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1 **Precipitation mediates sap flux sensitivity to evaporative demand in the neotropics**

2

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67 all authors contributed to revisions.

68 **Abstract**

69 Transpiration in humid tropical forests modulates the global water cycle and is a key driver of
70 climate regulation. Yet, our understanding of how tropical trees regulate sap flux in response to
71 climate variability remain elusive. With a progressively warming climate, atmospheric
72 evaporative demand (i.e., vapor pressure deficit, *VPD*) will be increasingly important for plant
73 functioning, becoming the major control of plant water use in the 21st century. Using
74 measurements in 34 tree species at seven sites across a precipitation gradient in the neotropics,
75 we determined how the maximum sap flux velocity (v_{max}) and the *VPD* threshold at which v_{max} is
76 reached (VPD_{max}) vary with precipitation regime (mean annual precipitation, *MAP*; seasonal
77 drought intensity, P_{DRY}) and two functional traits related to foliar and wood economics spectra
78 (leaf mass per area, *LMA*; wood specific gravity, *WSG*). We show that, even though v_{max} is
79 highly variable within sites, it follows a negative trend in response to increasing *MAP* and P_{DRY}
80 across sites. *LMA* and *WSG* exerted little effect on v_{max} and VPD_{max} , suggesting that these
81 widely-used functional traits provide limited explanatory power of dynamic plant responses to
82 environmental variation within hyper-diverse forests. This study demonstrates that long-term
83 precipitation plays an important role in the sap flux response of humid tropical forests to *VPD*.
84 Our findings suggest that under higher evaporative demand, trees growing in wetter
85 environments in humid tropical regions may be subjected to reduced water exchange with the
86 atmosphere relative to trees growing in drier climates.

87

88 **Keywords:** evapotranspiration, plant functional traits, transpiration, vapor pressure deficit.

89 **Introduction**

90 Humid tropical forests cover approximately 12% of global ice-free land surface area
91 (Mayaux et al. 2005) and are characterized by high mean annual precipitation (> 1500 mm) with
92 low variability in atmospheric temperature ($\approx 25 \pm 5^\circ\text{C}$) (Richards 1952; Murphy and Lugo,
93 1986). The majority of water entering tropical forests through precipitation or rivers is returned
94 to the atmosphere via evapotranspiration (Moreira et al. 1997; Kumagai et al. 2016). Water
95 released by trees in their transpiration flux largely contributes to total evapotranspiration in the
96 tropics (Schlesinger and Jasechko 2014), 35% of which is cycled back to the biome as
97 precipitation (Eltahir and Bras 1994; Zemp et al. 2014). As such, tree transpiration in tropical
98 forests is a major modulator of the global water cycle and plays a central role in climate
99 regulation (Foley et al, 2007). Yet, despite our efforts in understanding transpiration patterns of
100 tropical trees (e.g., Meinzer et al. 2003; Stahl et al. 2013a; Maréchaux et al. 2018), how trees
101 regulate water use in these ecosystems remains one of the largest uncertainty components in
102 models of tropical evapotranspiration.

103 At daily to seasonal time-scales, trees regulate their transpiration flux in response to
104 variation in atmospheric evaporative demand (i.e., vapor pressure deficit, *VPD*), radiation, wind
105 and available soil water (Oren et al. 1999; Meinzer et al. 2001). Under non-limiting soil water
106 availability, radiation and *VPD* are usually the most significant climate variables controlling
107 water flux in tropical trees (e.g., Meinzer et al. 2008). However, global warming will result in an
108 exponential climb in *VPD* in the next decades (Zhang et al. 2015), and the relative role of these
109 two abiotic drivers (i.e., radiation *vs.* *VPD*) is expected to shift in the future with *VPD* becoming
110 the major control of plant water use in the 21st century (Novick et al. 2016). Therefore,
111 improving our understanding of water use patterns and their response to *VPD*, including the

112 linkages to predictive plant traits, is an important next step with major implications for global
113 climate and vegetation predictions.

114 While over long periods (i.e. years to decades), stand water use is mainly regulated by
115 changes in leaf area and species composition, over short-term periods (i.e. hours to days), trees
116 regulate sap flux velocity (v) (Edwards et al. 1996) through changes in stomatal conductance.
117 Thus, v response to daily VPD variation directly depends on the degree of stomatal closure
118 (Schulze et al. 1972). Under low VPD conditions, plant stomata are fully open and v increases
119 linearly with VPD (Franks et al. 1997), until v reaches a saturation rate (v_{max} , Fig. 1) at a given
120 VPD threshold (VPD_{max} , Fig. 1). As VPD increases, trees progressively start closing their
121 stomata, and for some species, including tropical trees, stomatal closure can be so pronounced as
122 to result in a decreased rate of v (Fig. 1) (Schulze et al. 1972; Franks et al. 1997). The degree of
123 sap flux response to VPD varies both within and between species because of differences in local
124 climatic adjustments and ecological strategy. For instance, trees originating from distinct
125 precipitation regimes should differ in their sap flux responses to VPD because of adaptive
126 mechanisms in response to moisture conditions, including wood hydraulic properties and foliar
127 traits (Mencuccini 2003; Poyatos et al. 2007). Trees growing in drier climates may produce
128 xylem elements with reduced lumen areas relative to trees from wetter climates to reduce the risk
129 of xylem embolism and promote overall hydraulic safety (Hacke et al. 2004; Fonti and Jansen
130 2012). Anatomical changes in these conductive tissues will directly alter the sap flux patterns of
131 trees (i.e. reduced v in drier systems), and have been associated to reduced VPD_{max} and v_{max} in
132 dry ecosystems (Grossiord et al. 2017; 2018). Similarly, reductions in soil moisture during dry
133 periods have been linked with changes in stomatal density (Luomala et al. 2005) and in the
134 synthesis of chemical signals inducing stomatal closure (Schachtman and Goodger 2008), which

135 should also reduce VPD_{max} and v_{max} in forests that are subjected to seasonal droughts. In humid
136 tropical forests, regional variability in annual precipitation (from 1500 to > 4000 mm annually)
137 and in dry season intensity is high, suggesting large variation in plant physiological and
138 structural adjustments to moisture status, and thus potentially important differences in VPD_{max}
139 and v_{max} between ecosystems. However, soil moisture is usually less limiting in humid tropical
140 forests than in temperate and semiarid regions where reductions in VPD_{max} and v_{max} following
141 precipitation reduction have been reported (Grossiord et al. 2018). As such, this characteristic
142 physiological or hydraulic adjustment to soil moisture limitation may not occur in this biome,
143 suggesting that acclimation processes to water stress would only occur under a given
144 precipitation and/or drought intensity threshold.

145 A difficulty in making predictions on the functioning of humid tropical forests lies in the
146 fact that these ecosystems host more tree species than any other terrestrial ecosystem (Myers et
147 al. 2000). Large species diversity in the tropics is accompanied by large diversity in plant
148 functional traits (Wright et al. 2007; Baraloto et al. 2010; Fortunel et al. 2012; 2014; Zhu et al.
149 2013; Cosme et al. 2017). Functional differences that directly alter v regulation include rooting
150 properties (e.g. water uptake depth, Stahl et al. 2013b; Brum et al. 2019), hydraulic properties
151 (e.g. lumen area or water potential at 50% loss of hydraulic conductivity P_{50} ; Litvak et al. 2012)
152 and foliar characteristics (e.g. stomatal density or leaf turgor loss point; Bartlett et al. 2012,
153 Maréchaux et al. 2018). However, while such mechanistic trait data are growing in availability
154 for tropical forests, they remain poorly quantified relative to more easily measurable traits such
155 as leaf mass per area (LMA) and wood specific gravity (WSG) (Wright et al. 2004; Chave et al.
156 2014). LMA and WSG respectively comprise the well-studied leaf and wood economics spectra,
157 which have been successfully related to various aspects of plant function along a fast (resource-

158 acquisitive, low *LMA* and *WSG*)-to-slow (resource-conservative, high *LMA* and *WSG*) continuum
159 (Reich et al. 1997; but see Baraloto et al. 2010; Fortunel et al. 2012). These traits only indirectly
160 relate to dynamic physiological processes such as F_D (Brodribb 2017), however *LMA* and *WSG*
161 can be used to support mechanistic theory of moisture adjustments in modelling frameworks by
162 correlating with other plant traits related to hydraulic transport (Christoffersen et al. 2016). As
163 such, we might expect trees originating from drier regions in humid tropical forests, and thus
164 with lower VPD_{max} and v_{max} , to have higher *LMA* and *WSG* (i.e. two typical adjustment responses
165 to reduced moisture, Wright et al. 2005) relative to trees with higher VPD_{max} and v_{max} .

166 Here we analyzed how trees regulate sap flux velocity in response to *VPD* variation in 34
167 species originating from seven sites along a precipitation gradient in the neotropics. Our
168 objectives were to test how long-term local precipitation regime (annual precipitation and
169 intensity of the dry season) modulate VPD_{max} and v_{max} , and detect whether variation in VPD_{max}
170 and v_{max} across sites can be related to the variability in two easy-to-measure functional traits:
171 *LMA* and *WSG*. We hypothesized that:

- 172 1) trees growing in relatively dry regions and that are subjected to more frequent and intense
173 droughts would show reduced VPD_{max} and v_{max} compared to trees originating from wetter
174 areas because of long-term physiological and structural adjustments to reduced soil
175 moisture availability (Mencuccini 2003) (Fig. 1),
- 176 2) across all sites, trees with higher *LMA* and *WSG* would show reduced VPD_{max} and v_{max}
177 relative to trees with low *LMA* and *WSG*.

178 **Material and methods**

179 *Study sites*

180 We used data collected from mature humid tropical forests in seven sites spanning from
181 Puerto Rico to northern Brazil (Table 1, Figs. S1 & S2). The focal sites are located in Puerto
182 Rico (SAB hereafter), Costa Rica (SOL), Panama (SLZ, BCI and PNM), French Guiana (FRG)
183 and Brazil (MAN). The target tree species pool (representing among the most abundant tree
184 species within each site) varied between four and nine per site (Table 2), leading to a total of 34
185 tree species included in this study with only one species being present at multiple sites (Table
186 S1). Climatic conditions (rainfall, air temperature, atmospheric humidity and solar radiation)
187 were measured continuously and recorded by local weather stations at all sites during the
188 measurements.

189 All sites, apart from the SOL site, experience a dry season (i.e., monthly precipitation <
190 100 mm) of approx. three months. Long-term precipitation was used to characterize long-term
191 annual moisture status and drought intensity in each site using the site-level average in annual
192 sum of precipitation (*MAP*) and monthly precipitation during the dry season (P_{DRY}) over the
193 1950-2010 period. When long-term site-specific data was not available (all sites except PNM,
194 BCI and SLZ), long-term precipitation was extracted for each site using Twentieth Century
195 Reanalysis Project, a 2.0-degree latitude and 2.0-degree longitude global climate dataset (Compo
196 et al. 2011). The sites were characterized by contrasting precipitation regimes varying between
197 1826 and 4200 mm on average annually over the 1950-2010 period, with the PNM site (Panama)
198 being the driest and the SOL site (Costa Rica) the wettest (PNM < MAN < BCI < SLZ < FRG <
199 SAB < SOL) (Table 1). See Table 1 for more details on site characteristics and site-specific
200 references.

201

202 *Sap flux measurements*

203 In each site between four and nine trees that occupied dominant positions in the canopy (to
204 avoid effects related to crown exposure) were selected for this study, leading to a total of 43 trees
205 (Table 2). At all sites, tree sap flux velocity (v ; cm h^{-1}) was measured every 10 min, 15 min, 30
206 min or hour using either the thermal dissipation method (Granier 1987) or the heat ratio method
207 (Burgess et al. 1998). Depending on the site, sensors were bought from manufacturers (SFM1,
208 ICT International, NSW, Australia; UP-Gmbh, Cottbus, Germany; PS-GP, PlantSensors, Nakara,
209 Australia) or lab-built. Measurements were conducted continuously for periods varying between
210 two and 24 months (Table 1) between January 2014 and January 2017. For the thermal
211 dissipation method, sensors (i.e. one sensor per tree except for the SOL site where two sensors
212 per tree were installed, 10- or 20-mm long) were installed in the sapwood at 1.3 m aboveground
213 or above buttresses with a 10 cm vertical spacing between probes. For the heat-ratio method (i.e.
214 one sensor per tree), each set of sensors consisted of two or three thermocouples and one-line
215 heater probe. The thermocouples were inserted at 1.3 m aboveground at depths varying between
216 2.2 and 3 cm below the cambium. The sensors were covered with reflective insulation to reduce
217 the risk of direct sunlight causing thermal gradients. The data were recorded continuously by
218 dataloggers (CR800, CR10X and CR1000, Campbell Scientific Corp., Logan, UT, USA), apart
219 from the SFM1 sensors that contain a stand-alone datalogger. For more details see the site-
220 specific references in Table 1.

221

222 *Sap flux data processing*

223 Each site's sap flux data files were accompanied by a standardized metadata reporting
224 framework, consisting of three associated metadata files, respectively describing the data files,
225 the columns of each data file, and field observations of tree size, canopy position, and species
226 identity, if available (Christianson et al. 2017). We collated the raw data for all sites via a series
227 of R scripts, which interpreted each dataset in terms of its associated metadata file (code
228 available in the supplement of Christianson et al. 2017).

229 We started data processing using the raw mV values outputted by the sap flux sensors.
230 Sap flux velocity data from the SOL site had already been converted to v (cm h^{-1}) using the
231 Granier equation (1987) (see Aparecido et al. 2016 for more details). The open-source *Baseliner*
232 software (Oishi et al. 2016) was used to calculate v values for each tree following the equation
233 proposed by Granier (1987). No species-specific equations are available for the tropical species
234 included in this study, and thus care must be taken when interpreting v results as the empirically
235 derived coefficients in the Granier equation may introduce errors in v calculations (Bush et al.
236 2010). *Baseliner* enables users to control the quality and process data using a combination of
237 automated steps and manual editing (Oishi et al. 2016). Missing data were gap filled when they
238 were shorter than two hours using linear interpolation (Oishi et al. 2016). Estimation of baseline
239 nighttime flow is done automatically in *Baseliner* based on a joint set of conditions, including
240 nighttime hours (characterized by near-zero radiation), stable temperature differential between
241 probes (estimated using coefficient of variation) and low *VPD* (see Oishi et al. 2016 for more
242 details).

243 After converting all values into v , we conducted a systematic removal of values
244 associated with measurement failures and sensor removals in the field. For the MAN, PNM, SLZ
245 and BCI sites, we removed all days before DOY 175 in 2016 (corresponding to the 2015-2016

246 ENSO event) to avoid potential v responses to anomalously low soil moisture (Fig. S3). In
247 addition, sub-hourly v data was visually assessed for all trees to ensure no drought period was
248 included in the final dataset. The FRG site included semi-deciduous tree species, which
249 experienced leaf drop during the measurement periods. To avoid effects related to changes in
250 leaf area induced by significant leaf drop, these periods were removed from the analyses.
251 Individual-tree v time series are presented for each site in Fig. S4. The two methods used for
252 measuring v (heat ratio method vs. thermal dissipation method) have been shown to vary in their
253 accuracy to measure absolute v rates (Steppe et al. 2010). However, tests conducted at the MAN
254 and SLZ sites (i.e. the two sites where the heat ratio method was used), where both sensor types
255 were collocated on individual trees, indicated no significant differences in v rates between the
256 two methods (Fig. S5). No information on the depth of the active sapwood was available for the
257 target trees, but to our knowledge, no study reported radial changes in v patterns to VPD
258 variation.

259

260 *Estimation of maximum sap flux velocity and VPD at which sap flux velocity reaches maximum*
261 *values*

262 To avoid confounding effects of radiation we applied a radiation filter for each site by
263 removing all v data where sub-hourly radiation was below the 90th percentile of daytime
264 radiation values. For most sites this threshold was equal to 600 W m⁻² apart for the BCI and FRG
265 sites where the threshold was equal to 700 W m⁻² (Fig S6). Using sub-hourly v data, we estimated
266 the maximum sap flux velocity (v_{max} , Fig. 1) for each tree as the 95th percentile of v values after
267 applying the radiation filter (Fig. S7). The VPD value at which v reaches maximum levels
268 (VPD_{max} , Fig. 1) was estimated as the 2.5th percentile of VPD values corresponding to v_{max} (Fig.

269 S7). All the analysis was done using the R language for statistical computing (3.2.1, R
270 Development Core Team 2015).

271

272 *Functional traits*

273 To analyze how variation in VPD_{max} and v_{max} could be related to foliar and wood
274 functional traits, we used leaf mass per area (LMA , g m^{-2}) and wood specific gravity (WSG , g cm^{-3}).
275 Investigation of other traits (e.g., wood anatomy, leaf-to-sapwood area ratio) revealed a
276 paucity of data for the target tree species, thus we focused strictly on LMA and WSG . When
277 possible, we used direct measurements on the sampled trees during the sap flux measurements.
278 Conversely, when the trait measurements were not available for our focal trees, we used
279 previously published data originating from the same species (see sources in Table S1). In total,
280 data on LMA and WSG were gathered for 31 (73%) and 39 (91%) trees (for LMA and WSG ,
281 respectively) (Table S1).

282

283 *Statistical analyses*

284 The impacts of long-term MAP (or P_{DRY}), LMA and WSG on VPD_{max} and v_{max} were
285 determined first by fitting linear models, followed by closer examination using linear mixed
286 effect models (package *lme*) where MAP (or P_{DRY}), LMA , WSG , diameter at breast height (DBH ,
287 i.e. to account for effects related to tree size) and their interactions were used as fixed effects,
288 and trees nested in sites was used as a random effect. The model selection procedure started with
289 all variables and by progressively removing the variables with the lowest explanatory power
290 until the minimal model with the lowest Akaike Information Criterion (AIC) was obtained.

291 Models were compared using ‘anova’ test to select the least complex parsimonious model. In all
292 cases, the linear model (package *lm*) with *MAP* or *P_{DRY}* was selected. The same tests were used
293 to detect the impact of *MAP* (or *P_{DRY}*) on *LMA* and *WSG*, with *MAP* (or *P_{DRY}*), *DBH* and their
294 interaction used as fixed effects.

295 **Results**

296 *Climatic conditions*

297 Precipitation during the measurements was similar to the long-term average precipitation
298 (1950-2010) in all sites (Fig. S3). Mean daily air temperature and *VPD* ranged from 18 to 28°C,
299 and 0.47 to 2.94 kPa, respectively, during the measurement period, depending on the sites and
300 seasons (Fig. S8). The sites experienced a range of *VPD* values during sap flux measurements
301 varying between 0 and approx. 4.3 kPa (Fig. 2).

302

303 *Sap flux response to VPD variation*

304 Strong variability in sap flux velocity (v) was observed within sites, reflecting the
305 important diversity of water use strategies between species (Fig. S4). For most trees, v increased
306 linearly with *VPD* until reaching a saturation rate (v_{max}) at a given *VPD* threshold (VPD_{max} , Fig.
307 2). For a few trees, v decreased with rising *VPD* after reaching a saturation rate, suggesting
308 strong stomatal closure, while other trees showed no distinctive saturation rate with rising *VPD*
309 (Fig. 2). Trees displaying a decline in v at high *VPD* did not have significantly different *LMA* or
310 *WSG* from trees without such a decline (Welch's two-sided t-test: $t = 0.257$, $df = 4.05$, $P = 0.810$;
311 $t = 0.169$, $df = 4.75$, $P = 0.873$, respectively). In general, v_{max} was reached when VPD_{max} varied
312 between 0.6 and 2.0 kPa, depending on the trees (Fig. 2). v_{max} varied between 4.1 and 41.4 cm h⁻¹
313 ¹, depending on the individual tree (Fig. 2).

314 VPD_{max} and v_{max} were highly variable across sites, with a tendency for lower mean values
315 at wetter sites and higher values at drier sites. The driest site, PNM, had the highest values (mean
316 of 1.5 kPa and 24.7 cm h⁻¹ for VPD_{max} and v_{max} , respectively), while the wettest site, SOL, had

317 the lowest v_{max} (mean of 7.7 cm h⁻¹). There were significant negative effects of *MAP* on v_{max} ($r^2 =$
318 0.32, slope = -0.006, $P < 0.001$) but not on VPD_{max} ($r^2 = 0.10$, slope = -0.000, $P = 0.062$) (Fig. 3).
319 A significant negative effect of P_{DRY} was found for v_{max} ($r^2 = 0.21$, slope = -0.21, $P = 0.005$), but
320 not for VPD_{max} ($r^2 = 0.00$, slope = -0.000, $P = 0.842$) (Fig. 3). No relationship was found between
321 VPD_{max} and v_{max} (Fig. S9), indicating no trade-off between the *VPD* threshold at which v levels-
322 off at maximum rates and maximum v .

323

324 *Relationships with functional traits*

325 No effect of *LMA* on v_{max} ($r^2 = 0.00$, $P = 0.835$), and VPD_{max} ($r^2 = 0.00$, $P = 0.704$) was
326 found. Similarly, no relationship between *WSG* and v_{max} ($r^2 = 0.08$, $P = 0.167$), and VPD_{max} ($r^2 =$
327 0.02, $P = 0.542$) were found (Fig. 4). There was no effect of *MAP* or P_{DRY} on *LMA* ($P = 0.722$
328 and $P = 0.600$, respectively), nor on *WSG* ($P = 0.434$ and $P = 0.290$). A significant relationship
329 was observed between *LMA* and *WSG* (Fig. S9), suggesting a slight coupling between leaf and
330 stem economics in these trees (i.e. trees with higher *LMA* tend to grow denser wood).

331 **Discussion**

332 *Precipitation mediates sap flux response to evaporative demand in the neotropics*

333 Our findings highlight that sap flux response to *VPD* under non-depleted soil moisture
334 conditions in humid tropical forests partially depends on average *MAP* and *P_{DRY}* over the last 50
335 years, i.e., indicators of long-term moisture availability and drought stress intensity. More
336 specifically, our data show that as average site-level precipitation increases and seasonal drought
337 intensity decreases, trees attain lower maximum sap flux (v_{max}) when soil moisture is non-
338 limiting (Fig. 3). This relationship was not an artefact of reduced radiation at wetter sites because
339 of the radiation filter applied (Fig. S6). These findings contrast with previous observations from
340 Mediterranean and semiarid woodlands where increasing aridity resulted in reduced v_{max} (e.g.,
341 Poyatos et al. 2007; Grossiord et al. 2018), suggesting contrasting underlying adjustments to
342 moisture between supply-limited and demand-limited environments.

343 The negative response pattern of v_{max} to increasing *MAP* and *P_{DRY}* observed here implies
344 that compared to dry temperate forests, tree sap flux velocity in humid tropical forests does not
345 depend on drought-adjustments to local climate (i.e. adjustments reducing the vulnerability to
346 water shortage) (Grossiord et al. 2018). Instead, sap flux patterns in response to climate
347 variability are probably dependent on adjustments to high-moisture conditions. Indeed, in the
348 sites included here, *VPD* is usually low and precipitation is high compared to temperate and
349 semiarid regions, thus tree water relations are more rarely limited by high evaporative demand or
350 drought stress. One may therefore expect trees in this environment to have evolved functional
351 traits to deal with other limiting factors such as low radiation induced by the high cloud cover
352 (Moore et al. 2018). Furthermore, high atmospheric humidity can lead to sustained leaf wetness
353 with water films on leaves inhibiting gas exchanges, and resulting in reduced sensitivity to

354 atmospheric drivers (Dawson and Goldsmith 2018; Moore et al. 2018). Plants that grow in high
355 atmospheric humidity conditions have also been reported to show low levels of endogenous
356 abscisic acid (ABA) (Nejad and Van Meeteren 2007; Okamoto et al. 2009), and marginal
357 stomata regulation on carbon and water fluxes (Torre and Fjeld 2001; Torre et al. 2003).
358 Therefore, an important research topic for future work, in addition to exploring adjustment
359 mechanisms to reduced precipitation, is to understand how adaptive mechanisms related to high
360 moisture could relate to sap flux regulation in tropical trees.

361 Lower v_{max} under non-limiting soil moisture conditions could potentially result in reduced
362 water exchange with the atmosphere in humid tropical forests as more days with high VPD are
363 likely to occur in the future. Currently, Earth system models (ESM) are being developed to
364 incorporate plant hydraulic traits (Xu et al. 2016, Christoffersen et al. 2016, Kennedy et al.
365 2019), but it is not immediately clear if such traits will produce the patterns observed here for
366 humid tropical ecosystems. Incorporating traits related to adjustments to high-moisture
367 environments could potentially affect the differential responses of global precipitation to
368 vegetation changes (e.g., Kooperman et al. 2018). To gain further insight into the drivers of sap
369 flux variability, we suggest extending this work to more extreme sites, i.e. both wet and dry, and
370 exploring other relevant factors such as long-term indices of evaporative demand (Poyatos et al.
371 2007). Improved quantification of within-site variation, including systematic replication of
372 species sampled along environmental gradients would also be needed. Such an improved design
373 would be valuable for trait-enabled dynamic vegetation models (Fisher et al. 2018), even if
374 systematically sampling the same species in tropical forests may prove complicated considering
375 their high species diversity.

376

377 *Common functional traits provide limited insights into the mechanisms of sap flux regulation in*
378 *the neotropics*

379 We found a large variability in *LMA* and *WSG* within and across sites, reflecting the high
380 functional diversity present in these ecosystems (Fortunel et al. 2012). Nevertheless, the large
381 diversity in these functional traits could not be related to the variability in VPD_{max} and v_{max}
382 observed across sites (Fig. 4). This is not so surprising in light of a recent review (Moles 2018)
383 that highlights a remarkable degree of inconsistency in reported relationships of *LMA* and *WSG*
384 with other plant traits related to plant ecological strategy or the fast-slow economic spectrum
385 (Reich 2014). Moreover, we expect that stem and leaf traits more directly related to acquisition,
386 transport, and retention of water (hydraulic traits) would underpin the patterns observed here;
387 appropriate trait selection is therefore critical for uncovering trait-moisture relationships more
388 generally (Griffin-Nolan et al. 2018). Specifically, reduction in moisture across large
389 environmental gradients has been associated with shifts in mechanistic foliar traits such as
390 stomatal density (e.g. Luomala et al. 2005) or chemical compounds inducing stomatal closure
391 (Schachtman and Goodger 2008). Investigating such anatomical and chemical foliar adjustments
392 that provide stronger mechanistic basis than *LMA* will be needed to unravel the underlying
393 adaptive processes driving VPD_{max} and v_{max} patterns along our precipitation gradient (Fig. 3).
394 Similarly, *WSG* had no detectable impact on VPD_{max} and v_{max} (Fig. 4). Wood density is
395 considered an important modulator of xylem water transport as higher wood density has been
396 associated with reduced hydraulic conductivity and higher resistance to xylem cavitation (Hacke
397 et al. 2004). As such, this property could constrain the maximum flux of water movement in
398 trees (Barbour and Whitehead 2003). However, most *WSG* measurements, including the ones
399 used in this study, are made using main stems. Yet, to be relevant for water transport, this trait

400 should represent all woody tissues, from the roots to the canopy (Fortunel et al. 2012).
401 Furthermore, the interpretation of *WSG* as an indicator of plant hydraulic functions is debated
402 (Larjavaara and Muller-Landau 2010), since a given *WSG* can be achieved under various
403 combinations of wood anatomy which do not necessarily impact water transport, but instead
404 reflect variability in the competing demands of strength and storage (Fortunel et al. 2014;
405 Zieminska et al. 2015; Morris et al. 2016; Dias et al. 2019).

406 Therefore, although *LMA* and *WSG* are useful for indicating, respectively, placement on
407 the leaf economics spectrum (Wright et al. 2004) and successional status in productivity models
408 (Moorcroft et al. 2001), they do so only at global scales and do not consistently relate to other
409 plant traits at local and regional scales (Moles 2018), as our findings also confirm here. They
410 appear to provide limited interpretation of dynamic plant responses to environmental variation
411 within hyper-diverse tropical forests (Brodribb 2017). While incorporation of such local
412 adjustments in ESMs is possible via trait-mediated plant responses to the environment (e.g.,
413 Fisher et al. 2015), the functional traits explored here, *LMA* and *WSG*, show little promise.
414 Focused data collection on more mechanistic traits associated with plant hydraulics and stomatal
415 function like for instance P_{50} , leaf turgor loss point, cuticular conductance, sapwood anatomy,
416 stomatal density or foliar chemical compounds are likely to reveal mechanistic controls on the
417 interspecific differences in sap flow observed here, which can be used to refine existing plant
418 hydraulic models (Christoffersen et al. 2016; Wolf et al. 2016; Xu et al. 2016; Sperry et al.
419 2017).

420

421 *Conclusion*

422 This study demonstrates that local climate plays an important role in the sap flux
423 response of humid tropical forests to evaporative demand. Moreover, we highlight that trees
424 growing in wetter regions in the tropics may be subjected to a reduced sap flux velocity with the
425 high evaporative demand predicted by most climate models. We expect incorporating these
426 regulation strategies in models could improve our prediction accuracy of both vegetation
427 dynamics and water cycles. This study also shows that easy-to-measure functional traits provide
428 little interpretation in dynamic sap flux response to *VPD*, suggesting that more mechanistic traits
429 should be investigated to build predictors in future models. Finally, it is important to note that
430 although our sampling included a large number of species relative to previous studies
431 investigating sap flux-climate responses, our work still covers only a limited range of the
432 incredible diversity present in humid tropical forests. Extending sap flux measurements in more
433 regions in the tropics and developing large databases of plant water use (e.g. SAPFLUXNET,
434 Poyatos et al. 2016) is an important next step if we want to improve our predictive capacity of
435 tropical forest responses to climate change.

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699 e0124892.

700 **Table 1:** Characteristics of the study sites

<i>Site code</i>	PNM	MAN	BCI	FRG	SLZ	SAB	SOL
<i>Country</i>	Panama	Brazil	Panama	French Guiana	Panama	Puerto Rico	Costa Rica
<i>MAT*</i> (°C), <i>MAP*</i> (mm)	26, 1826	27, 2200	26, 2640	26, 3102	25, 3286	24, 3500	24, 4200
<i>P_{DRY}*</i> (mm)	53	95	60	72	70	90	100
<i>Topography</i>	Light slope	Flat	Flat	Light slope	Steep	Light slope	Steep
<i>Soil depth (m)</i>	> 6	> 20	NA	> 15	> 3	> 20	1.5
<i>Elevation (m)</i>	30	100	170	40	130	130	540
<i>Mean LAI*</i> (m ² m ⁻²)	NA	6.0	6	6.7	NA	6.47	3.32
<i>Soil type</i>	Mollisol	Latosol	Oxisol	Acrisols	Oxisol	Ultisol	Andisol
<i>MET station (m)*</i>	25	50	48	56	52	2	42
<i>Sap flux method</i>	TD	HR	TD	TD	HR	TD*	TD
<i>Duration of the measurements (months)</i>	12	2-5	16	24	13	12	21
<i>References</i>	Slot & Winter, 2017	Luizão <i>et al.</i> , 2004	Detto <i>et al.</i> , 2018	Bonal <i>et al.</i> , 2008	Slot & Winter, 2017	Kimball <i>et al.</i> , 2018	Aparecido <i>et al.</i> , 2016

701 *MAP, mean annual sum of precipitation (1950-2010); MAT, mean annual temperature (1950-2010); *P_{DRY}*, mean monthly sum of precipitation
702 during the dry season; LAI, leaf area index; HR, heat-ratio method; TD, thermal dissipation method; *MET station*, height of the meteorological
703 station (m).

704 **Table 2:** Characteristics of the study trees (\pm SE).

Site	Number of measured trees	Mean tree height (m)	Mean <i>DBH</i> * (cm)	Number of target species
PNM	4	30.7 \pm 2.7	83.9 \pm 18.9	4
MAN	4	32.2 \pm 1.5	59.9 \pm 9.6	4
BCI	6	26.6 \pm 2.0	47.3 \pm 6.7	5
FRG	5	27.8 \pm 2.1	40.3 \pm 10.9	5
SLZ	6	28.1 \pm 1.5	49.9 \pm 4.5	6
SAB	9	23.4 \pm 0.9	28.8 \pm 1.8	8
SOL	8	30.1 \pm 1.1	96.7 \pm 24.5	4

715 **DBH* = diameter at breast height

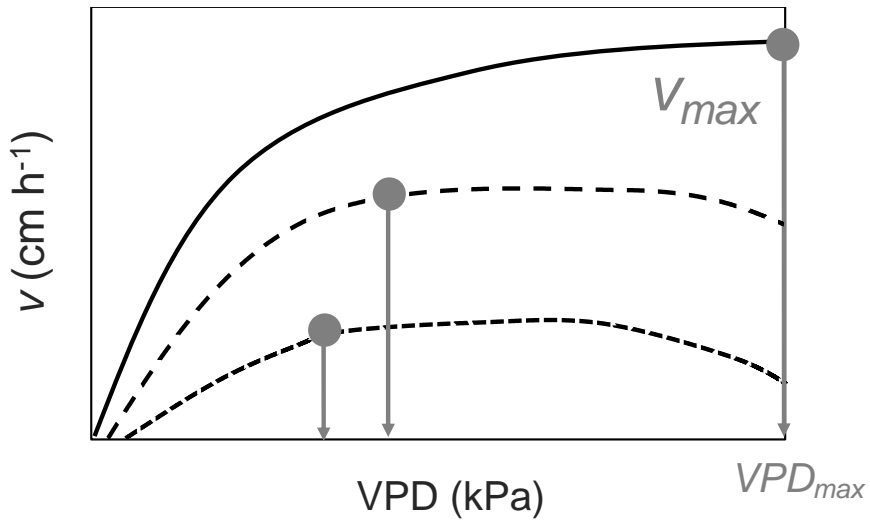
716 **Figure legends**

717 **Figure 1:** Theoretical variation in sap flux velocity (v) response to VPD : under low VPD
718 conditions, v increases linearly with rising VPD until v reaches a saturation rate (v_{max} , grey circle)
719 at a given VPD threshold (VPD_{max} , grey arrow). As VPD progressively increases v will either
720 level-off at a maximum rate or start dropping progressively. Differences in v responses to
721 increasing VPD between trees (highlighted by different dotted and bold lines) emerge from long-
722 term adjustments to local moisture conditions (i.e. reflecting differences in foliar and wood
723 hydraulic properties), with reductions in moisture expected to result in lower VPD_{max} and v_{max} .

724 **Figure 2:** Sub-hourly sap flux velocity (v , cm h^{-1}) as a function of vapor pressure deficit (VPD ,
725 kPa) for each site. Sites are organized going from the driest (b) to the wettest (h) (i.e. in terms of
726 MAP). Dashed lines represent fitted curves using local regression function for each individual
727 tree.

728 **Figure 3:** Relationships between the VPD threshold at which sap flux levels-off at maximum
729 levels ($VPD_{max} \pm \text{SD}$, kPa) and maximum sap flux ($v_{max} \pm \text{SD}$, cm h^{-1}), and mean annual
730 precipitation (MAP , mm) (panels a and c) or monthly precipitation during the dry season (P_{DRY} ,
731 mm) (panels b and d). Asterisks, situated next to the r^2 values, denote the significance of the
732 relationships (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

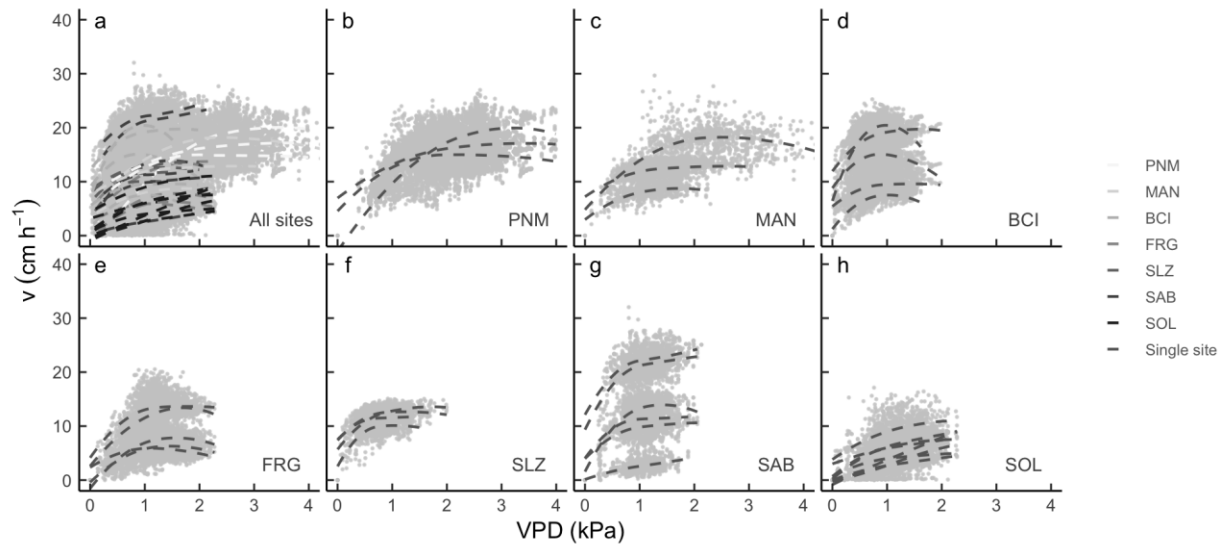
733 **Figure 4:** Relationships between VPD threshold at which sap flux levels-off at maximum levels
734 (VPD_{max} , kPa) and maximum sap flux (v_{max} , cm h^{-1}), and wood specific gravity (WSG , g cm^{-3})
735 (panels a and c) or leaf mass per area (LMA , g m^{-2}) (panels b and c), across all sites. Each point
736 represents a different individual tree.



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Figure 1



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Figure 2

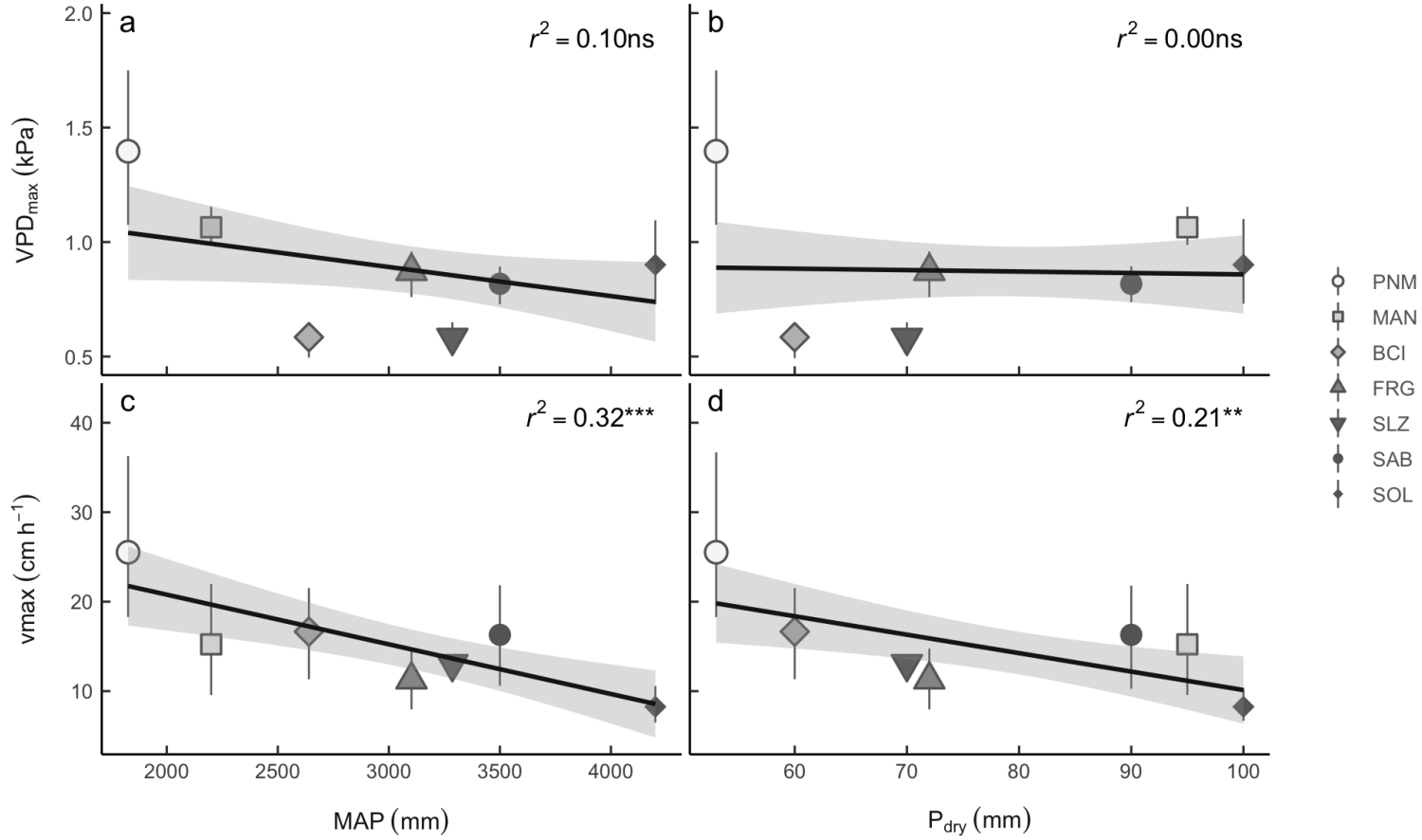


Figure 3

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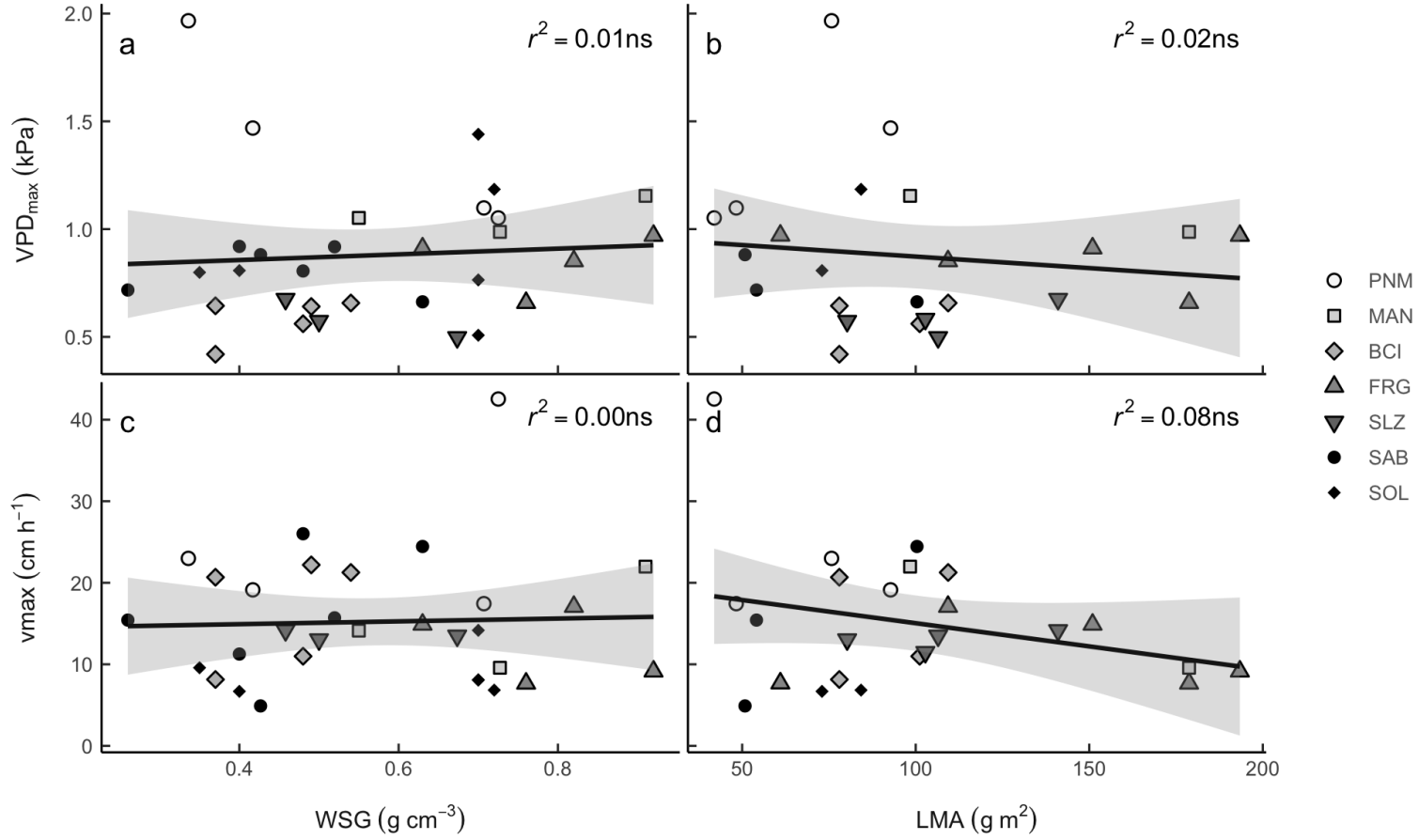


Figure 4

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