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Partitioning controls on Amazon forest photosynthesis between environmental and biotic factors at hourly to interannual timescales

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50 **Keywords:** light-use efficiency; physiology; phenology; temperature sensitivity on productivity;
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52

53 **Type of Paper:** Primary Research Article

54 **Abstract**

55 Gross ecosystem productivity (GEP) in tropical forests varies both with the environment and
56 with biotic changes in photosynthetic infrastructure, but our understanding of the relative effects
57 of these factors across timescales is limited. Here, we used a statistical model to partition the
58 variability of seven years of eddy covariance-derived GEP in a central Amazon evergreen forest
59 into two main causes: variation in environmental drivers (solar radiation, diffuse light fraction,
60 and vapor pressure deficit) that interact with model parameters that govern photosynthesis, and

61 biotic variation in canopy photosynthetic light-use efficiency associated with changes in the
62 parameters themselves. Our fitted model was able to explain most of the variability in GEP at
63 hourly ($R^2=0.77$) to inter-annual ($R^2=0.80$) timescales. At hourly timescales, we found that 75%
64 of observed GEP variability could be attributed to environmental variability. When aggregating
65 GEP to the longer timescales (daily, monthly, and yearly), however, environmental variation
66 explained progressively less GEP variability: at monthly timescales, it explained only 3%, much
67 less than biotic variation in canopy photosynthetic light-use efficiency, which accounted for
68 63%. These results challenge modeling approaches that assume GEP is primarily controlled by
69 the environment at both short and long timescales. Our approach distinguishing biotic from
70 environmental variability can help to resolve debates about environmental limitations to tropical
71 forest photosynthesis. For example, we found that biotically regulated canopy photosynthetic
72 light-use efficiency (associated with leaf phenology) increased with sunlight during dry seasons
73 (consistent with light but not water limitation of canopy development), but that realized GEP was
74 nonetheless lower relative to its potential efficiency during dry than wet seasons (consistent with
75 water limitation of photosynthesis in given assemblages of leaves). This work highlights the
76 importance of accounting for differential regulation of GEP at different timescales, and of
77 identifying the underlying feedbacks and adaptive mechanisms.

78

79 **Introduction**

80 The Amazon basin stores half of global tropical forest biomass (Saatchi *et al.*, 2011), harbors
81 vegetation that substantially influences large-scale carbon and water budgets (Phillips *et al.*,
82 2009; Lee & Boyce, 2010; Fu *et al.*, 2013), and exchanges mass and energy with the atmosphere
83 in ways that may amplify or mute climate change (Bonan, 2008; Lee & Boyce, 2010; Fu *et al.*,
84 2013). A majority of the climate model projections from the Coupled Model Intercomparison
85 Project Phase 5 (CMIP 5) showed a drier and warmer future for the central and eastern Amazon
86 region with an increased dry season length (Diffenbaugh & Field, 2013; Joetzjer *et al.*, 2013;
87 Duffy *et al.*, 2015). However, large uncertainties exist in the projected responses of Amazon
88 forests to this climatic change, primarily driven by different representation of plant physiological
89 processes among vegetation models (Powell *et al.*, 2013; Huntingford *et al.*, 2013). Our limited
90 confidence in model predictions calls for increased observations to more broadly test mechanistic

91 models of physiological and ecological processes that underlie the response of tropical forests to
92 global change.

93 Seasonal and multiyear datasets of eddy covariance (EC) derived fluxes of carbon, water,
94 and energy in tropical evergreen forests (Goulden *et al.*, 2004; Hutyra *et al.*, 2007; Doughty &
95 Goulden, 2008a; von Randow *et al.*, 2013; Restrepo-Coupe *et al.*, 2013; Zeri *et al.*, 2014) are a
96 powerful tool for investigating factors limiting biosphere-atmosphere exchange in tropical
97 forests, including photosynthesis (gross ecosystem productivity, GEP), important for predicting
98 tropical vegetation responses to climatic change (Nemani *et al.*, 2003). To date, however, most
99 EC-based studies in the tropics have focused on photosynthetic responses to variation in
100 individual environmental drivers, including solar radiation and diffuse light fraction (Graham *et*
101 *al.*, 2003; Goulden *et al.*, 2004; Hutyra *et al.*, 2007; Oliveira *et al.* 2007; Cirino *et al.*, 2014),
102 temperature (Doughty & Goulden, 2008a), and vapor pressure deficit (VPD; Hutyra *et al.*, 2007).
103 Despite high correlation among these drivers, few analyses (Lloyd & Farquhar, 2008) considered
104 the covariation among them.

105 Besides environmental factors, biotic changes in canopy photosynthetic efficiency
106 associated with leaf phenology are also important for forest photosynthesis, but have been
107 largely neglected in studies of tropical evergreen forests. Leaf development and senescence, and
108 associated leaf demography (i.e. the distribution of leaf ages within a forest canopy) can cause
109 seasonal changes in both leaf quantity (i.e. canopy leaf area) and leaf quality (i.e. per-area
110 photosynthetic capacity) (Baldocchi & Amthor, 2001; Gu *et al.*, 2003a; Goulden *et al.*, 2004;
111 Richardson *et al.*, 2007; Kitajima *et al.*, 1997; Doughty & Goulden, 2008b; Wu *et al.*, 2016).
112 With few exceptions (e.g. Kim *et al.*, 2012; de Weirdt *et al.*, 2012; Xu *et al.*, 2016), phenology of
113 leaf quantity and quality in the tropics has been assumed constant in both modelling (Powell *et*
114 *al.*, 2013; Sitch *et al.*, 2015) and empirical studies (Doughty & Goulden, 2008b; Doughty *et al.*,
115 2010; Lee *et al.*, 2013).

116 Accurate identification of the causes of tropical forest GEP variability may help resolve
117 several longstanding debates in tropical ecology. We focus here on two key debates about
118 tropical forest function: First is the question of whether light or water resources are more limiting
119 to tropical forest metabolism. Most modeling studies have represented tropical forest systems as
120 water-limited, simulating dry season declines in ecosystem-scale GEP and evapotranspiration
121 (Werth & Avissar, 2004; Lee *et al.*, 2005; Christoffersen *et al.*, 2014). By contrast, many *in-situ*

122 and satellite studies show dry season increases in GEP or evapotranspiration in Amazon forests
123 (Shuttleworth, 1988; Saleska *et al.*, 2003; Huete *et al.*, 2006; Restrepo-Coupe *et al.*, 2013; Guan
124 *et al.*, 2015), but these findings are still controversial in the remote sensing literature (Morton *et*
125 *al.*, 2014; Bi *et al.*, 2015; Saleska *et al.*, 2016).

126 The second debate is about whether tropical forests operate close to a temperature
127 threshold, above which performance diminishes. Observational studies report declines in forest
128 productivity and CO₂ uptake as temperature increases toward the upper end of the range under
129 current climates, and conclude that tropical forests operate close to a high temperature limit that
130 may easily be exceeded under climate change (Clark, 2004; Doughty & Goulden, 2008a; Clark *et*
131 *al.*, 2013; Cavaleri *et al.*, 2015). There are also studies arguing that the observed forest response
132 to high temperature is likely a stomatal response to VPD due to its correlation with temperature
133 (Lloyd & Farquhar, 2008). High VPD can induce stomatal closure and thus reduce GEP and
134 evapotranspiration. Hence, the observed decline in photosynthesis might not be a direct
135 temperature response, and might be ameliorated by higher future CO₂ concentrations under
136 climate change (Ainsworth & Long, 2005; Lewis *et al.*, 2009; Zhang *et al.*, 2015).

137 The goal of this study is to advance understanding of how environmental variation and
138 biotic change in canopy photosynthetic efficiency independently and jointly regulate tropical
139 forest photosynthetic metabolism, in order to provide new insights into the two longstanding
140 debates mentioned above. We ask: (1) How do environmental variables control hourly
141 photosynthesis in tropical evergreen forests? (2) What are the relative contributions of
142 environmental and biotic factors in controlling tropical photosynthesis on timescales from hours
143 to years? (3) Given the context of 1 and 2, what can we say about environmental limitations and
144 the temperature sensitivity of tropical forest photosynthesis? In order to address these questions,
145 we used a seven-year dataset of EC measurements from a central-eastern Amazonian evergreen
146 forest in Brazil (Hutyra *et al.*, 2007; Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016), and
147 partitioned the variability of GEP into responses to various causes at different timescales.

148

149 **Materials and Methods**

150 *Overview*

151 Here, we summarize the approach we developed in this study for partitioning the variability of
152 GEP into responses to both environmental and biotic (i.e. canopy photosynthetic efficiency)

153 causes at different timescales. Our strategy was to first apply the approach of Wu *et al* (2016) to
154 derive an estimate of canopy photosynthetic efficiency at monthly timescales, namely LUE_{ref} ,
155 the light-use efficiency ($LUE = GEP/PAR$) under reference environmental conditions. We then
156 normalized hourly GEP by LUE_{ref} within each month to provide a metric for photosynthetic
157 sensitivity to environmental drivers. At hourly timescales, we then used path analysis (Bassow &
158 Bazzaz, 1998; Huxman *et al.*, 2003) to statistically identify which environmental drivers
159 influenced GEP and the LUE_{ref} -normalized GEP, and to quantify their relative importance. We
160 used these results to develop a parsimonious, physiologically-based light-use-efficiency (LUE)
161 model for hourly GEP. We then used Analysis of Variance (ANOVA) to partition the observed
162 hourly GEP across different timescales (Hui *et al.*, 2003; Richardson *et al.*, 2007) to determine
163 the relative importance of environmental and biotic controls at timescales ranging from hours to
164 years. Finally, we tested whether there existed any environmental control on the inter-annual
165 dynamics of the biotic factor (i.e. monthly LUE_{ref}). The whole analysis flow is shown in Fig. 1.

166 167 *Site description*

168 The study site is the Tapajós National Forest, k67 eddy covariance tower site ($54^{\circ}58'W$, $2^{\circ}51'S$),
169 near Santarém, Pará, Brazil. It is an evergreen tropical forest on a well-drained clay-soil plateau,
170 with a mean upper canopy height of ~40 m (Hutyra *et al.*, 2007). Mean annual precipitation is
171 ~2000 mm/year with a 5-month dry season (monthly precipitation < monthly evapotranspiration)
172 from approximately mid-July to mid-December. Additional local site information can be found
173 in Hutyra *et al* (2007) and Restrepo-Coupe *et al* (2013).

174 175 *Measurements of fluxes and environmental drivers*

176 The eddy covariance (EC) method was used to measure the CO_2 exchange between forest and
177 the atmosphere from a 64-m high tower at Tapajós k67 site (Saleska *et al.*, 2003; Hutyra *et al.*,
178 2007; Restrepo-Coupe *et al.*, 2013). Our tower dataset includes flux and meteorological
179 measurements from January 2002 through December 2011, except for periods when operation
180 was interrupted (most significantly, from January 2006 to August 2008, due to a big tree fall). In
181 total, seven years of hourly EC observations (2002-2005 and 2009-2011) were used in this study.
182 The high-frequency raw EC data was processed and aggregated to hourly level. Detailed

183 description of the instrumentation and data pre-processing protocol can be found in (Hutyra *et*
184 *al.*, 2007; Restrepo-Coupe *et al.*, 2013).

185 After systematic data quality control and outlier removal (Wu *et al.*, 2016), hourly GEP
186 was estimated by separating hourly net ecosystem exchange (NEE, in $\mu\text{mol CO}_2/\text{m}^2/\text{s}$, with
187 fluxes to the atmosphere defined as positive) into two components: ecosystem respiration (Reco)
188 and GEP, where $\text{GEP} = \text{Reco} - \text{NEE}$. Reco was approximated by the average of valid nighttime
189 NEE during well-mixed periods (u^* criterion: ≥ 0.22 m/s; Hutyra *et al.*, 2007), interpolated into
190 the daytime following the approach described in Restrepo-Coupe *et al.* (2013). Hourly GEP
191 ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$) was further aggregated to daily steps ($\text{gC}/\text{m}^2/\text{d}$) by summing up all the
192 effective measurements (u^* criterion: ≥ 0.22 m/s) within a day. We also calculated the average
193 daily GEP for each month during our study period.

194 The EC observations also included environmental drivers: photosynthetically active radiation
195 (PAR), air temperature (T_a), and vapor pressure deficit (VPD) (Saleska *et al.*, 2003; Hutyra *et*
196 *al.*, 2007). Diffuse light fraction is also available from June 2004 to December 2005, which was
197 measured using a BF5 Sunshine Sensor (Delta-T Devices Ltd, Cambridge, UK) mounted at the
198 tower. As diffuse light fraction (the ratio between diffuse and total PAR) can influence canopy-
199 scale photosynthesis (Gu *et al.*, 2002, 2003b; Oliveira *et al.*, 2007; Mercado *et al.*, 2009; Cirino
200 *et al.*, 2014) but was only measured for a short portion of the EC record, we used a simple
201 “Cloudiness Index” (acronym as “CI” hereafter) as a proxy of light quality:

$$202 \quad CI = 1 - \frac{PAR_{obs}}{PAR_{clearsky}} \quad (1)$$

203 where the observed PAR (PAR_{obs}) was obtained from the tower-mounted PAR sensor, and the
204 theoretical PAR ($PAR_{clearsky}$) for clear-sky conditions at local elevation was estimated using an
205 established model (Weiss & Norman, 1985). CI was highly correlated with measured diffuse
206 light fraction (Fig. S1c, $R^2=0.60$, $p<10^{-5}$), so we take it as a proxy of diffuse light fraction in our
207 analysis, with observed values ranging from 0.1 (direct sun) to 0.8 (fully diffuse light).

208 We used rainfall measurements from the Tropical Rainfall Measuring Mission (TRMM)
209 Multi-satellite Precipitation Analysis (TMPA) (product 3b42V6, integrating microwave and
210 infrared satellite data with gauge data), which provides 0.25 degree and 3-hourly rainfall
211 estimate for the Amazon from 1998 to the present (Huffman *et al.*, 2007). The monthly TRMM

212 rainfall measurements centered on the k67 tower site from years 2002-2005, and years 2009-
 213 2011 were used in this study.

214

215 *LAI measurements*

216 Leaf area index (LAI), the quantity component of leaf phenology, influences ecosystem
 217 photosynthesis primarily by regulating the fraction of PAR absorbed by the forest canopy
 218 (FAPAR). Here, we used a classic LAI-FAPAR relationship (Doughty & Goulden, 2008b; Xiao
 219 *et al.*, 2004) for estimating FAPAR:

$$220 \quad FAPAR = 0.95 - \exp\left(-\frac{k \times LAI}{\cos(SZA)}\right) \quad (2)$$

221 where SZA is solar zenith angle, and $k(=0.5)$ is the extinction coefficient.

222 Monthly data of LAI was measured with an LAI-2000 instrument (LICOR) (2001-2005;
 223 Brando *et al.*, 2010) at 100 grid points within a one-hectare control plot of the Seca-Floresta
 224 drought experiment, about 5 kms away from the k67 eddy covariance tower. A five-year mean
 225 annual cycle of monthly LAI (range: 5.35-6.15 m^2/m^2) was used for deriving a mean annual
 226 cycle of FAPAR at k67 (Fig. S2). Since FAPAR showed very small seasonal variability (< 2%),
 227 we thus assumed the effect of LAI on FAPAR seasonality at this forest site could be ignored.

228

229 *Overview of the LUE-based photosynthesis modeling*

230 This study uses the LUE-based photosynthesis modeling approach (Eq. 3; Monteith, 1972;
 231 Monteith & Moss, 1977):

$$232 \quad GEP = \mathcal{E} \times PAR \quad (3)$$

233 where \mathcal{E} , or LUE, is the efficiency (mol CO₂/mol photons) with which solar radiation (PAR) is
 234 used in photosynthesis (GEP). The term \mathcal{E} was calculated by Eq. 4 (Jarvis, 1976; Field *et al.*,
 235 1995):

$$236 \quad \mathcal{E} = \frac{GEP}{PAR} = \mathcal{E}_0 \times FAPAR \times f_{env} \quad (4)$$

237 where \mathcal{E}_0 is the intrinsic LUE of the canopy under non-stressed or reference environment
 238 condition, which is influenced by internal leaf properties such as leaf nitrogen (Field, 1983) or
 239 leaf age (Wilson *et al.*, 2001; Doughty & Goulden, 2008b). FAPAR is described by a classic
 240 LAI-FAPAR relationship in Eq. 2; f_{env} represents the joint environmental effects that down-

241 regulate \mathcal{E} (Jarvis, 1976; Field *et al.*, 1995; Gu *et al.*, 2002; Xiao *et al.*, 2005; Mahadevan *et al.*,
 242 2008). The LUE-based photosynthesis model used here thus incorporates two kinds of control on
 243 vegetation photosynthesis: (1) a shorter-timescale photosynthetic response driven by light
 244 quantity (PAR) and other environmental drivers f_{env} , and (2) a longer-timescale response driven
 245 by changes in leaf quantity (which affects FAPAR) and leaf quality (which affects \mathcal{E}_0).

246

247 *LUE_{ref} and GEP_{norm}*

248 To represent the capability of the canopy to photosynthetically assimilate CO₂ independent of
 249 fluctuations in environmental drivers, we estimated the incident light-use efficiency of the
 250 canopy under reference conditions (LUE_{ref}). LUE_{ref} was estimated, following Wu *et al.* (2016)
 251 (where it was called canopy photosynthetic capacity, or PC), as the ratio of EC-derived GEP and
 252 PAR under reference environmental conditions. The definition of LUE_{ref} (from Wu *et al.*, 2016)
 253 generalizes previous studies that removed the influence of varying PAR on GEP (Hutyra *et al.*,
 254 2007; Doughty & Goulden, 2008b; Restrepo-Coupe *et al.*, 2013; Jones *et al.*, 2014) by further
 255 removing the influence of variation in other important environmental drivers (i.e. VPD, Ta, and
 256 CI) and SZA. The reference environmental conditions were taken as narrow bins of each driver:
 257 PAR=1320±200 μmol/m²/s, CI=0.40±0.10, VPD=874±200 Pa, and Ta=27.7±1.0 °C (8.1% of all
 258 hourly GEP observations, about 20 observations per month, on average). We assumed that
 259 LUE_{ref} is constant within a month (roughly the timescale needed for significant canopy changes)
 260 but that it can vary between months, following changes in LAI or in per-area photosynthetic
 261 efficiency. Because LUE_{ref} is derived from EC measurements, the question arises as to whether it
 262 is an adequately independent predictor of GEP, which is also derived from EC. However,
 263 changes in independent measurements of leaf-level photosynthetic capacity (or maximum
 264 carboxylation capacity of Rubisco, V_{cmax}), scaled to the canopy, are consistent with changes in
 265 LUE_{ref} (Wu *et al.*, 2016), lending confidence to our interpretation of LUE_{ref} as an accurate
 266 measure of ecosystem-scale photosynthetic infrastructure.

267 We note that the EC-derived LUE_{ref}, interpreted in the context of the LUE-based
 268 photosynthesis modeling (Eqs. 3-4), is proportional to $\mathcal{E}_0 \times FAPAR$ with a scaling constant $f_{env,ref}$
 269 (Eq. 5; the environmental effect under reference conditions):

$$270 \quad LUE_{ref} = \varepsilon_0 \times FAPAR \times f_{env,ref} \quad (5)$$

271 Combining Eqs. 3-5, we can further derive GEP and \mathcal{E} as functions of LUE_{ref}:

272
$$GEP = \frac{1}{f_{env,ref}} \times LUE_{ref} \times PAR \times f_{env} \quad (6)$$

273
$$\mathcal{E} = \frac{1}{f_{env,ref}} \times LUE_{ref} \times f_{env} \quad (7)$$

274 Eqs. 6-7 thus summarize the photosynthesis process subject to the joint controls from longer-
 275 timescale biotic change in canopy photosynthetic efficiency (i.e. monthly LUE_{ref} , which captures
 276 changes in LAI as well as changes in leaf-level photosynthetic efficiency aggregated to the
 277 canopy scale) and shorter-timescale environmental drivers (including hourly measurements of
 278 PAR and other variables). By using the EC-derived monthly LUE_{ref} over the seven-year
 279 timeseries, we further separated the shorter-timescale physiological response to environmental
 280 drivers from the longer-timescale biotic changes in canopy photosynthetic efficiency:

281
$$GEP_{norm} = \frac{GEP}{LUE_{ref}} \times LUE_{ref,avg} = \frac{LUE_{ref,avg}}{LUE_{ref}} \times PAR \times f_{env} \quad (8)$$

282
$$\mathcal{E}_{norm} = \frac{GEP_{norm}}{PAR} = \frac{LUE_{ref,avg}}{LUE_{ref}} \times f_{env} \quad (9)$$

283 where $LUE_{ref,avg}$ is the mean value of monthly LUE_{ref} over the seven-year time series, and
 284 GEP_{norm} and \mathcal{E}_{norm} were GEP and \mathcal{E} normalized by LUE_{ref} respectively. Therefore, according to
 285 Eqs. 8-9, GEP_{norm} is proportional to $PAR \times f_{env}$, representing variability in GEP due to shorter-
 286 timescale environmental variability alone. Likewise, \mathcal{E}_{norm} is proportional to the environmental
 287 response function f_{env} , representing variability in \mathcal{E} caused by shorter-timescale environmental
 288 variability alone.

289

290 *Path analysis for environmental controls on shorter-timescale photosynthesis*

291 Path analysis is similar to multiple regression approaches, and is especially useful when a *priori*
 292 causal or correlative information is known among variables (Li, 1975). It has been used to
 293 evaluate environmental controls on plant gas exchange in a temperate deciduous forest (Bassow
 294 & Bazzaz, 1998) and a high-elevation subalpine forest (Huxman *et al.*, 2003). In this study, we
 295 applied it in a tropical forest to investigate environmental controls on tropical forest
 296 photosynthesis.

297 Four environmental variables were considered in our path analysis, including PAR, VPD,
 298 Ta, and CI, due to their important roles in regulating tropical forest photosynthesis processes

299 (Graham *et al.*, 2003; Goulden *et al.*, 2004; Hutrya *et al.*, 2007; Doughty & Goulden, 2008a;
 300 Lloyd & Farquhar, 2008; Oliveira *et al.* 2007; Cirino *et al.*, 2014). We firstly designed the path
 301 structure for their correlations as follows: (1) atmospheric conditions (indicated by CI) and SZA
 302 determine the above-canopy PAR, (2) PAR drives Ta, and (3) CI and Ta influence VPD. While
 303 other path structures may be conceptually feasible, our intent was not to explore the relative
 304 goodness-of-fit of different models, but instead to identify the primary interaction pattern among
 305 these environmental drivers.

306 We then designed two path diagrams to explore environmental effects on EC-derived
 307 GEP_{norm} and ε_{norm} (Eqs. 8-9), respectively. We applied a log transformation to ε_{norm} to achieve
 308 the normality assumption for path analysis (Terborgh *et al.*, 2014). All environmental variables
 309 were initially assumed to directly control GEP_{norm} (or ε_{norm}). To derive the final path diagram,
 310 we ran the path analysis multiple times, removing insignificant paths (p -value>0.05) on each
 311 iteration, until all remaining paths were statistically significant.

312 The path value (PV, arrow thickness in Fig. 2) was derived from the standardized partial
 313 regression coefficients, representing the relative strength of a given relationship. Therefore, PV
 314 in our study allowed us to quantitatively compare the relative influence of various environmental
 315 variables on the photosynthesis. All the path diagrams were solved with IBM SPSS AMOS 22
 316 (Chicago, Ill., USA) software, by using full-information maximum-likelihood estimation.

317

318 *The LUE-based photosynthesis model*

319 To represent how multiple environmental drivers affect shorter-timescale tropical forest
 320 photosynthesis, we adopted the methods from previous studies, and described f_{env} as the product
 321 of scalar functions of PAR (L_{scalar}), VPD (W_{scalar}), Ta (T_{scalar}), and CI (CI_{scalar}) (Jarvis, 1976;
 322 Field *et al.*, 1995; Gu *et al.*, 2002; Xiao *et al.*, 2005; Mahadevan *et al.*, 2008):

$$323 \quad f_{env} = L_{scalar} \times W_{scalar} \times T_{scalar} \times CI_{scalar} \quad (10)$$

$$324 \quad L_{scalar} = \frac{1}{1 + PAR / PAR_0} \quad (11)$$

$$325 \quad W_{scalar} = 1 - k_w \times VPD \quad (12)$$

$$326 \quad T_{scalar} = 1 - k_T \times (T - T_{opt})^2 \quad (13)$$

$$327 \quad CI_{scalar} = 1 + k_{CI} \times CI \quad (14)$$

328 The coefficients in Eqs. 11 –14 were: PAR_0 , which describes the Michaelis-Menten constraint of
329 PAR on photosynthesis (Mahadevan *et al.*, 2008); k_w , k_T and k_{CI} , defined as the strength of the
330 environmental constraints from VPD, Ta and CI, respectively; and T_{opt} , which is the optimal Ta
331 for photosynthesis.

332 However, the default f_{env} (shown in Eq. 10) did not consider the fact of environmental
333 correlations (Lloyd & Farquhar, 2008). To overcome this problem, we turned to the path
334 analysis. Only those environmental drivers, which were significantly related with GEP_{norm} or
335 ϵ_{norm} in path analysis, were selected for the final form of f_{env} , by retaining their scalar functions
336 while setting the other scalar functions equal to 1. We called the final LUE-based photosynthesis
337 model as “the reference LUE model”.

338 To explore photosynthetic sensitivity response to environmental change, we used the
339 reference LUE model to simulate GEP_{norm} as a function of a single proxy CI, assuming that other
340 environmental variables change linearly with CI, following their currently observed joint
341 distribution (including correlations) (Table S1). The analysis would allow us to explore how each
342 environmental driver independently and jointly controls photosynthetic activity, and to perform a
343 more realistic sensitivity analysis of environmental effect on photosynthesis.

344

345 *Model runs and posterior analysis*

346 To quantify the effects of both environmental and biotic (i.e. LUE_{ref}) drivers on modeled
347 GEP, we ran our reference LUE model at hourly timescales for a training dataset (years 2003,
348 2005, 2009, and 2011), and validated the model using an independent dataset (years 2002, 2004,
349 and 2010). We optimized the model by minimizing the Euclidian distance between modeled and
350 observed GEP, using “NonLinearModel.fit” (Holland & Welsch, 1977) in Matlab R2014a. After
351 the optimization, we ran the LUE model with the fitted model parameters for full 7-year hourly
352 measurements but with three different scenarios: (1) the full model (or “full”; forced by time-
353 varying environmental drivers interacting with time-varying LUE_{ref}); (2) only with
354 environmental effects (or “Env”; forced only by time-varying environment drivers, assuming
355 LUE_{ref} is constant for all the months); (3) only with canopy photosynthetic efficiency effect (or
356 “PE”; forced only by time-varying LUE_{ref} , assuming environmental drivers are constant).

357 For the simulated GEP from each scenario, we aggregated the hourly GEP to the daily,
358 monthly, and yearly values, respectively. We then applied ANOVA analysis (Eqs. 15-21) to

359 partition the variance of EC-derived GEP into different causes (“full”, “Env”, and “PE”),
 360 following the approach used by a similar study in a temperate deciduous forest (Richardson *et*
 361 *al.*, 2007). We repeated the analysis for the three different periods of integration at daily,
 362 monthly, and yearly timescales.

$$363 \quad SS_T = \sum_{i=1}^N (y_{i,obs} - \overline{y_{obs}})^2 \quad (15)$$

$$364 \quad SS_{full} = \sum_{i=1}^N (y_{i,obs} - \widehat{y}_{i,full})^2 \quad (16)$$

$$365 \quad SS_{Env} = \sum_{i=1}^N (y_{i,obs} - \widehat{y}_{i,Env})^2 \quad (17)$$

$$366 \quad SS_{PE} = \sum_{i=1}^N (y_{i,obs} - \widehat{y}_{i,PE})^2 \quad (18)$$

$$367 \quad R_{full}^2 = 1 - \frac{SS_{full}}{SS_T} \quad (19)$$

$$368 \quad R_{Env}^2 = 1 - \frac{SS_{Env}}{SS_T} \quad (20)$$

$$369 \quad R_{PE}^2 = 1 - \frac{SS_{PE}}{SS_T} \quad (21)$$

370 where $y_{i,obs}$ refers to EC-derived (observed) GEP, and $\widehat{y}_{i,full}$, $\widehat{y}_{i,Env}$, and $\widehat{y}_{i,PE}$ refer to the modeled
 371 GEP for the *i*th observation under the model scenarios of “full”, “Env”, and “PE” respectively.
 372 $\overline{y_{obs}}$ is the mean of EC-derived GEP. N is the total number of observation under given integrated
 373 timescales. SS_T denotes the total sum of squares for EC-derived GEP; SS_{full} denotes the total
 374 sum of squared error of modeled GEP between observed and “full” scenario; SS_{Env} denotes the
 375 total sum of squared error of modeled GEP between observed and “Env” scenario; SS_{PE} denotes
 376 the total sum of squared error of modeled GEP between observed and “PE” scenario. Finally,
 377 R_{full}^2 , R_{Env}^2 , and R_{PE}^2 denote the fraction of EC-derived GEP variability explained by full model,
 378 environmental drivers, and LUE_{ref} respectively.

379

380 *Decoupling the effects of Ta and VPD on EC-derived GEP_{norm}*

381 To assess the effects of Ta and VPD on photosynthesis, we firstly normalized hourly EC-derived
382 GEP to derive GEP_{norm} . We then filtered the full 7-year hourly GEP_{norm} dataset to focus only on
383 those measurements with high light ($PAR \geq 1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). This treatment can tease
384 out the effect of environmental factors other than VPD and Ta. Then, we did two tests to assess
385 the effects of VPD and Ta on GEP_{norm} . In test 1, we binned GEP_{norm} by Ta, with a 1°C interval
386 from 25.5°C to 31.5°C , and plotted GEP_{norm} against VPD within each bin. In test 2, we binned
387 GEP_{norm} by VPD, with a 200 pa interval from 0 pa to 2200 pa, and plotted GEP_{norm} against Ta
388 within each bin. This analysis allowed us to separate the effects of VPD and Ta on GEP_{norm} .

389

390 *Exploring environmental controls on inter-annual LUE_{ref} variability*

391 We also analyzed the correlations between key environmental drivers and LUE_{ref} at the monthly
392 scale across all our seven-year data record to explore whether there exists any environmental
393 control on LUE_{ref} inter-annual variability.

394

395 **Results**

396 *Relationships among environmental variables*

397 The four environmental variables at our near-equatorial tropical forest site were highly correlated
398 (Figs. S3-S4 and Table S1). The path analysis (Fig. 2) revealed that: (1) PAR had a significant
399 positive effect on Ta (path value, $PV=0.53$, $p < 10^{-5}$), and (2) Ta had a significant positive effect
400 on VPD ($PV=0.86$, $p < 10^{-5}$). In addition, there was a secondary path between CI and VPD ($PV=-$
401 0.03 ; $p < 10^{-5}$). Finally, CI had a direct effect on PAR ($PV=-0.69$, $p < 10^{-5}$), as expected because CI
402 is defined to be negatively correlated with PAR in Eq. 1. CI also had an indirect effect on Ta
403 ($PV=-0.37$; $p < 10^{-5}$) and VPD ($PV=-0.36$; $p < 10^{-5}$). These quantitative results are consistent with
404 previous findings that clouds and aerosols (positively correlated with CI) influenced both the
405 surface energy balance and the hydrologic cycle (Benner & Curry, 1998; Gu *et al.*, 2002).

406

407 *Environmental controls on shorter-timescale photosynthesis*

408 We observed that three environmental variables significantly controlled the normalized light-use-
409 efficiency (ϵ_{norm}) at hourly timescales (Fig. 2a): (1) CI had a positive effect on ϵ_{norm} ($PV=0.34$,
410 $p < 10^{-5}$), and (2) VPD and PAR had negative effects on ϵ_{norm} with $PV=-0.23$ and -0.18
411 respectively. The absolute PV of CI on ϵ_{norm} was significantly larger than that of VPD and PAR

412 on ε_{norm} , indicating that diffuse light fraction (approximated by CI in this study) might be the
 413 dominant control on ε_{norm} .

414 We observed that only two environmental variables controlled the normalized GEP
 415 (GEP_{norm}) at hourly timescales (Fig. 2b): (1) PAR had the expected strongly positive effect on
 416 GEP_{norm} ($PV=0.84$, $p<10^{-5}$) and likewise (2) VPD had a significantly negative effect on GEP_{norm}
 417 ($PV=-0.35$, $p<10^{-5}$). The absolute PV of PAR on GEP_{norm} was more than twice that of VPD on
 418 GEP_{norm} , indicating that PAR was the dominant control. Our analysis of environmental controls
 419 on raw light-use-efficiency (ε) and GEP respectively (Fig. S5) showed that both relationships,
 420 LUE versus environmental drivers and GEP versus environmental drivers, were identical to ε_{norm}
 421 versus environment and GEP_{norm} versus environment, respectively.

422 Our path analyses therefore revealed that three environmental variables (CI, VPD and PAR)
 423 significantly controlled hourly photosynthesis at our tropical forest site: CI and VPD affected
 424 photosynthetic activity primarily through influencing ε_{norm} , and PAR affected photosynthetic
 425 activity primarily through its direct effect on GEP_{norm} .

426

427 *LUE modeling: synthesis and validation from hourly to inter-annual timescales*

428 Given the results of our path analysis and Eq. 5, we were able to omit the temperature response
 429 function from the overall environmental response function (Eq. 10), yielding:

$$430 \quad GEP = \frac{LUE_{ref}}{f_{env,ref}} \times PAR \times (1 + k_{CI} \times CI) \times (1 - k_w \times VPD) \times \left(\frac{1}{1 + PAR / PAR_0} \right) \quad (22)$$

431 Eq. 22 constituted our final form of the LUE-based photosynthesis model, or the reference LUE
 432 model.

433 We first validated the model performance. We found that the reference LUE model (Eq.
 434 22) forced by time-varying environmental drivers and monthly LUE_{ref} (or “full” model)
 435 explained 77% of variability in EC-derived GEP at hourly timescale (Fig. 3a). When aggregating
 436 the modeled and EC-derived GEP to longer timescales (days to years), our results indicated good
 437 agreement between these two metrics at daily, monthly and yearly timescales ($R^2=0.71$, 0.73, and
 438 0.80 respectively) (Fig. 3b-d). We also found that the reference LUE model (Eq. 22) forced only
 439 by time-varying environmental drivers with a constant LUE_{ref} (or “Env” model) did similarly
 440 well in explaining the hourly variability in EC-derived GEP ($R^2=0.75$; Fig. 3e). However, when
 441 aggregating to longer (daily and monthly) timescales, the “Env” model explains much less of the

442 variability in EC-derived GEP than does the “full” model, with strong evidence at monthly
443 timescales (Fig. 3c and Fig. 3g). A similar contrast is apparent at annual timescales (Fig. 3d and
444 Fig. 3h), but the evidence is relatively weaker, as we only have seven-year observations (data
445 size=7) for annual timescale comparisons.

446 We also ran the LUE model (Eq. 22) driven by the same hourly environmental drivers but
447 with three temporal resolutions of LUE_{ref} (monthly, to a mean seasonal cycle (one data point for
448 each month of the year), to a constant LUE_{ref} derived as the mean of the entire monthly
449 timeseries; Fig. 4b). Our results indicated that the LUE model with the highest temporal
450 resolution of LUE_{ref} could best capture inter-annual variability of monthly GEP ($R^2=0.74$; Fig.
451 4c), followed by a mean LUE_{ref} seasonal cycle ($R^2=0.61$), and a constant LUE_{ref} ($R^2=0.14$).

452 We then used our reference LUE model to partition GEP variability to different causes.
453 We found that at hourly timescales, modeled GEP of “full” scenario (driven by both
454 environmental and biotic factors, explaining 77% of EC-derived GEP) was most sensitive to
455 variation in environmental drivers (explaining 75 % of variance in EC-derived GEP), and as
456 expected, least sensitive to variation in LUE_{ref} (1% of variance in EC-derived GEP explained),
457 which is assumed to be constant within a month (Fig. 5). The environmental variability becomes
458 less important in affecting modeled GEP at progressively longer timescales, with 58%, 3%, and
459 11% of the variance in EC-derived GEP attributable to variation in environmental drivers at
460 daily, monthly, and yearly timescales respectively (Fig. 5). Meanwhile, variation in the biotic
461 response becomes progressively more important in determining EC-derived GEP, with 6%, 63%,
462 and 76% of the variance in EC-derived GEP can be attributed to variation in LUE_{ref} at daily,
463 monthly, and yearly timescales respectively (Fig. 5).

464

465 *LUE modeling: characterizing environmental responses*

466 The coefficients for the “full” model driven by both time varying environmental drivers and
467 monthly LUE_{ref} were reported in Table S2, including $f_{env,ref}$ (the scaling constant in Eq. 5), k_{CI}
468 (the coefficient of GEP sensitivity to CI), k_w (the coefficient of GEP sensitivity to VPD), and
469 PAR_0 (the Michaelis-Menten constraint of PAR on photosynthesis). These coefficients indicated
470 that photosynthesis was: (1) ~3.06 times as efficient under fully diffuse light as under fully direct
471 light, and (2) ~1.92 times as efficient without VPD stress as under the maximum VPD stress
472 (~2.5 kpa at k67 site).

473 With the model coefficients (Tables S2) and empirical correlations among environmental
474 variables (Table S1), we then assessed how environmental variables independently and jointly
475 controlled photosynthesis. Fig. 6a shows that photosynthesis responds monotonically to CI,
476 VPD, and PAR individually. However, when considering the correlations among environmental
477 variables (Fig. 6b), we found that: (1) the combined effect of PAR and CI led to a concave
478 photosynthetic response, with the maximum photosynthesis at the moderate CI; and (2) the
479 combined effect of PAR, CI, and VPD also led to a concave response, but with increased
480 curvature and with the maximum photosynthesis reached when CI is around 0.42. This optimal
481 CI value differentiated a “light limited regime” from a “stomatal limited regime” (Fig. 6b).

482 The hump-shaped relationship of Fig. 6b has important implications for the environmental
483 sensitivity of tropical forest physiological response in wet vs. dry seasons. Relative to current
484 seven-year environmental conditions, we simulated how the k67 forest GEP_{norm} responded to a
485 reduction in CI (typically associated with more sunlight, less rainfall, and higher VPD; Table
486 S3), generally seen during atmospheric drought conditions in the Amazon basin. Our results
487 showed that with CI reduction and associated increase in PAR, VPD and T_a (Fig. S6), the
488 integrated environmental effect led to an initial increase and then a decrease in wet season
489 modeled GEP_{norm} and a continuous decrease in dry season modeled GEP_{norm} (Fig. 6d). This is
490 because wet season environmental conditions tend to be cool, humid, and less bright, while the
491 dry season conditions are already hotter, less humid, and brighter (Fig. 6c). In addition, our
492 results also indicated that modeled GEP_{norm} at k67 had small sensitivity to moderate fluctuations
493 in CI; a reduction of CI by 0.1 (a ~20% change in CI), associated with an increase in midday
494 PAR of ~220 $\mu\text{mol}/\text{m}^2/\text{s}$ and an increase in midday VPD of ~170 Pa (Fig. S6), causing absolute
495 changes of less than 3% in modeled GEP_{norm} in both wet and dry seasons (Fig. 6d and Table S3).

496 Since modeled GEP_{norm} of this forest had small sensitivity to environmental variability (Fig.
497 6d), and dry season of this forest is more likely to be within its “stomatal limited regime” (Fig.
498 6b and Fig. 6c), we found, as expected, that the mean seasonality of modeled GEP driven by
499 environment alone showed inadequate seasonal variation (Fig. 7), accounting for only ~15% of
500 mean seasonality of observed GEP. By contrast, the model driven by biotically-controlled LUE_{ref}
501 alone well tracked the mean seasonality of observed GEP ($R^2=0.90$; Fig. 7), due to a strong dry-
502 season increase in canopy photosynthetic infrastructure, not captured by the environment-only
503 model. The main deviation for biotic-only model was late in the dry season (October to

504 December), when observed GEP fell significantly below that predicted by LUE_{ref} , consistent
505 with environment-driven stomatal limitation that prevented the canopy's full photosynthetic
506 efficiency from being utilized (Fig. 6b and Fig. 6c). This late dry-season suppression of GEP by
507 stomatal limitation was captured by both models which included environmental drivers (the
508 environment-only model and the full model).

509

510 *Decoupling the effects of T_a and VPD on GEP_{norm}*

511 Our analysis indicated that GEP_{norm} showed a nearly monotonic decline with VPD when
512 adjusted for T_a (and PAR and CI) (Fig. 8a; t-test for slopes under each reference T_a is
513 significantly different from 0, with $p=0.0251$), but that GEP_{norm} showed little change with T_a ,
514 when adjusted for VPD (and PAR and CI) (Fig. 8b; t-test for slopes under reference VPD is
515 insignificantly different from 0, with $p=0.0875$). These results together suggest that VPD is even
516 more direct control on GEP_{norm} . This analysis is consistent with the results from path analysis
517 (Fig. 2), suggesting that VPD is the direct control on GEP_{norm} .

518

519 *Environmental controls on inter-annual variability of monthly LUE_{ref}*

520 Our analysis showed that there was a strong, but lagged, correlation between environmental
521 variables (PAR, VPD, and Rainfall) and LUE_{ref} at monthly timescales over seven-year
522 observations at k67 (Fig. 4 and Table 1), with LUE_{ref} best tracking PAR from 3 months earlier
523 ($R^2=0.38$, $p<10^{-5}$), VPD from 3 months earlier ($R^2=0.24$, $p<10^{-5}$), CI from 4 months earlier
524 ($R^2=0.38$, $p<10^{-5}$), and Rainfall from 4 months earlier ($R^2=0.42$, $p<10^{-5}$).

525

526 **Discussion**

527 This work allows us to address three main questions about the regulation of photosynthesis in
528 tropical forests, and also to consider limitations in our ability to answer these questions.

529

530 *How do environmental drivers control hourly GEP in an evergreen tropical forest?*

531 Our analysis confirms that variation of environmental drivers is the dominant control on the
532 variation of tropical forest GEP at hourly to daily timescales (through direct plant physiological
533 response), as suggested by previous studies (Goulden *et al.*, 2004; Hutyyra *et al.*, 2007; Oliveira *et*
534 *al.*, 2007; Doughty & Goulden, 2008a; Cirino *et al.*, 2014). This shorter-timescale physiological

535 response follows a positive response to variations in light availability (PAR and CI) and a
536 negative response to atmospheric water deficit (VPD) (Figs. 2 and Fig. 6). We are also able to
537 model these responses by a parsimonious LUE-based photosynthesis model (Eq. 22; explaining
538 $R^2=77\%$ of EC-derived GEP; Fig. 3a).

539 This analysis allows us to investigate the cause for previously reported observations (at a
540 nearby evergreen forest site) that at given PAR, hourly GEP is higher in the morning than in the
541 afternoon (Doughty *et al.*, 2006). It had been suggested that a combination of increased
542 evapotranspiration demand and plant-endogenous circadian rhythms might explain the afternoon
543 decline in light sensitivity of GEP in this tropical forest (Goulden *et al.*, 2004; Doughty *et al.*,
544 2006). Our LUE-based photosynthesis model, by including environmental variables beyond
545 PAR, can well simulate the diel patterns of GEP (Fig. 3a and Fig. S7), confirming that
546 physiological response to higher afternoon evaporative demand is sufficient to account for
547 observed diel patterns in GEP. In addition, our analysis confirms the positive effect of moderate
548 cloudiness on GEP as reported by earlier studies (Gu *et al.* 2002, 2003; Mercado *et al.*, 2009;
549 Oliveira *et al.*, 2009; Cirino *et al.*, 2014).

550 Our study highlights the importance of accounting for correlations among environmental
551 drivers (e.g., CI, PAR, and VPD), and between these drivers and the underlying biotic factor (i.e.
552 LUE_{ref}) on which these drivers act. Such accounting shows that the normalized GEP (GEP_{norm})
553 is much less sensitive to environmental variability than previously reported -- e.g. a reference
554 20% change in CI has only <3% effect on GEP_{norm} (Fig. 6d, Fig. S6, and Table S3), about four-
555 fold less than in other studies (Oliveira *et al.*, 2007; Doughty & Goulden, 2008a; Lee *et al.*,
556 2013; Cirino *et al.*, 2014). The underlying reason for low sensitivity of GEP_{norm} to environmental
557 variation is twofold: (1) the correlated changes in CI, PAR, and VPD tend to compensate for one
558 another when acting on given LUE_{ref} (e.g. the positive effect of increasing PAR is partly
559 canceled by the correlated negative effect of increasing VPD), reducing the overall effect of
560 changing climate on GEP_{norm} , and (2) normalizing for biotic changes in canopy photosynthetic
561 efficiency allowed us to more accurately quantify the effects of environmental variation on that
562 canopy infrastructure, without being confounded by simultaneous changes in both drivers and
563 the model parameters to respond to those drivers (Wu *et al.*, 2016). Since GEP_{norm} had much
564 lower seasonal variation than did raw GEP (Fig. 7), our work further highlights the importance

565 of representing variation of the biotic factor (LUE_{ref}) in explaining GEP variability over longer
566 timescales in the tropics (see the question below).

567

568 *What are the relative contributions of environmental and biotic factors in controlling GEP*
569 *across timescales?*

570 Our finding that environmental variation alone explains progressively less GEP variability at
571 longer and longer timescales is consistent with similar findings in temperate biomes (Hui *et al.*,
572 2003; Richardson *et al.*, 2007; Urbanski *et al.*, 2007; Teklemariam *et al.*, 2010; Marcolla *et al.*,
573 2011; Wu *et al.*, 2012). However, this trend is much more pronounced at this tropical site, with
574 environmental variation accounting for only ~10% or less of GEP at longer timescales (i.e.
575 monthly and yearly), as compared to ~30% or more in a temperate forest (Richardson *et al.*,
576 2007; Urbanski *et al.*, 2007). This difference might be attributed to much smaller environmental
577 variability in the tropics, and to canopy photosynthetic efficiency in the tropics being less tightly
578 synchronized with environmental variability (Table 1). Our seven-year dataset is not long
579 enough to draw strong inferences about the controls on inter-annual GEP variability, and so the
580 pattern found in this study remains to be tested with a longer data record and more tropical forest
581 sites in future. However, this work shows that the environmental responses that explain most of
582 the hourly variability in GEP do not explain its seasonal or inter-annual variability, highlighting
583 that understanding and modeling the long term dynamics of GEP in response to environmental
584 drivers may be especially challenging in the tropics.

585 Variation in canopy photosynthetic efficiency (i.e. monthly LUE_{ref}) may arise from
586 seasonal and inter-annual patterns of leaf dynamics (flushing and abscission drive variations in
587 canopy leaf area and changes in the age composition of the canopy). Wu *et al.* (2016) suggested
588 that seasonal variation in leaf demography (i.e. leaf age composition) and in leaf ontogeny (i.e.
589 age-dependent photosynthetic efficiency) jointly explained as much as 91% of average LUE_{ref}
590 seasonal variability. This suggests that one way to improve model representation is the direct
591 inclusion of prognostic modeling of demographic processes in leaves and canopies (e.g. Kim *et*
592 *al.*, 2012).

593 However, understanding and quantitative representation of the biological mechanisms
594 underlying this demographically-induced LUE_{ref} seasonality and inter-annual variability are still
595 largely lacking. Our analysis showed that there is no direct instantaneous environmental control

596 on inter-annual variability of monthly LUE_{ref} (Table 1). Instead, LUE_{ref} well tracked preceding
597 environmental drivers (i.e. PAR with $R^2=0.38$) of 3 months at k67 site (Table 1). This preceding
598 environmental control on LUE_{ref} inter-annual variability might be as a consequence of leaf
599 maturation time to transfer from newly flushing leaves of low photosynthetic efficiency to
600 mature leaves with maximum photosynthetic efficiency (Wu *et al.*, 2016). In addition, leaf
601 demography may also arise from other biological mechanisms, including adaptations to avoid
602 herbivores or pathogens (Lieberei, 2007) or for optimal carbon acquisition under seasonally and
603 inter-annually varying resource availability (Kikuzawa, 1991; Wright & van Schaik., 1994;
604 Kikuzawa, 1995; Wright, 1996; Guan *et al.*, 2015; Brienen *et al.*, 2015). To empirically test
605 environmental control on LUE_{ref} variability, and, also to reconcile different mechanisms of leaf
606 demography (and demography induced LUE_{ref}) thus require an inter-disciplinary approach to
607 expand our observation skills across time, space, and spatial resolutions, and will be critical to
608 understanding the long-term response and resiliency of tropical forests to changing climate.

609 In addition to demography (Wu *et al.*, 2016), LUE_{ref} might also be sensitive to physiological
610 acclimation of given assemblages of leaves to seasonal or inter-annual environmental variability,
611 as well as physiological response to extreme climatic events. The physiological acclimation
612 might be associated with the plasticity response of tropical trees to longer-timescale
613 environmental variability (e.g. Strauss-Debenedetti & Bazzaz, 1991), which might be embedded
614 in the tradeoffs among covarying environmental variables, and biotic versus environmental
615 controls on response to those tradeoffs, which is too complex to objectively resolve from tower-
616 flux observations and the simple modeling proposed here. Therefore, it is yet pending to be
617 tested and quantified on the role of physiological acclimation over longer-timescale
618 photosynthetic response in future studies (and, ideally, manipulative experiments). Moreover, the
619 extreme events, such as drought in Amazon, could influence LUE_{ref} variability by forcing the
620 variation in carbon allocation among roots, stems, and leaves as a response to climatic stress
621 (Doughty *et al.*, 2015), or imposing the forest disturbance and associated tree mortality, and thus
622 changing LUE_{ref} through the changes in both leaf demography and canopy leaf area. A thorough
623 understanding of how LUE_{ref} varies with climate extremes and how LUE_{ref} changes during
624 forest post-disturbance recovery is thus greatly needed.

625

626 *Can canopy photosynthetic efficiency-normalized GEP help to resolve longstanding debates*
627 *about environmental limitations and sensitivity to temperature in tropical evergreen forests?*

628 As discussed above, separating the effects of changing environmental drivers from biotic
629 changes in canopy photosynthetic efficiency allows for a more accurate quantification of the
630 effects of environmental variability. Results from this holistic approach enable us to revisit two
631 long-running debates in tropical forest function.

632 a. Water versus light limitation. Whether tropical evergreen forests are light limited or water
633 limited has been a longstanding and controversial question in tropical ecology, as tropical
634 evergreen forests maintain high GEP and evapotranspiration during the dry season while most
635 earth system models simulate dry season declines in GEP and evapotranspiration (Saleska *et al.*,
636 2003; Baker *et al.*, 2008; Lee *et al.*, 2013; Wu *et al.*, 2016; Restrepo-Coupe *et al.*, 2016). Our
637 results here suggest that both light and water limitations co-occur and operate at different
638 timescales in tropical evergreen forests.

639 Fig. 6a shows that light availability (via $PAR \times CI$) and water deficit (via VPD and VPD
640 induced stomatal closure) are jointly associated with increases and decreases, respectively, in
641 hourly GEP. At monthly timescales, we observed increases in both GEP and canopy
642 photosynthetic efficiency (LUE_{ref}) during periods with higher sunlight, even during the dry
643 season (Fig. 4 and Fig. 7). This observation suggests that even during the dry season, water
644 supplies are sufficient to support canopy development, which increases LUE_{ref} . However,
645 simulations that only consider the variation of LUE_{ref} overestimate GEP in the dry season (Fig.
646 7). This pattern suggests that dry season LUE_{ref} is not water-limited (as LUE_{ref} increases with
647 increasing water deficit in the dry seasons), but that dry season GEP_{norm} , relative to its potential
648 photosynthetic efficiency, is water limited (e.g. decreases with increasing water deficiency, or
649 higher VPD, in the dry season; Fig. 6c, Fig. 6d and Fig. 7). The increase in LUE_{ref} during dry
650 season might be facilitated because ground water storage (recharged by excess wet-season
651 precipitation input) is enough to support the evapotranspiration demand, and thus the forest as a
652 whole overbuilds the capability to take advantage of excess light availability in the dry season
653 (Kikuzawa, 1995; Guan *et al.*, 2015; Doughty *et al.*, 2015). Our analysis is thus consistent with
654 light limitation of canopy development of photosynthetic efficiency (LUE_{ref}), and with water
655 limitation of stomatal conductance, both simultaneously operating during the dry season.

656

657 *b. Tropical forest sensitivity to temperature.* Our finding that temperature had no detectable
658 direct effect on GEP_{norm} (only the indirect effect via VPD; Fig. 2 and Fig. 8) has important
659 implications for the ongoing debate about the temperature sensitivity of tropical forests. Doughty
660 & Goulden (2008a) and Clark *et al* (2013) argued that carbon uptake in tropical forest was
661 limited by high temperature, while Lloyd & Farquhar (2008) argued that observed declines in
662 uptake with temperature were not due to high temperature *per se*, but to the associated increase
663 in VPD that induced stomatal closure. Our path analysis suggests that in our record of
664 observations, temperature affects GEP indirectly through its effect on VPD (Fig. 2). This
665 interpretation is confirmed by bivariate analysis of temperature and VPD, which could detect no
666 effect of temperature that was independent of VPD (Fig. 8). Tropical forest carbon uptake may
667 still be limited by temperature, but that limit is not evident over the range of temperatures
668 observed at this forest site.

669

670 *Possible caveats and limitations*

671 The current study has two interpretive limitations. One is the lack of explicit consideration of soil
672 moisture. Soil moisture can have an important influence on photosynthesis (Kapos, 1989; Baker
673 *et al.*, 2008; Brando *et al.*, 2008); excluding it from analysis might affect our derived canopy
674 photosynthetic efficiency (LUE_{ref}) and f_{env} terms in the LUE-based photosynthesis modeling.
675 However, even if not explicitly included, its effects are likely well represented indirectly: VPD
676 and soil moisture are highly correlated in tropical forests, and they both regulate plant
677 physiological processes through stomatal conductance (Meir *et al.*, 2009; Brando *et al.*, 2010;
678 Lee *et al.*, 2013). This suggests that much of the soil moisture effect on photosynthesis might
679 already be captured by the inclusion of VPD in our analysis. Second, even if a substantial soil
680 moisture effect was not captured by VPD, our results are likely robust. As soil moisture should
681 be lower in the dry season than in the wet season (Baker *et al.*, 2008; Meir *et al.*, 2009; Brando *et al.*,
682 2010), the consideration of soil moisture should reduce modeled dry-season photosynthesis
683 (i.e. our current LUE model might overestimate dry season photosynthesis) and increase the
684 estimate of dry-season canopy photosynthetic efficiency (e.g. Fig. S4 in Wu *et al.*, 2016). Thus
685 our observation of dry-season green-up (increase in LUE_{ref}) would be even larger, and the effects
686 we see resulting from LUE_{ref} on GEP would if anything be stronger than reported here, relative
687 to the effect of environmental variation on GEP (Wu *et al.*, 2016).

688 The other possible limitation comes from our LUE-based photosynthesis modeling approach,
689 which is a simplified representation of canopy photosynthesis. We assumed that the
690 environmental effects on canopy photosynthesis could be represented by the multiplication of
691 environmental stressors (Eq. 22), each described by a linear function. Possible nonlinear
692 responses and feedbacks are thus neglected in this parameterization. In addition, it is still
693 uncertain whether the model parameterized at one site can be extended to other tropical forest
694 sites, or into the future climate beyond the current environmental range. However, with these
695 caveats aside, it is clear that the model successfully reproduces the measured fluxes across a
696 range of time scales (Fig. 3a-d).

697

698 *Implications*

699 In contrast to modeling approaches that assume metabolic variation in tropical evergreen forests
700 can be represented largely as a response to environmental variation, our case study of forest
701 photosynthesis suggests that metabolism in these systems is importantly driven by both
702 environmental variation (at shorter timescales) and by longer-timescale biological rhythms that
703 are decoupled from the environment. By accounting for this decoupling, our approach can
704 reframe longstanding debates about functioning of tropical evergreen forests. It suggests, for
705 example: (1) that water availability limits instantaneous photosynthetic activity of existing
706 leaves, but not canopy scale development of overall photosynthetic function (which is driven by
707 the phenology of leaf production, development, and abscission); and (2) that although forest
708 photosynthesis is limited by atmospheric water deficit which in turn limits canopy conductance,
709 these forests are not currently reaching a temperature threshold above which photosynthetic
710 activity declines due to thermal stress.

711 The method used here to partition environmental and biotic controls on photosynthesis
712 could also be used to tackle a range of questions about tropical forest function. For example, it
713 may be applicable to the study of ecosystem respiration and transpiration, processes also subject
714 to these controls (Hutyra *et al.*, 2007; Phillips *et al.*, 2009; Brienen *et al.*, 2015). In addition, this
715 partitioning approach might provide insight into whether there are systematic differences
716 between temperate and tropical zones in the relative importance of environmental and biotic
717 controls on ecosystem metabolism—the biotic control in temperate biomes (i.e. leaf phenology)
718 being more tightly synchronized with environmental seasonality than in tropical biomes (Cleland

719 *et al.*, 2007). Finally, our results also suggest that failing to account for biotically regulated
720 variations in canopy photosynthetic light-use efficiency (i.e. LUE_{ref}), risks inaccurate model
721 predictions of tropical forest GEP at longer timescales. We have shown that the variation in
722 monthly LUE_{ref} —arising from phenology of leaf quality (Wu *et al.*, 2016) and possibly from
723 biological responses to climate extremes (Doughty *et al.*, 2015) and disturbance (Anderegg *et al.*,
724 2015)—is a key driver of seasonal and inter-annual changes in tropical evergreen forest GEP.
725 Therefore models that accurately simulate seasonal and inter-annual changes in biotically
726 regulated functions like LUE_{ref} will be critical to predicting future tropical forest carbon
727 dynamics.

728

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738

739 **Author contributions**

740 J.W., S.R.S., K.G., and M.H. designed the research. J.W., S.R.S., N. R., M.H., K.T. W., R.da.S.,
741 A.C.A., R.C.O., and P.B.C. contributed to installation, maintenance, or processing of eddy
742 covariance data. J.W. performed the data analysis. J.W. drafted the manuscript, and S.R.S., K.G.,
743 X.X., B.O.C., M.H., N.R., R.W., A.R.H., R.K.M., K.T.W., and M.G. contributed to writing the
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984
 985 **Table 1.** Environmental controls on inter-annual variation of monthly LUE_{ref} over seven years
 986 at k67 site. Two metrics, R² (coefficient of determination) and p (significant level) were used for
 987 measuring the correlations between environmental drivers and LUE_{ref}. Four environmental
 988 variables were analyzed including EC-derived PAR, VPD, and CI, and satellite TRMM derived
 989 Rainfall. Time lapse i refers to the variation in environmental drivers is the ith month preceding
 990 the variation on LUE_{ref}.

991

	lapse 0	lapse 1	lapse 2	lapse 3	lapse 4	lapse 5	lapse 6
LUE _{ref} -PAR	(R ² =0.04; p=0.07)	(R ² =0.05; p=0.04)	(R ² =0.23; p<10 ⁻⁵)	(R ² =0.38; p<10 ⁻⁵)	(R ² =0.34; p<10 ⁻⁵)	(R ² =0.17; p=0.0003)	(R ² =0.01; p=0.34)
LUE _{ref} -VPD	(R ² =0.00; p=0.93)	(R ² =0.02; p=0.0004)	(R ² =0.14; p<10 ⁻⁵)	(R ² =0.24; p<10 ⁻⁵)	(R ² =0.19; p<10 ⁻⁵)	(R ² =0.05; p=0.00002)	(R ² =0.00; p=0.68)
LUE _{ref} -CI	(R ² =0.31; p=0.005)	(R ² =0.00; p=0.79)	(R ² =0.08; p=0.01)	(R ² =0.28; p<10 ⁻⁵)	(R ² =0.38; p<10 ⁻⁵)	(R ² =0.32; p<10 ⁻⁵)	(R ² =0.09; p=0.01)
LUE _{ref} - Rainfall	(R ² =0.03; p=0.14)	(R ² =0.01; p=0.40)	(R ² =0.14; p=0.0005)	(R ² =0.30; p<10 ⁻⁵)	(R ² =0.42; p<10 ⁻⁵)	(R ² =0.34; p<10 ⁻⁵)	(R ² =0.05; p=0.06)

992

993

994

995 **Figure captions**

996

997 **Figure 1:** Flow-chart of the analysis of photosynthesis-environment relationships in a tropical
998 evergreen forest.

999

1000 **Figure 2:** Path diagrams illustrate environmental controls on (a) the logarithm of the canopy
1001 photosynthetic efficiency-normalized light-use-efficiency, or $\text{Log}(\varepsilon_{norm})$, and (b) the canopy
1002 photosynthetic efficiency-normalized GEP (GEP_{norm}). We use seven years of hourly daytime
1003 measurements at k67 site for the analysis. The thickness of each arrow indicates standardized
1004 correlation coefficients, or path value, (see legend). All the paths shown here are statistically
1005 significant ($p < 0.001$). The sub-diagram of environmental variables is colored grey.

1006

1007 **Figure 3:** GEP-model validation across a wide range of timescales: (a, e) hourly, (b, f) daily, (c,
1008 g) monthly, and (d, h) yearly timescales. GEP models used here include the “full” model (top
1009 panel; using the reference LUE-based photosynthesis model, driven by both time-varying
1010 environmental drivers and monthly LUE_{ref}) and the “Env” model (bottom panel; using reference
1011 LUE-based photosynthesis model, driven by time-varying environmental drivers only with a
1012 constant LUE_{ref}). The model is trained by the data of years 2003, 2005, 2009, and 2011, and
1013 validated by the independent data of years 2002, 2004, and 2010. Observed GEP refers to eddy
1014 covariance derived GEP. Fig. 3a-c and Fig. 3e-g shown for the validation data, and Fig. 3d and
1015 Fig. 3h shown for all 7-year data.

1016

1017 **Figure 4:** Inter-annual variation of monthly environmental variables, biotic factor (LUE_{ref}), eddy
1018 covariance (EC) derived GEP, and LUE-based model simulated GEP. (a) Inter-annual variation
1019 of four monthly environmental drivers: satellite TRMM based Rainfall (grey bar) and EC-
1020 derived PAR (red), VPD (blue), and CI (light blue); (b) Inter-annual variation in biotic factor
1021 represented by three temporal resolutions of LUE_{ref} (monthly in green, to a mean seasonal cycle
1022 (one data point for each month of the year) in blue, to a constant LUE_{ref} derived as the mean of
1023 the entire monthly timeseries in orange) at k67 site; (c) Inter-annual variation in EC-derived GEP
1024 (black), explained by LUE-based model simulated GEP driven by time varying environmental
1025 drivers and a constant LUE_{ref} (orange; $R^2=0.14$; $p < 10^{-5}$), driven by time varying environmental

1026 drivers and a mean seasonal cycle of LUE_{ref} (blue; $R^2=0.61$; $p<10^{-5}$), and driven by time varying
1027 environmental drivers and monthly LUE_{ref} (green; $R^2=0.74$; $p<10^{-5}$).

1028

1029 **Figure 5:** Fraction of EC-derived GEP explained by environmental drivers (grey squares), by the
1030 biotic factor (LUE_{ref} , grey triangles), and by a full LUE-based model that includes both
1031 components (black circles), as a function of timescale of observation. Partitioning among model
1032 components used a sums-of-squares approach, as given by Eqs 19-21.

1033

1034 **Figure 6:** Model simulated photosynthetic response to environmental drivers (f_{env}) under given
1035 biotic control (i.e. a fixed LUE_{ref}) based on the reference LUE-based photosynthesis model (Eq.
1036 22; coefficients from Table S2) and correlations among environmental drivers (Table S1),
1037 expressed as a function of CI (with PAR and VPD being expressed as a linear function of CI; see
1038 Table S1). (a) Model simulated environmental response to each environmental driver [CI in
1039 black squares (CI_{scalar} ; Eq. 14); PAR in grey circles ($L_{scalar} \times PAR$; Eq. 11); VPD in grey triangles
1040 (W_{scalar} ; Eq. 12)]; (b) Model simulated environmental response to joint environmental effects
1041 [total light effect in grey line ($CI_{scalar} \times L_{scalar} \times PAR$); joint light and water effect in black line
1042 $CI_{scalar} \times L_{scalar} \times PAR \times W_{scalar}$]; (c) Probability distribution of hourly CI observations for a given
1043 SZA bin ($20^\circ \leq SZA \leq 40^\circ$) for the wet season (black) and the dry season (grey) under current
1044 seven-year conditions; (d) Modeled GEP_{norm} response to CI reduction (corresponding to the
1045 increase in PAR and VPD; Fig. S6) relative to current seven-year conditions, for the wet season
1046 (black) and the dry season (grey). The grey dashed line in (b) and (c) indicate the optimal CI
1047 where GEP_{norm} is at its maximum.

1048

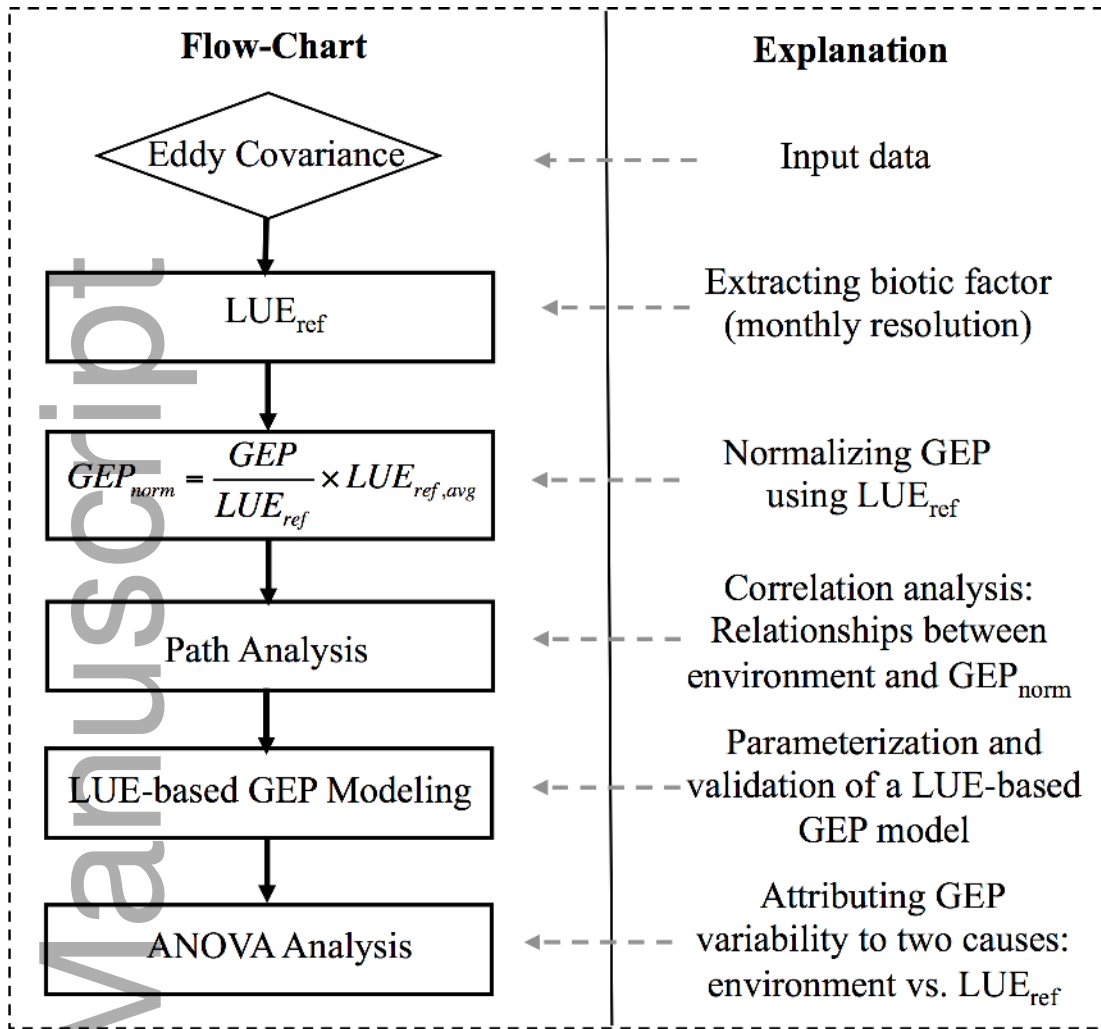
1049 **Figure 7:** Seven-year mean annual cycles of monthly EC-derived GEP (black squares, named as
1050 “EC-derived GEP”), modeled GEP with a constant LUE_{ref} and varying environmental drivers
1051 (grey triangles, named as “Env-modeled GEP”), and modeled GEP with monthly LUE_{ref} and
1052 constant environmental drivers (grey circles, named as “ LUE_{ref} -modeled GEP”). The dry season
1053 increase in LUE_{ref} (grey circles) is evidently not prevented by water limitation, but consistent
1054 with leaf/canopy physiological response (e.g. dry season stomatal closure), the realized GEP is

1055 lower, relative to LUE_{ref} in the dry season than in the wet season. Error bars are for 95%
1056 confidence intervals; Dry season is shaded in grey.

1057

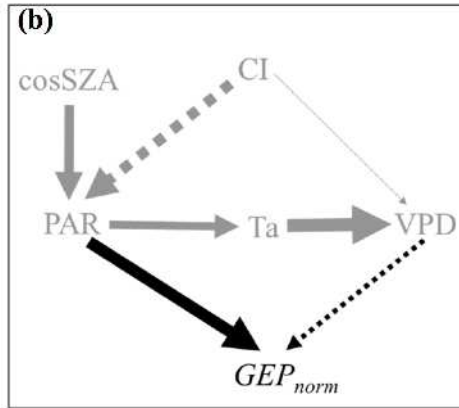
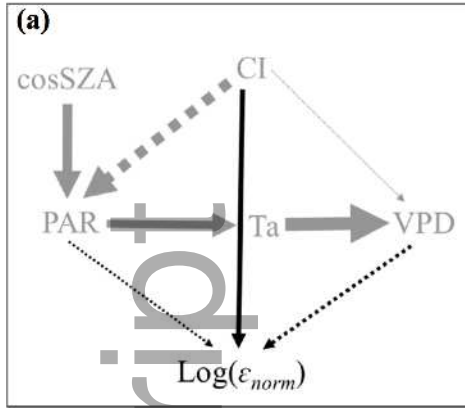
1058 **Figure 8:** Relationships between canopy photosynthetic efficiency normalized GEP (GEP_{norm} ,
1059 filtered by $PAR \geq 1500 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and VPD in (a), and GEP_{norm} and T_a in (b). All the
1060 hourly measurements at k67 site (years 2002-2005, 2009-2011) were used. Different colored
1061 lines in (a) represent different temperature (T_a) bins (1 °C bin). Different colored lines and
1062 symbols in (b) represent different VPD bins (200 pa bin). The central grey line indicates the
1063 overall bivariate relationship between GEP_{norm} and VPD (a) and T_a (b), without being
1064 conditioned by T_a in (a), or VPD in (b). Uncertainty bars indicate 95% confidence interval. The
1065 mean of all GEP_{norm} vs. VPD slopes in (a), each from a separate T_a bin, is significantly negative
1066 (t-test, $p=0.0251$), while the mean of all GEP_{norm} vs. T_a slopes in (b), each from a separate VPD
1067 bin, is statistically indistinguishable from 0 (t-test, $p=0.0875$).

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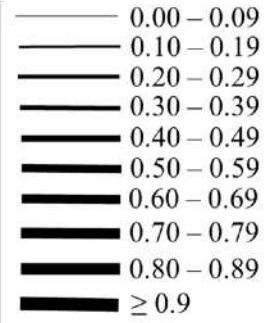


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Path Value (PV)

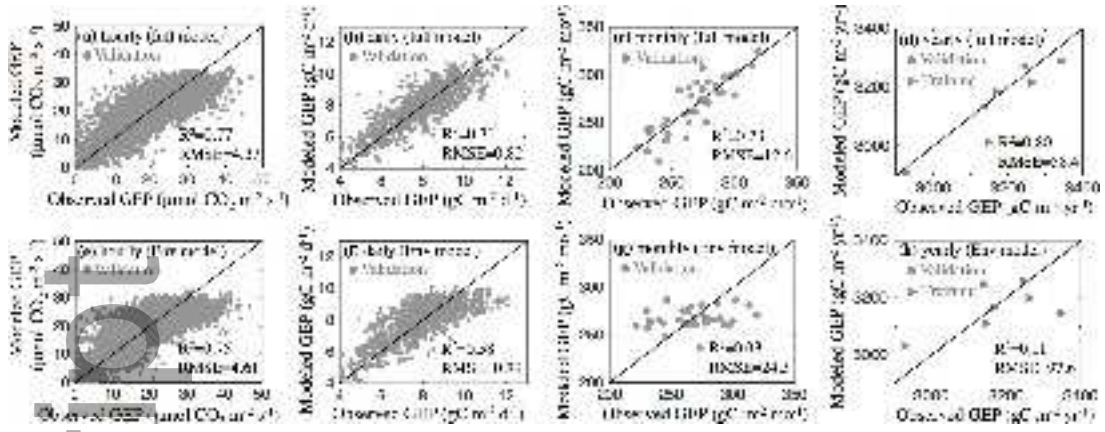


PV=standardized partial correlation coefficients

Dash line =negative PV

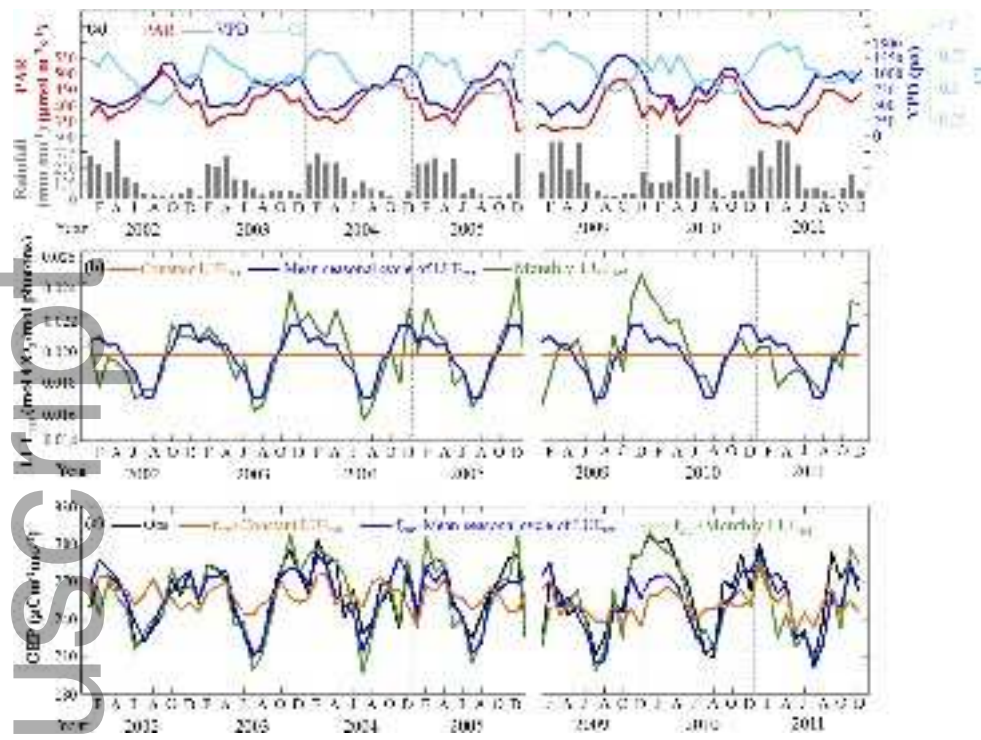
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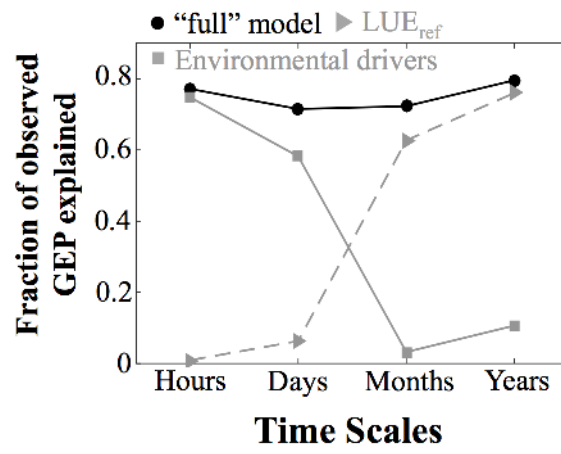


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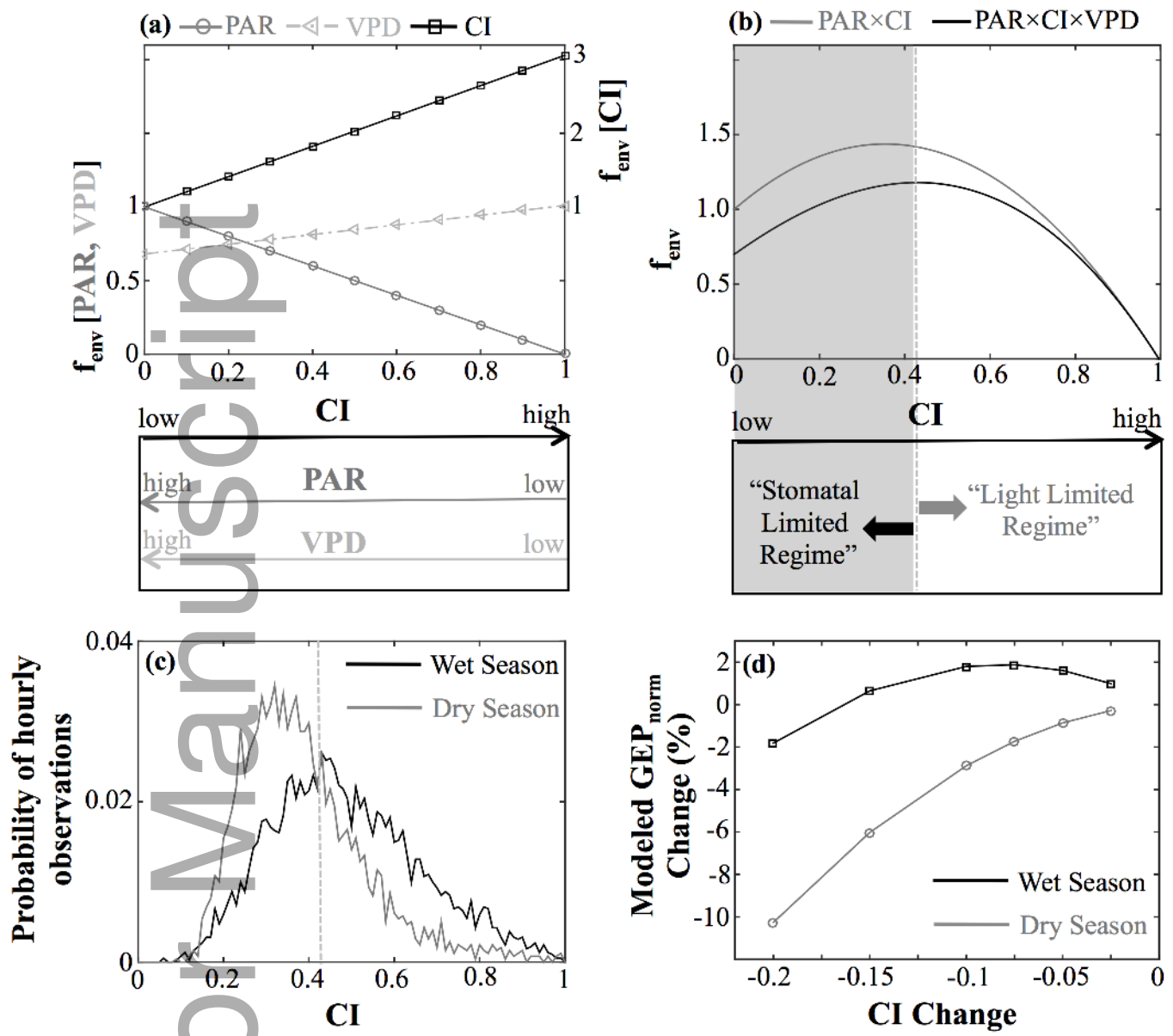
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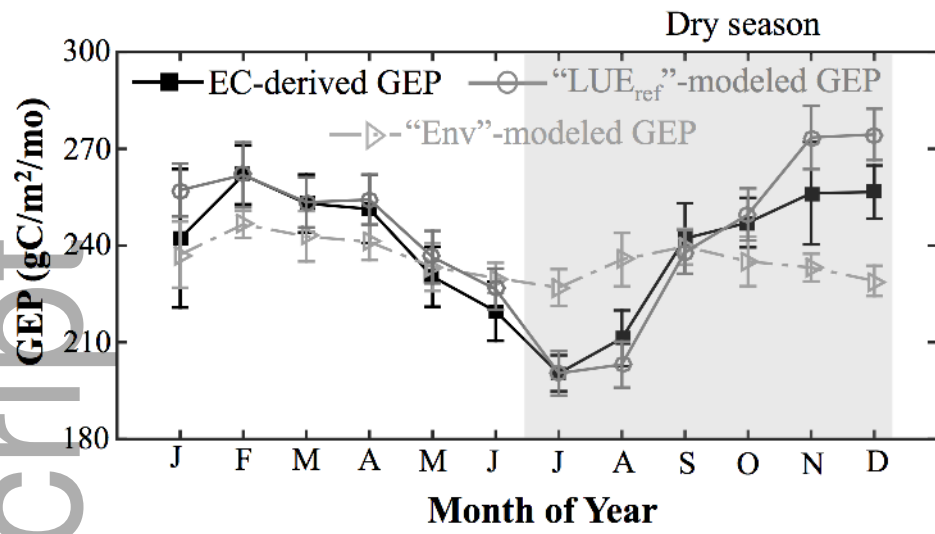
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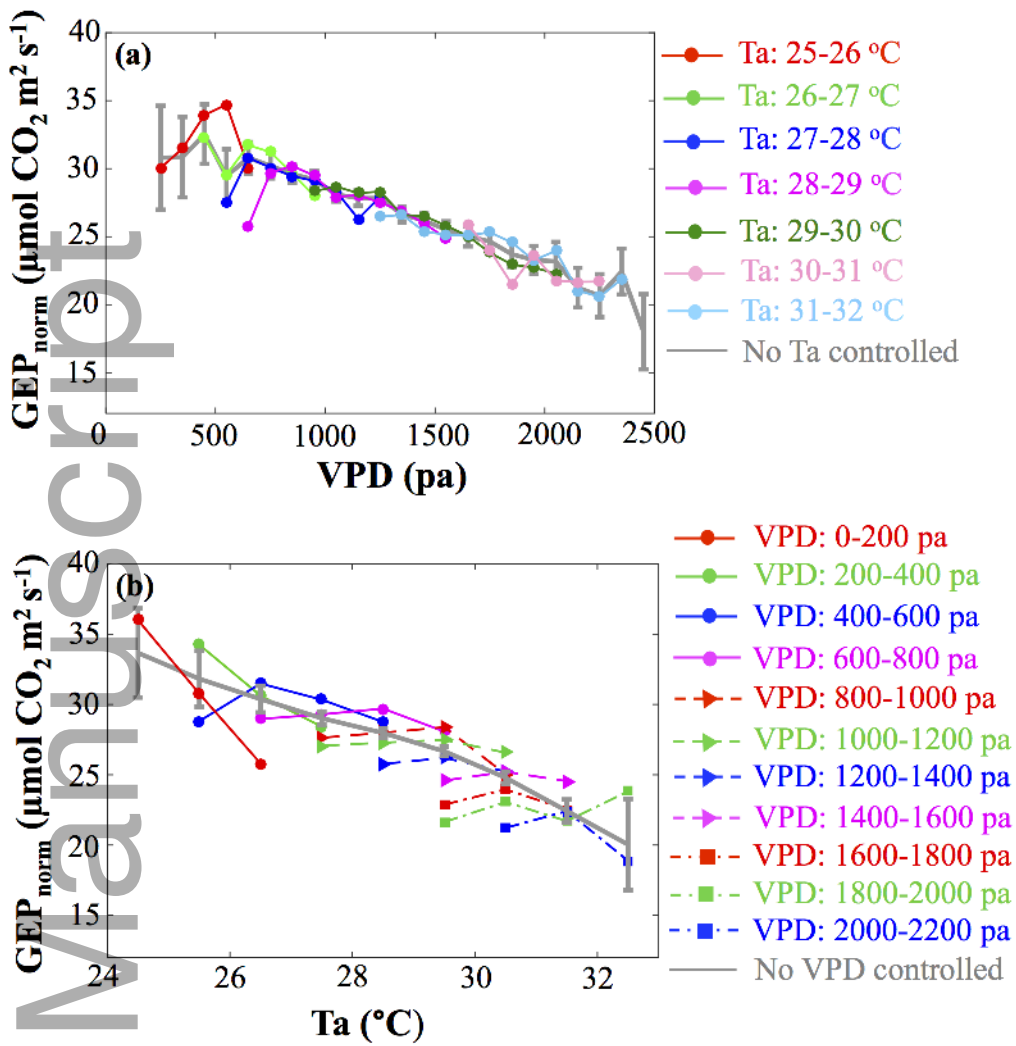
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