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When a tree dies in the forest: Scaling climate-driven tree mortality to ecosystem water and carbon fluxes

William R. L. Anderegg[1*], Jordi Martinez-Vilalta[2,3], Maxime Cailleret[4], Jesus Julio Camarero[5], Brent Ewers[6], David Galbraith[7], Arthur Gessler[8,9], Rüdiger Grote[10], Cho-ying Huang[11], Shaun Levick[12], Thomas L. Powell[13], Lucy Rowland[14], Raúl Sánchez-Salguero[15], Volodymyr Trotsiuk[16]

Affiliations:

[1]Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08544, USA; [2]CREAF, Cerdanyola del Vallès 08193, Spain; [3]Univ. Autònoma Barcelona, Cerdanyola del Vallès 08193, Spain; [4]Department of Environmental Systems Sciences, ETH Zürich, 8092 Zürich, Switzerland; [5]Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50192 Zaragoza, Spain; [6]Department of Botany, University of Wyoming, Laramie, WY 82071, USA; [7]School of Geography, University of Leeds, Leeds, LS2 9JT, UK; [8]Research Unit Forest Dynamics, Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland; [9]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany; [10]Institute for Meteorology and Climate Research (IMK-IFU), Karlsruhe Institute of Technology, 19, 82467 Garmisch-Partenkirchen, Germany; [11]Department of Geography, National Taiwan University, Taipei 10617, Taiwan; [12]Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745

Jena, Germany; [13]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA; [14]School of Geosciences, University of Edinburgh, Edinburgh, EH9 3FF, UK; [15]Dpto. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Ctra. Utrera Km 1, E-41013 Sevilla, Spain; [16]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamycka 129, Praha6–Suchdol, Prague, 16521, Czech Republic

*Corresponding author: Room 106 A, Guyot Hall, Princeton University, Princeton, NJ 08544, USA; phone: 01-970-739-4954; email: anderegg@princeton.edu

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

Introduction

Tree mortality is a critical demographic rate for determining forest dynamics and, consequently, ecosystem function and carbon cycling (Stephenson & van Mantgem, 2005). Mortality is the dominant driver of aboveground carbon turnover (Carvalhais *et al.*, 2014). Furthermore, mortality has wide-ranging consequences for biodiversity, ecosystem structure and function, and ecosystem services provided by forests (Anderegg *et al.*, 2013a). Yet the effects of mortality remain much less studied than causes of mortality (Anderegg *et al.*, 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 *et al.*, 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 *et al.*, 2010; Hicke *et al.*, 2012). Long-term forest plots have detected increasing mortality rates associated with temperature and drought stress in tropical, temperate, and boreal forests (van Mantgem *et al.*, 2009; Peng *et al.*, 2011; Brienen *et al.*, 2015). Gradual "press" effects of mortality are predicted to occur alongside episodic "pulse" mortality events triggered by climate extremes (Smith *et al.*, 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 *et al.*, 2010; Phillips *et al.*, 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 *et al.*, 2008). In this review, we draw upon the disturbance literature (e.g. Harmon *et al.*, 2011; Edburg *et al.*, 2012; Goetz *et al.*, 2012) to place climate-driven tree mortality in a

92 disturbance context and outline a framework for assessing the effects of climate-driven mortality
93 on ecosystem function and fluxes of carbon and water. This framework posits that the effects of
94 mortality are a function of 1) mortality attributes, such as the patch size and functional role of
95 trees killed, and 2) ecosystem properties, such as the system productivity and diversity. We use
96 remote-sensing datasets and synthesize flux data from multiple disturbance types to illustrate this
97 framework and propose cross-system hypotheses.

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

107 We focus primarily on climate-driven tree mortality, especially from drought, heat, and
108 climate-influenced insect infestations, because these are globally important but poorly
109 understood mortality events, although other global change drivers can induce mortality increases
110 as well. Some aspects of the consequences of tree mortality from drought (Adams *et al.*, 2010;
111 Anderegg *et al.*, 2013a) and insect outbreaks (Amiro *et al.*, 2010; Edburg *et al.*, 2012; Hicke *et*
112 *al.*, 2012) have been examined, but have been based primarily on a small number of individual
113 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 et al. 2011; Goetz et al. 2012; Fig 1). Drought-related forest mortality is a disturbance and can be described using classical disturbance theory (White & 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 (Fig 1a, #1). GPP recovers as surviving trees and understory vegetation produce more leaves (Anderegg *et al.*, 2012) and enhance their light use efficiency (Gough *et al.*, 2013) to better take advantage of newly available light resources and as new trees regenerate into the ecosystem (Stuart-Haëntjens *et al.*, 2015). Lower ecosystem-level leaf area and growth rates will tend to drive decreases in autotrophic respiration (R_a; Fig 1a, #2). Mortality also leads to a pulse input of leaf litter and coarse woody debris (Norton *et al.*, 2015), and thus decomposition of this plant matter is expected to drive lagged increases in heterotrophic respiration (R_h; Fig 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 *et al.*, 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 & Hua, 1991), and an additional pulse of R_h would be expected (Fig 1a, #4). Net ecosystem

137 productivity (NEP) should follow the trajectory outlined by GPP minus R_a and R_h, likely
138 experiencing an initial decline, followed by a period of positive uptake and a gradual return to
139 near equilibrium. Our framework assumes that the ecosystem is able to recover to near
140 equilibrium conditions, as assumed by almost all dynamic vegetation models, where GPP is
141 roughly in balance with R, such that NEP tends towards zero in the long-term (Odum, 1969).
142 Some ecosystems may, however, transition to alternate stable states (i.e. non-forest) after certain
143 types or magnitudes of climate-triggered mortality (Allen *et al.*, 2010), which we do not discuss
144 here.

145 Changes in ecosystem water fluxes following mortality commence with declines in the
146 sum of plant-level transpiration (E_{plant}) across the ecological community (Fig 1b, #1). In many
147 cases of both drought and insect-induced mortality, the mortality agent itself will drive this
148 decrease in transpiration even before leaf area losses are observed, for example through
149 extensive xylem cavitation (Martínez-Vilalta *et al.*, 2002; Anderegg *et al.*, 2014) or through
150 interruption of water transport by fungal pathogens associated with insects (Frank *et al.*, 2014),
151 both in trees that die and potentially in those that survive. Lower transpiration rates are predicted
152 to drive increased run-off – both surface run-off and streamflow (Fig 1b, #2) (Adams *et al.*,
153 2012). Declines in transpiration should also lead to increases in soil moisture, which is widely
154 supported by the timber harvest literature (Amiro *et al.*, 2010), although the changes are complex
155 throughout the soil profile (Miller *et al.*, 2011). In ecosystems with lower leaf area indices, there
156 also may be increases in soil evaporation rates (E_{soil}) due to increased radiation and temperature
157 exposure on bare soils (Raz-Yaseef *et al.*, 2010) (Fig 1b). If snags remain standing, a second
158 pulse of increased run-off is possible as snagfall may allow further erosion and increased surface
159 water transport (*cf.* Edburg *et al.* 2012) (Fig 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 Fig 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 analogues. There is growing evidence that thinning and defoliation may have relatively minor and short-lived effects on ecosystem fluxes (Amiro *et al.*, 2010; Miller *et al.*, 2011; Nave *et al.*, 2011; Dore *et al.*, 2012; Gough *et al.*, 2013; Templeton *et al.*, 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 *et al.*, 2005). While the direct effects of drought on ecosystem physiology can be large (Ciais *et al.*, 2005; Schwalm *et al.*, 2012; Gatti *et al.*, 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 *et al.*, 2013; Biederman *et al.*, 2014; Reed *et al.*, 2014).

183 Several compensatory mechanisms explain why substantial tree mortality may not
184 necessarily translate into major changes in ecosystem fluxes (Gough *et al.*, 2013; Rhoades *et al.*,
185 2013; Reed *et al.*, 2014) (Table 1). Firstly, moderate disturbances may increase canopy structural
186 heterogeneity and diffuse light penetration, improving light use efficiency and also resulting in
187 higher photosynthetic performance per unit leaf area (Gough *et al.*, 2013; Frank *et al.*, 2014). In
188 addition, higher resource availability (both water and nutrients) per unit of leaf area normally
189 results in higher photosynthetic and growth performance of remaining trees (Martínez-Vilalta *et*
190 *al.*, 2007; Dore *et al.*, 2012). Third, changes in ecosystem water use efficiency (WUE) can
191 modify the relative magnitude of changes in water and carbon fluxes after disturbance shown in
192 Fig 1 (Mkhabela *et al.*, 2009). Finally, leaf area index (LAI) may recover quickly due to the
193 regrowth of vegetation following disturbance, including both remaining trees and new
194 regeneration (Templeton *et al.*, 2015). Many forests have a huge capacity to recover leaf area
195 after disturbance if soil fertility is not negatively affected or even enhanced (Norton *et al.*, 2015).
196 This is particularly true if resprouting species are involved. For instance, LAI recovered
197 completely in a coppiced Mediterranean holm oak forest within 6 years after removing ~80% of
198 the forest basal area by thinning, despite the fact that the studied system was heavily water-
199 limited and that the strongest drought on record occurred two years after the thinning was
200 performed (López *et al.*, 2009).
201 Using the compensatory mechanisms discussed above, we outline a framework to predict
202 the changes in ecosystem fluxes within and across ecosystems after a pulse of mortality (Table 1,
203 Fig 2). These scaling variables (Table 1) should be considered as hypotheses of the mechanistic
204 effects of each variable when all other factors are roughly held constant (i.e. the slopes of a
205 partial regression between the scaling variable and ecosystem flux, while accounting for other

206 variables). Quantifying mortality severity is the first crucial component needed to scale from the
207 population to the ecosystem. While a population-level mortality rate (stems yr^{-1} ha^{-1}) is the
208 relevant metric to use in demographic studies aimed at predicting long-term community
209 dynamics, we suggest that in most cases the amount of biomass or basal area (g or m^2 yr^{-1} ha^{-1})
210 killed is a more useful quantification of severity of mortality and more likely to be related to
211 ecosystem-level functional consequences in the short- to mid-term. In this paper, we define
212 mortality broadly, including the complete loss of aboveground biomass (absent death of
213 meristem tissue), as this will affect ecosystem fluxes even if resprouting or clonal meristems do
214 not die. It is self-evident that the amount of mortality matters for the magnitude of ecosystem
215 response, but less clear about the timescales of ecosystem recovery, which may start to occur
216 while the mortality event is ongoing. In addition, the functional form of the relationship between
217 mortality severity and effects on ecosystem fluxes is largely unknown (Fig 2b). How mortality
218 scales to affect fluxes could be linear, non-linear, or threshold-driven (Fig 2b, dashed lines) and
219 will almost certainly depend on the ecosystem type and characteristics of mortality. Importantly,
220 the factors promoting fast recovery after mortality do not necessarily coincide with those
221 minimizing the initial effects.
222

223 **Mortality characteristics' influence on ecosystem flux trajectories**

224 We predict that the patch size and the timing of mortality, as well as the size-classes and
225 functional role of the trees killed will influence subsequent changes in ecosystem fluxes (Table
226 1). Tree mortality has long been known to be unevenly distributed in space and time (Franklin *et*
227 *al.*, 1987). Some mortality drivers, particularly fire and windthrow, yield large patches of forest
228 loss (Chambers *et al.*, 2013). Other drivers, such as mortality from competition or gap dynamics,

229 are likely to yield more dispersed and random patterns of mortality (Espírito-Santo *et al.*, 2014).
230 We posit that the spatial clustering (patch size distribution) of tree mortality will play a central
231 role in determining the effects on ecosystem fluxes (Table 1). All else being equal, large patches
232 of forest loss should have larger and longer effects on ecosystem fluxes than the same amount of
233 biomass lost from mortality in many more smaller patches. The theory underlying this essentially
234 derives from the relative importance of patch edge perimeter versus patch area because more
235 edges would be expected to facilitate both the utilization of newly available resources (water,
236 light, etc.) by neighboring trees as well as dispersal and colonization into the disturbed area,
237 leading to faster recovery of ecosystem fluxes (Franklin & Forman, 1987; Turner *et al.*, 1997).
238 The distribution of mortality patch sizes from disturbance has been quantified in some
239 ecosystems, notably the Amazon rainforest. Medium and large-scale disturbances (>1 ha) in the
240 Amazon roughly follow power-law relationships (Chambers *et al.*, 2013; Espírito-Santo *et al.*,
241 2014) (Fig 3). The shape and slope of this relationship is crucial in determining the effects on
242 ecosystem fluxes because the relationship describes the relative frequency of small versus large
243 disturbances and thus their relative impact on regional carbon fluxes (Espírito-Santo *et al.*,
244 2014).
245 We characterized the disturbance size and frequency for forest loss in a major temperate
246 region where drought- and insect-induced tree mortality has been exceptionally prominent (Allen
247 *et al.*, 2010) from two datasets: 1) Landsat estimates of forest loss from 2000–2013 (Hansen *et*
248 *al.*, 2013)(which also includes fire-driven losses) across the intermountain west, USA, and 2) an
249 individual widespread drought-driven tree mortality event of trembling aspen (*Populus*
250 *tremuloides*) (Huang & Anderegg, 2012). We observe that drought-, insect-, and fire-driven
251 forest loss across the intermountain western United States also appears to follow a power-law

252 relationship (Fig 3, dark green). Notably, however, the exponent of this relationship is $\alpha = -0.9$,
253 whereas the exponent in the Landsat-based analysis of the Amazon is $\alpha = -2.1$ (Fig 3) (Espírito-
254 Santo *et al.*, 2014). The less-steep exponent in this temperate region reveals that drought-, insect-
255 , and fire-induced mortality, which are the dominant causes of forest loss (Hicke *et al.*, 2013),
256 causes proportionally greater large disturbances than the disturbance distribution observed in the
257 Amazon, where small-scale disturbances dominate (Fig 3). The inclusion of fire-driven forest
258 losses could influence the slope of this power-law by increasing the relative proportion of large
259 patch disturbances. However, the Amazon disturbance data is roughly comparable in that it also
260 includes fires and windthrow disturbances. We also observed a power-law relationship in a
261 specific drought-driven mortality event of trembling aspen (*Populus tremuloides*) in Colorado,
262 USA, which has an exponent of $\alpha = -1.3$ (Fig 3; blue line). Forests in this temperate region
263 exhibit much higher frequency of large-scale disturbance than in the Amazon, which would favor
264 larger effects of mortality on ecosystem fluxes (note that the absolute numbers of disturbances
265 per hectare should not be compared between the Amazon and western US due to different bin
266 widths) (Fig 3).

267 The timing of the mortality event, particularly in relation to climatic conditions is also
268 likely to be relevant for ecosystem recovery and fluxes. A clear difference between drought-
269 induced mortality and other disturbances, such as commercial thinning, is that stressful
270 conditions are likely to prevail even after the mortality episode has come to an end, implying
271 legacy effects (Breda *et al.*, 2006; Anderegg *et al.*, 2013b, 2015a). In principle, recovery should
272 be faster if favorable climatic conditions, particularly with regards to water availability, occur
273 shortly after the mortality event, as increased water availability for the remaining vegetation
274 should promote the recovery of leaf area (Breda *et al.*, 2006). This leads to the prediction that

275 mortality episodes occurring relatively late during the dry season are likely to involve shorter
276 recovery times, provided that the rains return to normal levels at the beginning of the wet season.
277 The functional role of the trees killed will also impact the response of ecosystem fluxes to
278 a mortality event. Trees fill diverse functional roles and niches in forests, and thus a preferential
279 mortality of some species, which is common in drought- and insect-induced tree mortality (da
280 Costa *et al.*, 2010; Phillips *et al.*, 2010; Anderegg *et al.*, 2013a), may have important
281 consequences. Mortality of trees that fill functionally unique roles – for example in rooting
282 distribution, nitrogen fixation, flammability, a given successional status, or hydraulic
283 redistribution – should have larger effects on ecosystem fluxes. In general, we expect faster
284 recovery times if species with traits favoring regeneration after disturbance (e.g., resprouting) are
285 affected, as has been widely established for wildfires (Pausas *et al.*, 2009). Which other axes of
286 species' niches matter, however, is likely to vary from system to system and depend on the
287 relative importance of different abiotic constraints of the ecosystem.
288 Finally, the size class of trees affected by mortality is likely to be critical in evaluating
289 the ecosystem effects. Large trees play critical roles in many ecosystems and store
290 disproportionately large amounts of carbon (Slik *et al.*, 2013; Stephenson *et al.*, 2014) and,
291 obviously, they take longer to be replaced. Larger trees are also likely more susceptible to
292 drought stress, probably because disproportionally larger evaporation demands relative to their
293 larger uptake potential, leading to higher tension in water conducting systems (Merlin *et al.*,
294 2015). We thus hypothesize that mortality of larger trees is not only more likely under drought
295 stress but will also generally translate to larger effects on ecosystem fluxes. Consistent with this
296 prediction, simulations of the impacts of insect-driven mortality of *Pinus contorta*, which
297 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 *et al.*, 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 *et al.*, 2007; da Costa *et al.*, 2010; Phillips *et al.*, 2010) and elsewhere (Merlin *et al.*, 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.

Ecosystem properties' influence 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 *et al.*, 2013), where inputs from gross primary productivity tend to be higher (Carvalhais *et al.*, 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 *et al.*, 2013). Thus, structural and

321 compositional changes that occur following mortality will have important impacts on the long-
322 term trajectories of ecosystem fluxes.
323 Finally, higher functional diversity in an ecosystem and associated higher niche
324 redundancy should lead to faster recovery times and more muted ecosystem consequences. In
325 particular, we hypothesize that functional diversity specifically pertaining to drought tolerance
326 and recovery strategies should be one of the most important components of diversity. Theoretical
327 and empirical work has shown that biodiversity is crucial in helping systems reorganize and
328 return to a pre-disturbance state (Folke *et al.*, 2004). For example, the occurrence of isohydric
329 and anisophydric species or the mix between both has been found a key property to drought
330 vulnerability (Roman *et al.*, 2015). A prominent mechanism underlying the role of biodiversity is
331 termed the "insurance value of biodiversity," describing the observation that the presence in a
332 community of a diverse set of species allows for higher likelihoods that some species will be able
333 to a) tolerate a given disturbance and b) utilize available resources post-disturbance to regrow
334 quickly (Morin *et al.*, 2014).
335
336 **Recovery times of climate-induced tree mortality compared to other disturbances**
337 It has only been quite recently that severe drought and drought-induced tree mortality has
338 been widely considered in the disturbance literature. In order to locate climate-driven tree
339 mortality (drought-triggered and insect-triggered where insect-driven mortality is related to
340 climate) in context with other disturbances, we performed a literature review to identify studies
341 where: 1) mortality of trees occurred and was quantified and 2) the recovery of ecosystem fluxes
342 of carbon or water after disturbances were measured (Supplemental Material). We located 37
343 studies that met these criteria and spanned disturbances of drought, insects, windthrow, fire, and

344 timber harvest. We present results from 21 studies that included the most widely-reported and
345 relevant carbon flux – Net Ecosystem Productivity (NEP), but similar results were obtained if
346 other ecosystem fluxes were considered (Table S1). We classified disturbances as insect/drought-
347 driven, low severity fire/harvest, and high severity (i.e. stand clearing) fire/harvest.

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

362 Considering carbon fluxes in light of Fig. 1, declines in GPP were broadly observed
363 during and following drought-induced and insect-induced tree mortality in multiple conifer-
364 dominated ecosystems in North America, ranging from arid woodlands (Krofcheck *et al.*, 2014)
365 to montane pine forests (Brown *et al.*, 2012; Moore *et al.*, 2013) to high elevation forests (Frank
366 *et al.*, 2014). In the tropics, NPP was observed to recover within about 1 year after drought-

driven tree mortality (Brando *et al.*, 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 *et al.*, 2013) or recovery of the ecosystem to a net sink within 2-4 years post-outbreak (Brown *et al.*, 2012). In this case, the limitations of inputs from GPP to R_a appeared to lead to falling total respiration (Moore *et al.*, 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 *et al.*, 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 *et al.*, 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 (Fig 1; *cf.* Edburg et al., 2012).

Examining water fluxes following mortality, declines in transpiration and increases in soil moisture have been observed following extensive insect-driven tree mortality (Biederman *et al.*, 2014; Frank *et al.*, 2014). In most cases, increases in run-off are observed following drought- and insect-driven tree mortality (Adams *et al.*, 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 *et al.*, 2011; Biederman *et al.*, 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 while 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 (e.g. constant mortality rate independent of climate) or relatively simplistic (e.g. mortality increases outside an arbitrary climate envelope) in most current models (McDowell *et al.*, 2011), this is an active area of research (Fisher *et al.*, 2010; Anderegg *et al.*, 2015b; Mackay *et al.*, 2015). In particular, simulation 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 *et al.*, 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 (e.g. IBIS, SIB), to multi canopy-layer models (e.g. SPA JULES, CLM, ORCHIDAE), to models which dynamically simulate canopy gaps (e.g. 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

413 reaction and response to climate-induced mortality events (Powell *et al.*, 2013; Rowland *et al.*,
414 2015). In many models water stress is simplified to the impact of a soil water stress factor (Table
415 2), which is used to down-regulate stomatal conductance and/or photosynthesis in stressed
416 conditions, alongside the direct effects of changes in VPD on stomatal conductance (e.g.,
417 JULES, CLM, ED). Other vegetation models take a more process-based approach, for example
418 simulating a connection between leaf and soil water potential in which stomatal conductance is
419 maximized without allowing leaf water potential to fall below a critical threshold (SPA); or
420 simulating the hydraulic pathway from soil to leaf, with multiple resistances (Sperry *et al.*, 1998)
421 (Table 2). Variability in both canopy structure and water relations within models will alter both
422 the initial pulse response to a morality event, as well as the feedbacks which control the recovery
423 time, such as gaps allowing increased availability of light (Table 2).

424 Considering the elements of mortality that most impact fluxes (Fig 2), some of the critical
425 processes needed to capture ecosystem flux dynamics after mortality are currently present in
426 ecosystem models (Table 2), but other key processes are not well-represented. No large-scale
427 ecosystem models to our knowledge can currently represent spatial clustering of mortality
428 (Fisher *et al.*, 2010), although gap models, such as ED, can go some way towards representing
429 mortality patterns through a statistical representation of the spatial distribution of trees of
430 differing canopy heights. Large-scale gradients in productivity are well-represented in most
431 models, however currently none of the models represented in Table 2 sufficiently represent
432 functional diversity in a forest and therefore full diversity of variation in drought-response and
433 post-disturbance regeneration strategies between plant functional types (Fisher *et al.*, 2010;
434 Powell *et al.*, 2013; Anderegg, 2014). Individual stem or cohort-based models (e.g. ED, PPA)
435 may be able to represent functional diversity more effectively through using a continuum of trait

436 variation (Fyllas *et al.*, 2014), rather than through 1 or 2 discrete types of tree or plant, with the
437 trade-off that increased representation of diversity is computationally challenging at regional to
438 global scales.

439 Considering the key compensating mechanisms that would buffer flux responses, we
440 highlighted above the key roles of changes in photosynthetic performance of surviving trees,
441 increased resource availability, and changes in allocation to allow rapid recovery of LAI. Similar
442 to the challenge of simulating the full functional diversity of forests, most models in Table 2
443 have fixed photosynthetic traits, which would result in slower recovery of carbon uptake.
444 Dynamic LAI is generally incorporated into most vegetation models (Table 2), albeit with large
445 inter-model variability in absolute values and dynamic changes (Rowland *et al.*, 2015). However,
446 many models have constant carbon allocation to different tissues, which is potentially a major
447 limitation in simulating recovery of radial growth after drought (Anderegg *et al.*, 2015a). Finally,
448 in relation to recovery to mortality many of these mechanisms remain relatively untested against
449 observational data, and we suggest that the development of datasets and frameworks for
450 calibrating models to simulate such processes may be necessary.

451 Two major techniques provide most of the observational evidence examining changes in
452 ecosystem fluxes in carbon and water following tree mortality. First, several studies have used
453 spatial gradients in mortality severity across regions and/or across different times since mortality
454 (i.e. chronosequences) (Hansen *et al.*, 2015). These studies allow examination of ecosystem
455 stocks and fluxes well after mortality occurred and also integrate large spatial scales, such as
456 watersheds. However, the extent to which mortality also covaried with other ecosystem attributes
457 that would affect subsequent fluxes, such as soil type or stand density, is largely unknown and a
458 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). While 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 *et al.*, 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 *et al.*, 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 (e.g. 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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726 # Tables

727 **Table 1.** Hypothesized mortality characteristics (A) and ecosystem properties (B) that affect the

728 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 *et al*. (1997)
Timing (in relation to climate)	Mortality is followed by a relatively favorable period, particularly with regards to water availability	Increased resource availability and faster recovery of leaf area	Bréda *et al*. (2006)
Size-class of trees killed	Mortality affects preferentially small trees	Increased resource availability for the remaining trees	Pfeifer *et al*. (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 *et al.* (2015) Matheny *et al.* (2014)
(B) Ecosystem properties			
Turnover time (productivity)	Productivity is high	Faster dynamics; higher capacity to build up biomass after disturbance	Brando *et al.* (2008)
Diversity	Diversity is high, particularly concerning drought-response functional diversity	Insurance effect	Morin *et al.* (2014)

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731 **Table 2.** Key responses/mechanisms that will influence the effects of mortality on ecosystem
732 fluxes and how they are simulated in some current examples of widely-used ecosystem models
733 (not an exhaustive list of models that include these processes). Abbreviations match those of Fig.
734 1.

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
		Senesence	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 modelled 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
Runoff		Simulation of runoff	CLM, ED, JULES, ORCHIDAE

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Figure Legends

Figure 1: Expected changes in ecosystem fluxes of carbon (a) and water (b) during and following a tree mortality event (after Harmon et al. 2011; Edburg et al. 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 leaf area index (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).

Figure 2: Cross ecosystem-scaling of the effect of mortality on fluxes. (a) Flux (e.g. 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) (e.g. Table 1); white lines represent hypothetical linear and non-linear scaling.

Figure 3: Mortality frequency versus area affected (events per bin width per hectare per year) in the Amazon basin (light green; data from from Espirito-Santo *et al*. 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-

759 induced tree mortality, and a drought-driven widespread mortality event (blue) of
760 trembling aspen (*Populus tremuloides*) in Colorado, USA. Red lines are best fit
761 regressions for a power law relationship.
762 Figure 4: Observed recovery time in years of net ecosystem productivity (NEP) after disturbance
763 from insect/drought-driven mortality, low severity fire or harvest, and high severity (i.e.
764 stand- clearing) fire or harvest. Letters indicate statistically significant differences (Tukey
765 HSD $p<0.05$). Numbers beneath indicate the number of studies and number of sites (in
766 parentheses).
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Figures

Figure 1

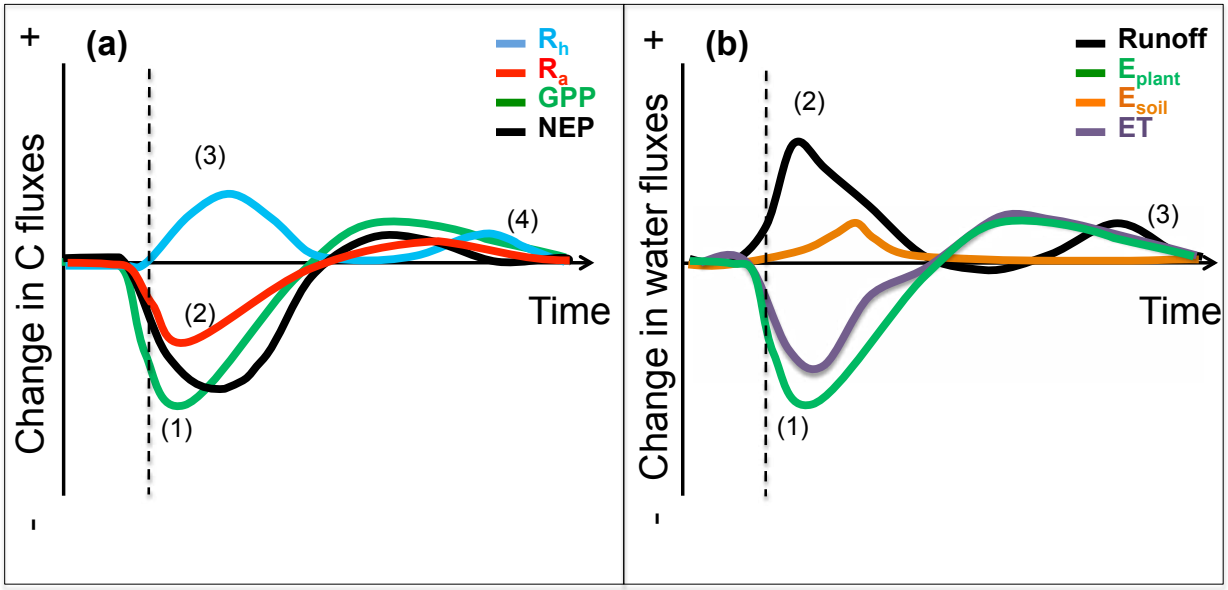


Figure 2

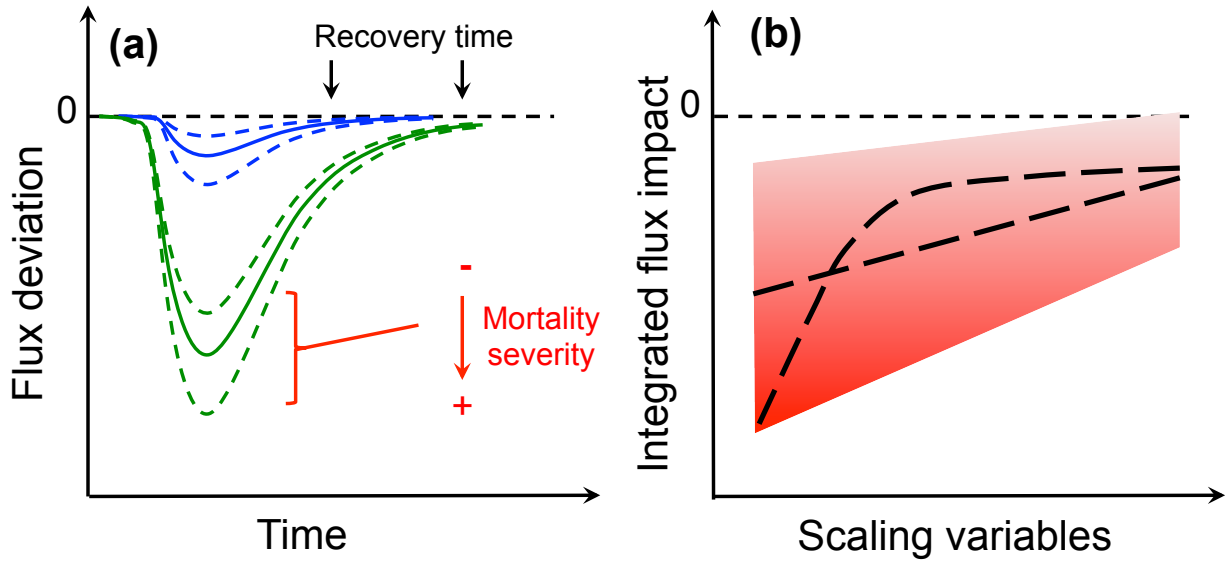
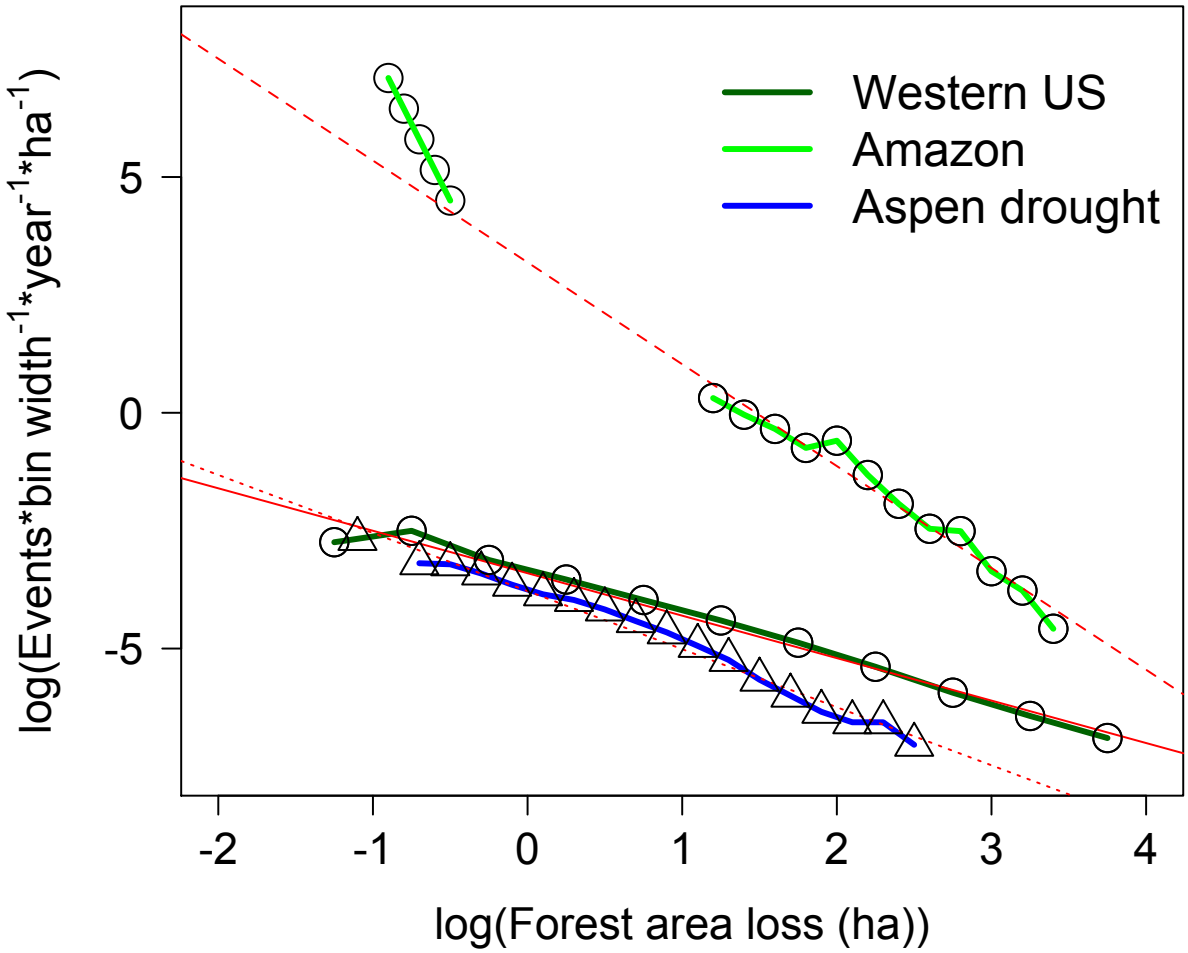

(a)
Recovery time
0
Flux deviation
Mortality
severity
-
+
Time
(b)
0
Integrated flux impact
Scaling variables

Figure 3


Western US
Amazon
Aspen drought
log(Events*bin width^{-1}*year^{-1}*ha^{-1})
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-1
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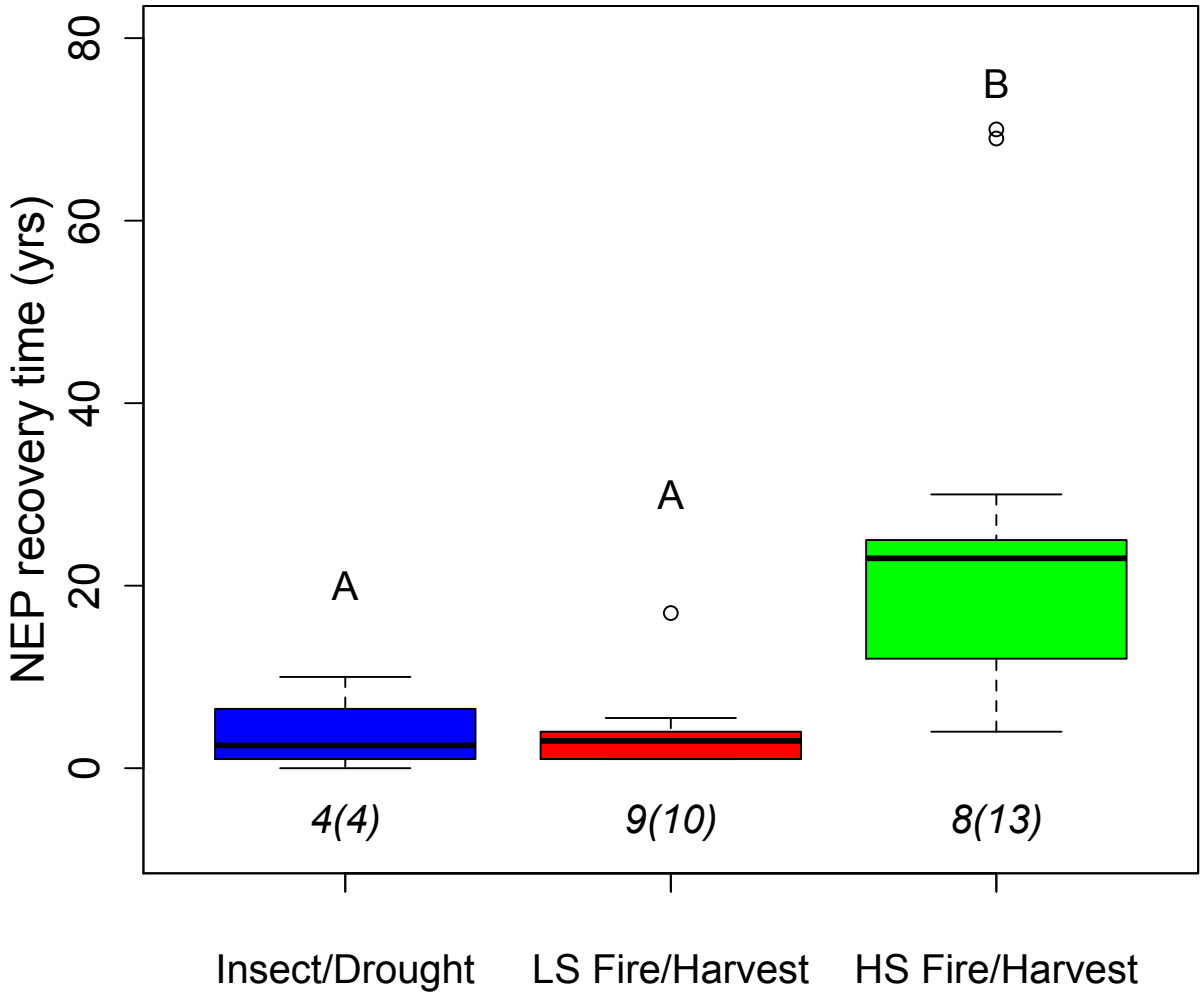
log(Forest area loss (ha))

Figure 4


NEP recovery time (yrs)
0
20
40
60
80
A
A
B
4(4)
9(10)
8(13)
Insect/Drought
LS Fire/Harvest
HS Fire/Harvest