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3 **Running head:** model stomatal response to seasonal drought

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41 Abstract

42 Stomata regulate CO₂ uptake for photosynthesis and water loss through transpiration. The
43 approaches used to represent stomatal conductance (g_s) in models vary. In particular, current
44 understanding of drivers of the variation in a key parameter in those models, the slope parameter
45 (i.e. a measure of intrinsic plant water-use-efficiency), is still limited, particularly in the tropics.
46 Here we collected diurnal measurements of leaf gas exchange and leaf water potential (Ψ_{leaf}), and
47 a suite of plant traits from the upper canopy of 15 tropical trees in two contrasting Panamanian
48 forests throughout the dry season of the 2016 El Niño. The plant traits included wood density,
49 leaf-mass-per-area (LMA), leaf carboxylation capacity ($V_{c,max}$), leaf water content, the degree of
50 isohydry, and predawn Ψ_{leaf} . We first investigated how the choice of four commonly used leaf-
51 level g_s models with and without the inclusion of Ψ_{leaf} as an additional predictor variable
52 influence the ability to predict g_s , and then explored the abiotic (i.e. month, site-month
53 interaction) and biotic (i.e. tree-species-specific characteristics) drivers of slope parameter
54 variation. Our results show that the inclusion of Ψ_{leaf} did not improve model performance and
55 that the models that represent the response of g_s to vapor pressure deficit performed better than
56 corresponding models that respond to relative humidity. Within each g_s model, we found large
57 variation in the slope parameter, and this variation was attributable to the biotic driver, rather
58 than abiotic drivers. We further investigated potential relationships between the slope parameter
59 and the six available plant traits mentioned above, and found that only one trait, LMA, had a
60 significant correlation with the slope parameter ($R^2=0.66$, $n=15$), highlighting a potential path
61 towards improved model parameterization. This study advances understanding of g_s dynamics
62 over seasonal drought, and identifies a practical, trait-based approach to improve modeling of
63 carbon and water exchange in tropical forests.

64 **Introduction**

65 Stomata regulate the exchange of carbon and water between plants and the atmosphere
66 (Cowan & Farquhar, 1977; Lawson & Vialet-Chabrand, 2018; Sperry et al., 2017). At large
67 scales, control of stomatal aperture regulates regional and global biogeochemical cycles of
68 carbon, water and energy, and influences the climate through vegetation-mediated climate
69 feedbacks (Bonan, 2008; Pielke et al., 1998; Zeng et al., 2017). Therefore, the representation of
70 stomatal conductance (g_s) is a fundamental component of Terrestrial Biosphere Models (TBMs),
71 and is essential to formulate correctly because it also captures the impacts of ongoing global
72 change on the climate system.

73 Four previously developed and widely used leaf-level models of g_s have been adopted by
74 current TBMs. These include the phenomenological Ball-Berry (BB; Ball, Woodrow, & Berry,
75 1987), Ball-Berry-Katul (BBK; Katul, Manzoni, Palmroth, & Oren, 2010), and Ball-Berry-
76 Leuning (BBL; Leuning, 1995) models, and the optimality-based unified stomatal optimization
77 model (USO; Medlyn et al., 2011). The phenomenological models are based on empirical
78 observations of stomatal behavior in response to environmental stimuli, whereas the optimality
79 model is based on the principle that stomata act to maximize carbon gain while minimizing water
80 loss (Cowan & Farquhar, 1977). Among these models, the BB and BBK formulations use
81 relative humidity (RH) while the BBL and USO formulations represent g_s responses to vapor
82 pressure deficit (D). Although D -type models more closely reflect stomatal mechanics and are
83 directly proportional to water loss (e.g. Aphalo & Jarvis, 1991; Eamus, Taylor, Macinnis-NG,
84 Shanahan, & de Silva, 2008), both RH -type and D -type g_s models are still widely used in TBMs
85 (e.g. Franks et al., 2018; Knauer et al., 2017; Rogers et al., 2017). Moreover, the performance of
86 RH -type and D -type models has rarely been evaluated in natural forests across diverse species

87 with *in-situ* gas exchange measurements, particularly in tropical forest biomes where changes in
88 RH and D are typically tightly coupled. Despite these fundamental differences,
89 phenomenological and optimality-based g_s models are structurally similar (Medlyn et al., 2011)
90 and they generate comparable g_s predictions under many biotic and abiotic conditions (Sperry et
91 al., 2017). Common to all these models is a representation of g_s that varies approximately
92 linearly with net CO_2 assimilation rate (A) for a given set of environmental conditions
93 (temperature, humidity and leaf-surface CO_2 concentration). Therefore, the slope parameter of
94 this coupled g_s - A relationship, which is an indicator of intrinsic plant water use efficiency
95 (referring to the amount of water release through stomata for given A and environmental
96 conditions as shown in Fig. 1), is fundamental to all these models.

97 Although it has been shown that the value of the slope parameter can have a large impact
98 on simulated carbon and water fluxes (Bauerle, Daniels, & Barnard, 2014; Franks et al., 2018;
99 Jefferson, Maxwell, & Constantine, 2017), our understanding of the variability in the slope
100 parameter is far from complete. Particularly, it is unclear what drives variation in the slope
101 parameter, which has been shown to change with both biotic (i.e. tree-species identification and
102 associated leaf characteristics) and abiotic factors (i.e. growth environment, and seasonal and
103 inter-annual environmental variability such as drought and warming) (e.g. Heroult, Lin, Bourne,
104 Medlyn, & Ellsworth, 2013; Lin et al., 2015; Medlyn et al., 2011; Pantin, Simonneau, & Muller,
105 2012; Wolz, Wertin, Abordo, Wang, & Leakey, 2017). This lack of a clear understanding of the
106 impact of biotic and abiotic controls on the slope parameter has contributed to the current
107 controversy on the choice of the most appropriate and parsimonious formulation of g_s models to
108 implement in TBMs. For example, recent experimental and seasonal drought-based studies have
109 shown that the abiotic control of the slope parameter can be as important as the biotic control,

110 especially under soil moisture stress (e.g. Drake et al., 2017; Heroult, Lin, Bourne, Medlyn, &
111 Ellsworth, 2013; Zhou, Medlyn, Sabaté, Sperlich, & Prentice, 2014). This can arise either from
112 the shorter timescale (e.g. diurnal) coordinated variation between leaf water potential and D
113 (Anderegg et al., 2017), from the increasing soil moisture stress that can induce the associated
114 change in plant water potential which down-regulates g_s and thus the slope parameters (e.g.
115 Drake et al., 2017; Heroult, Lin, Bourne, Medlyn, & Ellsworth, 2013; Zhou, Medlyn, Sabaté,
116 Sperlich, & Prentice, 2014), or there is coordinated acclimation of the slope parameter with
117 seasonal variation in soil moisture and plant water potential (e.g. Koepke & Kolb, 2012; Xu &
118 Baldocchi, 2003). Regardless of the reasons, the inclusion of a plant or leaf water potential
119 variable with the original g_s formulations has recently been increasingly advocated as a way to
120 improve prediction of g_s (Anderegg et al., 2017; Drake et al., 2017; Zhou, Medlyn, Sabaté,
121 Sperlich, & Prentice, 2014). Despite the recommendation of these previous studies, it remains
122 unclear whether these results are representative of wider natural plant communities, and
123 importantly, systems such as the tropics where tall canopy evergreen trees have evolved root
124 systems to adapt to seasonal variability in soil moisture content (Giardina et al., 2018; Meinzer et
125 al., 1999).

126 Although large variability in the slope parameter has been previously observed within
127 and across biomes (Dietze et al., 2014; Lin et al., 2015), many TBMs use just two slope
128 parameters to differentiate between vegetation with the C3 and C4 photosynthetic pathways (e.g.
129 Kowalczyk et al., 2006; Oleson et al., 2013; Sitch et al., 2003). Other TBMs incorporate
130 additional slope values for different plant functional types (PFTs), for example needleleaf
131 evergreen trees, broadleaf deciduous trees and C3 crops (Baldocchi & Mayers, 1998; Oleson et
132 al., 2010), or by using different slope parameters for temperate and tropical plants (Medvigy,

133 Wofsy, Munger, Hollinger, & Moorcroft, 2009). While past efforts to define the values of
134 stomatal slope across different PFTs were limited by data, recent syntheses and analyses have
135 provided improved understanding of global-scale variation in the slope parameter, enabling the
136 data-driven parameterization of stomata control in up to ten different global PFTs (Lin et al.,
137 2015; Miner, Bauerle, & Baldocchi, 2017).

138 Tropical forests account for around one-third of annual terrestrial photosynthesis (Beer et
139 al., 2010), and, through stomatal control of transpiration, mediate tropical convection and the
140 timing of dry-to-wet season transitions—a potentially important climate feedback (Wright et al.,
141 2017). However, for such a globally important and hyperdiverse biome, typically only one value
142 for the slope parameter is assigned in current TBMs (Lin et al., 2015; Miner, Bauerle, &
143 Baldocchi, 2017; Rogers et al., 2017). One approach to improve the representation of stomatal
144 response in TBMs is to establish empirical relationships between the slope parameter and other
145 plant traits (e.g. Lin et al., 2015). Not only do such relationships provide an empirical way to link
146 plant traits to the variability in the slope parameter within vegetation communities (Xu, Medvigy,
147 Powers, Becknell, & Guan, 2016), but they might also elucidate the biological mechanisms
148 underlying such variability (Lin et al., 2015). However, whether the previously observed global-
149 scale relationships between the slope parameter and key plant traits as shown in Lin et al. (2015)
150 also holds within forest communities, i.e. across tropical tree-species and forest sites, remains
151 uncertain.

152 The goal of this study was to identify the best potential model representation, and explore
153 the underlying ecological understanding, of the response of g_s to seasonal drought in tropical
154 forests. Specifically, we examined the impact of stomatal model choice (i.e. BB, BBK, BBL or
155 USO), inclusion of leaf water potential (Ψ_{leaf}), as well as abiotic and biotic drivers of variation in

156 the slope parameter on the ability to predict g_s dynamics in the tropics. We collected a unique
157 field dataset consisting of fifteen evergreen tree-species in two forests over the course of the
158 2016 dry season, which due to a strong 2015-2016 El Niño event (Liu et al., 2017) was drier than
159 the historical mean. Since both growth environment and leaf phenology might affect stomatal
160 response to diurnal and seasonal environmental variability, here we aim to first standardize these
161 effects by focusing solely on canopy-top, sunlit leaves at their fully mature status. By controlling
162 the leaf age variation in this way together with environmental variability captured by the g_s
163 models, the primary abiotic drivers of the slope parameter that we considered included forest
164 sites and the month of measurement (which represented seasonal variability in soil moisture
165 content and atmospheric humidity). The biotic factors included tree-species specific response and
166 their associated plant traits, which are either mechanistically or phenomenologically linked to
167 photosynthesis or transpiration (e.g. Xu, Medvigy, Powers, Becknell, & Guan, 2016; Wright et
168 al., 2004). The six plant traits we considered include wood density, leaf-mass-per-area (LMA),
169 leaf carboxylation capacity ($V_{c,max25}$), leaf water content, the degree of isohydry (Martinez-
170 Vilalta, Povatos, Aguadé, Retana, & Mencuccini, 2014), and predawn Ψ_{leaf} . We asked four
171 questions: (i) Does the inclusion of Ψ_{leaf} as an additional predictor variable improve the
172 simulation of g_s of tropical trees? (ii) Which model formulation best captures observed g_s ? (iii)
173 How do abiotic and biotic drivers of variation in the slope parameter influence the ability to
174 predict g_s ? (iv) Are there any key relationships with plant traits, particularly those widely
175 observed or easily measured, that could be used to constrain variation in the slope parameter
176 within models? Through answering these questions, we aim to improve understanding of g_s
177 dynamics in tropical forests, and potentially provide a practical approach to advance TBM

178 representation of g_s , thereby enabling a more accurate representation of carbon and water
179 dynamics in tropical ecosystems.

180

181 **Materials and methods**

182 *Sites and materials*

183 This study was conducted at two lowland tropical moist forest sites separated by 80 km
184 on opposite sides of the Isthmus of Panama. At each site, the Smithsonian Tropical Research
185 Institute maintains a canopy-access crane that enables access to the forest canopy. These sites
186 include a seasonally dry forest in the Parque Natural Metropolitano (PNM; 8°59'41.55" N,
187 79°32'35.22" W) near Panama City and a wet evergreen forest in the San Lorenzo Protected Area
188 (SLZ; 9°16'51.71" N, 79°58'28.27" W), Colon Province. Historic (1998-2015) mean annual air
189 temperature is 26.3 °C and 25.8 °C, and mean annual precipitation is 1826 mm and 3286 mm for
190 PNM and SLZ, respectively, with ~90% of the rainfall in the May-December wet season (Fig. 2).
191 For more details on these sites see Wright et al. (2003).

192 Fifteen evergreen canopy tree-species with no within species replication ($n=7$ for PNM
193 and $n=8$ for SLZ; Table 1) were selected for intensive field measurements of leaf gas exchange
194 and plant traits. These tree species were within the canopy crane access footprint and were
195 selected to capture the diversity of tree species and plant trait space present at each site. In order
196 to minimize the effects of leaf phenology and canopy environments on variation in field-
197 measured stomatal conductance, we restricted measurements to current-season, fully-expanded,
198 upper canopy sunlit foliage. We conducted four campaigns in 2016 at monthly intervals from
199 mid-February until mid-May, covering the middle of dry-season to the beginning of wet-season
200 (Figs. 2 and S2). We spent two days at each location each month and conducted diurnal

201 measurements of leaf gas exchange and leaf water potential (Ψ_{leaf}), measured photosynthetic CO₂
202 response curves and collected additional leaf traits. The May campaign had a reduced scope and
203 only focused on measurements of diurnal leaf gas exchange and Ψ_{leaf} .

204

205 *Measurements of leaf gas exchange and traits*

206 We used six portable gas exchange systems (LI-6400XT, LI-COR Inc., Lincoln, NE,
207 USA) equipped with a 2x3 cm² leaf chamber and red-blue light source. These gas exchange
208 systems were zeroed with a common nitrogen standard prior to each campaign. Diurnal leaf gas
209 exchange measurements were made *in-situ* using cranes to access the canopy throughout the day.
210 Each tree-species was measured five to seven times per day, and at each time point two leaves
211 were measured and then harvested for subsequent trait measurements. Measurements of diurnal
212 gas exchange, including A , g_s , leaf surface CO₂ concentration (C_a), intercellular CO₂
213 concentration (C_i), relative humidity (RH), leaf-to-air vapor pressure deficit (D) and leaf
214 temperature, followed the method of Bernacchi et al. (2006), and were used to evaluate leaf level
215 g_s models (see below). Prior to the gas exchange measurements, the temperature of each
216 measured leaf was recorded, and chamber conditions were matched to the ambient environment.
217 For each measurement round (time point), the sample chamber temperature (T_{block}) was set to the
218 ambient air temperature. For each tree, the sample chamber light was set to the
219 photosynthetically active radiation (PAR) incident on the leaf. This was adjusted throughout
220 each measurement time point to account for changing light conditions due to intermittent cloud
221 cover and leaf aspect. For each tree-species, chamber CO₂ concentration was set to ambient CO₂
222 concentration plus the differential expected due to CO₂ assimilation. The relative humidity of the
223 air entering the leaf chamber was not reduced so as to keep it close to ambient conditions. A high

224 flow rate ($500 \mu\text{mol s}^{-1}$) was used to minimize the time taken for A and g_s to stabilize. After
225 clamping in the chamber, rates were monitored using the instrument's graphical interface and
226 statistical output, and data logged after A and g_s reached stability. To ensure we were capturing
227 gas exchange rates representative of ambient conditions data were logged within a maximum of
228 90 seconds after clamping the leaf in the measurement chamber.

229 Over the course of the season we made c. 46 measurements per tree-species for a total
230 694 individual measurements. Prior to data analysis we filtered our initial dataset of survey
231 measurements by removing spurious data (e.g. negative values) and data where we believed
232 values were not reliable due to a mismatch between sample and reference IRGAs, or where
233 measured values indicated an artifact (e.g. dew on the leaves early in the morning, or poor
234 contact with the leaf thermocouple) or poor replication of ambient conditions. These data were
235 identified by flagging data where the $C_i:C_a$ ratio was <0.2 or >0.9 , or where RH was $<35\%$
236 or $>90\%$. Following examination of these flagged data records 83% of the total dataset remained
237 and was used for subsequent analysis.

238 Measurement of the response of A to C_i , commonly known as $A-C_i$ curves, was conducted
239 on detached branch sections. All branches were sampled before dawn using the canopy crane.
240 We took steps to protect the samples from xylem embolism, and where possible branches were
241 cut underwater by bending the branch into a bucket filled with water. In all cases $>1\text{m}$ of branch
242 was removed within 15 minutes of the initial cut by recutting the branch section underwater in a
243 large container. Samples were stored in individual buckets and kept in deep shade until used for
244 measurements. Measurement of $A-C_i$ curves closely followed the approach recently described by
245 Rogers, Serbin, Ely, Sloan, & Wullschleger (2017). Apparent maximum photosynthetic capacity
246 standardized to a reference temperature of 25°C ($V_{c,\text{max}25}$) was estimated using the kinetic

247 constants and temperature response functions presented by Bernacchi et al. (2013) as described
248 by Rogers, Serbin, Ely, Sloan, & Wullschleger (2017). A total of 120 estimates of $V_{c,max25}$ were
249 used in this study (c. 8 per tree-species), with tree-species-specific mean and standard deviation
250 summarized in Table 1.

251 Following *in-situ* gas exchange measurement, the leaves were immediately harvested for
252 Ψ_{leaf} and trait measurement. Leaves were sealed in humidified plastic bags and stored in the dark
253 on ice for a maximum of two hours before further processing. Ψ_{leaf} was measured using a
254 Scholander-type pressure chamber (PMS, Albany, OR, USA) as described previously
255 (McDowell, Brooks, Fitzgerald, & Bond, 2003). We also tested the robustness of our
256 methodology used to measure Ψ_{leaf} through an experimental test by examining the impact of the
257 time duration of wait time prior to measurement on the Ψ_{leaf} observed, and the results showed
258 that within the 2-hours, leaf storage in the dark on ice had little impact on the estimated Ψ_{leaf} .
259 These experimental results were summarized in Methods S1 and Fig. S3. We then sampled a
260 known leaf area using cork borers and weighed leaf fresh mass with a precision balance (Fisher
261 Science Education, Model SLF303, Hanover Park, IL). Once weighed, the samples were dried to
262 constant mass at 70°C. We then determined dry mass to calculate LMA (g m^{-2}) and leaf water
263 content (LWC; as a percentage of fresh mass, %). We also collected leaf samples (2-3 replicates
264 per tree-species per campaign) before dawn to measure pre-dawn Ψ_{leaf} . Based on the predawn
265 and diurnal measurements of Ψ_{leaf} , we derived a tree-species-specific plant hydrological trait,
266 degree of isohydry, which is defined by the slope of pre-dawn and mid-day Ψ_{leaf} , following the
267 approach as Martinez-Vilalta, Povatos, Aguadé, Retana, & Mencuccini (2014). In addition, we
268 used the existing data on stem wood density for our target tree-species collected from the same

269 forests (Wright et al., 2010). Canopy height and diameter at breast height (DBH) for the target
270 tree-species referred to Dickman et al. (2019).

271 Independent of the diurnal measurement campaigns, for the same tree-species at each site,
272 we also measured stem hydraulic conductivity as a function of stem water potential (i.e.
273 hydraulic vulnerability curves) in terminal branches of canopy trees. Following the approach
274 described by Wolfe, Sperry, & Kursar (2016), we measured hydraulic conductivity on 20–52
275 stem segments per tree-species (mean stem diameter = 5.9 mm) that had been air dried to reach
276 varying stem water potential. For each tree-species, stem hydraulic conductivity was plotted as a
277 function of stem water potential and a Weibull function was fit through the 90th percentile to
278 obtain the vulnerability curve parameters (summarized in Table 1).

279 We recognize that there are alternative approaches to deriving fitted parameters and
280 additional value in many of the traits we have collected. Therefore, all the data associated with
281 this study including raw gas exchange data, fitted photosynthetic parameters and leaf trait are
282 publicly available at the NGEE-Tropics dataset archive (Ely et al., 2018a,b; Rogers et al.,
283 2018a,b; Wolfe et al., 2018), the TRY database (Kattge et al., 2011) and the database
284 (www.BETYd.org) associated with the PEcAn project (LeBauer et al., 2018).

285

286 *Stomatal conductance models*

287 We utilized the four common models to describe the coupled g_s - A relationship to
288 environmental variables, including BB, BBK, BBL and USO (as described in the introduction).

289 The BB model (Ball, Woodrow, & Berry, 1987) is formulated as follows:

$$g_s = g_0 + m \times \frac{A \times RH}{C_a} \quad (1)$$

where RH is the leaf-surface relative humidity, C_a is the leaf-surface CO_2 concentration ($\mu\text{mol mol}^{-1}$), A is the net photosynthesis rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), m is the slope parameter (unitless), and g_0 ($\text{mol m}^{-2} \text{ s}^{-1}$) is the intercept of the regression, representing baseline g_s .

The BBK model (Katul, Manzoni, Palmroth, & Oren, 2010) as equation 2 is an extended version of the BB model that also accounts for the CO_2 compensation point (Γ^*) of assimilation in the absence of dark respiration.

$$g_s = g_0 + m_1 \times \frac{A \times RH}{(C_a - \Gamma^*)} \quad (2)$$

where m_1 is the slope parameter, and Γ^* is a function of leaf temperature using the same formula as Leuning (1995), shown in Table S1.

The BBL model (Leuning, 1995) is an alternative way to relate g_s to the environment incorporating an empirical dependence on leaf-to-air vapor pressure deficit (D , KPa) as follows:

$$g_s = g_0 + a_1 \times \frac{A}{(C_a - \Gamma^*) \times (1 + D/D_0)} \quad (3)$$

where a_1 is the slope parameter and D_0 is a fitted parameter. A practical issue with equation 3 is that the parameters a_1 and D_0 are highly correlated (Medlyn, Robinson, Clement, & McMurtrie, 2005) and thus not statistically valid to interpret values of a_1 across different tree-species when D_0 is fitted simultaneously. To avoid this issue, we employed a two-stage fitting procedure where we initially fitted BBL for the full dataset to derive D_0 ($=0.61$), and then assigned the same D_0 throughout all tree-species when estimating tree-species-specific a_1 .

309 The USO model as follows is an optimality model developed by Medlyn et al. (2011)),
 310 with the slope parameter of g_l .

$$311 \quad g_s = g_0 + 1.6 \times \left(1 + \frac{g_l}{\sqrt{D}}\right) \times \frac{A}{C_a} \quad (4)$$

312 Of particular note, in the original derivation of the g_s models shown above, the intercept
 313 term g_0 ensures correct g_s response when A approaches zero. The term g_0 is often thought to
 314 represent the cuticular g_s , or the conductance with closed stomata. Similar to Lin et al. (2015),
 315 we did not fit g_0 . First, fitted values of g_0 and the slope parameter tend to be correlated, meaning
 316 that the estimated slope parameters can be ill-posed and differences in the slope parameters
 317 among datasets cannot be clearly interpreted. Second, measuring cuticular conductance instead
 318 of fitting the parameter is likely a better means to capture g_0 . Since we did not measure cuticular
 319 conductance, in our data analysis, we assume $g_0=0$ for all tree-species.

320 To evaluate whether inclusion of Ψ_{leaf} as an additional model variable improves
 321 predictions of the four g_s models (Eqns. 1-4), we adapted the equation below from Anderegg et
 322 al. (2017):

$$323 \quad f_{\Psi_{leaf}} = e^{-\left(\frac{-\Psi_{leaf}}{c}\right)^b} \quad (5)$$

324 where b and c are two tree-species-specific parameters, which describe the Weibull form of the
 325 xylem conductivity functions, and hydraulic conductivity = $k_{max} \times f_{\Psi_{leaf}}$, where k_{max} describes the
 326 maximum rate of hydraulic conductance in the absence of water stress, i.e. $\Psi_{leaf}=0$ MPa (Sperry
 327 et al., 2017).

328 Taking BBL as an example, the model that incorporates Ψ_{leaf} is shown below:

$$329 \quad g_s = g_0 + a_1 \times \frac{A}{(C_a - \Gamma^*) \times (1 + D / D_0)} \times f_{\Psi_{leaf}} \quad (6)$$

330

331 *Modeling experiments, model fit and drivers of the slope parameter variation*

332 We first evaluated model choice and whether inclusion of Ψ_{leaf} would improve
 333 predictions of the four g_s models through the following three tests: (i) we calculated the model
 334 residuals (that we defined as the modeled g_s minus observed g_s) for the modeling scenarios
 335 without Ψ_{leaf} and quantified the extent to which these model residuals can be explained by
 336 measured Ψ_{leaf} ; (ii) we performed model optimization for each of the four g_s models with
 337 (including three parameters: the slope parameter, b and c) and without (that has just one
 338 parameter: the slope parameter) Ψ_{leaf} , and evaluated the model selection with the coefficient of
 339 determination (R^2), the root-mean-squared error (RMSE) of the model and the Akaike
 340 information criterion (AIC). AIC allows for the determination of relative statistical model
 341 robustness and parsimony by estimating the degree to which the inclusion of additional
 342 parameters between models improves model fit versus the loss of statistical power; and (iii)
 343 performed a second model optimization at the tree-species level, but instead of using the
 344 optimized Weibull parameters (b and c ; Eqn. 5) for describing the xylem conductivity function
 345 as in the second test, we used the tree-species-specific Weibull parameters derived from
 346 laboratory-measured stem hydraulic vulnerability curves (Table 1). The model selection was then
 347 evaluated through corresponding R^2 , RMSE, and AIC.

348 In addition to the tests including Ψ_{leaf} , we also evaluated the models in their original
 349 forms (Eqns. 1-4). For each g_s model we examined how the abiotic (i.e. site: PNM and SLZ;

350 month-of-measurement: February, March, April and May) and biotic (i.e. tree-species, $n=15$)
351 factors separately and jointly influence the estimation of the slope parameter used to predict g_s .
352 We started with the scenario that only accounts for the fixed effect, i.e. assuming a common
353 slope parameter for the full dataset. We then performed the analysis iteratively by adding one
354 level of the random effects (i.e. allowing for variation in the slope parameter associated with
355 different abiotic and/or biotic factors) in each analytical scenario, following the order of random
356 effects induced by month, site-month interaction, tree-species and tree-species-month interaction,
357 respectively, until the full random effects were represented in the final analysis. Three metrics
358 (R^2 , RMSE and AIC) were also calculated to compare different analytical scenarios.

359 Additionally, we bootstrapped the full dataset 1000 times for cross-model performance
360 comparisons. For each bootstrap, we randomly selected 70% of the data to fit parameters and
361 used the remaining 30% for validation. For the validation results (quantified using both the R^2
362 and RMSE statistics calculated for each iteration), statistical differences between model pairs
363 were identified with t -tests.

364 Last, we derived tree-species-specific slope parameters for each of the four g_s models in
365 their original forms using the ordinary least squared nonlinear model fit. We assessed these slope
366 parameter correlations with all six available plant traits, which have previously been linked with
367 either plant photosynthesis or transpiration. These six plant traits included wood density, LMA,
368 $V_{c,max25}$, LWC, degree of isohydry and pre-dawn Ψ_{leaf} .

369

370 **Results**

371 *g_s model performance with and without Ψ_{leaf} as an additional model variable*

372 Regardless of the g_s model chosen, our results showed that adding Ψ_{leaf} as an additional
373 model predictor variable did not appreciably improve model predictions of g_s across all three of
374 our tests of inclusion, i.e. (i) examining the relationships between the model residuals of g_s
375 resulting from predictions of g_s by the original model formulations (Eqns. 1-4) and from model
376 formulations that included representation of field measured Ψ_{leaf} (Fig. S4), (ii) adding in a single
377 pair of statistically optimized additional parameters (i.e. Weibull parameters b and c ; Eqn. 5) to
378 describe xylem conductivity response to Ψ_{leaf} (Fig. 3), and (iii) adding in tree-species-specific
379 Weibull parameters derived from laboratory-measured stem hydraulic vulnerability curves
380 (Table 1) to describe xylem conductivity response to Ψ_{leaf} (Figs. 4 and S5). As shown in Fig. S4,
381 we found that the model residuals showed no or very weak relationships ($R^2=0.00-0.04$) with
382 Ψ_{leaf} across all the four g_s models analyzed here. This thus provides direct evidence that
383 accounting for the variability in Ψ_{leaf} did not appreciably improve model predictions of g_s for
384 these tropical trees.

385 When using the optimized tree-species-specific Weibull parameters (Fig. 3), we found
386 the optimization results for the model formulations that include Ψ_{leaf} have very similar predictive
387 power (in terms of R^2 and RMSE) compared with the corresponding cases without Ψ_{leaf} , while
388 AIC values indicated that the inclusion of Ψ_{leaf} did not significantly improve model fit and
389 instead reduced model parsimony. This is especially apparent for the scenario of “tree-species-
390 month interaction” (Fig. 3c). For each of the four g_s models the AIC value when including Ψ_{leaf} is
391 far higher than the corresponding case without Ψ_{leaf} , and is also even higher than the scenario of
392 “all” (Fig. 3c; which assumes a common slope parameter for the full dataset), indicating that the
393 models with Ψ_{leaf} were over parameterized.

394 When using the derived tree-species-specific Weibull parameters (as in Table 1) rather
395 than optimized parameters, we found that the performance of g_s models coupled with Ψ_{leaf} was
396 markedly lower than the corresponding cases without Ψ_{leaf} (Figs. 4 and S5, and Table S2).
397 Particularly, at the tree-species level, regardless of the g_s model chosen, the former cases (with
398 Ψ_{leaf}) only have the predictive power of $R^2=0.17-0.19$ across all 15 tree-species (Fig. 4b,d,f and
399 h), while the later cases (without Ψ_{leaf}) have much better model performance ($R^2=0.64-0.74$; Fig.
400 4a,c,e and g).

401

402 *RH-type vs. VPD-type g_s models*

403 We now focused on the original g_s models, without further consideration of the addition
404 of a leaf water potential formulation (i.e. eqn. 5). When using a common, model specific, slope
405 parameter for the full dataset, the g_s models captured 56% (BB), 55% (BBK), 64% (BBL) and 65%
406 (USO) of the variability in field-measured g_s (Fig. 3). Notably, the two *D*-type models (BBL and
407 USO), which represent the g_s response to vapor pressure deficit, outperformed the other two *RH*-
408 type models (BB and BBK), which represent the g_s response to relative humidity. Our
409 bootstrapping analysis and associated *t*-tests also suggested the *D*-type models had significantly
410 higher model performance compared to the *RH*-type models (Fig. S6 and Table S3), with the
411 relative rank among these four models as follows: USO>BBL>>BB>BBK.

412

413 *Abiotic vs. biotic control on the stomatal slope parameter*

414 We examined the relative impacts of biotic (i.e. tree-species) and abiotic (i.e. month, site-
415 month interaction) drivers of variation of the slope parameters used in the four g_s models on the
416 ability to predict g_s . For all four models, we observed that accounting for tree-species-specific

417 and tree-species-month-specific variation in the slope parameter provided the most significant
418 improvement in the prediction of field-observed g_s , with a >10% increase in R^2 and ~20%
419 decrease in RMSE% (Fig. 3), relative to a common, model specific, slope parameter for the full
420 dataset. In contrast, accounting for month-specific variation in the slope parameter did not
421 improve g_s prediction (Fig. 3). In addition, our results showed that accounting for site-month-
422 specific variation in the slope parameter improved g_s prediction only for the two *RH*-type models
423 but not for the two *D*-type models. In addition, our results also showed that the two *RH*-type
424 models had similar model performance, but consistently yielded lower R^2 and higher RMSE than
425 the two *D*-type models (Fig. 3).

426

427 *Large inter-tree-specific variation in slope parameters and their relationships with plant traits*

428 Given the role of tree-species in driving stomatal slope variation (Fig. 3), we further
429 explored the potential for important relationships between stomatal slope and tree-species-
430 specific plant traits. To do this we first examined inter-tree-specific variation in the slope
431 parameters and then assessed their correlations with six field-collected plant traits. We found
432 large inter-tree-specific variation in the slope parameters (Figs. 5, and S7-S9; Table 2), with
433 around 2-3 fold variation depending on the model choice. Such high inter-tree-specific variation
434 in the slope parameter was also found within each of the two tropical forests, with seven-tree-
435 species average slope parameters and standard deviations of 7.38 ± 1.12 (BB), 6.34 ± 0.95 (BBK),
436 12.65 ± 2.18 (BBL), and 2.68 ± 0.59 (USO) for PNM, and eight-tree-species average slope
437 parameters and standard deviations of 6.64 ± 1.55 (BB), 5.78 ± 1.35 (BBK), 10.72 ± 2.40 (BBL),
438 and 2.17 ± 0.70 (USO) for SLZ. Similarly, we also observed relatively high inter-tree-specific
439 variation in our plant traits (see Table 1 and Fig. 5), including wood density ranging from 0.34 g

440 m^{-3} to 0.75 g m^{-3} , LMA ($84\text{-}154 \text{ g m}^{-2}$), $V_{c,\text{max}25}$ ($18\text{-}85 \mu\text{mol m}^{-2} \text{ s}^{-1}$), LWC ($46\text{-}65\%$), degree of
441 isohydry (-0.21 to 1.96 ; unitless) and pre-dawn Ψ_{leaf} (-1.9 to -0.8 MPa). Exploring the
442 relationship between derived tree-species-specific slope parameters and plant traits (Figs. 5 and
443 S7-S9) yielded only one significant correlation, LMA ($R^2=0.66\text{-}0.67$), consistent among all four
444 g_s models. The other five traits we examined, i.e. a wood trait (wood density), a leaf
445 photosynthetic trait ($V_{c,\text{max}25}$), and three hydraulic traits (LWC, degree of isohydry and pre-dawn
446 Ψ_{leaf}), showed no significant relationships with the slope parameters.

447

448 Discussion

449 Understanding abiotic and biotic controls of g_s and exploring accurate representation of
450 g_s in TBMs has been a core focus in ecology of climate regulation and plant physiology ecology.
451 Here, we used data from two contrasting tropical forests that spanned a large range of
452 environmental conditions associated with diurnal and seasonal variation. We demonstrated that
453 in tropical forests, including Ψ_{leaf} in model formulations did not improve predictions of g_s , and
454 the models that represent g_s response to vapor pressure deficit (i.e. *D*-type models, BBL and USO)
455 performed better than the models based on relative humidity (i.e. *RH*-type models, BB and BBK).
456 Additionally, we demonstrated that accounting for the variation in the slope parameters across
457 tree-species significantly improved model estimates of g_s , while accounting for the variation in
458 the slope parameters induced by abiotic factors (i.e. month and site-month interaction) did not
459 appreciably improve model performance. Finally, we explored potential relationships between
460 the slope parameters and six plant traits that correlate with photosynthesis or transpiration, and

461 identified only one leaf trait, LMA, that had a significant correlation with the slope parameter
462 derived from each of the four g_s model formulations.

463

464 *Modeling g_s with or without Ψ_{leaf}*

465 Several recent studies have suggested that Ψ_{leaf} should be incorporated into models of g_s
466 (e.g. Anderegg et al., 2017; Drake et al., 2017; Sperry et al., 2017; Venturas, et al., 2018; Zhou,
467 Medlyn, Sabaté, Sperlich, & Prentice, 2014). However, in our study the data do not support this
468 argument, at least for the tropical evergreen canopy trees analyzed here (Figs. 3, 4 and S5). This
469 result, while in contrast with previous work, is not unexpected. For example, in a recent
470 synthesis study, Anderegg et al. (2017) used a dataset of 24 woody plant species spanning global
471 forest biomes to examine the effect of Ψ_{leaf} on model prediction of g_s . Their results showed that
472 for the majority of tree species analyzed, inclusion of Ψ_{leaf} did not significantly improve
473 prediction of g_s , which is consistent with what we found here. Meanwhile, they did find that for
474 four tree-species g_s prediction was significantly improved with Ψ_{leaf} (i.e. delta-AIC>3 with
475 increase in R^2 by 10% or more). We note that those four tree-species were derived from studies
476 that examined drought impacts on a water-limited glasshouse plant (Arango-Velez, Zwiazek,
477 Thomas, & Tyree, 2011), saplings (Wolfe, Sperry, & Kursar, 2016), and two woody plants
478 (including an evergreen tree in an Australian tropical dry forest, and a juniper tree in northern
479 Arizona pinyon-juniper woodland) without explicitly accounting for the interactive effect of both
480 leaf phenology and seasonal variability in soil moisture content (Choat, Ball, Lully, Donnelly, &
481 Holtum, 2006; Koepke & Kolb, 2012).

482 Since our analysis focused on evergreen tropical canopy trees that experience seasonal
483 variability in soil moisture content (Fig. 2), we hypothesize that there are two major reasons for

484 the discrepancy between previous results and those of this study. First, including Ψ_{leaf} in g_s
485 formulations might be more important for water-limited plants (Arango-Velez, Zwiazek, Thomas,
486 & Tyree, 2011; Venturas et al., 2018; Zhou, Medlyn, Sabaté, Sperlich, & Prentice, 2014), e.g.
487 saplings or glasshouse plants, but might not improve model predictions for mature trees. This is
488 especially relevant for evergreen tropical trees that can maintain green leaves year-round, and
489 have deep and extensive root systems that enable access to moist soil during seasonal droughts
490 (Giardina et al., 2018; Guan et al., 2015; Meinzer et al., 1999; Nepstad et al., 1994). Therefore,
491 conclusions drawn from glasshouse plants or saplings should be used with caution when
492 considering natural forest ecosystems, particularly tropical forests. Second, the slope parameters
493 in the original g_s models (i.e. Eqns. 1-4) likely vary with leaf age (e.g. Albert et al., 2018), which
494 covaries with Ψ_{leaf} (and many other traits) over the season in seasonal forests (e.g. Koepke &
495 Kolb, 2012; Xu & Baldocchi, 2003), but not in evergreen forests where mixed leaf ages are often
496 found year round (e.g. Lopes et al. 2016; Wu et al., 2016). Thus, including Ψ_{leaf} can improve
497 predictions of g_s seasonality over leaves of different ages, but may not be a significant factor
498 when controlling for leaf age as this study. This hypothesis is consistent with several studies (e.g.
499 Albert et al., 2018; Jordan, Brown, & Thomas, 1975; Pantin, Simonneau, & Muller, 2012;
500 Rogers et al., 2012) that show a strong age-dependence of leaf g_s under controlled environmental
501 conditions. However, additional field and manipulation studies are needed to fully elucidate the
502 mechanisms and scales at which leaf properties, such as Ψ_{leaf} , may regulate g_s in addition to other,
503 potentially correlated leaf properties.

504 There was still a weak but significant relationship between Ψ_{leaf} and the g_s residuals in
505 three of the four g_s models in their original forms (Fig. S4). Higher residuals at lower Ψ_{leaf}
506 indicate that the models tended to overestimate g_s at low Ψ_{leaf} and suggest that there is indeed

507 room to improve the models by incorporating Ψ_{leaf} . However, the proposed model improvements
508 with Ψ_{leaf} (i.e. Anderegg et al., 2017) that we tested failed to improve model performance (Figs. 3,
509 4, S5, Table S2). We identified three potential reasons. First, it is likely true that Ψ_{leaf} can help
510 regulate g_s variation, particularly when leaf or soil water potential is below certain thresholds (e.g.
511 under severe droughts or when Ψ_{leaf} is close to leaf turgor loss point; Brodribb & Holbrook, 2003;
512 Rodriguez-Dominguez et al., 2016; Venturas et al., 2018), but not within the range of variability
513 we witnessed. As such, Ψ_{leaf} does not play a large role in regulating the range of observed g_s
514 values in this study (Figs. 3 and S4). Second, the additional parameters (i.e. Weibull parameters
515 of b and c as shown in Eqn. 5) required to fit the model come with their own uncertainties, since
516 they are based on the laboratory-measured hydraulic conductivity responses (e.g. Wolfe, Sperry,
517 & Kursar, 2016). Such uncertainty can propagate into the fitting scheme leading to a lower
518 model performance as observed in Figs. 4 and S5. Lastly, the water potential in the leaves can be
519 more negative than the water potential in the stem xylem, and this should be taken into account
520 when using Ψ_{leaf} to parameterize stem vulnerability curves within g_s models. For example, as in
521 Fig. S5, the stem hydraulic vulnerability curves suggest that most of trees we studied would
522 close their stomata (i.e. $f_{\Psi_{leaf}} = 0$) when Ψ_{leaf} is lower than -2MPa, while field observations
523 showed that the stomata were still open and that leaves were photosynthesizing, even when Ψ_{leaf}
524 <-2MPa. The difference in water potential between leaf and stem is quite difficult to quantify in
525 nature, as it varies largely with tree-species, growth environment and plant traits (Christoffersen
526 et al., 2016; Nolf et al., 2015). For example, in tropical plants, water storage and plant
527 atmospheric water absorption have been shown to be effective in buffering diurnal fluctuation of
528 xylem water potential (Bartlett, Detto, & Pacala, 2018; Binks et al., 2019; Meinzer, James,
529 Goldstein, & Woodruff, 2003). Thus, including Ψ_{leaf} in the g_s models should be done by

530 considering a more comprehensive quantification of the entire soil-plant-atmosphere continuum
531 (e.g. Giardina et al., 2018).

532 Regardless of the above-mentioned limitations, plant hydraulics models (e.g. Sperry et al.,
533 2017; Wolf, Anderegg, & Pacala, 2016) that rely on stem xylem conductivity response functions
534 (as Eqn. 5) can still provide a useful framework for theoretical simulation or deduction of plant
535 optimal response to soil and atmospheric water stress. However, the uncertainty associated with
536 the Weibull parameters (based on direct measurements of hydraulic conductivity), the fact that
537 the optimal theory of stomata control might operate at a longer timescale (e.g. Buckley, Sack, &
538 Farquhar, 2017; Lin et al., 2018), rather than at the instantaneous timescale as explored here, as
539 well as that the exact biological mechanisms that contribute to the hydraulic cost (e.g. damage,
540 repair or loss of opportunity) underlying the optimality theory have not yet been identified or
541 readily measured, further suggests that more research is needed to determine the most
542 appropriate means of incorporating such optimal plant hydraulics theory into process-based g_s
543 models that are integrated into TBMs.

544

545 *Stomatal model choice: D-type vs. RH-type g_s models*

546 Although *D*-type models have been increasingly advocated by plant physiologists (e.g.
547 Medlyn et al., 2011; Rogers et al., 2017), both *D*-type vs. *RH*-type models are still widely used in
548 many TBMs (e.g. Franks et al., 2018; Knauer et al., 2017). Meanwhile, *in-situ* gas exchange
549 measurements from mature tall trees to examine the difference across these two model types are
550 rare. Furthermore, in moist tropical forests, seasonal variation in air temperature is small (e.g.
551 Fig. S2b), and consequently *D* and *RH* are typically more correlated than in other biomes;
552 therefore, we expected only minor differences in performance between *D*- and *RH*-type models

553 in the tropics. To evaluate the correlation between *RH*- and *D*-type models, we made
554 measurements over full diurnal cycles and a dry season in a particularly dry El Niño year (Fig. 2),
555 which captured a wide range of natural variability in *RH* and *D* experienced in these forests. The
556 two *D*-type models significantly outperformed the two *RH*-type models both across and within
557 our dataset ($n=15$ tree-species; Fig. 3 and Table 2), suggesting that *D*-type models should be
558 used for modeling carbon and water fluxes in tropical forest ecosystems, and potentially, also in
559 many other ecosystems, particularly those where *D* and *RH* are not tightly correlated, e.g.
560 savanna. The cross-model comparisons between BB (which accounts for the *RH* effect) and BBK
561 (which accounts for *RH* and includes CO_2 compensation point, Γ^*), shows that including Γ^* did
562 not improve model performance (Fig. 3). Therefore, the improved performance of BBL (which
563 accounts for *D* and Γ^* effects) relative to BB was primarily because BBL captures g_s response to
564 *D*, consistent with the concept that stomata respond directly to *D* rather than to *RH* (Aphalo &
565 Jarvis, 1991; Eamus, Taylor, Macinnis-NG, Shanahan, & de Silva, 2008).

566 Our results also show that the two *D*-type models generated comparable model
567 performance for our dataset, with USO yielding a small but significantly better model
568 performance than BBL (Figs. 3 and S6, and Table S3). This finding is consistent with several
569 recent studies both relying on empirical observations (e.g. Medlyn et al., 2011) and mathematical
570 simulations of optimal stomatal behavior (e.g. Wolf, Anderegg, & Pacala, 2016) for a range of
571 environmental conditions (e.g. C_a within the range of 375-425 ppm). However, as Wolf,
572 Anderegg, & Pacala (2016) point out, due to the fundamental difference in the forms of *D*
573 response in BBL ($\sim D^{-1}$) and USO ($\sim D^{-1/2}$), the predictions of BBL and USO models will differ
574 when C_a exceeds 425 ppm, which is expected to occur in the next 1-2 decades. Therefore, we

575 advocate that USO should be favored for modeling g_s response to D , particularly in TBMs that
576 aim to capture the impact of global change on the climate system.

577

578 *Variation in the slope parameter, sources of variability, and its impact on g_s modeling*

579 We observed large variation in the slope parameter across the sampled 15 tree-species.
580 Such biotic slope parameter variation (e.g. g_I used in USO varied from 1.14 to 3.58) is present at
581 both sites (Fig. 5 and Table 2), and corresponds roughly to the range assigned to six of ten global
582 PFTs in a recent synthesis using the USO approach (Lin et al., 2015). In particular, our observed
583 g_I range encompasses the g_I value of 1.84 for a tropical tree in Caxiuana National Forest Reserve
584 in the eastern Amazon (Lin et al., 2015), overlaps extensively with the g_I (3.00 to 3.79) for three
585 tropical tree-species in Australia (Lin et al., 2015), and is within the range of g_I (0.9 to 6.2) for
586 21 tree-species surveyed in central tropical Africa (Hasper et al., 2017), including canopy and
587 understory trees. Such agreement with previous findings suggests that our results could be
588 broadly applicable to other forests in the tropics. Additionally, we observed that our g_I range is
589 largely lower than an average g_I of 4.23 across a set of tree species sampled in a tropical forest in
590 French Guiana. This might be attributable to the inconsistent approach used for g_I estimate, e.g.
591 only one g_I value was estimated for the whole dataset due to insufficient replication (Lin et al.,
592 2015). In the analysis presented by Lin et al. (2015) they estimated a g_I of 3.77 for a generic
593 tropical rainforest PFT, which is higher than our observed g_I range (1.14 to 3.58). However, this
594 mean g_I included the high estimate from French Guiana. When excluding the French Guiana
595 data-point, the mean g_I estimate based on Lin et al. (2017) is 3.02, which is well within our g_I
596 range. The particularly lower g_I values (i.e. all lower than 3.77 and 13/15 tree-species lower than
597 3.02) observed in our study could also reflect an acclimation to interannual climate variability

598 (e.g. Reyer et al., 2013), e.g. the drier El Niño year experienced in our study, which started at the
599 end of 2014, peaked in late 2015, and ended in May 2016 (Liu et al., 2017). The increasing
600 atmospheric water deficit in the drought year could push plants to evolve a more conservative
601 strategy in order to cope with increasing hydrological stress with El Niño droughts (Cowan &
602 Farquhar, 1977). Clearly there is a need for a deeper understanding of variation in g_l in tropical
603 forests, of particularly value would be replicated measurements that span variation in soil fertility,
604 climate, canopy structure, and leaf phenology and morphology.

605 With the observed large inter-tree-specific variation in slope parameter, we further
606 showed that accounting for such biotic variation led to improved model estimates of g_s (Fig. 3).
607 This finding is consistent with previous work, which illustrated the diversity in stomatal slope is
608 integral to modelling plant water fluxes (Wolz, Wertin, Abordo, Wang, & Leakey, 2017). Our
609 results did not show that accounting for the abiotic (e.g. month, site-month interaction) effects of
610 slope parameter variation improved D -type g_s modeling (Fig. 3). However, we observed that
611 variation in the slope parameter induced by the tree-species-month interaction was the second
612 most important factor for improving g_s modeling of the full dataset. This may reflect differential
613 drought-induced acclimation of the slope parameter across tree-species as reported previously
614 (e.g. Heroult, Lin, Bourne, Medlyn, & Ellsworth, 2013; Zhou, Medlyn, & Prentice, 2015).
615 Furthermore, we controlled for leaf age in our experimental design but it is clear that accounting
616 for potential phenological variation in the slope parameter at the longer timescale will be critical
617 to more accurately represent the seasonal variation in canopy fluxes and the modeling of g_s under
618 natural conditions (Albert et al., 2018) and warrants further exploration.

619 We did not find that month-associated (i.e. month-specific and site-month-specific) slope
620 parameter variation was important for g_s modeling, particularly for D -type models. This suggests

621 that D -type g_s models are able to accurately represent g_s response to seasonal environmental
622 variability. Further extension of our leaf-level findings to interpret ecosystem-scale transpiration
623 seasonality would require the understanding of leaf phenology and forest composition, in
624 particular how the slope parameter varies with different phenophases, including leaf age (as
625 discussed above) and leaf habits (evergreen vs. deciduous trees; Bohlman, 2010), as well as the
626 seasonal and interannual variation in these phenophases (e.g. Lopes et al., 2016; Wu et al., 2018;
627 Detto, Wright, Calderón, & Muller-Landau, 2018).

628

629 *Plant trait relationships with the inter-tree-specific slope parameter*

630 Our results show that LMA was highly correlated with the inter-tree-specific slope
631 parameter for all four g_s models (Figs. 5 and S7-S9). The five other traits we investigated showed
632 weak or no correlation with the slope parameter. Wood density has recently been shown to have
633 a significant relationship with the slope parameter at the global scale (Lin et al., 2015), but was
634 not significantly correlated with the slope parameter in this study. It is possible that over a
635 narrower geographic range with less variability in wood density (the range of wood density is
636 0.34-0.75 in this study vs. 0.35-1.1 in Lin et al., 2015) the relationship may not hold. We
637 hypothesized that $V_{c,max25}$ may have a negative relationship with the slope parameter because as
638 the slope parameter decreases, water use efficiency rises and the effective C_i/C_a in a low slope
639 parameter tree-species (with a lower g_s for a given A) might require a higher $V_{c,max25}$ in order to
640 maintain the same A compared with plant with a larger value of the slope parameter. The lack of
641 a relationship may imply that it will be important to consider the role of mesophyll conductance,
642 especially for model applications (Sun et al., 2014). We also anticipated that measurements of
643 leaf hydrological traits, i.e. leaf water content, degree of isohydry and pre-dawn Ψ_{leaf} , may have

644 correlations with the slope parameter, given the link between these parameters and model
645 formulations that include hydraulic limitations (e.g. Rogers et al., 2017; Tuzet, Perrier, &
646 Luening, 2003; Williams et al., 1996). The lack of a correlation in this study suggests that Ψ_{leaf} ,
647 which changes markedly during the day, may not share a clear mechanistic link to the slope
648 parameter, which likely acclimates to the environment over much longer timescales.

649 The underlying reason for the observed slope parameter-LMA relationship might be that
650 LMA is subject to hydrological constraints (Cavaleri, Oberbauer, Clark, Clark, & Ryan, 2010),
651 and results from a long term evolutionary tradeoff between carbon gain and water loss
652 (Terashima, Miyazawa, & Hanba, 2001). As such, thicker leaves (with higher LMA) are more
653 resistant to water loss, resulting in a higher intrinsic water use efficiency (and a lower slope
654 parameter; Fig. 1). Consequently, a negative slope parameter-LMA relationship was observed in
655 this study. Likewise, higher LMA enables leaf temperature to remain nearer to the
656 photosynthetic optimum under conditions of varying air temperature (Michaletz et al., 2015,
657 2016), again maximizing water use efficiency and promoting a negative slope parameter-LMA
658 relationship. Furthermore, leaves with higher LMA generally have lower mesophyll conductance
659 (Niinemets, Díaz-Espejo, Flexas, Galmés, & Warren, 2009), which could increase
660 photosynthesis without excessive water cost. Consequently, photosynthesis of high LMA tree-
661 species might be less sensitive to stomatal conductance, resulting in a lower slope parameter
662 value. Although these previous studies provide some explanation of the observed slope
663 parameter-LMA relationship, elucidation of the mechanism underlying this relationship is still
664 required. In addition, the LMA-slope parameter relationship presented in this study is based on
665 upper canopy leaf samples of only 15 evergreen canopy tree-species. Therefore, whether the

666 relationship can be extended to broader scenarios, e.g. across vertical canopy profiles, different
667 tropical forests, variation in leaf age and soil moisture content, is pending further examination.

668 The finding that LMA correlates with the slope parameter is encouraging, as LMA is an
669 easy-to-measure leaf trait that is widely used in the plant ecology community and well
670 represented in plant trait databases; e.g., the TRY database has LMA entries for over 10,000
671 species (Díaz et al., 2016). Our observation suggests that it might be possible for next generation
672 TBMs to implement trait-based parameterization of the slope parameter following the approach
673 used for other trait-based modeling components (e.g. photosynthesis, phenology and plant
674 hydraulics) already explored in TBMs (e.g. Fisher et al., 2015; Franks et al., 2018; Xu, Medvigy,
675 Powers, Becknell, & Guan, 2016) and thereby improve representation of carbon and water
676 dynamics in tropical ecosystems. Additionally, recent work on spectroscopic remote sensing
677 suggests that it is feasible to remotely estimate LMA at the leaf and canopy scales (Asner et al.,
678 2011; Serbin, Singh, McNeil, Kingdon, & Townsend, 2014; Singh, Serbin, McNeil, Kingdon, &
679 Townsend, 2015), and as such, if this LMA-stomatal slope relationship holds it may be possible
680 to derive large-scale estimates of the slope parameter across space and time using the suite of
681 current and planned remote sensing systems (Stavros et al., 2017).

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688

689 **Author contributions**

690 J.W., S.P.S., B.T.W., and A.R. designed the research. All authors contributed to data collection.
691 J.W., S.P.S., K.S.E., B.T.W., M.D., S.J.W. and A.R. performed the data analysis. J.W. drafted
692 the paper and all authors contributed to writing of the manuscript.

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1003

1004 **Table 1** Species, canopy status and plant traits (mean \pm standard deviation) for all tree-species
 1005 sampled at the two crane sites (the Parque Natural Metropolitano site, PNM and the San Lorenzo
 1006 site, SLZ) in Panama.

Site	Species	Family	Height (m)	DBH (cm)	LMA (g m ⁻²)	LWC (%)	$V_c, max25$ ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Wood Density (g cm ⁻³)	Predawn Ψ_{leaf} (MPa)	degree of isohydry (slope of Ψ_{leaf} :mid-day Ψ_{leaf})	Stem vulnerability curve parameter b	Stem vulnerability curve parameter c
PNM	<i>Albizia adinocephala</i>	Fabaceae	29.4	29.5	89 \pm 11	48 \pm 5	53 \pm 10	N/A	-1.9 \pm 0.5	1.96	1.3 \pm 0.3	2.8 \pm 1.6
PNM	<i>Pittoniotis trichantha</i>	Rubiaceae	19	21.0	91 \pm 16	53 \pm 5	31 \pm 2	0.60	-1.0 \pm 0.4	1.46	1.9 \pm 0.5	10.3 \pm 21.3
PNM	<i>Calycophyllum candidissimum</i>	Rubiaceae	20.1	39.5	92 \pm 9	56 \pm 4	44 \pm 23	0.75	-1.4 \pm 0.8	1.02	1.7 \pm 15.8	15.8 \pm 824.9
PNM	<i>Castilla elastica</i>	Moraceae	23.5	38.0	102 \pm 5	58 \pm 2	46 \pm 13	0.34	-1.0 \pm 0.4	0.48	1.3 \pm 0.6	2.0 \pm 2.1
PNM	<i>Cordia alliodora</i>	Boraginaceae	22	28.3	92 \pm 11	53 \pm 4	75 \pm 6	0.46	-1.7 \pm 0.3	0.78	3.3 \pm 1.7	6.1 \pm 13.9
PNM	<i>Ficus insipida</i>	Moraceae	31.2	95.4	119 \pm 14	65 \pm 3	78 \pm 10	0.34	-1.4 \pm 0.3	-0.21	1.0 \pm 11.6	1.2 \pm 15.9
PNM	<i>Luehea seemannii</i>	Tiliaceae	26	63.2	147 \pm 11	47 \pm 2	85 \pm 8	0.57	-1.4 \pm 0.6	0.52	3.0 \pm 2.0	10.8 \pm 29.1
SLZ	<i>Carapa guianensis</i>	Meliaceae	33.9	62.0	152 \pm 16	52 \pm 4	25 \pm 4	0.55	-0.8 \pm 0.2	0.19	1.3 \pm 0.5	21.4 \pm 119.9
SLZ	<i>Guatteria dumetorum</i>	Annonaceae	35	59.0	84 \pm 7	55 \pm 5	35 \pm 4	0.45	-1.1 \pm 0.6	0.04	1.3 \pm 0.6	2.1 \pm 1.4
SLZ	<i>Miconia borealis</i>	Melastomataceae	24.8	34.0	99 \pm 9	51 \pm 3	59 \pm 1	N/A	-1.6 \pm 0.7	0.37	1.6 \pm 0.8	1.5 \pm 1.1
SLZ	<i>Tachigali versicolor</i>	Fabaceae	30.4	57.4	95 \pm 10	46 \pm 4	36 \pm 4	0.58	-1.2 \pm 0.5	0.47	0.8 \pm 1.2	1.1 \pm 1.3
SLZ	<i>Terminalia amazonia</i>	Combretaceae	27	52.9	131 \pm 13	52 \pm 4	47 \pm 16	0.67	-0.9 \pm 0.3	1.32	1.2 \pm 0.4	2.0 \pm 1.6
SLZ	<i>Tocoyena pittieri</i>	Rubiaceae	26.6	53.3	93 \pm 10	62 \pm 3	38 \pm 6	0.64	-0.9 \pm 0.4	0.53	3.6 \pm 2.0	4.0 \pm 7.3
SLZ	<i>Virola multiflora</i>	Myristicaceae	22.7	35.1	154 \pm 10	55 \pm 3	18 \pm 1	0.45	-0.9 \pm 0.5	0.19	1.4 \pm 0.4	3.9 \pm 4.4
SLZ	<i>Vochysia ferruginea</i>	Vochysiaceae	29.4	58.0	114 \pm 11	61 \pm 4	51 \pm 14	0.39	-0.8 \pm 0.3	0.38	1.0 \pm 0.3	3.5 \pm 3.4

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1008

1009 **Table 2** Tree-species-specific model optimization results for all four g_s models (i.e. BB, BBK,
 1010 BBL and USO) using the ordinary least squares nonlinear model fit. The model results shown
 1011 below including the two statistic metrics for model performance (R^2 and RMSE) and the best
 1012 fitted stomatal slope (mean \pm standard deviation).

Site	Species Name	# of observations	BB			BBK			BBL			USO		
			slope (m)	R^2	RMSE	slope (m_1)	R^2	RMSE	slope (a_1)	R^2	RMSE	slope (g_1)	R^2	RMSE
PNM	<i>A. adinocephala</i>	36	7.92 \pm 0.09	0.42	0.07	6.82 \pm 0.08	0.39	0.07	12.91 \pm 0.10	0.60	0.06	2.78 \pm 0.03	0.60	0.06
PNM	<i>P. trichantha</i>	35	8.58 \pm 0.10	0.53	0.06	7.38 \pm 0.09	0.52	0.07	14.33 \pm 0.17	0.57	0.06	3.14 \pm 0.04	0.60	0.06
PNM	<i>C. candidissimum</i>	35	7.00 \pm 0.15	0.12	0.06	6.00 \pm 0.14	0.11	0.06	12.58 \pm 0.20	0.37	0.05	2.61 \pm 0.06	0.30	0.05
PNM	<i>C. elastica</i>	23	7.20 \pm 0.16	0.57	0.06	6.19 \pm 0.14	0.56	0.06	12.63 \pm 0.24	0.76	0.05	2.72 \pm 0.07	0.73	0.05
PNM	<i>C. alliodora</i>	35	8.85 \pm 0.21	0.30	0.07	7.55 \pm 0.19	0.28	0.07	16.08 \pm 0.24	0.53	0.05	3.58 \pm 0.07	0.50	0.05
PNM	<i>F. insipida</i>	35	6.13 \pm 0.08	0.60	0.06	5.31 \pm 0.07	0.59	0.06	9.88 \pm 0.12	0.70	0.05	1.95 \pm 0.03	0.68	0.06
PNM	<i>L. seemannii</i>	32	5.98 \pm 0.04	0.74	0.04	5.12 \pm 0.03	0.74	0.04	10.17 \pm 0.07	0.66	0.05	1.96 \pm 0.02	0.77	0.04
SLZ	<i>C. guianensis</i>	41	5.01 \pm 0.06	0.56	0.03	4.38 \pm 0.06	0.55	0.03	8.18 \pm 0.10	0.65	0.03	1.44 \pm 0.03	0.63	0.03
SLZ	<i>G. dumetorum</i>	44	7.90 \pm 0.06	0.34	0.05	6.88 \pm 0.05	0.32	0.06	13.00 \pm 0.09	0.50	0.05	2.80 \pm 0.02	0.48	0.05
SLZ	<i>M. borealis</i>	41	6.79 \pm 0.06	0.47	0.06	5.91 \pm 0.05	0.47	0.06	11.20 \pm 0.10	0.55	0.06	2.28 \pm 0.03	0.53	0.06
SLZ	<i>T. versicolor</i>	45	8.30 \pm 0.08	0.44	0.06	7.25 \pm 0.07	0.43	0.06	13.03 \pm 0.12	0.53	0.05	2.85 \pm 0.03	0.51	0.06
SLZ	<i>T. amazonia</i>	45	4.43 \pm 0.03	0.73	0.02	3.86 \pm 0.03	0.72	0.02	7.31 \pm 0.04	0.77	0.02	1.14 \pm 0.01	0.76	0.02
SLZ	<i>T. pittieri</i>	44	7.19 \pm 0.08	0.56	0.06	6.26 \pm 0.07	0.55	0.06	11.92 \pm 0.14	0.60	0.06	2.48 \pm 0.04	0.62	0.05
SLZ	<i>V. multiflora</i>	43	5.23 \pm 0.07	0.52	0.04	4.55 \pm 0.06	0.51	0.04	8.32 \pm 0.11	0.62	0.03	1.53 \pm 0.03	0.59	0.03
SLZ	<i>V. ferruginea</i>	46	8.26 \pm 0.05	0.56	0.07	7.18 \pm 0.04	0.55	0.07	12.80 \pm 0.08	0.62	0.06	2.83 \pm 0.02	0.62	0.06

1013 The four g_s models are Ball-Berry (BB), Ball-Berry-Katul (BBK), Ball-Berry-Leuning (BBL),
 1014 and Unified Stomatal Optimization (USO), and the two crane sites in Panama include the Parque
 1015 Natural Metropolitano site, PNM and the San Lorenzo site, SLZ.

1016

1017 **Figure captions**

1018 **Figure 1.** The slope parameter of the USO model (Medlyn et al., 2011) is an indicator of
 1019 intrinsic water use efficiency. The regression slope between stomatal conductance (g_s) and the
 1020 USO model index ($1.6 \times \frac{A}{C_a \times \sqrt{D}}$) shown below is almost linearly proportional to the stomatal

1021 slope of the USO model (see Fig. S1). For a given CO_2 assimilation rate (A), atmospheric CO_2
 1022 concentration (C_a), and leaf-to-air vapor pressure deficit (D) a higher regression slope (and thus
 1023 stomatal slope) means that plants maintain a higher g_s to keep the same photosynthetic rate. As
 1024 such, the stomatal slope parameter is an indicator of intrinsic plant water use efficiency, and a
 1025 greater stomatal slope equates to a lower intrinsic water use efficiency. The background
 1026 scatterplots include diurnal gas exchange measurements for two example tree-species
 1027 (*V.ferruginea*, blue and *T.amazonia*, red) at the San Lorenzo site in Panama (see Table 1 for
 1028 more details), and the regression coefficients and model performance were summarized in Table
 1029 2.

1030

1031 **Figure 2.** Four field campaigns were conducted in each of the two Panamanian crane sites in
 1032 2016. These are (a) the Parque Natural Metropolitano crane site (PNM) and (b) the San Lorenzo
 1033 crane site (SLZ). Campaigns included diurnal measurements of gas exchange, leaf water
 1034 potential and leaf traits. The rainfall data for historic (1998-2015; black broken line) and 2016
 1035 (red line) trends were obtained from biogeodb.stri.si.edu/physical_monitoring; the shading
 1036 indicates one standard deviation (std) of the historic mean. The soil moisture index (blue line)
 1037 measures the relative soil water content, where 1 = fully saturated soil. The soil moisture index
 1038 was calculated using a daily integrated value, and was obtained by averaging soil moisture
 1039 values across three different soil depths (at 10, 40, and 100 cm) and time (at 5 minutes interval
 1040 across the day), divided by the maximum value in the record.

1041

1042 **Figure 3.** Model performance comparisons across different g_s models and with/without including
 1043 leaf water potential (ψ_{leaf}). Statistics for the four g_s models (color symbols) that exclude (solid
 1044 lines) or include (dash lines) ψ_{leaf} as an additional model predictor variable, including (a) the
 1045 coefficient of determination (R^2), (b) root-mean-square-error (RMSE) between modeled and
 1046 observed g_s , and (c) Akaike Information Criterion (AIC), for the entire dataset ($n=574$
 1047 observations from 15 tree tree-species). The x-axis represents different scenarios for model
 1048 treatments of the whole dataset, by separating them according to different combinations among
 1049 month, site and tree-species. The results shown here are based on the statistically optimized
 1050 nonlinear model fitting. AIC is a statistic metric that allows inference on the relative quality of
 1051 statistical models, and the models with relatively lower AIC values are generally chosen over
 1052 another. The four g_s models are Ball-Berry (BB), Ball-Berry-Katul (BBK), Ball-Berry-Leuning
 1053 (BBL), and Unified Stomatal Optimization (USO).

1054 **Figure 4.** Model performance comparisons across g_s models with and without tree-species-
 1055 specific Weibull parameters. The tree-species-specific Weibull parameters were derived from
 1056 laboratory-measured stem hydraulic vulnerability response curves (parameters are shown in
 1057 Table 1) and field measurements of leaf water potential (ψ_{leaf}). The left hand panels (a,c,e,g)
 1058 show the results from the four models in their original forms (see Eqns. 1-4), and the right panels
 1059 (b,d,f,h) show those same models with formulations that include ψ_{leaf} and derived Weibull
 1060 parameters. The four g_s models are Ball-Berry (BB), Ball-Berry-Katul (BBK), Ball-Berry-

1061 Leuning (BBL), and Unified Stomatal Optimization (USO). The model results shown here are
1062 based on the entire dataset ($n=574$ observations from 15 tree-species); tree-species-specific
1063 model evaluation is reported in Fig. S5 and Table S2. R^2 for coefficient of determination, RMSE
1064 for root-mean-square-error, and p for significance level of modeled vs. observed g_s correlations.
1065 Black lines indicate the 1:1 relationships.

1066 **Figure 5.** Correlations between the tree-species-specific slope parameter (g_1 ; using the USO
1067 model; Medlyn et al., 2011) and associated plant traits, including (a) wood density, (b) leaf mass
1068 per area, (c) $V_{c,max25}$, (d) leaf water content, (e) degree of isohydry (approximated by the slope
1069 between predawn and mid-day leaf water potential; Martinez-Vilalta, Povatos, Aguadé, Retana,
1070 & Mencuccini, 2014), and (f) predawn leaf water potential (ψ_{leaf}). Points show tree-species
1071 means from the PNM (dry) site ($n=7$ tree-species, circles), and the SLZ site ($n=8$ tree-species,
1072 triangles). R^2 for coefficient of determination, and p for significance level of slope parameter-
1073 trait correlation. Fitted lines (ordinary least square regression, OLS) were only shown for
1074 significant relationships. Similar results were found for the Ball-Berry model (Fig. S7), the Ball-
1075 Berry-Katul model (Fig. S8), and the Ball-Berry-Leuning model (Fig. S9).