

Drivers and mechanisms of tree mortality in moist tropical forests

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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) and
2 could have significant consequences for the global carbon cycle. We review the state of
3 knowledge regarding the drivers of MTF tree mortality, create a conceptual framework with
4 testable hypotheses regarding the drivers, mechanisms, and interactions that may underlie
5 increasing MTF mortality rates, and identify next steps for improved understanding and reduced
6 predictive uncertainty. Increasing mortality rates are associated with rising temperature and
7 vapor pressure deficit, liana abundance, drought frequency, wind events, fire, and possibly CO₂
8 fertilization-induced increases in stand thinning or acceleration of trees reaching larger, more
9 vulnerable heights. These mortality drivers alter plant physical structure or physiological
10 processes such as carbon starvation and hydraulic failure. The relative importance of each driver
11 is unknown and collectively they are a major knowledge gap. High species diversity may buffer
12 MTFs against large-scale mortality events relative to the extratropics, but the historical and
13 expected trends in mortality drivers give reason for concern regarding increasing mortality
14 within MTFs. Models of tropical tree mortality are advancing representation of hydraulics,
15 carbon, and demography, but require more empirical knowledge regarding the most common
16 drivers and their subsequent mechanisms. We outline critical datasets and model developments
17 required to test hypotheses regarding the underlying causes of increasing MTF mortality rates,
18 and improve prediction of future mortality under climate change.

19

20 II) Introduction

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

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

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

57

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

59 Mortality of individual trees within intact, old-growth forests has been rising during
60 recent decades in the Amazon basin (Figure 2; see Glossary for definitions of mortality rates;
61 unless otherwise specified mortality rate in this manuscript is always defined as % individuals
62 died per total number of live and dead individuals per year), having a significant impact on
63 biomass carbon loss (Figure SI1) and net ecosystem carbon storage (Phillips and Gentry 1994,
64 Phillips et al. 2004, Brienen et al. 2015). The trends for the Amazon basin are similar whether
65 plotted as percent mortality rates or biomass mortality (Figure 2 and Figure SI1). These results
66 from 100s of plots across the Amazon are consistent with observed pulse-mortality events in SE
67 Asia (Phillips et al. 2010), and declines in remotely sensed indices (assumed to be correlated
68 with canopy or whole-tree loss) of canopy biomass post-drought in the Amazon (Saatchi et al.
69 2013) and canopy health in the Congo attributed to drought and warming (Zhou et al. 2014).
70 However, not all tropical forests have exhibited increasing mortality recently (in Panama; Condit
71 et al. 2006, Meakem et al. 2017). The drivers and mechanism(s) underlying this increasing rate
72 of tree death in some areas (while not in others) are currently unknown (Phillips and Gentry
73 1994; Stephenson et al. 2011; Feldpausch et al. 2016).

74 At the coarsest level, increasing mortality rates in the Amazon are consistent with
75 observed forest inventory results from old-growth boreal and temperate forests of North America
76 (Figure 2; Luo and Chen 2015). Direct statistical comparison of the lines for the Amazon and for
77 North America is precluded by many limitations (see SI for details), but the similar general
78 trends for the two regions allows for the possibility of similar drivers and mechanisms across
79 North and South America. The Amazon basin has higher mortality rates than North America
80 (Figure 2), which may be expected based on the observed correlation between productivity and
81 turnover at regional (Amazon, Figure 3, and see alternative versions of Figure 3 (Figure SI2A,

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

89

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

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

106

107 **IV.I) Global Driver--Temperature and vapor pressure deficit:** Temperature is expected to rise
 108 in tropical forests (Figure 4A; Figure 5A-C). MTFs reside in the warmest latitudes on Earth,
 109 thus rising temperature will push them into a new temperature regime that has no current analog
 110 (Diffenbaugh and Charland 2016). Rising temperature and vapor pressure deficit (VPD) are
 111 forcing drivers associated with the multi-decadal increases in tree mortality rates throughout the
 112 Americas (Figure 2). There are multiple mechanisms by which rising temperature could cause

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

128
129 **IV.II) Global-Regional Driver-Drought:** Drought, i.e. precipitation decline that impacts soil
130 moisture, is arguably the best-studied driver of MTF tree mortality. Two critical aspects of
131 drought as a mortality driver are that it episodically occurs everywhere globally, and that the
132 severity of drought extremes is expected to worsen under future conditions (Trenberth et al.
133 2014; also see Mitigating Factors section below for more details on precipitation forecasts). In
134 particularly wet or anoxic soils the drying may benefit growth and survival, but in many areas
135 this will result in regional increases in mortality (Phillips et al. 2010, Brienen et al. 2015,
136 Doughty et al. 2015, Johnson et al. 2016, Powell et al. 2013, Thurner et al. 2017). Droughts
137 happen in MTFs particularly during El Niño events (Ropelewski and Halpert 1987, Ronchail et
138 al. 2002) and periods of warm North Atlantic sea-surface temperatures (Marengo et al. 2011).
139 The most consistent predictions of climate in tropical forests suggest increasing total
140 precipitation (Kitoh et al. 2013, Gloor et al. 2013), but stronger and longer dry seasons over the
141 next century (Boisier et al. 2015; Duffy et al. 2015, Rauscher et al. 2015, Pascale et al. 2016).
142 Due to atmospheric warming (and possibly due to lower relative humidity, see Figure SI3), these
143 future droughts will include higher so-called baseline temperature and VPD than historically

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

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

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

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

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

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

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

211

212 **IV.IV) Regional Driver--Lianas:** Lianas (woody vines) are much more common in tropical
213 forests than in temperate or boreal forests (Schnitzer 2005). Lianas reduce productivity and
214 increase mortality of host trees (Figure 1F; Ingwell et al. 2010; van der Heijden et al. 2015,
215 Wright et al. 2015). The total contribution of lianas to tropical tree mortality is difficult to
216 estimate because of wide variation in liana abundance among tropical forests, the relatively small
217 number of studies that have quantified liana influences on tree mortality, differences among
218 studies that make direct comparisons difficult, and the inherent difficulties of quantifying the full
219 impact of lianas on tree mortality. However, Wright et al. (2015) found that 64% of studies had
220 shown liana abundance to be increasing (also see Phillips et al. 2002, Schnitzer and Bongers
221 2011). Lianas outcompete host trees for resources such as light, water, and nutrients (Johnson et
222 al. 2013), thus they potentially promote both carbon starvation and hydraulic failure of host trees.
223 Furthermore, lianas break limbs and expose fresh wounds for infection by biotic agents. Thus
224 interdependent mechanisms between liana invasion, carbon starvation (e.g. shading), hydraulic
225 failure (e.g. reduced water availability), and biotic agent attack are likely (interactions in Figure
226 4B-E). Lianas may also increase mortality rates of neighboring uninfested trees, insofar as they
227 increase the rates of treefalls – which can be lethal to smaller neighbors – while competing
228 belowground for water and nutrients (Johnson et al. 2013). Liana abundance tends to increase
229 with dry season length, land use change, and with increasing CO₂ (DeWalt et al. 2015, Granados
230 and Körner 2002, Schnitzer 2014) and thus is expected to increase in the future (Figure 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 by
235 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 forests
237 during drought years tend to be larger (Silvestrini et al. 2011, Alencar et al. 2015), more intense,
238 and kill more trees than the ones occurring in non-drought years (Brando et al. 2014). Several
239 lines of evidence suggest that fire seasons in tropical forests have increased over the past few
240 decades (Jolly et al. 2015) resulting in larger (Cochrane and 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 and 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. 2003,
245 Balch et al. 2015, Brando et al. 2016). It is likely that rising temperatures and climate extremes
246 and decreasing surface water content (Figure 5) are increasing forest flammability (Chen et al.
247 2011). Clear linkages between hydraulic failure and post-fire mortality are now established (Bar
248 et al. 2017) suggesting again that interactions across mechanisms (in this case hydraulic failure
249 and fire) are likely (Figure 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 and 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 in
262 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 SI
268 Figure SI4) with warming-driven increases in atmospheric latent heat, indicating a shift toward
269 more intense wind disturbance regimes in MTFs (Figure 4D).

270

271 **IV.VII) Regional Driver-Biotic agents:** Pathogens, insects, and other biotic agents contribute to
272 tree mortality (Coley and Barone 1996) and play a strong role in structuring tropical forests
273 (Mangan et al. 2010, Coley and 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 (Figure 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% (Figure SI1), 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 and 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 (Figure 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; Figure 1D). Shading
301 is presumed to be the dominant driver of the high mortality rates of seedlings and understory
302 plants (Figure 1A, Panama example), however the mechanisms of the interactions between
303 shade, herbivory, biotic agents, and the physiological mechanisms of carbon starvation and
304 hydraulic failure (O'Brien et al. 2014) within the ultimate mortality process is poorly known.
305 Solar 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) and
309 higher leaf area. Thus, there is large uncertainty in the trajectory of shading in the future (Figure
310 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 (Figure 3) may all possibly increase under future climate change (Figure, 4). However,
317 the 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 (Figure 2) a challenge both
320 historically 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; Figure 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 (Figure 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 and Korner 2005). Biotic
339 agents may successfully invade trees that have low carbohydrates from the carbon starvation
340 process and low sap pressure (Lorio and 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 **V) 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
354 al. 2015), rising CO₂ impacts on carbon and water relations (Keenan et al. 2016), and the
355 potential of increasing mean annual precipitation (Figure SI5).

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 promotes
361 resistance (ability to withstand change) and resilience (ability to recover) are thought to lie in the
362 greater capacity of the forest community to tolerate new conditions due to a wider range of traits
363 that enable survival (e.g. hydraulic traits that promote drought tolerance; Christoffersen et al.
364 2016; Powell et al. 2017). Evidence on the role of diversity in global patterns of mortality comes
365 from comparison of rates of drought-induced death in the moist tropics, where mortality rates (on
366 an individual basis) are rarely above 5% in inventory plots even after droughts (Figure SI1B) and
367 only up to 15% in drought experiments (Nepstad et al. 2007, Rowland et al. 2015a), versus the
368 temperate zone where mortality rates can exceed >90% (Breshears et al. 2005; Plaut et al. 2012).

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

378 Increasing mean annual precipitation may occur in some tropical regions (Figure SI5).
379 This would act to only partially buffer the large increase in evaporative demand due to
380 temperature (Figure 5A), which results in significant reductions in soil moisture (Figure 5B)
381 based on the Coupled-Model Intercomparison Study (CMIP5, Collins et al. 2013). As reviewed
382 earlier, the occurrence of droughts that are warmer than previously will increase, thus their
383 impact will be more severe (Trenberth et al. 2014). There is some prediction of shifts to longer
384 drought lengths (Boisier et al. 2015; Duffy et al. 2015, Rauscher et al. 2015, Pascale et al. 2016).
385 Note that increasing precipitation, when it does occur, also results in greater shade, more soil
386 anoxia, and greater windthrow, so it is not clear that there will be much net benefit of increasing
387 precipitation on survival of moist-tropical forest trees.

388

389 **VI) The state of ESM simulations of moist tropical tree mortality**

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

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

410 Among the newer generation of ESMs, two representations of mortality are common.
411 The first is shifting from one plant functional type (PFT) to another (representative of mortality
412 and regeneration by a new type) based on climate envelopes (Sitch et al., 2003). The second is
413 the use of constant biomass residence times (see Kucharik et al., 2006), which is tantamount to
414 assuming "senescence" mortality, in which a genetically predisposed age threshold is used. Both
415 of these approaches risk over-simplification. Climate envelopes do not capture spatial variability
416 such as with different climates, species, or topography, and may not be realistic in a future,
417 warmer, higher CO₂ world. Age-driven mortality, while it may capture the statistical odds of
418 dying from pathogen infestation, wind, or lightning, is not mechanistically representative
419 (Mencuccini et al. 2005) and may thus also fail under a novel climate.

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

430

431 **VII) Next steps**

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

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

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

448

449 **VII.I) Observations:** We do not know the relative importance of the various drivers of MTF
450 mortality (Figures 1-4) nor do we have sufficient confidence in the trajectory of these mortality

451 drivers in the future to make rigorous predictions (Figure 4). Quantifying the various mortality
452 mechanisms in MTFs is limited by a scarcity of temporal and spatial data sufficient to overcome
453 the high signal-to-noise ratio inherent in field observations of plant mortality. Long-term and
454 high-temporal frequency observations (e.g. annual) at the plot-level are essential to reveal the
455 long-term spatial and temporal patterns of mortality in relation to climate dynamics. Plot
456 networks, although challenging to run, are arguably the lowest cost, highest impact investment
457 one could make to refine the uncertainty in moist-tropical mortality drivers. Plot networks
458 provide information regarding the dynamics of growth and death in response to droughts (Condit
459 et al. 1995, Phillips et al. 2009; Brienen et al. 2015, Anderson-Teixeira et al. 2015), and with
460 appropriate measurements, they can unveil mechanisms driving mortality (Doughty et al. 2015).
461 A relatively low-cost addition to inventory networks could be assessment of the “modes” of
462 death (snapped, died standing, windthrow, presence of rot, etc), determination fraction of crown
463 shaded (by neighbors or lianas), and dendrometer measurements prior to death. Plot-level work
464 can in some cases include tree rings, even for tropical trees (Schöngart et al. 2006, van der Sleen
465 et al. 2015; Brienen et al. 2016), which can provide proxy measurements of physiology
466 proceeding death (Gaylord et al. 2015). Similarly, remotely-sensed data provide unparalleled
467 spatial coverage of drought impacts, such as the long-term decline in canopy health associated
468 with declining precipitation and increasing temperature in the Congo Basin (Zhou et al. 2014)
469 and the sustained loss of biomass observed post-drought in the Amazon (Saatchi et al. 2013). A
470 key step is validation of remote sensing estimates of mortality against ground-based data such as
471 mortality rates, leaf area, canopy height, and canopy biomass and correlations of remotely sensed
472 indices of dying and surviving trees at the crown scales e.g. using high-resolution (<10m)
473 satellite products now available (McDowell et al. 2015).

474
475 **VII.II) Experiments:** Cause-and-effect experiments that manipulate mortality drivers (Meir et al.
476 2015, van der Heijden et al. 2015) are valuable because they can reveal the mechanisms
477 underlying mortality, and can be employed for model evaluation under novel climate conditions.
478 The few moist tropical drought experiments (Nepstad et al. 2007, Moser et al. 2014, Rowland et
479 al. 2015a, Meir et al. 2015), cannot be representative of the diverse MTFs and thus experiments
480 replicated across a broad range of soils, topographic relief, and proximity to groundwater (Nobre
481 et al., 2011) are needed. Replication of such experiments across a wider range of sites in the

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

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

503
504 **VII.IV) *ESM drought, temperature, VPD and CO₂:*** Given that mortality is downstream of the
505 majority of other physiological processes (assimilation, respiration, allocation), predictions are
506 sensitive to assumptions about photosynthesis, respiration, carbon allocation, and carbon storage
507 (Fisher et al. 2010), all of which are heavily influenced by plant hydraulics (Christoffersen et al.
508 2016; see text below on hydraulic modeling limitations and developments) and so predictions
509 tend to be extremely divergent among models (Galbraith et al. 2010, Huntingford et al. 2013).
510 To improve accuracy under non-linear changes (and complex interactions) of future drought,
511 temperature, VPD, CO₂, and hopefully someday wind, fire, and lianas, next-generation models
512 are now including more realism such as carbon starvation and hydraulic failure (Fisher et al.

513 2010, 2015; McDowell et al. 2013; Sperry et al. 2016; Xu et al. 2016), though evaluation in
514 MTFs is needed. Simulating these mortality mechanisms requires representing water transport,
515 xylem embolism, photosynthesis, and carbon storage accurately.

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

544 drought and mortality responses (see an example approach for future ESM hydraulic
545 development in the supplemental information).

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

561
562 **VII.V) *ESM trait-based modeling in the diverse moist tropics:*** Modeling the myriad set of
563 mortality drivers and mechanisms (Figure 4) is challenging as it requires identification and
564 incorporation of the trade-off and coordination among different traits targeted for different
565 survival strategies (Fisher et al. 2015). This is a particularly important issue in the particularly
566 diverse tropics, where the variety of species and thus traits are greatest, but are represented by
567 only a limited number of PFTs used to model MTFs i.e. evergreen vs. deciduous trees. Next
568 generation models are moving towards becoming trait-enabled such that trait-trade-offs facilitate
569 simulation of diversity impacts on carbon and water balance of forests (Sakschewski et al. 2016).
570 Data to parameterize these models is becoming available at the global scale, with discovery of
571 quantitative relationships among plant traits (Wright et al. 2004, Christoffersen et al. 2016), the
572 inter- and intra-specific and biogeographical components to their variation (Anderegg 2015c),
573 the number of independent axes of trait variation in forest communities (Wright et al. 2007,
574 Baraloto et al. 2010, Reich 2014), and relationships of plant traits to tree mortality (Wright et al.

2010). For example, many parameters required for simulating plant hydraulics (such as pressure-volume relationships) can be estimated from traits such as wood density (Christoffersen et al. 2016). This understanding informs us 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 developing 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, Langan & Higgins 2013) because of mounting evidence showing that key aspects of ecosystem-level properties (e.g., C storage, overall resiliency) 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 (Figure 4).

587

VII.VI) *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, CO₂, 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 liana's 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 likely impact hydraulic failure through drawing down soil moisture via their high transpiration rates (Chen et al. 2015), and carbon starvation via shading, but determining the fraction of host-crown shaded, and impacts on water consumption, are required to inform model mechanism.

599

VII.VII) *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

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

615
616 **VII.VIII) *ESM Biotic agents:*** Most ESMs have not simulated biotic attacks (insects and
617 pathogens; but see Dietze and Matthes 2014, Landry et al. 2016) but a path forward can be
618 derived from a few key observations. Insect outbreaks often occur after droughts in the moist
619 tropics (Anderegg et al. 2015b), exhibit a correlation between host tree defense and outbreak
620 success in both temperate (Herms and Mattson 1992, Raffa et al. 2008) and tropical regions
621 (Dyer et al. 2007), and outbreaks (i.e. widespread attacks on one or more species) decline with
622 increasing diversity at the global scale (Jactel and Brockerhoff 2007). Less is known about the
623 processes driving biotic agents such as heartrot and rootrot, but we may presume that infection
624 by these agents is similar in physiological regulation to that of insects (see McDowell et al.
625 2011). Thus an initial ESM approach could be to simulate defense (perhaps using available
626 carbon as a surrogate) and assume (for now) that biotic agents are ubiquitous in presence.
627 However, in addition to predisposition by plant stress, outbreaks of tropical tree-killing insects
628 are also more likely after other types of disturbances that open the canopy and increase the
629 abundance of light, new foliage, and juvenile trees (Dyer et al. 2012), which suggests that the
630 dynamics of canopy gap formation in demographic models may be used for outbreak initiation.
631 Although these bottom-up controls by plant defenses and stand structure play a role in outbreaks
632 of tropical tree killing insects, top-down predator control appears particularly important in the
633 tropics in constraining the magnitude of outbreaks (Van Bael et al. 2004). Thus an idealized
634 model might include a function associated with host tree defense capability, host-tree abundance
635 (Dyer et al. 2012), forest structure (Dyer et al. 2012), insect thermal optima (Goodsman et al. in
636 revision), and top-down insect predator abundance, all influenced by environment.

637

638 **VII.IX) *ESM Wind*:** Arguably the hardest ESM challenge is to downscale maximum wind
639 speeds from atmospheric models that simulate average wind speeds over the scale of individual
640 grid cells (e.g. Figure SI4) and are formulated using a hydrostatic approximation that prevents
641 explicit representation of processes that generate high wind extremes. At the canopy-scale, the
642 ability to model either loss of foliage, loss of major branches, snapped-stems, standing dead
643 stems, or an uprooted tree is valuable for capturing recovery processes, gap light dynamics, and
644 carbon cycling from wind mortality (Holm et al. 2017), which can be most aptly simulated in
645 demographic models. Opportunities to further improve predictions of wind mortality lie in
646 representing abiotic and biotic conditions (e.g., soil conditions, prior exposure to stress, presence
647 of heartrot) that enhance vulnerability to wind, traits that confer susceptibility or resistance to
648 wind, and the wind fields that can topple canopy trees (Ribeiro et al. 2016).

649

650 **VIII) Conclusions**

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

665

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671

For Peer Review

672 **Box 1. Glossary**

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

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

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

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

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

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

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

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

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

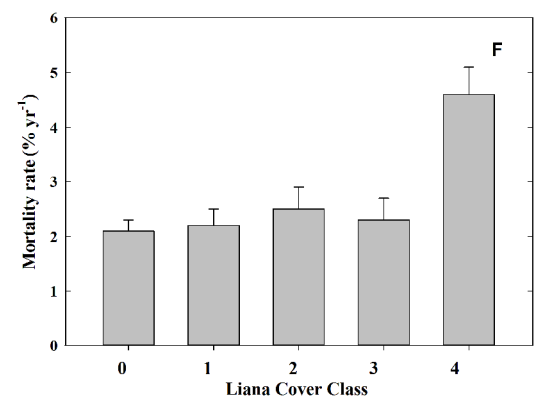
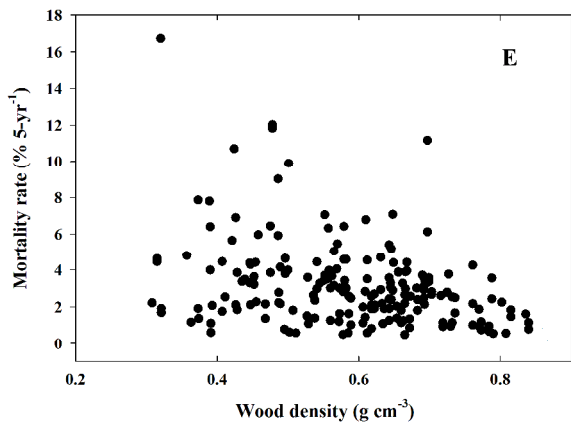
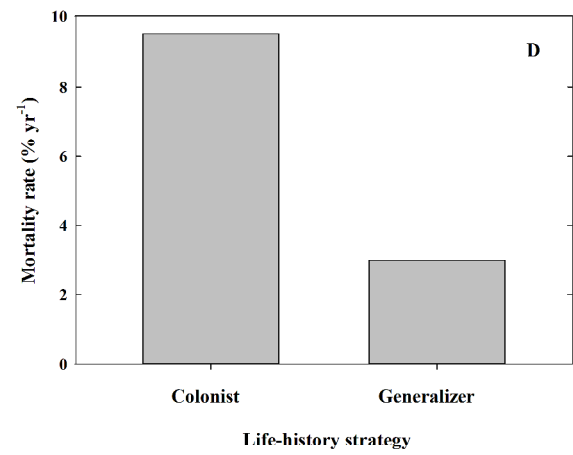
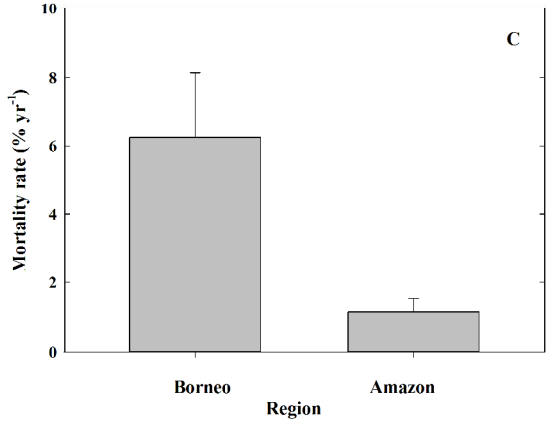
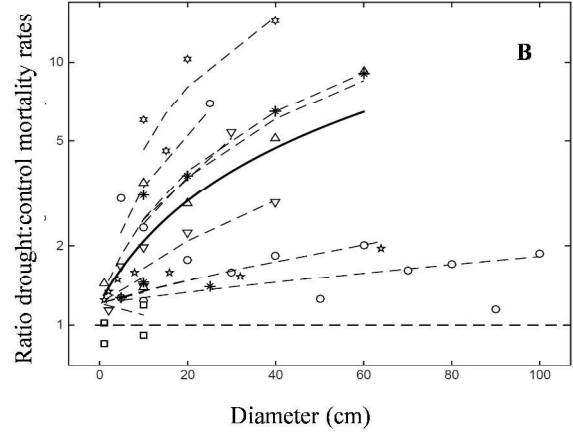
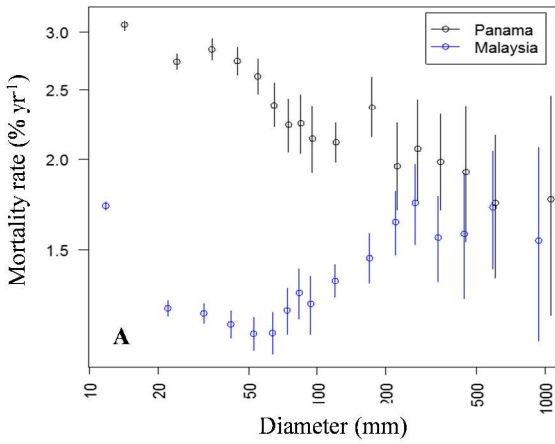
696 Mortality rate: Can be defined using many units, typically % yr⁻¹ (number of trees died per
697 number of total individuals live and dead per year) or in units of basal area (m² basal area
698 died/m² of total stems/year) or biomass (kg C died/kg C standing biomass/year). Corrections for
699 biomass weighting, non-balanced plot sizes or sampling periods over time and space are often
700 employed when calculating mortality rates from inventory data. See Supplemental Information
701 for equations.

702

703 **Figure 1. Axes of variability in tropical tree mortality.** A) Mortality rate [as $\log(\text{initial}$
704 $\text{number}) - \log(\text{number survivors})/(\text{years})$] versus stem diameter in Pasoh, Malaysia and Barro
705 Colorado, Panama (bars are 95% CI, no major droughts during censuses); this highlights that
706 both negative and positive mortality rates as a function of diameter can be found (from Muller-
707 Landau et al. 2006). B) Mortality rates (# individuals died per number of total individuals per
708 year; all subsequent figures use this calculation; see Glossary and SI for information on mortality
709 rate calculations) plotted as the ratio of mortality rate during drought relative to a control period
710 across a range of stem diameters for 12 sites across the tropics (symbols represent different
711 sites), showing the clear pattern size-mortality relationships *during droughts* (from Bennett et al.
712 2015). C) The mortality rates in forests in Borneo and the Amazon measured post-drought,
713 highlighting regional differences (from Phillips et al. 2010). D) Mortality rate versus life-history
714 strategy in Barro Colorado, Panama, highlighting the role of successional strategy on long-term
715 mortality rates (from Condit et al. 1995). E) Mortality rate versus wood density in Barro
716 Colorado, Panama, highlighting a significant but weak relationship ($p < 0.05$; from Wright et al.
717 2010). F) Mortality rate as a function of liana cover class in Pasoh, Malaysia, highlighting the
718 influence of lianas on mortality. Liana cover class 0 indicates no lianas, 1 indicates up to 25% of
719 the crown covered by lianas, 2 = 26-50%, 3=51-75%, and 4=76-100% (from Wright et al. 2015).

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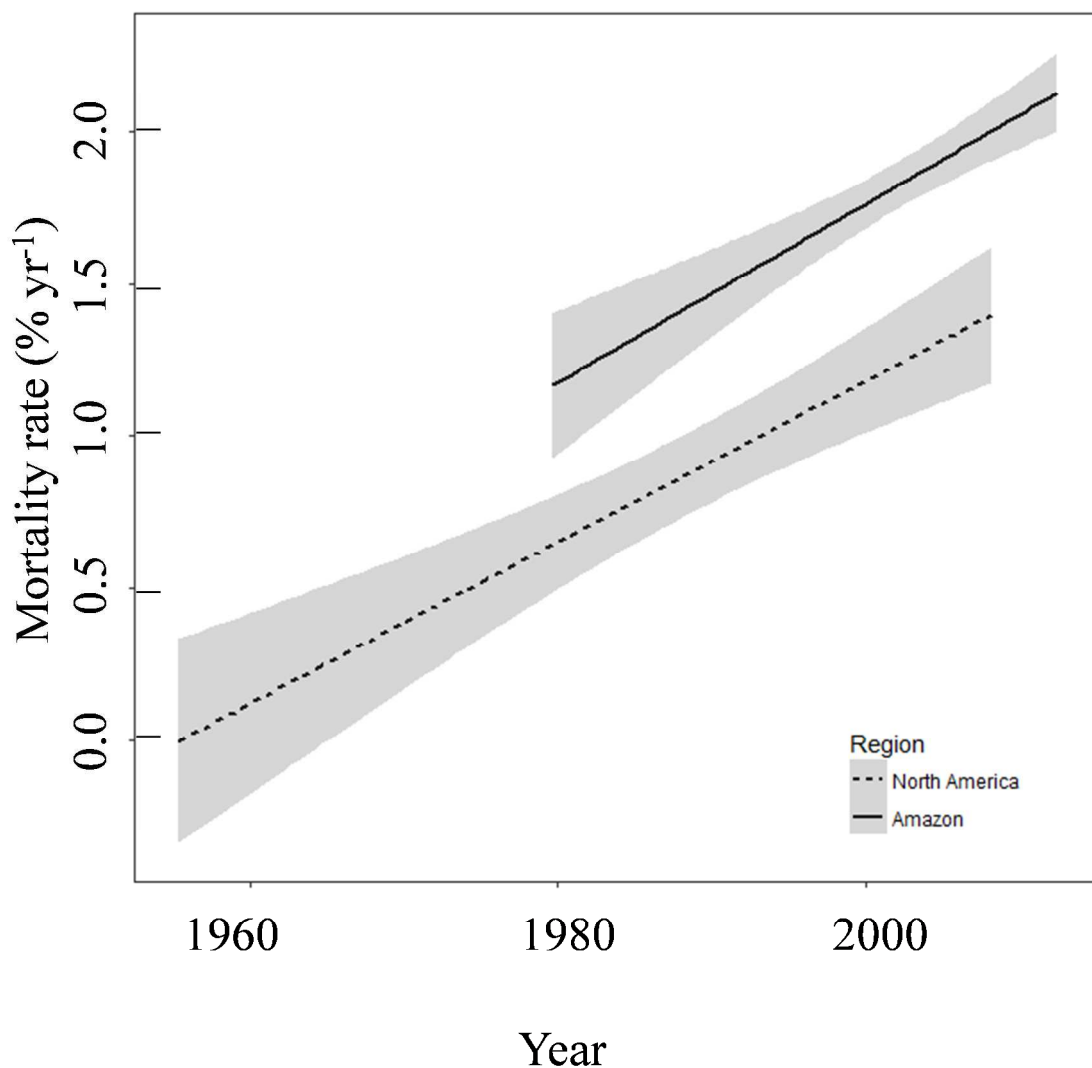
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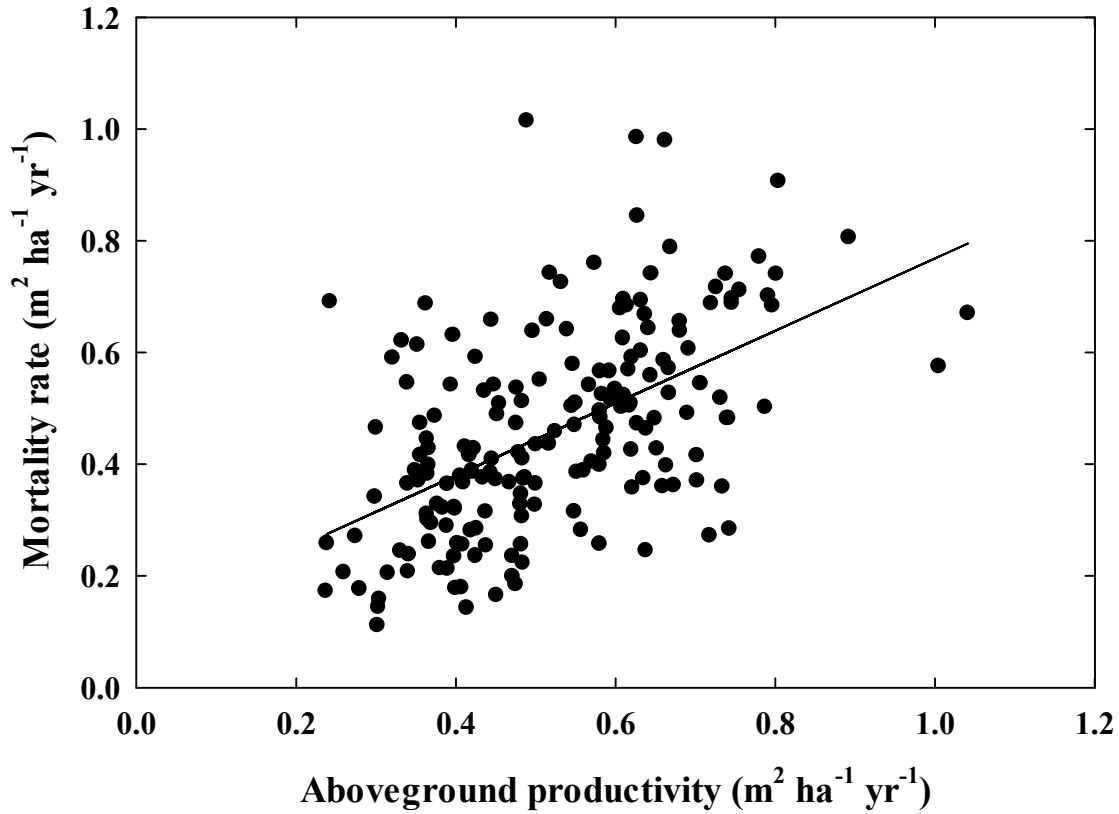
726 **Figure 2. Consistent increases in mortality rate (% individuals died per total number of**
 727 **individuals per year) across the America's.** Regression lines fitted to observations of stem
 728 mortality rate for the Amazon basin (solid line; Brienen et al. 2015, slope of 0.029) and for
 729 temperate and boreal North America (dashed line; average values from all five sub-regions
 730 within van Mantgem et al. 2009, Peng et al. 2011, slope of 0.027). Linear regressions were used
 731 for simplicity, though a case can be made for non-linear (exponential) lines because zero-
 732 intercepts on the time-axis are not realistic (e.g. there is always some mortality occurring; see
 733 text). See supplemental information for methods details and for versions of this figure using
 734 different units.

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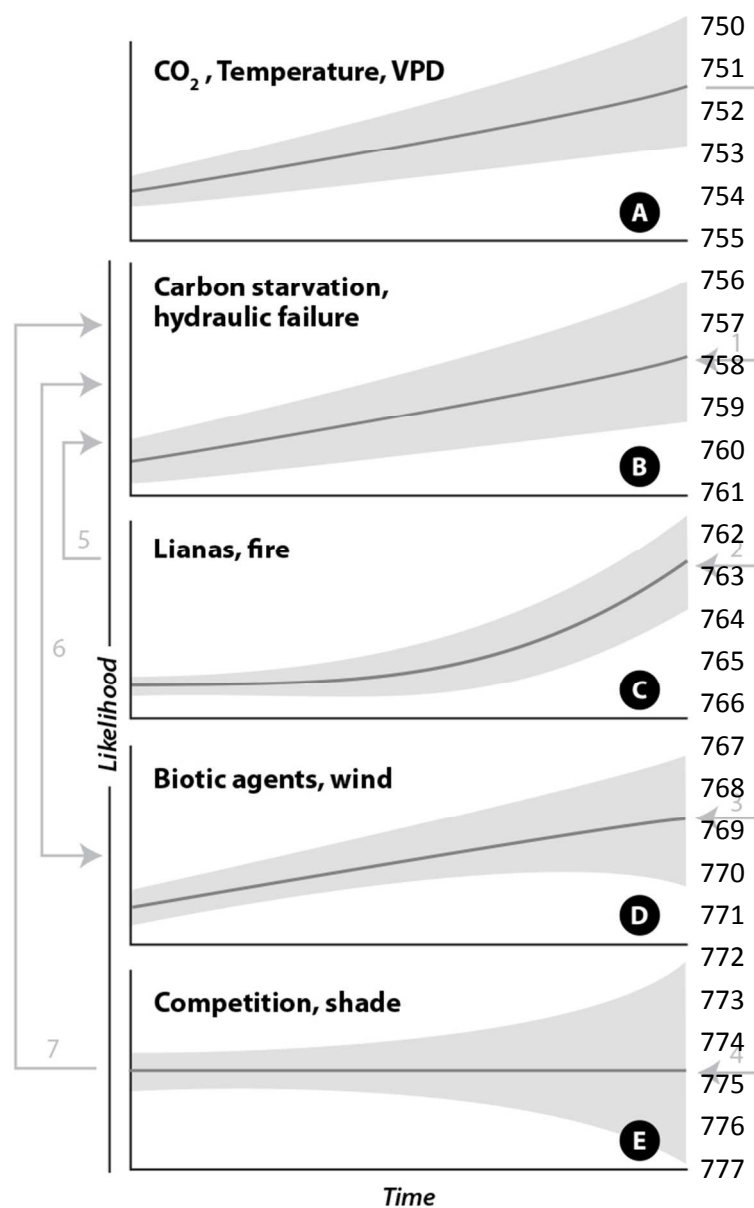
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737 **Figure 3: Basal area mortality rate is correlated with basal area productivity across the**
738 **Amazon basin ($r^2 = 0.29$).** Data from Brien et al. 2015. Data represent stand dynamics as
739 recorded for individual plots. See supplemental information for methods details.



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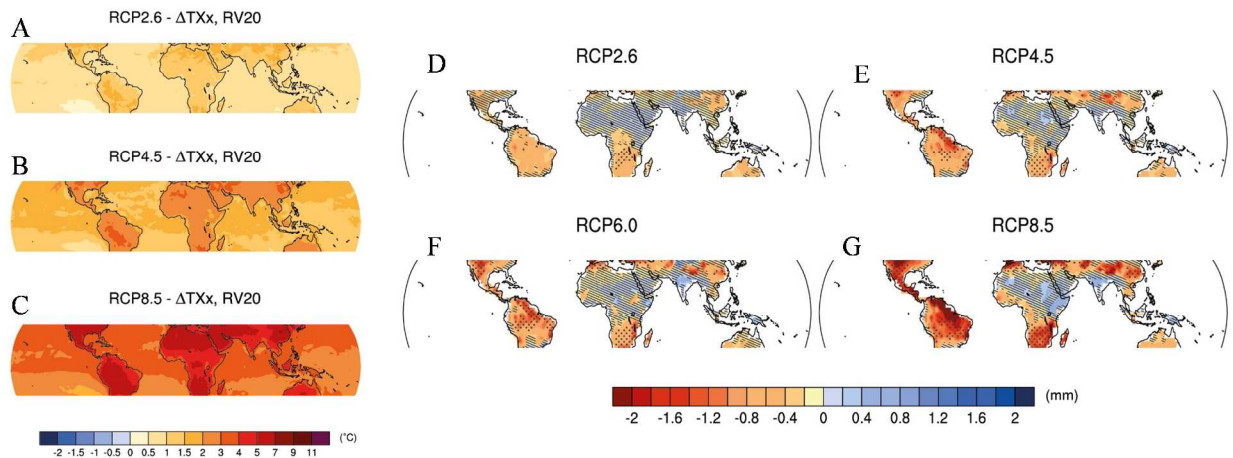
741 **Figure 4. A graphical summary of the literature evidence of changing mortality drivers**
 742 **and potential mechanisms over future conditions in moist -tropical forests.** Shown are the
 743 expected trends in A) the forcing drivers of CO₂, temperature and VPD, and associated
 744 likelihoods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



750 increasing shade and higher water-
 751 use efficiency) that may negate
 752 influences. The numbered gray
 753 lines denote potential interactions
 754 across panels based on the
 755 literature evidence. Rising
 756 temperature and VPD promote (1)
 757 carbon starvation and hydraulic
 758 failure, (2) liana encroachment and
 759 fires, and (3) biotic agent attack
 760 and wind events. (4) Rising CO₂
 761 may promote competition and
 762 shade. (5) Lianas may promote
 763 carbon starvation via shade and
 764 fires may promote hydraulic failure
 765 via xylem damage, (6) biotic
 766 agents promote carbon starvation
 767 and hydraulic failure and vice
 768 versa; wind promotes carbon
 769 starvation via canopy loss, and (7)
 770 competition and shade promote
 771 carbon starvation. Not shown is
 772 potential long-term precipitation
 773 trends; but there is high likelihood
 774 of continued droughts at some
 775 periodicity and frequency, which
 776 will be more severe due to rising
 777 temperature and VPD (Panel A).

778

779 **Figure 5.** Coupled-Model Intercomparison Project (5) multi-model ensemble means of pan-
 780 tropical temperature and soil moisture in 2081-2100 relative to 1986-2005. **A-C)** The CMIP5
 781 multi-model median change in 20-year return intervals of annual warm temperature extremes as
 782 simulated for 2081-2100 in RCP2.6 (top), RCP4.5 (middle), and RCP8.5 (bottom). **D-G)**
 783 Change in annual mean soil moisture (mass of water in the uppermost 10cm) (mm) for 2081-
 784 2100 relative to 1986-2005 from the CMIP5 ensemble (RCP2.6, 4.5, 6.0, and 8.5). Hatching
 785 indicates regions where the multi-model mean change is less than one standard deviation of
 786 internal variability and where at least 90% of models agree on the sign of change. Between 22
 787 and 35 models were used depending on the scenario. Re-printed courtesy of Collins et al.
 788 (2013).



789

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review

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1620

1621 **Supplemental information**

1622 Table of contents:

1623 -Figure 2 methods descriptions

1624 -Figure SI1

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1626 -Figure SI2

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1630 -Figure SI4

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1632

1633 **Figure 2 and Figure 3 Methods.** Inventory data on the number of trees live and dead on a plot,
 1634 censused at periodic intervals, can be converted into mortality rates using the equation

1635

$$1636 \text{ mortality rate (year}^{-1}\text{)} = (d/n)/t \qquad \text{Eqn S1}$$

1637

1638 where n is the number of living trees at the start of the census interval, d is the number of those
 1639 trees that died during the census interval, and t is the number of years in the census interval.

1640 However, this “arithmetic mortality” (as used by Brien et al. 2015) and also the commonly

1641 used “instantaneous mortality” rate (Eq S2), systematically underestimate mortality rate and can

1642 introduce systematic biases if the lengths of the census intervals change through time (Sheil et al.

1643 1995).

1644 This bias can be reduced by calculating the true annual mortality rate as

1645

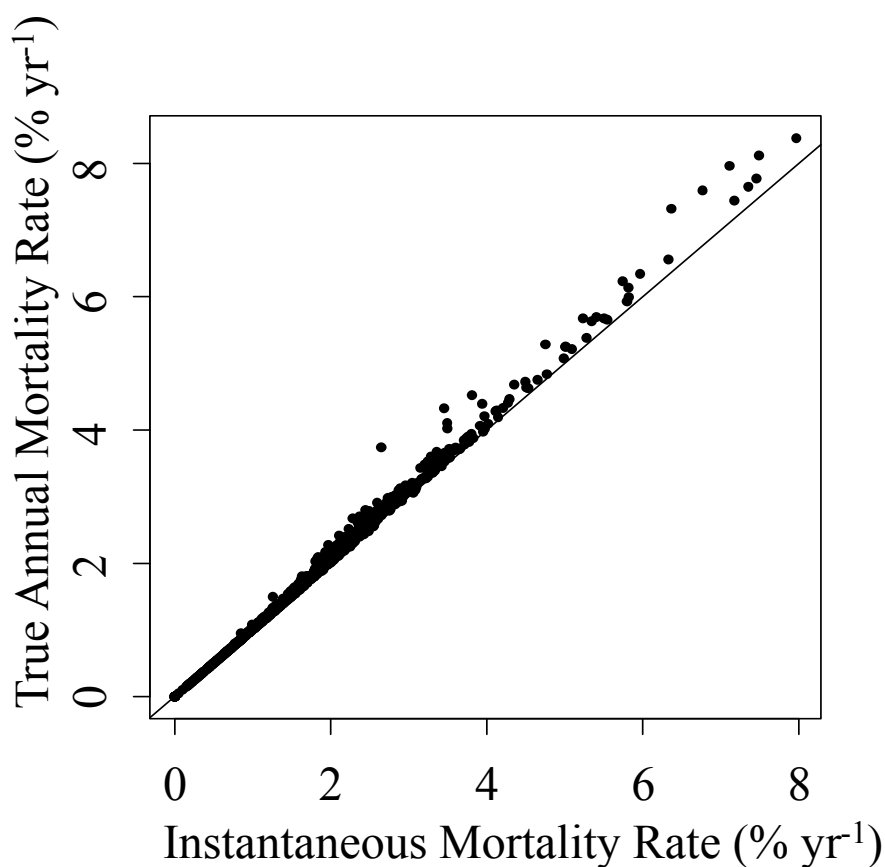
1646 mortality rate (year^{-1}) = $(\text{LN}(n) - (\text{LN}(n - d)))/t$ Eq. S2.

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1648 (equation 4 in Sheil et al. 1995). The difference in estimates is generally small in absolute terms,

1649 especially when mortality rates are low (e.g., Figure SII).

1650



1651

1652 **Figure SII.** Comparison of the true annual mortality rate (Eq. S2) and the rate calculated under
 1653 the arithmetic formula (Eq. S1) for the Amazon tree dataset analyzed by Brien et al. (2015).
 1654 The mortality rate using Eq S1 is virtually indistinguishable from this result and is therefore not
 1655 shown. Each point represents a single plot and census interval. The line is the 1:1 line.

1656 Alternative versions of the Amazon data shown in Figure (2) are presented below in
1657 Figure SI2, including biomass mortality, percent mortality with all data shown, and percent
1658 biomass mortality (panels A, B, C respectively). Amazon mortality trends shown in Figure 2 are
1659 based on census data from 321 plots from across the Amazon basin from Brienen et al. (2015).
1660 The trends are calculated using linear mixed effects models (lme4 package: Bates et al. 2013)
1661 with weightings applied based on sampling effort (plot size and monitoring length) as described
1662 in Brienen et al. (2015). Mortality rates were calculated using equation S2 (Sheil et al. 1995;
1663 Kohyama et al. 2017).

1664 We did not conduct a formal test to compare the Amazonian and the N. American lines.
1665 We chose not to conduct this test based on limitations associated with the different time periods
1666 of the two datasets, and issues associated with new sites being added to each dataset throughout
1667 the life of the dataset. Formal comparison of global inventory datasets is a large but important
1668 future challenge.

1669 To assess whether the long-term trends in mortality rates for Amazon trees better fit a
1670 linear or non-linear model, we compared two mixed effects model fits. First, we performed a
1671 simple regression of the mid-point of each census interval against the mortality rate for that
1672 interval, using the lme4 package (Bates et al. 2013). This model accounted explicitly for plot
1673 effects (as random effect in the model) and for variation in sampling effort (plot size and census
1674 interval length) as outlined in Brienen et al. 2015. We then rerun the same model, but adding a
1675 quadratic term to the explanatory variable (mid-point of census interval), in effect creating a non-
1676 linear fit. The two mixed effect models were then compared using ANOVA.

1677 The implications of different equations to fit long-term mortality data (e.g. Figure 2) are
1678 substantial. Four possible interpretations of these data could be taken.

- 1679 1) This time-window happened to capture an increase in mortality, but this is really part
1680 of long-term variation that is stationary. Mortality rates will continue to bounce
1681 around, with no fundamental change in their probabilities. .
- 1682 2) The change in mortality rates during this time period is best fit by a step function; that
1683 is, mortality rates were previously stable at a lower rate, and transitioned or are
1684 transitioning to a new higher rates (say 2% instead of 1% for the Amazon). A
1685 doubling in mortality corresponds to a halving in residence time if all else is equal,
1686 thus this would have significant impacts on carbon storage.
- 1687 3) Mortality rates increased linearly during this time period. If this increase continues
1688 for the foreseeable future, the rate will continue to rise as depicted in Figure (2), and
1689 we can expect another doubling in the near future. Clearly a linear increase cannot be
1690 extrapolated far backward in time, as mortality was never zero historically and cannot
1691 ever be negative.
- 1692 4) Mortality rates increased exponentially during this time period. An exponential
1693 function is the best fit at low mortality rates (e.g. decades ago in Figure 2). Such an
1694 increase could be extrapolated backwards in time (it will never reach zero), although
1695 we lack data to support such extrapolation. Continued exponential growth in
1696 mortality would result in massive reductions in turnover time and biomass stocks.

1697 Ultimately, understanding the proper relationships to fit to these long-term mortality data with an
1698 upward trend over time is more than simply a statistical exercise, but has implications for our
1699 understanding of the trajectory of mortality.

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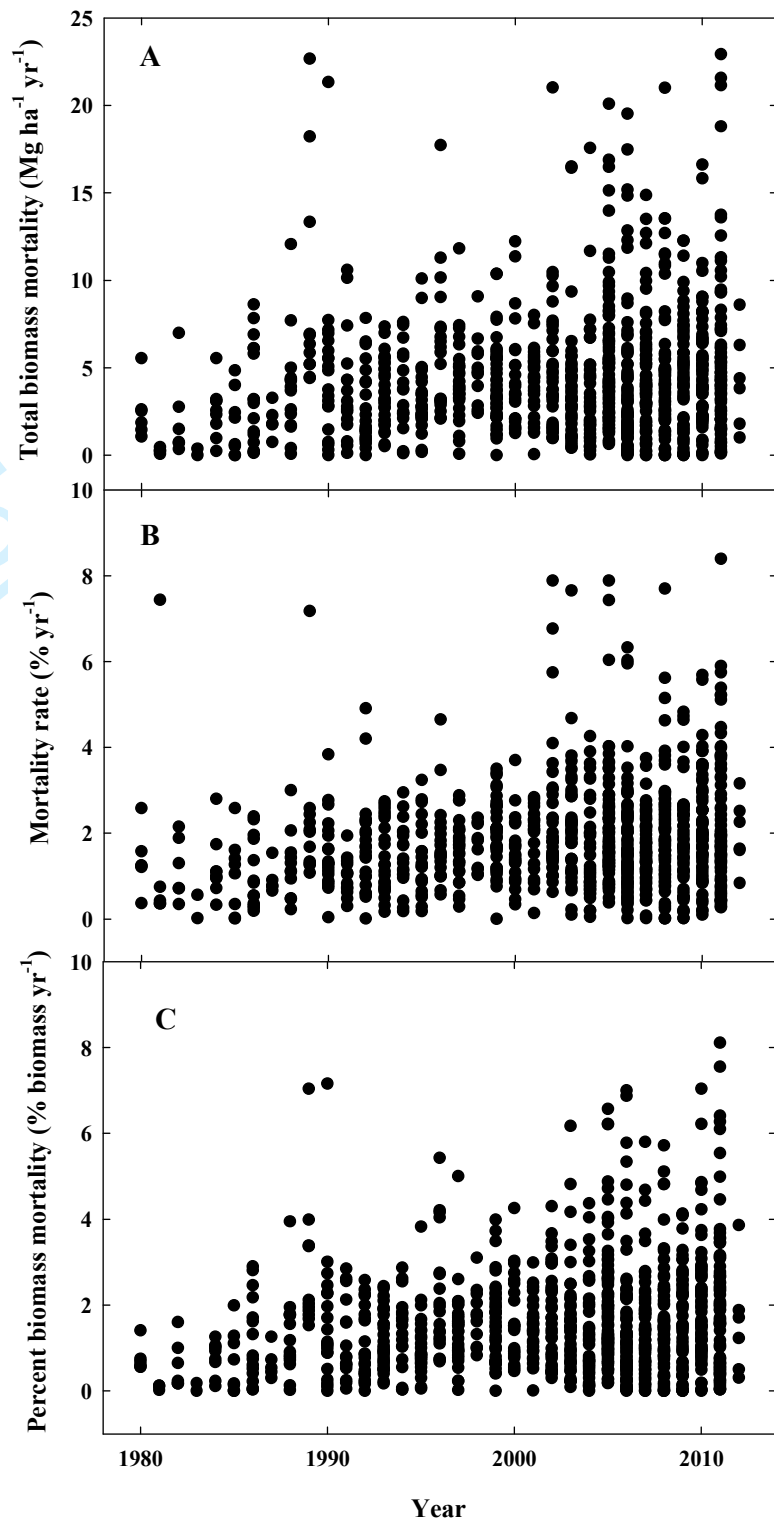
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1701 **Figure SI2.** Alternative
 1702 approaches to presenting %
 1703 mortality in units of # of
 1704 individuals died / total number
 1705 of individuals / year is to
 1706 calculate the mortality in rates
 1707 of biomass loss (Brienen et al.
 1708 2015). For completeness, we
 1709 plotted multiple metrics of
 1710 mortality using the Brienen et
 1711 al. (2015) dataset in Figure
 1712 SI1: A) biomass mortality
 1713 (arithmetic equation SI1), B) %
 1714 mortality, as shown in Figure
 1715 (2) but with all data included to
 1716 highlight both the trend and the
 1717 variability, and C) percent of
 1718 biomass lost to mortality.
 1719 Census dates were rounded to
 1720 the nearest year.

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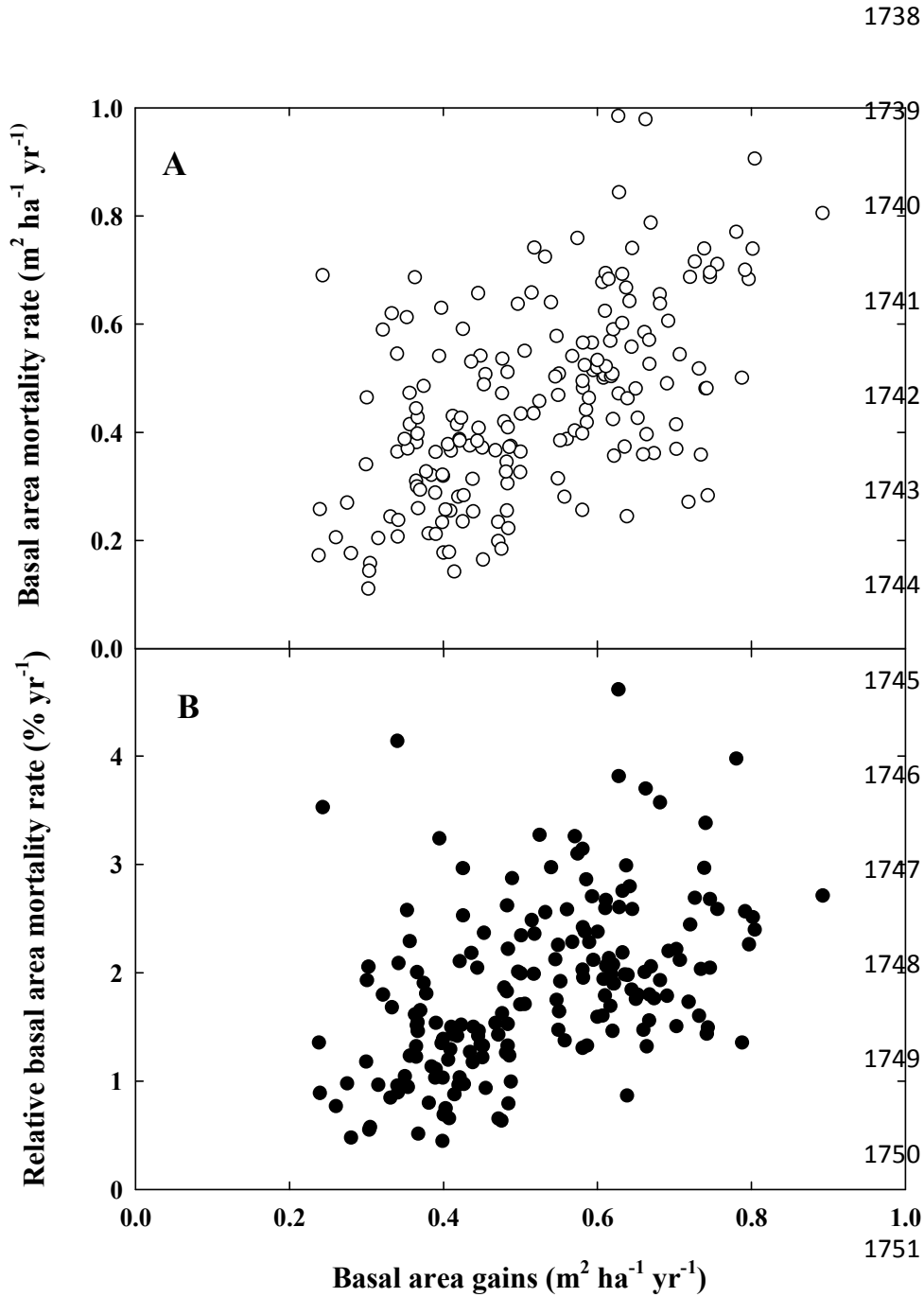


1724 The relationship between mortality and productivity shown in Fig. 3 was based on the
1725 same set of Amazon plot data from Brienen et al. (2015). Mortality rates of individual plots were
1726 calculated as the basal area of trees that died between censuses allowing for census interval
1727 effects (see Talbot et al. 2014). Plot level productivity was calculated as the sum of basal area
1728 growth of surviving trees, plus trees that recruited (that is reached > 100 mm in diameter)
1729 between censuses, and also included interval corrections as described in Talbot et al. 2014). We
1730 used a standard major axis regression (SMATR package: Warton and Weber 2002) to account
1731 for the errors in both productivity and mortality (x and y). The North American data are
1732 reproduced from van Mantgem et al. 2009 and Peng et al. 2011.

1733 Alternative presentations of Figure (3) are shown in Figures SI3A, B.

1734 **Figure SI3.** The relationship between mortality and productivity can be shown as it is in Figure
1735 (3) or in units of basal area gain (for productivity) and loss (for mortality), which more closely
1736 approximate biomass fluxes in absolute values (panel A) or relative to the total stand basal area
1737 (panel B).

review



1752

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1768 **On nutrients**

1769 It is possible that elevated nitrogen availability is also driving increased growth and hence
1770 mortality. Measurements in Thailand and Panama have found that increased nitrogen deposition
1771 was associated with increased plant tissue nitrogen concentrations and nitrogen cycling rates
1772 without increasing productivity (Hietz et al. 2011). N deposition reduces cation availability and
1773 may thereby increase tree stress. N (and other particulate) deposition may increase or decrease
1774 the likelihood of mortality (Dietze and Moorcroft 2011, Gessler et al. 2017). No literature was
1775 available regarding phosphorous and mortality. Thus, atmospheric deposition may be partially
1776 responsible for trends in tree mortality, but its impact remains poorly studied in the tropics.

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1784

1785 **A potential new approach to ESM modeling of hydraulics:** Inclusion of plant
1786 hydraulics in ESMs (or schemes capable of incorporation in ESMs) is drawing increased
1787 attention (Hickler et al. 2006, Alton et al. 2009, McDowell et al. 2013; Bonan et al. 2014,
1788 Mirfenderesgi et al., 2016, Christoffersen et al., 2016; Xu et al. 2016). These approaches apply
1789 Darcy's law to the coupled plant-soil continuum, which states that the rate of water supplied
1790 from the soil to the leaves is the product of the conductance in the xylem and the soil-leaf water
1791 potential gradient. A common theme to emerge from these model development studies is the
1792 improved realism of simulations, either with respect to transpiration at seasonal and interannual
1793 timescales, ecosystem response to water deficits, or drought-deciduous leaf phenology. A
1794 common challenge faced by any process-based representation of plant hydraulics in ESMs is
1795 maintaining a minimum level of complexity sufficient for capturing the first-order effect that
1796 plant hydraulics has on modulating ecosystem responses to water deficits. Sperry and Love
1797 (2015) have proposed a novel approach, attractive for ESMs, in which a simple integral
1798 transform is used to integrate the variable hydraulic properties from roots to stems and leaves to
1799 derive a representation of water delivery to the site of transpiration (the 'supply function'). A
1800 corresponding 'demand function' (and the ensuing modeled stomatal response to water deficits)
1801 then follows from theory suggesting that stomata operate in such a way to prevent catastrophic
1802 xylem failure, in which case hydraulic failure occurs through prolonged cuticular loss of water.
1803 This pragmatic approach to plant hydraulics well-simulates observed drought responses in
1804 tropical trees (Sperry and Love 2015). A recent extension of this work incorporates stomatal
1805 optimization of photosynthetic profit relative to hydraulic cost (Sperry et al. 2017), and
1806 provides an example for how hydraulics can potentially simplify simulating responses to a wide
1807 range of environmental cues (i.e., CO₂, light, temperature, as well as water deficits). In summary,

1808 all evidence points to the inclusion of plant hydraulics in ESMs as a promising avenue for
 1809 developing more mechanistic bases for tree mortality in the tropics.

1810

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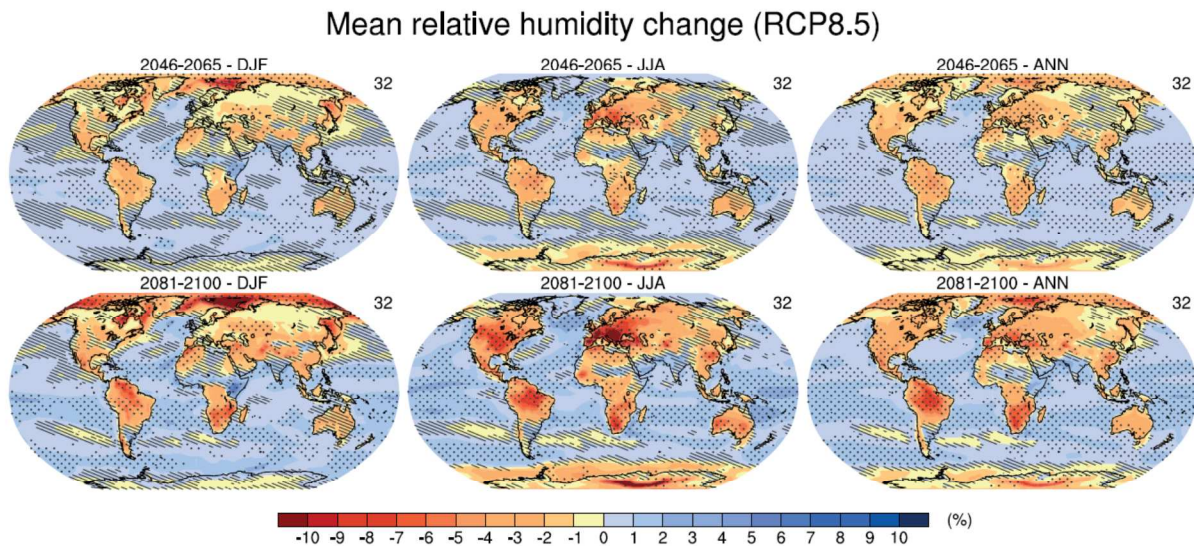
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1845 **Figure SI3.** Projected changes in near-surface relative humidity percentage from CMIP5 models
 1846 under RCP8.5 for the December, January, and February period (DJF, left), June, July, and
 1847 August period (JJA, middle), and annual mean (ANN, right) averages relative to 1986-2005 for
 1848 the periods 2046-2065 (top row) and 2081-2100 (bottom row). Hatching indicates regions where
 1849 the multi-model mean change is less than one standard deviation of internal variability.
 1850 Stippling indicates regions where the multi-model mean change is less than two standard
 1851 deviations of internal variability and where 90% of models agree on the sign of change. Re-
 1852 printed courtesy of Collins et al. (2013).

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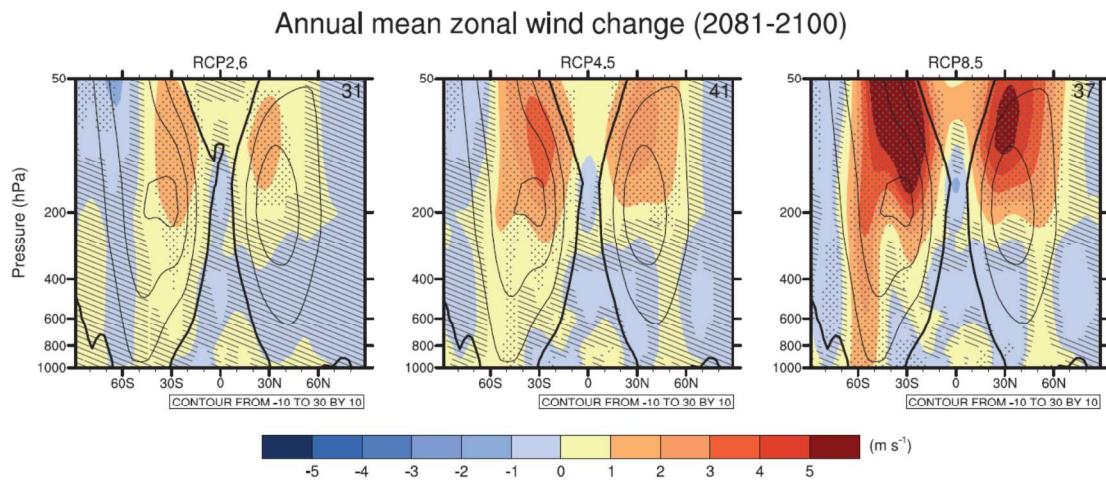
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1860 **Figure SI4.** CMIP5 multi-model ensemble average of zonal and annual mean wind change
 1861 (2081-2100 minus 1986-2005) for, from left to right, RCP2.6, 4.5, and 8.5. Black contours
 1862 represent the average for 1986-2005. Hatching indicates regions where the multi-model mean
 1863 change is less than one standard deviation of internal variability, and stippling indicates regions
 1864 where the multi-model mean change is greater than two standard deviation of internal variability
 1865 and where at least 90% of models agree on the sign of change. Re-printed courtesy of Collins et
 1866 al. (2013).

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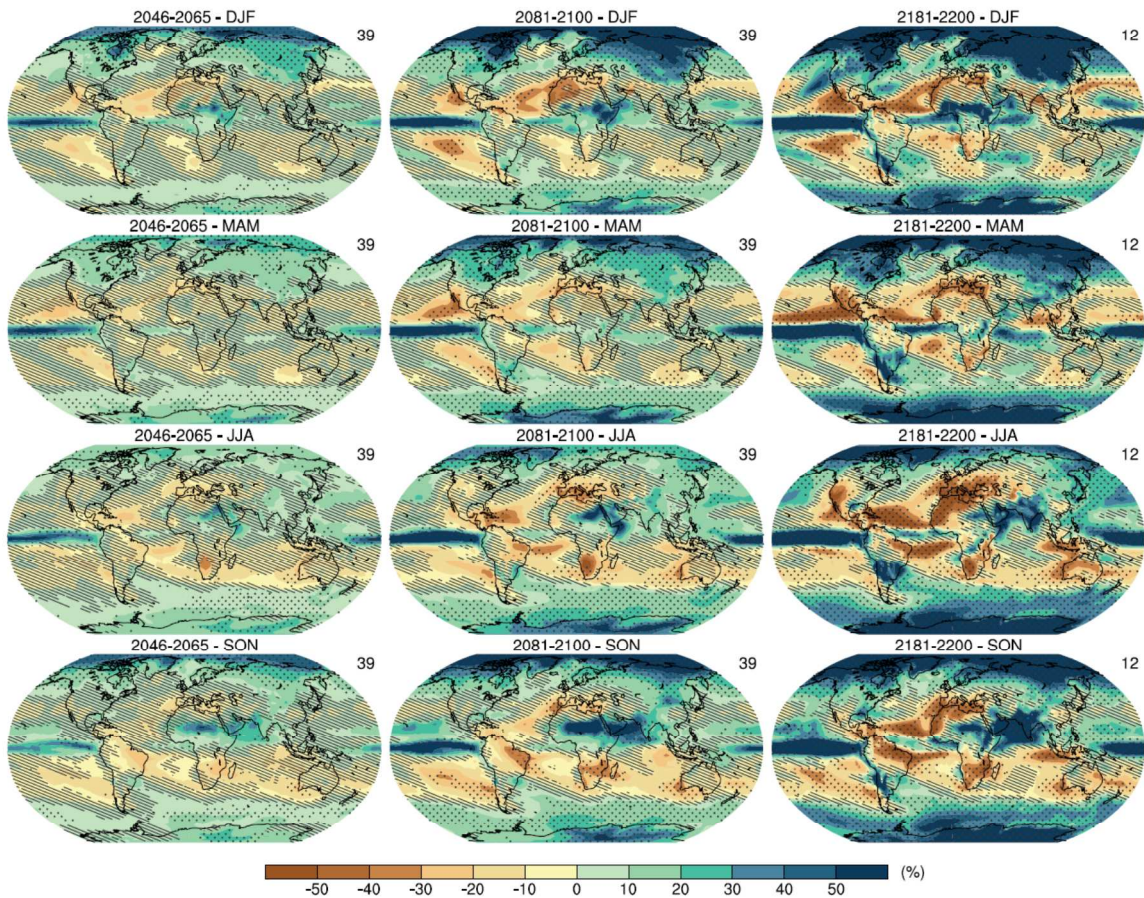
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1871 **Figure SI5.** The CMIP5 multi-model average percentage change in seasonal mean precipitation
 1872 relative to the reference period 1986-2005 averaged for 2045-2065, 2081-2100, and 2181-2100
 1873 under the RCP8.5 forcing scenario. Hatching indicates regions where the multi-model mean
 1874 change is less than one standard deviation of internal variability. Stippling indicates regions
 1875 where the multi-model mean change is greater than two standard deviations of internal
 1876 variability and where at least 90% of models agree on the sign of change. The number of models
 1877 used in the analyses are shown in the upper right-hand corner of each figure. Re-printed courtesy
 1878 of Collins et al. (2013).

1879

Seasonal mean percentage precipitation change (RCP8.5)



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