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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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46   *Abstract*

47   Drought- and heat-driven tree mortality, along with associated insect outbreaks, have

48   been observed globally in recent decades and are expected to increase in future climates. Despite

49   its potential to profoundly alter ecosystem carbon and water cycles, how tree mortality scales up

50   to ecosystem functions and fluxes is uncertain. We describe a framework for this scaling where

51   the effects of mortality are a function of the mortality attributes, such as spatial clustering and

52   functional role of the trees killed, and ecosystem properties, such as productivity and diversity.

53   We draw upon remote sensing data and ecosystem flux data to illustrate this framework and

54   place climate-driven tree mortality in the context of other major disturbances. We find that

55   emerging evidence suggests that climate-driven tree mortality impacts may be relatively small

56   and recovery times are remarkably fast (~4 years for net ecosystem production). We review the

57   key processes in ecosystem models necessary to simulate the effects of mortality on ecosystem

58   fluxes and highlight key research gaps in modeling. Overall, our results highlight the key axes of

59   variation needed for better monitoring and modeling of the impacts of tree mortality and provide

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

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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

114   synthesis and perspective necessary for predicting when and where the functional impacts of tree

115   mortality will be most severe, which is largely missing to date.

116

117   **How tree mortality affects ecosystem fluxes**

118   The general trajectory of the effects of tree mortality on forest ecosystem fluxes of carbon

119   and water can be predicted from first principles and ecological theory (Harmon et al. 2011;

120   Goetz et al. 2012; Fig 1). Drought-related forest mortality is a disturbance and can be described

121   using classical disturbance theory (White & Pickett, 1985). As trees die, independent of the

122   causal agent of mortality, leaf area in an ecosystem will temporarily decline. The corresponding

123   decline of ecosystem photosynthesis leads to declines in gross primary productivity (GPP) over

124   some time period (Fig 1a, #1). GPP recovers as surviving trees and understory vegetation

125   produce more leaves (Anderegg *et al.*, 2012) and enhance their light use efficiency (Gough *et al.*,

126   2013) to better take advantage of newly available light resources and as new trees regenerate into

127   the ecosystem (Stuart-Haëntjens *et al.*, 2015). Lower ecosystem-level leaf area and growth rates

128   will tend to drive decreases in autotrophic respiration (R_a; Fig 1a, #2). Mortality also leads to a

129   pulse input of leaf litter and coarse woody debris (Norton *et al.*, 2015), and thus decomposition

130   of this plant matter is expected to drive lagged increases in heterotrophic respiration (R_h; Fig 1a,

131   #3). The direct effects of drought, however, will act to suppress R_h due to soil moisture

132   limitations, which could counteract this litter decomposition pulse in the short term (Rowland *et*

133   *al.*, 2014). Finally, in ecosystems with slower turnover and decomposition rates – particularly

134   colder and drier ecosystems – dead bole snags may remain standing for relatively long periods of

135   time. When these snags fall to the ground their decomposition may be relatively fast (Harmon &

136   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

160   sum of precipitation (assumed to be constant in our hypothetical example) minus run-off,

161   groundwater infiltration (also assumed constant, although in reality this could change due to

162   changes in canopy openness), and plant and soil water loss. ET is predicted to decline during and

163   after the disturbance and then to gradually recover afterwards.

164

165   **Scaling mortality to fluxes across ecosystems**

166   The net effect of mortality on ecosystem fluxes is the integral of the trajectories in Fig 1

167   over time. This highlights that two key characteristics will determine the magnitude of the

168   impacts: 1) the magnitude of the initial "pulse" response and 2) the recovery rate of the

169   ecosystem (Table 1). Both of these characteristics are likely to vary substantially across

170   ecosystems and mortality events. The functional impacts of drought-related tree mortality are

171   likely to differ from those of stand-clearing disturbances, such as fire or clearcut harvests,

172   whereas stand-thinning disturbances such as thinning harvests, low-intensity fires, or storms may

173   provide better analogues. There is growing evidence that thinning and defoliation may have

174   relatively minor and short-lived effects on ecosystem fluxes (Amiro *et al.*, 2010; Miller *et al.*,

175   2011; Nave *et al.*, 2011; Dore *et al.*, 2012; Gough *et al.*, 2013; Templeton *et al.*, 2015), in

176   agreement with studies showing that ecosystem structure, such as canopy height and root

177   biomass, may recover more slowly than ecosystem function, such as NEP, after disturbance

178   (Beard *et al.*, 2005). While the direct effects of drought on ecosystem physiology can be large

179   (Ciais *et al.*, 2005; Schwalm *et al.*, 2012; Gatti *et al.*, 2014), we hypothesize that the functional

180   impacts of drought-related *tree mortality* itself may be relatively mild, at least in some

181   ecosystems, as has been recently shown for climate-triggered mountain pine beetle infestations

182   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

298 distribution of diameter size classes living and killed had the largest impact on simulated carbon

299 fluxes (Pfeifer *et al.*, 2011). Critically, both plot networks and drought experiments have

300 indicated that drought-induced mortality is likely to preferentially affect large trees in tropical

301 forests (Nepstad *et al.*, 2007; da Costa *et al.*, 2010; Phillips *et al.*, 2010) and elsewhere (Merlin *et

302 al.*, 2015), which may induce larger ecosystem effects than if mortality were random. Scaling

303 from the individual tree to ecosystem level responses is, however, far from trivial, implying that

304 the association between larger trees being affected and higher overall functional impacts may not

305 be universal.

306

307 **Ecosystem properties' influence on ecosystem flux responses**

308 We hypothesize that properties of different ecosystem and biomes, particularly

309 productivity/turnover time and tree species diversity, will strongly affect ecosystem flux

310 trajectories after mortality. Ecosystems that exhibit higher productivity and faster turnover times

311 should, all else being equal, recover more quickly. Aboveground plant carbon turnover times

312 vary substantially across ecosystems and are generally faster in tropical ecosystems (Galbraith *et

313 al.*, 2013), where inputs from gross primary productivity tend to be higher (Carvalhais *et al.*,

314 2014). The speed of regrowth and regeneration is generally thought to be much slower in cold-

315 limited and water-limited ecosystems, correlating with growth rate differences (Reich, 2014).

316 The degree of "competitor release" triggered by tree mortality and the growth rates of these

317 competitors should greatly influence ecosystem recovery from mortality. For example, thinning

318 and the related reduction in competition for light and water increased growth of the remaining

319 trees in xeric pine stands for up to three decades after the treatment, with higher and longer

320 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-

367 driven tree mortality (Brando *et al.*, 2008). Flux tower studies in *Pinus contorta* dominated

368 forests, which have experienced the largest insect-triggered mortality events ever documented,

369 found that total ecosystem respiration (sum of R_a and R_h) declined in parallel with GPP and thus

370 found little net change in NEP (Moore *et al.*, 2013) or recovery of the ecosystem to a net sink

371 within 2-4 years post-outbreak (Brown *et al.*, 2012). In this case, the limitations of inputs from

372 GPP to R_a appeared to lead to falling total respiration (Moore *et al.*, 2013). Despite extremely

373 high mortality rates, 60-90% of trees killed at these sites, and relatively low diversity in the plant

374 community, the studies observed that remaining vegetation and regrowth caused GPP and thus

375 NEP to recover relatively rapidly at an ecosystem scale (Brown *et al.*, 2010, 2012). However,

376 recent evidence has highlighted large differences between eddy flux estimates and direct

377 chamber measurements of respiration in insect-attacked forests, indicating uncertainty in

378 ecosystem respiration and thus NEP quantification (Speckman *et al.*, 2014). In addition, large

379 amounts of trees in these ecosystems are still standing and thus the short timescale of most

380 studies (most are <6 years post-disturbance) may not capture a second peak or extended period

381 of respiration after tree fall (Fig 1; *cf.* Edburg et al., 2012).

382   Examining water fluxes following mortality, declines in transpiration and increases in

383 soil moisture have been observed following extensive insect-driven tree mortality (Biederman *et*

384 *al.*, 2014; Frank *et al.*, 2014). In most cases, increases in run-off are observed following drought-

385 and insect-driven tree mortality (Adams *et al.*, 2012), however in some systems increases in soil

386 evaporation and snow sublimation appear to outweigh the declines in transpiration, leading to

387 muted or even declines in run-off and streamflow (Guardiola-Claramonte *et al.*, 2011;

388 Biederman *et al.*, 2014). The average recovery time of run-off and water yield from harvest and

389 fire disturbances was 5.4 years (range 2-16 years) (Table S1), and while no studies to our

390 knowledge have quantified recovery of run-off after drought-induced mortality, the relatively

391 fast NEP recovery times we observed suggest that the recovery times from these other

392 disturbances are a reasonable approximation.

393

394 **Research gaps in mortality-flux data and current ecosystem models**

395   Models provide useful frameworks for performing scaling and testing scaling hypotheses,

396 as they include some representation of the biotic and abiotic effects on tree physiology,

397 demography, and forest fluxes (Table 2). How models simulate drought-induced mortality is one

398 of the largest areas of uncertainty and while this is either absent (e.g. constant mortality rate

399 independent of climate) or relatively simplistic (e.g. mortality increases outside an arbitrary

400 climate envelope) in most current models (McDowell *et al.*, 2011), this is an active area of

401 research (Fisher *et al.*, 2010; Anderegg *et al.*, 2015b; Mackay *et al.*, 2015). In particular,

402 simulation of canopy structure, such as whether trees or cohorts of trees are simulated, and of

403 plant physiology are critical elements that determine how and if models can simulate drought-

404 induced mortality and its effects (McDowell *et al.*, 2013).

405   Currently a variety of vegetation models exist which employ different representations of

406 canopy structure and ecosystem physiology in order to simulate ecosystem scale responses, some

407 of which we summarize in Table 2. In relation to canopy structure most commonly used

408 vegetation models vary from being a simple "big leaf" model, within which the canopy is

409 represented by a single canopy layer (e.g. IBIS, SIB), to multi canopy-layer models (e.g. SPA

410 JULES, CLM, ORCHIDAE), to models which dynamically simulate canopy gaps (e.g. ED,

411 PPA). The representation of water stress and its interaction with canopy structure in models is

412 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

459   measurement of ecosystem fluxes where mortality is occurring, using for instance eddy

460   covariance methods or streamflow gauges. These studies are more direct, but relatively rare

461   (Table S1). While some of this rarity is due to relatively few flux towers that can be

462   opportunistically placed in regions experiencing a pulse of drought- or insect-induced mortality

463   (Brown *et al.*, 2012), another major impediment is that many flux studies often do not report

464   mortality rates within the flux tower footprint, even when it has occurred (Ciais *et al.*, 2005).

465   Both reporting of mortality rates within existing flux towers and additional studies placing flux

466   towers in ongoing disturbance to monitor recovery are greatly needed.

467

468   **Conclusion**

469   We find here that mortality attributes and ecosystem properties interact to determine the

470   effect of climate-driven tree mortality on ecosystem fluxes. The magnitude of the initial impact

471   (e.g. drought) has been much better quantified than recovery dynamics, but both are critical in

472   determining ecosystem-level consequences. We argue that the functional effects of drought-

473   driven tree mortality are comparable to those of other, non stand-replacing disturbances and

474   should be put in the same theoretical framework, but it is unique in that it co-occurs with a direct

475   stress on ecosystems that can have large impacts on fluxes. Emerging evidence suggests that the

476   effect of tree mortality itself (not the inciting drought) on ecosystem fluxes may be smaller and

477   recovery times may be faster than previously thought, suggesting that compensating mechanisms

478   are very strong.

479

480

481

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725

Tables

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 *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)

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). Abbreviations match those of Fig.

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

736 **Figure Legends**

737 Figure 1: Expected changes in ecosystem fluxes of carbon (a) and water (b) during and following

738   a tree mortality event (after Harmon et al. 2011; Edburg et al. 2012). A dashed line

739   indicates the beginning of the mortality event. Carbon fluxes include a decline in gross

740   primary productivity (GPP) driven mostly by reductions in leaf area index (1), a decline

741   in autotrophic respiration (R_a) due mostly to reductions in leaf area and growth rates (2),

742   an increase in heterotrophic respiration (R_h) driven mostly by decomposition of dead

743   leaves and roots (3), a decrease in net ecosystem productivity (NEP), and in some

744   systems a second pulse of heterotrophic respiration driven mostly by decomposition of

745   fallen stems and snags (4). Water fluxes include a decline in plant transpiration (E_{plant})

746   driven mostly by reductions in leaf area (1), increases in run-off, including both run-off

747   and streamflow (2), and in some systems a potential secondary increase in run-off due to

748   increased surface water movement after snag fall (3).

749 Figure 2: Cross ecosystem-scaling of the effect of mortality on fluxes. (a) Flux (e.g. GPP, NEP,

750   ET) deviation from a baseline over time as a function of mortality severity (dashed versus

751   solid) and the ecosystem and mortality attribute scaling variables (green and blue). (b)

752   Integrated impact on ecosystem flux as a function of ecosystem and mortality attribute

753   scaling variables (polygon) (e.g. Table 1); white lines represent hypothetical linear and

754   non-linear scaling.

755 Figure 3: Mortality frequency versus area affected (events per bin width per hectare per year) in

756   the Amazon basin (light green; data from from Espirito-Santo *et al.* 2014 from lidar for

757   the upper line and satellite remote sensing for the lower line), intermountain western

758   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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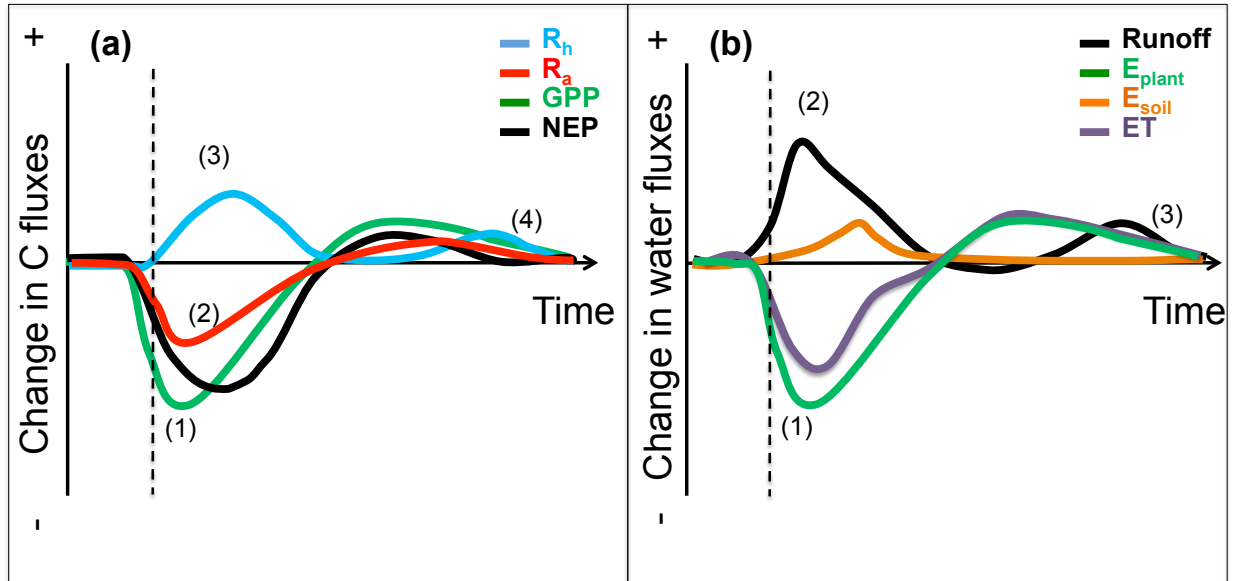
Figures

Figure 1

810   Figure 3
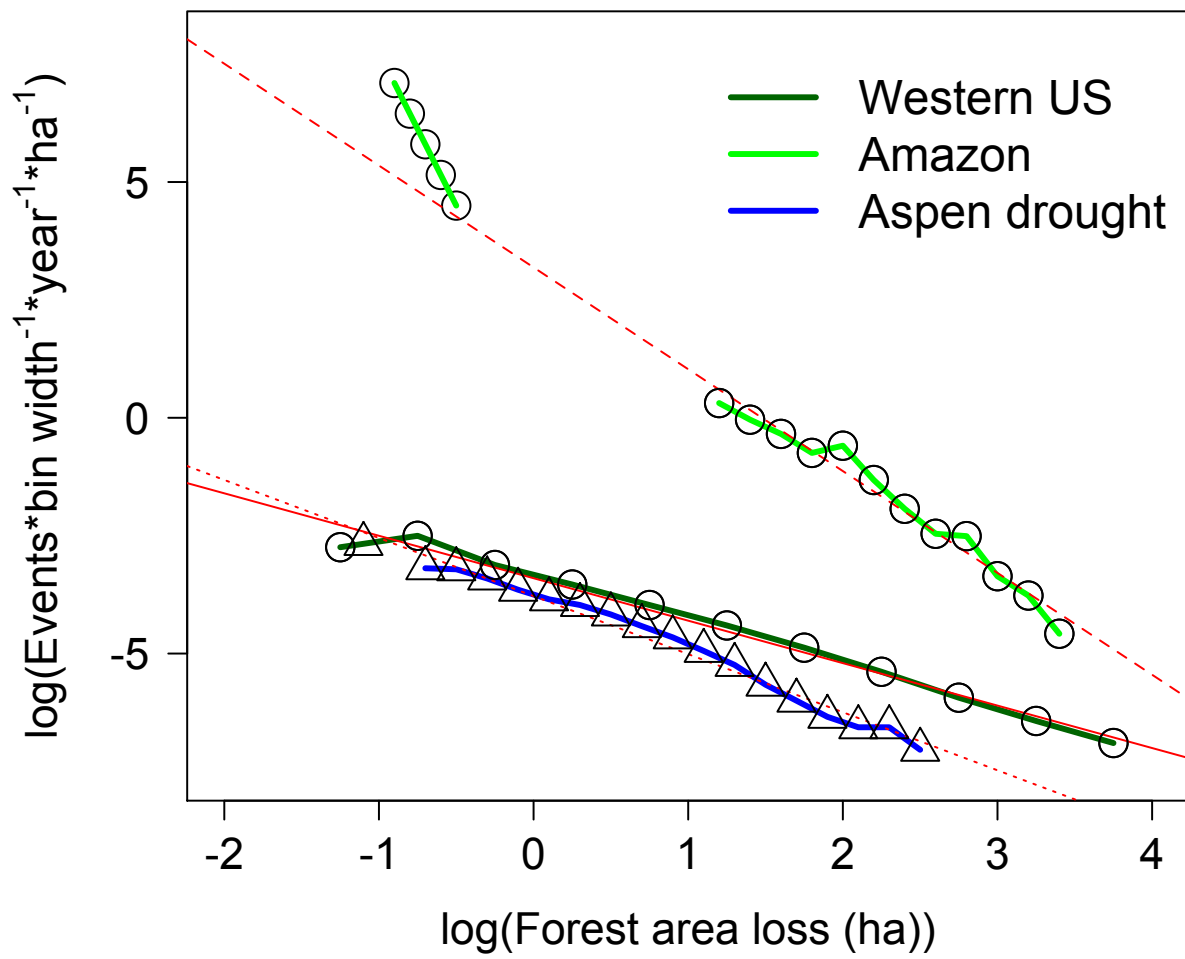
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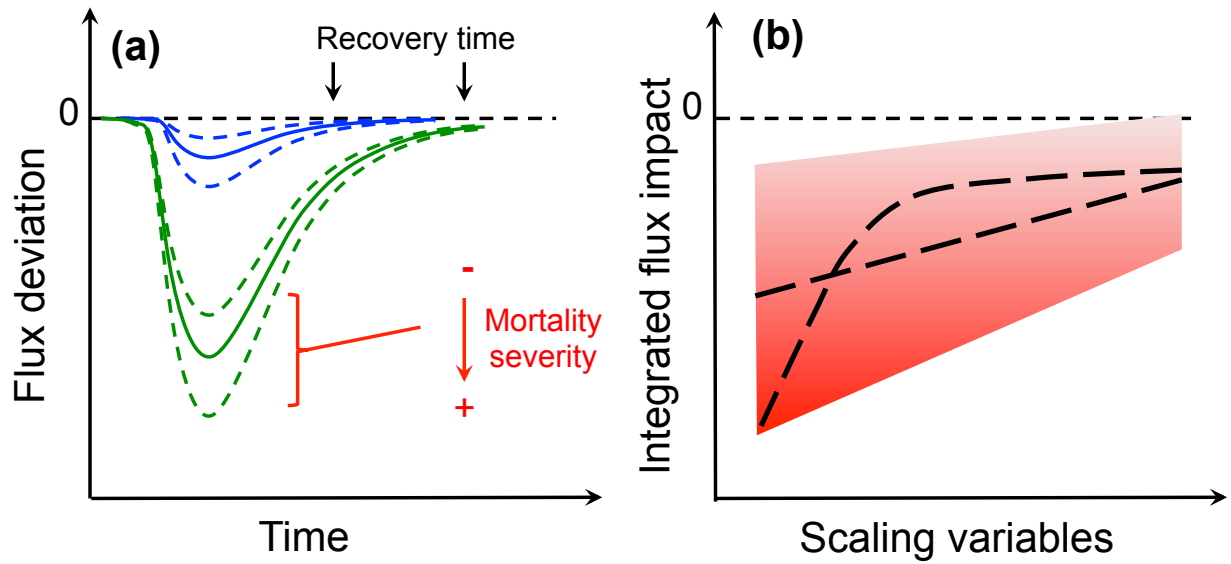
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