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Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Nino-induced drought

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Summary

(1) Reducing uncertainties in the response of tropical forests to global change requires understanding how intra- and interannual climatic variability selects for different species, community functional composition and ecosystem functioning, so that the response to climatic events of differing frequency and severity can be predicted.

(2) Here we present an extensive dataset of hydraulic traits of dominant species in two tropical Amazon forests with contrasting precipitation regimes—low seasonality forest (LSF) and high seasonality forest (HSF)—and relate them to community and ecosystem response to the El Niño-Southern Oscillation (ENSO) of 2015.

(3) Hydraulic traits indicated higher drought tolerance in the HSF than in the LSF. Despite more intense drought and lower plant water potentials in HSF during the 2015-ENSO, greater xylem embolism resistance maintained similar hydraulic safety margin as in LSF. This likely explains how ecosystem scale whole-forest canopy conductance at HSF maintained a similar response to atmospheric drought as at LSF despite their water transport systems operating at different water potentials.

(4) Our results indicate that contrasting precipitation regimes (at seasonal and interannual time scales) select for assemblies of hydraulic traits and taxa at the community level, which may have a significant role in modulating forest drought response at ecosystem scales.

Key-words: hydraulic traits; 2015-ENSO; drought; embolism resistance; Amazon tropical forest, plant functional diversity

Introduction

Increases in the frequency and duration of climatic anomalies, such as drought events induced by the El Niño Southern Oscillations (ENSO), are resulting in higher plant mortality, including in Amazonia, home of the world's largest contiguous tropical forests (Williamson *et al*., 2000; Phillips *et al.*, 2010; Lintner *et al*., 2012; Fu *et al.*, 2013). Amazon forests play a significant role in regional and global carbon and water cycles, and provide essential ecosystem services (Oyama and Nobre, 2003; Malhi *et al*., 2009; Davidson *et al*., 2011); many efforts thus seek to understand and predict how these forests respond to drought (da Costa *et al.*, 2010; Joetzjer *et al.*, 2014; Brienen *et al*., 2015; Rowland *et al.*, 2015).

Most early ecosystem modelling studies used "big leaf" approaches (in which whole forest responses are modelled after average growth responses of single plants or a small number of plants) that do not represent a diversity of functional strategies; these models tended to predict either large-scale catastrophic forest dieback (Cox *et al.*, 2004; Good *et al*., 2011) or forest persistence (Friedlingstein *et al*., 2006; Huntingford *et al*., 2013; Cox *et al*., 2013). More recent models which account for diversity in functional growth strategies and landscape heterogeneity tend to simulate more nuanced resilience emerging from trait-based selection among growth strategies (Sakschewski *et al*., 2016) and more heterogeneous transitions (Levine *et al*., 2016). The inclusion of functional traits in models is therefore expected to improve simulations of forest drought vulnerability and resilience (Fisher *et al*., 2015; Gentine *et al*., 2016; Xu *et al.*, 2016; Konings *et al.*, 2017; Manoli *et al.,* 2018).

Two empirical challenges face efforts to improve such models: the need to

increase knowledge of the composition of relevant functional traits of different systems (Medlyn *et al.*, 2016), and the need to test how such knowledge about functionally different individuals scales to ecosystem behaviour – the scale relevant to interactions with the atmosphere and regional climate. To address these challenges, we investigated two different tropical evergreen forests with contrasting climates and different species compositions by first, characterizing their differences in terms of functional traits, and then by testing hypotheses for how functional differences would affect whole-ecosystem responses.

For functional diversity, we focus on hydraulic traits, particularly those related to embolism resistance, which are key to explaining such important factors as tree mortality, drought resistance and species distribution (Anderegg *et al*., 2015, 2016; Rowland *et al*., 2015; Oliveira *et al.,* 2019). Embolism formation in the xylem decreases water supply to the leaves, forcing plants to reduce transpiration and, consequently, reducing photosynthesis and the energy available for physiological functions (Sperry *et al.*, 2002; McDowell *et al*., 2008). The water potentials at which plant tissues (i.e. stem xylem) lose 50 or 88 % of their conductance (P_{50} or P_{88}, respectively) are common measures of xylem embolism resistance (Tyree and Sperry, 1989; Sperry *et al.*, 2002), while hydraulic safety margins to P_{50} (HSM_{P50}) - the difference between the minimum water potential measured in field conditions and P_{50} - is a frequently used index of plant drought resistance (Meinzer *et al.*, 2009). Hydraulic safety margins (e.g. HSM_{P50}) are observed in a majority of sampled woody species around the globe to be maintained within a narrow range despite the large diversity of embolism resistance (quantified as P_{50}), which generally increases as mean annual precipitation declines (Choat *et al*., 2012). Drought-resistance is a key strategy affecting the distribution of species along water availability gradients which act as environmental filters, including or excluding species based on their traits (Engelbrecht *et al.*, 2005, 2007; Markesteijn *et al.*, 2011; Esquivel-Muelbert *et al.*, 2017, Oliveira *et al.,* 2019).

For ecosystem level behaviour, we focused on whole-forest canopy conductance (G_s), an ecosystem level trait that is both likely related to the hydraulic traits we are measuring and which plays a central role in coupling ecosystems to the atmosphere. Critically, canopy conductance includes stomatal conductance (aggregated across all leaves in the canopy), which controls plant water use and couples the plant water and carbon cycles (Collatz *et al.,* 1991; Lin *et al.,* 2015).

We ask whether different precipitation regimes in different Amazon forests lead to community scale differences in hydraulic traits, and in vegetation responses to extreme drought events. To address this question, we studied hydraulic traits of dominant tree species in two evergreen tropical forests sites with contrasting rainfall regimes: a low seasonality forest (LSF) characterized by low seasonal and interannual rainfall variability in central Amazon (near Manaus, Brazil), and a high seasonal forest (HSF) with substantial seasonal and interannual precipitation variability in Eastern Amazon (near Santarem, Brazil).

Then, we compared species, community and ecosystem-level responses at these two forests during a typical dry season period and during one of the most extreme drought-El Niño events (referred here as 2015-ENSO or just ENSO) ever recorded in Amazon rainforests (Jiménez-Muños *et al.*, 2016; Panisset *et al*., 2018). We hypothesized that:

(1) More variable precipitation regimes select for more drought resistant communities. We predict dominant species in the HSF have traits associated with higher drought tolerance than the LSF.

(2) Communities in environments with higher precipitation variability are less sensitive to extreme drought events than communities in environments with lower precipitation variability. We estimated sensitivity as the change in water potential from a regular year dry season to the 2015-ENSO dry season. We predict that HSF species and community are less sensitive to the 2015-ENSO than the LSF, and that embolism resistance modulates the magnitude of the response. Additionally, we hypothesize the species response to this El Niño event is mediated by their hydraulic traits.

(3) Community level water use responses to atmospheric and soil drought is less intense in forests with more variable precipitation. We predict ecosystem canopy conductance, a measure of plant community water use response to environment changes, is less sensitive to vapour pressure deficit and cumulative water deficit in HSF than in LSF.

To test these hypotheses, we combine a unique dataset of xylem embolism resistance, plant water potential (i.e. the physical driver of embolism formation) and canopy conductance in tropical forests species, in the novel context of a strong El Niño event. We propose an approach that allows us to scale species-level hydraulic traits to

community-level properties, contributing to the critical overarching goal of linking individual plant trait composition to ecosystem level functioning.

Materials and Methods

Study sites

This study was carried out at two Large-Scale Biosphere–Atmosphere Experiment in Amazon forest (LBA) sites, with contrasting precipitation regimes. The low seasonality forest (LSF) is located in central Amazonia, at the Cuieras Biological Reserve (K34 site), near Manaus, Amazonas, Brazil (60°21'W, 2°61'S). The mean annual precipitation is about 2,400 mm, with two months of dry season (precipitation < 100 mm) in July and August (De Gonçalves *et al.*, 2013, Araujo *et al.*, 2002). The higher seasonality forest (HSF) is located in the eastern Amazonia in the Tapajós National Forest (K67 site), near Santarém, Pará, Brazil (54°58'W, 2°51'S). It is drier than the Manaus region, with an annual mean precipitation of about 1,900 mm (Parrotta *et al*., 1995), a longer dry season (five months, on average) and higher interannual climatic variability. Average annual vapour pressure deficit (VPD) at the HSF site is slightly higher than at LSF (means ± standard deviation of 0.94 ± 0.3 kPa and 0.84 ± 0.34 kPa, respectively), however dry season VPDs do not differ between the sites (1.05 ± 0.18 kPa and 1.08 ± 0.26 kPa, for the HSF and LSF respectively; Fig. S1). The LSF soils are characterized by tertiary sediments covered by clayey Oxisols on the plateaus and sandy Spodosols on the valley bottoms (Araujo *et al.*, 2002), whereas the HSF soils are clayey Oxisols, deeply weathered with no concretions or impeding layers, at least in the upper 12 m (Oliveira *et al.*, 2005, Nepstad *et al*., 2007).

Species selection

At each site, we selected locally and regionally abundant woody species or genera, that contribute significantly to Amazon forest biomass (Ter Steege *et al.,* 2013; Fauset *et al*., 2015). We studied 17 species in the LSF and nine in the HSF (Table S1; see Brum *et al*., 2018), which correspond, respectively, to 13.7% and 35% of the total forest stem basal area. Embolism vulnerability curves were also measured for three additional species in the HSF (*Manilkara huberi, Tachigali chrysophylla* and *Minquartia guianensis*, representing 6.7%, 3.94%, and 0.07% of total forest stem basal area).

The LSF and HSF sites differ in species richness, but mainly in terms of dominance homogeneity (Carneiro, 2004; Vieira *et al.*, 2004; Longo, 2013), which led us to sample more species in the LSF to reach a minimum of 10% of forest stem basal area (Table S1). According to previous surveys, which used trees with stem diameter at breast height (DBH) >10 cm, the species density at the LSF is about 153.2 species ha^{-1} (based on 3.5-ha sampling, measured on the plateaus with total basal area of 28.3 m^2 ha^{-1}; Carneiro, 2004), while at the HSF the density was 133 species ha^{-1} (4 ha transects sampling, Vieira *et al*., 2004; with total basal area of 30.8 m^2 ha^{-1}, Pyle *et al*., 2008 updated by Longo, 2013). The dominance in the LSF is more homogeneous, and the most dominant tree species (i.e. *Eschweilera wachenheimii*) represents 3.02% of total basal area, followed by a few species between 1 and 2 % (Carneiro, 2004); whereas in the HSF, few species are locally hyperdominant (i.e., *Erisma uncinatum*, *Chamaecrista xinguensis*, and *Coussarea albescens*, corresponding to 11.1, 6.1, and 4.6% of the total basal area, respectively).

Hydraulic traits

Xylem vulnerability to embolism was assessed by the relationship between the percentage loss of xylem conductivity (PLC) and xylem water potential (Ψ). PLC was estimated from percentage air discharge (PAD) using the pneumatic method (Pereira *et al*., 2016). To obtain these curves, we collected sun-exposed branches longer than 1 m length early in the morning, from one to three individuals per tree species (Table S1) with DBH across species ranging from 2.7 to 98 cm. For some species, we sampled only one individual due to difficulties of access to very tall trees (e.g. >35 m height). We cut the branch under water inside a bucket and covered them with a plastic bag overnight prior to measurements (following Oliveira *et al.,* 2019 and Brum *et al.,* 2018). To induce cavitation, we used the bench dehydration method (Sperry *et al*., 1988). Stem Ψ was measured as leaf Ψ after equilibrating the branch inside a black plastic bag, for at least one hour prior to making the measurement. We measured leaf Ψ (MPa) with a pressure chamber (PMS 1000; PMS Instruments Co., Albany, OR, USA). We calculated P_{50} and P_{88}, defined as the water potentials at which the tissue loses 50 and 88% of its hydraulic conductivity, by fitting a sigmoidal function to the data (Pammenter and Willigen 1998):

248 $$PAD = \frac{100}{1 + exp\left(\frac{Sp}{25}(\psi x - \psi p50)\right)}$$

249 where PAD (percentage of air discharge) and Ψ_x (xylem water potential, MPa) are the
250 measurement data, to which the parameters Ψ_{p50} (xylem water potential (when PAD
251 equals to 50%) and S_p (slope of the curve, % PAD MPa^{-1}) were fitted.

252 The minimum leaf water potential (Ψ_{min}) was measured during the peak of the
253 dry season of an ENSO (Ψ_{ENSO}) and non-ENSO year ($\Psi_{nonENSO}$). The $\Psi_{nonENSO}$ was
254 measured during the dry season in August 2016 and December 2014, for the LSF and
255 HSF sites respectively. The Ψ_{ENSO} was measured during the driest period of the ENSO
256 event in October 2015 for the LSF and December 2015 for the HSF. The driest interval
257 was determined by the cumulative water deficits for both sites (Fig. 1) (CMWD; see
258 *Microclimatic and soil data* bellow). The leaf Ψ was measured with a pressure chamber
259 in two or three leaves of the same individuals we used to measure the vulnerability
260 curves. Leaves were collected between 12 and 2:30 pm from sun-exposed branches. For
261 both sites, the water potential was collected over an interval of less than seven days in
262 each period (ENSO or non ENSO). There were a few short and light rain events in the
263 LSF during this sampling period, however they were insufficient to increase soil
264 moisture. The water potential was always measured after at least one day without rain.
265 In the HSF there was no rain during the months during which Ψ was measured.

266 Species hydraulic safety margins (HSM) with respect to P_{50} and P_{88} (HSM_{P50}
267 and HSM_{P88}, respectively) were calculated as minimum leaf Ψ ($\Psi_{nonENSO}$ and Ψ_{ENSO})
268 minus P_{50}, or P_{88} respectively. The HSM of the non-ENSO period is thus referred to as
269 $HSM_{nonENSO}$ and that of the ENSO period, as HSM_{ENSO}. We assumed that leaf Ψ was a
270 suitable estimator of xylem Ψ in terminal branches.

271 *Wood anatomy*

272 We collected wood samples from 2nd or 3rd order branches (diameter from ~ 1 to
273 2 cm, i.e. the same as used for vulnerability curves) for anatomy. We kept the samples
274 on formalin-acetic acid alcohol (FAA) for a few days and then exchanged with 50%
275 alcohol to maintain the wood tissue integrity. We did cut the samples using a manual
276 microtome, dyed them with safranin and toluidine blue, and placed on microscope

277 slides. For each individual sample, we took pictures from three regions of different
278 xylem slices (three per individual), using a digital camera (Olympus DP71) coupled to a
279 polarizing microscope (Olympus BX51). The images were processed using the Image J
280 software (version 1.6.0_20) (Schneider *et al*., 2012). For each image, we measured the
281 area of each vessel, the total vessel area (VA; mm^2 of vessel area per mm^2 of xylem
282 area), and their density (VD; number of vessels per mm^2 of xylem area). We calculated
283 effective vessel diameters from the area, assuming vessels were circular. From these
284 data we calculated the vessel hydraulic diameter (D_h; μ) and the theoretical specific
285 hydraulic conductance of the xylem (K_h; kg MPa^{-1} s^{-1} m^{-1}), using the Poiseuille Law
286 (Scholz *et al*. 2013) as:

287 $$D_h = \left(\sum_1^n D_i^4\right)^{\frac{1}{4}}$$

288 $$K_h = \left(\frac{\pi\rho}{128\eta A}\right)\sum_1^n D_i^4$$

289 where D_i is each individual vessel diameter from 1 to *n* in the photographed xylem area
290 A; π is pi; ρ and η are the density of water (996.7867 kg m^{-3}) and water dynamic
291 viscosity (8.9 x 10^{-4} Pa s) at 26ºC, respectively.

292 *Dominance-weighted traits*

293 We used the species relative dominance (percentage stem basal area of each
294 species in each forest) to calculate the dominance-weighted mean (DWM) for each
295 hydraulic trait, which we use as an estimate of the community-weighted mean (CWM;
296 Garnier *et al.,* 2004). The DWM was calculated from a subsample of the species in each
297 community, once to achieve 50% of the hyperdiverse LSF dominance it would require
298 sampling at least 53 species. Our rationale relies on the fact that the DWM from a
299 subsample of species in the community is valid as long as: i) no single species and trait
300 value exerts stronger influence over the CWM value; or ii) sample weight and sample
301 value are independent, and the estimated weighted mean of a subsample of the data
302 should approximate the true weighted mean (see Supplementary Information Methods
303 S1).

304 For both LSF and HSF we did not detect any relationship between the trait value and
305 the species dominance and the most dominant species were not outliers. Furthermore, to

evaluate whether our results have biases due to the low coverage of basal area of the LSF, we carried out additional analyses to demonstrate that there was no change in the estimates when a larger data sample is considered. Since the contribution to the basal area is homogeneously distributed across many species and the traits are assumed to vary randomly, this enables us to assume the DWM as a good estimator of the CWM and scale results to the whole community. Additionally, we used the biogeographic dry-affiliation index as a trait of the genera in each site (Esquivel-Muelbert *et al.*, 2017, 2018; Supplementary Methods S2) to evaluate the community functional composition, *i.e*, the dry-affiliation of the whole community at each site.

Microclimatic and soil data

We measured meteorological conditions at both eddy flux towers sites (1999 to 2016; update from Restrepo-Coupe *et al.*, 2016; details in Methods S3). For each location we used the cumulative monthly water deficit (CMWD; mm) as a measure of soil water deficit, calculated as in Aragão *et al*., (2007), except that we used a positive sign to denote convention for the deficit. CMWD was calculated for each month as the cumulative excess of evapotranspiration less precipitation, starting in the wet season of 1999 for LSF, and 2002 for the HSF:

$$CMWD_m = CMWD_{m-1} + ET_m - P_m$$

where ET_m is monthly evapotranspiration (mm), P_m is monthly precipitation (mm) and $CMWD_m$ is the cumulative water deficit for month *m* (mm) and $CMWD_{m-1}$ is that for the previous month. $CMWD_m$ was initialized at zero for the first month and was reset to zero whenever it became negative (i.e., there was a water surplus and not deficit). The annual mean CMWD was 43.6 ± 47.3 for the LSF and, 109.1 ± 49.4 for the HSF, while the mean annual peak of CMWD was 154.8 ± 118.6 mm for LSF and, 333.1 ± 110.8 mm for the HSF (Fig. 1).

To verify that the estimated CMWD was a good proxy for the more physiologically-relevant soil moisture deficit, we assessed the correlation of CMWD with monthly-averaged soil volumetric water content (SWC) measurements (cm^3cm^{-3}) available at each site. The SWC was measured hourly from October 2015 to August 2016 at the LSF (depths of 0.8, 1.6, 2.4. m; L. Borma *et al*., unpublished data) and from August 2008 to March 2017 (with a 4-year gap from 2012-2015) at the HSF (depths of

0.1, 1.0, 2.0 m; Wu *et al*., 2016, B. Christoffersen *et al*., unpublished data). We obtained soil-water retention curves for LSF from L. Borma *et al*. (unpublished). Using the time series that overlap between the two sites (2015 and 2016), the monthly CMWD explained 46% ($F_{(1,9)} = 7.57$; $p = 0.02$ for LSF) and 65% ($F_{(1,52)} = 95.49$; $p < 0.001$ for HSF) of the variation in the soil water content (0 to 2-2.4 m soil depth) (Fig. S2), confirming that CMWD could be used as a suitable proxy for soil water deficit.

Canopy conductance

To obtain the ecosystem canopy conductance (G_S; mm s^{-1}) we used eddy covariance data from both sites (LBA data from 2002 to 2016, see Methods S3). We calculated G_S through the inversion of the Penman–Monteith (PM) equation (Methods S4). We restricted estimates of G_S to times when the canopy was dry (all data up to 12 hours after precipitation were removed), so we could justifiably assume that most of the flux was due to transpiration. Eddy covariance, microclimatic and soil data are available at LBA data repository (LBA DIS; see https://daac.ornl.gov/cgi-bin/dataset_lister.pl?p=11).

Data analysis

To address our first hypothesis, whether traits from LSF species had less drought resistant traits than HSF species, we used a one-tailed statistical Welch`s t-test and to evaluate the differences in dominance weighted means we used a Monte Carlo approach with the difference in weighted mean as the test statistic, randomizing the site and repeating 10000 times.

To evaluate our second hypothesis, whether the dry season leaf water potential (Ψ_{min}) of the species was affected by the 2015 ENSO in relation to a non-ENSO year and whether the effect differed between sites, we used a general mixed model with species as random factor affecting intercept to account for the same species being measured in the ENSO and non-ENSO year in each site. This has a similar effect of pairing the species in a paired t test. Additionally, to better understand ENSO effects, we evaluated whether Ψ_{min} variation could also be accounted by the atmospheric and soil water deficits (monthly maximum VPD and monthly CMWD) when the Ψ_{min} was measured. To evaluate if the species response to ENSO was modulated by hydraulic traits, we tested whether the difference in species Ψ_{min} from ENSO to non-ENSO year ($\Delta\Psi$) was related to hydraulic traits using general fixed effects model.

For the third hypothesis, we evaluated whether effects of vapour pressure deficit (VPD) and cumulative water deficit (CMWD), measures of atmospheric and soil water stress, on G_s differed between HSF and LSF. As periods of soil drought usually occur with atmospheric drought, we had to first remove the correlation between VPD and CMWD. For this we modelled VPD ~ CMWD and site to obtain a VPD independent from CMWD measure (VPD_r for VPD residuals). In the same way, we modelled CMWD ~ VPD and site to obtain a CMWD independent from VPD ($CMWD_r$). With independent VPD and CMWD measures, we tested whether G_s had a fixed VPD_r and $CMWD_r$ effect and whether site (HSF and LSF) had an additive or interactive effect on G_s. For the above analysis and for obtaining $CMWD_r$ and VPD_r, we used general mixed effect models, with month of the year as random factor affecting slope, to control for temporal autocorrelation of variables. The same analyses were performed to evapotranspiration (ET). Finally, to evaluate whether the ecosystem level water use (G_s) was modulated by hydraulic traits, we analysed if dominance-weighted P50 and hydraulic safety margin affected G_s.

Part of the difficulty analysing atmospheric and soil drought effects is that both are usually correlated (i.e. rainless periods usually have drier atmosphere). To remove this correlation from our dataset, we used only data with CMWD higher than 0, and observations from July to December of 2015. This approach was justified as our goal is to evaluate drought response of G_s, and the data from January to June is usually rainy (precipitation >100 $mm.month^{-1}$). Moreover, LSF had almost no data with CMWD > 0 mm in this wet period, and it would only carry information about G_s response to VPD in wet conditions. For all statistical analyses, data processing, and curve fitting, we used R (R Core Team 2018, version 3.5), and further information about the analysis functions and packages can be found in SI (Methods S5).

Results

Hydraulic trait differences between the two forests

The LSF had less embolism resistant hydraulic vulnerability curves than HSF due to higher P88 (-4.08 ± 1.83 MPa versus -5.33 ± 1.49 MPa, p = 0.027; Fig. 2), and a marginally significant difference in P50 between the two forests (-2.34 ± 0.89 MPa and -2.90 ± 1.15 MPa, respectively, p=0.085; Fig. 2, 3a; see Table S1 and S2 for results summary). Different P88, even if the P50 was similar, is only possible if HSF has a

shallower slope than LSF species hydraulic vulnerability curves, consistent with our observations of a marginally significant difference in slopes (Fig 2; slope difference $p = 0.07$; Table S2). Corroborating these results, the dry-affiliation index (represented by the probability of recording a higher dry-affiliated precipitation centre of gravity value than the observed by chance) revealed differences on the HSF and LSF community functional composition (details in Methods S2). We found a dominance of dry affiliated taxa for HSF compared to LSF (0.73±0.4 for HSF and 0.86±0.3 for LSF; $t = 4.8$, $df = 339.9$, $p < 0.001$) (Fig. 4).

The minimum water potential in the non-ENSO year ($\Psi_{nonENSO}$) was higher ($p < 0.01$) in the LSF (-1.09 ± 0.43 MPa) than in HSF (-1.88 ± 0.58 MPa), however the hydraulic safety margins (i.e. non-ENSO HSM_{P50} and HSM_{P88}) did not differ between the two forests ($p = 0.38$ and $p = 0.23$) (Fig. 3c-e and Table S2). The xylem anatomy of the HSF and LSF species also showed significantly differences for all inspected traits: vessel density, vessel area, potential specific hydraulic conductance and hydraulic diameter (Fig.3f-i and Table S2). Xylem vessel area was higher at the LSF site than at the HSF site ($p=0.03$), and so were the hydraulic diameter ($p = 0.04$) and the potential specific conductance ($p = 0.04$) (Fig.3, Table S2), while the vessel density was 71% higher at HSF ($p=0.01$; Fig. 3f and Table S2).

The analysis comparing the dominance-weighted mean of LSF and HSF showed similar patterns, with P88 of HSF forest being lower than LSF and P50 and slope marginally differently (see Table S2). However, it did not detect differences in anatomical traits, possible because of the lower statistical power of the test and the high value of the 95% confidence intervals of the mean for those traits.

Species and community level responses to the 2015 ENSO-induced drought

The 2015-ENSO climatic effects were observed in both forests, as the CMWD reached values greater than historical means of the driest months recorded since 1998 (Fig. 1). The 2015-ENSO induced CMWD was greatest in the HSF, but absolute and relative changes from the 1998-2014 average of annual maximum CMWD were higher in LSF, with an increase of 306.4 mm (197%; 154.8 to 461.2 mm) versus 155 mm in HSF (46%; 333.1 to 488.1 mm). The $\Psi_{nonENSO}$ and Ψ_{ENSO} measurements at the LSF site were performed during a CMWD of 67.4 mm, and 356.1 mm, respectively; whereas in the HSF, $\Psi_{nonENSO}$ and Ψ_{ENSO} were measured when the CMWD reached 303.2 mm, and

433 422.3 mm respectively (Fig. 1 and Fig. 5a), confirming the different CMWDs
434 conditions when the Ψ_{min} was measured in both forests.

435 At both LSF and HSF sites, Ψ_{min} was significantly reduced during the ENSO
436 period ($p < 0.001$; see Table S3 for statistical summaries), although the effect of ENSO
437 on Ψ_{min} was not very high (0.6 and 0.5 MPa drop for LSF and HSF, respectively). Site
438 had an additive effect on Ψ_{min} ($p = 0.006$) with the HSF Ψ_{min} being on average -0.72
439 MPa lower than LSF (Fig. 5a), but there was no interaction between site and ENSO ($p =$
440 0.12), indicating the 2015-ENSO effect on Ψ_{min} was similar in both areas. The model
441 explained 68% of Ψ_{min} variability with ENSO and site explained 32% (conditional and
442 marginal R^2, respectively).

443 At the species level, responses to the 2015-ENSO event were heterogeneous
444 (Fig. 5b-c). At the LSF site, Ψ_{min} declined in almost all species during ENSO, while at
445 HSF the responses were more diverse, with a majority of species (*Miconia* sp*., C.*
446 *albescens, E. uchi* and *R. pubiflora, M. itauba*) showing a steep drop in Ψ_{min}, while a
447 minority (4 of 9) showing no detectable change (the slight increases seen in Fig 5. are in
448 the range of the measurement error).

449 Monthly maximum VPD was related to Ψ_{min} ($p < 0.001$; Fig. 5c and Table S3)
450 but only with a significant site interactive ($p = 0.008$) and additive effect ($p = 0.001$) on
451 VPD. CMWD was related to Ψ_{min} ($p < 0.001$; Fig. 4b and Table S3) but site had no
452 interactive or additive effect on Ψ_{min} ($p = 0.31$ and $p = 0.11$). The CMWD and VPD of
453 this dataset were related ($r = 0.56$) as the month with higher VPD also had higher
454 CMWD, which precludes us to infer whether the VPD or CMWD effect is dominating
455 the Ψ_{min} variability. However, VPD requiring additional explanation of site to explain
456 Ψ_{min} suggests CMWD contains additional information not contained in VPD, possible
457 the correlation with site, which absorbed site effect on Ψ_{min}, making CMWD the only
458 significant effect on the model. This effect can be seen in Fig. 5b-c.

459 The leaf water potential change, comparing non-ENSO to 2015-ENSO ($\Delta\Psi$),
460 was related to embolism resistance for both P50 and P88 ($p = 0.017$; r^2=0.21 and p=
461 0.019; $r^2 = 0.21$, respectively; Fig. 6). Species with higher embolism resistance had
462 higher changes in $\Delta\Psi$. Site effects on P50 and P88 were not significant for additive
463 effect ($p = 0.77$ and $p = 0.32$) or interaction effect ($p = 0.15$ and $p = 0.13$), indicating
464 $\Delta\Psi$ is similarly modulated by embolism resistance in both sites. Anatomical traits were

not related to $\Delta\Psi$ ($p > 0.20$ for all anatomical traits). P50 and P88 had the same explanatory power of $\Delta\Psi$ ($r^2 = 0.21$), likely due to both being strongly correlated ($r = 0.74$).

Ecosystem level functional responses to drought

CMWD and VPD from July to December were highly correlated ($r = 0.41$), particularly for HSF ($r = 0.53$). This correlation was removed using the residuals of one variable modelled with the other as predictor and site as additive factor (Table S4). The residuals of VPD (VPD_r) did not carry any more signal of CMWD for both sites ($r < 0.01$) and the residuals of CMWD ($CMWD_r$) did not carry any VPD signal ($r = -0.07$).

Canopy conductance (G_s) was significantly affected by VPD_r ($p < 0.001$; $R^2m = 0.40$) with no additive or interactive site effect, while $CMWD_r$ was unrelated to Gs ($p = 0.10$; Fig. S3; Table S4). Given the lack of evidence for a VPD-independent signal of CMWD on G_s, we remodelled G_s as a function of VPD (Fig. 7). We found each unit VPD caused a decreased in G_s of 5.1 mm s^{-1} ($p < 0.001$) and VPD explained 40% of G_s variability. Site had no significant additive or interactive influence on G_s ($p = 0.91$ and $p = 0.08$), indicating HSF and LSF respond equally to VPD. Evapotranspiration (ET) was not affected by VPD_r neither $CMWD_r$ ($p = 0.32$ and $p = 0.29$), although site had a significant effect on ET ($p < 0.001$) (Table S5; Fig. S4).

The differences in ecosystem canopy conductance (G_s) values between the two forests correlated with the variation observed in community Ψ_{min}, as represented by the dominance-weighted trait (Fig. 8). For the same G_s value, the HSF had more negative community Ψ_{min} than LSF, and the G_S seems to respond linearly to HSM_{P50}, which explained 95% of G_s variability, when the two sites were considered together ($p = 0.02$) (Fig. 8b).

Discussion

We evaluated plant responses at the species, community, and ecosystem levels during usual years and one of the most severe drought events (El-Niño event in 2015) (Jiménez-Muñoz *et al*., 2016**)** ever recorded in Amazonia. We report species-level hydraulic traits that contributed to the observed differences in forest drought responses. Our findings highlight the role of rainfall seasonality and inter-annual variability in addition to mean annual precipitation as important filters selecting different hydraulic

traits, strategies and taxa across rainforest sites, and complement analyses based on MAP differences alone (Choat *et al.,* 2012; Ciemer *et al*., 2019). The dominant species at the high seasonality forest in Eastern Amazon (HSF) are more drought-affiliated and exhibit hydraulic traits with higher embolism resistance (i.e., lower P88), as compared to the low seasonal forest in the central Amazon (LSF).

Despite this difference in the hydraulic system of plants, both forests maintained the same sensitivity of canopy conductance (G_s) to atmospheric drought. Our data suggest this is possible because of the higher embolism resistance in HSF. Interestingly, the two forests had similar responses to the 2015-ENSO when we consider their change in water potential, and at both forests we showed species embolism resistance to modulate the species level response to ENSO. Importantly, despite the limitations of our sampling design, we were able to show that species-level hydraulic traits have the potential of being scaled up to community-level properties, which in turn could help explaining ecosystem-level water fluxes and drought response (Fig. 8).

Differences in drought resistance traits between low and high seasonality forests

Our results indicate that precipitation regime is an important filter in selecting contrasting embolism vulnerabilities. The drier condition and the marked seasonality and inter-annual rainfall variability in Eastern Amazon make the HSF an environment with more pronounced water limitation, which in turn, have shaped the dominance of traits related to embolism resistance, which allowed species to operate at more negative Ψ during water-limiting conditions. Consistent with these findings, our results indicate higher proportion of dry-affiliated taxa at the HSF when compared with LSF (Fig. 4) (Esquivel-Muelbert *et al*., 2017), and the dominance of drought-resistant taxa in the HSF also suggests that climate-driven community assembly may be the mechanism underlying the higher resilience to climatic disturbances observed for forests under higher rainfall variability regimes in the Amazon (Ciemer *et al.,* 2019).

The differences between P_{88} and P_{50} show that xylem embolism resistance (represented by the vulnerability curve) can be affected not only by shifting the curves towards a certain P_{50}, but also by modifying their shape (i.e., the slope and the difference between P_{50} and P_{88}) (Fig. 2). We observed a lower P_{88} in the HSF, which could be an evolutionary adjustment allowing the species to maintain xylem conductivity in highly seasonal environments where some embolism may be

528 unavoidable, mainly for shallow-rooted species in HSF (Brum *et al.*, 2018). Thus, we
529 emphasize the importance of xylem embolism resistance (represented by the
530 vulnerability curves) as one of key functional traits relevant for explaining the patterns
531 of plant distribution in biodiverse tropical ecosystems, as proposed for other
532 environments (Pockman and Sperry, 2000; Brodribb, 2017; Cosme *et al*., 2017; Trueba
533 *et al.*, 2017; Oliveira *et al*., 2019).

534 *Complex leaf water potential response to the 2015 ENSO-induced drought*

535 During the 2015-ENSO, the Amazon basin-wide average temperature reached a
536 record high (the annual monthly maximum was 2.5 ºC higher than the climatological
537 mean) for the last century, exacerbating the effect of the 2015-ENSO drought (Jiménez-
538 Muñoz *et al.*, 2016; Panisset *et al*., 2018). The warmer conditions increased the
539 evaporative demand (VPD) at both sites, affecting species hydraulic functioning. Our
540 results showed a site-specific condition affecting Ψ_{min} (Fig. 5), with the CMWD likely
541 incorporating both the atmospheric signal (VPD) and the soil signal (CMWD) in plant
542 water potential.

543 This difficulty of separating soil and atmospheric water stress, as both usually
544 occur together, is furthermore complicated by the non-linear effect of soil water content
545 (represented in our study sites by the CMWD) on soil water potential (van Genuchten,
546 1980), which means it is necessary to have substantial decrease in CMWD for the soil
547 water potential to increase to levels that induce embolism; and once this threshold is
548 reached a small change in CMWD implies in a large change in soil water potential. This
549 threshold has an important meaning for vegetation, as it represents the point when
550 plants start experiencing a strong soil drought signal, which depends on: i) soil type and
551 soil depth, ii) tree rooting depth, and iii) spatial variability, factors that can imply
552 landscape niches with different degrees of vulnerability. So, depending on the locations
553 and species, the CMWD can have different meanings, and should be used with caution
554 as universal index of drought stress for vegetation (Esquivel-Muelbert *et al*., 2017). For
555 example, the higher drop in Ψ observed for some species at the HSF could indicate the
556 placement of their roots in shallow soils and lower stomatal regulation, while deeply
557 rooted species probably avoid extreme intensity of droughts (e.g., Ivanov *et al*., 2012;
558 Nepstad *et al*., 1994; Oliveira *et al.*, 2005; Brum *et al*., 2018).

559 Although we observed a strong climatological drought, we cannot predict its

consequences to long term functioning of trees, as it does not immediately translate to ecohydrological drought (Nepstad *et al.*, 2007; da Costa *et al.*, 2010) and some species were still operating with some hydraulic safety margin. We found the drought was enough to cause a modest average drop in leaf Ψ (with Ψ stabilization), probably indicating species stomatal control with the major effect at gas exchange level, as observed with the decrease in G_s, which is likely maintaining ET constant despite changing VPD as predicted by stomatal optimization models (Sperry and Love 2015; Eller et al., 2018). We also show the xylem embolism resistance explained part of the response in leaf Ψ during the 2015-ENSO (Fig. 6), which means species with higher resistance to xylem embolism could withstand lower water potentials and maintain gas exchange under drier conditions. Thus, to have a more comprehensive understanding on the diversity of plant water potential responses, studies should consider traits that influence plant water supply, demand and storage, some of them very challenging to measure in the field.

Canopy conductance changes as an ecosystem level response

It is notable that, despite the HSF and LSF operating at different Ψ_{min}, both had the same canopy level response to VPD (Fig. 7). This difference between water supply function responses with no difference in the canopy level water control function responses is likely possible only because the HSF has a more embolism resistant water-transport system. This is theoretically expected, as the embolism resistance sets the water potentials plants can operate (Sperry and Love, 2015) and, consequently, modulate the atmospheric and soil climatic envelope they can tolerate.

In fact, we show here the Ψ_{min} and HSM are traits mechanistically involved in species physiological responses under different conditions of water availability (Fig. 8). Moreover, the result that both communities operate under the same safety margin, in ENSO and non-ENSO, suggests they can keep their gas exchange rates even under extreme drier conditions than the usual dry season, which probably directly influence forest productivity. This highlights the role of xylem embolism resistance traits in determining plant functioning and vegetation drought-response (Anderegg *et al.*, 2016; Anderegg *et al.*, 2018). Actually, including embolism resistance in plant models has improved the prediction of ecosystem transpiration drought responses in the Amazon Forest of Caxiuanã (Eller *et al.*, 2018), and they also predict lower sensitivity to drought

than do previous models, a result supported by our data.

Despite changes in the CMWD we did not detect its signal on canopy level response. In LSF, the effect of 2015-ENSO was only substantial in the superficial soil layers (around 80 cm depth), suggesting that a higher CMWD (than the one caused by the 2015-ENSO) is necessary to affect deeper soils and change the soil water content in a way that would induce notable changes in canopy conductance. On the other hand, in the HSF, the large variability on soil water content (at least to a depth of 2 m; Fig. S2) did not affect Gs either, emphasising the importance of more drought resistant traits and/or deep roots to modulate canopy water use. This suggests possibly extreme dry years, and not average years, contribute to filter plant communities, where trees have adapted their water transport system to drier than normal conditions, which they will likely experience during their lifespan (Grant *et al*. 2017). Moreover, as in HSF trees are currently operating at lower soil water availability, we believe an additional increase in CMWD may provoke extreme changes in soil water potential (Hutyra *et al.*, 2005) and consequently in forest functioning. Additional studies will need to consider interactions between rooting depth and soil moisture dynamics to gain insights on the behaviour of forest canopy conductance.

Conclusion

We report significant differences in hydraulic traits between two Amazon forests: low (LSF) and high seasonal forest (HSF). Our results demonstrate that the seasonal and inter-annual variability on water stress is a key factor driving hydraulic functional differences across tropical forest sites. Interestingly, despite differences in water transport operation and traits, this difference was not translated in different atmospheric drought responses, suggesting the more drought resistant hydraulic traits in HSF compensated for the drier soils, equalizing their safety margin and allowing them to maintain similar canopy level responses to a drier atmosphere in both forests.

Our study shows the importance of embolism resistance in explaining interspecific variability in drought responses of the two different communities of species that have contrasting seasonality of moisture availability, thereby linking relevant traits to species distribution, community assembly and ecosystem functioning. Further studies should address how spatial and temporal climatic variability at broader scales in the Amazon region filter a set of hydraulic traits that affect forest functioning,

which will permit better-informed predictions of vegetation response to climate change.

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Author Contributions

FVB, PRLB, MB and RSO conceived the research ideas, developed the project and wrote the manuscript. FVB, PRLB and MB collected, processed and analysed the data. NRC and SRS, with support from PG, derived the ecosystem analysis, principally metrics of whole forest water cycling (canopy conductance and cumulative water deficit) from eddy covariance data, after applying consistent processing and QA/QC protocols at both sites. LSB and BOC collected and processed soil data. DP, LP and GST collected and processed some tree hydraulic data. LFA, AJNL and VMCC collected, processed and analysed floristic data. LSML and ACA maintained instruments and acquired and processed raw eddy covariance data from the low-seasonality forest (K34), and SRS and NRC played this role at the HSF (K67). LCEOA, J-EL and VI and all authors revised the manuscript. FVB, PRLB and MB contributed equally to this work.

References

Anderegg WRL, Flint A, Huang C, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* **8**: 367–371.

Anderegg WR, Klein T, Bartlett M, Sack L, Pellegrini AF, Choat B, Jansen S. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences* **113**: 5024–5029.

Anderegg WRL, Konings AG, Trugman AT, Yu K, Bowling DR, Gabbitas R *et al*. 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature letter* **561**: 538-541.

Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE. 2007. Spatial patterns and fire response of recent Amazonian droughts. *Geophys. Res. Lett.* **34**: L07701.

Araujo AC, Nobre AD, Kruijt B, Elbers JA, Dallarosa R, Stefani P et al. 2002. Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. *Journal of Geophysical Research* **107**: 8090.

Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, Lloyd J, Lopez-Gonzalez G, Monteagudo-Menzoza A, Malhi Y, Martinez RA *et al.* 2015. Long-term decline of the Amazon carbon sink. *Nature* **519**: 344–348.

Brodribb TJ. 2017. Progressing from "functional" to mechanistic traits. *New Phytologist* **215**: 9–11.

Brum M, Vadeboncoeur MA, Ivanov V, Asbjornsen H, Saleska S, Alves LF, Penha D, Dias JD, Aragão LEOC, Barros F *et al.* 2018. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology.* **107**: 318-333.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci GS, Field TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–755.

Carneiro VMC. 2004. *Composição florística e análise estrutural da floresta primária de terra firme na bacia do Rio Cuieras, Manaus - AM*. Master dissertation, Universidade Federal do Amazonas, Manaus - AM.

Ciemer C, Boers N, Hirota M, Kurths J, Muller-Hansen F, Oliveira RS Winkelmann R. 2019. Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall. *Nature Geoscience* **12**: 174-179.

Collatz GJ, Ball JT, Grivet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agr. Forest Meteorol.* **54**:107–136.

Cosme LHM, Schietti J, Costa FRC, Oliveira RS. 2017. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytologist* **215**: 113–125.

Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology* **78**: 137-156.

Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**: 341–344.

Da Costa CL, Galbraith D, Almeida S, Tanaka Portela BT, da Costa M, de Athaydes SJ, Braga AP, Gonçalves PHL, Oliveira AAR, Fisher R *et al.* 2010. Effect of seven years of experimental drought on the aboveground biomass storage of an eastern Amazonian rainforest. *New Phytologist* **187**: 579–591.

Davidson E, Lefebvre PA, Brando PM, Ray DM, Trumbore SE, Solorzano LA, Ferreira JN, Bustamante MMC, Nepstad DC. 2011. Carbon inputs and water uptake in deep soils of an eastern Amazon forest. *For. Sci.* **57**: 51–58.

De Gonçalves LGG, Borak JS, Costa MH, Saleska SR, Baker I, Restrepo-Coupe N, Muza MN, Poulter B, Verbeeck H, Fisher JB *et al.* 2013. Overview of the large-scale biosphere-atmosphere experiment in Amazonia data model intercomparison project (LBA-DMIP). *Agricultural and Forest Meteorology* **182–183**: 111–127.

Eller CB, Rowland L, Oliveira RS, Bittencourt PRL, Barros FV, Friend AD,Mencuccini M, Sitch S, Cox P. 2018. Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics. *Philosophical Transactions of the Royal Society Biological Sciences* **373**: 20170315.

Engelbrecht BMJ, Kursar TA, Tyree MT. 2005. Drought effects on seedling survival in a tropical moist forest. *Trees* **19**: 312–321.

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**: 80–82.

Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, ter Steege H, Lopez-Gonzalez G, Mendoza AB, Brienen R, Feldpausch TR, Pitman N *et al.* 2017. Seasonal drought limits tree species across the Neotropics. *Ecography* **40**: 618–629.

Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, Brienen RJW, Feldpausch TR , Loyd J, Monteagudo-Mendoza A, Arroyo L, Álvarez-Dávila E *et al.* 2018. Compositional response of Amazon forests to climate change. *Global Change Biology* **25:** 39-56.

Fauset S, Johnson MO, Gloor M, Baker TR, Monteagudo A, Brienen RJW, Feldpausch TR, Lopez-Gonzalez G, Malhi Y, ter Steege H *et al.* 2015. Species contributions to stems, biomass and productivity in Amazon inventory plots. Hyperdominance in Amazonian forest carbon cycling. *Nature Communications* **6**: 6857.

Fisher RA, Muszala S, Verteinstein M, Lawrence P, Xu C, McDowell NG, Knox RG, Koven C, Holm J, Rogers BM *et al.* 2015. Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development* **8**: 3593–3619.

Friedlingstein P, Cox P, Betts R, Bopp L, von Bloh W, Brovkin V. *et al.* 2006. Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *J. of Climate* **19**: 3337-3353.

Fu R, Yin L, Li W, Arias PA, Dickinson RE, Huang L, Chakraborty S, Fernandes K, Liebmann B, Fisher R, Myneni RB. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences* **110**: 18110-18115.

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Gérard L, Blanchard A, Aubry D, Neill C *et al.* 2004. Plant Functional Markers Capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.

Gentine P, Guérin M, Uriarte M, Mcdowell NG, Pockman WT. 2016. An allometry-based model of the survival strategies of hydraulic failure and carbon starvation. *Ecohydrology* **9**: 529–546.

Good P, Jones C, Lowe J, Betts R, Booth B. 2011. Quantifying environmental drivers of future tropical forest extent. *Journal of Climate* **24**:1337–1349.

Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J. 2017. Evolution caused by extreme events. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**: 20160146.

Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Fisher R, Lomas M, Walker AP, Jones CD, Booth BBB *et al.* 2013. Simulated resilience of tropical rainforests to CO2-induced climate change. *Nature Geoscience* **6**: 268–273.

Hutyra LR, Munger JW, Nobre CA, Saleska SR, Vieira SA, Wofsy SC. 2005. Climatic variability and vegetation vulnerability in Amazônia. *Geophysical Research Letters* **32**: L24712.

Ivanov VY, Hutyra LR, Wofsy SC, Munger JW, Saleska SR, Oliveira Jr. RC, Camargo PB. 2012. Root niche separation can explain avoidance of seasonal drought stress and vulnerability of overstory trees to extended drought in a mature Amazonian forest. *Water Resources Research* **48**: W12507.

Jiménez-Muñoz JC, Mattar C, Barichivich J, Santamaría-Artigas A, Takahashi K, Malhi Y, Sobrino JA, van der Schrier G. 2016. Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. *Scientific Reports* **6**: 33130.

Joetzjer E, Delire C, Douville H, Ciais P, Decharme B, Fisher R, Christoffersen B, Calvet JC, da Costa ACL, Ferreira LV, Meir P. 2014. Predicting the response of the Amazon rainforest to persistent drought conditions under current and future climates: A major challenge for global land surface models. *Geoscientific Model Development* **7**: 2933–2950.

Konings AG, Williams AP, Gentine P. 2017. Sensitivity of grassland productivity to aridity controlled by stomatal and xylem regulation. *Nat. Geosci* **7**: 2193–2197.

Levine NM, Zhang K, Longo M, Baccini A, Phillips OL, Lewis SL, Alvarez-Dàvila E, Andrade ACG, Brienen RJW, Erwin TL *et al.* 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. P*roceedings of the National Academy of Sciences* **113**: 793–797.

Lin YS, Medlyn BE, Duursma RA, Prentice IC, Wang H, Baig S, Eamus D, Dios VR, Mitchell P, Ellsworth DS *et al.* 2015. Optimal stomatal behavior around the world. *Nature Climate Change* **5**: 459–464.

Lintner BR, Biasutti M, Diffenbaugh NS, Lee J-E, Niznik MJ, Findell KL. 2012. Amplification of wet and dry month occurrence over tropical land regions in response to global warming. *Journal of Geophysical Research* **117**: D11106

Longo, M. 2013. *Amazon Forest Response to Changes in Rainfall Regime: Results from an Individual-Based Dynamic Vegetation Model.* Dissertation Thesis, Harvard University, United States.

Malhi Y, Aragão LE, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences* **106**: 20610–20615.

Manoli G, Ivanov VY, Fatichi S. 2018. Dry-season greening and water stress in Amazonia: The role of modeling leaf phenology. *Journal of Geophysical Research* **123:** 1909–1926.

Markesteijn L, Poorter L, Bongers F, Paz H, Sack L. 2011. Hydraulics and life history of tropical dry forest tree species : coordination of species' drought and shade tolerance. *New Phytologist* **191**: 480-495.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA. 2008. Mechanisms of Plant Survival and Mortality during Drought : Why Do Some Plants Survive while Others Succumb to Drought ? *New Phytologist* **178**: 719–739.

Medlyn BE, De Kauwe MG, Duursma RA. 2016. New developments in the effort to model ecosystems under water stress. *New Phytologist* **212**: 5–7.

Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR. 2009. Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* **23**: 922–930.

Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Silva ED, Stone TA, Trumbore SE, Vieira S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**: 666–669.

Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon Forest. *Ecology* **88**: 2259-2269.

Oyama MD, Nobre CA. 2003. A new climate-vegetation equilibrium state for Tropical South America. *Geophys. Res. Lett.* **30**: 2199.

Oliveira RS, Dawson TE, Burgess SSO, Nepstad DC. 2005. Hydraulic redistribution in three Amazonian trees. *Oecologia* **145**: 354 – 363.

Oliveira RS, Costa FRC, Baalen E, Jonge A, Bittencourt PR, Almanza Y, Barros FV, Cordoba EC, Fagundes MV, Garcia S *et al.* 2019. Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytologist* **221**: 1457-1465.

Pammenter NW, Vander Willigen C. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree physiology* **18**: 589-593.

Panisset JS, Libonati R, Gouveia CMP, Machado-Silva F, França DA, França JRA, Peres LF. 2018. Contrasting patterns of the extreme drought episodes of 2005, 2010 and 2015 in the Amazon Basin. *International Journal of Climatology* **38**: 1096-1104.

Parrotta JA, Francis JK, DeAlmeida RR. 1995. Trees of the Tapajo´s: A photographic field guide. Gen. Tech. Rep. IITF-1, U. S. Dep. of Agric., Rio Piedras, Puerto Rico.

Pereira L, Bittencourt PRL, Oliveira RS, Junior MBM, Barros FV, Ribeiro

RV, Mazzafera P. 2016 Plant pneumatics: stem air flow is related to embolism – new perspectives on methods in plant hydraulics. *New Phytologist* **211:** 357-370.

Phillips OL, van der Heijden G, Lewis SL, López-González G, Aragão LEOC, Lloyd J, Malhi Y, Monteagudo A, Almeida S, Dávila EA *et al*. 2010. Drought mortality relationships for tropical forests. *New Phytologist* **187:** 631-646.

Pockman WT, Sperry JS. 2000. Vulnerability to Xylem cavitations and the distribution of Sonoran Desert vegetation. *American Journal of Botany* **87:** 1287–1299.

Pyle EH, Santoni GW, Nascimento HEM, Hutyra LR, Vieira S, Curran DJ, van Haren J, Saleska SR, Chow VY, Camargo PB. 2008. Dynamics of carbon, biomass, and structure in two Amazonian forests. *Journal of Geophysical Research: Biogeosciences* **114**:1–20.

Restrepo-Coupe N, Levine NM, Christoffersen BO, Albert LP, Wu J, Costa MH, Galbraith D, Imbuzeiro H, Martins G, Araujo AC *et al*. 2016. Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison. *Glob. Change Biol* 23:191-208.

Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS *et al*. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* **528**:119-122.

Sakschewski B, von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J, Thonicke K. 2016. Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change* **6**: 1032–1036.

Schneider CA, Rasband WS, Eliceiri KW. 2012. "NIH Image to ImageJ: 25 years of image analysis". *Nature methods* **9**: 671-675.

Scholz A, Klepsch M, Karimi Z, Jansen S. 2013. How to quantify conduits in wood? *Frontiers in Plant Science* **4**: 56.

Sperry JS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**:35–40.

Sperry JS, Hacke UG, Oren R, Comstock JP. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment* **25**: 251–263.

Sperry JS, Love DM. **2015**. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* **207**: 14–27.

Ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomao RP, Guevara JE, Philips OL, Castilho CV, Magnusson WE, Molino JF *et al*. 2013. Hyperdominance in the Amazonian Tree Flora. *Science* **342**: 1243092..

Trueba S, Pouteau R, Lens F, Feild TS, Isnard S, Olson ME, Delzon S. 2017. Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island. *Plant Cell and Environment* **40**: 277–289.

Tyree MT, Sperry JS. 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant. Phys. Mol. Bio*. **40**: 19-38

van Genuchten MT. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America* **44**:892-898.

Williamson GB, Laurance WF, Oliveira AA, Delamônica P, Gascon C, Lovejoy TE, Pohl L. 2000. Amazonian tree mortality during the 1997 El Niño drought. *Conservation Biology* **14**:1538–1542.

Vieira S, de Camargo PB, Selhorst D, da Silva R, Hutyra L, Chambers JQ, Brown IF, Higuchi N, dos Santos J, Wofsy SC *et al*. 2004. Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* **140**: 468-479.

Xu X, Medvigy D, Powers JS, Becknell JM, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80-95.

Figures

Figure 1. Monthly cumulative water deficit (mm) from 1999 to 2016 for Manaus (a), and Tapajos (b). Blue and red lines correspond to the periods of water potential measurements at each site for LSF (low seasonal forest; Manaus) and HSF (high seasonal forest; Tapajós), respectively: the solid line represents the non-ENSO year

(2014-2015 for Tapajós and 2016-2017 for Manaus), and the dashed line the 2015-2016 ENSO year. Grey lines represent all other years and the thick grey line is the mean across all years, including the ENSO year. Asterisks on blue and red lines denote the months during which the water potential data were collected. Boxplots inserts represent CMWD distribution for each site. Whiskers are either maximum/minimum value or, when outliers are present, 1.5 interquartile range above/bellow the quartiles 2 and 3.

Figure 2. Hydraulic vulnerability curves for different species at (a) LSF (low seasonal forest), and (b) HSF (high seasonal forest). The thicker lines denote the dominance-weighted vulnerability curve for each forest (blue for LSF and red for HSF).

Figure 3. Hydraulic and anatomical trait distributions for LSF (blue) and HSF (red): (a) P_{50} (MPa); (b) P_{88} (MPa); (c) minimum midday (12:00 - 2:30 PM) water potential for the non-ENSO year (MPa); (d) P_{50} hydraulic safety margin for the non-ENSO year (MPa); (e) P_{88} hydraulic safety margin for the non-ENSO year (MPa); (f) D_v -Hydraulic diameter (mm), (g) Vessel density (vessels per mm^{-2}); (h) Vessel area (% vessel area per xylem area); and (i) Potential specific conductance (K_h; kg MPa^{-1} s^{-1} m^{-1}). Whiskers are either maximum/minimum value or, when outliers are present, 1.5 interquartile range above/bellow the quartiles 2 and 3.

Figure 4. (a) The probability of recording a higher dry-affiliated precipitation center of gravity (PCG) value than observed by chance (PCG 2-tail p-value) for a range of genera in Amazonian sites varying with the Cumulative Water Deficit for the same sites obtained by Esquivel-Muelbert et al. (2017). Each point represents a different genus in the Amazon (grey points), where blue and red points represent the studied genera for LSF and HSF, respectively. (b) The PCG 2-tail p-value obtained from the database available at Esquivel-Muelbert et al. (2017) for the all the genera recorded at LSF (blue) and HSF (red). The higher the genus PCG 2-tail p-value, the lower its dry-affiliation index. We can see the lower dry-affiliation of LSF genera (higher PCG 2−tail P−value, $p < 0.001$), when compared with the HSF genera. Whiskers in b) are minimum value or, when outliers are present, 1.5 interquartile range bellow the quartile 2.

Figure 5. (a) Dry season minimum leaf water potential (Ψ_{min}; MPa) of high seasonality

forest (HSF; Tapajos) and the low seasonality forest (LSF; Manaus) species during non-ENSO year (blue) and the 2015 ENSO year (red). Change in minimum leaf water potential (Ψ_{min}; MPa) from non-ENSO (circles) to the 2015 ENSO year (triangles) in the low seasonality forest (LSF, Manaus; blue) and the high seasonality forest (HSF, Tapajos, red) as a function of monthly CMWD (b) and maximum monthly vapour pressure deficit (VPD); (c) Each pair of points (circle and triangle) represents a different species.

Figure 6. A relationship between change in minimum leaf water potential from non-ENSO year to 2015 ENSO year ($\Delta\Psi$; MPa) and embolism resistance for the low seasonality forest (LSF, Manaus, blue) and the high seasonality forest (HSF, Tapajos, red). Relationship between $\Delta\Psi$ and (a) P_{50}, and (b) P_{88}. The solid lines represent the best linear fit. Whiskers in a) are either maximum/minimum value or, when outliers are present, 1.5 interquartile range above/bellow the quartiles 2 and 3.

Figure 7. A relationship between July to December monthly mean canopy conductance (G_S) and cumulative water deficit (CMWD) in the (a) low seasonality forest (LSF, Manaus); and (b) high seasonality forest (HSF, Tapajos), and between canopy conductance (Gs) and monthly mean vapour pressure deficit (VPD) for (c) LSF and (d) HSF. The colour of the data points is proportional to the VPD value in plots (a) and (b) and to the CMWD values in plots (c) and (d), according to the colour charts bellow the panels. Note that high CMWD data points are redder, indicating they also have high VPD showing the correlation between VPD and CMWD. The p-values* are for the relationship between G_s and VPD_r and $CMWD_r$, which are the same variables after removing the correlation between VPD and CMWD using residuals (see data analysis and results section). Note both sites were modelled together and the p value in panel (a) also applies to panel (b), and p and R^2m values in panel (c) also apply to panel (d). Triangles points are data from 2015 ENSO. Circles points are monthly data from 1999 to 2016, excluding the 2015 ENSO period. Another version of this figure presenting G_s relationship to VPD_r and $CMWD_r$ is presented in Supporting Information Fig. S3.

Figure 8. Canopy conductance (mm s^{-1}) in non-ENSO (circles) and ENSO (triangles) years and for LSF (blue) and HSF (red) versus: (a) the dominance-weighted minimum leaf water potential (Ψ_{min}; MPa) and (b) P_{50} hydraulic safety margin (HSM_{P50}; MPa). The horizontal bars represent the confidence interval (*ci*) for the dominance-weighted mean of Ψ_{min} and HSM. The vertical bars represent the standard deviation (*sd*), across

usual years, of canopy conductance in August and December for LSF and HSF, respectively. We considered as usual (non ENSO) years the period from 1999 to 2016, excluding data from 2015 ENSO. As ENSO year, we considered October and December of 2015 for LSF and HSF, respectively, and then we had no monthly *sd*.

Supporting Information

Figure S1. Times series of climatic and hydrologic variables for the studied sites.

Figure S2. Soil water content time series for the studied sites.

Figure S3. Relationship between monthly mean canopy conductance and residuals of vapour pressure deficit and cumulative water deficit for the studied sites.

Figure S4. The relationship between monthly mean evapotranspiration and vapour pressure deficit and cumulative water deficit fo the studied sites.

Table S1. List of species name, family and mean hydraulic traits value for all studied species at low seasonal forest (LSF) and high seasonal forest (HSF).

Table S2. Summary of hydraulic traits and statistical results of hypothesis 1, that HSF has more drought resistant hydraulic traits than LSF.

Table S3. General mixed model result from the test of hypothesis 2, that species from HSF are less sensitive to ENSO than species from LSF.

Table S4. General mixed model result from the test of our hypothesis 3, that HSF forest is less sensitive to atmospheric drought and soil drought than the LSF forest.

Table S5. General mixed site-specific model results for evapotranspiration (ET) varying in function of atmospheric drought, soil drought.

Methods S1 Species dominance and trait distribution in the communities.

Methods S2. The biogeographic dry affiliation index as a trait to differ LSF and HSF community composition.

Methods S3 Eddy covariance flux measurements.

Methods S4 Canopy conductance calculation

Methods S5 Statistic functions and packages

a)

LSF (Manaus)

– non−ENSO

−−− 2015−2016 ENSO

CMWD (mm)

0

100

200

300

400

500

b)

HSF (Tapajos)

CMWD (mm)

0

100

200

300

400

500

Jul

Aug

Sep

Oct

Nov

Dec

Jan

Feb

Mar

Apr

May

Jun