



- 1 Quantification of hydraulic trait control on plant hydrodynamics and risk of hydraulic
- 2 failure within a demographic structured vegetation model in a tropical forest (FATES-
- 3 HYDRO V1.0)
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24 Abstract: Vegetation plays a key role in the global carbon cycle and thus is an important 25 component within Earth system models (ESMs) that project future climate. Many ESMs are 26 adopting methods to trace the size and succession-stage-structure of plants within demographic 27 models. These models make it feasible to conduct more realistic simulation of processes that 28 control vegetation dynamics. Separately, increasing understanding of the ecophysiological 29 processes governing plant water use, and the need to understand ecosystem responses to drought 30 in particular, has led to the adoption of physical plant hydrodynamic schemes within ESMs. In this 31 study, we report on a new hydrodynamics (HYDRO) model incorporated in the Functionally 32 Assembled Terrestrial Ecosystem simulator (FATES). The size and canopy structured 33 representation within FATES is able to simulate how plant size and hydraulic traits affect 34 vegetation dynamics and carbon/water fluxes. To better understand this new model system and its 35 functionality in tropical forest systems in particular, we conducted a global parameter sensitivity 36 analysis at Barro Colorado Island, Panama. We assembled observations of plant hydraulic traits 37 for stomata, leaves, stems, and roots, and determined the best-fit statistical distribution for each 38 trait. Our model analysis showed that the taper component determining hydraulic conductivity 39 tapering from trunk to branch, the water potential leading to 50% loss (P50) of stomatal 40 conductance, the maximum hydraulic conductivity for the stem, and the fraction of total hydraulic 41 resistance in the above ground section are the top 5 traits determining the simulated water potential 42 and loss of conductivity for different plant organs. For the risk of hydraulic failure and potential 43 tree mortality, we found that ensemble members with high risk of mortality generally have a higher 44 taper exponent and a higher xylem conductivity, less negative P₅₀ for stomata conductance, and 45 more negative P₅₀ for stem and transporting roots. We expect that our results will provide guidance on future modeling studies using plant hydrodynamic models to predict the forest responses to 46





- 47 droughts, and future field campaigns that aim to better parameterize the plant hydrodynamic
- 48 model.
- 49





50

51 1. Introduction

52 Tropical forests play a critical role in regulating regional and global climates (Bonan, 53 2008). Under ongoing and future climate change, they are subjected to substantial risks of 54 climate extremes such as drought and heat waves (Mcdowell et al., 2018). Studies have already shown that tropical forests were experiencing elevated tree mortality rates due to mega 55 56 droughts related to ENSO events. For example, the 2015-16 El Niño led to the death of an 57 estimated 2.5 ± 0.3 billion stems in the Lower Tapajós river basin of the Amazon and the 58 associated carbon loss had not yet been compensated by new plant growth three years after the 59 event (Berenguer et al., 2021). Such extreme climate events are projected to increase in 60 frequency and intensity under a warming future. A statistical analysis based on the projection 61 of 13 ESMs under a high greenhouse emission scenario showed that the frequency of extreme 62 droughts as defined by rhizosphere soil moisture (occurring once every 50 years) could increase by a factor of nearly 4 and this increase would have substantially more impact on 63 64 tropical forests (Xu et al., 2019). The high species diversity found in tropical forests may result 65 in increased resilience to climate extremes, based on the demonstrated resilience of temperate 66 forests in relationship to trait diversity (Anderegg et al., 2018). However, due to limited data to parametrize and constrain models for tropical forests, there is a large uncertainty in our 67 68 predictive understanding of how tropical forests will respond to these climate extremes (Bonal 69 et al., 2016). This uncertainty is considered to be a key source of uncertainty in our projection 70 of land carbon fluxes and future climates (Arora et al., 2020).

Earth System Models (ESMs) have been developed to project future changes to the coupled
 climate and biosphere system. Typically, 'big leaf' approximations of vegetation with no





73 explicit presentation of tree size and canopy structure have been used to predict the impact of 74 vegetation on carbon and water cycles. These models do not represent the fundamental 75 elements of vegetation dynamics including mortality, competition, and growth, and their 76 response to disturbances. In the last decade, many ESMs have incorporated vegetation 77 demographic models (VDMs) that represent plant size, canopy structure and disturbance 78 histories, with the goal of better representing the competitive dynamics among different size 79 classes of trees and plant functional types in response to climate and vegetation disturbance 80 (Fisher et al., 2018). Most of these VDMs can differentiate plants' light, water and carbon use 81 strategies and can thus represent some part of the functional diversity of tropical forests 82 (Massoud et al., 2019; Koven et al., 2020).

83 Following the 'big leaf' model, water limitation on plant gas exchange in these VDMs is 84 generally calculated based on three factors: 1) soil water potential; 2) root distribution; and 3) 85 water potential for stomata openness and closure, all of which differ by plant functional type 86 (Koven et al., 2020). While such water limitation functions are able to capture trait diversity 87 in leaf-level stomatal behaviors, they fail to capture plant functional diversity in many other 88 observable plant hydraulic traits, such as xylem capacitance, water potentials for loss of xylem 89 hydraulic conductivity, stem hydraulic safety margin, and turgor loss point (Hochberg et al., 90 2018). Many studies have shown that plant hydraulic traits play an important role in plant 91 responses to droughts (Su et al., 2022; Anderegg et al., 2016), which could shape the landscape 92 distribution of plant functional types (Kunert et al., 2021). In view of this limitation, plant 93 hydrodynamic models have been developed with the aim of better simulating forest response 94 to droughts (Powell et al., 2018; Christoffersen et al., 2016; Xu et al., 2016; Kennedy et al., 95 2019). These models not only allows us to better incorporate hydraulic functional diversity,





- 96 but also allow us to mechanistically simulate the risk of plant mortality due to hydraulic
- 97 functional failure resulting from embolism in xylem.
- 98 One key challenge for these plant hydrodynamic models is that they have many more 99 parameters than simple water limitation functions based on soil water potentials and thus 100 inherently possess more uncertainty in the model parameterization and subsequent simulations. 101 In this study, we describe the implementation of a hydrodynamic scheme within FATES, and 102 assess this new configuration with two goals: 1) assess the importance of different hydraulic 103 traits in determining plant hydrodynamics; and 2) identify key hydraulic traits that are 104 important for predicting the risk of mortality due to hydraulic failure. We expect that our results 105 will provide guidance on model parameterization for future modeling studies using plant 106 hydrodynamic models to predict tropical forest response to droughts, and future field 107 campaigns that aim to collect observational data that can be used to better parameterize and 108 benchmark plant hydrodynamic models.
- 109 **2.** Methodology

110 **2.1. Model description**

111 We use the functionally assembled terrestrial ecosystem simulator (FATES), a VDM that is coupled within the Energy Exascale Earth System Model (E3SM) (Caldwell et al., 2019). 112 FATES represents size-structured groups of plants (cohorts) and successional trajectory-based 113 114 patches using the ecosystem demography approach (Fisher et al., 2015; Moorcroft et al., 2001). 115 FATES simulates growth by integrating photosynthesis across different leaf layers for each 116 cohort. FATES allocates this photosynthate to different tissues including leaves, fine and 117 coarse roots, and stem, based on the allometry of different plant functional types, as well as a carbon storage pool (Fisher et al., 2015). Mortality within FATES is simulated by several 118





- mechanisms, including carbon starvation caused by depletion of the storage pool, hydraulic
 function failure, as well as impact mortality during disturbance, fire, logging, freezing, agerelated and 'background' constant turnover (Fisher et al., 2015; Huang et al., 2020; Fisher et
 al., 2010; Needham et al., 2020).
- The default model contains a simplistic algorithm that approximates plant hydraulic failure 123 124 thresholds based on soil water potential. An important feature of the plant hydrodynamic 125 scheme (HYDRO), which explicitly simulates water flow from the soil through leaves to the 126 atmosphere, is that it enables direct representation of percent loss conductance as a predictor 127 of hydraulic failure mortality rates. FATES-HYDRO is based on the hydrodynamic model 128 implemented in the Traits-based Forest Simulator (TFS) (Christoffersen et al., 2016). The 129 water flow is calculated based on water pressure gradients across different plant compartments 130 (rhizosphere, absorbing roots, transporting roots, stem, and leaf). Specifically, flow between 131 compartment *i* and $i + 1(Q_i)$ is given by

$$Q_i = -K_i \Delta h_i,\tag{1}$$

132 where K_i is the total conductance (kg MPa⁻¹ s⁻¹) at the boundary of compartments *i* and *i* + 1 133 and Δh_i is the total matric potential difference between the compartments:

$$\Delta h_i = \rho_w g(z_i - z_{i+1}) + (\psi_i - \psi_{i+1}), \tag{2}$$

where z_i is compartment elevation difference above (+) or below (-) the soil surface (m), ρ_w is the density of water (10³ kg m⁻³), g is acceleration due to gravity (9.8 m s⁻²), and ψ_i is tissue or soil matric water potential (MPa). K_i is treated here as the product of a maximum boundary conductance between compartments *i* and *i* + 1 ($K_{max,i}$), and the fractional maximum hydraulic conductance of the upstream compartments (*FMC_i* or *FMC_{i+1}*), which is a function of the tissue water content.





140	The plant hydrodynamic representation and numerical solver scheme within FATES-
141	HYDRO follows the 1-D solver laid out by Christoffersen et al. (2016). The equations are
142	solved for tissue water content at a 30 minutes time step. We made a few modifications to
143	accommodate the multiple-soil layers and improve the numerical stability. First, to
144	accommodate the multiple-soil layers, we sequentially solve the Richards' equation for each
145	individual soil layer, with each layer-specific solution proportional to each layer's contribution
146	to the total root-soil conductance. Second, to improve the numerical stability, we now linearly
147	interpolate the pressure/volume curve beyond the residual and saturated tissue water content
148	to avoid the rare cases of overshooting in the numerical scheme under very dry or wet
149	conditions. Please see the Supplementary Information [HYDRO_DESCRIPTION.pdf] for
150	details of the implementation.

151 In this study, as our focus is on the plant hydrodynamics, we used the static stand structure 152 mode of FATES that turns off the processes of competition, growth and mortality, to instead 153 hold the ecosystem structure constant. This reduced-complexity configuration (Fisher and 154 Koven, 2020) thus exercises only the primarily fast-timescale-processes of photosynthesis, 155 transpiration, water transport, and plant hydrodynamics (i.e., change in hydraulic conductivity, 156 water storage, and water potentials in plant tissues). By using static stand structure mode, as in 157 Chitra-Tarak et al. (2021), we isolate hydraulic trait controls on simulated hydrodynamics and 158 avoid confounding, and potentially biased, feedbacks from resulting changes in forest 159 structure. The forest stand structure include tree size and composition is initialized based on 160 the forest inventory data in 2017. As the majority of species in BCI is evergreen broad leave 161 trees, we run the model with one PFT with different hydraulic traits (Table 1) to assess their 162 impact on the hydrodynamically relevant outputs including water potentials and fraction of





168	2.2. Parametric uncertainty estimation
167	of diameter more than 60 cm.
166	environmental conditions in the canopy, here we focused on hydrodynamic behaviors for trees
165	for different size classes of trees. Because large trees experience more fluctuation in
164	stem, and leaves and risk of hydraulic failure. FATES simulates the carbon and water fluxes
163	maximum conductivity for different plant organs including absorbing root, transporting root,

169 We identified 36 parameters for the FATES-HYDRO model (Table 1). To estimate the 170 parameter distributions, we started with published meta-analyses (Christoffersen et al., 2016; 171 Choat et al., 2012; Bartlett et al., 2012; Bartlett et al., 2014; Bartlett et al., 2016; Klein, 2014) 172 and supplemented them with select new data from individual studies. Focal data were tissue-173 or individual-level hydraulic traits spanning water transport and embolism resistance, tissue 174 water storage and retention (PV curve traits), hydraulic architecture (i.e., leaf area to sapwood 175 area ratio), stomatal responses to dehydration, and fine root traits (Table 1). For each dataset, 176 we standardized taxonomic names using the TNRS package in R (Boyle et al., 2013). This allowed us to join datasets together based on species, averaging multiple observations per 177 178 species if necessary, resulting in a species-specific sparse matrix of all hydraulic traits for all 179 databases and individual studies that we compiled. This pantropical hydraulic trait dataset is 180 included in the Supporting Information [traits master trop.csv].

181 We then determined parametric distributions which best fit the trait data. Where necessary, 182 traits were transformed to be positive, and certain traits with well-defined upper and lower 183 bounds were normalized on [0, 1] according to (x - x.lowerbound)/(x.upperbound -184 x.lowerbound) for trait x (Table 1). For each trait, we used parameter estimates for the185 distribution with the largest log likelihood among all possible distributions using fitdistr





- 186 package in R. We augmented observations with extratropical data to increase sample size for 187 traits with less than three tropics-specific observations. Where trait data were mostly 188 unmeasured, we used a uniform distribution bounded on our best estimate of the theoretical 189 range (Table 1). As there is limited data on roots, we used the same distribution as that for 190 branches if data was missing. Because our goal is to understand the model behaviors as 191 determined by different hydraulic traits, we assumed independence among traits. As we 192 focused on the hydraulic traits in this study, we used non-hydraulic trait values based on an 193 optimal set of parameters that best fit observed water and carbon fluxes in FATES 194 implemented without hydrodynamics (Koven et al., 2020).
- 195 **2.3.** Sensitivity analysis

196 We used the Fourier Amplitude Sensitivity Test (FAST) to assess the relative importance 197 of parameters in determining the variance of model outputs (Xu and Gertner, 2011a). The main 198 idea of FAST is to assign periodic signals in the sampled parameter values and use Fourier 199 transformation to identify the signals in the outputs. Sampled parameter values are based on 200 Latin hypercube sampling from the fitted statistical distributions (see previous section for more 201 details). We ran 1000 ensemble simulations of the FATES-Hydro to derive model outputs of 202 water potential and fraction of maximum conductivity. We used the Uncertainty Analysis and 203 Sensitivyt Analysis (UASA) tool (https://sites.google.com/site/xuchongang/uasatoolbox) to 204 estimate the parameter importance, which is defined as the proportion of total model output 205 variance contributed by individual model parameters. For details, please refer to Xu and 206 Gertner (2011a). We run the model with 1000 ensemble members, in view that an order of 100 207 times effective important number of parameters, which we estimate to be ~ 10 , is needed to 208 achieve reasonable precision (Xu and Gertner, 2011b).





209 **2.4. Study area and climate drivers**

In this study, we used Barro Colorado Island (BCI), Panama, as our test site to evaluate model behavior. We chose BCI as it has moderately strong dry and wet seasons that allow us to assess the hydrodynamics under different levels of water availability. Moreover, extensive field campaigns in recent years have provided comprehensive data needed for model parameterization, initialization and climate drivers. Finally, we also leverage prior FATES studies of non-hydraulic parameters at BCI (Koven et al., 2020).

216 BCI has an annual mean temperature of 26.3°C and an annual mean precipitation of 2656 217 mm with a strong seasonal precipitation signal. The dry season lasts from January to April, 218 with a mean precipitation of 228mm, while the wet season lasts from May-December with a 219 mean precipitation of 2428mm (Paton, 2020). In this study, we used hourly in-situ climate data 220 from 2008-2016 to drive the model. To run the model to equilibrium (in terms of soil moisture 221 content) takes 5-6 years, thus we choose February of 2016 as the target for analysis of dry 222 season hydrodynamics and August of 2016 as the target for analysis of wet season 223 hydrodynamics. Using static stand structure mode means that we do not need to spin up 224 vegetation state and thus reducing the simulation time.

225 3. Results

Our results showed that the simulated ranges across the ensemble of leaf water potential (Fig. 1) and loss of conductivity (Fig. 2) are large. For leaf water potential, the 95% percentile ranges are from -5 MPa to -0.5 MPa and -3 MPa to -0.5 Mpa for February and August 2016, respectively. Correspondingly, the fraction of maximum stem hydraulic conductivity is much higher during August compared to February (Fig. 2); however, in both months, the modeled range spans almost the full range of between 0 and 1.





232	Based on the FAST sensitivity indices (i.e., the variance in model output contributed by
233	different parameters), the key parameters that control the water potentials of different plant
234	organs (leaf, stem and root) include the taper exponent for hydraulic conductivity (p_taper) ,
235	the water potential leading to 50% loss of stomatal conductance ($p50_gs$), maximum hydraulic
236	conductivity for the stem (<i>kmax_node_stem</i>), and the fraction of total hydraulic resistance in
237	the above ground section (<i>rfrac_stem</i>), in decreasing order (Fig. 3). For the fractional loss of
238	conductivity, the most important parameter is the water potential leading to 50% loss of
239	hydraulic conductance (P ₅₀) for the corresponding organs (Fig. 4). Other important parameters
240	are similar to those for simulated water potentials. Notably, the organ-specific P50 values are
241	more important for the dry month (February) compared to the wet month (August). For the wet
242	month of August, p_{taper} is the dominant parameter controlling the pre-dawn and midday loss
243	of hydraulic conductivity, while organ-specific P50 parameters are the second most important.
244	In terms of the risk of hydraulic failure, out of the 1000 ensemble members, 40-60% of the
245	simulations suggest that branches are the most vulnerable plant organ, based on highest loss of
246	conductivity across the continuum from root to branch (Fig. 5). For the dry month of February,
247	roots are at greater risk in comparison to the wet season. If we consider the loss of conductivity
248	more than 50% for February 2016 as a threshold for a high risk of mortality (Adams et al.,
249	2017), then 53% of ensemble simulations reach this threshold. The key parameters affecting
250	the risk of mortality, as measured by percentage difference in parameter values for ensemble
251	members reaching 50% loss of conductivity or not, include the water potential leading to 50%
252	loss of conductance for stomata ($p50_gs$), stem ($p50_node_stem$), and transporting roots
253	(p50_node_troot), maximum hydraulic conductivity of stem (kmax_node_stem), and the taper
254	exponent (p_taper) (Fig. 6). Ensemble members with high risk of mortality generally have a





higher *p_taper* and *kmax_node_stem*, less negative *p50_gs*, and more negative *p50* for stem

- and transporting roots (Fig. 7).
- 257 4. Discussion

258 Our analysis showed the importance of key plant hydraulic traits in simulating plant water 259 potential and risk of hydraulic failure. This analysis identifies these parameters as potential 260 targets of either model calibration or targeted measurement campaigns to achieve realistic simulations. In our sensitivity analysis, the most influential parameter for both water potential 261 262 and loss of conductivity is the tapering of the radius of conduit with increasing plant height 263 (p taper). As p taper increases, the conduit radius increases from the top of the tree to its base. 264 According to Hagen-Poiseuille's equation, this increases the theoretical maximum total 265 conductance. Low values of p taper thus limit the adverse effects of tree height by increasing 266 k max along the whole continuum and reducing the soil-to-leaf water potential needed to 267 maintain transpiration. Our inference is that *p* taper represents an overarching property of plant architecture that influences the relative effect of each of the other parameters with regard 268 269 to hydraulic safety and efficiency. While *p* taper is less directly related to plant adaptations to 270 drought, the architecture of the plant itself determines the range of values that give rise to 271 drought adaptive strategies. Another dimension of the hydraulic architecture with a critical role 272 in determining both water potential and loss of conductivity, though to a much lesser degree, 273 was the fraction of total tree resistance within the above-ground stem (rfrac stem). Generally, 274 a plant will maintain this resistance, matching the growth of trunk and crown height to maintain 275 total resistance as the distance water needs to travel increases (Yang and Tyree, 1993). In this 276 study, due to the lack of data on the belowground resistance, we assigned a quite large range





- for this trait, which could be impact by many factors such as belowground root biomass andinteraction between root, fungi and bacteria.
- 279 The second most sensitive parameter in determining loss of conductance was the leaf water 280 potential at 50% loss of stomatal conductance (p50 gs). The parameter controls the water loss 281 rate from leaf and a less negative value provides protection from hydraulic failure during water 282 limited periods. It has been shown to play a key role in tree survival during severe droughts 283 (Breshears et al., 2009; Rowland et al., 2015). The ability to withstand lower leaf water 284 potentials is also a key indicator of sapling and seedling survival during drought and 285 determines species distribution across a moisture gradient (Kursar et al., 2009). There may be 286 a trade-off between drought tolerance (with a lower p50 gs) and drought avoidance (a less 287 negative p50 gs but with a high capacitance; the amount of water released from reserves as 288 leaf water potential declines), a crucial aspect in determining species drought resistance 289 (Pineda-Garcia et al., 2013). Additionally, loss of conductivity was sensitive to the water 290 potential at 50% loss of max conductivity within the stem (p50 stem) as it can largely affect 291 the whole plant conductance and thus the water supply to the leaves. p50 stem negatively 292 correlates with wood density and may be a marker of the trade-off between hydraulic efficiency 293 and safety within the stem (Chen et al., 2009; Manzoni et al., 2013). Even though we did not 294 consider this trade-off as we mainly focused on the hydraulic traits in this study, this trade-off 295 could be important to consider for competitions and co-existence among different plant 296 functional types.

Leaf water potential and loss of conductance were both sensitive to the maximum xylem
 conductivity in the stem (*kmax_node_stem*). Higher maximum conductivity represents greater
 xylem efficiency, which in the absence of drought or light limitations would result in greater





potential photosynthesis and less negative water potentials (Gleason et al., 2016). However,
xylem with higher *kmax_node_stem* could be more vulnerable to embolism as water potential
declines (Sperry and Love, 2015). In tropical rainforests, species with higher conductivity per
unit leaf area generally are less desiccation tolerant and exhibit higher mortality rates (Kursar
et al., 2009). Low *kmax_node_stem* along with high leaf-to-sapwood area ratio (*la2sa*) also
represents a vulnerability to reduced conductance which increases with height (Christoffersen
et al., 2016).

307 Traits with lower order of impacts on water potential modulate the amount of stored water 308 available during drought. The fraction of water in the capillary reserve within the stem (f_{cap}) 309 determines the amount of water stored within the stem. Water storage in the stem has been 310 shown to help maintain higher water potentials as drought continues (Bartlett et al., 2019). The 311 bulk modulus of elasticity in the root (epsil node) determines the amount of water available 312 from cellular storage between complete hydration and loss of turgor (Powell et al., 2017). This 313 represents the ability of the roots to continually supply water to the rest of the plant as drought 314 occurs. It also represents an investment in cellular structure, which may be an additional 315 indicator of adaptations with non-hydraulic origin.

The sensitivity of vegetation to drought stress and hydraulic failure induced mortality is of paramount importance for understanding how ecosystems may respond to shifting temperature and rainfall patterns under a changing climate (Mcdowell et al., 2022). We recognize that parametric sensitivity could be different for different sites depending on climate driver, soil moisture and vegetation types. However, we expect the main parameter of importance could be could be useful to guide model calibration to select the candidate parameters for different sites. As understanding of plant hydrodynamics increases, linking





323	model predictions to observable plant traits has emerged as a promising means of constraining
324	predictions of ecosystem resilience. Such traits are challenging and costly to measure in the
325	field and thus resources must be directed carefully when planning measurement campaigns.
326	The identified parameters in this study could provide guidance on the limited measurement we
327	could target in the field.
328	5. Acknowledgment
329	This research was supported as part of the Next Generation Ecosystem Experiments-
330	Tropics, funded by the U.S. Department of Energy, Office of Science, Office of Biological and
331	Environmental Research.
332	6. CODE and Data Availability
333	The FATES-HYDRO code is available from https://doi.org/10.5281/zenodo.7686333. The
334	traits data are in the supplementary file [traits_master_trop.csv].
335	7. Supplement Information
336	Two supplementary file are included. The HYDRO_DESCRIPTION.pdf provide the
337	summary of the hydrodynamic implementation that is different from Christoffersen et al.
338	(2016). The traits_master_trop.csv file include all the hydraulic traits we assembled for the
339	tropical region.
340	8. Author contribution
341	CX and BC designed the sensitivity analysis experiments. BC collected the data and fitted
342	the trait distributions. CX conducted the analysis and drafted the manuscript. BC, CX, RF, RN
343	and CK designed the implementation of HDRO codes. BC implemented the majority of
344	HDRO codes with code improvement made by CX and RN. ZR conducted the ensemble model
345	simulations. MS provided the leaf cuticular conductance data. NM, CK and LK provided





- 346 guidance on the sensitivity analysis, code development and trait data synthesis. All authors
- 347 contributed to manuscript writing by providing edits and suggestions.
- **9. Competing interests**
- 349 The contact author has declared that none of the authors has any competing interests.
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352 Figures

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356 Figure 1: Simulated ranges of leaf water potential for February (a) and August (a), 2016. The percentiles are calculated

based on the monthly mean values of leaf water potentials for the 1000 ensemble simulations.





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361 Figure 2: Simulated ranges of fraction of maximum hydraulic conductivity of stem for February (a) and August (a),

- 362 2016. The percentiles are calculated based on the monthly mean values of leaf water potentials for the 1000 ensemble
- 363 simulations.
- 364







368 absorbing root (d). The sensitivity value refers to the proportion of total model output variance contributed by a specific

369 parameter (0-1). See Table 1 for the explanation of the parameters.

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372

- 374 absorbing root (d). The sensitivity value refers to the proportion of total model output variance contributed by a specific
- 375 parameter. See Table 1 for the explanation of the parameters. See Table 1 for the description of parameters.

³⁷³ Figure 4: Key parameters that control simulated loss of conductivity for branch (a), stem (b), transporting root (c) and







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378 Figure 5: Risk on the continuum for hydraulic failure as measured by percentage of total number of simulations with

379 highest loss of conductivity for a specific organ (branch, stem, transporting root and absorbing root). As the model does

380 not specifically simulate the branch, we calculated the risk of loss of conductivity based on the leaf water potential and hydraulic

381 vulnerability curve from xylem.





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- 387 Figure 6: Mean trait percentage difference for model ensemble simulations with loss of hydraulic conductivity larger
- 388 than 50% and ensemble simulations with loss of hydraulic conductivity less than 50%. See Table 1 for the description of
- 389 parameters.

390







393 Figure 7: Parameter difference for ensemble members with risk of mortality. Blue bars indicate parameter values with

394 lower mortality risk (<50% loss of hydraulic conductivity). Red bars indicate parameter values with higher mortality risk (>=

395 50% loss of hydraulic conductivity) and purple bars indicate parameter values stacked from transparent red/blue bars. See Table

396 1 for the description of parameters.

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399

400 Table 1 Hydraulic parameters considered in the sensitivity analysis

PARAMETER	Symbol	UNITS	DISTRIBUTION ¹	Sources& Notes
Pressure-Volume (PV) curve (water content – water				
saturated water content (thetas_node)	θ_s	cm ³ cm ⁻³	Leaf: Beta (9.69, 6.20)	Christoffersen et al. (2016)
			Stem: Beta (12.67, 7.4626)	Iversen et al. (2017)
			TRoot and AROOT: Beta	Wright et al. (2010)
			(22.98, 5.29)	Roderick et al. (1999)
				Sack et al. (2003)
				Binks et al. (2016)
turgor loss point (tlp_node)	$\pi_{_{tlp}}$	MPa	-	Bartlett et al. (2012);
				$\pi_{tlp} = (\pi_0 \boldsymbol{\varepsilon}) / (\pi_0 + \boldsymbol{\varepsilon})$
osmotic potential at full turgor (pinot_node)	π_{0}	MPa	Leaf: G [9.8,6.26], Stem,	Bartlett et al. (2012, 2014,
			TRoot, ARoot: LN	2016) and Christoffersen et al.
			[0.32,0.39]	(2016)
bulk elastic modulus (epsil_node)	3	MPa	Leaf: G (4.07, 4.12)	Bartlett et al. (2012, 2014), and
			Stem, TRoot and ARoot:	Christoffersen et al. (2016)
			G [3.57, 3.84]	
residual water fraction(resid_node)	RWC _r	unitless	Leaf: B [2.14,4.10]	Bartlett et al. (2012, 2014),
			Stem, TRoot and ARoot:	Christoffersen et al. (2016)
			B [2.71, 4.53]	
fraction of water in capillary reserve (fcap_node)	fcap	unitless	U [0.1, 0.7]	Christoffersen et al. (2016)
Vulnerability Curve (water potential – hydraulic c				
water potential at 50% loss of max conductivity	<i>P</i> _{50,<i>x</i>}	MPa	Stem, TRoot and ARoot:	Choat et al. (2012)
(p50_node)			G [2.07, 1.18]	
vulnerability curve shape parameter (avuln_node)	a _x	unitless	Stem, TRoot and ARoot:	Choat et al. (2012)
			LN [0.82,0.66]	





xylem conductivity per unit sapwood area	k _{s,max}	kg m ⁻¹ s ⁻¹	G [1.41, 2.37]	Choat et al. (2012)
(kmax_node_stem)		MPa ⁻¹		
Leaf hydraulics				
leaf water potential at 50% loss of max gs (p50_gs)	P _{50,gs}	MPa	G [5.73, 0.27]	Klein (2014)
stomatal vulnerability shape parameter(avuln_gs)	a _{gs}	unitless	-	Christoffersen et al. (2016); derived according to empirical equation: a_{gs} = -2.406 P50,gs (-P50,gs) ^{-1.25}
Leaf cuticular conductivity (k0_leaf)	k _{0,l}	umol m ⁻² s ⁻¹	LN [1.04,0.84]	This study, based on data measured by Martijn Slot
Plant Hydraulic Architecture				
Xylem taper exponent for sapwood (p_taper)	р	(-)	U (0.08, 0.5)	Savage et al. (2010)
Leaf area to sapwood area ratio (la2sa)	la2sa	(-)	LN (-0.48, 0.77)	Choat et al. (2012)
Root hydraulic Traits				
specific root length (srl)	srl	m g ⁻¹	G [1.70, 35.31]	Iversen et al. (2017)
absorbing root radius (rs2)	r	mm	LN [-1.91, 0.79]	Iversen et al. (2017)
fraction of total tree resistance that is aboveground (<i>rfrac_stem</i>)	frac	Unitless	U [0.1,0.7]	This study; empirical
root-soil interface conductivity per unit surface area (<i>Kr1</i>)	k _{r1,max}	kg m ⁻¹ s ⁻¹ MPa ⁻¹	G [1.41, 2.37]	This study; empirically set the same as xylem conductivity
maximum root water loss rate (<i>Kr2</i>)	k _{r2,max}	kg m ⁻¹ s ⁻¹ MPa ⁻¹	LN [-6.80, 0.92]	Wolfe (2020); Empirically set as 1/1000 bark water loss rate

401 Note: 1:B-Beta distribution; U- Uniform distribution [lower limit, upper limit]; N-Gaussian

402 distribution (mean, standard deviation); LN-Log Normal Distribution [mean, standard deviation];

403 G-Gamma distribution (lambda, scale); TRoot-Transporting root; ARoot-Absorbing root.





405 **Reference**

406	1.	Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhausser, S. M.,
407		Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D.
408		L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann,
409		H., Cobb, R. C., Collins, A. D., Dickman, L. T., Duan, H. L., Ewers, B. E., Galiano, L.,
410		Galvez, D. A., Garcia-Forner, N., Gavlord, M. L., Germino, M. J., Gessler, A., Hacke, U.
411		G., Hakamada, R., Hector, A., Jenkins, M. W., Kane, J. M., Kolb, T. E., Law, D. J.,
412		Lewis, J. D., Limousin, J. M., Love, D. M., Macalady, A. K., Martinez-Vilalta, J.,
413		Mencuccini, M., Mitchell, P. J., Muss, J. D., O'Brien, M. J., O'Grady, A. P., Pangle, R.
414		E., Pinkard, E. A., Piper, F. I., Plaut, J. A., Pockman, W. T., Ouirk, J., Reinhardt, K.,
415		Ripullone, F., Rvan, M. G., Sala, A., Sevanto, S., Sperry, J. S., Vargas, R., Vennetier, M.,
416		Way, D. A., Xu, C. G., Yepez, E. A., and McDowell, N. G.: A multi-species synthesis of
417		physiological mechanisms in drought-induced tree mortality, Nat Ecol Evol, 1, 1285-
418		1291, 10.1038/s41559-017-0248-x, 2017.
419	2.	Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and
420		Jansen, S.: Meta-analysis reveals that hydraulic traits explain cross-species patterns of
421		drought-induced tree mortality across the globe, P Natl Acad Sci USA, 113, 5024-5029,
422		10.1073/pnas.1525678113, 2016.
423	3.	Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K. L., Bowling, D. R.,
424		Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., and Zenes, N.:
425		Hydraulic diversity of forests regulates ecosystem resilience during drought, Nature, 561,
426		538–541, 10.1038/s41586-018-0539-7, 2018.
427	4.	Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein,
428		P., Schwinger, J., Bopp, L., Boucher, O., Cadule, P., Chamberlain, M. A., Christian, J. R.,
429		Delire, C., Fisher, R. A., Hajima, T., Ilyina, T., Joetzjer, E., Kawamiya, M., Koven, C.
430		D., Krasting, J. P., Law, R. M., Lawrence, D. M., Lenton, A., Lindsay, K., Pongratz, J.,
431		Raddatz, T., Seferian, R., Tachiiri, K., Tjiputra, J. F., Wiltshire, A., Wu, T. W., and
432		Ziehn, T.: Carbon-concentration and carbon-climate feedbacks in CMIP6 models and
433		their comparison to CMIP5 models, Biogeosciences, 17, 4173-4222, 10.5194/bg-17-
434		4173-2020, 2020.
435	5.	Bartlett, M. K., Detto, M., and Pacala, S. W.: Predicting shifts in the functional
436		composition of tropical forests under increased drought and CO2 from trade-offs among
437		plant hydraulic traits, Ecol Lett, 22, 67-77, 10.1111/ele.13168, 2019.
438	6.	Bartlett, M. K., Scoffoni, C., and Sack, L.: The determinants of leaf turgor loss point and
439		prediction of drought tolerance of species and biomes: a global meta-analysis, Ecol Lett,
440		15, 393-405, 10.1111/j.1461-0248.2012.01751.x, 2012.
441	7.	Bartlett, M. K., Klein, T., Jansen, S., Choat, B., and Sack, L.: The correlations and
442		sequence of plant stomatal, hydraulic, and wilting responses to drought, P Natl Acad Sci
443		USA, 113, 13098-13103, 10.1073/pnas.1604088113, 2016.
444	8.	Bartlett, M. K., Zhang, Y., Kreidler, N., Sun, S. W., Ardy, R., Cao, K. F., and Sack, L.:
445		Global analysis of plasticity in turgor loss point, a key drought tolerance trait, Ecol Lett,
446		17, 1580-1590, 10.1111/ele.12374, 2014.
447	9.	Berenguer, E., Lennox, G. D., Ferreira, J., Malhi, Y., Aragao, L. E. O. C., Barreto, J. R.,
448		Espirito-Santo, F. D., Figueiredo, A. E. S., Franca, F., Gardner, T. A., Joly, C. A.,
449		Palmeira, A. F., Quesada, C. A., Rossi, L. C., de Seixas, M. M. M., Smith, C. C., Withey,





450		K., and Barlow, J.: Tracking the impacts of El Nino drought and fire in human-modified
451		Amazonian forests, P Natl Acad Sci USA, 118, ARTN e2019377118:
452		10.1073/pnas.2019377118, 2021.
453	10.	Binks, O., Meir, P., Rowland, L., da Costa, A. C. L., Vasconcelos, S. S., de Oliveira, A.
454		A. R., Ferreira, L., Christoffersen, B., Nardini, A., and Mencuccini, M.: Plasticity in leaf-
455		level water relations of tropical rainforest trees in response to experimental drought, New
456		Phytol, 211, 477-488, 10.1111/nph.13927, 2016.
457	11.	Bonal, D., Burban, B., Stahl, C., Wagner, F., and Herault, B.: The response of tropical
458		rainforests to drought-lessons from recent research and future prospects, Ann Forest Sci,
459		73, 27-44, 10.1007/s13595-015-0522-5, 2016.
460	12.	Bonan, G. B.: Forests and climate change: Forcings, feedbacks, and the climate benefits
461		of forests, Science, 320, 1444-1449, 10.1126/science.1155121, 2008.
462	13.	Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., Matasci,
463		N., Narro, M. L., Piel, W. H., and Mckay, S. J.: The taxonomic name resolution service:
464		an online tool for automated standardization of plant names, BMC bioinformatics, 14, 1-
465		15, 2013.
466	14.	Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D.,
467		McDowell, N. G., and Pockman, W. T.: Tree die-off in response to global change-type
468		drought: mortality insights from a decade of plant water potential measurements, Front
469		Ecol Environ, 7, 185-189, 10.1890/080016, 2009.
470	15.	Caldwell, P. M., Mametjanov, A., Tang, Q., Van Roekel, L. P., Golaz, J. C., Lin, W. Y.,
471		Bader, D. C., Keen, N. D., Feng, Y., Jacob, R., Maltrud, M. E., Roberts, A. F., Taylor, M.
472		A., Veneziani, M., Wang, H. L., Wolfe, J. D., Balaguru, K., Cameron-Smith, P., Dong,
473		L., Klein, S. A., Leung, L. R., Li, H. Y., Li, Q., Liu, X. H., Neale, R. B., Pinheiro, M.,
474		Qian, Y., Ullrich, P. A., Xie, S. C., Yang, Y., Zhang, Y. Y., Zhang, K., and Zhou, T.: The
475		DOE E3SM Coupled Model Version 1: Description and Results at High Resolution, J
476		Adv Model Earth Sy, 11, 4095-4146, 10.1029/2019ms001870, 2019.
477	16.	Chen, J. W., Zhang, Q., Li, X. S., and Cao, K. F.: Independence of stem and leaf
478		hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology, Planta,
479		230, 459-468, 10.1007/s00425-009-0959-6, 2009.
480	17.	Chitra-Tarak, R., Xu, C. G., Aguilar, S., Anderson-Teixeira, K. J., Chambers, J., Detto,
481		M., Faybishenko, B., Fisher, R. A., Knox, R. G., Koven, C. D., Kueppers, L. M., Kunert,
482		N., Kupers, S. J., McDowell, N. G., Newman, B. D., Paton, S. R., Perez, R., Ruiz, L.,
483		Sack, L., Warren, J. M., Wolfe, B. T., Wright, C., Wright, S. J., Zailaa, J., and McMahon,
484		S. M.: Hydraulically-vulnerable trees survive on deep-water access during droughts in a
485		tropical forest, New Phytol, 231, 1798-1813, 10.1111/nph.17464, 2021.
486	18.	Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J.,
487		Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H.,
488		Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann,
489		J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global
490		convergence in the vulnerability of forests to drought, Nature, 491, 752-+,
491		10.1038/nature11688, 2012.
492	19.	Christoffersen, B. O., Gloor, M., Fauset, S., Fyllas, N. M., Galbraith, D. R., Baker, T. R.,
493		Kruijt, B., Rowland, L., Fisher, R. A., Binks, O. J., Sevanto, S., Xu, C. G., Jansen, S.,
494		Choat, B., Mencuccini, M., McDowell, N. G., and Meir, P.: Linking hydraulic traits to





495		tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro),
496		Geosci Model Dev, 9, 4227-4255, 10.5194/gmd-9-4227-2016, 2016.
497	20.	Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C.,
498		Meir, P., and Woodward, F. I.: Assessing uncertainties in a second-generation dynamic
499		vegetation model caused by ecological scale limitations. New Phytol, 187, 666-681,
500		10.1111/i.1469-8137.2010.03340.x. 2010.
501	21.	Fisher, R. A. and Koven, C. D.: Perspectives on the Future of Land Surface Models and
502		the Challenges of Representing Complex Terrestrial Systems. J Adv Model Earth Sy. 12.
503		ARTN e2018MS001453: 10.1029/2018MS001453. 2020.
504	22.	Fisher, R. A., Muszala, S., Verteinstein, M., Lawrence, P., Xu, C., McDowell, N. G.,
505		Knox, R. G., Koven, C., Holm, J., Rogers, B. M., Spessa, A., Lawrence, D., and Bonan,
506		G.: Taking off the training wheels: the properties of a dynamic vegetation model without
507		climate envelopes, CLM4.5(ED), Geosci Model Dev. 8, 3593-3619, 10.5194/gmd-8-
508		3593-2015, 2015.
509	23.	Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C.,
510		Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W.,
511		Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin,
512		S. P., Sato, H., Shuman, J. K., Smith, B., Trugman, A. T., Viskari, T., Verbeeck, H.,
513		Weng, E. S., Xu, C. G., Xu, X. T., Zhang, T., and Moorcroft, P. R.: Vegetation
514		demographics in Earth System Models: A review of progress and priorities, Global
515		Change Biol, 24, 35-54, 10.1111/gcb.13910, 2018.
516	24.	Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar,
517		R., Brodribb, T. J., Bucci, S. J., Cao, K. F., Cochard, H., Delzon, S., Domec, J. C., Fan,
518		Z. X., Feild, T. S., Jacobsen, A. L., Johnson, D. M., Lens, F., Maherali, H., Martinez-
519		Vilalta, J., Mayr, S., McCulloh, K. A., Mencuccini, M., Mitchell, P. J., Morris, H.,
520		Nardini, A., Pittermann, J., Plavcova, L., Schreiber, S. G., Sperry, J. S., Wright, I. J., and
521		Zanne, A. E.: Weak tradeoff between xylem safety and xylem-specific hydraulic
522		efficiency across the world's woody plant species, New Phytol, 209, 123-136,
523		10.1111/nph.13646, 2016.
524	25.	Hochberg, U., Rockwell, F. E., Holbrook, N. M., and Cochard, H.: Iso/Anisohydry: A
525		Plant-Environment Interaction Rather Than a Simple Hydraulic Trait, Trends Plant Sci,
526		23, 112-120, 10.1016/j.tplants.2017.11.002, 2018.
527	26.	Huang, M. Y., Xu, Y., Longo, M., Keller, M., Knox, R. G., Koven, C. D., and Fisher, R.
528		A.: Assessing impacts of selective logging on water, energy, and carbon budgets and
529		ecosystem dynamics in Amazon forests using the Functionally Assembled Terrestrial
530		Ecosystem Simulator, Biogeosciences, 17, 4999-5023, 10.5194/bg-17-4999-2020, 2020.
531	27.	. Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T.,
532		Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J.,
533		van Bodegom, P. M., and Violle, C.: A global Fine-Root Ecology Database to address
534		below-ground challenges in plant ecology, New Phytol, 215, 15-26, 10.1111/nph.14486,
535		2017.
536	28.	Kennedy, D., Swenson, S., Oleson, K. W., Lawrence, D. M., Fisher, R., da Costa, A. C.
537		L., and Gentine, P.: Implementing Plant Hydraulics in the Community Land Model,
538		Version 5, J Adv Model Earth Sy, 11, 485-513, 10.1029/2018ms001500, 2019.





539 29. Klein, T.: The variability of stomatal sensitivity to leaf water potential across tree sp	ecies
540 indicates a continuum between isohydric and anisohydric behaviours, Funct Ecol, 22	3,
541 1313-1320, 10.1111/1365-2435.12289, 2014.	
542 30. Koven, C. D., Knox, R. G., Fisher, R. A., Chambers, J. Q., Christoffersen, B. O., Da	vies,
543 S. J., Detto, M., Dietze, M. C., Faybishenko, B., Holm, J., Huang, M. Y., Kovenock	, M.,
544 Kueppers, L. M., Lemieux, G., Massoud, E., McDowel, N. G., Muller-Landau, H. C	•,
545 Needham, J. F., Norby, R. J., Powell, T., Rogers, A., Serbin, S. P., Shuman, J. K., S	vann,
546 A. L. S., Varadharajan, C., Walker, A. P., Wright, S. J., and Xu, C. G.: Benchmarkin	ıg
547 and parameter sensitivity of physiological and vegetation dynamics using the	
548 Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorad	lo
549 Island, Panama, Biogeosciences, 17, 3017-3044, 10.5194/bg-17-3017-2020, 2020.	
550 31. Kunert, N., Zailaa, J., Herrmann, V., Muller-Landau, H. C., Wright, S. J., Perez, R.,	
551 McMahon, S. M., Condit, R. C., Hubbell, S. P., Sack, L., Davies, S. J., and Anderso	n-
552 Teixeira, K. J.: Leaf turgor loss point shapes local and regional distributions of ever	green
553 but not deciduous tropical trees, New Phytol, 230, 485-496, 10.1111/nph.17187, 202	21.
554 32. Kursar, T. A., Engelbrecht, B. M. J., Burke, A., Tyree, M. T., El Omari, B., and Gira	aldo,
555 J. P.: Tolerance to low leaf water status of tropical tree seedlings is related to drough	it
556 performance and distribution, Funct Ecol. 23, 93-102, 10.1111/j.1365-	
557 2435.2008.01483.x. 2009.	
558 33. Manzoni, S., Vico, G., Katul, G., Palmroth, S., Jackson, R. B., and Porporato, A.:	
559 Hydraulic limits on maximum plant transpiration and the emergence of the safety-	
560 efficiency trade-off. New Phytol. 198, 169-178, 10,1111/nph,12126, 2013.	
561 34. Massoud, E. C., Xu, C. G., Fisher, R. A., Knox, R. G., Walker, A. P., Serbin, S. P.,	
562 Christoffersen, B. O., Holm, J. A., Kueppers, L. M., Ricciuto, D. M., Wei, L., Johns	on.
563 D. J., Chambers, J. O., Koven, C. D., McDowell, N. G., and Vrugt, J. A.: Identificat	ion of
564 key parameters controlling demographically structured vegetation dynamics in a lan	d
565 surface model: CLM4.5(FATES), Geosci Model Dev. 12, 4133-4164, 10.5194/gmd	-12-
566 4133-2019, 2019.	
567 35. McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chamb	ers.
568 J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher,	R.,
569 Fontes, C. G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J.,	,
570 Johnson, D. J., Kassim, A., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malh	i. Y
571 McMahon, S. M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H. C.,	-,,
572 Phillips, O. L., Powell, T., Sierra, C. A., Sperry, J., Warren, J., Xu, C. G., and Xu, X	. Т.:
573 Drivers and mechanisms of tree mortality in moist tropical forests, New Phytol, 219	. 851-
574 869. 10.1111/nph.15027. 2018.	,
575 36. McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg,	W.
576 R. L., Arend, M., Breshears, D. D., Brodribb, T., Choat, B., Cochard, H., De Cacere	s. M.
577 De Kauwe, M. G., Grossiord, C., Hammond, W. M., Hartmann, H., Hoch, G., Kahr	ien.
578 A., Klein, T., Mackay, D. S., Mantova M. Martinez-Vilalta I. Medlyn B. F.	· - · · ,
579 Mencuccini, M., Nardini, A., Oliveira, R. S., Sala, A., Tissue, D. T., Torres-Ruiz, J.	М.,
580 Trowbridge, A. M., Trugman, A. T., Wiley, E., and Xu, C. G. Mechanisms of wood	v-
581 plant mortality under rising drought CO2 and vapour pressure deficit. Nat Rev Fart	h
582 Env, 3, 294-308, 10.1038/s43017-022-00272-1, 2022.	-





583	37.	Moorcroft, P. R., Hurtt, G. C., and Pacala, S. W.: A method for scaling vegetation
584		dynamics: The ecosystem demography model (ED), Ecol Monogr, 71, 557-585,
585	20	10.1890/0012-9015(2001)0/1[055/:Amisva]2.0.06;2, 2001.
507	38.	Neednam, J. F., Chambers, J., Fisher, R., Knox, R., and Koven, C. D.: Forest responses to
58/		simulated elevated CO2 under alternate hypotheses of size- and age-dependent mortality,
588	20	Global Change Biol, 26, 5/34-5/53, 10.1111/gcb.15254, 2020.
589	39.	Paton, S.: Yearly Reports Barro Colorado Island, Smithsonian Tropical Research
590 501	40	Institute, <u>https://doi.org/10.255/3/data.11/99111.v3</u> , 2020.
591	40.	Pineda-Garcia, F., Paz, H., and Meinzer, F. C.: Drought resistance in early and late
592 502		secondary successional species from a tropical dry forest: the interplay between xylem
593		resistance to embolism, sapwood water storage and leaf shedding, Plant Cell Environ, 36,
594	41	405-418, 10.1111/j.1365-3040.2012.02582.X, 2013.
595	41.	Powell, I. L., wheeler, J. K., de Oliveira, A. A. K., da Costa, A. C. L., Saleska, S. K.,
590		Meir, P., and Moorcron, P. K.: Differences in Xylem and leaf hydraulic traits explain
509		differences in drought tolerance among mature Amazon rainforest trees, Global Change
598	10	Biol, 23, 4280-4293, 10.1111/gcb.13/31, 2017.
599	42.	Powell, I. L., Koven, C. D., Jonnson, D. J., Faybisnenko, B., Fisner, K. A., Knox, K. G.,
600		McDowell, N. G., Condil, K., Hubbell, S. P., Wright, S. J., Chambers, J. Q., and
601		Kueppers, L. M.: variation in hydroclimate sustains tropical forest biomass and promotes
602	12	Iunctional diversity, New Phytol, 219, 952-940, 10.1111/npn.152/1, 2018.
603	43.	hotevers the common sitism, mormhology and function of logy of Exact Each 12, 606,710
604 (05		between the composition, morphology and function of leaves, Funct Ecol, 13, 696-710,
605	11	DOI 10.1040/J.1303-2433.1999.00309.X, 1999.
607	44.	A A D Dullan A M Doughty C E Mataolfo D D Vagoonaolog S S Formaina I
608		A. A. K., Fullell, A. M., Doughty, C. E., Metcalle, D. B., Vascoliccios, S. S., Fellella, L. V. Malhi, V. Graan, I. Manauagini, M. and Mair, D. Daoth from drought in transal
600		forests is triggered by hydroulies not earbon steruction. Neture, 528, 110 ±
610		10.1038/nature15530, 2015
611	15	Sack I. Cowan P. D. Jaikumar N. and Halbrook N. M. The 'hydrology' of leaves:
612	45.	co ordination of structure and function in temperate woody species. Plant Cell Environ
613		$26 \cdot 1343 \cdot 1356$ DOI 10 1046/j 0016-8025 2003 01058 x 2003
614	16	Savage V M Bentley I P Enquist B I Sperry I S Smith D D Beich P B and
615	- 0.	von Allmen E. I. Hydraulic trade-offs and space filling enable better predictions of
616		vascular structure and function in plants. P Natl Acad Sci USA 107, 22722-22727
617		10 1073/ppas 1012194108 2010
618	47	Sperry I S and Love D M : What plant hydraulies can tell us about responses to
619	17.	climate-change droughts New Phytol 207 14-27 10 1111/nph 13354 2015
620	48	Su R Liu H Wang C Zhang H and Cui I: Leaf turgor loss point is one of the best
621	10.	predictors of drought-induced tree mortality in tropical forest Front Fool Fyol 10
622		$A R TN 974004 \cdot 10 3389/fevo 2022 974004 2022$
623	49	Wolfe B T · Bark water vanour conductance is associated with drought performance in
624		tropical trees Biol Letters 16 ARTN 20200263. 10 1098/rsbl 2020 0263. 2020
625	50	Wright S J Kitajima K Kraft N J B Reich P B Wright I I Runker D F
626	20.	Condit, R., Dalling, J. W., Davies, S. J., Diaz, S., Engelbrecht, B. M. J., Harms K. E.
627		Hubbell S P Marks C O Ruiz-Jaen M C Salvador C M and Zanne A F
<u> </u>		reaction, 2. r. a. reaction, constraint and frances of the state of th





628	Functional traits and the growth-mortality trade-off in tropical trees, Ecology, 91, 3664-
629	3674, Doi 10.1890/09-2335.1, 2010.
630	51. Xu, C. G. and Gertner, G.: Understanding and comparisons of different sampling
631	approaches for the Fourier Amplitudes Sensitivity Test (FAST), Comput Stat Data An,
632	55, 184-198, 10.1016/j.csda.2010.06.028, 2011a.
633	52. Xu, C. G. and Gertner, G. Z.: Reliability of global sensitivity indices, J Stat Comput Sim,
634	81, 1939-1969, 10.1080/00949655.2010.509317, 2011b.
635	53. Xu, C. G., McDowell, N. G., Fisher, R. A., Wei, L., Sevanto, S., Christoffersen, B. O.,
636	Weng, E. S., and Middleton, R. S.: Increasing impacts of extreme droughts on vegetation
637	productivity under climate change, Nat Clim Change, 9, 948-+, 10.1038/s41558-019-
638	0630-6, 2019.
639	54. Xu, X. T., Medvigy, D., Powers, J. S., Becknell, J. M., and Guan, K. Y.: Diversity in
640	plant hydraulic traits explains seasonal and inter-annual variations of vegetation
641	dynamics in seasonally dry tropical forests, New Phytol, 212, 80-95, 10.1111/nph.14009,
642	2016.
643	55. Yang, S. D. and Tyree, M. T.: Hydraulic Resistance in Acer-Saccharum Shoots and Its
644	Influence on Leaf Water Potential and Transpiration, Tree Physiol, 12, 231-242, DOI
645	10.1093/treephys/12.3.231, 1993.
646	