

1 **Canopy height and climate dryness parsimoniously**  
2 **explain spatial variation of unstressed stomatal**  
3 **conductance**

4 **Yanlan Liu**<sup>1,2</sup>, **Olivia Flournoy**<sup>3</sup>, **Quan Zhang**<sup>4</sup>, **Kimberly A. Novick**<sup>5</sup>,  
5 **Randal D. Koster**<sup>6</sup>, **Alexandra G. Konings**<sup>7</sup>

6 <sup>1</sup>School of Earth Sciences, The Ohio State University, Columbus, OH, USA

7 <sup>2</sup>School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA

8 <sup>3</sup>Department of Geophysics, Stanford University, Stanford, CA, USA

9 <sup>4</sup>State Key Laboratory of Water Resources and Hydropower Engineering Science, Wuhan University,  
10 Wuhan, China

11 <sup>5</sup>O'Neill School of Public and Environmental Affairs, Indiana University Bloomington, Bloomington, IN,  
12 USA

13 <sup>6</sup>Global Modeling and Assimilation Office, NASA GSFC, Greenbelt, MD, USA

14 <sup>7</sup>Department of Earth System Science, Stanford University, Stanford, CA, USA

15 **Key Points:**

- 16 • Many large-scale models represent the spatial patterns of unstressed stomatal con-  
17 ductance using plant functional types (PFTs)
- 18 • PFT-averages of unstressed stomatal conductance at FLUXNET sites only cap-  
19 ture seventeen percent of spatial variability
- 20 • Spatial variation of unstressed stomatal conductance is better explained using cli-  
21 mate dryness and canopy height

**Abstract**

The spatio-temporal variation of stomatal conductance directly regulates photosynthesis, water partitioning, and biosphere-atmosphere interactions. While many studies have focused on stomatal response to stresses, the spatial variation of unstressed stomatal conductance remains poorly determined, and is usually characterized in land surface models (LSMs) simply based on plant functional type (PFT). Here, we derived unstressed stomatal conductance at the ecosystem-scale using observations from 115 global FLUXNET sites. When aggregated by PFTs, the across-PFT pattern was highly consistent with the parameterizations of LSMs. However, PFTs alone captured only 17% of the variation in unstressed stomatal conductance across sites. Within the same PFT, unstressed stomatal conductance was negatively related to climate dryness and canopy height, which explained 45% of the total spatial variation. Our results highlight the importance of plant-environment interactions in shaping stomatal traits. The trait-environment relationship established here provides an empirical approach for improved parameterizations of stomatal conductance in LSMs.

**Plain Language Summary**

Stomatal conductance regulates the ease with which vegetation extracts water from the soil and releases it to the atmosphere. It thus helps determine the total evapotranspiration and plant uptake of carbon, which in turn significantly influences many aspects of ecosystem function, ranging from regional water resources to biodiversity and climate feedbacks. In particular, stomatal conductance under a stress-free condition (without limitations from water, light, or other factors) acts as the basis of all mathematical models of stomatal dynamics. It is important to understand what causes the unstressed conductance to vary from one place to the next. Large-scale models often assume the unstressed stomatal conductance is the same for all ecosystems belonging to the same plant functional type (for example, deciduous forests, grasslands, or croplands). However, based on observations at 115 sites across the globe, we showed that unstressed stomatal conductance varies significantly between sites within the same plant functional type. Sites located in drier climates and with taller canopies tended to have lower unstressed stomatal conductance. Accounting for climate dryness and canopy height helped better explain the spatial variation. Our results provide a useful approach to improving model descriptions of stomatal conductance.

## 1 Introduction

Stomatal conductance for water vapor and carbon dioxide is a primary control on transpiration and photosynthesis. Many aspects of ecosystem function, including water resources (Fowler et al., 2019; Mankin et al., 2019), carbon sink strength (Powell et al., 2013; Trugman et al., 2018), tree mortality (McDowell et al., 2011; Anderegg et al., 2018), regional climate feedbacks (Kala et al., 2016; Green et al., 2017), and ecoclimate telecommunications (Garcia et al., 2016; Stark et al., 2016), are directly regulated by the spatio-temporal variation of stomatal conductance. Representation of this variation has been recognized as the central link of biosphere-atmosphere interactions in observational and modeling studies (Hetherington & Woodward, 2003; Buckley & Mott, 2013; Bonan et al., 2014; Franks et al., 2018). Under reference conditions of low water stress and non-limiting radiation and temperature, the open apertures of stomata lead to unstressed stomatal conductance ( $g_{s,\text{ref}}$ ). During periods of water, light, or temperature stress, stomata close, thus downregulating stomatal conductance. Over the past decades, much attention has been focused on evaluating the reduction of stomatal conductance in response to meteorological conditions and water stress (Powell et al., 2013; Novick et al., 2016; Sperry et al., 2017; Konings et al., 2017; Trugman et al., 2018; Y. Liu et al., 2020). However, although  $g_{s,\text{ref}}$  is the reference basis for downregulation of stomatal conductance under all meteorological conditions, its spatial variation remains poorly understood. Due to the direct influence of  $g_{s,\text{ref}}$  on biosphere-atmosphere interactions during both stressed and non-stressed conditions, an accurate description of the spatial variation of  $g_{s,\text{ref}}$  is fundamental for predictions of ecosystem dynamics in space and time.

In-situ measurements have found a negative relationship between  $g_{s,\text{ref}}$  and canopy height at the tree scale (Ryan et al., 2000; Schäfer et al., 2000; Novick et al., 2009), supporting the hydraulic limitation hypothesis (Ryan et al., 2006). This theory predicts that, under steady-state flow conditions, the  $g_{s,\text{ref}}$  should be coordinated with xylem conductance, which itself is inversely related to the soil-to-leaf path length, i.e., canopy height. Nonetheless, observations suggesting a positive relationship between  $g_{s,\text{ref}}$  and canopy height also exist (McDowell et al., 2002). This may be because taller canopies have greater sapwood area per leaf area, thus contributing to a higher xylem conductance and thus greater  $g_{s,\text{ref}}$  (Fischer et al., 2002). The overall balance of these two factors remains unclear. Moreover, leaf-scale measurements have found that species in more arid climates tend to have lower stomatal density and area (Carlson et al., 2016; C. Liu et al., 2018).

87 Because  $g_{s,\text{ref}}$  is morphologically determined at the leaf scale by these factors (Franks  
88 et al., 2009; Lammertsma et al., 2011; Dow et al., 2014), these measurements suggest a  
89 negative relationship between  $g_{s,\text{ref}}$  and climate dryness. However, the observational stud-  
90 ies were based on measurements at leaf and tree scales with a limited number of species.  
91 It remains unclear whether these relationships explaining the spatial variation of  $g_{s,\text{ref}}$   
92 are generalizable to the ecosystem-scale. Furthermore, each of the observational stud-  
93 ies tested an independent correlation between  $g_{s,\text{ref}}$  and an individual covariate. The com-  
94 bined effect requires further investigation.

95 Addressing this gap is particularly relevant for land surface models (LSMs), which  
96 typically omit spatial variation of  $g_{s,\text{ref}}$  other than that due to the distribution of plant  
97 functional types (PFTs). Specifically,  $g_{s,\text{ref}}$  in LSMs corresponds to the stomatal con-  
98 ductance under optimal meteorological conditions and no soil moisture limitation, rep-  
99 resented using empirical or optimal approaches, e.g., the Jarvis, Ball-Berry and Medlyn  
100 models (Jarvis, 1976; Ball et al., 1987; Medlyn et al., 2011; Franks et al., 2018). The spa-  
101 tial pattern of  $g_{s,\text{ref}}$  is determined by a single parameter or an equivalent parameter set  
102 (e.g., the slope parameter, the maximum photosynthetic carboxylation rate  $V_{c,\text{max}}$ , etc.)  
103 assigned for each PFT. However, previous studies have found many related plant traits,  
104 such as  $V_{c,\text{max}}$  and multiple hydraulic traits, vary significantly within a PFT (Anderegg,  
105 2015; Walker et al., 2017; Konings & Gentine, 2017; Y. Liu et al., 2021), which can in-  
106 cur large errors in stomatal closure modeling (Wolz et al., 2017). These variations can,  
107 among others, emerge from plant-environment interactions and community dynamics,  
108 through which the environment can be considered as a filter in shaping the community-  
109 average traits (Cornwell et al., 2006; Ackerly & Cornwell, 2007). Such “environmental  
110 filtering” has previously been applied in large-scale models to improve the parameter-  
111 ization of photosynthetic traits and empirical evapotranspiration parameters by map-  
112 ping them to climate and environmental characteristics (Verheijen et al., 2015; Walker  
113 et al., 2017; Wu et al., 2020). In the same way,  $g_{s,\text{ref}}$  may also vary with ecological and  
114 environmental conditions as a result of plant-environment interactions.

115 Our objective is to explore the extent to which information about canopy height  
116 and climate dryness predict spatial variation in ecosystem scale  $g_{s,\text{ref}}$ . We use observa-  
117 tions at 115 FLUXNET sites to derive  $g_{s,\text{ref}}$  and hypothesize that  $g_{s,\text{ref}}$  varies with canopy  
118 height and climatic factors, including mean annual air temperature, mean annual pre-  
119 cipitation, and climate dryness across sites. We examine whether an environmental fil-

120 ter exists that could characterize the spatial variation of  $g_{s,\text{ref}}$  better than the PFT-based  
121 approach widely used in LSMs. Our analysis aims to parsimoniously explain the spatial  
122 variation of  $g_{s,\text{ref}}$  within PFTs using readily available datasets, thus providing a tractable  
123 approach to better parameterize stomatal conductance in LSMs.

## 124 **2 Methods**

### 125 **2.1 Sites and datasets**

126 The 115 global FLUXNET sites covered seven PFTs and a wide range of climates.  
127 Among the sites included in the FLUXNET2015 Tier1 dataset (FLUXNET, 2016), we  
128 analyzed only those with ET and relevant meteorological data available, and for which  
129 there were at least 100 valid observations satisfying the quality control filters described  
130 in Section 2.2. The PFT of each site is determined based on the International Geosphere-  
131 Biosphere Programme (IGBP) classification system. The sites include 31 evergreen needle-  
132 leaf forests, 12 deciduous broadleaf forests, 11 evergreen broadleaf forests, 10 shrublands,  
133 12 savannas, 25 grasslands, and 14 croplands. Leaf area index was extracted from the  
134 closest 500 m pixel from the MODIS (Moderate Resolution Imaging Spectroradiometer)  
135 product (MCD15A3H.006) using Google Earth Engine (Myneni et al., 2015) with a 4-  
136 day temporal resolution. It was then smoothed using the Savitzky–Golay filter to remove  
137 high-frequency noise and linearly interpolated to the same temporal resolution (half-hourly  
138 or hourly, depending on the site) as the flux measurements. Canopy height was obtained  
139 from the Biological, Ancillary, Disturbance and Metadata (BADM) associated with the  
140 FLUXNET2015 dataset.

### 141 **2.2 Derivation of unstressed stomatal conductance**

142 Ecosystem conductance ( $G_s$ ) was calculated by inverting the Penman-Monteith equa-  
143 tion (Penman, 1948; Monteith, 1965) using ET and relevant meteorological conditions  
144 at a half-hourly or hourly scale, including net radiation, air temperature, relative humid-  
145 ity, wind speed, and friction velocity. To control the uncertainty in the estimated con-  
146 ductance, only measurements taken between 10 am and 3 pm that satisfy the following  
147 filters were used: no rainfall in the previous two days, net radiation greater than half of  
148 the annual maximum, vapor pressure deficit greater than 0.6 kPa, and wind speed greater  
149 than 1 m/s. More details on the inversion method are described in Zhang et al. (2019).

150 We note that  $G_s$  estimated by inverting the Penman-Monteith equation is subject to bias,  
 151 which remains challenging to accurately quantify due to biased or unmeasured energy  
 152 budget components (Wehr & Saleska, 2021). While this bias has been shown to cause  
 153 skewed down-regulation sensitivities of stomatal conductance to light and moisture stresses  
 154 (Wehr & Saleska, 2021), we only analyze stomatal conductance under close-to-optimal  
 155 conditions at all sites here. Notably, for sites with available observations of energy bud-  
 156 get components, we tested only using the data when the energy closure error is below  
 157 average and found the main results remained fundamentally unchanged (Fig. S1). Thus,  
 158 this uncertainty will likely contribute to unexplained residuals but not qualitatively change  
 159 the derived relationships.

160 The ecosystem conductance was then partitioned into soil conductance and canopy  
 161 conductance using a data-driven approach that generalizes Leuning’s and Medlyn’s mod-  
 162 els of stomatal conductance (C. Lin et al., 2018; X. Li et al., 2019):

$$G_s = G_0 + G_1 \frac{\text{GPP}}{\text{VPD}^m} \quad (1)$$

163 where GPP is the gross primary production; VPD is the vapor pressure deficit; and  $G_0$ ,  
 164  $G_1$ , and  $m$  are parameters fitted by minimizing the root-mean-square error. As discussed  
 165 in more detail below, we assume that, at the ecosystem scale,  $G_0$  is dominated by soil  
 166 conductance. One set of fitting parameters was estimated for each site using all avail-  
 167 able data from the growing season, which was identified based on LAI being greater than  
 168 its median. Because  $G_0$  can vary with soil moisture, the parameters were fitted using  
 169 data binned by the quartiles of soil moisture measurements at each site for which soil  
 170 moisture measurements were available, and using all valid data otherwise (at 16 sites).  
 171 The accuracy of Eq. 1 was evaluated at each site. We subtracted the fitted constants  
 172  $G_0$  at different soil moisture levels from the hourly/half-hourly ecosystem conductance  
 173  $G_s$  to approximate canopy conductance, which preserves the original variation of  $G_s$  and  
 174 reduces the uncertainty introduced by fitting errors.

175 The canopy conductance was then scaled to stomatal conductance ( $g_s$ ) at leaf-scale  
 176 using LAI as follows.

$$g_s = \frac{(G_s - G_0)}{\min(\text{LAI}, 6)} \quad (2)$$

177 The cut-off point of  $\text{LAI} = 6$  was used to account for the nonlinear scaling between stom-  
 178 ata and canopy conductances due to shading in dense canopy (Granier et al., 2000; Novick  
 179 et al., 2009; Alam et al., 2021). Lastly, the unstressed stomatal conductance ( $g_{s,\text{ref}}$ ) was

180 quantified as the 90th percentile of the  $g_s$  time series satisfying all the filters described  
 181 above at each site. The 90th percentile was used to approximate the maximum stom-  
 182 atal conductance while minimizing the impact of outliers due to observational noise. We  
 183 note that because the optimal temperature, saturated radiation, and minimal water stress  
 184 rarely co-occur,  $g_{s,\text{ref}}$  is expected to be lower than but correlated to the maximum stom-  
 185 atal conductance, as also found in leaf-scale measurements (Dow et al., 2014; McElwain  
 186 et al., 2016). Thus, through this work, the term “unstressed conductance” may not rep-  
 187 resent the truly maximum conductance, but rather the conductance observed under en-  
 188 vironmental conditions that are reasonably close to optimal.

189 We adopted several approaches to evaluate the uncertainties inherent to our ap-  
 190 proach. First, we tested the robustness of our method to errors in the separation of soil  
 191 and canopy conductance, such as in the case where there is an intercept in the stomatal  
 192 conductance-GPP relationship due to cuticular conductance, incompletely closed stom-  
 193 ata, or other reasons (Medlyn et al., 2011; Duursma et al., 2019). In this case,  $G_0$  also  
 194 represents part of the canopy conductance. In the extreme case (i.e., no soil conductance  
 195 contribution to  $G_0$ ), instead of Eq. 2,  $g_s$  could be calculated as  $g_s = G_s / \min(\text{LAI}, 6)$ .  
 196 Combined with  $g_s$  derived from Eq. 2, these two estimates span the possible range of  
 197 zero to large contributions of stomatal conductance to  $G_0$ , allowing us to test the robust-  
 198 ness of our results to  $G_s$  partitioning uncertainty. Second, we tested different thresholds  
 199 for the cut-off point (LAI = 4, 6, and 8) used to scale the canopy conductance to stom-  
 200 atal conductance. Finally, while  $g_{s,\text{ref}}$  represents stomatal conductance under close-to-  
 201 optimal conditions at all sites, the hydroclimatic conditions when  $g_{s,\text{ref}}$  was achieved could  
 202 be farther away from the optima at some sites than others. For example, in most sites,  
 203  $g_s$  close to  $g_{s,\text{ref}}$  was found around VPD of 1 kPa, as expected theoretically (Oren et al.,  
 204 1999); however, in extremely dry sites, it was only found when VPD exceeded 1.5 kPa  
 205 (Fig. S2). To better understand whether this difference is attributable to real variations  
 206 or to the methodological choice to surrogate  $g_{s,\text{ref}}$  to the 90th percentile of  $g_{s,\text{ref}}$ , we cal-  
 207 culated an alternative  $g_{s,\text{ref}}$  as the envelope (90th quantile) of  $g_s$  under VPD = 1 kPa  
 208 using a quantile regression (Fig. S3) (Koenker, 2005).

### 209 **2.3 Baseline model and scaled model estimating $g_{s,\text{ref}}$ variation**

210 Two models for estimating spatial variation of  $g_{s,\text{ref}}$  were compared: a ‘baseline model’  
 211 that is an analogy of the PFT-based approach used in land models and a ‘scaled model’

212 that parsimoniously accounts for relations with canopy height and climate conditions,  
 213 i.e., environmental filters. The baseline model was derived by calculating the average of  
 214  $g_{s,\text{ref}}$  for all FLUXNET sites, and can be written as:

$$y_i^j = c^j + \delta_i \quad (3)$$

215 where  $y_i^j$  is the  $g_{s,\text{ref}}$  at the  $i$ th site belonging to the  $j$ th PFT;  $c^j$  is the  $j$ th PFT-specific  
 216 parameter, equal to the average  $g_{s,\text{ref}}$  of the  $j$ th PFT; and  $\delta_i$  is the model error.

217 To test whether an environmental filter could better estimate  $g_{s,\text{ref}}$  variation, a scaled  
 218 model was used, which describes  $g_{s,\text{ref}}$  as a fixed linear combination of explanatory vari-  
 219 ables that is multiplicatively scaled by a PFT-specific factor.

$$y_i^j = \alpha^j (\beta^T X_i) + \delta_i \quad (4)$$

220 where  $X_i$  is a vector containing z-scores of a set of explanatory variables for the  $i$ th site,  
 221 and  $\beta$  contains the corresponding coefficients. Z-scores rather than the original magni-  
 222 tudes of explanatory variables were used in  $X_i$  so that  $\beta^T$  reflects the relative sensitiv-  
 223 ities. Note that the vector  $\beta^T$  is independent of PFT  $j$ , maintaining the same ratio of  
 224 sensitivity to each of the possible explanatory variables  $X_i$ . By maintaining this consis-  
 225 tency, the number of necessary variables is reduced significantly, preserving the parsim-  
 226 onious nature of the model and preventing over-fitting. The PFT-specific parameter  
 227  $\alpha^j$  accounts for different scalings across PFTs. For  $X_i$ , we explored widely-available vari-  
 228 ables (to ensure a large dataset and tractability of the resulting model as an environmental  
 229 filter) of three categories: long-term average precipitation and air temperature, dryness  
 230 index, and canopy height (Table 1). Mean annual air temperature (MAT) and precip-  
 231 itation (MAP) were calculated using the FLUXNET2015 dataset as averages across the  
 232 entire record of each site. We considered six different metrics to quantify climate dry-  
 233 ness based on actual evapotranspiration (ET), potential evapotranspiration (PET) and  
 234 MAP. PET was calculated using the Penman-Monteith equation, and ET was calculated  
 235 as the average of the observations across the entire record period. The inverse of canopy  
 236 height ( $1/H_c$ ), rather than canopy height itself, was used because the inverse linearly con-  
 237 trols the xylem conductance from the root to the leaf, which affects stomatal conduc-  
 238 tance through hydraulic coordination (Brodribb & Jordan, 2011; Manzoni et al., 2013).  
 239 To identify the most informative variables, we conducted model selection by choosing  
 240 at most one variable within each of the three categories. The performance of models with  
 241 different variable combinations was evaluated using the coefficient of determination ( $R^2$ )

242 and the Akaike information criteria (AIC). We analyzed the top ten scaled models (based  
 243 on AIC) and compared their AIC and  $R^2$  to the baseline model. We further examined  
 244 the relation between  $g_{s,\text{ref}}$  and the selected independent variables as reflected by  $\beta$ . The  
 245 uncertainty of  $\beta$  of the best-performing model was estimated using seven-fold bootstrap-  
 246 ping (Efron, 1992).

**Table 1.** Candidate variables considered in the scaled model

	Candidate variables					
Canopy height	$1/H_c$					
Dryness index	PET/MAP	PET-MAP	PET/ET	PET-ET	ET/MAP	ET-MAP
Mean climate	MAP		MAT			

#### 247 **2.4 Unstressed stomatal conductance within land surface models**

248 We compared the baseline model derived here from FLUXNET sites to the actual  
 249 parameterizations used in land surface models and a global modeling system. The Global  
 250 Land Data Assimilation System (GLDAS) (Rodell et al., 2004), the Community Land  
 251 Model Version 4.5 (CLM4.5) (Oleson et al., 2013) and Version 5 (CLM5) (Lawrence et  
 252 al., 2019) were used as examples. The land model Noah v3.3 in GLDAS prescribes un-  
 253 stressed stomatal conductance per PFT, and these values were directly compared with  
 254  $g_{s,\text{ref}}$  here. CLM4.5 and CLM5 describe stomatal conductance using the Ball-Berry model  
 255 and the Medlyn model respectively; in these two models, the unstressed stomatal con-  
 256 ductance is not directly prescribed but primarily determined by the maximum rate of  
 257 Rubisco carboxylase activity  $V_{cmax}$  and the slope parameter  $g_1$ , which are specified by  
 258 PFT. We calculated the equivalent unstressed stomatal conductance of each PFT using  
 259 the PFT-specific parameters as in Oleson et al. (2013) and Lawrence et al. (2019) un-  
 260 der reference conditions, i.e., net radiation of  $600 \text{ W/m}^2$ , air and leaf temperature of  $25$   
 261  $^\circ\text{C}$ , VPD of  $0.6 \text{ kPa}$ , and without soil moisture limitation. The maximum rate of pho-  
 262 tosynthetic electron transport ( $J_{max}$ ) and the photorespiration rate were approximated  
 263 as 1.97 and 0.015 times  $V_{c,max}$ , respectively (Oleson et al., 2013).

### 3 Results and Discussion

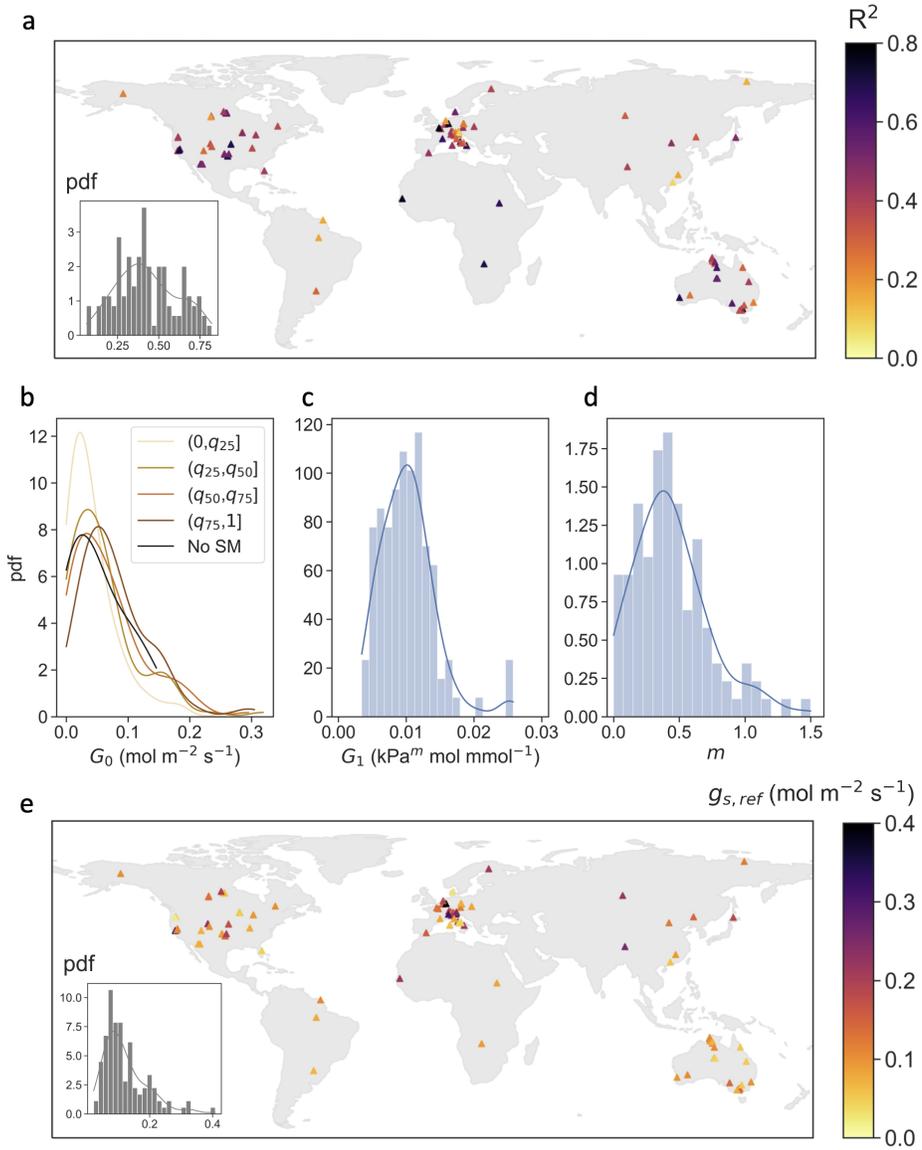
#### 3.1 Unstressed stomatal conductance across sites

Across sites, the ecosystem conductance model (Eq. 1) captures on average 43% and up to 82% of subdaily variation of the derived ecosystem conductance  $G_s$  (Fig. 1a). This is on par with an  $R^2$  of 0.52 at one site reported in C. Lin et al. (2018). The model  $R^2$  does not exhibit clear spatial clusters (Fig. 1a) and does not significantly differ for sites with and without soil moisture measurements ( $p > 0.1$  using a Kolmogorov–Smirnov test). At sites with available soil moisture measurements,  $G_0$  increases with soil moisture as expected. The across-sites medians of  $G_0$  are 0.043, 0.059, 0.066, and 0.080 mol/m<sup>2</sup>/s under soil moisture within the first to the fourth quartiles, respectively (Fig. 1b). The mid-50% of the slope ( $G_1$ ) and the exponent ( $m$ ) parameters range from 0.075 to 0.121 (kPa <sup>$m$</sup>  mol  $\mu$ mol<sup>-1</sup>), and from 0.240 to 0.584, respectively (Fig. 1c, d). The values of all three parameters estimated here are consistent with those in previous studies (C. Lin et al., 2018; X. Li et al., 2019).

The derived  $g_{s,\text{ref}}$  spans a wide range from 0.022 to 0.409 mol/m<sup>2</sup>/s (Fig. 1e) and is not clustered by PFT or climate type. Each of the tropical, temperate and boreal regions and all of the PFTs include both small (below the 25th percentile across all sites) and large (above the 75th percentile) values of  $g_{s,\text{ref}}$ . The large spatial variability of  $g_{s,\text{ref}}$  highlights the need for its appropriate characterization.

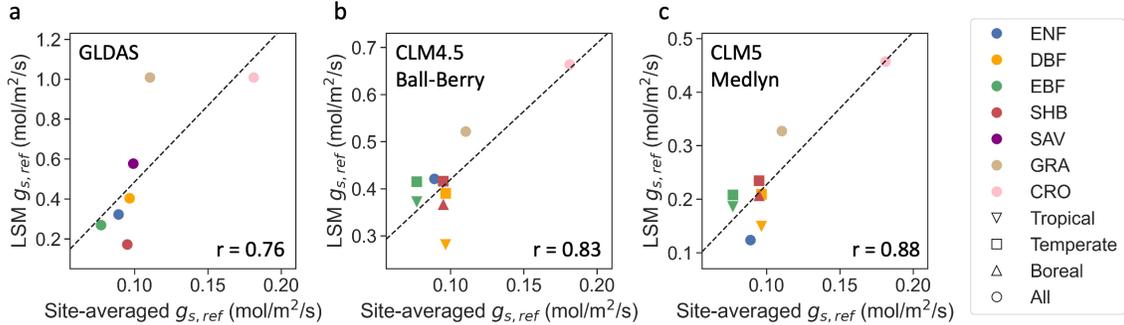
#### 3.2 Cross-PFT pattern and connection to parameterization of LSMs

The PFT-averaged  $g_{s,\text{ref}}$  is highest in croplands (0.186 mol/m<sup>2</sup>/s), followed by grasslands (0.135 mol/m<sup>2</sup>/s), and is lowest in evergreen broadleaf forests (0.083 mol/m<sup>2</sup>/s). This cross-PFT pattern is largely consistent with the parameterization of LSMs (Fig. 2). The equivalent  $g_{s,\text{ref}}$  from GLDAS, CLM4.5 and CLM5 are correlated with the site-averaged  $g_{s,\text{ref}}$  per PFT with Pearson correlation coefficients of 0.76, 0.83, and 0.88 respectively ( $p < 0.01$  for all), though these correspondences are in large part attributable to high  $g_{s,\text{ref}}$  in croplands. When excluding croplands, the correlations degrade to 0.78, 0.55, and 0.31 for the three model parameterizations, respectively. While the cross-PFT patterns derived here and the parametrization of LSMs are largely consistent, significant differences also remain. These may be attributable to the limited number of sites in each



**Figure 1.** (a) Temporal variation of ecosystem conductance  $G_s$  explained by the ecosystem conductance model (Eq. 1) for all investigated FLUXNET sites. Model accuracy was evaluated using the coefficient of determination ( $R^2$ ) between fitted  $G_s$  and that derived from observations. (b) Probability density function (pdf) of the fitted soil conductance ( $G_0$ ) across sites under measured soil moisture in the four quartiles separated by the 25th ( $q_{25}$ ), the 50th ( $q_{50}$ ), and the 75th ( $q_{75}$ ) quantiles of each site, and under all soil moisture conditions at sites without soil moisture measurement (no SM). (c) The pdf of the slope parameter  $G_1$ . (d) The pdf of the VPD-sensitivity parameter  $m$ . (e) The unstressed stomatal conductance ( $g_{s,ref}$ ) derived for FLUXNET sites.

294 PFT in this study and similarly, the small number of (possibly different) sites typically  
 295 used to tune parameters in LSMs.

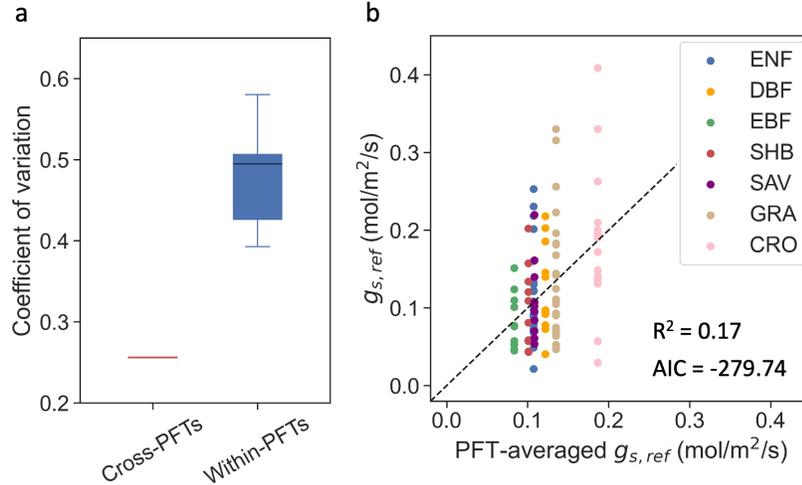


**Figure 2.** Relations between PFT-averaged unstressed stomatal conductance ( $g_{s,ref}$ ) of FLUXNET sites and the equivalent  $g_{s,ref}$  calculated using the parameterizations of (a) Noah v3.3 in GLDAS, (b) the Ball-Berry model in CLM4.5, and (c) the Medlyn model in CLM5. Black dashed lines denote the regression lines. Colored dots represent the seven PFTs, including evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF), evergreen broadleaf forests (EBF), shrublands (SHB, including both open and closed shrublands), savannas (SAV, including both savannas and woody savannas), grasslands (GRA), and croplands (CRO). Different symbol shapes denote parameterizations specific for tropical, temperate and boreal biomes. Each panel only shows available PFTs and biomes in the corresponding model.

296 On average, the cross-PFT variation of observed  $g_{s,ref}$  is only half of that seen within  
 297 each of the seven PFTs (Fig. 3a). As a result, the PFT-averages of  $g_{s,ref}$  only explain  
 298 17% of the total observed variation across all sites (Fig. 3b). This suggests that repre-  
 299 senting the unstressed stomatal conductance via PFT alone ignores significant sources  
 300 of spatial variation, which may result in spatial errors of simulated biosphere-atmosphere  
 301 interactions in LSMs.

### 302 3.3 Improved spatial estimation of unstressed stomatal conductance

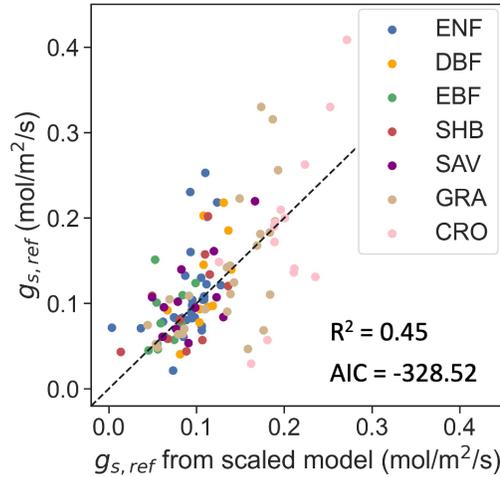
303 The most informative variable in explaining the spatial variation of  $g_{s,ref}$  is the dry-  
 304 ness index, calculated as the long-term averaged deficit between potential evapotranspi-  
 305 ration and the actual evapotranspiration (PET-ET), followed by canopy height. Using  
 306 these two variables, the scaled model (Eq. 4) explains 45% of the variation of  $g_{s,ref}$  across  
 307 all sites (Fig. 4), which more than doubles the  $R^2$  of 0.17 using PFT-averages (Fig. 3).



**Figure 3.** (a) The coefficient of variation of  $g_{s,ref}$  across- and within-PFTs. (b) Relation between PFT-averaged  $g_{s,ref}$  (the baseline model) and the  $g_{s,ref}$  across sites. Acronyms of PFTs are noted in the caption of Fig. 2.

308 Despite requiring more parameters, the best scaled model is also more informative ( $AIC=$   
 309  $-328.52$ ) than the baseline model ( $AIC= -279.74$ ). The  $g_{s,ref}$  is negatively related to  
 310  $PET-ET$  and positively related to  $1/H_c$ , with greater sensitivity to  $PET-ET$  ( $-0.198 \pm$   
 311  $0.018$ ) than to  $1/H_c$  ( $0.046 \pm 0.011$ ), where the sensitivity coefficients were calculated  
 312 using the variables' z-scores. We note that multiple variable combinations and the cor-  
 313 responding regression coefficients yield similar model accuracies (Table S1). However,  
 314 both  $1/H_c$  and the dryness index are selected in the majority of the top ten models. Across  
 315 models, the signs of the relationships between both  $1/H_c$  and the dryness index to  $g_{s,ref}$   
 316 are also consistent. Mean annual temperature and precipitation are also selected in eight  
 317 out of the ten top models, although  $g_{s,ref}$  is less sensitive to mean climate conditions than  
 318 to the dryness index. These findings are robust with respect to the alternative approx-  
 319 imations and thresholds for deriving  $g_{s,ref}$  described in Section 2.2. Climate dryness and  
 320 canopy height are still the most informative variables explaining 38% to 45% of  $g_{s,ref}$  vari-  
 321 ation, in contrast to 13% to 16% using PFT averages (Fig. S4–S7).

322 Our results indicate that accounting for climate dryness and canopy height explains  
 323 more than two times the  $g_{s,ref}$  variation explained by PFT alone. This suggests that a  
 324 simple and tractable equation can enable significantly more accurate  $g_{s,ref}$  assumptions  
 325 for use in LSMs. Plants in drier climates tend to exhibit lower  $g_{s,ref}$ , which provides the



**Figure 4.** Performance of the best scaled model in estimating  $g_{s,ref}$  using canopy height and climate dryness across sites. Acronyms of PFTs are noted in the caption of Fig. 2.

326 first ecosystem-scale evidence consistent with leaf scale measurements suggesting species  
 327 in drier climates tend to have lower stomatal density and area and thus lower unstressed  
 328 stomatal conductance (Carlson et al., 2016; C. Liu et al., 2018). Based on leaf-level gas  
 329 exchange, Y.-S. Lin et al. (2015) also found drier climates were correlated with higher  
 330 marginal water use efficiency, indicating low stomatal conductance under unstressed con-  
 331 ditions.

332 To our knowledge, our study is the first to present evidence on the coordination  
 333 between unstressed stomatal and xylem conductances (evidenced here through canopy  
 334 height) at the ecosystem scale. Previous studies have found strong coordination between  
 335 xylem and stomatal vulnerabilities to water stresses (Martin-StPaul et al., 2017; Bro-  
 336 dribb et al., 2017; Pivovarovff et al., 2018), and identified positive  $1/H_c - g_{s,ref}$  relation-  
 337 ships based on tree-scale measurements for each species (Schäfer et al., 2000; Ryan et  
 338 al., 2000; Phillips et al., 2003; Delzon et al., 2004). Our study extends these results by  
 339 showing that, even without distinguishing species within a PFT, canopy height explains  
 340  $g_{s,ref}$  variations at the ecosystem-scale. It further suggests that the direct effect of canopy  
 341 height on xylem conductance (which suggests a positive relationship between  $1/H_c$  and  
 342  $g_{s,ref}$ ) outweighs the influence of xylem conductance's dependence on the sapwood-to-  
 343 leaf area (which by itself suggests a negative relationship between  $1/H_c$  and  $g_{s,ref}$ ). Nev-

344 ertheless, these competing influences may explain why, at stand-scale,  $g_{s,\text{ref}}$  is less sen-  
345 sitive to canopy height than to climate dryness.

## 346 4 Conclusions and implications

347 This study investigated the spatial variation of stomatal conductance under un-  
348 stressed conditions ( $g_{s,\text{ref}}$ ) derived from FLUXNET sites across the globe. Differences  
349 between PFTs only account for a limited fraction of the total spatial variance. This high-  
350 lights the uncertainties introduced by PFT-based parameterization schemes commonly  
351 used in LSMs. In contrast, using PFT, canopy height and climate dryness significantly  
352 contribute to explaining the spatial variation of  $g_{s,\text{ref}}$ , even in the absence of any infor-  
353 mation about species composition, competition, soil type (which may affect rooting prop-  
354 erties), or other factors. Note that the predictive capabilities of this relationship are not  
355 obvious *a priori* from the existence of analogous univariate species-scale relationships.  
356 The large range of other factors varying at ecosystem-scale could have prevented the ex-  
357 istence of a tractable relationship for  $g_{s,\text{ref}}$  with climate dryness and canopy height. In-  
358 deed, for water use efficiency (WUE) – another stomatal trait – it has been shown that  
359 the WUE aridity index relationship is very different between leaf and ecosystem scales  
360 (H. Li et al., 2022). Greater  $g_{s,\text{ref}}$  is associated with lower canopy height and more mesic  
361 climates, which is supported by ecophysiological theory and is qualitatively consistent  
362 with previous evidence observed at leaf and tree scales. Our findings suggest that ex-  
363 plicitly considering canopy height and climate dryness can contribute to a more accu-  
364 rate description of unstressed stomatal conductance and its ecohydrological consequences  
365 in models. Additionally, an increasing number of land models have started to incorpo-  
366 rate plant hydraulics and therefore a mechanistic impact of canopy height on the equiv-  
367 alent  $g_{s,\text{ref}}$  (Kennedy et al., 2019; Eller et al., 2020; L. Li et al., 2021). The sensitivity  
368 of  $g_{s,\text{ref}}$  to canopy height estimated here can provide an observation-based diagnostic bench-  
369 mark for examining such parameterizations. Overall, the fact that climate and ecolog-  
370 ical state explain  $g_{s,\text{ref}}$  highlights the importance of plant-environment interactions and  
371 ecological dynamics in shaping community-average traits. Our findings motivate further  
372 studies accounting for these impacts to improve prediction of biosphere-atmosphere in-  
373 teractions.

## Open Research

All meteorological data and canopy height data were obtained from the FLUXNET2015 dataset (<https://fluxnet.org/data/fluxnet2015-dataset/>). Leaf area index was extracted from the MODIS product (MCD15A3H.006, <https://doi.org/10.5067/MODIS/MCD15A3H.006>).

## Acknowledgments

AGK was funded by the NASA Modeling, Analysis, and Prediction program, grant 80NSSC21K1523, and by NSF DEB-1942133. QZ was supported by the National Natural Science Foundation of China (no. U2243214). KAN acknowledges support from NSF-DEB 1552747. RDK's involvement with the study was supported by the NASA MAP program. The authors acknowledge the FLUXNET network for providing the FLUXNET2015 dataset.

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**Figure 1.**

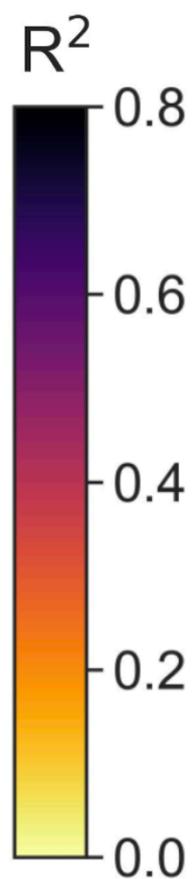
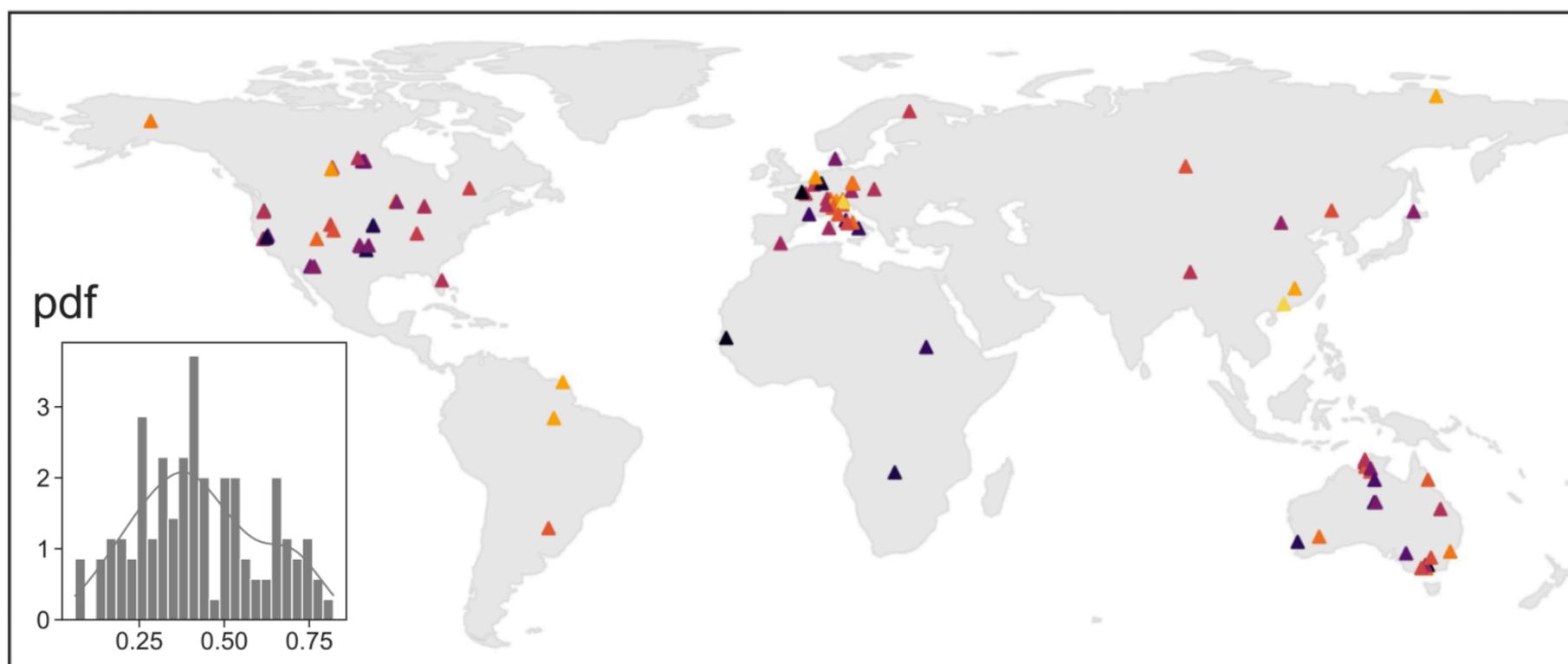
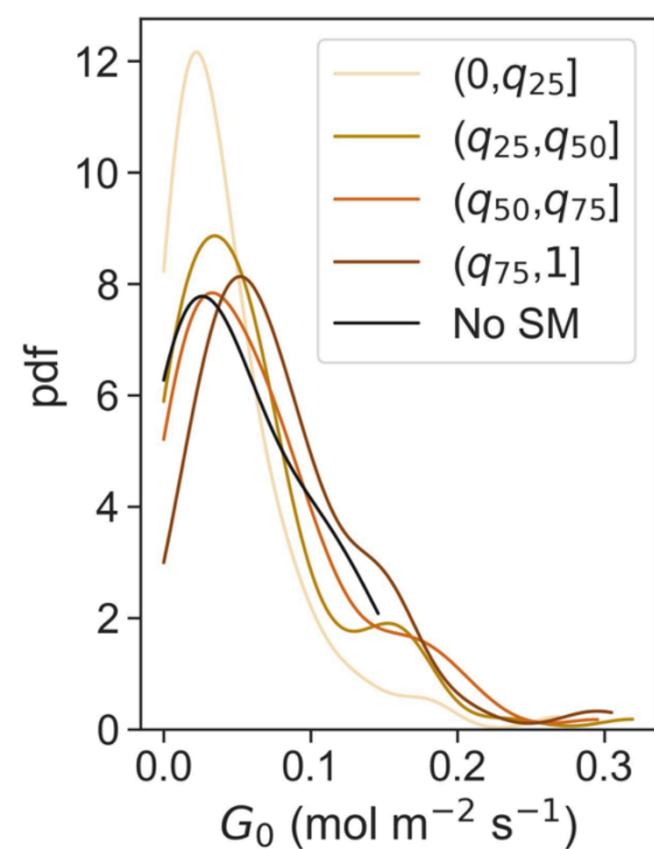
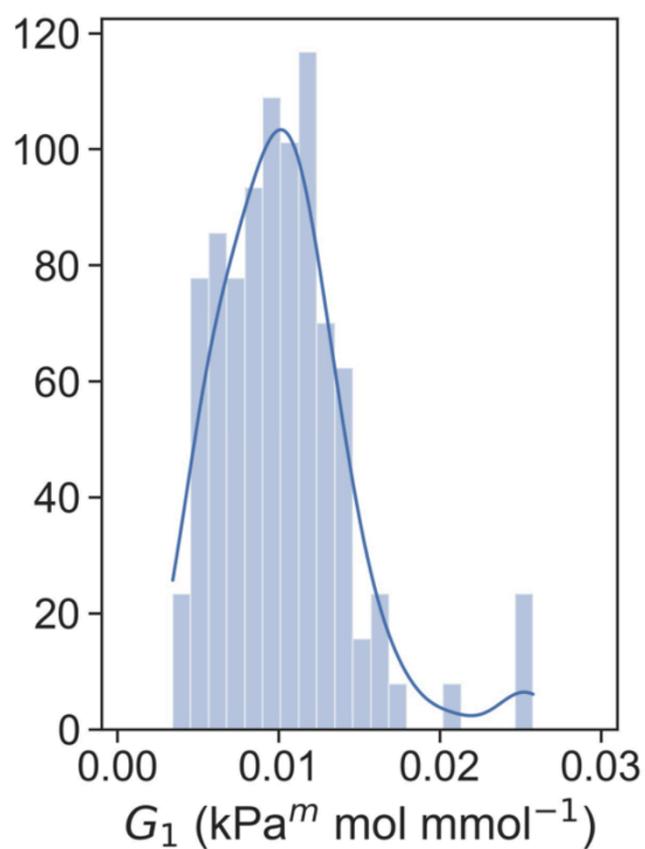
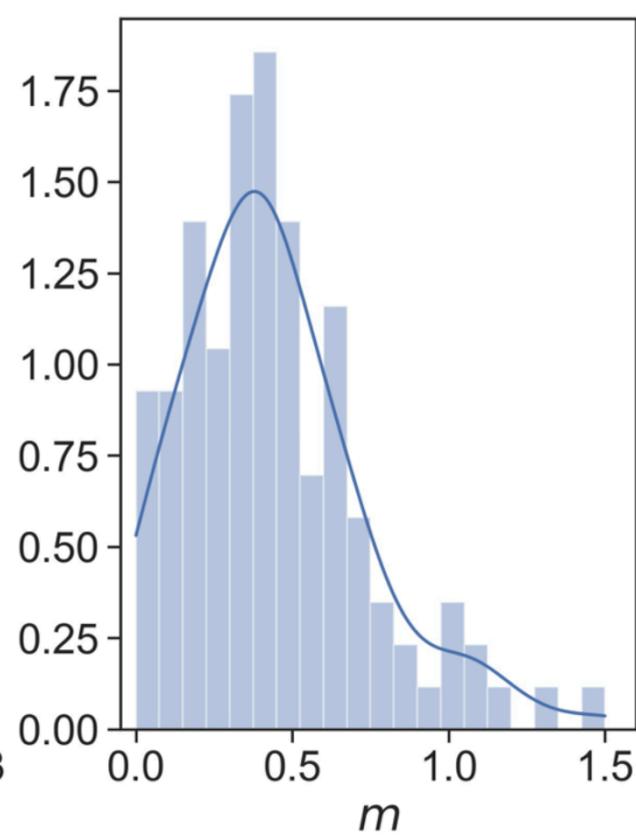
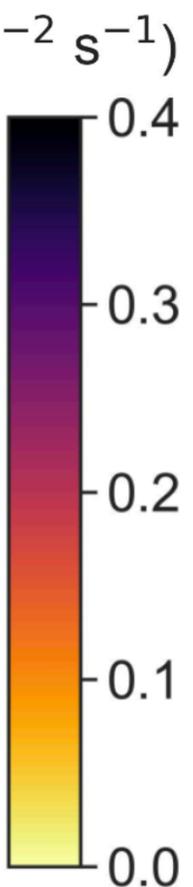
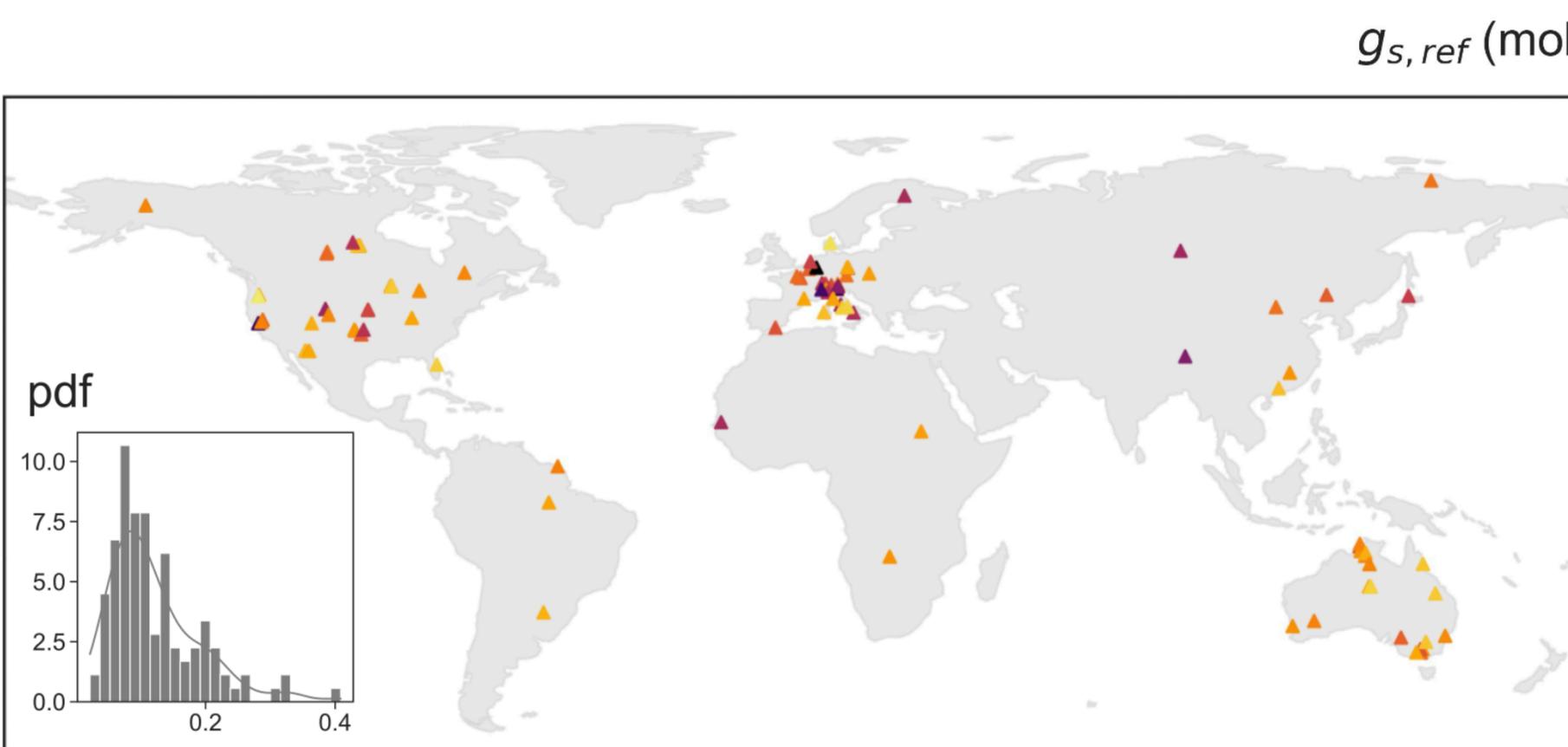
**a****b****c****d****e**

Figure 2.

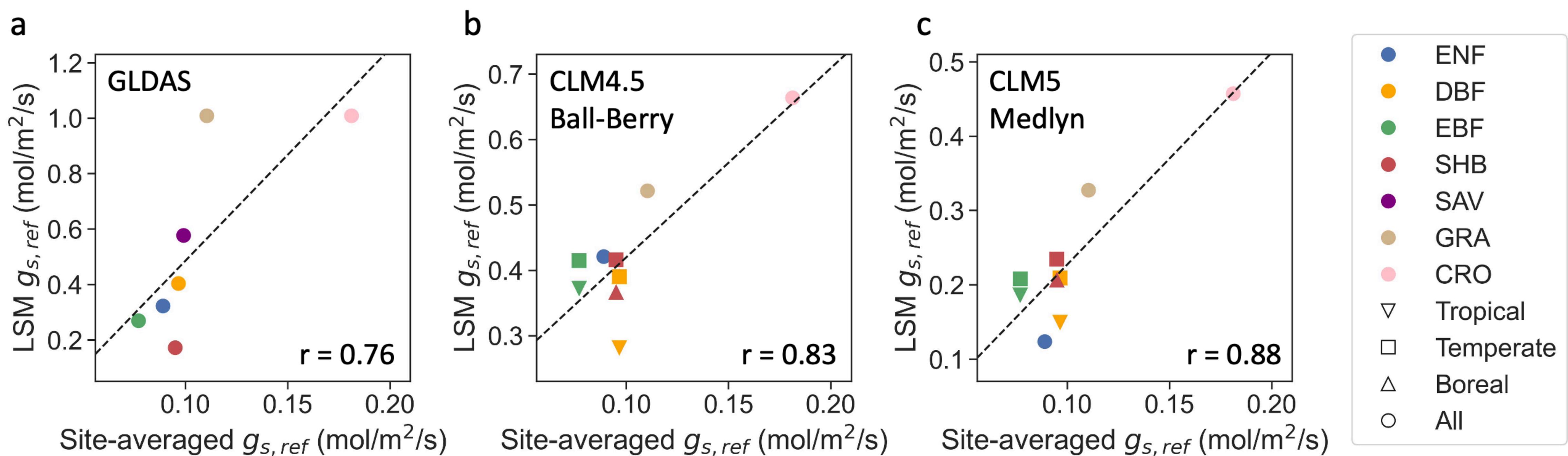


Figure 3.

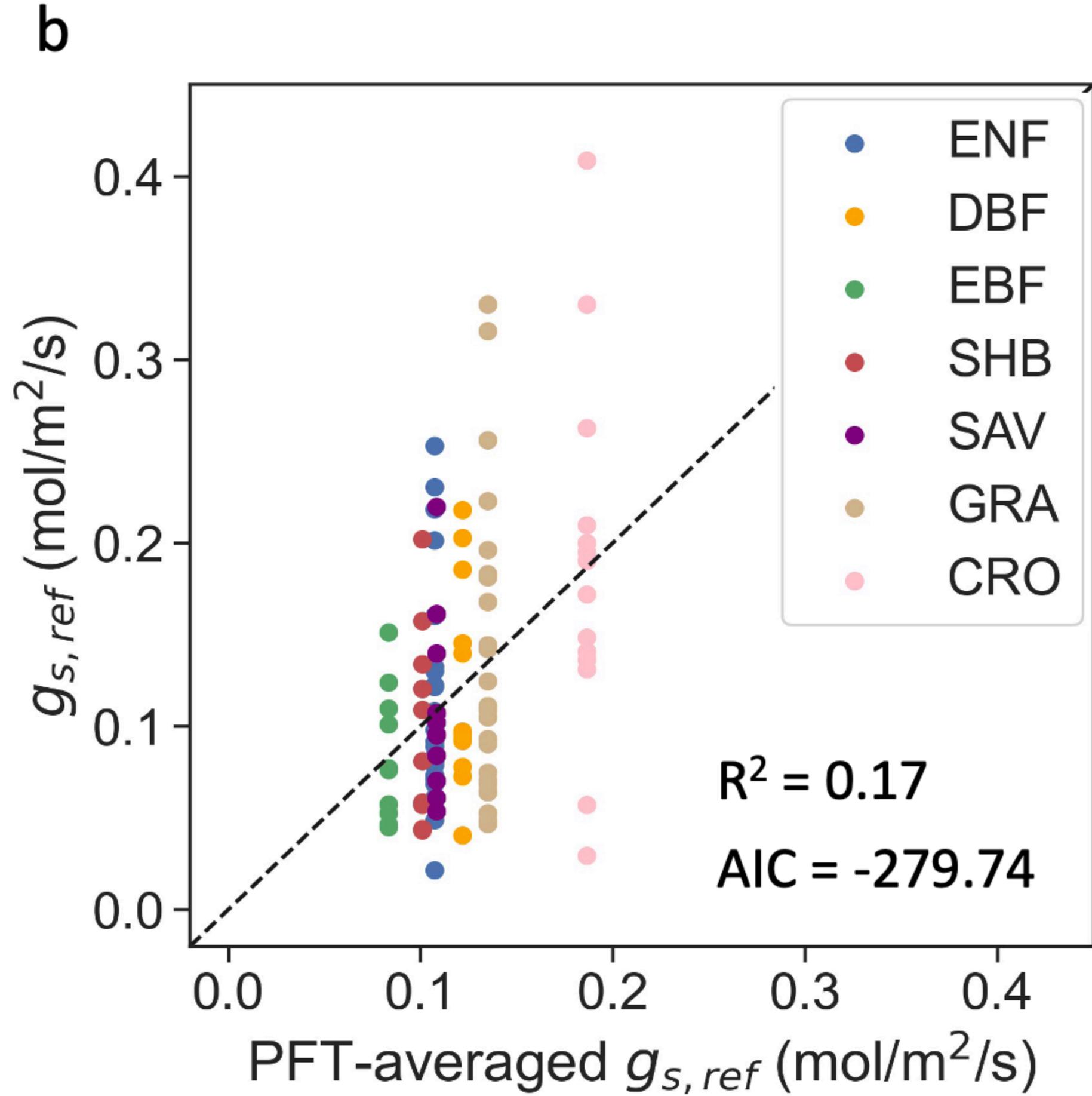
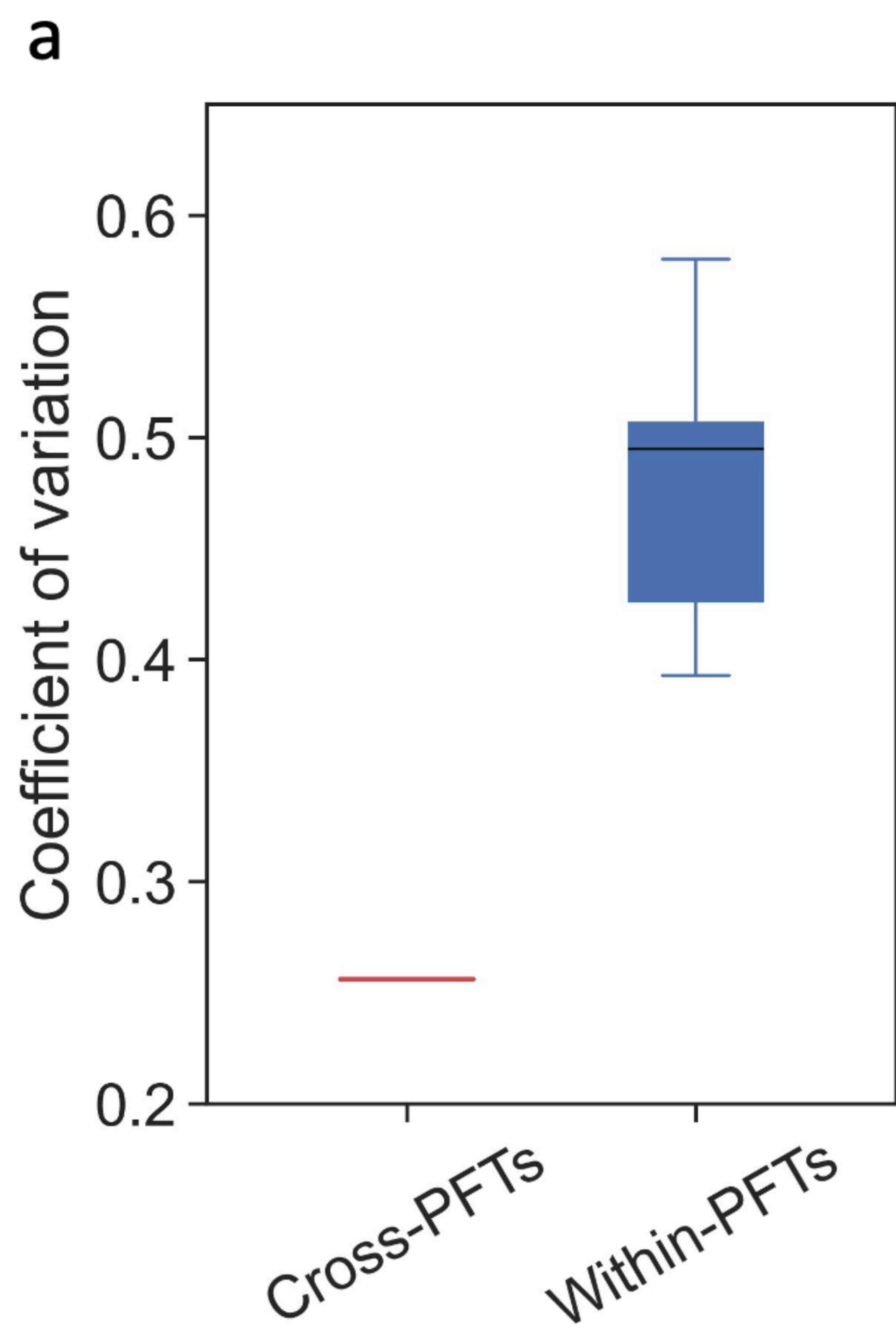


Figure 4.

