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Drivers and mechanisms of tree mortality in moist tropical forests

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1 **D) Summary** Tree mortality rates appear to be increasing in moist tropical forests (MTFs) with
2 significant carbon cycle consequences. We review the state of knowledge regarding MTF tree
3 mortality, create a conceptual framework with testable hypotheses regarding the drivers,
4 mechanisms, and interactions that may underlie increasing MTF mortality rates, and identify
5 next steps for improved understanding and reduced prediction. Increasing mortality rates are
6 associated with rising temperature and vapor pressure deficit, liana abundance, drought, wind
7 events, fire, and possibly CO₂ fertilization-induced increases in stand thinning or acceleration of
8 trees reaching larger, more vulnerable heights. The majority of these mortality drivers may kill
9 trees in part through carbon starvation and hydraulic failure. The relative importance of each
10 driver is unknown. High species diversity may buffer MTFs against large-scale mortality events,
11 but recent and expected trends in mortality drivers give reason for concern regarding increasing
12 mortality within MTFs. Models of tropical tree mortality are advancing representation of
13 hydraulics, carbon, and demography, but require more empirical knowledge regarding the most
14 common drivers and their subsequent mechanisms. We outline critical datasets and model
15 developments required to test hypotheses regarding the underlying causes of increasing MTF
16 mortality rates, and improve prediction of future mortality under climate change.
17

18 **II) Introduction**

19 Moist tropical forests (MTFs, see Glossary) are the largest terrestrial carbon sink in the
20 world (Pan *et al.*, 2011) and house the majority of Earth’s terrestrial biodiversity (Myers *et al.*,
21 2000; Krefl & Jetz, 2007). The spatial patterns of biomass carbon storage in MTFs are primarily
22 driven by mortality (see Glossary) rather than productivity (Galbraith *et al.*, 2013; Johnson *et al.*,
23 2016). The climatic and ecological benefits of intact MTFs are potentially threatened by
24 increasing tree mortality due to environmental and biotic changes (Phillips *et al.*, 2009; Lewis *et*
25 *al.*, 2011; Davidson *et al.*, 2012; Chambers *et al.*, 2013; Erb *et al.*, 2016). Valuable tools for
26 predicting the future of MTF tree mortality are ecosystem and earth-system models (see
27 Glossary; Seiler *et al.*, 2015; Sperry & Love, 2015; Levine *et al.*, 2016; Xu *et al.*, 2016). These
28 “next-generation” models have enabled progress on mortality prediction, yet these advances have
29 also revealed multiple questions, particularly regarding MTF tree mortality drivers and
30 mechanisms, that must be addressed to enable accurate prediction (Powell *et al.*, 2013; Thurner
31 *et al.*, 2017). Improving our understanding and model prediction is challenged in part by the
32 enormous variability in mortality temporally, regionally, and within sites according to tree size
33 and other traits (Fig. 1).

34 Accurate prediction of the global climate warming trajectory is challenged by non-
35 mechanistic understanding and simulation of future MTF carbon balance as influenced by tree
36 death (Friedlingstein *et al.*, 2006; Friend *et al.*, 2014). To address this challenge, we describe the
37 state of knowledge of (non-harvest) MTF tree mortality drivers and their associated
38 physiological mechanisms, and investigate the likelihood that these drivers will strengthen in the
39 future. We use empirical and simulation evidence. Through this review, we generate a
40 conceptual framework that provides testable hypotheses regarding the causes, mechanisms, and
41 interactions associated with increasing mortality rates. We briefly investigate factors that may
42 promote survival, and propose a path forward for both empirical and modeling work to better
43 understand the future of MTF tree mortality. Our focus is on intact (primary or old-growth)
44 forests, including aseasonal (wet) and seasonally dry forests, because of their large role in the
45 global carbon cycle (Pan *et al.*, 2011). We are focused on intact forests so that we may
46 investigate if global drivers are associated with mortality, in the absence of direct human
47 intervention. We draw an outer boundary to our geographic scope at the dry margin where forest
48 fires historically occurred. Our scope includes all evidence available from the MTFs in South

49 America, Africa, and Southeast Asia. We are focused only on mortality; we do not discuss
50 resilience and recovery rates from mortality events, though these are critical questions relative to
51 the terrestrial carbon sink. We use evidence from the extra-tropics when a process appears to be
52 global in nature (e.g. warming impacts on carbon balance) and when tropical evidence is scarce.
53 This ultimately allowed hypothesis generation as to the trends in MTF tree mortality drivers and
54 their mechanisms.

55

56 **III) Increasing mortality rates in the Amazon Basin**

57 Mortality of individual trees within intact, old-growth forests has been rising during
58 recent decades in the Amazon basin (Fig. 2; see Glossary and Methods S1 for definitions of
59 mortality rates; unless otherwise specified mortality rate in this manuscript is always defined as
60 % individuals died per total number of live and dead individuals per year), having a significant
61 impact on biomass carbon loss (Fig. S1) and net ecosystem carbon storage (Phillips & Gentry,
62 1994; Phillips *et al.*, 2004; Brienen *et al.*, 2015). The trends for the Amazon basin are similar
63 whether plotted as percent mortality rates or biomass mortality (Figs 2, S2). These results from
64 100s of plots across the Amazon are consistent with observed pulse-mortality events in SE Asia
65 (Phillips *et al.*, 2010), and declines in remotely sensed indices (assumed to be correlated with
66 canopy or whole-tree loss) of canopy biomass post-drought in the Amazon (Saatchi *et al.*, 2013)
67 and canopy health in the Congo attributed to drought and warming (Zhou *et al.*, 2014). However,
68 not all tropical forests have exhibited increasing mortality recently (in Panama; Condit *et al.*,
69 2006; Meakem *et al.*, 2017). The drivers and mechanism(s) underlying this increasing rate of tree
70 death in some areas (while not in others) are currently unknown (Phillips & Gentry, 1994;
71 Stephenson *et al.*, 2011; Feldpausch *et al.*, 2016).

72 At the coarsest level, increasing mortality rates in the Amazon are consistent with
73 observed forest inventory results from old-growth boreal and temperate forests of North America
74 (Fig. 2; Luo & Chen, 2015). Direct statistical comparison of the lines for the Amazon and for
75 North America is precluded by many limitations (see Notes S1 for details), but the similar
76 general trends for the two regions allows for the possibility of similar drivers and mechanisms
77 across North and South America. The Amazon basin has higher mortality rates than North
78 America (Fig. 2), which may be expected based on the observed correlation between
79 productivity and turnover at regional (Amazon, Fig. 3, and see alternative versions of Fig. 3 (Fig.

80 S3A,B)) and global scales (Phillips & Gentry, 1994; Stephenson & van Mantgem, 2005; Phillips
81 *et al.*, 2004). We note that an important question arises from Fig. 2: is the relationship of
82 mortality rate over time non-linear or linear (our analysis of Brienen *et al.*'s data shows no
83 significant difference between linear and non-linear fits ($p=0.36$; see Notes S1 for statistical
84 details). A non-linear pattern is logical because mortality never reaches zero historically,
85 however, a continued non-linear or exponential relationship is also unsustainable. Further
86 discussion of the implications of different statistical fits for Fig. 2 are discussed in the Notes S1.

87

88 **IV) Global and regional mortality drivers and mechanisms**

89 We review mortality drivers that are significant factors in MTFs with the objective of
90 assessing the likelihood that they could already be increasing mortality rates (Fig. 2), and
91 ultimately to generate testable hypotheses regarding future mortality rates, their drivers and
92 associated mechanistic processes (Fig. 4). We draw upon empirical and simulation evidence of
93 both historical and likely future trends in mortality drivers to aid in generating hypotheses as to
94 the drivers of increasing mortality. In many cases, these expected trajectories are based on
95 limited data (e.g. from the Neotropics) or inferred from uncertain climate forecasts (e.g. wind
96 disturbance) and we have attempted to represent this uncertainty for each trajectory in Fig. 4.
97 We review the evidence supporting and conflicting with Fig. 4 in the following sections, and
98 include a critical assessment of the data and model limitations. We cannot rank the importance
99 of mortality drivers because there is too little evidence (even at single sites). We focus on
100 tropical evidence throughout our review; however, some drivers (temperature, VPD, and CO₂ in
101 particular) are all rising globally and thus we also use knowledge from the extra-tropics to fill in
102 knowledge gaps when appropriate. While potentially important, nutrient impacts were so poorly
103 covered in the literature that we relegated that text to the supplemental information (Notes S1).

104

105 **IV.I) Global Driver--Temperature and vapor pressure deficit:** Temperature is expected to rise
106 in tropical forests (Figs 4A, 5A–C). MTFs reside in the warmest latitudes on Earth, thus rising
107 temperature will push them into a new temperature regime that has no current analog
108 (Diffenbaugh & Charland, 2016). Rising temperature and vapor pressure deficit (VPD) are
109 forcing drivers associated with the multi-decadal increases in tree mortality rates throughout the
110 Americas (Fig. 2). VPD rises due to temperature rise (e.g. Trenberth *et al.*, 2014) and due to

111 changes in relative humidity (Fig. S4). There are multiple mechanisms by which rising
112 temperature could cause rising mortality. First, rising temperature can drive increased respiratory
113 carbon costs via the dependence of respiration on temperature (Clark *et al.*, 2010) and via high-
114 temperature impacts on photosynthetic metabolism, both exacerbating carbon starvation (see
115 Glossary; Fig. 4B; Galbraith *et al.*, 2010). Second, rising temperature also causes elevated VPD
116 (Trenberth *et al.*, 2014), forcing greater risk of carbon starvation and hydraulic failure (see
117 Glossary; Fig. 4B) via greater stomatal closure and evaporative demand, respectively (McDowell
118 & Allen, 2015). Model analyses suggest the impacts of rising VPD on photosynthesis are
119 substantially greater than the impacts of rising temperature *per se* in tropical forests (Lloyd &
120 Farquhar, 2008). Rising temperature and VPD can cause a negative carbon balance even at
121 relatively high soil water availability (Zhao *et al.*, 2013). Rising temperatures and VPD may
122 promote biotic attacks (Raffa *et al.*, 2008), though this has not been tested in MTFs. Rising
123 temperature and VPD is also particularly relevant in the mountainous tropics, where mountain
124 tops may limit migration (Feeley *et al.*, 2011; Duque *et al.*, 2015), but also because the range of
125 microhabitats are greater, which could provide refugia under climate change. Impacts of rising
126 temperature and VPD on other mechanisms of mortality are described below (see Fig. 4B–E).

127

128 **IV.II) Global-Regional Driver-Drought:** Drought, i.e. precipitation decline that impacts soil
129 moisture, is arguably the best-studied driver of MTF tree mortality. Two critical aspects of
130 drought as a mortality driver are that it episodically occurs everywhere globally, and that the
131 severity of drought extremes is expected to worsen under future conditions (Trenberth *et al.*,
132 2014; also see Mitigating Factors section below and Fig. S5 for more details on precipitation
133 forecasts). In particularly wet or anoxic soils the drying may benefit growth and survival, but in
134 many areas this will result in regional increases in mortality (Phillips *et al.*, 2010; Brienens *et al.*,
135 2015; Doughty *et al.*, 2015; Johnson *et al.*, 2016; Powell *et al.*, 2013; Thurner *et al.*, 2017).
136 Droughts happen in MTFs particularly during El Niño events (Ropelewski & Halpert, 1987;
137 Ronchail *et al.*, 2002) and periods of warm North Atlantic sea-surface temperatures (Marengo *et al.*,
138 2011). The most consistent predictions of climate in tropical forests suggest increasing total
139 precipitation (Gloor *et al.*, 2013; Kitoh *et al.*, 2013), but stronger and longer dry seasons over the
140 next century (Boisier *et al.*, 2015; Duffy *et al.*, 2015; Rauscher *et al.*, 2015; Pascale *et al.*, 2016).
141 Due to atmospheric warming (and possibly due to lower relative humidity, see Fig. S3), these

142 future droughts will include higher so-called baseline temperature and VPD than historically
143 experienced by MTFs (Trenberth *et al.*, 2014; McDowell & Allen, 2015), which is the primary
144 driver of the modeled soil drying pan-tropically after 2081 (Fig. 5D–G). Thus tropical droughts
145 will be superimposed upon chronically drier soils. In the Amazon basin, dry season length is
146 increasing (Fu *et al.*, 2013), and anomalous droughts occurred in 1997, 2005, 2010 (Marengo *et*
147 *al.*, 2011), and 2015. In both drought experiments and in observational datasets, the largest trees
148 have disproportionately higher mortality rates under drought stress, with associated large impacts
149 on carbon storage (Nepstad *et al.*, 2007; da Costa *et al.*, 2010; Meir *et al.*, 2015; Bennett *et al.*,
150 2015; Rowland *et al.*, 2015a; Meakem *et al.*, 2017; Fig. 1B). Drought has both positive and
151 negative impacts on the other mortality mechanisms (Fig. 4, see text below).

152 Drought, temperature, and VPD are expected to kill trees alone or via a combination of
153 physiological stress and biotic attack (McDowell *et al.*, 2011). These inter-related mechanisms
154 occur in part via carbon starvation and hydraulic failure (see Glossary; Fig. 4B). In particular,
155 sustained periods of severe loss of hydraulic conductivity are a strong predictor of drought
156 mortality in temperate forests (McDowell *et al.*, 2013; Anderegg *et al.*, 2015a; Sperry & Love,
157 2015; Adams *et al.*, 2017), with consistent evidence from the tropics (Rowland, 2015a).
158 Carbohydrate status was a strong predictor of mortality in a study of tropical seedlings, with
159 higher carbohydrate content leading to more favorable water status and longer survival (O'Brien
160 *et al.*, 2014).

161 Moist tropical forests often display paradoxical autotrophic carbon cycle responses to
162 drought. Seasonal and interannual droughts cause greater respiratory carbon loss (Metcalf *et*
163 *al.*, 2010), lower leaf-level photosynthesis (Doughty *et al.*, 2014), increases in mortality (Phillips
164 *et al.*, 2009; Brienen *et al.*, 2015), and reduced regional carbon uptake (Gatti *et al.*, 2014).
165 Nonetheless, droughts sometimes result in stable growth (Doughty *et al.*, 2015, but see
166 Feldpausch *et al.*, 2016 for evidence of decreasing growth) in part via increasing canopy
167 photosynthetic capacity (Clark & Clark, 1994; Graham *et al.*, 2003; Saleska *et al.*, 2007, 2016;
168 Huete *et al.*, 2006; Brando *et al.*, 2010), flushing of young leaves (Wu *et al.*, 2016), and greater
169 solar radiation (Guan *et al.*, 2015). This paradoxical strategy of prioritizing growth during
170 periods of drought, presumably to compete for light, may accelerate risk of hydraulic failure,
171 carbon starvation, or vulnerability to biotic attack (Doughty *et al.*, 2015). Rowland *et al.* (2015a)
172 found that both growth and carbohydrate concentrations of trees that survived drought were

173 unchanged relative to control trees, suggesting that survival may either depend on maintenance
174 of a positive carbon balance, or vice versa, mortality of surrounding trees promotes higher
175 carbon balance in those that survive. Because carbon starvation and hydraulic failure can be
176 induced or exacerbated by myriad drivers, including increases in these processes after fire (Bar *et*
177 *al.*, 2017), biotic attack (McDowell *et al.*, 2011), and defoliation and shading (Kobe *et al.*, 1997),
178 we hypothesize that carbon starvation and/or hydraulic failure may underlie the mortality
179 resulting from many of the drivers (Fig. 4A–E; see hypotheses descriptions below).

180 **IV.III) Global Driver--Carbon Dioxide:** Like rising temperature, VPD, and possibly drought,
181 atmospheric CO₂ is rising globally and thus is a candidate driver of the observed increasing
182 mortality rates throughout the America's (Fig. 2). But how could rising CO₂ cause elevated
183 mortality rates, when it promotes increased water-use efficiency (Lloyd & Farquhar, 2008) and
184 growth? At least two candidate explanations exist. First, at the stand level, rising CO₂ may drive
185 elevated mortality through enhanced growth, which accelerates successional dynamics by
186 driving faster thinning via increased competition for resources (light, water, nutrients). In such a
187 case, the suppressed trees that die experience carbon starvation, hydraulic failure, or biotic attack
188 due to reduced light, water, and nutrients due to increased competition (i.e. the interdependent
189 processes across panels in Fig. 4A, B, D, E). Second, rising CO₂ may allow greater growth per
190 individual, thus accelerating the speed at which trees reach large heights, and therefore the rate at
191 which they experience the increased risks of lightning, windthrow, dry-upper canopy
192 environments, and the physiological impacts associated with large size (Nepstad *et al.*, 2007;
193 Bennett *et al.*, 2015; Rowland *et al.*, 2015a). The hypothesis that rising CO₂ may partially drive
194 increasing mortality rates is consistent with 1) the observed mortality rate increase (Fig. 2), 2)
195 the relationship between mortality rate and productivity (Fig. 3), 3) the relationship between
196 mortality and stand density (Lugo & Scatena, 1996), 4) the lag between increases in productivity
197 (first) and then mortality (second) in Amazonia (Brienen *et al.*, 2015), 5) with observed increases
198 in recruitment in Amazonia (Phillips *et al.*, 2004), and 6) the consistent observation that drought-
199 CO₂ studies find little benefit of CO₂ upon survival (reviewed in Allen *et al.*, 2015, but see Liu *et*
200 *al.*, 2017 for a contrasting model-based result). For these mechanisms to be driving increased
201 mortality, they also must be driving faster stand-level growth but this has only been shown
202 unambiguously for the Amazon basin thus far (Brienen *et al.*, 2015); we lack such tests for
203 African and Asian forests. This idea is not new (Phillips *et al.*, 2004; Stephenson & van

204 Mantgem, 2005; Stephenson *et al.*, 2011), but could be an important driver of increased mortality
205 and thus merits further study.

206 If either CO₂ (via the enhanced-productivity mechanism), temperature, or VPD drive
207 mortality, then we can expect mortality rates to continue increasing as these drivers are expected
208 to continue rising (IPCC, 2014). The remaining mortality drivers discussed below are less
209 certain at the global scale, but evidence exists for them at regional scales.

210
211 **IV.IV) Regional Driver--Lianas:** Lianas (woody vines) are much more common in tropical
212 forests than in temperate or boreal forests (Schnitzer, 2005). Lianas reduce productivity and
213 increase mortality of host trees (Fig. 1F; Ingwell *et al.*, 2010; van der Heijden *et al.*, 2015,
214 Wright *et al.*, 2015). The total contribution of lianas to tropical tree mortality is difficult to
215 estimate because of wide variation in liana abundance among tropical forests, the relatively small
216 number of studies that have quantified liana influences on tree mortality, differences among
217 studies that make direct comparisons difficult, and the inherent difficulties of quantifying the full
218 impact of lianas on tree mortality. However, Wright *et al.* (2015) found that 64% of studies had
219 shown liana abundance to be increasing (also see Phillips *et al.*, 2002; Schnitzer & Bongers,
220 2011). Lianas outcompete host trees for resources such as light, water, and nutrients (Johnson *et*
221 *al.*, 2013), thus they potentially promote both carbon starvation and hydraulic failure of host
222 trees. Furthermore, lianas break limbs and expose fresh wounds for infection by biotic agents.
223 Thus interdependent mechanisms between liana invasion, carbon starvation (e.g. shading),
224 hydraulic failure (e.g. reduced water availability), and biotic agent attack are likely (interactions
225 in Fig. 4B–E). Lianas may also increase mortality rates of neighboring uninfested trees, insofar
226 as they increase the rates of treefalls – which can be lethal to smaller neighbors – while
227 competing belowground for water and nutrients (Johnson *et al.*, 2013). Liana abundance tends to
228 increase with dry season length, land use change, and with increasing CO₂ (DeWalt *et al.*, 2015;
229 Granados & Körner, 2002; Schnitzer, 2014) and thus is expected to increase in the future (Fig.
230 4C).

231
232 **IV.V) Regional Driver-Fire:** Although fires in MTFs are influenced by anthropogenic ignitions,
233 there is a significant role played by climate through drying and increasing fuels (Cochrane, 2003;
234 Nepstad *et al.*, 2004; Slik *et al.*, 2010; Brando *et al.*, 2014). Droughts increase MTF flammability

235 by reducing understory air and fuel moisture (Ray *et al.*, 2010) and increasing fuel accumulation
236 from litterfall and mortality (Ray *et al.*, 2005). As a result, forest fires occurring in tropical
237 forests during drought years tend to be larger (Silvestrini *et al.*, 2011; Alencar *et al.*, 2015), more
238 intense, and kill more trees than the ones occurring in non-drought years (Brando *et al.*, 2014).
239 Several lines of evidence suggest that fire seasons in tropical forests have increased over the past
240 few decades (Jolly *et al.*, 2015) resulting in larger (Cochrane & Barber, 2009) and more frequent
241 fires (Alencar *et al.*, 2015). MTF species have few adaptations to resist fires (Barlow *et al.*, 2003;
242 Brando *et al.*, 2012), resulting in even low-intensity understory fires killing a high proportion of
243 the forest community (Barlow *et al.*, 2003; Cochrane & Barber, 2009; Slik *et al.*, 2010).
244 Estimates of fire-induced tree mortality rates range from 5% yr⁻¹ to 90% yr⁻¹ (Barlow *et al.*,
245 2003; Balch *et al.*, 2015; Brando *et al.*, 2016). It is likely that rising temperatures and climate
246 extremes and decreasing surface water content (Fig. 5) are increasing forest flammability (Chen
247 *et al.*, 2011). Clear linkages between hydraulic failure and post-fire mortality are now
248 established (Bar *et al.*, 2017) suggesting again that interactions across mechanisms (in this case
249 hydraulic failure and fire) are likely (Fig. 4B,C).

250

251 **IV.VI) Regional Driver--Wind:** Wind Convective storms, hurricanes, and typhoons that
252 generate high winds, water logging, and lightning cause tree mortality from individual wind-
253 thrown trees to large blowdown patches (Lugo & Scatena, 1996; Chao *et al.*, 2009; Chambers *et*
254 *al.*, 2013; Marra *et al.*, 2014). Treefall clusters ranging from individual treefalls to <10 trees per
255 gap represented more than 90% of wind-driven mortality for a Central Amazon landscape
256 (Chambers *et al.*, 2013; consistent with Espirito-Santo, 2014a, b). Hurricanes and typhoons also
257 damage forests in coastal and island forests, though these forests are adapted to these events and
258 tend to shed leaves and even branches without complete mortality during wind events
259 (Zimmerman *et al.*, 1994; Yap *et al.*, 2016). Storms are associated in some cases with
260 waterlogging, which promote trees tipping over. Storm-associated lightning also kills trees and
261 damages tree crowns (Magnusson *et al.*, 1996; Yanoviak *et al.*, 2015), but has been little studied
262 in MTFs even though lightning frequencies are higher in the tropics (Christian *et al.*, 2003). No
263 study has yet determined if wind-associated mortality has a latitudinal trend at the global scale,
264 though there is a latitudinal trend in average wind speed, average wind speed declines towards
265 the tropics (<http://globalwindatlas.com/datasets.html>) and equatorial regions (≤ 10 degrees from

266 the equator) rarely experience hurricanes/typhoons. Extreme storm events are expected to
267 become stronger and more frequent with climate warming (Emanuel, 2013; IPCC, 2014, see Fig.
268 S6) with warming-driven increases in atmospheric latent heat, indicating a shift toward more
269 intense wind disturbance regimes in MTFs (Fig. 4D).

270

271 **IV.VII) Regional Driver-Biotic agents:** Pathogens, insects, and other biotic agents contribute to
272 tree mortality (Coley & Barone, 1996) and play a strong role in structuring tropical forests
273 (Mangan *et al.*, 2010; Coley & Kursar, 2014). While only rarely studied, heart rot is associated
274 with >50% of stems in a forest in Borneo, and may be strongly associated with susceptibility to
275 wind events that cause loss of branches, stem breakage, or windthrow (Heineman *et al.*, 2015).
276 Far less is known about tropical outbreaks of biotic agents than temperate outbreaks leading to
277 unclear expectations of their response to future climate (Fig. 4D), due in part to the great
278 diversity of species that kill trees (Dyer *et al.*, 2012) and the historic focus on defoliators that
279 often do not kill trees (Anderegg *et al.*, 2015b). However, attack by insects was greater in a
280 drought experiment in the Amazon (Brando *et al.*, 2006) and tends to follow droughts (Anderegg
281 *et al.*, 2015b). Biotic agents often cause widespread tree mortality events in the temperate and
282 boreal zones (Kautz *et al.*, 2017), but die-offs of the magnitude observed in low-diversity forests
283 (Breshears *et al.*, 2005) have not been observed in tropical forests. The largest mortality rates
284 observed in moist tropical forests rarely exceed 5% (Fig. S1), whereas mortality events
285 exceeding 90% of individuals lost have occurred in the extratropics (Breshears *et al.*, 2005),
286 generally the result of a drought-facilitated insect (e.g. bark beetle) outbreak upon single or
287 multiple species. The relatively low rates of mortality in MTFs (compared to the extra-tropics)
288 may be due to the high species diversity and the relatively high specificity of biotic agent-host
289 tree relationships, coupled to the asynchronous timing of outbreaks of biotic agents (Dyer *et al.*,
290 2007; Coley & Kursar, 2014). Alternatively, the rate of biotic-attack driven mortality may be
291 higher but less detectable in the tropics than in the extra-tropics. Thus while biotic agents are
292 clearly important mortality drivers in MTFs, their historical or expected future trends in attack
293 rates are poorly constrained (Fig. 4D).

294

295 **IV.VIII) Regional Driver--Shading:** Shading in light-limited MTFs is an expected driver of
296 mortality (Wright *et al.*, 2010; Ruger *et al.*, 2011) and has been associated with carbon starvation

297 in four species of angiosperms (Kobe, 1997). The dichotomy between the low light environment
298 and the high light environment when gaps form has had a distinct impact on evolutionary
299 strategy of species (Richards, 1952). Slow-growing, shade-tolerant trees tend to live longer than
300 fast-growing, shade-intolerant trees (Condit *et al.*, 1995; Wright *et al.*, 2010; Fig. 1D). Shading
301 is presumed to be the dominant driver of the high mortality rates of seedlings and understory
302 plants (Fig. 1A, Panama example), however the mechanisms of the interactions between shade,
303 herbivory, biotic agents, and the physiological mechanisms of carbon starvation and hydraulic
304 failure (O'Brien *et al.*, 2014) within the ultimate mortality process is poorly known. Solar
305 radiation is expected to increase in much of the tropics (Collins *et al.*, 2013), and rising
306 temperature and VPD would act to further reduce shading by inducing mortality (or lower leaf
307 area) of competing vegetation. In contrast, the competitive dynamics that drive mortality via
308 shading may be speeding up due to CO₂ induced increased productivity (Brienen *et al.*, 2015)
309 and higher leaf area. Thus, there is large uncertainty in the trajectory of shading in the future
310 (Fig. 4E).

311 **IV.IX) Summary – mortality drivers**

312 In summary, amongst the identified mortality drivers in tropical forests, most appear to
313 be increasing in potential or frequency, thus there is reasonable evidence to conclude that risks to
314 continued increases in tree mortality within moist-tropical forests are likely. Temperature, VPD,
315 fire, wind, biotic agents, lianas, and potentially CO₂-induced thinning and accelerated height
316 growth (Fig. 3) may all possibly increase under future climate change (Fig. 4). However, the
317 lack of knowledge of the relative impacts and interactions of each process on MTF tree
318 mortality, and inadequate evidence of their trajectories (particularly for competition) make
319 determination of the relative causes of rising mortality rates (Fig. 2) a challenge both historically
320 and in the future.

321

322 **V) On the coupling of mortality drivers and mechanisms**

323 Mortality drivers and mortality mechanisms (see Glossary for definitions) are coupled
324 through a chain of events, starting from an initial forcing variable that promotes an increase in a
325 mortality driver (e.g. rising CO₂ forces rising temperature), and the mortality driver subsequently
326 impacting plants via structural (e.g. windthrow) or physiological mechanisms (e.g. liana-shading

327 reducing photosynthesis; Fig. 4). Understanding these linkages is valuable both from a
328 fundamental knowledge perspective and for advancing mechanistic-mortality simulation within
329 newer ESMs. We previously explained the linkage between carbon starvation, hydraulic failure,
330 and temperature, VPD and drought, and now hypothesize on how these mechanisms are tied to
331 the other mortality drivers (Fig. 4).

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

350

351 **VI) Mitigating factors that may promote future survival**

352 There are potential mitigating factors that may promote survival of trees in MTFs that
353 should be considered. The three most obvious mitigating factors are species diversity (Poorter *et al.*
354 *et al.*, 2015), rising CO₂ impacts on carbon and water relations (Keenan *et al.*, 2016), and the
355 potential of increasing mean annual precipitation (Fig. S5).

356 Higher species richness and hence physiological traits are expected to reduce
357 vulnerability to large-scale mortality events (Mori *et al.*, 2013). Empirical data from tropical

358 forests suggests higher diversity does beget greater resistance to drought in terms of individual
359 mortality rates (Williamson *et al.*, 2000; Fauset *et al.*, 2012) and sometimes carbon storage
360 (Poorter *et al.*, 2015, but see Sullivan *et al.*, 2017). The mechanisms by which diversity
361 promotes resistance (ability to withstand change) and resilience (ability to recover) are thought to
362 lie in the greater capacity of the forest community to tolerate new conditions due to a wider
363 range of traits that enable survival (e.g. hydraulic traits that promote drought tolerance;
364 Christoffersen *et al.*, 2016; Powell *et al.*, 2017). Evidence on the role of diversity in global
365 patterns of mortality comes from comparison of rates of drought-induced death in the moist
366 tropics, where mortality rates (on an individual basis) are rarely above 5% in inventory plots
367 even after droughts (Fig. S1B) and only up to 15% in drought experiments (Nepstad *et al.*, 2007,
368 Rowland *et al.*, 2015a), versus the temperate zone where mortality rates can exceed >90%
369 (Breshears *et al.*, 2005; Plaut *et al.*, 2012).

370 As reviewed earlier, elevated CO₂ benefits water-use efficiency (Ehrlinger & Cerling,
371 1995; Lloyd & Farquahar, 2008), but the degree to which this results in changed growth at the
372 individual tree level remains disputed (van der Sleen *et al.*, 2015; Brienen *et al.*, 2016).
373 Enhanced growth should result in less risk of mortality of the trees that are rapidly growing
374 (Chao *et al.*, 2008), as should enhanced water-use efficiency through reducing the risk of both
375 hydraulic failure and carbon starvation. However, CO₂ manipulation studies that imposed
376 drought and killed trees rarely found any effect of CO₂ on survival (all greenhouse studies;
377 reviewed in Allen *et al.*, 2015). It remains a large question what the impact of CO₂ is on moist-
378 tropical tree mortality and this introduces uncertainty into the associated drivers (Fig. 4).

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

389

390 **VII) The state of ESM simulations of moist tropical tree mortality**

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

401 Most tropical ESM projections highlight the interaction between the fertilization impacts
402 of rising CO₂ and the deleterious impacts of increasing drought and heat stress (Cox *et al.*, 2004;
403 Huntingford *et al.*, 2008; Fisher *et al.*, 2010; Rowland *et al.*, 2015b). However, many earlier-
404 generation ESMs simply assume a fixed mortality rate (often called background mortality, see
405 Glossary), leading to a growth-only driven estimate of forest carbon fluxes and stocks (i.e. they
406 cannot capture the trends in Fig. 2; de Almeida Castanho *et al.*, 2016; Johnson *et al.*, 2016; see
407 Table 1 within McDowell *et al.*, 2011 for a brief summary of mortality mechanisms in ESMs).
408 This is a significant problem because ESMs must simulate mortality sufficiently well to properly
409 predict ecosystem biomass (Galbraith *et al.*, 2013; Johnson *et al.*, 2016), particularly if mortality
410 drivers are changing (Fig. 4).

411 Among the newer generation of ESMs, two representations of mortality are common.
412 The first is shifting from one plant functional type (PFT) to another (representative of mortality
413 and regeneration by a new type) based on climate envelopes (Sitch *et al.*, 2003). The second is
414 the use of constant biomass residence times (see Kucharik *et al.*, 2006), which is tantamount to
415 assuming “senescence” mortality, in which a genetically predisposed age threshold is used. Both
416 of these approaches risk over-simplification. Climate envelopes do not capture spatial variability
417 such as with different climates, species, or topography, and may not be realistic in a future,
418 warmer, higher CO₂ world. Age-driven mortality, while it may capture the statistical odds of

419 dying from pathogen infestation, wind, or lightning, is not mechanistically representative
420 (Mencuccini *et al.*, 2005) and may thus also fail under a novel climate.

421 A more sophisticated yet common approach to simulate tree mortality in ESMs is the use
422 of growth efficiency, in which a PFT is replaced if its stemwood growth per individual leaf area
423 is below a threshold (McDowell *et al.*, 2011). The low growth-efficiency approach is
424 mechanistic and supported because trees that die tend to grow more slowly (per unit leaf area)
425 than those that live (Chao *et al.*, 2008; McDowell *et al.*, 2008; Cailleret *et al.*, 2016) and because
426 growth is intimately tied to carbon starvation (McDowell, 2011). Furthermore, the growth-
427 efficiency approach responds to most if not all climate drivers that limit growth, including CO₂,
428 light limitation, drought, and VPD. Next-generation approaches that are under current or
429 planned development, as well as new ideas on ESM developments that have not yet been
430 attempted, are discussed in the ensuing sections on specific ESM development needs.

431

432 **VIII) Next steps**

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

- 437 1) MTF mortality rates are increasing linearly and will continue under projected climate
438 change (Fig. 2);
- 439 2) mechanisms of mortality e.g. lianas, fire, biotic agents, wind, competition, and shade,
440 are increasing
- 441 3) with the exception of death from direct physical destruction (e.g. windthrow or
442 intense fire), mortality involve a cascade of impacts from driver (Fig. 4A) through a
443 mechanism (Fig. 4C–E) to a physiological death process (Fig. 4B);
- 444 4) uncertainty can be reduced through quantifying the primary mechanisms and
445 processes underlying rising mortality rates in MTFs.

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

449

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

475
476 **VIII.II) Experiments:** Cause-and-effect experiments that manipulate mortality drivers (Meir *et*
477 *al.*, 2015; van der Heijden *et al.*, 2015) are valuable because they can reveal the mechanisms
478 underlying mortality, and can be employed for model evaluation under novel climate conditions.
479 The few moist tropical drought experiments (Nepstad *et al.*, 2007; Moser *et al.*, 2014; Rowland
480 *et al.*, 2015a; Meir *et al.*, 2015), cannot be representative of the diverse MTFs and thus

481 experiments replicated across a broad range of soils, topographic relief, and proximity to
482 groundwater (Nobre *et al.*, 2011) are needed. Replication of such experiments across a wider
483 range of sites in the moist-tropics could be achieved economically if the measurement intensity
484 was low. However, in addition to replication, some of the next generation experiments must
485 address the multi-factorial climate changes expected in the future e.g. low precipitation and
486 elevated CO₂ or rising temperature (and associated rising VPD), and should push drought to
487 extreme levels to understand acute impacts and threshold responses (Knapp *et al.*, 2016)
488 including mortality. Otherwise, such experiments manipulate only one of the many variables
489 that are changing, and thus determining the net effects under future climate scenarios is
490 challenged. Multi-factorial and replicated experiments have not been conducted in mature
491 tropical forests for financial, technical, and logistical reasons. The most challenging aspects of
492 manipulative experiments are their inability to control all environmental conditions, and their
493 minimal replication relative to the hyper-diversity of tree species in MTFs.

494 **VIII.III) *ESM Demographics:*** To allow simulation of competition, shading, lianas, and size-
495 dependence of mortality as they may change over time (Fig. 4), ESMs should represent
496 demographic heterogeneity in vegetation (horizontal and vertical size variation, Moorcroft *et al.*,
497 2001; Fisher *et al.*, 2015; Levine *et al.*, 2016). Big-leaf (no demography) model simulations
498 predict trees fail to die (Powell *et al.*, 2013) or die more often and faster than is observed
499 (Galbraith *et al.*, 2010; Poulter *et al.*, 2010), whereas the addition of demographic variation in
500 size and environment results in more realistic, gradual mortality (Powell *et al.*, 2013; Levine *et al.*,
501 2016). Simulating demography allows more realistic spatial heterogeneity in resource
502 capture and loss and thus better simulations of mortality against observations, for example,
503 prediction of taller trees dying in a drought experiment (Longo, 2013).

504
505 **VIII.IV) *ESM drought, temperature, VPD and CO₂:*** Given that mortality is downstream of the
506 majority of other physiological processes (assimilation, respiration, allocation), predictions are
507 sensitive to assumptions about photosynthesis, respiration, carbon allocation, and carbon storage
508 (Fisher *et al.*, 2010), all of which are heavily influenced by plant hydraulics (Christoffersen *et al.*,
509 2016; see text below on hydraulic modeling limitations and developments) and so predictions
510 tend to be extremely divergent among models (Galbraith *et al.*, 2010; Huntingford *et al.*, 2013).
511 To improve accuracy under non-linear changes (and complex interactions) of future drought,

512 temperature, VPD, CO₂, and hopefully someday wind, fire, and lianas, next-generation models
513 are now including more realism such as carbon starvation and hydraulic failure (Fisher *et al.*,
514 2010, 2015; McDowell *et al.*, 2013; Sperry *et al.*, 2016; Xu *et al.*, 2016), though evaluation in
515 MTFs is needed. Simulating these mortality mechanisms requires representing water transport,
516 xylem embolism, photosynthesis, and carbon storage accurately.

517 Inclusion of plant hydraulics allows more realistic simulation of mortality (McDowell *et*
518 *al.*, 2013; Anderegg *et al.*, 2015a) and photosynthesis (Bonan *et al.*, 2014). Thus simulating
519 plant hydraulics allows more accurate representation of both the risk of hydraulic failure and the
520 likelihood of carbon starvation under changing climate, and of the interactions of these processes
521 with external drivers such as lianas, shading, biotic agents, wind, and climate. Most land
522 components of ESMs model plant response to drought as a function of the vertical profile of
523 prescribed fine root biomass ('root fraction' in models) and soil moisture, and collapse these two
524 profiles into a single non-dimensional ('beta') multiplier [0,1] that is applied to Ball-Berry
525 stomatal parameters or to carbon assimilation (Sitch *et al.*, 2003; Krinner *et al.*, 2005; Kucharik
526 *et al.*, 2006; Oleson *et al.*, 2010). Three main reasons exist why this approach is insufficient for
527 modeling tropical forest hydraulic and subsequent carbon assimilation responses to reductions in
528 moisture. First, these models poorly capture observed experimentally-induced patterns of
529 mortality (Powell *et al.*, 2013; Joetzjer *et al.*, 2014) in contrast to site-specific models that
530 include plant hydraulics (Williams *et al.*, 1998; Fisher *et al.*, 2006, 2007). This model-
531 observation mismatch is due in part to the 'beta' approach: because all trees' drought response is
532 considered equivalent and shares the same threshold response, causing an all-or-nothing response
533 to drought. Second, current approaches lack the ability to model a well-documented negative
534 interactive effect of soil moisture and VPD (Sperry & Love, 2015; Sperry *et al.*, 2016), which
535 plays an important role in regulating tree response to typical droughts. Finally, a wealth of
536 knowledge regarding plant hydraulic traits that govern how tropical trees transport and use water
537 under a range of moisture conditions has been synthesized in multiple databases that quantify
538 inter- and intra-specific variation (Bartlett *et al.*, 2012, 2014, 2016; Choat *et al.*, 2012; Gleason *et*
539 *al.*, 2016; Christoffersen *et al.*, 2016; Wolfe *et al.*, 2016). While the typical argument against
540 increasing model process complexity usually states that a host of unknown parameters are
541 introduced, the case of plant hydraulics represents the opposite: parameter central tendencies,
542 ranges, and variances are already known but most current model structures are incapable of

543 exploiting this information. Inclusion of biophysically-based representations of water
544 acquisition, transport, and use holds great promise for increasing the realism of tropical forest
545 drought and mortality responses (see an example approach for future ESM hydraulic
546 development in Notes S2).

547 Carbon starvation is sensitive to shade, temperature, VPD, and CO₂ (Fig. 4; reviewed by
548 McDowell *et al.*, 2011) among other factors. In practice, carbon starvation mortality is simulated
549 as a response to nonstructural carbohydrate stores; i.e., trees die when nonstructural carbohydrate
550 stores reach zero (Weng *et al.*, 2015), or when carbon storage is less than leaf biomass carbon
551 (Fisher *et al.*, 2010), though these thresholds are arbitrary and more work is required to
552 determine if a universal threshold exists under field conditions (Adams *et al.*, 2017). The
553 accuracy of carbohydrate simulations can be high (e.g. McDowell *et al.*, 2013), but observations
554 of carbohydrate content at death are required to tune models to simulate mortality via carbon
555 starvation, because the carbohydrate concentrations at death are variable (Adams *et al.*, 2017)
556 and because carbohydrate results vary between labs/studies (Quentin *et al.*, 2015). Furthermore,
557 the role of carbon in mortality remains in question, therefore carbon starvation by itself may not
558 be the appropriate mechanism to simulate tree death (Rowland *et al.*, 2015a), but rather an
559 interdependency of carbon starvation and hydraulic failure, and linkages to phloem failure may
560 be required to improve model simulations during drought or under low light (O'Brien *et al.*,
561 2014; Sevanto *et al.*, 2014; Mencuccini *et al.*, 2015; Adams *et al.*, 2017).

562

563 **VIII.V) ESM trait-based modeling in the diverse moist tropics:** Modeling the myriad set of
564 mortality drivers and mechanisms (Fig. 4) is challenging as it requires identification and
565 incorporation of the trade-off and coordination among different traits targeted for different
566 survival strategies (Fisher *et al.*, 2015). This is a particularly important issue in the particularly
567 diverse tropics, where the variety of species and thus traits are greatest, but are represented by
568 only a limited number of PFTs used to model MTFs i.e. evergreen vs. deciduous trees. Next
569 generation models are moving towards becoming trait-enabled such that trait-trade-offs facilitate
570 simulation of diversity impacts on carbon and water balance of forests (Sakschewski *et al.*,
571 2016). Data to parameterize these models is becoming available at the global scale, with
572 discovery of quantitative relationships among plant traits (Wright *et al.*, 2004; Christoffersen *et*
573 *al.*, 2016), the inter- and intra-specific and biogeographical components to their variation

574 (Anderegg, 2015c), the number of independent axes of trait variation in forest communities
575 (Wright *et al.*, 2007; Baraloto *et al.*, 2010; Reich, 2014), and relationships of plant traits to tree
576 mortality (Wright *et al.*, 2010). For example, many parameters required for simulating plant
577 hydraulics (such as pressure-volume relationships) can be estimated from traits such as wood
578 density (Christoffersen *et al.*, 2016). This understanding informs us how models can
579 represent new and flexible PFT definitions (Pavlick *et al.*, 2013; Verheijen *et al.*, 2013; Harper *et al.*,
580 *et al.*, 2016; Powell *et al.*, 2017), which is a critical prerequisite for developing modeling capability
581 to represent ecological sorting mediated by plant traits (i.e., trait-mediated environmental
582 filtering *sensu* Sommer *et al.*, 2014). It is important for next-generation ESMs to predict shifts in
583 trait distributions through time (Scheiter *et al.*, 2013) because of mounting evidence showing that
584 key aspects of ecosystem-level properties (e.g., C storage, overall resiliency) depend on the
585 functional community composition (Fauset *et al.*, 2012). A critical challenge, however, is for us
586 to better understand what traits, their trade-offs, and their plasticity (Lloyd *et al.*, 2010), result in
587 tolerance or susceptibility to mortality drivers (Fig. 4).

588

589 **VIII.VI) ESM Lianas:** No ESMs have yet attempted to explicitly represent lianas (Verbeeck &
590 Kearsley, 2016). The empirical knowledge base for modeling lianas is incomplete, but our
591 existing knowledge regarding the role of gaps, CO₂, and drought on liana abundance can provide
592 some simulation potential for liana succession. With demographic ESMs it may be possible to
593 simulate the succession and impacts of liana's on upper-canopy trees through shading and
594 breakage, particularly in gaps. Trait-enabled hydraulic models will be able to simulate the high
595 rates of soil water acquisition by lianas (Johnson *et al.*, 2013) and subsequent impacts on host
596 tree water availability. For mortality mechanisms, lianas likely impact hydraulic failure through
597 drawing down soil moisture via their high transpiration rates (Chen *et al.*, 2015), and carbon
598 starvation via shading, but determining the fraction of host-crown shaded, and impacts on water
599 consumption, are required to inform model mechanism.

600

601 **VIII.VII) ESM Fire:** Most ESMs include representations of fire, but the majority of these
602 models are parameterized from limited studies in boreal and temperate regions, and their
603 applicability to tropical systems is largely unknown (Hantson *et al.*, 2016). Improvements in the
604 simulation of fires for the tropical forests should focus on 1) mechanism-scale validation of fire

605 spread and tree mortality simulations against fire experiment data, 2) tests of how fire-vegetation
606 interactions are simulated at stand-to-ecosystem scales, and 3) developments that focus on the
607 landscape-scale determinants of fire durations, maximum fire extent, the geographical spread of
608 ignition events and interactions with human activity. The latter problem in particular poses
609 significant issues concerned with how to attribute patterns observed through remote sensing to
610 variation in different processes (ignition, suppression, fragmentation), and with predictive
611 models of interactions with human behaviors. Increasing abundance of regional and global fire
612 remote sensing products (Alencar *et al.*, 2015; Bloom *et al.*, 2015) allows at least the possibility
613 of better landscape-scale calibration of the higher-level features of such models, while more
614 robust testing of physical models of fire spread should increase confidence in our ability to
615 predict responses to altered climatic drivers in future scenarios.

616

617 **VIII.VIII) *ESM Biotic agents:*** Most ESMs have not simulated biotic attacks (insects and
618 pathogens; but see Dietze & Matthes, 2014; Landry *et al.*, 2016) but a path forward can be
619 derived from a few key observations. Insect outbreaks often occur after droughts in the moist
620 tropics (Anderegg *et al.*, 2015b), exhibit a correlation between host tree defense and outbreak
621 success in both temperate (Herms & Mattson, 1992; Raffa *et al.*, 2008) and tropical regions
622 (Dyer *et al.*, 2007), and outbreaks (i.e. widespread attacks on one or more species) decline with
623 increasing diversity at the global scale (Jactel & Brockerhoff, 2007). Less is known about the
624 processes driving biotic agents such as heartrot and rootrot, but we may presume that infection
625 by these agents is similar in physiological regulation to that of insects (see McDowell *et al.*,
626 2011). Thus an initial ESM approach could be to simulate defense (perhaps using available
627 carbon as a surrogate) and assume (for now) that biotic agents are ubiquitous in presence.
628 However, in addition to predisposition by plant stress, outbreaks of tropical tree-killing insects
629 are also more likely after other types of disturbances that open the canopy and increase the
630 abundance of light, new foliage, and juvenile trees (Dyer *et al.*, 2012), which suggests that the
631 dynamics of canopy gap formation in demographic models may be used for outbreak initiation.
632 Although these bottom-up controls by plant defenses and stand structure play a role in outbreaks
633 of tropical tree killing insects, top-down predator control appears particularly important in the
634 tropics in constraining the magnitude of outbreaks (Van Bael *et al.*, 2004). Thus an idealized
635 model might include a function associated with host tree defense capability, host-tree abundance

636 (Dyer *et al.*, 2012), forest structure (Dyer *et al.*, 2012), insect thermal optima (Goodsman *et al.*
637 2017), and top-down insect predator abundance, all influenced by environment.

638
639 **VIII.IX) *ESM Wind*:** Arguably the hardest ESM challenge is to downscale maximum wind
640 speeds from atmospheric models that simulate average wind speeds over the scale of individual
641 grid cells (e.g. Fig. S4) and are formulated using a hydrostatic approximation that prevents
642 explicit representation of processes that generate high wind extremes. At the canopy-scale, the
643 ability to model either loss of foliage, loss of major branches, snapped-stems, standing dead
644 stems, or an uprooted tree is valuable for capturing recovery processes, gap light dynamics, and
645 carbon cycling from wind mortality (Holm *et al.*, 2017), which can be most aptly simulated in
646 demographic models. Opportunities to further improve predictions of wind mortality lie in
647 representing abiotic and biotic conditions (e.g., soil conditions, prior exposure to stress, presence
648 of heartrot) that enhance vulnerability to wind, traits that confer susceptibility or resistance to
649 wind, and the wind fields that can topple canopy trees (Ribeiro *et al.*, 2016).

650

651 **IV) Conclusions**

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

666

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1485

1486 **Supporting Information**

1487

1488 Additional Supporting Information may be found online in the Supporting Information tab for this
1489 article:

1490

1491 **Methods S1** A review of how inventory data are converted into mortality rate estimates and the
1492 implications of differing calculations and statistics (in relation to Fig. 2 within the main text).

1493

1494 **Fig. S1** Comparison of two approaches to calculating mortality rates from inventory data reveals
1495 only negligible impacts on the final estimates.

1496 **Fig. S2** Representation of Fig. 2 from the main text using different metrics such as biomass
1497 mortality.

1498 **Methods S2** Description of methods used for Fig. 3 from the main text.

1499

1500 **Fig. S3** Representation of Fig. 3 from the main text using different metrics such as basal area.

1501 **Notes S1** On the role of nutrients in MTF mortality

1502 **Notes S2.** A potential approach to ESM modeling of hydraulics

1503

1504 **Fig. S4** Projected changes in atmospheric relative humidity from CMIP5 models under RCP8.5

1505

1506 **Fig. S5** Projected changes in precipitation from CMIP5 models under RCP8.5

1507 **Fig. S6** Projected changes in atmospheric wind speeds from CMIP5 models under RCP8.5

1508

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1511 be directed to the *New Phytologist* Central Office

1512 **Box 1 Glossary**

1513 Background mortality: also considered a fixed mortality rate (e.g. % year⁻¹, carbon m⁻² yr⁻¹) in
1514 models and referred to as such in this manuscript; this is the theoretically stable mortality rate
1515 under a non-changing environment.

1516 Biotic agents: insects, fungi, and other pathogens that attack and sometimes kill trees directly or
1517 by weakening them (e.g. defoliation, or rot impacts on wind resistance).

1518 Carbon starvation: the *process* by which limited carbon uptake (e.g. due to stomatal closure,
1519 shade, or leaf area loss to wind damage) relative to carbon demand (e.g. growth, respiration,
1520 defense) results in a decline in carbon-driven metabolism, hydraulic repair, or ability to defend
1521 against pests, and ultimately promotes mortality (McDowell *et al.*, 2011).

1522 Earth System Model (ESM): models designed to simulate the coupled influences and feedbacks
1523 of climate, land and ocean. Land surface models operate within ESMs.

1524 Hydraulic failure: mortality via dehydration; often associated with prolonged periods of xylem
1525 conductivity loss >60% in field studies (McDowell *et al.*, 2013).

1526 Lianas: woody plants that utilize free-standing hosts to support their weight as they grow into
1527 the canopy. Lianas are typically aggressive consumers of light, water, and nutrients.

1528 Moist-tropical forests (MTFs): forests with mean annual precipitation > 1500 mm, including
1529 both aseasonal and seasonal precipitation regimes (e.g. with a dry season < 100mm/month for
1530 five months or less; Vitousek & Sanford, 1986).

1531 Mortality drivers: factors that when they experience a directional change so do mortality rates.
1532 Examples include decreasing precipitation, increasing temperature, and increasing biotic attack.

1533 Mortality mechanisms: mortality drivers cause changes in mechanisms that lead to mortality,
1534 such as altering plant structure (e.g. via windthrow, fire) or physiology (e.g. shade-induced
1535 carbon starvation, drought-induced hydraulic failure).

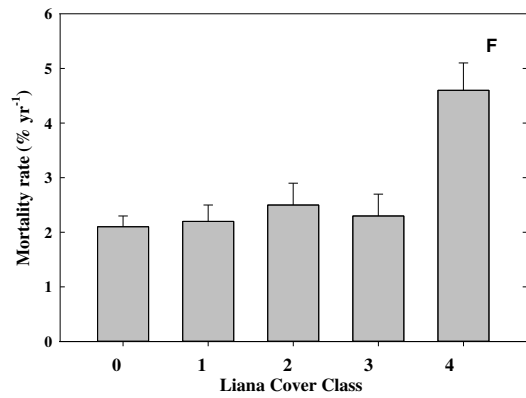
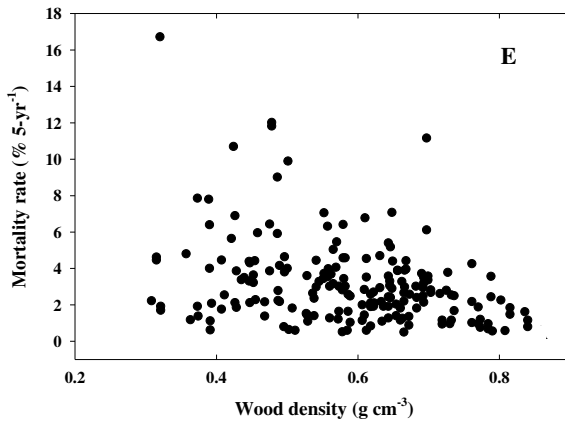
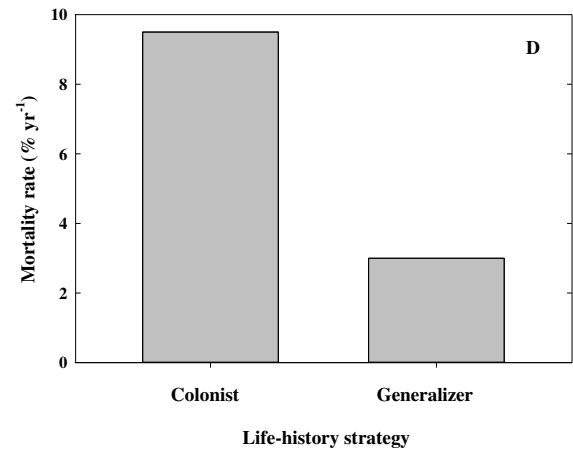
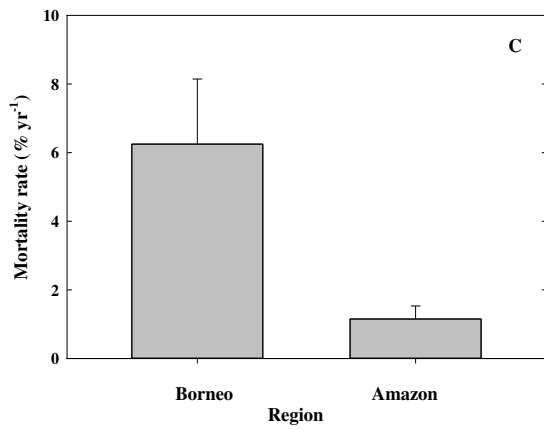
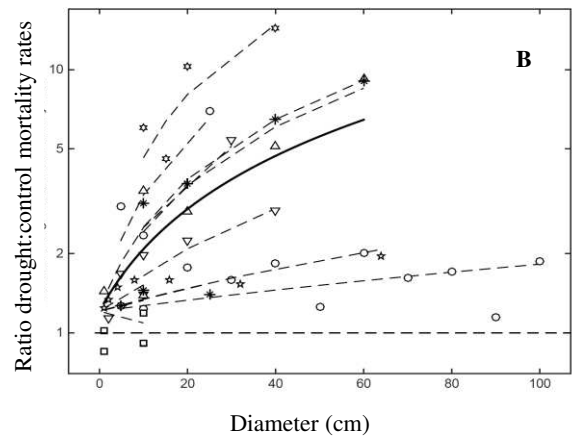
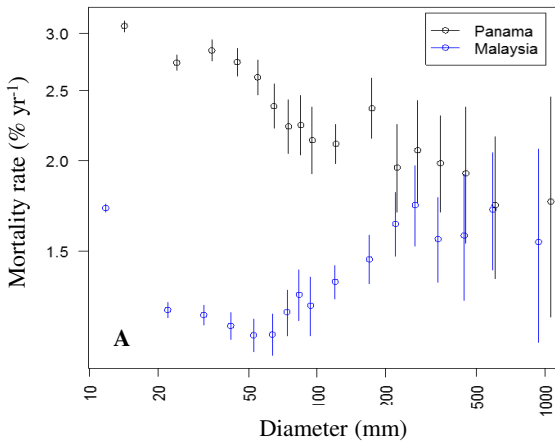
1536 Mortality rate: Can be defined using many units, typically % yr⁻¹ (number of trees died per
1537 number of total individuals live and dead per year) or in units of basal area (m² basal area died
1538 per m² of total stems per year) or biomass (kg C died per kg C standing biomass per year).
1539 Corrections for biomass weighting, non-balanced plot sizes or sampling periods over time and
1540 space are often employed when calculating mortality rates from inventory data. See Supporting
1541 Information Methods S1 for equations.

1542

1543 **Fig. 1 Axes of variability in tropical tree mortality.** A) Mortality rate [as $\log(\text{initial number}) -$
1544 $\log(\text{number survivors})/(\text{years})$] versus stem diameter in Pasoh, Malaysia and Barro Colorado,
1545 Panama (bars are 95% CI, no major droughts during censuses); this highlights that both negative
1546 and positive mortality rates as a function of diameter can be found (from Muller-Landau et al.
1547 2006). B) Mortality rates (# individuals died per number of total individuals per year; all
1548 subsequent figures use this calculation; see Glossary and Supporting Information Methods S1 on
1549 mortality rate calculations) plotted as the ratio of mortality rate during drought relative to a
1550 control period across a range of stem diameters for 12 sites across the tropics (symbols represent
1551 different sites), showing the clear pattern size-mortality relationships *during droughts* (from
1552 Bennett *et al.*, 2015). C) The mortality rates in forests in Borneo and the Amazon measured post-
1553 drought, highlighting regional differences (from Phillips *et al.*, 2010). D) Mortality rate versus
1554 life-history strategy in Barro Colorado, Panama, highlighting the role of successional strategy on
1555 long-term mortality rates (from Condit *et al.*, 1995). E) Mortality rate versus wood density in
1556 Barro Colorado, Panama, highlighting a significant but weak relationship ($p < 0.05$; from Wright
1557 *et al.*, 2010). F) Mortality rate as a function of liana cover class in Pasoh, Malaysia, highlighting
1558 the influence of lianas on mortality. Liana cover class 0 indicates no lianas, 1 indicates up to
1559 25% of the crown covered by lianas, 2 = 26-50%, 3=51-75%, and 4=76-100% (from Wright *et*
1560 *al.*, 2015).

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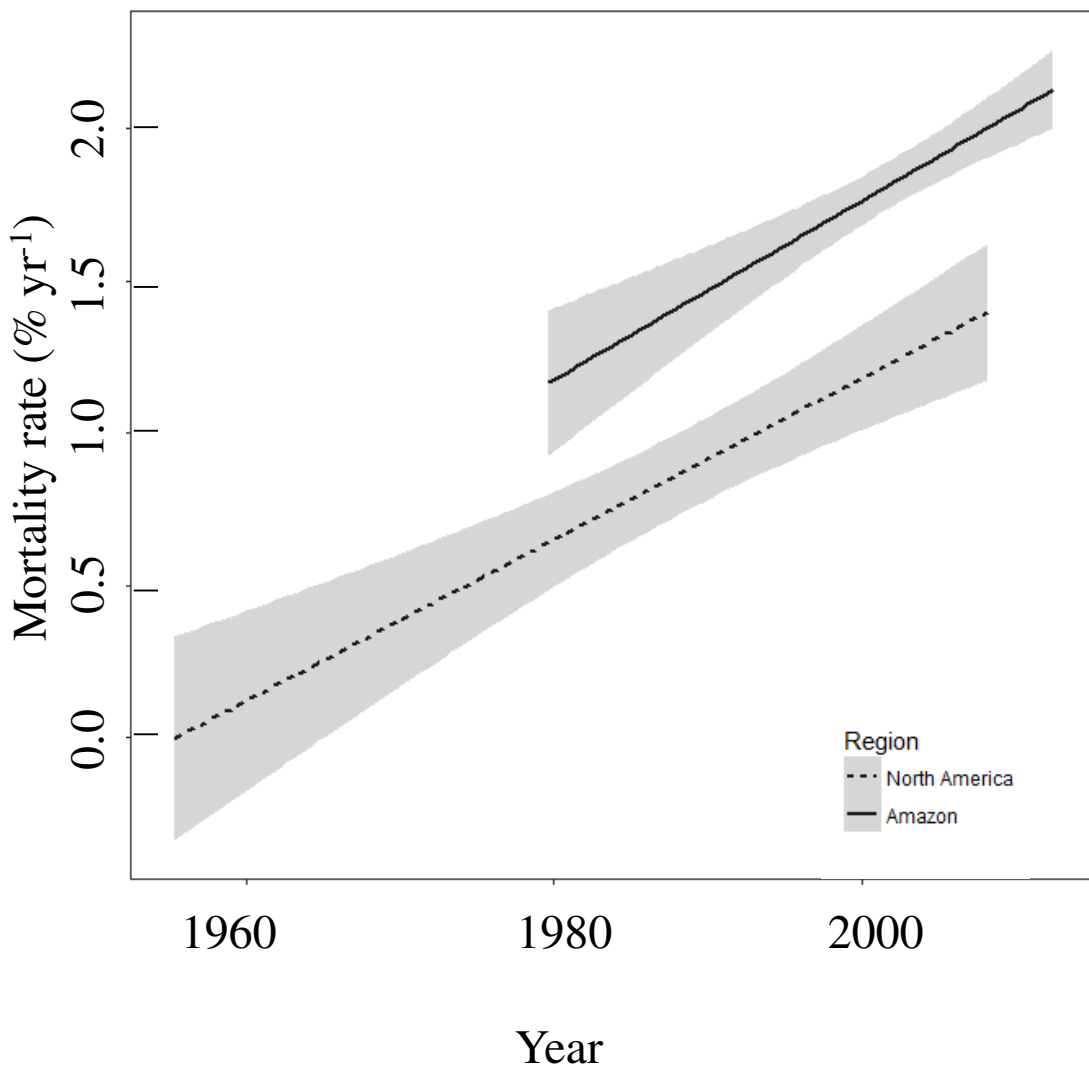
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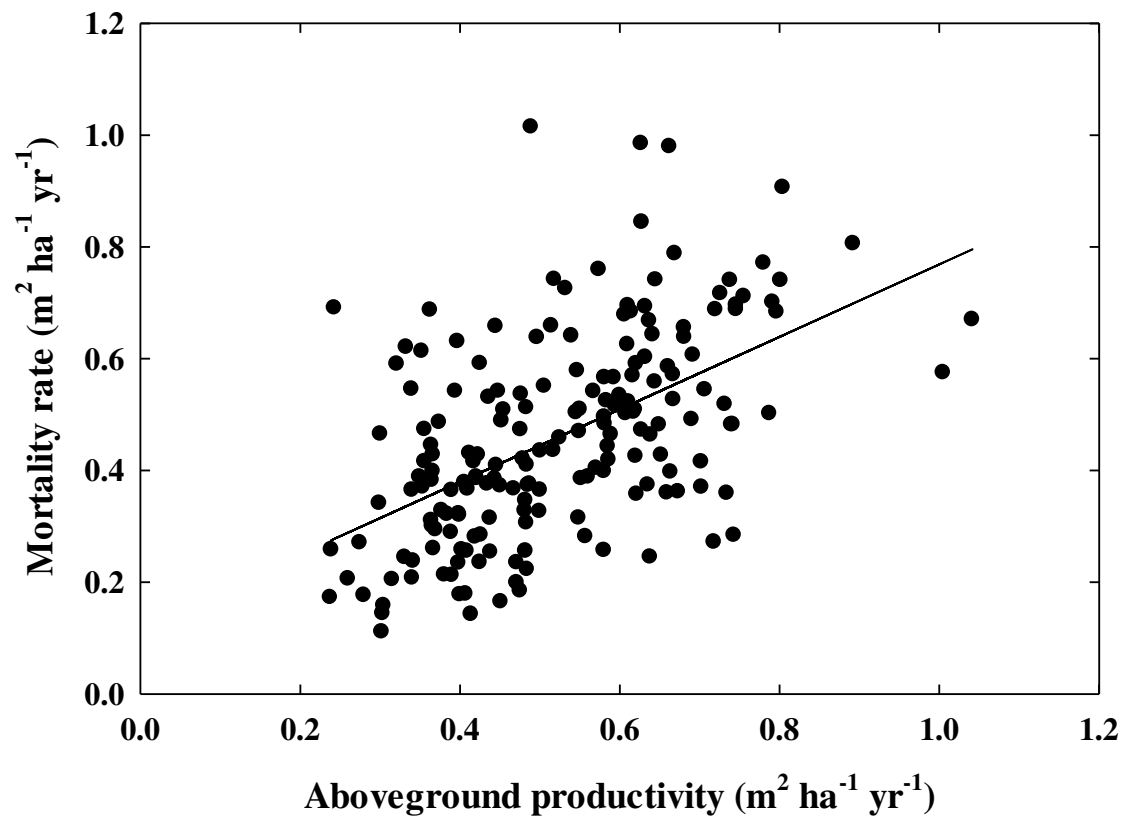
1567 **Fig. 2. Consistent increases in mortality rate (% individuals died per total number of**
1568 **individuals per year) across the America's.** Regression lines fitted to observations of stem
1569 mortality rate for the Amazon basin (solid line; Brienen *et al.*, 2015, slope of 0.029) and for
1570 temperate and boreal North America (dashed line; average values from all five sub-regions
1571 within van Mantgem *et al.*, 2009, Peng *et al.*, 2011, slope of 0.027). Linear regressions were
1572 used for simplicity, though a case can be made for non-linear (exponential) lines because zero-
1573 intercepts on the time-axis are not realistic (e.g. there is always some mortality occurring; see
1574 text). See Supporting Information Methods S1 and S2 for methods details and for versions of
1575 this figure using different units.

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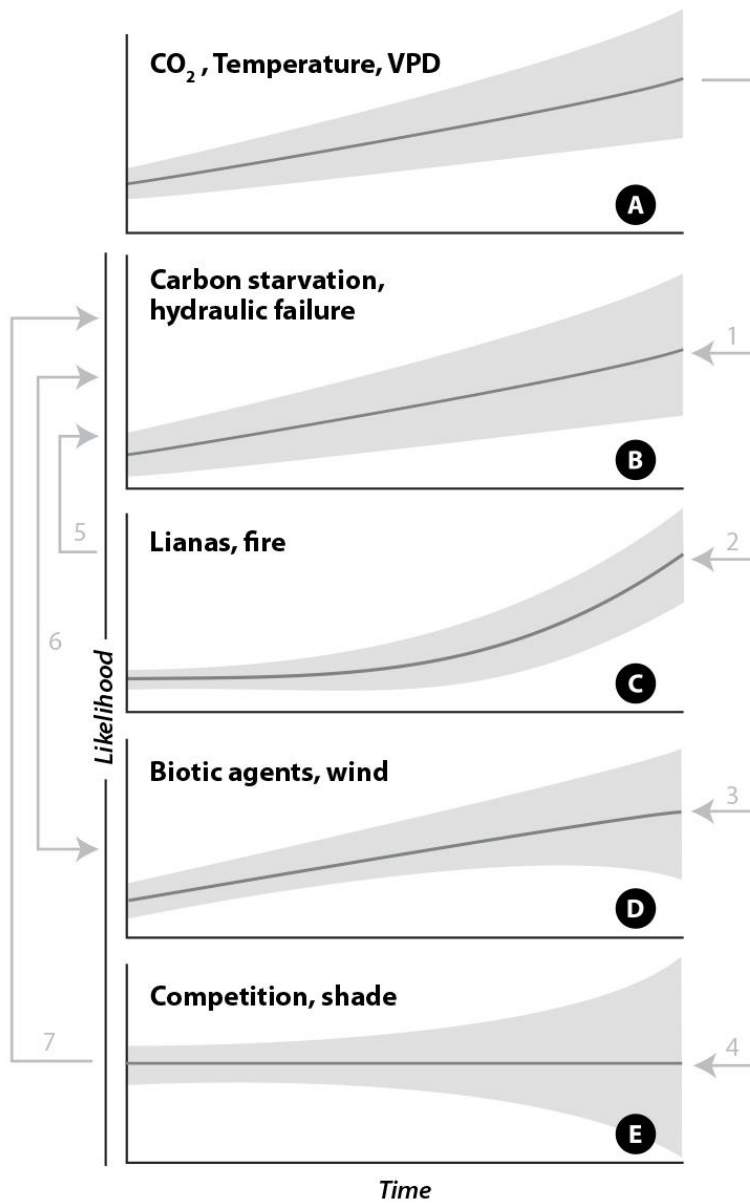
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1578 **Fig. 3: Basal area mortality rate is correlated with basal area productivity across the**
1579 **Amazon basin ($r^2 = 0.29$).** Data from Brien *et al.* (2015). Data represent stand dynamics as
1580 recorded for individual plots. See Supporting Information Methods S2 for details.



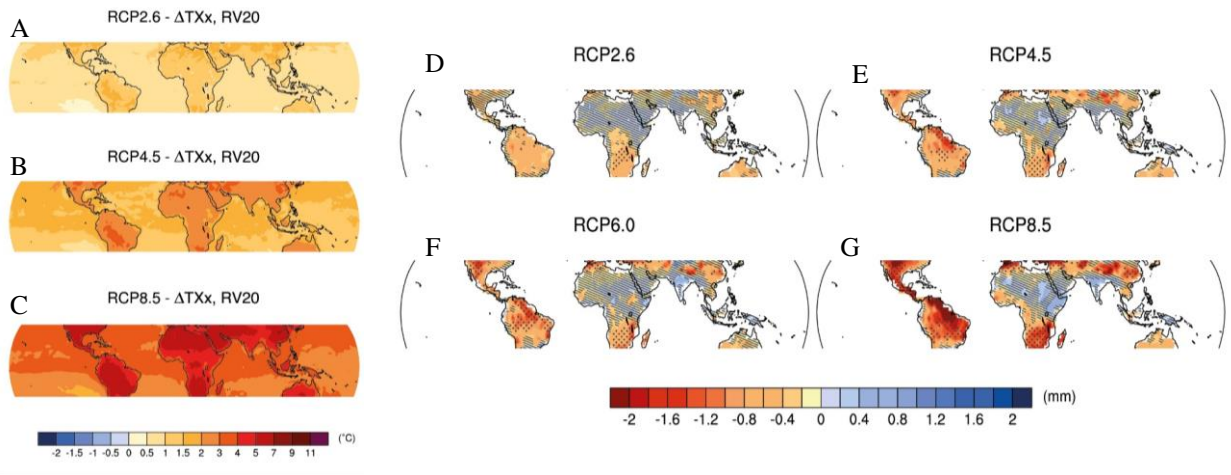
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1582 **Fig. 4. A graphical summary of the literature evidence of changing mortality drivers and**
 1583 **potential mechanisms over future conditions in moist -tropical forests.** Shown are the
 1584 expected trends in A) the forcing drivers of CO₂, temperature and VPD, and associated
 1585 likelihoods of B) carbon starvation and/or hydraulic failure, C) liana abundance and fire
 1586 frequency, D) biotic agent attack rates and destructive wind events, and E) competition for
 1587 resources including shade. See references in text that support the general trends and their
 1588 associated uncertainty. Panels C-E have widening uncertainty around the mean expectations due
 1589 to lack of consistent projections (e.g. wind and biotic agents) or due to logical feedbacks (e.g.
 1590 shade is enhanced by CO₂ but reduced by rising temperature and VPD; and CO₂ causes both



increasing shade and higher water-use efficiency) that 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 CO₂ 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, and (7) competition and shade promote carbon starvation. Not shown is potential long-term precipitation trends; but there is high likelihood of continued droughts at some periodicity and frequency, which will be more severe due to rising temperature and VPD (Panel A).

1620 **Fig. 5.** Coupled-Model Intercomparison Project (5) multi-model ensemble means of pan-tropical
 1621 temperature and soil moisture in 2081-2100 relative to 1986-2005. **A-C)** The CMIP5 multi-
 1622 model median change in 20-year return intervals of annual warm temperature extremes as
 1623 simulated for 2081-2100 in RCP2.6 (top), RCP4.5 (middle), and RCP8.5 (bottom). **D-G)**
 1624 Change in annual mean soil moisture (mass of water in the uppermost 10cm) (mm) for 2081-
 1625 2100 relative to 1986-2005 from the CMIP5 ensemble (RCP2.6, 4.5, 6.0, and 8.5). Hatching
 1626 indicates regions where the multi-model mean change is less than one standard deviation of
 1627 internal variability and where at least 90% of models agree on the sign of change. Between 22
 1628 and 35 models were used depending on the scenario. Re-printed courtesy of Collins *et al.*
 1629 (2013).



1630