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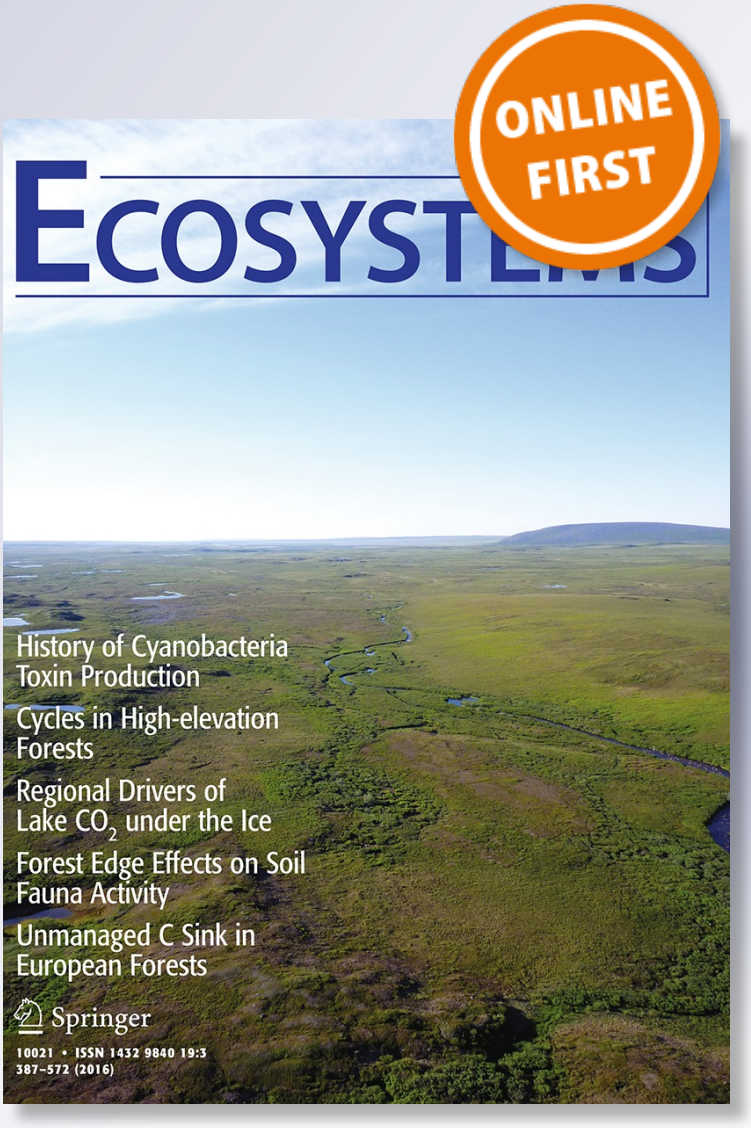

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When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes

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Abstract

Drought- and heat-driven tree mortality, along with associated insect outbreaks, have been observed globally in recent decades and are expected to increase in future climates. Despite its potential to profoundly alter ecosystem carbon and water cycles, how tree mortality scales up to ecosystem functions and fluxes is uncertain. We describe a framework for this scaling where the effects of mortality are a function of the mortality attributes, such as spatial clustering and functional role of the trees killed, and ecosystem properties, such as productivity and diversity. We draw upon remote-sensing data and ecosystem flux data to illustrate this framework and place climate-driven tree mortality in the context of other major disturbances. We find that emerging evidence suggests that climate-driven tree mortality impacts may be relatively small and recovery times are remarkably fast (~4 years for net ecosystem production). We review the key processes in ecosystem models necessary to simulate the effects of mortality on ecosystem fluxes and highlight key research gaps in modeling. Overall, our results highlight the key axes of variation needed for better monitoring and modeling of the impacts of tree mortality and provide a founda-

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Author Contributions WRLA, JMV, MC, JJC, BE, DG, AG, RG, CH, SL, TLP, LR, RSS, and VT conceived of the study. WRLA, JMV, MC, and CY performed research. WRLA analyzed the data. WRLA, JMV, MC, JJC, BE, DG, AG, RG, CH, SL, TLP, LR, RSS, and VT wrote the paper.

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tion for including climate-driven tree mortality in a disturbance framework.

Key words: disturbance; recovery; resilience; productivity; biodiversity; carbon and water fluxes.

Introduction

Tree mortality is a critical demographic rate for determining forest dynamics and, consequently, ecosystem function and carbon cycling (Stephenson and van Mantgem 2005). Mortality is the dominant driver of aboveground carbon turnover (Carvalhais and others 2014). Furthermore, mortality has wide-ranging consequences for biodiversity, ecosystem structure and function, and ecosystem services provided by forests (Anderegg and others 2013a). Yet, the effects of mortality remain much less studied than causes of mortality (Anderegg and others 2013a). Reducing this uncertainty requires more empirical data and long-term monitoring. Mortality is currently poorly monitored compared to forest growth and productivity because of its highly stochastic nature (Allen and others 2010).

Climate change is expected to alter tree mortality rates through stress on individual plants, biotic interactions among plants, attacks by pests and pathogens, and shifting disturbance regimes (Allen and others 2010; Hicke and others 2012). Long-term forest plots have detected increasing mortality rates associated with temperature and drought stress in tropical, temperate, and boreal forests (van Mantgem and others 2009; Peng and others 2011; Brienen and others 2015). Gradual ''press'' effects of mortality are predicted to occur alongside episodic ''pulse'' mortality events triggered by climate extremes (Smith and others 2009). Indeed, widespread ''pulse'' mortality events linked with drought and heat stress have already been widely documented in many regions in the past few decades (Allen and others 2010; Phillips and others 2010).

The actual effects of tree mortality on ecosystem function and fluxes are still not well understood despite the recognized central role of tree mortality in forest ecosystem carbon cycling (Kurz and others 2008; Frank and others 2015). In this review, we draw upon the disturbance literature (for example, Harmon and others 2011; Edburg and others 2012; Goetz and others 2012) to place climate-driven tree mortality in a disturbance context and outline a framework for assessing the effects of climate-driven mortality on ecosystem function and fluxes of carbon and water. This framework posits that the effects of mortality are a function of (1) mortality attributes, such as the patch size and functional role of trees killed, and (2) ecosystem properties, such as the system productivity and diversity. We use remote-sensing datasets and synthesize flux data from multiple disturbance types to illustrate this framework and propose cross-system hypotheses.

We first summarize the extensive disturbance literature of how tree losses should affect ecosystem carbon and water fluxes. We next outline our framework for assessing the effects of climate-driven mortality on ecosystem function; we place particular focus on compensating mechanisms that could buffer the effect of climate-induced mortality on ecosystem fluxes. We then present hypotheses on how mortality attributes and ecosystem properties will influence the impact of mortality on fluxes. Next, we quantitatively synthesize the available flux literature to compare climate-induced tree mortality to other disturbances, such as fire and harvest. We conclude with research gaps and promising research avenues in modeling and monitoring of tree mortality.

We focus primarily on climate-driven tree mortality, especially from drought, heat, and climate-influenced insect infestations, because these are globally important but poorly understood mortality events, although other global change drivers can induce mortality increases as well. Some aspects of the consequences of tree mortality from drought (Adams and others 2010; Anderegg and others 2013a) and insect outbreaks (Amiro and others 2010; Edburg and others 2012; Hicke and others 2012) have been examined, but have been based primarily on a small number of individual cases or mortality events. Thus, our review is timely because it provides a cross-ecosystem synthesis and perspective necessary for predicting when and where the functional impacts of tree mortality will be most severe, which is largely missing to date.

How Tree Mortality Affects Ecosystem Fluxes

The general trajectory of the effects of tree mortality on forest ecosystem fluxes of carbon and water can be predicted from first principles and ecological theory (Harmon and others 2011; Goetz and others 2012; Figure 1). Drought-related forest mortality is a disturbance and can be described

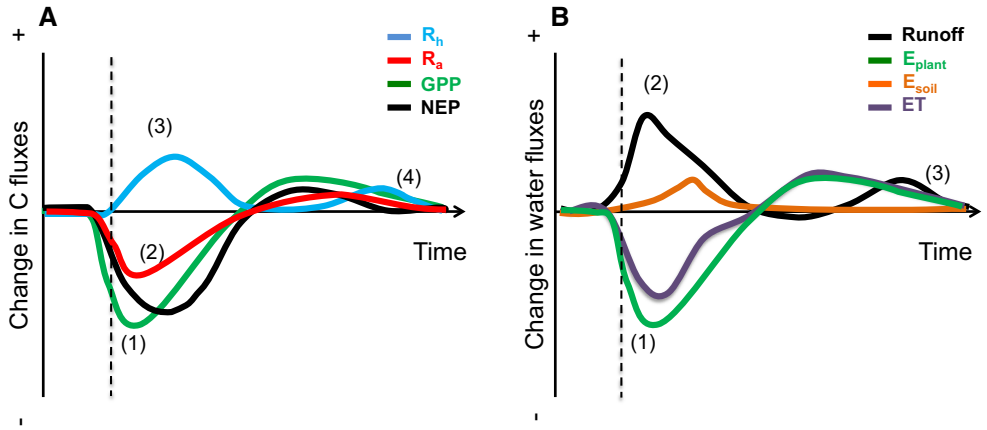

Figure 1. Expected changes in ecosystem fluxes of carbon (**A**) and water (**B**) during and following a tree mortality event (after Harmon and others 2011; Edburg and others 2012). A *dashed line* indicates the beginning of the mortality event. Carbon fluxes include a decline in gross primary productivity (GPP) driven mostly by reductions in LAI (1), a decline in autotrophic respiration (R_a) due mostly to reductions in leaf area and growth rates (2), an increase in heterotrophic respiration (R_h) driven mostly by decomposition of dead leaves and roots (3), a decrease in net ecosystem productivity (NEP), and in some systems a second pulse of heterotrophic respiration driven mostly by decomposition of fallen stems and snags (4). Water fluxes include a decline in plant transpiration (E_{plant}) driven mostly by reductions in leaf area (1), increases in run-off, including both run-off and streamflow (2), and in some systems a potential secondary increase in run-off due to increased surface water movement after snag fall (3) (Color figure online)

using classical disturbance theory (White and Pickett 1985). As trees die, independent of the causal agent of mortality, leaf area in an ecosystem will temporarily decline. The corresponding decline of ecosystem photosynthesis leads to declines in gross primary productivity (GPP) over some time period (Figure 1A, #1). GPP recovers as surviving trees and understory vegetation produce more leaves (Anderegg and others 2012) and enhance their light use efficiency (Gough and others 2013) to better take advantage of newly available light resources and as new trees regenerate into the ecosystem (Stuart-Haëntjens and others 2015). Lower ecosystem-level leaf area and growth rates will tend to drive decreases in autotrophic respiration (R_a; Figure 1A, #2). Mortality also leads to a pulse input of leaf litter and coarse woody debris (Norton and others 2015), and thus decomposition of this plant matter is expected to drive lagged increases in heterotrophic respiration (R_h; Figure 1A, #3). The direct effects of drought, however, will act to suppress R_h due to soil moisture limitations, which could counteract this litter decomposition pulse in the short term (Rowland and others 2014). Finally, in ecosystems with slower turnover and decomposition rates—particularly colder and drier ecosystems—dead bole snags may remain standing for relatively long periods of time. When these snags fall to the ground, their decomposition may be relatively fast (Harmon and Hua 1991), and an additional pulse of R_h would be expected (Figure 1A, #4). Net ecosystem productivity (NEP) should follow the trajectory outlined by GPP minus R_a and R_h, likely experiencing an initial decline, followed by a period of positive uptake and a gradual return to near equilibrium. Our framework assumes that the ecosystem is able to recover to near-equilibrium conditions, as assumed by almost all dynamic vegetation models, where GPP is roughly in balance with R, such that NEP tends towards zero in the long term (Odum 1969). Some ecosystems may, however, transition to alternate stable states (that is, non-forest) after certain types or magnitudes of climate-triggered mortality (Allen and others 2010), which we do not discuss here.

Changes in ecosystem water fluxes following mortality commence with declines in the sum of plant-level transpiration (E_{plant}) across the ecological community (Figure 1B, #1). In many cases of both drought and insect-induced mortality, the mortality agent itself will drive this decrease in transpiration even before leaf area losses are observed, for example through extensive xylem cavitation (MartínezVilalta and others 2002; Anderegg and others 2014) or through interruption of water transport by fungal pathogens associated with insects (Frank and others 2014), both in trees that die and potentially in those that survive. Lower transpiration rates are predicted to drive increased run-off—both surface run-off and streamflow (Fig-

ure 1B, #2) (Adams and others 2012). Declines in transpiration should also lead to increases in soil moisture, which is widely supported by the timber harvest literature (Amiro and others 2010), although the changes are complex throughout the soil profile (Miller and others 2011). In ecosystems with lower leaf area indices, there also may be increases in soil evaporation rates (E_{soil}) due to increased radiation and temperature exposure on bare soils (Raz-Yaseef and others 2010) (Figure 1B). If snags remain standing, a second pulse of increased run-off is possible as snagfall may allow further erosion and increased surface water transport (compare Edburg and others 2012) (Figure 1B, #3). Ecosystem evapotranspiration (ET) is the sum of precipitation (assumed to be constant in our hypothetical example) minus run-off, groundwater infiltration (also assumed constant, although in reality this could change due to changes in canopy openness), and plant and soil water loss. ET is predicted to decline during and after the disturbance and then to gradually recover afterwards.

Scaling Mortality to Fluxes Across Ecosystems

The net effect of mortality on ecosystem fluxes is the integral of the trajectories in Figure 1 over time. This highlights that two key characteristics will determine the magnitude of the impacts: (1) the magnitude of the initial ''pulse'' response and (2) the recovery rate of the ecosystem (Table 1). Both of these characteristics are likely to vary substantially across ecosystems and mortality events. The functional impacts of drought-related tree mortality are likely to differ from those of stand-clearing disturbances, such as fire or clearcut harvests, whereas stand-thinning disturbances such as thinning harvests, low-intensity fires, or storms may provide better analogs. There is growing evidence that thinning and defoliation may have relatively minor and short-lived effects on ecosystem fluxes (Amiro and others 2010; Miller and others 2011; Nave and others 2011; Dore and others 2012; Gough and others 2013; Templeton and others 2015), in agreement with studies showing that ecosystem structure, such as canopy height and root biomass, may recover more slowly than ecosystem function, such as NEP, after disturbance (Beard and others 2005). Although the direct effects of drought on ecosystem physiology can be large (Ciais and others, 2005; Schwalm and others 2012; Gatti and others 2014), we hypothesize that the functional impacts of drought-related *tree mortality* itself may be relatively mild, at least in some ecosystems, as has been recently shown for climate-triggered mountain pine beetle infestations in North America (Rhoades and others 2013; Biederman and others 2014; Reed and others 2014).

Several compensatory mechanisms explain why substantial tree mortality may not necessarily translate into major changes in ecosystem fluxes (Gough and others 2013; Rhoades and others 2013; Reed and others 2014) (Table 1). Firstly, moderate disturbances may increase canopy structural heterogeneity and diffuse light penetration, improving light use efficiency and also resulting in higher photosynthetic performance per unit leaf area (Gough and others 2013; Frank and others 2014). In addition, higher resource availability (both water and nutrients) per unit of leaf area normally results in higher photosynthetic and growth performance of remaining trees (Martínez-Vilalta and others 2007; Dore and others 2012). Third, changes in ecosystem water use efficiency (WUE) can modify the relative magnitude of changes in water and carbon fluxes after disturbance shown in Figure 1 (Mkhabela and others 2009). Finally, leaf area index (LAI) may recover quickly due to the regrowth of vegetation following disturbance, including both remaining trees and new regeneration (Templeton and others 2015). Many forests have a huge capacity to recover leaf area after disturbance if soil fertility is not negatively affected or even enhanced (Norton and others 2015). This is particularly true if resprouting species are involved. For instance, LAI recovered completely in a coppiced Mediterranean holm oak forest within 6 years after removing approximately 80 % of the forest basal area by thinning, despite the fact that the studied system was heavily water limited and that the strongest drought on record occurred 2 years after the thinning was performed (López and others 2009).

Using the compensatory mechanisms discussed above, we outline a framework to predict the changes in ecosystem fluxes within and across ecosystems after a pulse of mortality (Table 1; Figure 2). These scaling variables (Table 1) should be considered as hypotheses of the mechanistic effects of each variable when all other factors are roughly held constant (that is, the slopes of a partial regression between the scaling variable and ecosystem flux, while accounting for other variables). Quantifying mortality severity is the first crucial component needed to scale from the population to the ecosystem. While a population-level mortality rate (stems y^{-1} ha^{-1}) is the relevant metric to use in demographic studies aimed at

predicting long-term community dynamics, we suggest that in most cases the amount of biomass or basal area (g or $m^2\ y^{-1}\ ha^{-1}$) killed is a more useful quantification of severity of mortality and more likely to be related to ecosystem-level functional consequences in the short to mid-term. In this paper, we define mortality broadly, including the complete loss of aboveground biomass (absent death of meristem tissue), as this will affect ecosystem fluxes even if resprouting or clonal meristems do not die. It is self-evident that the amount of mortality matters for the magnitude of ecosystem response, but less clear about the time-scales of ecosystem recovery, which may start to occur while the mortality event is ongoing. In addition, the functional form of the relationship between mortality severity and effects on ecosystem fluxes is largely unknown (Figure 2B). How mortality scales to affect fluxes could be linear, non-linear, or threshold driven (Figure 2B, dashed lines) and will almost certainly depend on the ecosystem type and characteristics of mortality. Importantly, the factors promoting fast recovery after mortality do not necessarily coincide with those minimizing the initial effects.

Influence of Mortality Characteristics on Ecosystem Flux Trajectories

We predict that the patch size and the timing of mortality, as well as the size classes and the functional role of the trees killed, will influence subsequent changes in ecosystem fluxes (Table 1). Tree mortality has long been known to be unevenly distributed in space and time (Franklin and others 1987). Some mortality drivers, particularly fire and windthrow, yield large patches of forest loss (Chambers and others 2013). Other drivers, such as mortality from competition or gap dynamics, are likely to yield more dispersed and random patterns of mortality (Espírito-Santo and others 2014). We posit that the spatial clustering (patch size distribution) of tree mortality will play a central role in determining the effects on ecosystem fluxes (Table 1). All else being equal, large patches of forest loss should have larger and longer effects on ecosystem fluxes than the same amount of biomass lost from mortality in many more smaller patches. The theory underlying this essentially derives from the relative importance of patch edge perimeter versus patch area because more edges would be expected to facilitate both the utilization of newly available resources (water, light, and so on) by neighboring trees as well as dispersal and colonization into the disturbed area, leading to faster recovery of ecosystem fluxes (Franklin and Forman 1987; Turner and others 1997).

The distribution of mortality patch sizes from disturbance has been quantified in some ecosystems, notably the Amazon rainforest. Medium- and large-scale disturbances (>1 ha) in the Amazon roughly follow power-law relationships (Chambers and others 2013; Espírito-Santo and others 2014) (Figure 3). The shape and slope of this relationship are crucial in determining the effects on ecosystem fluxes because the relationship describes the relative frequency of small versus large disturbances and thus their relative impact on regional carbon fluxes (Espírito-Santo and others 2014).

We characterized the disturbance size and frequency for forest loss in a major temperate region where drought- and insect-induced tree mortality has been exceptionally prominent (Allen and others 2010) from two datasets: (1) Landsat estimates of forest loss from 2000–2013 (Hansen and others 2013) (which also includes fire-driven losses) across the intermountain west, USA, and (2) an individual widespread drought-driven tree mortality event of trembling aspen (*Populus tremuloides*) (Huang and Anderegg 2012). We observe that drought-, insect-, and fire-driven forest loss across the intermountain western United States also appears to follow a power-law relationship (Figure 3, dark green). Notably, however, the exponent of this relationship is $\alpha = -0.9$, whereas the exponent in the Landsat-based analysis of the Amazon is $\alpha = -2.1$ (Figure 3) (Espírito-Santo and others 2014). The less-steep exponent in this temperate region reveals that drought-, insect-, and fire-induced mortality, which are the dominant causes of forest loss (Hicke and others 2013), causes proportionally greater large disturbances than the disturbance distribution observed in the Amazon, where small-scale disturbances dominate (Figure 3). The inclusion of fire-driven forest losses could influence the slope of this power law by increasing the relative proportion of large patch disturbances. However, the Amazon disturbance data are roughly comparable in that they also include fires and windthrow disturbances. We also observed a power-law relationship in a specific drought-driven mortality event of trembling aspen (*Populus tremuloides*) in Colorado, USA, which has an exponent of $\alpha = -1.3$ (Figure 3; blue line). Forests in this temperate region exhibit much higher frequency of large-scale disturbance than in the Amazon, which would favor larger effects of mortality on ecosystem fluxes (note that the absolute numbers of disturbances per hectare

Table 1. Hypothesized Mortality Characteristics (A) and Ecosystem Properties (B) that Affect the Scaling of Tree Mortality (% Basal Area Killed is Assumed to be Fixed) into Ecosystem Fluxes

Variable	Smaller and less durable effects expected whenever …	Compensatory mechanism involved	Examples from the literature
(A) Mortality characteristics			
Size distribution and spatial clustering	Mortality occurs in relatively small clusters	Easier utilization of newly available resources, enhanced gap colonization, and recovery of canopy cover	Turner and others (1997)
Timing (in relation to climate)	Mortality is followed by a relatively favorable period, particularly with regard to water availability	Increased resource availability and faster recovery of leaf area	Bréda and others (2006)
Size class of trees killed	Mortality affects preferentially small trees	Increased resource availability for the remaining trees	Pfeifer and others (2011)
Functional role of trees killed	Mortality affects species with redundant (as opposed to unique) functional roles or with a high capacity to regrow after canopy loss (e.g., resprouting species)	Niche overlap/redundancy and complementarity; ability to use newly available resources	Roman and others (2015) Matheny and others (2014)
(B) Ecosystem properties			
Turnover time (productivity)	Productivity is high	Faster dynamics; higher capacity to build up biomass after disturbance	Brando and others (2008)
Diversity	Diversity is high, particularly concerning drought-response functional diversity	Insurance effect	Morin and others (2014)

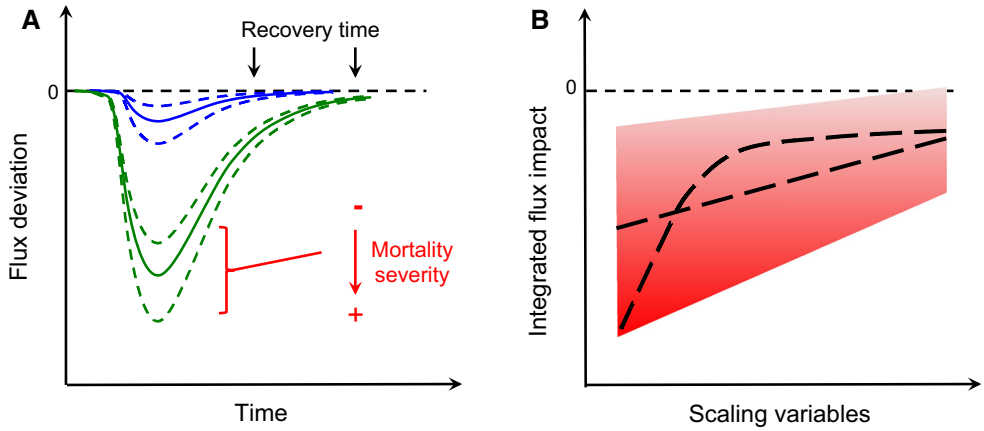

Figure 2. Cross-ecosystem scaling of the effect of mortality on fluxes. (**A**) Flux (for example, GPP, NEP, ET) deviation from a baseline over time as a function of mortality severity (*dashed* versus *solid*) and the ecosystem and mortality attribute scaling variables (*green* and *blue*). (**B**) Integrated impact on ecosystem flux as a function of ecosystem and mortality attribute scaling variables (*polygon*) (for example, Table 1); *white lines* represent hypothetical linear and non-linear scaling (Color figure online)

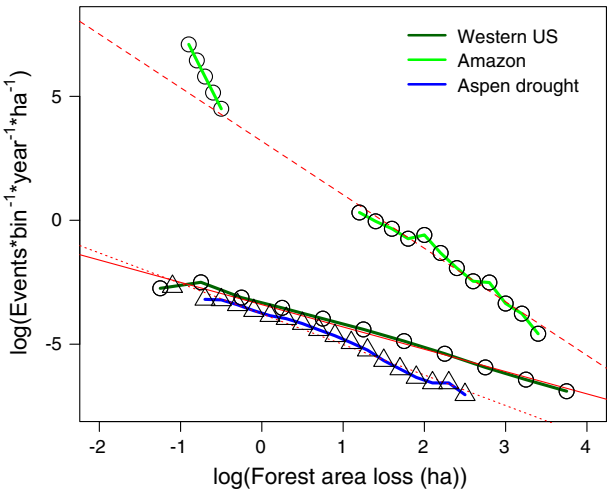

Figure 3. Mortality frequency versus area affected (events per bin per hectare per year) in the Amazon basin (*light green*; data from Espirito-Santo and others 2014 from lidar for the *upper line* and satellite remote sensing for the *lower line*), intermountain western United States (*dark green*), which has been affected by large-scale drought- and insect-induced tree mortality, and a drought-driven widespread mortality event (*blue*) of trembling aspen (*Populus tremuloides*) in Colorado, USA. *Red lines* are best fit regressions for a power-law relationship (Color figure online)

should not be compared between the Amazon and western US due to different bin widths) (Figure 3).

The timing of the mortality event, particularly in relation to climatic conditions, is also likely to be relevant for ecosystem recovery and fluxes. A clear difference between drought-induced mortality and other disturbances, such as commercial thinning, is that stressful conditions are likely to prevail even after the mortality episode has come to an end, implying legacy effects (Breda and others 2006; Anderegg and others 2013b, 2015a). In principle, recovery should be faster if favorable climatic conditions, particularly with regard to water availability, occur shortly after the mortality event, as increased water availability for the remaining vegetation should promote the recovery of leaf area (Breda and others 2006). This leads to the prediction that mortality episodes occurring relatively late during the dry season are likely to involve shorter recovery times, provided that the rains return to normal levels at the beginning of the wet season.

The functional role of the trees killed will also impact the response of ecosystem fluxes to a mortality event. Trees fill diverse functional roles and niches in forests, and thus a preferential mortality of some species, which is common in drought- and insect-induced tree mortality (da Costa and others 2010; Phillips and others 2010; Anderegg and others 2013a), may have important consequences. Mortality of trees that fill functionally unique roles—for example in rooting distribution, nitrogen fixation, flammability, a given successional status, or hydraulic redistribution—should have larger effects on ecosystem fluxes. In general, we expect faster recovery times if species with traits favoring regeneration after disturbance (for example, resprouting) are affected, as has been widely established for wildfires (Pausas and others 2009). Which other axes of species' niches matter, however, is likely to vary from system to system and depend on the relative importance of different abiotic constraints of the ecosystem.

Finally, the size class of trees affected by mortality is likely to be critical in evaluating the ecosystem effects. Large trees play critical roles in many ecosystems and store disproportionately large amounts of carbon (Slik and others 2013; Stephenson and others 2014) and, obviously, they take longer to be replaced. Larger trees are also likely more susceptible to drought stress, probably because disproportionally larger evaporation demands relative to their larger uptake potential, leading to higher tension in water conducting systems (Merlin and others 2015). We thus hypothesize that mortality of larger trees is not only more likely under drought stress but will also generally translate to larger effects on ecosystem fluxes. Consistent with this prediction, simulations of the impacts of insect-driven mortality of *Pinus contorta*, which recently affected more than 20 million ha of forests in North America, revealed that the distribution of diameter size classes living and killed had the largest impact on simulated carbon fluxes (Pfeifer and others 2011). Critically, both plot networks and drought experiments have indicated that drought-induced mortality is likely to preferentially affect large trees in tropical forests (Nepstad and others 2007; da Costa and others 2010; Phillips and others 2010) and elsewhere (Merlin and others 2015), which may induce larger ecosystem effects than if mortality were random. Scaling from the individual tree to ecosystem-level responses is, however, far from trivial, implying that the association between larger trees being affected and higher overall functional impacts may not be universal.

Influence of Ecosystem Properties on Ecosystem Flux Responses

We hypothesize that properties of different ecosystem and biomes, particularly productivity/turnover time and tree species diversity, will strongly affect ecosystem flux trajectories after mortality. Ecosystems that exhibit higher productivity and faster turnover times should, all else being equal, recover more quickly. Aboveground plant carbon turnover times vary substantially across ecosystems and are generally faster in tropical ecosystems (Galbraith and others 2013), where inputs from GPP tend to be higher (Carvalhais and others 2014). The speed of regrowth and regeneration is generally thought to be much slower in cold-limited and water-limited ecosystems, correlating with growth rate differences (Reich 2014). The degree of ''competitor release'' triggered by tree mortality and the growth rates of these competitors should greatly influence ecosystem recovery from mortality. For example, thinning and the related reduction in competition for light and water increased growth of the remaining trees in xeric pine stands for up to three decades after the treatment, with higher and longer lasting effects in higher thinning intensities (Giuggiola and others 2013). Thus, structural and compositional changes that occur following mortality will have important impacts on the long-term trajectories of ecosystem fluxes.

Finally, higher functional diversity in an ecosystem and associated higher niche redundancy should lead to faster recovery times and more muted ecosystem consequences. In particular, we hypothesize that functional diversity specifically pertaining to drought tolerance and recovery strategies should be one of the most important components of diversity. Theoretical and empirical work has shown that biodiversity is crucial in helping systems reorganize and return to a pre-disturbance state (Folke and others 2004). For example, the occurrence of isohydric and anisohydric species or the mix between both has been found as a key property to drought vulnerability (Roman and others 2015). A prominent mechanism underlying the role of biodiversity is termed the ''insurance value of biodiversity,'' describing the observation that the presence in a community of a diverse set of species allows for higher likelihoods that some species will be able to (a) tolerate a given disturbance and (b) utilize available resources post-disturbance to regrow quickly (Morin and others 2014).

Recovery Times of Climate-Induced Tree Mortality Compared to Other Disturbances

It has only been quite recently that severe drought and drought-induced tree mortality have been widely considered in the disturbance literature. In order to locate climate-driven tree mortality (drought triggered and insect triggered where insect-driven mortality is related to climate) in context with other disturbances, we performed a literature review to identify studies where (1) mortality of trees occurred and was quantified and (2) the recovery of ecosystem fluxes of carbon or water after disturbances were measured (Supplemental Material). We located 37 studies that met these criteria and spanned disturbances of drought, insects, windthrow, fire, and timber harvest. We

present results from 21 studies that included the most widely reported and relevant carbon flux—net ecosystem productivity (NEP), but similar results were obtained if other ecosystem fluxes were considered (Table S1). We classified disturbances as insect/drought driven, low-severity fire/harvest, and high-severity (that is, stand-clearing) fire/harvest.

We found that recovery times differed across these disturbance classes (ANOVA; $F = 7.13$, $P = 0.004$), with the main difference being significantly slower recovery times in high-severity fire/harvest (Tukey HSD high severity–low severity: $P = 0.007$; Tukey HSD high-severity insect/drought: $P = 0.04$). Recovery time to where NEP first reached pre-disturbance or control values for insect- and drought-driven tree mortality was relatively short, around 4 years on average (Figure 4). This was comparable to low-severity fire or harvest, also around 4 years, but much faster than high-severity fire or harvest, which was around 26 years (Figure 4). Strikingly, these recovery times occurred despite relatively high levels (~60–90 % of stems) of tree mortality driven by insects and drought (Table S1). Our sample of studies is likely biased—due to data availability—towards temperate and coniferous forests (Table S1), which has several implications. Such forests might be expected to fall along the slower end of recovery rates and tend to have relatively lower productivity. Thus, the impacts of mortality could be of a larger magnitude in more mesic, broad-leaved forests, but we would generally predict recovery times to be faster in those systems.

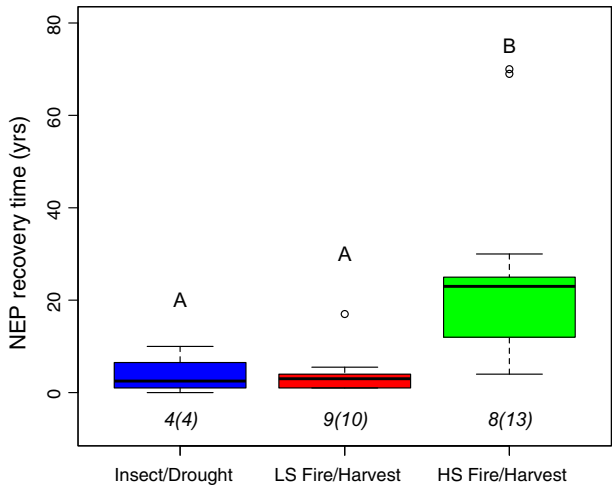

Figure 4. Observed recovery time in years of net ecosystem productivity (NEP) after disturbance from insect/drought-driven mortality, low-severity fire or harvest, and high-severity (that is, stand-clearing) fire or harvest. *Letters* indicate statistically significant differences (Tukey HSD $P < 0.05$). Numbers beneath indicate the number of studies and the number of sites (*in parentheses*)

Considering carbon fluxes in light of Figure 1, declines in GPP were broadly observed during and following drought-induced and insect-induced tree mortality in multiple conifer-dominated ecosystems in North America, ranging from arid woodlands (Krofcheck and others 2014) to montane pine forests (Brown and others 2012; Moore and others 2013) to high-elevation forests (Frank and others 2014). In the tropics, NPP was observed to recover within about 1 year after drought-driven tree mortality (Brando and others 2008). Flux tower studies in *Pinus contorta*-dominated forests, which have experienced the largest insect-triggered mortality events ever documented, found that total ecosystem respiration (sum of R_a and R_h) declined in parallel with GPP and thus found little net change in NEP (Moore and others 2013) or recovery of the ecosystem to a net sink within 2–4 years post-outbreak (Brown and others 2012). In this case, the limitations of inputs from GPP to R_a appeared to lead to falling total respiration (Moore and others 2013). Despite extremely high mortality rates, 60–90 % of trees killed at these sites, and relatively low diversity in the plant community, the studies observed that remaining vegetation and regrowth caused GPP and thus NEP to recover relatively rapidly at an ecosystem scale (Brown and others 2010, 2012). However, recent evidence has highlighted large differences between eddy flux estimates and direct chamber measurements of respiration in insect-attacked forests, indicating uncertainty in ecosystem respiration and thus NEP quantification (Speckman and others 2014). In addition, large amounts of trees in these ecosystems are still standing and thus the short timescale of most studies (most are <6 years post-disturbance) may not capture a second peak or extended period of respiration after tree fall (Figure 1; compare Edburg and others 2012).

Examining water fluxes following mortality, declines in transpiration and increases in soil moisture have been observed following extensive insect-driven tree mortality (Biederman and others 2014; Frank and others 2014). In most cases, increases in run-off are observed following drought- and insect-driven tree mortality (Adams and others 2012); however, in some systems increases in soil evaporation and snow sublimation appear to outweigh the declines in transpiration, leading to muted or even declines in run-off and streamflow (Guardiola-Claramonte and others 2011; Biederman and others 2014). The average recovery time

of run-off and water yield from harvest and fire disturbances was 5.4 years (range 2–16 years) (Table S1), and although no studies to our knowledge have quantified recovery of run-off after drought-induced mortality, the relatively fast NEP recovery times we observed suggest that the recovery times from these other disturbances are a reasonable approximation.

Research Gaps in Mortality-Flux Data and Current Ecosystem Models

Models provide useful frameworks for performing scaling and testing scaling hypotheses, as they include some representation of the biotic and abiotic effects on tree physiology, demography, and forest fluxes (Table 2). How models simulate drought-induced mortality is one of the largest areas of uncertainty and while this is either absent (for example, constant mortality rate independent of climate) or relatively simplistic (for example, mortality increases outside an arbitrary climate envelope) in most current models (McDowell and others 2011), this is an active area of research (Fisher and others 2010; Anderegg and others 2015b; Mackay and others 2015). In particular, simulations of canopy structure, such as whether trees or cohorts of trees are simulated, and of plant physiology are critical elements that determine how and if models can simulate drought-induced mortality and its effects (McDowell and others 2013).

Currently, a variety of vegetation models exist which employ different representations of canopy structure and ecosystem physiology in order to simulate ecosystem scale responses, some of which we summarize in Table 2. In relation to canopy structure, most commonly used vegetation models vary from being a simple ''big leaf'' model, within which the canopy is represented by a single canopy layer (for example, IBIS, SIB), to multi canopy-layer models (for example, SPA JULES, CLM, ORCHIDAE), to models which dynamically simulate canopy gaps (for example, ED, PPA). The representation of water stress and its interaction with canopy structure in models is arguably one of the most important determinants of variation in how ecosystem models simulate reaction and response to climate-induced mortality events (Powell and others 2013; Rowland and others 2015). In many models, water stress is simplified to the impact of a soil water stress factor (Table 2), which is used to down-regulate stomatal conductance and/or photosynthesis in stressed conditions, alongside the direct effects of changes in VPD on stomatal conductance (for example, JULES, CLM, ED). Other vegetation models take a more process-based approach, for example simulating a connection between leaf and soil water potential in which stomatal conductance is maximized without allowing leaf water potential to fall below a critical threshold (SPA); or simulating the hydraulic pathway from soil to leaf, with multiple resistances (Sperry and others 1998) (Table 2). Variability in both canopy structure and water relations within models will alter both the initial pulse response to a morality event, as well as the feedbacks which control the recovery time, such as gaps allowing increased availability of light (Table 2).

Considering the elements of mortality that most impact fluxes (Figure 2), some of the critical processes needed to capture ecosystem flux dynamics after mortality are currently present in ecosystem models (Table 2), but other key processes are not well represented. No large-scale ecosystem models to our knowledge can currently represent spatial clustering of mortality (Fisher and others 2010), although gap models, such as ED, can go some way towards representing mortality patterns through a statistical representation of the spatial distribution of trees of differing canopy heights. Large-scale gradients in productivity are well represented in most models; however, currently none of the models represented in Table 2 sufficiently represent functional diversity in a forest and therefore full diversity of variation in drought-response and post-disturbance regeneration strategies between plant functional types (Fisher and others 2010; Powell and others 2013; Anderegg 2014). Individual stem or cohort-based models (for example, ED, PPA) may be able to represent functional diversity more effectively through the use of a continuum of trait variation (Fyllas and others 2014), rather than through 1 or 2 discrete types of tree or plant, with the trade-off that increased representation of diversity is computationally challenging at regional to global scales.

Considering the key compensating mechanisms that would buffer flux responses, we highlighted above the key roles of changes in photosynthetic performance of surviving trees, increased resource availability, and changes in allocation to allow rapid recovery of LAI. Similar to the challenge of simulating the full functional diversity of forests, most models in Table 2 have fixed photosynthetic traits, which would result in slower recovery of carbon uptake. Dynamic LAI is generally incorporated into most vegetation models (Table 2), albeit with large inter-model variability in absolute values and dynamic changes (Rowland and others

Table 2. Key Responses/Mechanisms that Will Influence the Effects of Mortality on Ecosystem Fluxes and How They Are Simulated in Some Current Examples of Widely Used Ecosystem Models (Not an Exhaustive List of Models that Include These Processes)

Flux	Response	Model function	Example models
GPP	(1) Competition for light	Dynamic LAI	SPA, CLM, ED, JULES, ORCHIDAE
		Canopy layers	SPA, CLM, ED, JULES, ORCHIDAE
		Different PFTs	CLM, ED
		Simulation of gap development (i.e., succession)	ED
		Senescence	ORCHIDAE
	(2) Competition for water	Representation of rooting profile	SPA, CLM, ED, JULES, ORCHIDAE
		Different rooting profiles for different size classes (not PFTs)	ED
		Dynamic root water uptake	SPA
		Senescence	ORCHIDAE
	(3) Impact of water stress on stomatal conductance and gross primary productivity	Water stress factor	ED, CLM, JULES, ORCHIDAE
		Minimum leaf water potential	SPA
		Water potential and hydraulic pathway simulated	Sperry model
R_h	(1) Impact of temperature	Temperature response function	SPA, CLM, ED, JULES, ORCHIDAE
	(2) Impact of moisture	Moisture response function	Many models
	(3) Impact of decomposers	Separate microbial model/decomposition model	
R_a	(1) Impact of temperature	Temperature response function	SPA, CLM, ED, JULES, ORCHIDAE
	(2) Impact of moisture	Moisture response function	JULES
	(3) Impact of GPP on Ra	Ra fixed fraction of GPP	SPA
		Ra a function of GPP + temp	SPA, CLM, ED, JULES
		Ra a function of GPP + temp + water stress	
		Ra modeled independently	
ΔSWC	(1) Changes in evapotranspiration	Representation of rooting profile	SPA, CLM, ED, JULES, ORCHIDAE
		Different rooting profiles for PFTs	
		Soil hydraulic properties	SPA, CLM, ED, JULES, ORCHIDAE
E_{soil}		Simulation of canopy gaps	ED
E_{plant}		Representation of plant surface area	SPA, CLM, ED, JULES, ORCHIDAE
		Representation of plant height/surface roughness	SPA, CLM, ED, JULES, ORCHIDAE
Run-off		Simulation of run-off	CLM, ED, JULES, ORCHIDAE

Abbreviations match those of Figure 1

2015). However, many models have constant carbon allocation to different tissues, which is potentially a major limitation in simulating recovery of radial growth after drought (Anderegg and others 2015a). Finally, in relation to recovery to mortality many of these mechanisms remain relatively untested against observational data, and we suggest that the development of datasets and frameworks for calibrating models to simulate such processes may be necessary.

Two major techniques provide most of the observational evidence examining changes in ecosystem fluxes in carbon and water following tree mortality. First, several studies have used spatial gradients in mortality severity across regions and/or across different times since mortality (that is, chronosequences) (Hansen and others 2015). These studies allow examination of ecosystem stocks and fluxes well after mortality occurred and also integrate large spatial scales, such as watersheds. However, the extent to which mortality also covaried with other ecosystem attributes that would affect subsequent fluxes, such as soil type or stand density, is largely unknown, which is a potentially major confounding factor. The second technique involves the continuous measurement of ecosystem fluxes where mortality is occurring, using for instance eddy covariance methods or streamflow gauges. These studies are more direct, but relatively rare (Table S1). Although some of this rarity is due to relatively few flux towers that can be opportunistically placed in regions experiencing a pulse of drought- or insect-induced mortality (Brown and others 2012), another major impediment is that many flux studies often do not report mortality rates within the flux tower footprint, even when it has occurred (Ciais and others 2005). Both reporting of mortality rates within existing flux towers and additional studies placing flux towers in ongoing disturbance to monitor recovery are greatly needed.

Conclusion

We find here that mortality attributes and ecosystem properties interact to determine the effect of climate-driven tree mortality on ecosystem fluxes. The magnitude of the initial impact (for example, drought) has been much better quantified than recovery dynamics, but both are critical in determining ecosystem-level consequences. We argue that the functional effects of drought-driven tree mortality are comparable to those of other, non-stand-replacing disturbances and should be put in the same theoretical framework, but it is unique in that it co-occurs with a direct stress on ecosystems that can have large impacts on fluxes. Emerging evidence suggests that the effect of tree mortality itself (not the inciting drought) on ecosystem fluxes may be smaller and recovery times may be faster than previously thought, suggesting that compensating mechanisms are very strong.

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