Tansley review

Drivers and mechanisms of tree mortality in moist tropical forests

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Summary

Tree mortality rates appear to be increasing in moist tropical forests (MTFs) with significant carbon cycle consequences. Here, we review the state of knowledge regarding MTF tree mortality, create a conceptual framework with testable hypotheses regarding the drivers, mechanisms and interactions that may underlie increasing MTF mortality rates, and identify the next steps for improved understanding and reduced prediction. Increasing mortality rates are associated with rising temperature and vapor pressure deficit, liana abundance, drought, wind events, fire and, possibly, CO_2 fertilization-induced increases in stand thinning or acceleration of trees reaching larger, more vulnerable heights. The majority of these mortality drivers may kill trees in part through carbon starvation and hydraulic failure. The relative importance of each driver is unknown. High species diversity may buffer MTFs against large-scale mortality events, but recent and expected trends in mortality drivers give reason for concern regarding increasing mortality within MTFs. Models of tropical tree mortality are advancing the representation of hydraulics, carbon and demography, but require more empirical knowledge regarding the most common drivers and their subsequent mechanisms. We outline critical datasets and model developments required to test hypotheses regarding the underlying causes of increasing MTF mortality rates, and improve prediction of future mortality under climate change.

I. Introduction

Moist tropical forests (MTFs, see Box 1 Glossary) are the largest terrestrial carbon sink in the world (Pan *et al.*, 2011) and house the majority of Earth's terrestrial biodiversity (Myers *et al.*, 2000; Kreft & Jetz, 2007). The spatial patterns of biomass carbon storage in MTFs are primarily driven by mortality (see Box 1 Glossary) rather than productivity (Galbraith *et al.*, 2013; Johnson *et al.*, 2016). The

Box 1 Glossary

Background mortality: also considered a fixed mortality rate (e.g. % yr^{-1}, carbon m^{-2} yr^{-1}) in models and referred to as such in this article; this is the theoretically stable mortality rate under a non-changing environment.
Biotic agents: insects, fungi and other pathogens that attack and sometimes kill trees directly or by weakening them (e.g. defoliation, or rot impacts on wind resistance).
Carbon starvation: the *process* by which limited carbon uptake (e.g. as a result of stomatal closure, shade or leaf area loss to wind damage) relative to carbon demand (e.g. growth, respiration, defense) results in a decline in carbon-driven metabolism, hydraulic repair or ability to defend against pests, and ultimately promotes mortality (McDowell *et al.*, 2011).
Earth system model (ESM): models designed to simulate the coupled influences and feedbacks of climate, land and ocean. Land surface models operate within ESMs.
Hydraulic failure: mortality via dehydration; often associated with prolonged periods of xylem conductivity loss > 60% in field studies (McDowell *et al.*, 2013).
Lianas: woody plants that utilize free-standing hosts to support their weight as they grow into the canopy. Lianas are typically aggressive consumers of light, water and nutrients.
Moist tropical forests (MTFs): forests with mean annual precipitation > 1500 mm, including both aseasonal and seasonal precipitation regimes (e.g. with a dry season < 100 mm per month for 5 months or less; Vitousek & Sanford, 1986).
Mortality drivers: factors which, when they experience a directional change, so do mortality rates. Examples include decreasing precipitation, increasing temperature and increasing biotic attack.
Mortality mechanisms: mortality drivers cause changes in mechanisms that lead to mortality, such as altering plant structure (e.g. via windthrow, fire) or physiology (e.g. shade-induced carbon starvation, drought-induced hydraulic failure).
Mortality rate: can be defined using many units, typically % yr^{-1} (number of trees died per number of total individuals live and dead per year), or basal area (m^2 basal area died per m^2 of total stems per year) or biomass (kg C died per kg C standing biomass per year). Corrections for biomass weighting, non-balanced plot sizes or sampling periods over time and space are often employed when calculating mortality rates from inventory data. See Supporting Information Methods S1 for equations.

climatic and ecological benefits of intact MTFs are potentially threatened by increasing tree mortality as a result of environmental and biotic changes (Phillips *et al.*, 2009; Lewis *et al.*, 2011; Davidson *et al.*, 2012; Chambers *et al.*, 2013; Erb *et al.*, 2016). Valuable tools for the prediction of the future of MTF tree mortality are ecosystem and Earth system models (ESMs; see Box 1 Glossary; Seiler *et al.*, 2015; Sperry & Love, 2015; Levine *et al.*, 2016; Xu *et al.*, 2016). These 'next-generation' models have enabled progress on mortality prediction, yet these advances have also revealed multiple questions, particularly regarding MTF tree mortality drivers and mechanisms, which must be addressed to enable accurate prediction (Powell *et al.*, 2013; Thurner *et al.*, 2017). Improving our understanding and model prediction is challenged in part by the enormous variability in mortality, temporally, regionally and within sites, according to tree size and other traits (Fig. 1).

Accurate prediction of the global climate warming trajectory is challenged by non-mechanistic understanding and simulation of future MTF carbon balance as influenced by tree death (Friedlingstein *et al.*, 2006; Friend *et al.*, 2014). To address this challenge, we describe the state of knowledge of (non-harvest) MTF tree mortality drivers and their associated physiological mechanisms, and investigate the likelihood that these drivers will strengthen in the future. We use empirical and simulation evidence. Throughout this review, we generate a conceptual framework that provides testable hypotheses regarding the causes, mechanisms and interactions associated with increasing mortality rates. We briefly investigate

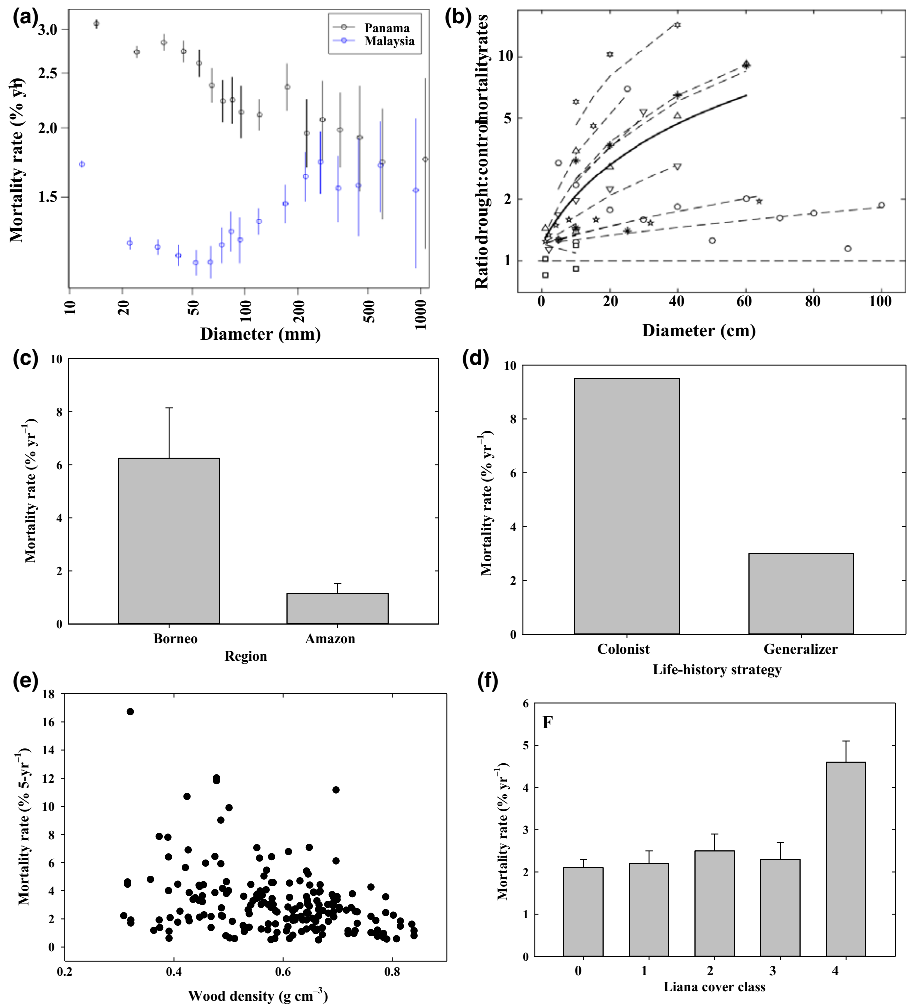

Fig. 1 Axes of variability in tropical tree mortality. (a) Mortality rate (as log(initial number) – log(number survivors))/(years)) vs stem diameter in Pasoh, Malaysia and Barro Colorado, Panama (bars are 95% confidence intervals (CIs), no major droughts during censuses); this highlights that both negative and positive mortality rates as a function of diameter can be found (data from Muller-Landau *et al.*, 2006). (b) Mortality rates (number of individuals died per number of total individuals per year; all subsequent figures use this calculation; see Box 1 Glossary and Supporting Information Methods S1 on mortality rate calculations) plotted as the ratio of mortality rate during drought relative to a control period across a range of stem diameters for 12 sites across the tropics (symbols represent different sites), showing the clear pattern of size–mortality relationships *during droughts* (data from Bennett *et al.*, 2015). (c) The mortality rates in forests in Borneo and the Amazon measured post-drought, highlighting regional differences (data from Phillips *et al.*, 2010). (d) Mortality rate vs life-history strategy in Barro Colorado, Panama, highlighting the role of successional strategy on long-term mortality rates (data from Condit *et al.*, 1995). (e) Mortality rate vs wood density in Barro Colorado, Panama, highlighting a significant but weak relationship ($P < 0.05$; data from Wright *et al.*, 2010). (f) Mortality rate as a function of liana cover class in Pasoh, Malaysia, highlighting the influence of lianas on mortality. Liana cover class: 0, no lianas; 1, up to 25% of the crown covered by lianas; 2, 26–50%; 3, 51–75%; 4, 76–100% (data from Wright *et al.*, 2015). All error bars are ± SE.

factors that may promote survival, and propose a path forward for both empirical and modeling work to better understand the future of MTF tree mortality. Our focus is on intact (primary or old-growth) forests, including aseasonal (wet) and seasonally dry forests, because of their large role in the global carbon cycle (Pan *et al.*, 2011). We are focused on intact forests, so that we may investigate whether global drivers are associated with mortality in the absence of direct human intervention. We draw an outer boundary to our geographic scope at the dry margin at which forest fires historically occurred. Our scope includes all evidence available from the MTFs in South America, Africa and Southeast Asia. We are focused only on mortality; we do not discuss resilience and recovery rates from mortality events, although these are critical questions relative to the terrestrial carbon sink. We use evidence from the extra-tropics when a process appears to be global in nature (e.g. warming impacts on carbon balance) and when tropical evidence is scarce. This ultimately allows hypothesis generation with regard to the trends in MTF tree mortality drivers and their mechanisms.

II. Increasing mortality rates in the Amazon Basin

The mortality of individual trees within intact, old-growth forests has been increasing during recent decades in the Amazon Basin (Fig. 2; see Box 1 Glossary and Supporting Information Methods S1 for definitions of mortality rates; unless otherwise specified, the mortality rate in this article is always defined as the percentage individuals died per total number of live and dead individuals per year), having a significant impact on biomass carbon loss (Fig. S1) and net ecosystem carbon storage (Phillips & Gentry, 1994; Phillips *et al.*, 2004; Brienen *et al.*, 2015). The trends for the Amazon Basin are similar whether plotted as percentage mortality rates or biomass mortality (Figs 2, S2). These results from hundreds of plots across the Amazon are consistent with observed pulse mortality events in Southeast Asia (Phillips *et al.*, 2010), and declines in remotely sensed indices (assumed to be correlated with canopy or whole-tree loss) of canopy biomass post-drought in the Amazon (Saatchi *et al.*, 2013) and canopy health in the Congo attributed to drought and warming (Zhou *et al.*, 2014). However, not all tropical forests have exhibited increasing mortality recently (in Panama; Condit *et al.*, 2006; Meakem *et al.*, 2017). The drivers and mechanism(s) underlying this increasing rate of tree death in some areas (but not in others) are currently unknown (Phillips & Gentry, 1994; Stephenson *et al.*, 2011; Feldpausch *et al.*, 2016).

At the coarsest level, increasing mortality rates in the Amazon are consistent with observed forest inventory results from old-growth boreal and temperate forests of North America (Fig. 2; Luo & Chen, 2015). Direct statistical comparison of the lines for the Amazon and for North America is precluded by many limitations (see Notes S1 for details), but the similar general trends for the two regions allow for the possibility of similar drivers and mechanisms across North and South America. The Amazon Basin has higher mortality rates than North America (Fig. 2), which may be expected based on the observed correlation between productivity and turnover at regional (Amazon, Fig. 3, and see alternative versions of Fig. 3 (Fig. S3A,B)) and global (Phillips & Gentry, 1994; Phillips *et al.*, 2004; Stephenson & van Mantgem, 2005) scales. We note that an important question arises from Fig. 2: is the relationship of mortality rate over time non-linear or linear (our analysis of the data of Brienen *et al.* 2015 shows no significant difference between linear and non-linear fits ($P = 0.36$; see Notes S1 for statistical details)). A non-linear pattern is logical because mortality never reaches zero historically; however, a continued non-linear or exponential relationship is also unsustainable. Further discussion of the implications of different statistical fits for Fig. 2 is given in Notes S1.

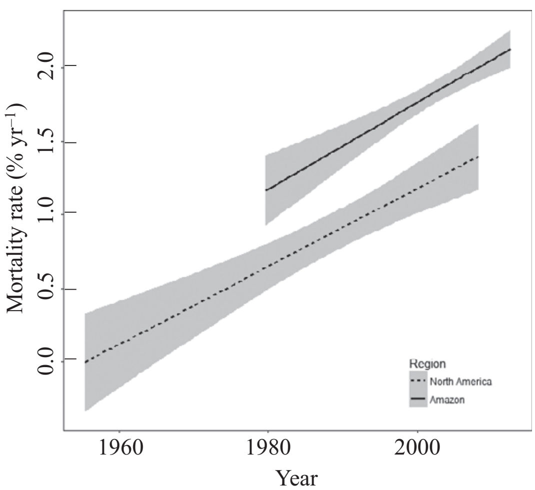

Fig. 2 Consistent increases in mortality rate (% individuals died per total number of individuals per year) across the Americas. Regression lines fitted to observations of stem mortality rate for the Amazon Basin (solid line; data from Brienen *et al.*, 2015; slope of 0.029) and for temperate and boreal North America (dashed line; average values from all five sub-regions within van Mantgem *et al.*, 2009; Peng *et al.*, 2011; slope of 0.027). Linear regressions were used for simplicity, although a case can be made for non-linear (exponential) lines because zero intercepts on the time axis are not realistic (e.g. there is always some mortality occurring; see text). Gray shading represents the 95% confidence intervals. See Supporting Information Methods S1 and S2 for method details and for versions of this figure using different units.

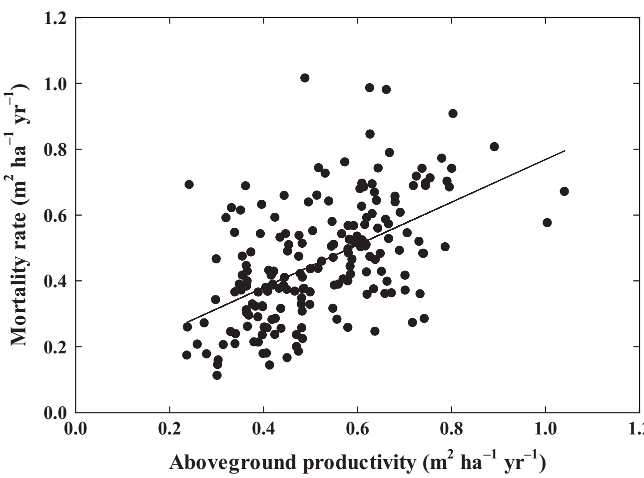

Fig. 3 Basal area mortality rate is correlated with basal area productivity across the Amazon Basin ($r^2 = 0.29$). Data from Brienen *et al.* (2015). Data represent stand dynamics as recorded for individual plots. See Supporting Information Methods S2 for details.

III. Global and regional mortality drivers and mechanisms

We review mortality drivers that are significant factors in MTFs with the objective of assessing the likelihood that they could already be increasing mortality rates (Fig. 2), and ultimately to generate testable hypotheses regarding future mortality rates, their drivers and associated mechanistic processes (Fig. 4). We draw upon empirical and simulation evidence of both historical and likely future trends in mortality drivers to aid in the generation of hypotheses with regard to the drivers of increasing mortality. In many cases, these expected trajectories are based on limited data (e.g. from the Neotropics) or inferred from uncertain climate forecasts (e.g. wind disturbance), and we have attempted to represent this uncertainty for each trajectory in Fig. 4. We review the evidence supporting and conflicting with Fig. 4 in the following sections, and include a critical assessment of the data and model limitations. We cannot rank the importance of mortality drivers because there is too little evidence (even at single sites). We focus on tropical evidence throughout our review; however, some drivers (temperature, vapor pressure deficit (VPD) and CO_2 in particular) are all rising globally, and thus we also use knowledge from the extra-tropics to fill in knowledge gaps when appropriate. Although potentially important, nutrient impacts were so poorly covered in the literature that we relegated this text to the supporting information (Notes S1).

1. Global driver – temperature and VPD

Temperature is expected to rise in tropical forests (Figs 4a, 5a–c). MTFs reside in the warmest latitudes on Earth; thus rising temperature will push them into a new temperature regime that has no current analog (Diffenbaugh & Charland, 2016). Rising temperature and VPD are forcing drivers associated with the multi-decadal increases in tree mortality rates throughout the Americas (Fig. 2). VPD rises as a result of temperature rise (e.g. Trenberth *et al.*, 2014) and because of changes in relative humidity (Fig. S4). There are multiple mechanisms by which rising temperature could cause rising mortality. First, rising temperature can drive increased respiratory carbon costs via the dependence of respiration on temperature (Clark *et al.*, 2010) and via high-temperature impacts on photosynthetic metabolism, both exacerbating carbon starvation (see Box 1 Glossary; Fig. 4b; Galbraith *et al.*, 2010). Second, rising temperature also causes elevated VPD (Trenberth *et al.*, 2014), forcing greater risk of carbon starvation and hydraulic failure (see Box 1 Glossary; Fig. 4b) via greater stomatal closure and evaporative demand, respectively (McDowell & Allen, 2015). Model analyses suggest that the impacts of rising VPD on photosynthesis are substantially greater than the impacts of rising temperature *per se* in tropical forests (Lloyd & Farquhar, 2008). Rising temperature and VPD can cause a negative carbon balance even at relatively high soil water availability (Zhao *et al.*, 2013). Rising temperatures and VPD may promote biotic attacks (Raffa *et al.*, 2008), although this has not been tested in MTFs. Rising temperature and VPD are also particularly relevant in the mountainous tropics, where mountain tops may limit migration

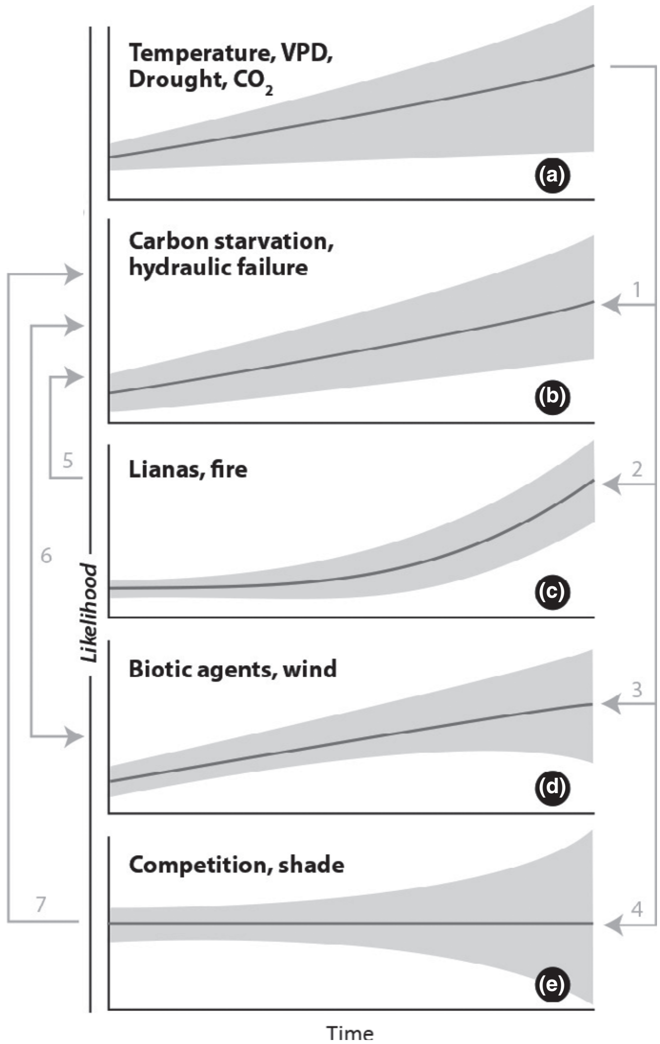

Fig. 4 A graphical summary of the literature evidence of changing mortality drivers and potential mechanisms over future conditions in moist tropical forests. Shown are the expected trends in (a) the forcing drivers of CO_2, temperature and vapor pressure deficit (VPD), and associated likelihoods of (b) carbon starvation and/or hydraulic failure, (c) liana abundance and fire frequency, (d) biotic agent attack rates and destructive wind events, and (e) competition for resources including shade. See references in text that support the general trends and their associated uncertainty (represented by the gray shading). Panels (c–e) have widening uncertainty around the mean expectations because of a lack of consistent projections (e.g. wind and biotic agents) or logical feedbacks (e.g. shade is enhanced by CO_2, but reduced by rising temperature and VPD, and CO_2 causes both increasing shade and higher water-use efficiency), which may negate influences. The numbered gray lines denote potential interactions across panels based on the literature evidence. Rising temperature and VPD promote (1) carbon starvation and hydraulic failure, (2) liana encroachment and fires, and (3) biotic agent attack and wind events. (4) Rising CO_2 may promote competition and shade. (5) Lianas may promote carbon starvation via shade and fires may promote hydraulic failure via xylem damage. (6) Biotic agents promote carbon starvation and hydraulic failure and vice versa; wind promotes carbon starvation via canopy loss. (7) Competition and shade promote carbon starvation. Not shown are the potential long-term precipitation trends, but there is a high likelihood of continued droughts at some periodicity and frequency, which will be more severe as a result of rising temperature and VPD (a).

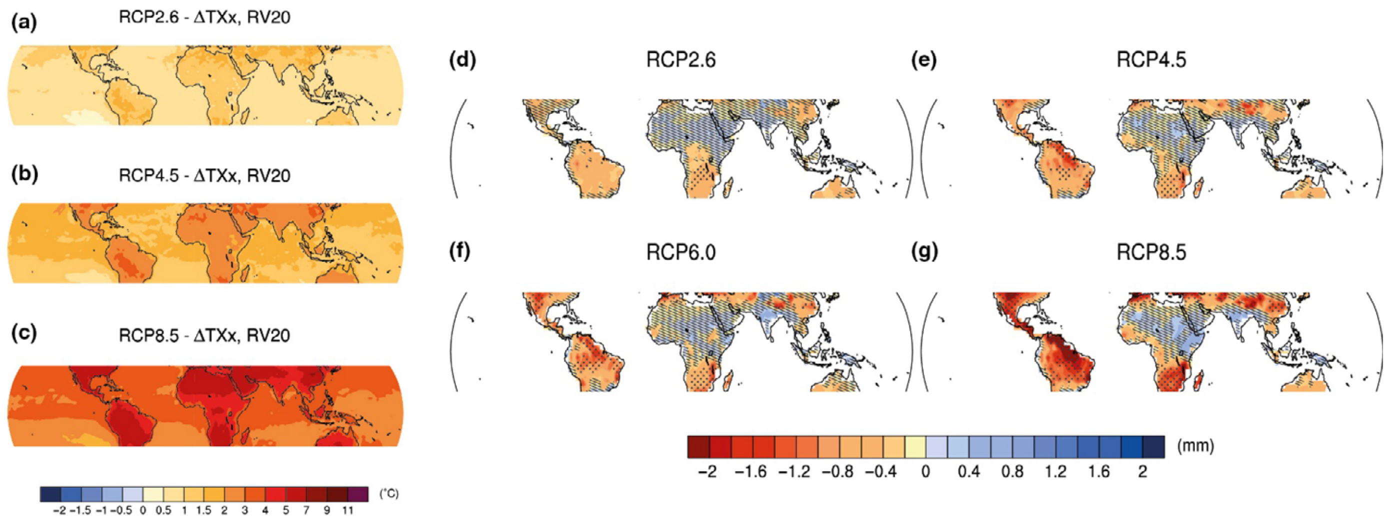

Fig. 5 Coupled-Model Intercomparison Project (5) (CMIP5) multi-model ensemble means of pan-tropical temperature and soil moisture in 2081–2100 relative to 1986–2005. (a–c) The CMIP5 multi-model median change in 20-yr return intervals of annual warm temperature extremes as simulated for 2081–2100 in RCP2.6 (top), RCP4.5 (middle) and RCP8.5 (bottom). (d–g) Change in annual mean soil moisture (mass of water in the uppermost 10 cm) (mm) for 2081–2100 relative to 1986–2005 from the CMIP5 ensemble (RCP2.6, 4.5, 6.0 and 8.5). Hatching indicates regions in which the multi-model mean change is less than one standard deviation of internal variability and where at least 90% of models agree on the sign of change. Between 22 and 35 models were used depending on the scenario. Re-printed courtesy of Collins *et al.* (2013).

(Feeley *et al.*, 2011; Duque *et al.*, 2015), but also because the range of microhabitats is greater, which could provide refugia under climate change. Impacts of rising temperature and VPD on other mechanisms of mortality are described below (see Fig. 4b–e).

2. Global–regional driver – drought

Drought, i.e. precipitation decline that impacts soil moisture, is arguably the best-studied driver of MTF tree mortality. Two critical aspects of drought as a mortality driver are that it episodically occurs everywhere globally, and that the severity of drought extremes is expected to worsen under future conditions (Trenberth *et al.*, 2014; also see 'Mitigating factors' section below and Fig. S5 for more details on precipitation forecasts). In particularly wet or anoxic soils, drying may benefit growth and survival, but, in many areas, this will result in regional increases in mortality (Phillips *et al.*, 2010; Powell *et al.*, 2013; Brienen *et al.*, 2015; Doughty *et al.*, 2015; Johnson *et al.*, 2016; Thurner *et al.*, 2017). Droughts happen in MTFs, particularly during El Niño events (Ropelewski & Halpert, 1987; Ronchail *et al.*, 2002) and periods of warm North Atlantic sea surface temperatures (Marengo *et al.*, 2011). The most consistent predictions of climate in tropical forests suggest increasing total precipitation (Gloor *et al.*, 2013; Kitoh *et al.*, 2013), but stronger and longer dry seasons over the next century (Boisier *et al.*, 2015; Duffy *et al.*, 2015; Rauscher *et al.*, 2015; Pascale *et al.*, 2016). As a result of atmospheric warming (and possibly lower relative humidity, see Fig. S3), these future droughts will include higher so-called baseline temperature and VPD than historically experienced by MTFs (Trenberth *et al.*, 2014; McDowell & Allen, 2015), and represent the primary driver of the modeled soil drying pan-tropically after 2081 (Fig. 5d–g). Thus, tropical droughts will be superimposed on chronically drier soils. In the Amazon Basin, dry season length is increasing (Fu *et al.*, 2013), and anomalous droughts occurred in 1997, 2005, 2010 (Marengo *et al.*, 2011) and 2015. In both drought experiments and in observational datasets, the largest trees have disproportionately higher mortality rates under drought stress, with associated large impacts on carbon storage (Nepstad *et al.*, 2007; da Costa *et al.*, 2010; Bennett *et al.*, 2015; Meir *et al.*, 2015; Rowland *et al.*, 2015a; Meakem *et al.*, 2017; Fig. 1b). Drought has both positive and negative impacts on the other mortality mechanisms (Fig. 4, see text below).

Drought, temperature and VPD are expected to kill trees alone or via a combination of physiological stress and biotic attack (McDowell *et al.*, 2011). These inter-related mechanisms occur in part via carbon starvation and hydraulic failure (see Box 1 Glossary; Fig. 4b). In particular, sustained periods of severe loss of hydraulic conductivity are a strong predictor of drought mortality in temperate forests (McDowell *et al.*, 2013; Anderegg *et al.*, 2015a; Sperry & Love, 2015; Adams *et al.*, 2017), with consistent evidence from the tropics (Rowland *et al.*, 2015a). Carbohydrate status was a strong predictor of mortality in a study of tropical seedlings, with higher carbohydrate content leading to more favorable water status and longer survival (O'Brien *et al.*, 2014).

Moist tropical forests often display paradoxical autotrophic carbon cycle responses to drought. Seasonal and interannual droughts cause greater respiratory carbon loss (Metcalfe *et al.*, 2010), lower leaf-level photosynthesis (Doughty *et al.*, 2014), increases in mortality (Phillips *et al.*, 2009; Brienen *et al.*, 2015) and reduced regional carbon uptake (Gatti *et al.*, 2014). Nonetheless, droughts sometimes result in stable growth (Doughty *et al.*, 2015; but see Feldpausch *et al.*, 2016 for evidence of decreasing growth) in part via increasing canopy photosynthetic capacity (Clark & Clark, 1994; Graham *et al.*, 2003; Huete *et al.*, 2006; Saleska *et al.*, 2007, 2016; Brando *et al.*, 2010), flushing of young leaves (Wu *et al.*, 2016) and greater solar radiation (Guan *et al.*, 2015). This paradoxical strategy of prioritizing growth during periods of drought, presumably to compete for light, may accelerate the risk of hydraulic failure, carbon starvation or vulnerability to biotic attack (Doughty *et al.*, 2015). Rowland *et al.* (2015a) found that both growth and carbohydrate concentrations of trees that survived drought were unchanged relative to control trees, suggesting that survival may either depend on the maintenance of a positive carbon balance, or vice versa, the mortality of surrounding trees promotes higher carbon balance in those that survive. Because carbon starvation and hydraulic failure can be induced or exacerbated by myriad drivers, including increases in these processes after fire (Bär *et al.*, 2018), biotic attack (McDowell *et al.*, 2011), and defoliation and shading (Kobe, 1997), we hypothesize that carbon starvation and/or hydraulic failure may underlie the mortality resulting from many of the drivers (Fig. 4a–e; see hypotheses descriptions below).

3. Global driver – carbon dioxide

Like rising temperature, VPD and, possibly, drought, atmospheric CO_2 is rising globally and thus is a candidate driver of the observed increasing mortality rates throughout the Americas (Fig. 2). But how could rising CO_2 cause elevated mortality rates, when it promotes increased water-use efficiency (Lloyd & Farquhar, 2008) and growth? At least two candidate explanations exist. First, at the stand level, rising CO_2 may drive elevated mortality through enhanced growth, which accelerates successional dynamics by driving faster thinning via increased competition for resources (light, water, nutrients). In such a case, the suppressed trees that die experience carbon starvation, hydraulic failure or biotic attack as a result of reduced light, water and nutrients because of increased competition (i.e. the interdependent processes across panels in Fig. 4a,b,d,e). Second, rising CO_2 may allow greater growth per individual, thus accelerating the speed at which trees reach large heights, and therefore the rate at which they experience the increased risks of lightning, windthrow, dry upper canopy environments and the physiological impacts associated with large size (Nepstad *et al.*, 2007; Bennett *et al.*, 2015; Rowland *et al.*, 2015a). The hypothesis that rising CO_2 may partially drive increasing mortality rates is consistent with: (1) the observed mortality rate increase (Fig. 2), (2) the relationship between mortality rate and productivity (Fig. 3), (3) the relationship between mortality and stand density (Lugo & Scatena, 1996), (4) the lag between increases in productivity (first) and mortality (second) in Amazonia (Brienen *et al.*, 2015), (5) the observed increases in recruitment in Amazonia (Phillips *et al.*, 2004), and (6) the consistent observation that drought–CO_2 studies find little benefit of CO_2 on survival (reviewed in Allen *et al.*, 2015; but see Liu *et al.*, 2017 for a contrasting model-based result). For these mechanisms to be driving increased mortality, they also must be driving faster stand-level growth, but this has only been shown unambiguously for the Amazon Basin thus far (Brienen *et al.*, 2015); we lack such tests for African and Asian forests. This idea is not new (Phillips *et al.*, 2004; Stephenson & van Mantgem, 2005; Stephenson *et al.*, 2011), but could be an important driver of increased mortality, and thus merits further study.

If CO_2 (via the enhanced productivity mechanism), temperature or VPD drive mortality, we can expect mortality rates to continue to increase as these drivers are expected to continue to rise (IPCC, 2014). The remaining mortality drivers discussed below are less certain at the global scale, but evidence exists for them at regional scales.

4. Regional driver – lianas

Lianas (woody vines) are much more common in tropical forests than in temperate or boreal forests (Schnitzer, 2005). Lianas reduce productivity and increase mortality of host trees (Fig. 1f; Ingwell *et al.*, 2010; van der Heijden *et al.*, 2015; Wright *et al.*, 2015). The total contribution of lianas to tropical tree mortality is difficult to estimate because of the wide variation in liana abundance among tropical forests, the relatively small number of studies that have quantified liana influences on tree mortality, differences among studies that make direct comparisons difficult, and the inherent difficulties of quantifying the full impact of lianas on tree mortality. However, Wright *et al.* (2015) found that 64% of studies showed liana abundance to be increasing (also see Phillips *et al.*, 2002; Schnitzer & Bongers, 2011). Lianas outcompete host trees for resources such as light, water and nutrients (Johnson *et al.*, 2013), and thus they potentially promote both carbon starvation and the hydraulic failure of host trees. Furthermore, lianas break limbs and expose fresh wounds for infection by biotic agents. Thus, interdependent mechanisms between liana invasion, carbon starvation (e.g. shading), hydraulic failure (e.g. reduced water availability) and biotic agent attack are likely (interactions in Fig. 4b–e). Lianas may also increase the mortality rates of neighboring uninfested trees, insofar as they increase the rates of treefall – which can be lethal to smaller neighbors – whilst competing below ground for water and nutrients (Johnson *et al.*, 2013). Liana abundance tends to increase with dry season length, land use change and increasing CO_2 (Granados & Körner, 2002; Schnitzer, 2014; DeWalt *et al.*, 2015) and thus is expected to increase in the future (Fig. 4c).

5. Regional driver – fire

Although fires in MTFs are influenced by anthropogenic ignitions, there is a significant role played by climate through drying and increasing fuels (Cochrane, 2003; Nepstad *et al.*, 2004; Slik *et al.*, 2010; Brando *et al.*, 2014). Droughts increase MTF flammability by reducing understory air and fuel moisture (Ray *et al.*, 2010) and increasing fuel accumulation from litterfall and mortality (Ray *et al.*, 2005). As a result, forest fires occurring in tropical forests during drought years tend to be larger (Silvestrini *et al.*, 2011; Alencar *et al.*, 2015), more intense and kill more trees than those occurring in non-drought years (Brando *et al.*, 2014). Several lines of evidence suggest that fire seasons in tropical forests have increased over the past few decades (Jolly *et al.*, 2015), resulting in larger (Cochrane & Barber, 2009) and more frequent (Alencar *et al.*, 2015) fires. MTF species have few adaptations to resist fires (Barlow *et al.*, 2003; Brando *et al.*, 2012), resulting in even low-intensity understory fires killing a high proportion of the forest community (Barlow *et al.*, 2003; Cochrane & Barber, 2009; Slik *et al.*, 2010). Estimates of fire-induced tree mortality rates range from 5% yr^{-1} to 90% yr^{-1} (Barlow *et al.*, 2003; Balch *et al.*, 2015; Brando *et al.*, 2016). It is likely that rising temperatures and climate extremes and decreasing surface water content (Fig. 5) are increasing forest flammability (Chen *et al.*, 2011). Clear linkages between hydraulic failure and post-fire mortality are now established (Bär *et al.*, 2018), suggesting again that interactions across mechanisms (in this case hydraulic failure and fire) are likely (Fig. 4b,c).

6. Regional driver – wind

Convective storms, hurricanes and typhoons that generate high winds, waterlogging and lightning cause tree mortality from individual wind-thrown trees to large blowdown patches (Lugo & Scatena, 1996; Chao *et al.*, 2009; Chambers *et al.*, 2013; Marra *et al.*, 2014). Treefall clusters ranging from individual treefalls to < 10 trees per gap represented > 90% of wind-driven mortality for a central Amazon landscape (Chambers *et al.*, 2013; consistent with Espírito-Santo *et al.*, 2014a,b). Hurricanes and typhoons also damage forests in coastal and island forests, although these forests are adapted to these events and tend to shed leaves and even branches without complete mortality during wind events (Zimmerman *et al.*, 1994; Yap *et al.*, 2016). Storms are associated in some cases with waterlogging, which promotes trees tipping over. Storm-associated lightning also kills trees and damages tree crowns (Yanoviak *et al.*, 2015), but has been little studied in MTFs, even though lightning frequencies are higher in the tropics (Christian *et al.*, 2003). No study has yet determined whether wind-associated mortality has a latitudinal trend at the global scale, although there is a latitudinal trend in average wind speed, average wind speed declines towards the tropics (http://globalwindatlas.com/datasets.html) and equatorial regions (≤ 10° from the equator) rarely experience hurricanes/typhoons. Extreme storm events are expected to become stronger and more frequent with climate warming (Emanuel, 2013; IPCC, 2014, see Fig. S6), with warming-driven increases in atmospheric latent heat, indicating a shift towards more intense wind disturbance regimes in MTFs (Fig. 4d).

7. Regional driver – biotic agents

Pathogens, insects and other biotic agents contribute to tree mortality (Coley & Barone, 1996) and play a strong role in structuring tropical forests (Mangan *et al.*, 2010; Coley & Kursar, 2014). Although only rarely studied, heart rot was associated with > 50% of stems in a forest in Borneo, and may be strongly associated with susceptibility to wind events, which cause a loss of branches, stem breakage or windthrow (Heineman *et al.*, 2015). Far less is known about tropical outbreaks of biotic agents than about temperate outbreaks, leading to unclear expectations of their response to future climate (Fig. 4d), in part because of the great diversity of species that kill trees (Dyer *et al.*, 2012) and the historic focus on defoliators that often do not kill trees (Anderegg *et al.*, 2015b). However, attack by insects was greater in a drought experiment in the Amazon (Brando *et al.*, 2006) and tends to follow droughts (Anderegg *et al.*, 2015b). Biotic agents often cause widespread tree mortality events in the temperate and boreal zones (Kautz *et al.*, 2017), but die-offs of the magnitude observed in low-diversity forests (Breshears *et al.*, 2005) have not been observed in tropical forests. The largest mortality rates observed in MTFs rarely exceed 5% (Fig. S1), whereas mortality events exceeding 90% of individuals lost have occurred in the extra-tropics (Breshears *et al.*, 2005), generally the result of a drought-facilitated insect (e.g. bark beetle) outbreak on single or multiple species. The relatively low rates of mortality in MTFs (compared with the extra-tropics) may be a result of the high species diversity and the relatively high specificity of biotic agent–host tree relationships, coupled with the asynchronous timing of outbreaks of biotic agents (Dyer *et al.*, 2007; Coley & Kursar, 2014). Alternatively, the rate of biotic attack-driven mortality may be higher but less detectable in the tropics than in the extra-tropics. Thus, although biotic agents are clearly important mortality drivers in MTFs, their historical or expected future trends in attack rates are poorly constrained (Fig. 4d).

8. Regional driver – shading

Shading in light-limited MTFs is an expected driver of mortality (Wright *et al.*, 2010; Rüger *et al.*, 2011) and has been associated with carbon starvation in four species of angiosperm (Kobe, 1997). The dichotomy between the low-light environment and the high-light environment when gaps form has had a distinct impact on the evolutionary strategy of species (Richards, 1952). Slow-growing, shade-tolerant trees tend to live longer than fast-growing, shade-intolerant trees (Condit *et al.*, 1995; Wright *et al.*, 2010; Fig. 1d). Shading is presumed to be the dominant driver of the high mortality rates of seedlings and understory plants (Fig. 1a, Panama example); however, the mechanisms of the interactions between shade, herbivory, biotic agents and the physiological mechanisms of carbon starvation and hydraulic failure (O'Brien *et al.*, 2014) within the ultimate mortality process is poorly known. Solar radiation is expected to increase in much of the tropics (Collins *et al.*, 2013), and rising temperature and VPD would act to further reduce shading by inducing mortality (or lower leaf area) of competing vegetation. By contrast, the competitive dynamics that drive mortality via shading may be speeding up as a result of CO_2-induced increased productivity (Brienen *et al.*, 2015) and higher leaf area. Thus, there is large uncertainty in the trajectory of shading in the future (Fig. 4e).

9. Summary – mortality drivers

In summary, amongst the identified mortality drivers in tropical forests, most appear to be increasing in potential or frequency, and there is reasonable evidence to conclude that risks to continued increases in tree mortality within MTFs are likely. Temperature, VPD, fire, wind, biotic agents, lianas and, potentially, CO_2-induced thinning and accelerated height growth (Fig. 3) may all possibly increase under future climate change (Fig. 4). However, the lack of knowledge of the relative impacts and interactions of each process on MTF tree mortality, and inadequate evidence of their trajectories (particularly for competition), make the determination of the relative causes of rising mortality rates (Fig. 2) a challenge both historically and in the future.

IV. On the coupling of mortality drivers and mechanisms

Mortality drivers and mortality mechanisms (see Box 1 Glossary for definitions) are coupled through a chain of events, starting from an initial forcing variable that promotes an increase in a mortality driver (e.g. rising CO_2 forces rising temperature), and the mortality driver subsequently impacting plants via structural (e.g. windthrow) or physiological (e.g. liana shading reducing photosynthesis; Fig. 4) mechanisms. An understanding of these linkages is valuable both from a fundamental knowledge perspective and for advancing mechanistic mortality simulation within newer ESMs. We have previously explained the linkage between carbon starvation, hydraulic failure, temperature, VPD and drought, and now hypothesize on how these mechanisms are tied to the other mortality drivers (Fig. 4).

Fires and wind events can destroy entire trees via simple structural breakage. For the other mortality drivers, we propose that drivers kill trees via the mechanisms of carbon starvation (and phloem failure) and hydraulic failure (see Box 1 Glossary for definitions). Carbon starvation should be promoted by increased shade from neighboring trees or lianas, and can be further exacerbated if lianas girdle the phloem. Defoliation from wind and insects promotes carbon starvation if sufficient canopy is removed, although such disturbances may need to be repeated at high frequency to sufficiently deplete stored carbohydrates (Würth *et al.*, 2005). Biotic agents may successfully invade trees that have low carbohydrates from the carbon starvation process and low sap pressure (Lorio & Hodges, 1968). Hydraulic failure may be promoted by increased competition for soil water, such as from lianas, and fire promotes hydraulic failure in partially burned trees (Michaletz *et al.*, 2012), thus resulting in greater death than the consumed stems alone. The carbon starvation and hydraulic failure framework has had a growing impact on ESMs (Fisher *et al.*, 2010, 2015; McDowell *et al.*, 2013) because it is logical and consistent with available data; however, extending it (including validation) to include the interactions with lianas, wind, fire, shade and other drivers has yet to be attempted. Whether the representation of carbon starvation and hydraulic failure associated with the myriad mortality drivers will improve model predictions over simpler empirical functions is an emergent question as we begin to uncover mechanisms.

V. Mitigating factors that may promote future survival

There are potential mitigating factors that may promote the survival of trees in MTFs which should be considered. The three most obvious mitigating factors are species diversity (Poorter *et al.*, 2015), rising CO_2 impacts on carbon and water relations (Keenan *et al.*, 2016) and the potential of increasing mean annual precipitation (Fig. S5).

Higher species richness and hence physiological traits are expected to reduce vulnerability to large-scale mortality events (Mori *et al.*, 2013). Empirical data from tropical forests suggest that higher diversity does beget greater resistance to drought in terms of individual mortality rates (Williamson *et al.*, 2000; Fauset *et al.*, 2012) and sometimes carbon storage (Poorter *et al.*, 2015; but see Sullivan *et al.*, 2017). The mechanisms by which diversity promotes resistance (ability to withstand change) and resilience (ability to recover) are thought to lie in the greater capacity of the forest community to tolerate new conditions as a result of a wider range of traits that enable survival (e.g. hydraulic traits that promote drought tolerance; Christoffersen *et al.*, 2016; Powell *et al.*, 2017). Evidence on the role of diversity in global patterns of mortality comes from a comparison of rates of drought-induced death in the moist tropics, where mortality rates (on an individual basis) are rarely above 5% in inventory plots even after droughts (Fig. S1B), and only up to 15% in drought experiments (Nepstad *et al.*, 2007; Rowland *et al.*, 2015a), vs the temperate zone, where mortality rates can exceed > 90% (Breshears *et al.*, 2005; Plaut *et al.*, 2012).

As reviewed earlier, elevated CO_2 benefits water-use efficiency (Ehleringer & Cerling, 1995; Lloyd & Farquhar, 2008), but the degree to which this results in changed growth at the individual tree level remains disputed (van der Sleen *et al.*, 2015; Brienen *et al.*, 2016). Enhanced growth should result in less risk of mortality of the trees that are rapidly growing (Chao *et al.*, 2008), as should enhanced water-use efficiency, through reduction in the risk of both hydraulic failure and carbon starvation. However, CO_2 manipulation studies that imposed drought and killed trees rarely found any effect of CO_2 on survival (all glasshouse studies; reviewed in Allen *et al.*, 2015). It remains a large question as to what is the impact of CO_2 on moist tropical tree mortality, and this introduces uncertainty into the associated drivers (Fig. 4).

Increasing mean annual precipitation may occur in some tropical regions (Fig. S5). This would act to only partially buffer the large increase in evaporative demand as a result of temperature (Fig. 5a), which would lead to significant reductions in soil moisture (Fig. 5b) based on the Coupled-Model Intercomparison Study (CMIP5, Collins *et al.*, 2013). As reviewed earlier, the occurrence of droughts that are warmer than previously will increase, and thus their impact will be more severe (Trenberth *et al.*, 2014). There is some prediction of shifts to longer drought lengths (Boisier *et al.*, 2015; Duffy *et al.*, 2015; Rauscher *et al.*, 2015; Pascale *et al.*, 2016). It should be noted that increasing precipitation, when it does occur, also results in greater shade, more soil anoxia and greater windthrow, and so it is unclear what the net benefit of increasing precipitation, if it occurs, will be on the survival of MTF trees.

VI. The state of ESM simulations of moist tropical tree mortality

ESMs are the required tool to predict moist tropical tree mortality pan-tropically. However, many ESM processes, including those relevant to mortality, draw on ecosystem- and individual plant-scale models, in part, because they provide mechanistic simulation capabilities at appropriate scales (e.g. the individual plant). As discussed above, although there is evidence of increasing likelihood of mortality drivers, we still need substantially more data on these processes in order to understand them sufficiently to model them. As a result, many of the mortality drivers and mechanisms discussed here (Figs 1–4) are not represented in ESMs, and thus accurate simulation of the future mortality-related carbon flux requires process development. Before discussing the next steps in empirical and model developments, we briefly review the state of ESM simulations of mortality in MTFs.

Most tropical ESM projections highlight the interaction between the fertilization impacts of rising CO_2 and the deleterious impacts of increasing drought and heat stress (Cox *et al.*, 2004; Huntingford *et al.*, 2008; Fisher *et al.*, 2010; Rowland *et al.*, 2015b). However, many earlier generation ESMs simply assume a fixed mortality rate (often called background mortality, see Box 1 Glossary), leading to a growth-only-driven estimate of forest carbon fluxes and stocks (i.e. they cannot capture the trends in Fig. 2; de Almeida Castanho *et al.*, 2016; Johnson *et al.*, 2016; see table 1 within McDowell *et al.*, 2011 for a brief summary of mortality mechanisms in ESMs). This is a significant problem because ESMs must simulate mortality sufficiently well to properly predict ecosystem biomass (Galbraith *et al.*, 2013; Johnson *et al.*, 2016), particularly if mortality drivers are changing (Fig. 4).

Among the newer generation of ESMs, two representations of mortality are common. The first is the shift from one plant functional type (PFT) to another (representative of mortality and regeneration by a new type) based on climate envelopes (Sitch *et al.*, 2003). The second is the use of constant biomass residence times (see Kucharik *et al.*, 2006), which is tantamount to assuming 'senescence' mortality, in which a genetically predisposed age threshold is used. Both of these approaches risk over-simplification. Climate envelopes do not capture spatial variability, such as with different climates, species or topography, and may not be realistic in a future, warmer, higher CO_2 world. Age-driven mortality, although it may capture the statistical odds of dying from pathogen infestation, wind or lightning, is not mechanistically representative (Mencuccini *et al.*, 2005), and may thus also fail under a novel climate.

A more sophisticated, yet common, approach to simulate tree mortality in ESMs is the use of growth efficiency, in which a PFT is replaced if its stemwood growth per individual leaf area is below a threshold (McDowell *et al.*, 2011). The low growth efficiency approach is mechanistic and supported because trees that die tend to grow more slowly (per unit leaf area) than those that live (Chao *et al.*, 2008; McDowell *et al.*, 2008; Cailleret *et al.*, 2017), and because growth is intimately tied to carbon starvation (McDowell *et al.*, 2011). Furthermore, the growth efficiency approach responds to most, if not all, climate drivers that limit growth, including CO_2, light limitation, drought and VPD. Next-generation approaches that are under current or planned development, as well as new ideas on ESM developments that have not yet been attempted, are discussed in the ensuing sections on specific ESM development needs.

VII. Next steps

There are numerous hypotheses regarding the possibility of increasing future MTF mortality rates (e.g. continuation of trends in Fig. 2) that revolve around the dependence of mortality process changes, and subsequent mortality rate changes, on chronic or punctuated changes in mortality drivers (Fig. 4). We outline our highest level hypotheses here:

- MTF mortality rates are increasing linearly and will continue under projected climate change (Fig. 2);
- mechanisms of mortality, e.g. lianas, fire, biotic agents, wind, competition and shade, are increasing;
- with the exception of death from direct physical destruction (e.g. windthrow or intense fire), mortality involves a cascade of impacts from a driver (Fig. 4a) through a mechanism (Fig. 4c–e) to a physiological death process (Fig. 4b);
- uncertainty can be reduced through the quantification of the primary mechanisms and processes underlying rising mortality rates in MTFs.

Many sub-hypotheses have been outlined previously and will be expanded upon below, but all revolve around the trajectories and interactions between expected drivers, their mechanisms and physiological end points (Fig. 4).

1. Observations

We do not know the relative importance of the various drivers of MTF mortality (Figs 1–4), nor do we have sufficient confidence in the trajectory of these mortality drivers in the future to make rigorous predictions (Fig. 4). Quantification of the various mortality mechanisms in MTFs is limited by a scarcity of temporal and spatial data sufficient to overcome the high signal-to-noise ratio inherent in field observations of plant mortality. Long-term and high-temporal-frequency observations (e.g. annual) at the plot level are essential to reveal the long-term spatial and temporal patterns of mortality in relation to climate dynamics. Plot networks, although challenging to run, are arguably the lowest cost, highest impact investment we could make to refine the uncertainty in MTF mortality drivers. Plot networks provide information regarding the dynamics of growth and death in response to droughts (Condit *et al.*, 1995; Phillips *et al.*, 2009; Anderson-Teixeira *et al.*, 2015; Brienen *et al.*, 2015) and, with appropriate measurements, can unveil the mechanisms driving mortality (Doughty *et al.*, 2015). A relatively low-cost addition to inventory networks could be the assessment of the 'modes' of death (snapped, died standing, windthrow, presence of rot, etc.), the determination of the fraction of crown that is shaded (by neighbors or lianas) and dendrometer measurements before death. Plot-level work can, in some cases, include tree rings, even for tropical trees (Schöngart *et al.*, 2006; van der Sleen *et al.*, 2015; Brienen *et al.*, 2016), which can provide proxy measurements of physiology preceding death (Gaylord *et al.*, 2015). Similarly, remotely sensed data provide unparalleled spatial coverage of drought impacts, such as the long-term decline in canopy health associated with declining precipitation and increasing temperature in the Congo Basin (Zhou *et al.*, 2014) and the sustained loss of biomass observed post-drought in the Amazon (Saatchi *et al.*, 2013). A key step is the validation of remote sensing estimates of mortality against ground-based data, such as mortality rates, leaf area, canopy height and canopy biomass, and correlations of remotely sensed indices of dying and surviving trees at the crown scales, e.g. using the high-resolution (< 10 m) satellite products now available (McDowell *et al.*, 2015).

2. Experiments

Cause-and-effect experiments that manipulate mortality drivers (van der Heijden *et al.*, 2015; Meir *et al.*, 2015) are valuable because they can reveal the mechanisms underlying mortality, and can be employed for model evaluation under novel climatic conditions. The few moist tropical drought experiments (Nepstad *et al.*, 2007; Moser *et al.*, 2014; Meir *et al.*, 2015; Rowland *et al.*, 2015a) cannot be representative of the diverse MTFs, and thus experiments replicated across a broad range of soils, topographic relief and proximity to groundwater (Nobre *et al.*, 2011) are needed. Replication of such experiments across a wider range of sites in the moist tropics could be achieved economically if the measurement intensity was low. However, in addition to replication, some of the next-generation experiments must address the multifactorial climate changes expected in the future, e.g. low precipitation and elevated CO_2 or rising temperature (and associated rising VPD), and should push drought to extreme levels to understand acute impacts and threshold responses (Knapp *et al.*, 2016), including mortality. Otherwise, such experiments manipulate only one of the many variables that are changing, and thus the determination of the net effects under future climate scenarios is challenged. Multifactorial and replicated experiments have not been conducted in mature tropical forests for financial, technical and logistical reasons. The most challenging aspects of manipulative experiments are their inability to control all environmental conditions, and their minimal replication relative to the hyperdiversity of tree species in MTFs.

3. ESM demographics

To allow the simulation of competition, shading, lianas and size dependence of mortality, as they may change over time (Fig. 4), ESMs should represent demographic heterogeneity in vegetation (horizontal and vertical size variation; Moorcroft *et al.*, 2001; Fisher *et al.*, 2015; Levine *et al.*, 2016). Big leaf (no demography) model simulations predict that trees fail to die (Powell *et al.*, 2013) or die more often and faster than is observed (Galbraith *et al.*, 2010; Poulter *et al.*, 2010), whereas the addition of demographic variation in size and environment results in more realistic, gradual mortality (Powell *et al.*, 2013; Levine *et al.*, 2016). Simulation of demography allows more realistic spatial heterogeneity in resource capture and loss, and thus better simulations of mortality against observations, for example, the prediction of taller trees dying in a drought experiment (Longo, 2013).

4. ESM drought, temperature, VPD and CO_2

Given that mortality is downstream of the majority of other physiological processes (assimilation, respiration, allocation), predictions are sensitive to assumptions about photosynthesis, respiration, carbon allocation and carbon storage (Fisher *et al.*, 2010), all of which are heavily influenced by plant hydraulics (Christoffersen *et al.*, 2016; see text below on hydraulic modeling limitations and developments), and so predictions tend to be extremely divergent among models (Galbraith *et al.*, 2010; Huntingford *et al.*, 2013). To improve accuracy under non-linear changes (and complex interactions) of future drought, temperature, VPD, CO_2 and, hopefully some day, wind, fire and lianas, next-generation models are now including more realism, such as carbon starvation and hydraulic failure (Fisher *et al.*, 2010, 2015; McDowell *et al.*, 2013; Sperry *et al.*, 2016; Xu *et al.*, 2016), although evaluation in MTFs is needed. Simulation of these mortality mechanisms requires the accurate representation of water transport, xylem embolism, photosynthesis and carbon storage.

The inclusion of plant hydraulics allows more realistic simulation of mortality (McDowell *et al.*, 2013; Anderegg *et al.*, 2015a) and photosynthesis (Bonan *et al.*, 2014). Thus, the simulation of plant hydraulics allows more accurate representation of both the risk of hydraulic failure and the likelihood of carbon starvation under changing climate, and of the interactions of these processes with external drivers, such as lianas, shading, biotic agents, wind and climate. Most land components of ESMs model plant response to drought as a function of the vertical profile of prescribed fine root biomass ('root fraction' in models) and soil moisture, and collapse these two profiles into a single non-dimensional ('beta') multiplier [0,1] that is applied to Ball–Berry stomatal parameters or to carbon assimilation (Sitch *et al.*, 2003; Krinner *et al.*, 2005; Kucharik *et al.*, 2006; Oleson *et al.*, 2010). Three main reasons exist as to why this approach is insufficient for modeling tropical forest hydraulic and subsequent carbon assimilation responses to reductions in moisture. First, these models poorly capture the observed experimentally induced patterns of mortality (Powell *et al.*, 2013; Joetzjer *et al.*, 2014), in contrast with site-specific models that include plant hydraulics (Williams *et al.*, 1998; Fisher *et al.*, 2006, 2007). This model–observation mismatch is caused, in part, by the 'beta' approach: because all drought responses of trees are considered to be equivalent and to share the same threshold response in the model, the model causes an all-or-nothing response to drought. Second, current approaches lack the ability to model a well-documented negative interactive effect of soil moisture and VPD (Sperry & Love, 2015; Sperry *et al.*, 2016), which plays an important role in regulating the tree response to typical droughts. Finally, a wealth of knowledge regarding plant hydraulic traits, which govern how tropical trees transport and use water under a range of moisture conditions, has been synthesized in multiple databases that quantify inter- and intra-specific variation (Bartlett *et al.*, 2012, 2014, 2016; Choat *et al.*, 2012; Christoffersen *et al.*, 2016; Gleason *et al.*, 2016; Wolfe *et al.*, 2016). Although the typical argument against increasing model process complexity usually states that a host of unknown parameters are introduced, the case of plant hydraulics represents the opposite: parameter central tendencies, ranges and variances are already known, but most current model structures are incapable of exploiting this information. The inclusion of biophysically based representations of water acquisition, transport and use holds great promise for increasing the realism of tropical forest drought and mortality responses (see an example approach for future ESM hydraulic development in Notes S2).

Carbon starvation is sensitive to shade, temperature, VPD and CO_2 (Fig. 4; reviewed by McDowell *et al.*, 2011), amongst other factors. In practice, carbon starvation mortality is simulated as a response to non-structural carbohydrate stores, i.e. trees die when non-structural carbohydrate stores reach zero (Weng *et al.*, 2015), or when carbon storage is less than leaf biomass carbon (Fisher *et al.*, 2010), although these thresholds are arbitrary and more work is required to determine whether a universal threshold exists under field conditions (Adams *et al.*, 2017). The accuracy of carbohydrate simulations can be high (e.g. McDowell *et al.*, 2013), but observations of carbohydrate content at death are required to tune models to simulate mortality via carbon starvation, because the carbohydrate concentrations at death are variable (Adams *et al.*, 2017), and because carbohydrate results vary between laboratories/studies (Quentin *et al.*, 2015). Furthermore, the role of carbon in mortality remains in question, and therefore carbon starvation by itself may not be the appropriate mechanism to simulate tree death (Rowland *et al.*, 2015a), but rather an interdependence of carbon starvation and hydraulic failure, and linkages to phloem failure, may be required to improve model simulations during drought or under low light (O'Brien *et al.*, 2014; Sevanto *et al.*, 2014; Mencuccini *et al.*, 2015; Adams *et al.*, 2017).

5. ESM trait-based modeling in the diverse moist tropics

Modeling the myriad set of mortality drivers and mechanisms (Fig. 4) is challenging, as it requires the identification and incorporation of the trade-off and coordination among different traits targeted for different survival strategies (Fisher *et al.*, 2015). This is a particularly important issue in the particularly diverse tropics, where the variety of species, and thus traits, is greatest, but is represented by only a limited number of PFTs used to model MTFs, i.e. evergreen vs deciduous trees. Next-generation models are moving towards becoming trait enabled, such that trait trade-offs facilitate the simulation of diversity impacts on the carbon and water balance of forests (Sakschewski *et al.*, 2016). Data to parameterize these models are becoming available at the global scale, with the discovery of quantitative relationships among plant traits (Wright *et al.*, 2004; Christoffersen *et al.*, 2016), the inter- and intra-specific and biogeographical components to their variation (Anderegg, 2015), the number of independent axes of trait variation in forest communities (Wright *et al.*, 2007; Baraloto *et al.*, 2010; Reich, 2014) and relationships of plant traits to tree mortality (Wright *et al.*, 2010). For example, many parameters required for the simulation of plant hydraulics (such as pressure–volume relationships) can be estimated from traits such as wood density (Christoffersen *et al.*, 2016). This understanding informs us as to how models can represent new and flexible PFT definitions (Pavlick *et al.*, 2013; Verheijen *et al.*, 2013; Harper *et al.*, 2016; Powell *et al.*, 2017), which is a critical prerequisite for the development of modeling capability to represent ecological sorting mediated by plant traits (i.e. trait-mediated environmental filtering *sensu* Sommer *et al.*, 2014). It is important for next-generation ESMs to predict shifts in trait distributions through time (Scheiter *et al.*, 2013) because of mounting evidence showing that key aspects of ecosystem-level properties (e.g. carbon storage, overall resilience) depend on the functional community composition (Fauset *et al.*, 2012). A critical challenge, however, is for us to better understand what traits, their trade-offs and their plasticity (Lloyd *et al.*, 2010) result in tolerance or susceptibility to mortality drivers (Fig. 4).

6. ESM lianas

No ESMs have yet attempted to explicitly represent lianas (Verbeeck & Kearsley, 2016). The empirical knowledge base for modeling lianas is incomplete, but our existing knowledge regarding the role of gaps, CO_2 and drought on liana abundance can provide some simulation potential for liana succession. With demographic ESMs, it may be possible to simulate the succession and impacts of lianas on upper canopy trees through shading and breakage, particularly in gaps. Trait-enabled hydraulic models will be able to simulate the high rates of soil water acquisition by lianas (Johnson *et al.*, 2013) and subsequent impacts on host tree water availability. For mortality mechanisms, lianas probably impact hydraulic failure through the drawing down of soil moisture via their high transpiration rates (Chen *et al.*, 2015), and carbon starvation via shading (Fig. 4), but the determination of the fraction of host crown that is shaded, and impacts on water consumption, is required to inform the model mechanism.

7. ESM fire

Most ESMs include representations of fire, but the majority of these models are parameterized from limited studies in boreal and temperate regions, and their applicability to tropical systems is largely unknown (Hantson *et al.*, 2016). Improvements in the simulation of fires for the tropical forests should focus on: (1) mechanism-scale validation of fire spread and tree mortality simulations against fire experiment data, (2) tests of how fire–vegetation interactions are simulated at stand to ecosystem scales, and (3) developments that focus on the landscape-scale determinants of fire durations, maximum fire extent, the geographical spread of ignition events and interactions with human activity. The latter problem, in particular, poses significant issues concerned with how to attribute patterns observed through remote sensing to variation in different processes (ignition, suppression, fragmentation), and with predictive models of interactions with human behaviors. The increasing abundance of regional and global fire remote-sensing products (Alencar *et al.*, 2015; Bloom *et al.*, 2015) at least allows the possibility of better landscape-scale calibration of the higher level features of such models, and more robust testing of physical models of fire spread should increase confidence in our ability to predict responses to altered climatic drivers in future scenarios.

8. ESM biotic agents

Most ESMs have not simulated biotic attacks (insects and pathogens; but see Dietze & Matthes, 2014; Landry *et al.*, 2016), but a path forward can be derived from a few key observations. Insect outbreaks often occur after droughts in the moist tropics (Anderegg *et al.*, 2015b), exhibit a correlation between host tree defense and outbreak success in both temperate (Herms & Mattson, 1992; Raffa *et al.*, 2008) and tropical (Dyer *et al.*,

2007) regions, and outbreaks (i.e. widespread attacks on one or more species) decline with increasing diversity at the global scale (Jactel & Brockerhoff, 2007). Less is known about the processes driving biotic agents, such as heart rot and root rot, but we may presume that infection by these agents is similar in physiological regulation to that of insects (see McDowell *et al.*, 2011). Thus, an initial ESM approach could be to simulate defense (perhaps using available carbon as a surrogate) and assume (for now) that biotic agents are ubiquitous in presence. However, in addition to predisposition by plant stress, outbreaks of tropical tree-killing insects are also more likely after other types of disturbances that open the canopy and increase the abundance of light, new foliage and juvenile trees (Dyer *et al.*, 2012), which suggests that the dynamics of canopy gap formation in demographic models may be used for outbreak initiation. Although these bottom-up controls by plant defenses and stand structure play a role in outbreaks of tropical tree-killing insects, top-down predator control appears to be particularly important in the tropics in constraining the magnitude of outbreaks (Van Bael *et al.*, 2004). Thus, an idealized model might include a function associated with host tree defense capability, host tree abundance (Dyer *et al.*, 2012), forest structure (Dyer *et al.*, 2012), insect thermal optima (Goodsman *et al.*, 2018) and top-down insect predator abundance, all influenced by environment.

9. ESM wind

Arguably the hardest ESM challenge is to downscale maximum wind speeds from atmospheric models that simulate average wind speeds over the scale of individual grid cells (e.g. Fig. S4) and are formulated using a hydrostatic approximation that prevents explicit representation of processes that generate high wind extremes. At the canopy scale, the ability to model loss of foliage, loss of major branches, snapped stems, standing dead stems or an uprooted tree is valuable for the capture of recovery processes, gap light dynamics and carbon cycling from wind mortality (Holm *et al.*, 2017), which can be most aptly simulated in demographic models. Opportunities to further improve predictions of wind mortality lie in the representation of abiotic and biotic conditions (e.g. soil conditions, prior exposure to stress, presence of heart rot) that enhance vulnerability to wind, traits that confer susceptibility or resistance to wind and the wind fields that can topple canopy trees (Ribeiro *et al.*, 2016).

VIII. Conclusions

Many of the drivers of MTF tree mortality appear to be increasing (Fig. 4, although with large uncertainties), and thus there is some confidence that mortality rates may increase over time. These mortality drivers may include productivity-driven thinning and increase in height growth, rising temperature and VPD, increasing frequency and severity of droughts, increasing liana competition, fire, wind disturbance and biotic attacks. The determination of the relative importance of these drivers is critical to enable mechanistic prediction of future mortality. The simulation of future tropical forest mortality under climate change is daunting because of this lack of knowledge, coupled with the complexity of processes in hyperdiverse tropical systems. Some model mechanisms require improvement, such as the inclusion of refined hydraulics and demographics, whereas other model processes have yet to be included, such as wind, insects and liana competition. Model structures that include demographic representation and represent the diversity of physiological traits should provide a useful foundation for rapid model development, but such development must progress hand in hand with increasing empirical knowledge of the key processes that regulate tropical forest mortality under climate change.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Comparison of two approaches for calculating mortality rates from inventory data reveals only negligible impacts on the final estimates.

Fig. S2 Representation of Fig. 2 from the main text using different metrics, such as biomass mortality.

Fig. S3 Representation of Fig. 3 from the main text using different metrics, such as basal area.

Fig. S4 Projected changes in atmospheric relative humidity from CMIP5 models under RCP8.5.

Fig. S5 Projected changes in precipitation from CMIP5 models under RCP8.5.

Fig. S6 Projected changes in atmospheric wind speeds from CMIP5 models under RCP8.5.

Methods S1 A review of how inventory data are converted into mortality rate estimates and the implications of differing calculations and statistics (in relation to Fig. 2 within the main text).

Methods S2 Description of methods used for Fig. 3 from the main text.

Notes S1 On the role of nutrients in moist tropical forest (MTF) mortality.

Notes S2 A potential approach to Earth system model (ESM) modeling of hydraulics.

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