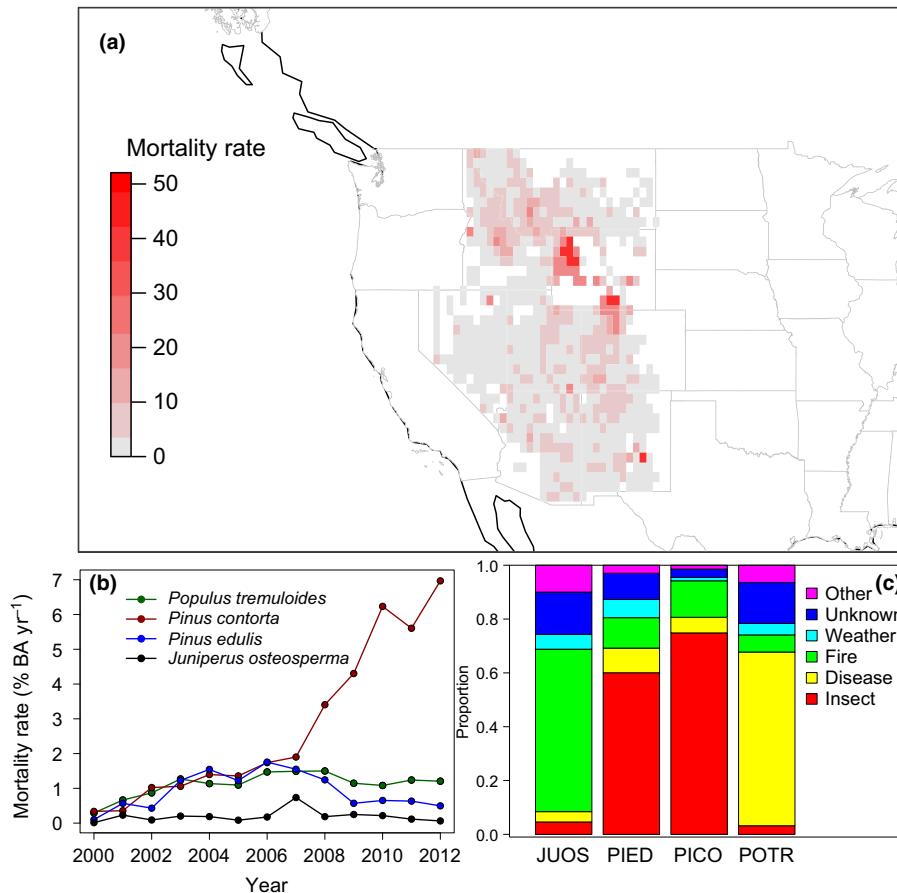
Although existing broad frameworks include drought, insects, and their interactions in driving tree mortality (e.g. Manion, 1981; McDowell *et al.*, 2008), there is as yet no general method for attributing their relative importance in tree death. We present a general two-axis framework for attributing the relative roles of drought, insects, and their interactions. Our framework revolves around two central questions. How many trees would have died in a given mortality event with drought but without insects? Conversely, how many trees would have died in a given mortality event with insects but without drought? This gives rise to two hypothetical numbers of dead trees in a focal region. In practice, these quantities can be difficult to determine but can be estimated from sensitivities observed in field experiments (Gaylord *et al.*, 2013; Netherer *et al.*, 2015) or from empirical relationships derived from previous insect outbreaks or mortality events (Chapman *et al.*, 2012; Creeden *et al.*, 2014). Then, based on inventory plots, aerial surveys, or satellite remote sensing, the observed number of dead

trees can be estimated. By comparing the relative sizes of the insect-free and drought-free hypothetical cases and the observed mortality rates, it should be possible to determine the relative influence of each stressor on mortality rates.

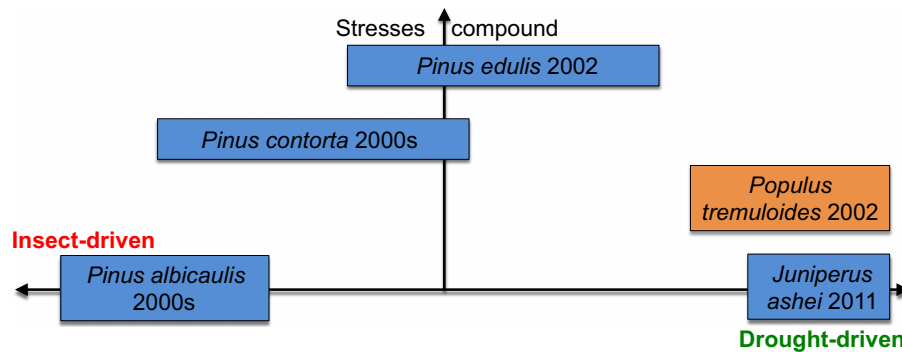
Several techniques and lines of evidence have been used to determine where mortality events fall along a continuum, from where the dominant driver of mortality was climate stress on the tree to where it was climate influence on insect populations. Postmortem assessments of trees that died using field plots or inventory networks provide the most basic pieces of information – were dead trees attacked by insects based on evidence such as bore holes or resin exudates and, if so, at what densities and by which insect species? Fig. 1 presents such information as collected by the US Forest Inventory and Analysis plot network. This network assigns a proximate mortality agent based on visible evidence (e.g. insect galleries, fire scars) (Fig. 1), although drought-kill can be difficult to determine visually and is thus more uncertain (Supporting Information Notes S1). System knowledge of the ecosystem from previous mortality events can also be informative. Are the insect species known to be primary agents that kill trees outright, or secondary agents that typically require stressed trees to be lethal? For example, several major die-offs were strongly associated with physiological impacts of drought stress on trees, such as widespread juniper, oak, and pine mortality in Texas in 2011, with relatively few signs of insect attack (Twidwell *et al.*, 2014). In recent widespread trembling aspen (*Populus tremuloides*)

mortality in the Rocky Mountains and boreal forest in Canada, all observed biotic agents for aspen are considered to be secondary (Marchetti *et al.*, 2011) and up to 20% of dead ramets had no signs of biotic attack (Anderegg *et al.*, 2012b), indicating a major role of drought. Finally, spatial patterns of mortality in relation to drought stress patterns or insect outbreak and dispersal patterns also provide an insight into the dominant drivers of mortality. For example, high mortality at lower elevations, south-facing slopes, and in regions of the highest drought stress all support a prominent role of drought stress driving mortality – although improved conditions for tree-killing insects and pathogens on these warmer sites might also affect these patterns. On the other end of the drought–insect continuum (Fig. 2), climate influences on insect populations may be the dominant driver in other mortality events. For example, in aggressive bark beetles, the combination of warm temperatures that directly benefit beetle population success, and a supply of susceptible, nutritionally optimal host trees is often necessary to shift insect populations across the endemic to epidemic threshold (Raffa *et al.*, 2008). Warming has also allowed the mountain pine beetle's northward expansion into Canadian jack pine (Cullingham *et al.*, 2011) and enhanced beetle survival in western high-elevation pine forests (Bentz *et al.*, 2013), in the absence of any major drought effects (Fig. 2).

Drought and insect stresses may also interact and lead to compounding effects on mortality (Fig. 2). The timing of mortality relative to climate anomalies is a crucial piece of



**Fig. 1** (a) Cumulative mortality rates (% basal area, BA) four major forest types (below) in western US forests averaged over 2000–2013, with fire-caused mortality removed from US Forest Service Forest Inventory and Analysis data. (b) Annual mortality rates (% BA yr<sup>-1</sup>) of major tree species in the western US from US Forest Service Forest Inventory and Analysis data. (c) Field-ascribed proximate cause of mortality that crews noted about individual dead trees in *Juniperus osteosperma* (JUOS), *Pinus edulis* (PIED), *Pinus contorta* (PICO), and *Populus tremuloides* (POTR) (Supporting Information Notes S1).



**Fig. 2** Example attribution of the relative roles of drought stress, insect attack, and their interactions in recent angiosperm (orange box) and gymnosperm (blue boxes) mortality events in western North America. References for episodes: *Juniperus ashei* mortality in Texas (Twidwell *et al.*, 2014); *Populus tremuloides* mortality (Worrall *et al.*, 2008, 2013; Anderegg *et al.*, 2012b, Anderegg *et al.*, 2013); *Pinus edulis* mortality (Breshears *et al.*, 2005; Gaylord *et al.*, 2013; Meddens *et al.*, 2015); *Pinus contorta* mortality (Chapman *et al.*, 2012); and *Pinus albicaulis* mortality (Bentz *et al.*, 2013).

information. For example, in lodgepole pine (*P. contorta*), the correlation with drought extent and mortality illustrates an important role for drought stress (Chapman *et al.*, 2012; Hart *et al.*, 2013), but the mortality event continued long after the observed drought stress had abated (Raffa *et al.*, 2008; Creeden *et al.*, 2014). This indicates that the presence of higher insect populations prolonged the mortality event, and thus might be categorized as a situation with compounding stress. Experimental evidence can also reveal when and where drought and insects interact. For example, a manipulative drought experiment revealed that drought stress predisposed piñon pine (*P. edulis*) trees to attack by piñon ips beetles (*Ips confusus*) (Gaylord *et al.*, 2013), highlighting that drought–insect interactions were critical in this recent widespread mortality event (Breshears *et al.*, 2005; Meddens *et al.*, 2015).

Thus, in recent tree mortality events in western North America, we found examples of drought-driven, insect-driven, and drought–insect interaction-driven tree mortality (Fig. 2). This brief survey illustrates the importance of understanding not just the role of plant physiological stress but also the wider context of insect population dynamics and tree physiology pertaining to insect attack when studying climate-induced tree mortality.

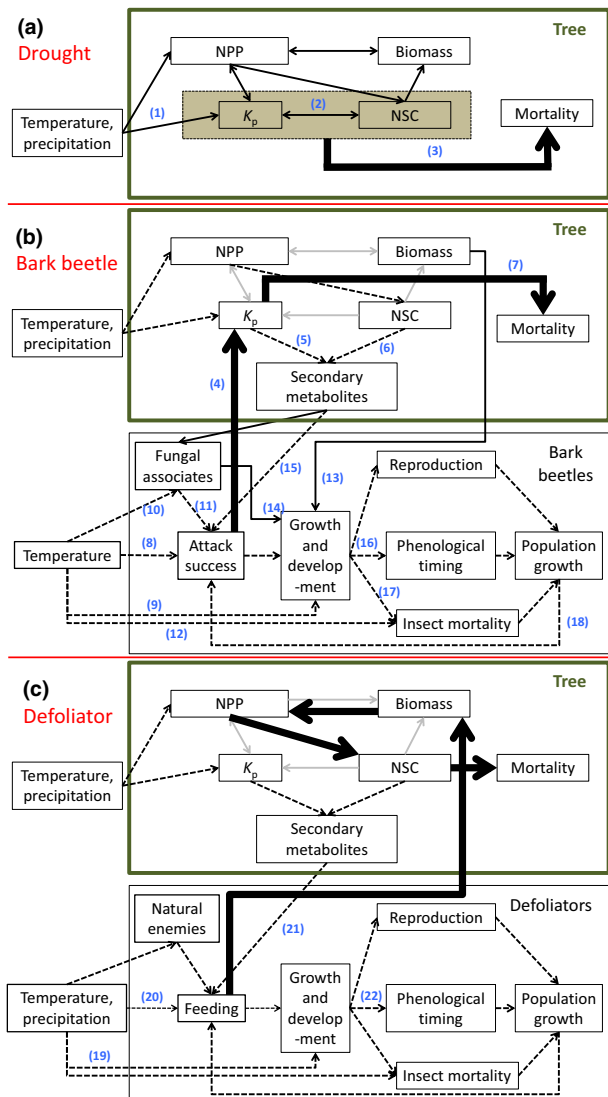
## Drought and insect mortality pathways

### Overview

Most vegetation models do not explicitly consider the effects of insects, but instead implicitly assume that the impact of insects on plant death is accounted for in the temporally and spatially averaged ‘background’ mortality rate (McDowell *et al.*, 2011). Moving beyond this assumption will require both theoretical and empirical advances, ideally operating in tandem. To this end, Dietze & Matthes (2014) propose a theoretical framework for modeling drought–insect interactions in trees. The framework examines the effects of different insect functional groups via changes in leaf area, phloem flow, xylem flow, stem turnover, and root biomass (Dietze & Matthes, 2014). This useful framework could be extended by including a limited set of additional processes for different

insect feeding guilds (Koricheva *et al.*, 1998). First, in addition to direct effects of climate on tree hosts, it could incorporate a mechanistic description of insect population dynamics as a function of climate (direct effects of climate on insects; Fig. 3). Second, and most importantly, it could incorporate the interaction between insects and tree physiology and their consequences on mortality (indirect nonadditive effects; *y*-axis in Fig. 2). We propose that such an interaction may be modeled with a basic physiological framework of the physiology of plant defense, such as the growth-differentiation balance hypothesis (GDBH; see later) (Herms & Mattson, 1992).

We begin with a baseline pathway that attributes mortality solely to drought stress on tree physiology. As discussed earlier and previously (McDowell *et al.*, 2011; Anderegg *et al.*, 2012a; Sala *et al.*, 2012), changes in plant hydraulics and carbon metabolism probably mediate the multitude of drought mortality pathways. In ecosystem models, whole-plant hydraulic conductivity ( $K_p$ ), the hydraulic conductance of water within plant xylem vessels from the root surface to the stomata, has frequently been used to represent both reductions in productivity with drought and hydraulic failure (Martínez-Vilalta *et al.*, 2002). This concept integrates the combined effects of water availability on biomass allocation to conducting tissue, transpiration, and inherent xylem hydraulic properties. Similarly, nonstructural carbohydrate (NSC) reserves may provide a time-integrated measure of the carbon status of a plant (Tague *et al.*, 2013).  $K_p$  and NSC, however, are interdependent: changes in  $K_p$  will affect carbon assimilation, and NSCs have been implicated in xylem repair (Salleo *et al.*, 2009; Secchi *et al.*, 2011; Trifilò *et al.*, 2014), as well as in overall plant hydraulic integrity (O’Brien *et al.*, 2014). Future research should focus on the interaction between  $K_p$  and NSC to better understand their respective influence on each other and the subsequent specific thresholds that lead to mortality. In addition to capturing tree physiological status, these two variables allow incorporation of several important interconnections between trees and insect populations, particularly through secondary metabolites (Fig. 3a), although other interconnections may also be important.



**Fig. 3** Conceptual framework of tree interactions with two insect guilds, illustrating tree mortality caused by climate and insects. Drought-induced tree mortality (a) occurs when climate variables influence net primary productivity (NPP) and plant hydraulic conductivity ( $K_p$ ), which are interlinked with nonstructural carbohydrate (NSC) reserves and biomass. In (b) and (c), insect feeding guilds of bark beetles and defoliators, respectively, are coupled with the tree model (green box) to lead to mortality. Thick black lines indicate pathways of tree mortality. In insect feeding guilds, dashed black lines indicate common links in both bark beetles and defoliators; solid black lines indicate differences between bark beetles and defoliators. Example references for process arrows: (1) McDowell *et al.* (2011), Anderegg *et al.* (2014); (2) McDowell *et al.* (2011), Anderegg & Callaway (2012); (3) Anderegg *et al.* (2012b), Sevanto *et al.* (2013), O'Brien *et al.* (2014); (4) Safranyik & Carroll (2006), Gaylord *et al.* (2013); (5) Goodsman *et al.* (2013); (6) Wright *et al.* (1979), Koricheva *et al.* (1998); (7) Uri *et al.* (2013), Frank *et al.* (2014); (8) Bentz *et al.* (2013); (9) Bentz *et al.* (1991), Hansen *et al.* (2001); (10) Paine *et al.* (1997), Addison *et al.* (2013); (11) Paine *et al.* (1997), Safranyik & Carroll (2006); (12) Bentz & Mullins (1999), Ungerer *et al.* (1999); (13) Safranyik & Carroll (2006); (14) Safranyik & Carroll (2006), Six (2013); (15) Raffa & Berryman (1983), Safranyik & Carroll (2006); (16) Logan & Powell (2001); (17) Bentz *et al.* (2010); (18) Raffa & Berryman (1983), Safranyik & Carroll (2006); (19) Thomson *et al.* (1984), Bentz *et al.* (2013); (20) Thomson *et al.* (1984); (21) Wagner *et al.* (1983), Lindroth (2010); (22) Thomson *et al.* (1984), Bentz *et al.* (2013).

## Bark beetles

Climate, particularly temperature, directly influences bark beetle populations, and therefore tree mortality, through various processes: larval growth and development; phenological timing that affects the degree of synchrony of emergence and mass attack; and cold- and heat-induced insect mortality (Bentz *et al.*, 2010) (Fig. 3b). Climate also influences development and growth of fungal associates that contribute to a successful attack and provide vital nutrients to developing larvae (Addison *et al.*, 2014). These elements of the conceptual model are distinct from tree vulnerability and thus apply even in situations without much drought-related host tree stress. Beetle populations are indirectly influenced by climate via stress to the host tree, most notably drought, mediated primarily by tree secondary metabolites (Fig. 3b). The likelihood of successful attack increases under drought conditions when reduction of carbon assimilation and water transport decreases the tree's capacity to produce NSC and mobilize secondary metabolites for defense production (Raffa & Berryman, 1983; Safranyik & Carroll, 2006). Developing larvae feed in the phloem while beetle fungal associates colonize both the xylem and the phloem; both decrease  $K_p$ , leading to eventual tree death (Reed *et al.*, 2014).

## Defoliators

Similar processes occur with defoliator-induced tree mortality, yet important differences exist. For spring-feeding defoliators, phenology (larval emergence) must be synchronized with key physiological processes of host trees (e.g. bud burst) for optimal insect population growth (Van Asch & Visser, 2007). Phenological synchrony can be highly sensitive to temperature, with insects and host plants sometimes responding to warming at different rates (Schwartzberg *et al.*, 2014). Defoliator consumption of leaves depends on leaf nutritional quality and palatability, which are influenced by secondary metabolites and plant nutrient status (Fig. 3c) (Wallin & Raffa, 2001). By reducing leaf biomass, defoliators reduce net primary production (NPP) and NSC production. Unlike bark beetle attacks, which typically kill trees quickly, severe defoliation over multiple years is usually required to kill trees, particularly in deciduous species (Van Asch & Visser, 2007). Natural enemies, which generally have a larger limiting effect on defoliator population dynamics than on bark beetles, are affected by temperature (especially predators and parasites) and precipitation (especially entomopathogens) (Jamieson *et al.*, 2012; Reilly *et al.*, 2014).

## Linking insects and tree physiology through secondary metabolites

Theories of plant defense postulate allocation tradeoffs between defense and other plant functions, shifts in allocation depending on abiotic resource availability (e.g. nutrients, water), and host fitness implications depending on resource availability, rates of herbivory and the competitive environment (Loomis, 1932; Lorio, 1986; Bazzaz *et al.*, 1987; Berryman, 1988; Herms & Mattson, 1992; Tuomi, 1992). The expanded GDBH provides a useful framework

to predict plant defenses. Because drought slows growth before photosynthesis, moderate drought will increase secondary metabolites, which include defensive structures and compounds (Herms & Mattson, 1992). Empirical and model-based tests of plant carbon balance during drought support GDBH predictions in some systems (Koricheva *et al.*, 1998). However, changes in defenses as a result of nutrient availability, CO<sub>2</sub> enrichment, and temperature have been tested more rigorously than drought stress, and it appears that the GDBH is less adept at predicting tree defenses *vis-à-vis* drought, but adequate tests of this are rare. Defense levels did not appear to conform to the predictions of the GDBH in one study that used two thresholds of water availability (Hale *et al.*, 2005). Resin flow in *P. edulis* across three experimental drought levels matched the pattern predicted by the GDBH, but the hypothesis could not be tested because growth rate was not measured (Gaylord *et al.*, 2013). Applicability of GDBH also varies among different groups of defense compounds (Koricheva *et al.*, 1998) and between constitutive and inducible defenses (Lewinsohn *et al.*, 1993). Thus, the GDBH may provide a useful mechanistic link for connecting climate stress and tree defenses based on recently assimilated vs stored carbon concentrations, but more tests are needed.

### Cross-biome patterns in insects' roles in tree mortality

How the mechanisms articulated in Fig. 3 operate in different biomes is uncertain. Given the importance of insects as herbivores in tropical forests, a better understanding of drought–insect interactions in tropical forests is probably crucial if we are to represent global biogeochemical dynamics more realistically, because of the significant contribution of these forests to the global carbon cycle – but most recent literature on insect outbreaks has focused on temperate forests. How do the relative roles of insects and drought vary across ecosystems and across the globe? Cross-biome patterns of the relative roles of insects vs drought in causing tree mortality are hampered by available data in tropical forests, but some generalizations can be made across biomes. Compared with the insect outbreaks in temperate forests previously described, tropical outbreaks usually affect fewer trees, largely because tropical forests are more diverse in species composition and most herbivores are limited to one or a few related tree genera (Dyer *et al.*, 2012). Thus, we hypothesize that the relative severity of climate-sensitive, insect-caused mortality should increase with latitude as tree species diversity declines and the number of host trees increases. Insects at high latitudes are also predicted to have relatively greater fitness as climate warms, because they are currently living below their thermal optima, compared with insects at low latitudes that currently live very close to their thermal optima and face greater extinction risks (Deutsch *et al.*, 2008). Although tropical outbreaks are usually most severe in areas of highest host tree density (Dyer *et al.*, 2012), they can still occur in diffusely distributed host species that comprise 1% or less of trees in a forest (Wong *et al.*, 1990). Importantly, generalized outbreaks also do sometimes occur, with several different insect species simultaneously attacking a taxonomically diverse array of tree species (Van Bael *et al.*, 2004; Dyer *et al.*, 2012).

Although our understanding of outbreaks in species-rich tropical forests is less than in the temperate and boreal zones (Dyer *et al.*, 2012), available information hints at some important contrasts between tropical and temperate forests. For example, although several species of tropical bark beetles and wood borers are known to undergo outbreaks (Nair, 2007; Dyer *et al.*, 2012), most published information on tropical outbreaks focuses on defoliators. The dominance of publications on defoliators may be a consequence of defoliator outbreaks being more common or it may reflect a reporting bias as a result of easier detection of defoliator outbreaks.

Many outbreaks in tropical forests – at least of defoliators – appear to be triggered by drought. However, outbreaks often occur during the rainy season immediately following the drought, perhaps in response to postdrought leaf flushes or delayed postdrought recovery of the outbreaking herbivores' enemies (predators, parasitoids, and pathogens; Coley, 1998; Van Bael *et al.*, 2004). Tropical outbreaks may generally be shorter than temperate outbreaks (weeks or months rather than years; Wong *et al.*, 1990; Van Bael *et al.*, 2004), perhaps as a result of rapid top-down control by enemies (Van Bael *et al.*, 2004). Tropical outbreaks might also, on average, be more spatially restricted than temperate outbreaks. For example, Van Bael *et al.* (2004) reported localized outbreaks along the Pacific Coast of Panama following a drought, but found no outbreaks among the same host species in moister interior forests. A few tropical outbreaks have been documented as long-lived and spatially extensive, particularly when host-tree densities are high. Nair (2007) summarized a century's worth of outbreaks of *Hoplocerambyx spinicornis* (a cerambycid beetle) in one of its host trees in India and found that the largest outbreak spanned > 6 yr and 500 000 ha, killing millions of trees.

Finally, the role of higher trophic levels as negative feedbacks that control insect outbreaks appears to be more important in tropical forests than in extratropical forests. Predicting the effects of climatic changes in these systems will thus depend on an improved understanding of climatic effects on trophic cascades. For example, if climatic changes disrupt the synchronization of top-down control of outbreaking insects by their enemies (Coley, 1998; Stireman *et al.*, 2005), we might expect more frequent, extensive, generalized, and long-lasting outbreaks in the future.

### Tools and approaches for moving forward

Multiple experimental, observational, and modeling approaches appear promising for attributing tree mortality to drought, insects, and their interactions, although each approach has its limitations. Factorial experiments that manipulate both drought and insects have good potential to improve understanding of tree drought response, insect population dynamics, and tree–insect interactions, but to date these have been rare and expensive. Rainfall exclusion experiments have been widely used to impose drought stress on forest ecosystems (Beier *et al.*, 2012; Zeppel *et al.*, 2014) and have, in some cases, induced mortality in concert with insect attacks (Gaylord *et al.*, 2013; Netherer *et al.*, 2015). Insecticide sprays or manipulated insect introductions can control for insect attack on certain trees, and factorial drought experiments with and without

insect attack may be a useful tool to disentangle the relative roles and climatic underpinnings of tree stress and insect attack in mortality (Raffa & Berryman, 1983; Netherer *et al.*, 2015).

Observational data that include both tree mortality and insect abundances or presence in dying trees, especially across different locations and ecosystem scales over longer time periods, will help to advance our understanding. A few data sets are available that cover landscape and broader scales over multiple years (Shaw *et al.*, 2005; Meddens *et al.*, 2012) (Fig. 1). Satellite remote sensing, particularly time series of imagery, can be especially useful when accuracy is evaluated against other observations, such as field data, and when attribution of tree mortality to a disturbance agent is identified (Hansen *et al.*, 2013; McDowell *et al.*, 2014). Quantification of insect abundance along with tree mortality is a critical data gap, and would be especially useful if collected in concert with large-scale forest inventory networks. Empirical studies of the causes of tree mortality that consider multiple factors, including climate, stand structure, soil characteristics, and insect populations, will be particularly valuable.

Mechanistic models exist that simulate the internal physiology of tree hydraulic and carbon status (McDowell *et al.*, 2013; Powell *et al.*, 2013) but will probably require substantial empirical calibration (Fisher *et al.*, 2010) to account for uncertainty in meteorology and soil physical properties that affect plant water supply and therefore accurate representation of drought (Lichstein *et al.*, 2014). We posit that better modeling of internal plant physiology, such as plant hydraulics, along with coupling to mechanistic insect dynamics models (Fig. 2), will improve higher-scale modeling of mortality resulting from drought, insects, and their interactions. For example, a hydrological model that incorporated a plant hydraulic threshold was able to predict spatial patterns in drought-driven mortality of *P. tremuloides* with 75% accuracy and was a big improvement on prediction from soil moisture, precipitation, or temperature alone (Anderegg *et al.*, 2015).

Mechanistic models have also incorporated insect outbreaks in several studies in different ways (for a review, see Hicke *et al.*, 2012). One way involves prescribing insect-caused tree mortality to study the effects on vegetation structure and function by bark beetles (Kurz *et al.*, 2008; Edburg *et al.*, 2011) and other feeding guilds (Hogg, 1999; Keith *et al.*, 2012). Sensitivity studies are useful for identifying key processes missing from models, such as the inclusion of snags that have a large effect on heterotrophic respiration fluxes (Edburg *et al.*, 2011). Studies of past events document the impacts of insect outbreaks on vegetation dynamics, including influences on carbon fluxes that may affect national policy (Kurz *et al.*, 2008), although adequate information about the extent, severity, and duration of tree mortality is needed. Investigations have illustrated the advantages of detailed tree-based models run at stand scales (Pfeifer *et al.*, 2011), as well as less detailed growth and yield models (Kurz *et al.*, 2008) or global land surface models (Edburg *et al.*, 2011) that permit large-scale assessments and/or linkages to Earth system models. Effects of future outbreaks can be assessed by prescribing the timing and severity of these events using scenarios, which is particularly effective with defoliator outbreaks given their cyclical

nature (Dymond *et al.*, 2010; Hennigar & MacLean, 2010). A disadvantage of the scenario approach is that any coupling with climate may be limited.

A second means of incorporating insect outbreaks in mechanistic vegetation models is by developing and including a prognostic insect outbreak model. Insect models to predict the probability, extent, and/or severity of tree mortality that incorporate climate variables to predict insect-caused tree mortality have used a mix of temperature and precipitation variables (Jewett *et al.*, 2011; Preisler *et al.*, 2012). More recent mechanistic insect models also include spatially explicit host tree densities (Powell & Bentz, 2014) and fungal associates (Addison *et al.*, 2014). Inclusion of insect models in vegetation models allows us to assess the degree of ecological understanding (when results are evaluated against historical events) as well as to estimate the impacts of future climate change and management decisions. However, such studies are rare given the state of knowledge. A notable exception is the inclusion of European spruce bark beetle (*Ips typographus*) in LPJ-GUESS (Jönsson *et al.*, 2012). Thus, more detailed coupling of tree and insect models and additional applications to case studies should be possible, at least in some ecosystems, in the near future (Fig. 2).

A key decision is when and how best to model insect population dynamics. The status quo approach for typical vegetation models is that insect-induced death is implicitly included in background mortality rates, but in reality that insect-caused mortality is not constant, but rather often aggregated in space and time and nonlinear. One approach relies on the dominance of temperature as a significant driver of insect life cycles, and information on temperature-dependent development times in outbreaking insect populations that are well studied (Powell & Bentz, 2009). These climate-driven insect population models can be coupled with ecosystem models (Jönsson *et al.*, 2012). Further complexity can be added by considering diffusion or spread, where the probability of infestation varies as a function of proximity to other currently infested trees (Preisler *et al.*, 2012; Powell & Bentz, 2014). Advantages of spatially modeling insect population dynamics include the capacity to incorporate density-dependent factors and the potential to better capture spatial and temporal variation in tree mortality that results from climate-driven insect population growth. Disadvantages include the need for additional parameters and model complexity, the lack of scientific understanding for many processes, and the possibility of introducing erratic and unpredictable model behavior as a result of greater model complexity.

## Conclusion

Advancing our understanding of drought, biotic disturbance agents, and their interactions is critical to developing and applying models that predict future patterns of tree mortality in a changing world. Recent developments in tree mortality research have focused separately on the physiology of trees under stress and on insects as tree-killing agents, yet these processes are linked. Insects play many critical roles in physiology, demography, and disturbance of forest ecosystems, although they are often not explicitly included in ecosystem models used to make predictions of vegetation change or carbon cycling under climate scenarios. Furthermore, insect

outbreaks are strongly influenced by climate (both warming and drought), and the role of drought varies by insect species. An important first step in predicting future mortality is to identify situations where considering both agents is necessary. We argue that a fully coupled approach is needed when: insect and tree physiologies exhibit different responses to climate drivers; nonlinear thresholds can be passed where drought processes may incite but not be needed to continue tree mortality: or interactions between insects and tree physiology lead to nonadditive effects on tree mortality rates. We present examples of different types of events throughout western North America, and argue that it will be essential to study mortality in other biomes, particularly the tropics, to improve mortality modeling under climate change. Our conceptual model that links internal tree physiology with insect feeding guilds offers a pathway for modeling drought-induced tree mortality, insect outbreaks, and their interaction in a fully coupled approach. The representation of insect diversity according to their functional interaction with trees (feeding guilds) offers a useful way to focus effort on understanding plant–insect interactions at large spatial and temporal scales, and provides a much-needed common point of interaction for cross-disciplinary science.

## Acknowledgements

This work was conducted as part of the Tree Mortality Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by the NSF (grant no. EF-0553768), the University of California, Santa Barbara, and the State of California. Additional support was also provided for J.A., the NCEAS Postdoctoral Associate in the Group. W.R.L.A. was supported in part by a National Oceanic and Atmospheric Administration Climate and Global Change Postdoctoral fellowship, administered by the University Corporation of Atmospheric Research. J.A.H. was supported by a grant from the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture (grant no. 2013-67003-20652), the United States Geological Survey (USGS) Climate Research and Development Program through the Western Mountain Initiative, and the Department of the Interior Northwest Climate Science Center through a Cooperative Agreement (G12AC20481) from the USGS. We also acknowledge the support of the US Geological Survey's Ecosystems and Climate and Land Use Change mission areas.

## References

Adams HD, Macalady AK, Breshears DD, Allen CD, Stephenson NL, Saleska SR, Huxman TE, McDowell NG. 2010. Climate-induced tree mortality: earth system consequences. *Eos, Transactions American Geophysical Union* 91: 153–154.

Addison A, Powell JA, Bentz BJ, Six DL. 2014. Integrating models to investigate critical phenological overlaps in complex ecological interactions: the mountain pine beetle–fungus symbiosis. *Journal of Theoretical Biology* 368: 55–66.

Addison A, Powell J, Six D, Moore M, Bentz B. 2013. The role of temperature variability in stabilizing the mountain pine beetle–fungus mutualism. *Journal of Theoretical Biology* 335: 40–50.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Venetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH *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.

Anderegg WRL, Anderegg LD, Berry JA, Field CB. 2014. Loss of whole-tree hydraulic conductance during severe drought and multi-year forest die-off. *Oecologia* 175: 11–23.

Anderegg WRL, Berry JA, Field CB. 2012a. Linking definitions, mechanisms, and modeling of drought-induced tree death. *Trends in Plant Science* 17: 693–700.

Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB. 2012b. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences, USA* 109: 233–237.

Anderegg WRL, Callaway E. 2012. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology* 159: 1866–1874.

Anderegg WRL, Flint A, Huang C-y, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* 8: 367–371.

Anderegg WRL, Kane JM, Anderegg LDL. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* 3: 30–36.

Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. 1987. Allocating resources to reproduction and defense. *BioScience* 37: 58–67.

Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C, Boeck H, Christensen JH, Leuzinger S, Janssens IA. 2012. Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters* 15: 899–911.

Bentz B, Vandygriff J, Jensen C, Coleman T, Maloney P, Smith S, Grady A, Schen-Langenheim G. 2013. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. *Forest Science* 60: 434–449.

Bentz BJ, Logan JA, Amman GD. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Canadian Entomologist* 123: 1083–1094.

Bentz BJ, Mullins D. 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the intermountain west. *Environmental Entomology* 28: 577–587.

Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF, Seybold SJ. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *BioScience* 60: 602–613.

Berryman AA. 1988. Towards a unified theory of plant defense. In: Mattson WJ, Levieux J, Bernard-Dagan C, eds. *Mechanisms of woody plant defenses against insects*. New York, NY, USA: Springer, 39–55.

Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J *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.

Chapman TB, Veblen TT, Schoennagel T. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93: 2175–2185.

Coley PD. 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change* 39: 455–472.

Creeden EP, Hicke JA, Buotte PC. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecology and Management* 312: 239–251.

Cullingham CI, Cooke JE, Dang S, Davis CS, Cooke BJ, Coltman DW. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology* 20: 2157–2171.

Davidson CB, Gottschalk KW, Johnson JE. 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *Forest Science* 45: 74–84.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences, USA* 105: 6668–6672.

Dietze MC, Matthes JH. 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters* 17: 1418–1426.

Dyer LA, Carson WP, Leigh EG Jr. 2012. Insect outbreaks in tropical forests: patterns, mechanisms, and consequences. *Insect Outbreaks Revisited* 10: 219–245.



- Dymond CC, Neilson ET, Stinson G, Porter K, MacLean DA, Gray DR, Campagna M, Kurz WA. 2010. Future spruce budworm outbreak may create a carbon source in eastern Canadian forests. *Ecosystems* 13: 917–931.
- Edburg SL, Hicke JA, Lawrence DM, Thornton PE. 2011. Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. *Journal of Geophysical Research: Biogeosciences* 116: 4033.
- Fisher R, McDowell N, Purves D, Moorcroft P, Sitch S, Cox P, Huntingford C, Meir P, Ian Woodward F. 2010. Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. *New Phytologist* 187: 666–681.
- Frank JM, Massman WJ, Ewers BE, Huckaby LS, Negrón JF. 2014. Ecosystem CO<sub>2</sub>/H<sub>2</sub>O fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce bark beetles. *Journal of Geophysical Research: Biogeosciences* 119: 1195–1215.
- Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yezpe EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist* 198: 567–578.
- Goodsman DW, Lusebrink I, Landhäuser SM, Erbilgin N, Lieffers VJ. 2013. Variation in carbon availability, defense chemistry and susceptibility to fungal invasion along the stems of mature trees. *New Phytologist* 197: 586–594.
- Hajek A. 1999. Pathology and epizootiology of the Lepidoptera-specific mycopathogen *Entomophaga maimaiga*. *Microbiology and Molecular Biology Reviews* 63: 814–835.
- Hale BK, Herms DA, Hansen RC, Clausen TP, Arnold D. 2005. Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. *Journal of Chemical Ecology* 31: 2601–2620.
- Hansen EM, Bentz BJ, Turner DL. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist* 133: 827–841.
- Hansen MC, Potapov P, Moore R, Hancher M, Turubanova S, Tyukavina A, Thau D, Stehman S, Goetz S, Loveland T. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853.
- Hart SJ, Veblen TT, Eisenhart KS, Jarvis D, Kulakowski D. 2013. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95: 930–939.
- Hennigar CR, MacLean DA. 2010. Spruce budworm and management effects on forest and wood product carbon for an intensively managed forest. *Canadian Journal of Forest Research* 40: 1736–1750.
- Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.
- Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Kashian DM, Moore D, Raffa KF, Sturrock RN, Vogelmann J. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* 18: 7–34.
- Hogg EH. 1999. Simulation of interannual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. *Ecological Modelling* 114: 175–193.
- Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL. 2012. Consequences of climate warming and altered precipitation patterns for plant–insect and multitrophic interactions. *Plant Physiology* 160: 1719–1727.
- Jewett JT, Lawrence RL, Marshall LA, Gessler PE, Powell SL, Savage SL. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *Forest Science* 57: 320–335.
- Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B. 2012. Guess the impact of *Ips typographus* – an ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agricultural and Forest Meteorology* 166: 188–200.
- Keith H, Van Gorsel E, Jacobsen KL, Cleugh HA. 2012. Dynamics of carbon exchange in a Eucalyptus forest in response to interacting disturbance factors. *Agricultural and Forest Meteorology* 153: 67–81.
- Koricheva J, Larsson S, Haukioja E, Keinänen M. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos* 160: 212–226.
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.
- Lewinsohn E, Gijzen M, Muzika RM, Barton K, Croteau R. 1993. Oleoresinosis in Grand Fir (*Abies grandis*) saplings and mature trees (modulation of this wound response by light and water stresses). *Plant Physiology* 101: 1021–1028.
- Lichstein JW, Golaz N-Z, Malyshev S, Shevliakova E, Zhang T, Sheffield J, Birdsey RA, Sarmiento JL, Pacala SW. 2014. Confronting terrestrial biosphere models with forest inventory data. *Ecological Applications* 24: 699–715.
- Lindroth RL. 2010. Impacts of elevated atmospheric CO<sub>2</sub> and O<sub>3</sub> on forests: phytochemistry, trophic interactions, and ecosystem dynamics. *Journal of Chemical Ecology* 36: 2–21.
- Logan JA, Powell JA. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47: 160.
- Loomis WE. 1932. Growth-differentiation balance vs. carbohydrate–nitrogen ratio. *Proceedings of the American Society of Horticultural Sciences* 29: 240–245.
- Lorio PL Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle–tree interactions. *Forest Ecology and Management* 14: 259–273.
- Manion P. 1981. *Tree disease concepts*. Englewood Cliffs, NJ, USA: Prentice-Hall.
- Marchetti SB, Worrall JJ, Eager T. 2011. Secondary insects and diseases contribute to sudden aspen decline in southwestern Colorado, USA. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 41: 2315–2325.
- Martínez-Vilalta J, Piñol J, Beven K. 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecological Modelling* 155: 127–147.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 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 NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26: 523–532.
- McDowell NG, Coops NC, Beck PS, Chambers JQ, Gangodagamage C, Hicke JA, Huang C, Kennedy R, Krofcheck DJ, Litvak M *et al.* 2014. Global satellite monitoring of climate-induced vegetation disturbances. *Trends in Plant Science* 20: 114–123.
- McDowell NG, Fisher RA, Xu C, Domec J, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* 200: 304–321.
- Meddens AJ, Hicke JA, Ferguson CA. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22: 1876–1891.
- Meddens AJ, Hicke JA, Macalady AK, Buotte PC, Cowles TR, Allen CD. 2015. Patterns and causes of observed piñon pine mortality in the southwestern United States. *New Phytologist* 206: 91–97.
- Muilenburg VL, Herms DA. 2012. A review of bronze birch borer (Coleoptera: Buprestidae) life history, ecology, and management. *Environmental Entomology* 41: 1372–1385.
- Nair KS. 2007. *Tropical forest insect pests: ecology, impact, and management*. Cambridge, UK: Cambridge University Press.
- Nardini A, Battistuzzo M, Savi T. 2013. Shoot desiccation and hydraulic failure in temperate woody angiosperms during an extreme summer drought. *New Phytologist* 200: 322–329.
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H *et al.* 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* 205: 1128–1141.
- O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4: 710–714.
- Paine T, Raffa K, Harrington T. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Reviews of Entomology* 42: 179–206.
- Pfeifer EM, Hicke JA, Meddens AJ. 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global Change Biology* 17: 339–350.

- Powell JA, Bentz BJ. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology* 24: 657–672.
- Powell JA, Bentz BJ. 2014. Phenology and density-dependent dispersal predict patterns of mountain pine beetle (*Dendroctonus ponderosae*) impact. *Ecological Modelling* 273: 173–185.
- Powell TL, Galbraith DR, Christoffersen BO, Harper A, Imbuzeiro H, Rowland L, Almeida S, Brando PM, Costa ACL, Costa MH. 2013. Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist* 200: 350–365.
- Preisler HK, Hicke JA, Ager AA, Hayes JL. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* 93: 2421–2434.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58: 501–517.
- Raffa KF, Berryman A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 79: 27–49.
- Reed DE, Ewers BE, Pendall E. 2014. Impact of mountain pine beetle induced mortality on forest carbon and water fluxes. *Environmental Research Letters* 9: 105004–105008.
- Régnière J, Bentz B. 2007. Modeling cold tolerance in the Mountain Pine Beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology* 53: 559–572.
- Régnière J, Nealis V. 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecological Entomology* 32: 461–477.
- Reilly JR, Hajek AE, Liebhold AM, Plymale R. 2014. Impact of *Entomophaga maimaiga* (Entomophthorales: Entomophthoraceae) on outbreak gypsy moth populations (Lepidoptera: Erebidae): the role of weather. *Environmental Entomology* 43: 632–641.
- Safranyik L, Carroll AL. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik L, Wilson WR, eds. *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine*. Victoria, BC, Canada: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 3–66.
- Sala A, Woodruff DR, Meinzer FC. 2012. Carbon dynamics in trees: feast or famine? *Tree Physiology* 32: 764–775.
- Salleo S, Trifilò P, Esposito S, Nardini A, Gullo MAL. 2009. Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? *Functional Plant Biology* 36: 815–825.
- Schwartzberg EG, Jamieson MA, Raffa KF, Reich PB, Montgomery RA, Lindroth RL. 2014. Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia* 175: 1041–1049.
- Secchi F, Gilbert ME, Zwieniecki MA. 2011. Transcriptome response to embolism formation in stems of *Populus trichocarpa* provides insight into signaling and the biology of refilling. *Plant Physiology* 157: 1419–1429.
- Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. 2013. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment* 37: 153–161.
- Shaw JD, Steed BE, DeBlander LT. 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: what is happening to Pinyon–Juniper woodlands? *Journal of Forestry* 103: 280–285.
- Six DL. 2013. The bark beetle holobiont: why microbes matter. *Journal of Chemical Ecology* 39: 989–1002.
- Stireman J, Dyer L, Janzen D, Singer M, Lill J, Marquis R, Ricklefs R, Gentry G, Hallwachs W, Coley P. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proceedings of the National Academy of Sciences, USA* 102: 17384–17387.
- Tague CL, McDowell NG, Allen CD. 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: e80286.
- Thomson AJ, Shepherd RF, Harris JWE, Silversides RH. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera, Tortricidae), in British Columbia. *Canadian Entomologist* 116: 375–381.
- Trifilò P, Barbera PM, Raimondo F, Nardini A, Gullo MAL. 2014. Coping with drought-induced xylem cavitation: coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiology* 34: 109–122.
- Tuomi J. 1992. Toward integration of plant defence theories. *Trends in Ecology & Evolution* 7: 365–367.
- Twidwell D, Wonkka CL, Taylor CA, Zou CB, Twidwell JJ, Rogers WE. 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.
- Ungerer MJ, Ayres MP, Lombardero MJ. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography* 26: 1133–1145.
- Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* 33: 672–683.
- Van Asch M, Visser ME. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Reviews of Entomology* 52: 37–55.
- Van Bael SA, Aiello A, Valderrama A, Medianero E, Samaniego M, Wright SJ. 2004. General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest. *Journal of Tropical Ecology* 20: 625–633.
- Wagner MR, Benjamin DM, Clancy KM, Schuh BA. 1983. Influence of diterpene resin acids on feeding and growth of larch sawfly, *Pristiphora erichsonii* (Hartig). *Journal of Chemical Ecology* 9: 119–127.
- Wallin KF, Raffa KF. 2001. Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology* 82: 1387–1400.
- Weed AS, Ayres MP, Hicke J. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83: 441–470.
- Wong M, Wright SJ, Hubbell SP, Foster RB. 1990. The spatial pattern and reproductive consequences of outbreak defoliation in *Quararibea asterolepis*, a tropical tree. *Journal of Ecology* 78: 579–588.
- Worrall JJ, Egeland L, Eager T, Mask RA, Johnson EW, Kemp PA, Shepperd WD. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *Forest Ecology and Management* 255: 686–696.
- Worrall JJ, Rehfeldt GE, Hamann A, Hogg EH, Marchetti SB, Michaelian M, Gray LK. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management* 299: 35–51.
- Wright L, Berryman A, Gurusiddaiah S. 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae): 4. Effect of defoliation on wound monoterpane and inner bark carbohydrate concentrations. *Canadian Entomologist* 111: 1255–1262.
- Zeppel MJB, Wilks JV, Lewis JD. 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. *Biogeosciences* 11: 3083–3093.

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Notes S1** Details concerning the cause of mortality data as collected by the US Forest Service Forest Inventory and Analysis (FIA) program.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.