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

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Abstract

Gross ecosystem productivity (GEP) in tropical forests varies both with the environment and with biotic changes in photosynthetic infrastructure, but our understanding of the relative effects of these factors across timescales is limited. Here, we used a statistical model to partition the variability of seven years of eddy covariance-derived GEP in a central Amazon evergreen forest into two main causes: variation in environmental drivers (solar radiation, diffuse light fraction, and vapor pressure deficit) that interact with model parameters that govern photosynthesis and biotic variation in canopy photosynthetic light-use efficiency associated with changes in the parameters themselves. Our fitted model was able to explain most of the variability in GEP at hourly ($R^2 = 0.77$) to interannual ($R^2 = 0.80$) timescales. At hourly timescales, we found that 75% of observed GEP variability could be attributed to environmental variability. When aggregating GEP to the longer timescales (daily, monthly, and yearly), however, environmental variation explained progressively less GEP variability: At monthly timescales, it explained only 3%, much less than biotic variation in canopy photosynthetic light-use efficiency, which accounted for 63%. These results challenge modeling approaches that assume GEP is primarily controlled by the environment at both short and long timescales. Our approach distinguishing biotic from environmental variability can help to resolve debates about environmental limitations to tropical forest photosynthesis. For example, we found that biotically regulated canopy photosynthetic light-use efficiency (associated with leaf phenology) increased with sunlight during dry seasons (consistent with light but not water limitation of canopy development) but that realized GEP was nonetheless lower relative to its potential efficiency during dry than wet seasons (consistent with water limitation of photosynthesis in given assemblages of leaves). This work highlights the importance of accounting for differential regulation of GEP at different timescales and of identifying the underlying feedbacks and adaptive mechanisms.

Keywords: environmental limitation, leaf demography, leaf quality, leaf quantity, light-use efficiency, phenology, physiology, temperature sensitivity on productivity

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Introduction

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

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

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

Accurate identification of the causes of tropical forest GEP variability may help resolve several long-standing debates in tropical ecology. We focus here on two key debates about tropical forest function: First is the question of whether light or water resources are more limiting to tropical forest metabolism. Most modeling studies have represented tropical forest systems as water-limited, simulating dry-season declines in ecosystem-scale GEP and evapotranspiration (Werth & Avissar, 2004; Lee *et al.*, 2005; Christoffersen *et al.*, 2014). By contrast, many *in situ* and satellite studies show dry season increases in GEP or evapotranspiration in Amazon forests (Shuttleworth, 1988; Saleska *et al.*, 2003; Huete *et al.*, 2006; Restrepo-Coupe *et al.*, 2013; Guan *et al.*, 2015), but these findings are still controversial in the remote sensing literature (Morton *et al.*, 2014; Bi *et al.*, 2015; Saleska *et al.*, 2016).

The second debate is about whether tropical forests operate close to a temperature threshold, above which performance diminishes. Observational studies report declines in forest productivity and CO_2 uptake as temperature increases toward the upper end of the range under current climates and conclude that tropical forests operate close to a high temperature limit that may easily be exceeded under climate change (Clark, 2004; Doughty & Goulden, 2008a; Clark *et al.*, 2013; Cavaleri *et al.*, 2015). There are also studies arguing that the observed forest response to high temperature is likely a stomatal response to VPD due to its correlation with temperature (Lloyd & Farquhar, 2008). High VPD can induce stomatal closure and thus reduce GEP and evapotranspiration. Hence, the observed decline in photosynthesis might not be a direct temperature response and might be ameliorated by higher future CO_2 concentrations under climate change (Ainsworth & Long, 2005; Lewis *et al.*, 2009; Zhang *et al.*, 2015).

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

Materials and methods

Overview

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

Site description

The study site is the Tapajós National Forest, k67 eddy covariance tower site (54°58′W, 2°51′S), near Santarém, Pará, Brazil. It is an evergreen tropical forest on a well-drained clay-soil plateau, with a mean upper canopy height of ~40 m (Hutyra *et al.*, 2007). Mean annual precipitation is ~2000 mm yr^{-1} with a 5-month dry season (monthly precipitation < monthly evapotranspiration) from approximately mid-July to mid-December. Additional local site information can be found in Hutyra *et al.* (2007) and Restrepo-Coupe *et al.* (2013).

Measurements of fluxes and environmental drivers

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

After systematic data quality control and outlier removal (Wu *et al.*, 2016), hourly GEP was estimated by separating hourly net ecosystem exchange (NEE, in μmol CO_2 m^{-2} s^{-1}, with fluxes to the atmosphere defined as positive) into two components: ecosystem respiration (Reco) and GEP, where GEP = Reco - NEE. Reco was approximated by the average of valid nighttime NEE during well-mixed periods (u* criterion: ≥0.22 m s^{-1}; Hutyra *et al.*, 2007), interpolated into the daytime following the approach described in Restrepo-Coupe *et al.* (2013). Hourly GEP (μmol CO_2 m^{-2} s^{-1}) was further aggregated to daily steps (gC m^{-2} day^{-1}) by summing up all the effective measurements (u* criterion: ≥0.22 m s^{-1}) within a day. We also calculated the average daily GEP for each month during our study period.

The EC observations also included environmental drivers: photosynthetically active radiation (PAR), air temperature (Ta), and vapor pressure deficit (VPD) (Saleska *et al.*, 2003; Hutyra *et al.*, 2007). Diffuse light fraction is also available from June 2004 to December 2005, which was measured using a BF5 Sunshine Sensor (Delta-T Devices Ltd, Cambridge, UK) mounted at the tower. As diffuse light fraction (the ratio between diffuse and total PAR) can influence canopy-scale photosynthesis (Gu *et al.*, 2002, 2003b; Oliveira *et al.*, 2007; Mercado *et al.*, 2009; Cirino *et al.*, 2014) but was only measured for a short portion of the EC record, we used a simple 'Cloudiness Index' (acronym as 'CI' hereafter) as a proxy of light quality:

$$\text{CI} = 1 - \frac{\text{PAR}_{\text{obs}}}{\text{PAR}_{\text{clearsky}}} \tag{1}$$

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

We used rainfall measurements from the Tropical Rainfall Measuring Mission (TRMM) Multi-satellite Precipitation Analysis (TMPA) (product 3b42V6, integrating microwave and infrared satellite data with gauge data), which provides 0.25 degree and 3-hourly rainfall estimate for the Amazon from 1998 to the present (Huffman *et al.*, 2007). The monthly TRMM rainfall measurements centered on the k67 tower site from years 2002–2005 and years 2009–2011 were used in this study.

LAI measurements

Leaf area index (LAI), the quantity component of leaf phenology, influences ecosystem photosynthesis primarily by

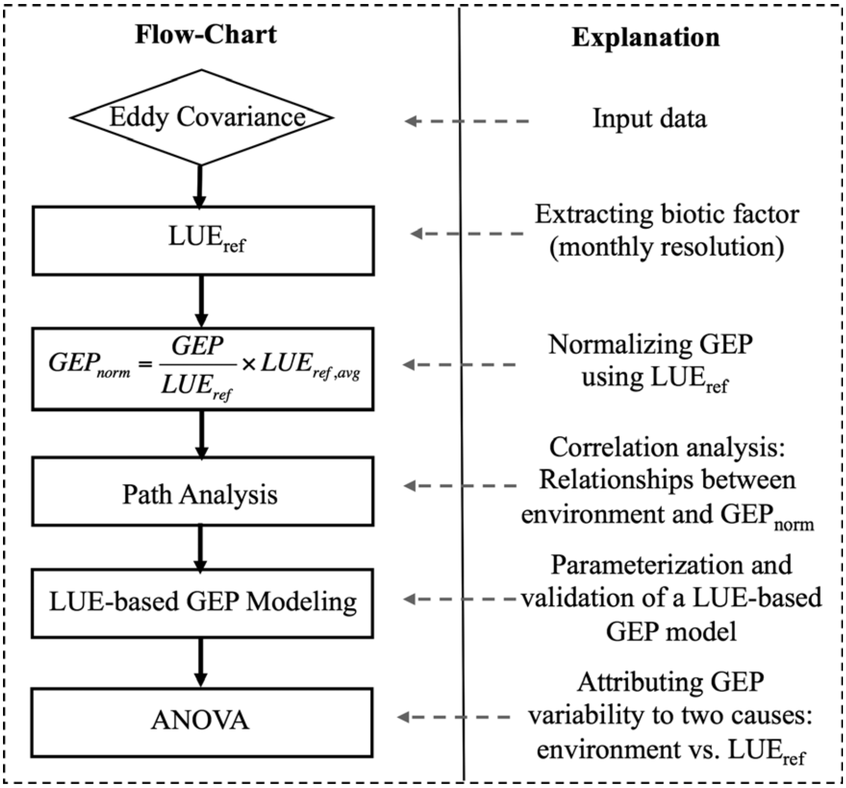

Fig. 1 Flowchart of the analysis of photosynthesis–environment relationships in a tropical evergreen forest.

regulating the fraction of PAR absorbed by the forest canopy (FAPAR). Here, we used a classic LAI-FAPAR relationship (Xiao *et al.*, 2004; Doughty & Goulden, 2008b) for estimating FAPAR:

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

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

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

Overview of the LUE-based photosynthesis modeling

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

$$\mathrm{GEP} = \varepsilon \times \mathrm{PAR} \tag{3}$$

where ε, or LUE, is the efficiency (mol CO_2 per mol photons) with which solar radiation (PAR) is used in photosynthesis (GEP). The term ε was calculated by Eqn (4) (Jarvis, 1976; Field *et al.*, 1995):

$$\varepsilon = \frac{\mathrm{GEP}}{\mathrm{PAR}} = \varepsilon_0 \times \mathrm{FAPAR} \times f_{\mathrm{env}} \tag{4}$$

where ε_0 is the intrinsic LUE of the canopy under nonstressed or reference environment condition, which is influenced by internal leaf properties such as leaf nitrogen (Field, 1983) or leaf age (Wilson *et al.*, 2001; Doughty & Goulden, 2008b). FAPAR is described by a classic LAI-FAPAR relationship in Eqn (2); f_{env} represents the joint environmental effects that downregulate ε (Jarvis, 1976; Field *et al.*, 1995; Gu *et al.*, 2002; Xiao *et al.*, 2005; Mahadevan *et al.*, 2008). The LUE-based photosynthesis model used here thus incorporates two kinds of control on vegetation photosynthesis: (i) a shorter-timescale photosynthetic response driven by light quantity (PAR) and other environmental drivers f_{env} and (ii) a longer-timescale response driven by changes in leaf quantity (which affects FAPAR) and leaf quality (which affects ε_0).

LUE$_{ref}$ and GEP$_{norm}$

To represent the capability of the canopy to photosynthetically assimilate CO_2 independent of fluctuations in environmental drivers, we estimated the incident light-use efficiency of the canopy under reference conditions (LUE$_{\mathrm{ref}}$). LUE$_{\mathrm{ref}}$ was estimated, following Wu *et al.* (2016) (where it was called canopy photosynthetic capacity, or PC), as the ratio of EC-derived

GEP and PAR under reference environmental conditions. The definition of $\mathrm{LUE_{ref}}$ (from Wu *et al.*, 2016) generalizes previous studies that removed the influence of varying PAR on GEP (Hutyra *et al.*, 2007; Doughty & Goulden, 2008b; Restrepo-Coupe *et al.*, 2013; Jones *et al.*, 2014) by further removing the influence of variation in other important environmental drivers (i.e., VPD, Ta, and CI) and SZA. The reference environmental conditions were taken as narrow bins of each driver: PAR = 1320 ± 200 μmol $\mathrm{m^{-2}}$ $\mathrm{s^{-1}}$, CI = 0.40 ± 0.10, VPD = 874 ± 200 Pa, and Ta = 27.7 ± 1.0 °C (8.1% of all hourly GEP observations, about 20 observations per month, on average). We assumed that $\mathrm{LUE_{ref}}$ is constant within a month (roughly the timescale needed for significant canopy changes) but that it can vary between months, following changes in LAI or in per-area photosynthetic efficiency. Because $\mathrm{LUE_{ref}}$ is derived from EC measurements, the question arises as to whether it is an adequately independent predictor of GEP, which is also derived from EC. However, changes in independent measurements of leaf-level photosynthetic capacity (or maximum carboxylation capacity of Rubisco, V_{cmax}), scaled to the canopy, are consistent with changes in $\mathrm{LUE_{ref}}$ (Wu *et al.*, 2016), lending confidence to our interpretation of $\mathrm{LUE_{ref}}$ as an accurate measure of ecosystem-scale photosynthetic infrastructure.

We note that the EC-derived $\mathrm{LUE_{ref}}$, interpreted in the context of the LUE-based photosynthesis modeling (Eqns 3 and 4), is proportional to $\varepsilon_0 \times \mathrm{FAPAR}$ with a scaling constant $f_{\mathrm{env,ref}}$ (Eqn 5; the environmental effect under reference conditions):

$$\mathrm{LUE_{ref}} = \varepsilon_0 \times \mathrm{FAPAR} \times f_{\mathrm{env,ref}} \tag{5}$$

Combining Eqns (3–5), we can further derive GEP and ε as functions of $\mathrm{LUE_{ref}}$:

$$\mathrm{GEP} = \frac{1}{f_{\mathrm{env,ref}}} \times \mathrm{LUE_{ref}} \times \mathrm{PAR} \times f_{\mathrm{env}} \tag{6}$$

$$\varepsilon = \frac{1}{f_{\mathrm{env,ref}}} \times \mathrm{LUE_{ref}} \times f_{\mathrm{env}} \tag{7}$$

Equations (6 and 7) thus summarize the photosynthesis process subject to the joint controls from longer-timescale biotic change in canopy photosynthetic efficiency (i.e., monthly $\mathrm{LUE_{ref}}$, which captures changes in LAI as well as changes in leaf-level photosynthetic efficiency aggregated to the canopy scale) and shorter-timescale environmental drivers (including hourly measurements of PAR and other variables). Using the EC-derived monthly $\mathrm{LUE_{ref}}$ over the seven-year time series, we further separated the shorter-timescale physiological response to environmental drivers from the longer-timescale biotic changes in canopy photosynthetic efficiency:

$$\mathrm{GEP_{norm}} = \frac{\mathrm{GEP}}{\mathrm{LUE_{ref}}} \times \mathrm{LUE_{ref,avg}} = \frac{\mathrm{LUE_{ref,avg}}}{f_{\mathrm{env,ref}}} \times \mathrm{PAR} \times f_{\mathrm{env}} \tag{8}$$

$$\varepsilon_{\mathrm{norm}} = \frac{\mathrm{GEP_{norm}}}{\mathrm{PAR}} = \frac{\mathrm{LUE_{ref,avg}}}{f_{\mathrm{env,ref}}} \times f_{\mathrm{env}} \tag{9}$$

where $\mathrm{LUE_{ref,avg}}$ is the mean value of monthly $\mathrm{LUE_{ref}}$ over the seven-year time series, and $\mathrm{GEP_{norm}}$ and $\varepsilon_{\mathrm{norm}}$ were GEP and ε normalized by $\mathrm{LUE_{ref}}$, respectively. Therefore, according to Eqns 8 and 9, $\mathrm{GEP_{norm}}$ is proportional to $\mathrm{PAR} \times f_{\mathrm{env}}$, representing variability in GEP due to shorter-timescale environmental variability alone. Likewise, $\varepsilon_{\mathrm{norm}}$ is proportional to the environmental response function f_{env}, representing variability in ε caused by shorter-timescale environmental variability alone.

Path analysis for environmental controls on shorter-timescale photosynthesis

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

Four environmental variables were considered in our path analysis, including PAR, VPD, Ta, and CI, due to their important roles in regulating tropical forest photosynthesis processes (Graham *et al.*, 2003; Goulden *et al.*, 2004; Hutyra *et al.*, 2007; Oliveira *et al.*, 2007; Doughty & Goulden, 2008a; Lloyd & Farquhar, 2008; Cirino *et al.*, 2014). We firstly designed the path structure for their correlations as follows: (i) atmospheric conditions (indicated by CI) and SZA determine the above-canopy PAR, (ii) PAR drives Ta, and (iii) CI and Ta influence VPD. While other path structures may be conceptually feasible, our intent was not to explore the relative goodness of fit of different models, but instead to identify the primary interaction pattern among these environmental drivers.

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

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

The LUE-based photosynthesis model

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

$$f_{\mathrm{env}} = L_{\mathrm{scalar}} \times W_{\mathrm{scalar}} \times T_{\mathrm{scalar}} \times \mathrm{CI}_{\mathrm{scalar}} \quad (10)$$

$$L_{\mathrm{scalar}} = \frac{1}{1 + \mathrm{PAR}/\mathrm{PAR}_0} \quad (11)$$

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

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

$$\mathrm{CI}_{\mathrm{scalar}} = 1 + k_{\mathrm{CI}} \times \mathrm{CI} \quad (14)$$

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

However, the default f_{env} (shown in Eqn 10) did not consider the fact of environmental correlations (Lloyd & Farquhar, 2008). To overcome this problem, we turned to the path analysis. Only those environmental drivers, which were significantly related with $\mathrm{GEP}_{\mathrm{norm}}$ or $\varepsilon_{\mathrm{norm}}$ in path analysis, were selected for the final form of f_{env}, by retaining their scalar functions while setting the other scalar functions equal to 1. We called the final LUE-based photosynthesis model as ‘the reference LUE model’.

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

Model runs and posterior analysis

To quantify the effects of both environmental and biotic (i.e., $\mathrm{LUE}_{\mathrm{ref}}$) drivers on modeled GEP, we ran our reference LUE model at hourly timescales for a training dataset (years 2003, 2005, 2009, and 2011) and validated the model using an independent dataset (years 2002, 2004, and 2010). We optimized the model by minimizing the Euclidian distance between modeled and observed GEP, using ‘NonLinearModel.fit’ (Holland & Welsch, 1977) in MATLAB R2014a. After the optimization, we ran the LUE model with the fitted model parameters for full 7-year hourly measurements but with three different scenarios: (i) the full model (or ‘full’; forced by time-varying environmental drivers interacting with time-varying $\mathrm{LUE}_{\mathrm{ref}}$), (ii) only with environmental effects (or ‘Env’; forced only by time-varying environment drivers, assuming $\mathrm{LUE}_{\mathrm{ref}}$ is constant for all the months), and (iii) only with canopy photosynthetic efficiency effect (or ‘PE’; forced only by time-varying $\mathrm{LUE}_{\mathrm{ref}}$, assuming environmental drivers are constant).

For the simulated GEP from each scenario, we aggregated the hourly GEP to the daily, monthly, and yearly values, respectively. We then applied ANOVA (Eqns 15–21) to partition the variance of EC-derived GEP into different causes (‘full’, ‘Env’, and ‘PE’), following the approach used by a similar study in a temperate deciduous forest (Richardson *et al.*, 2007). We repeated the analysis for the three different periods of integration at daily, monthly, and yearly timescales.

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

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

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

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

$$R^2_{\mathrm{full}} = 1 - \frac{\mathrm{SS}_{\mathrm{full}}}{\mathrm{SS}_T} \quad (19)$$

$$R^2_{\mathrm{Env}} = 1 - \frac{\mathrm{SS}_{\mathrm{Env}}}{\mathrm{SS}_T} \quad (20)$$

$$R^2_{\mathrm{PE}} = 1 - \frac{\mathrm{SS}_{\mathrm{PE}}}{\mathrm{SS}_T} \quad (21)$$

where $y_{i,\mathrm{obs}}$ refers to EC-derived (observed) GEP, and $\widehat{y}_{i,\mathrm{full}}$, $\widehat{y}_{i,\mathrm{Env}}$, and $\widehat{y}_{i,\mathrm{PE}}$ refer to the modeled GEP for the *i*th observation under the model scenarios of ‘full’, ‘Env’, and ‘PE’ respectively. $\overline{y_{\mathrm{obs}}}$ is the mean of EC-derived GEP. *N* is the total number of observation under given integrated timescales. SS_T denotes the total sum of squares for EC-derived GEP; $\mathrm{SS}_{\mathrm{full}}$ denotes the total sum of squared error of modeled GEP between observed and ‘full’ scenario; $\mathrm{SS}_{\mathrm{Env}}$ denotes the total sum of squared error of modeled GEP between observed and ‘Env’ scenario; $\mathrm{SS}_{\mathrm{PE}}$ denotes the total sum of squared error of modeled GEP between observed and ‘PE’ scenario. Finally, R^2_{full}, R^2_{Env}, and R^2_{PE} denote the fraction of EC-derived GEP variability explained by full model, environmental drivers, and $\mathrm{LUE}_{\mathrm{ref}}$, respectively.

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

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

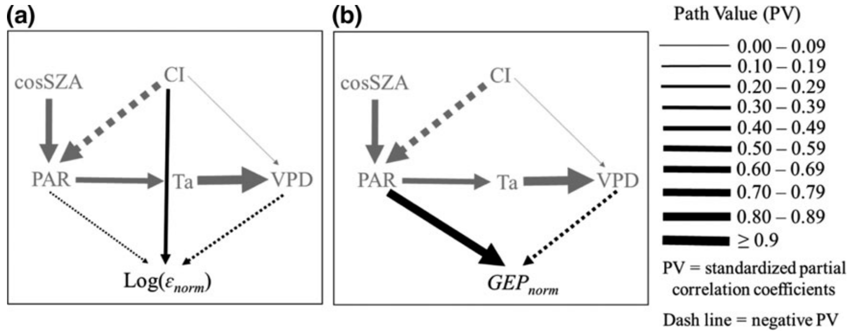

Fig. 2 Path diagrams illustrate environmental controls on (a) the logarithm of the canopy photosynthetic efficiency-normalized light-use efficiency, or Log($\varepsilon_{\mathrm{norm}}$), and (b) the canopy photosynthetic efficiency-normalized GEP ($\mathrm{GEP}_{\mathrm{norm}}$). We use seven years of hourly daytime measurements at k67 site for the analysis. The thickness of each arrow indicates standardized correlation coefficients, or path value, (see legend). All the paths shown here are statistically significant ($P < 0.001$). The subdiagram of environmental variables is colored gray.

Exploring environmental controls on interannual LUE_{ref} variability

We also analyzed the correlations between key environmental drivers and $\mathrm{LUE}_{\mathrm{ref}}$ at the monthly scale across all our seven-year data record to explore whether there exists any environmental control on $\mathrm{LUE}_{\mathrm{ref}}$ interannual variability.

Results

Relationships among environmental variables

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

Environmental controls on shorter-timescale photosynthesis

We observed that three environmental variables significantly controlled the normalized light-use efficiency ($\varepsilon_{\mathrm{norm}}$) at hourly timescales (Fig. 2a): (i) CI had a positive effect on $\varepsilon_{\mathrm{norm}}$ (PV = 0.34, $P < 10^{-5}$), and (ii) VPD and PAR had negative effects on $\varepsilon_{\mathrm{norm}}$ with PV = −0.23 and −0.18, respectively. The absolute PV of CI on $\varepsilon_{\mathrm{norm}}$ was significantly larger than that of VPD and PAR on $\varepsilon_{\mathrm{norm}}$, indicating that diffuse light fraction (approximated by CI in this study) might be the dominant control on $\varepsilon_{\mathrm{norm}}$.

We observed that only two environmental variables controlled the normalized GEP ($\mathrm{GEP}_{\mathrm{norm}}$) at hourly timescales (Fig. 2b): (i) PAR had the expected strongly positive effect on $\mathrm{GEP}_{\mathrm{norm}}$ (PV = 0.84, $P < 10^{-5}$) and likewise (ii) VPD had a significantly negative effect on $\mathrm{GEP}_{\mathrm{norm}}$ (PV = −0.35, $P < 10^{-5}$). The absolute PV of PAR on $\mathrm{GEP}_{\mathrm{norm}}$ was more than twice that of VPD on $\mathrm{GEP}_{\mathrm{norm}}$, indicating that PAR was the dominant control. Our analysis of environmental controls on raw light-use efficiency (ε) and GEP, respectively (Fig. S5), showed that both relationships, LUE vs. environmental drivers and GEP vs. environmental drivers, were identical to $\varepsilon_{\mathrm{norm}}$ vs. environment and $\mathrm{GEP}_{\mathrm{norm}}$ vs. environment, respectively.

Our path analyses therefore revealed that three environmental variables (CI, VPD, and PAR) significantly controlled hourly photosynthesis at our tropical forest site: CI and VPD affected photosynthetic activity primarily through influencing $\varepsilon_{\mathrm{norm}}$, and PAR affected photosynthetic activity primarily through its direct effect on $\mathrm{GEP}_{\mathrm{norm}}$.

LUE modeling: synthesis and validation from hourly to interannual timescales

Given the results of our path analysis, we were able to omit the temperature response function from the overall environmental response function (Eqn 10), yielding the following:

$$\mathrm{GEP} = \frac{\mathrm{LUE_{ref}}}{f_{\mathrm{env,ref}}} \times \mathrm{PAR} \times (1 + k_{\mathrm{CI}} \times \mathrm{CI}) \times (1 - k_w \times \mathrm{VPD}) \times \left(\frac{1}{1+\mathrm{PAR}/\mathrm{PAR}_0}\right) \qquad (22)$$

Equation (22) constituted our final form of the LUE-based photosynthesis model or the reference LUE model.

We first validated the model performance. We found that the reference LUE model (Eqn 22) forced by time-varying environmental drivers and monthly $\mathrm{LUE_{ref}}$ (or 'full' model) explained 77% of variability in EC-derived GEP at hourly timescale (Fig. 3a). When aggregating the modeled and EC-derived GEP to longer timescales (days to years), our results indicated good agreement between these two metrics at daily, monthly, and yearly timescales ($R^2 = 0.71$, 0.73, and 0.80, respectively) (Fig. 3b–d). We also found that the reference LUE model (Eqn 22) forced only by time-varying environmental drivers with a constant $\mathrm{LUE_{ref}}$ (or 'Env' model) did similarly well in explaining the hourly variability in EC-derived GEP ($R^2 = 0.75$; Fig. 3e). However, when aggregating to longer (daily and monthly) timescales, the 'Env' model explains much less of the variability in EC-derived GEP than does the 'full' model, with strong evidence at monthly timescales (Fig. 3c, g). A similar contrast is apparent at annual timescales (Fig. 3d, h), but the evidence is relatively weaker, as we only have seven-year observations (data size = 7) for annual timescale comparisons.

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

We then used our reference LUE model to partition GEP variability to different causes. We found that at hourly timescales, modeled GEP of 'full' scenario (driven by both environmental and biotic factors, explaining 77% of EC-derived GEP) was most sensitive to variation in environmental drivers (explaining 75% of variance in EC-derived GEP) and, as expected, least sensitive to variation in $\mathrm{LUE_{ref}}$ (1% of variance in EC-derived GEP explained), which is assumed to be constant within a month (Fig. 5). The environmental variability becomes less important in affecting modeled GEP at progressively longer timescales, with 58%, 3%, and 11% of the variance in EC-derived GEP attributable to variation in environmental drivers at daily, monthly, and yearly timescales, respectively (Fig. 5). Meanwhile, variation in the biotic response becomes progressively more important in determining EC-derived GEP, with

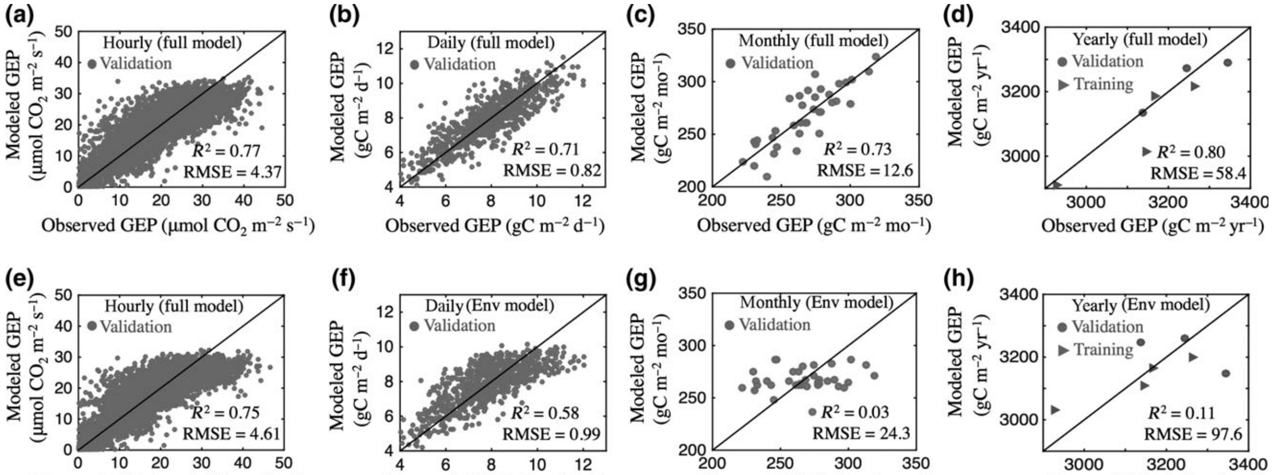

Fig. 3 GEP-model validation across a wide range of timescales: (a, e) hourly, (b, f) daily, (c, g) monthly, and (d, h) yearly timescales. GEP models used here include the 'full' model (top panel; using the reference LUE-based photosynthesis model, driven by both time-varying environmental drivers and monthly $\mathrm{LUE_{ref}}$) and the 'Env' model (bottom panel; using reference LUE-based photosynthesis model, driven by time-varying environmental drivers only with a constant $\mathrm{LUE_{ref}}$). The model is trained by the data of years 2003, 2005, 2009, and 2011 and validated by the independent data of years 2002, 2004, and 2010. Observed GEP refers to eddy covariance-derived GEP. Fig. 3a–c and e–g shows the validation data, and Fig. 3d, h shows all 7-year data.

6%, 63%, and 76% of the variance in EC-derived GEP can be attributed to variation in LUE_{ref} at daily, monthly, and yearly timescales, respectively (Fig. 5).

LUE modeling: characterizing environmental responses

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

With the model coefficients (Tables S2) and empirical correlations among environmental variables (Table S1), we then assessed how environmental variables independently and jointly controlled photosynthesis. Fig. 6a shows that photosynthesis responds monotonically to CI, VPD, and PAR individually. However, when considering the correlations among environmental variables (Fig. 6b), we found that (i) the combined effect of

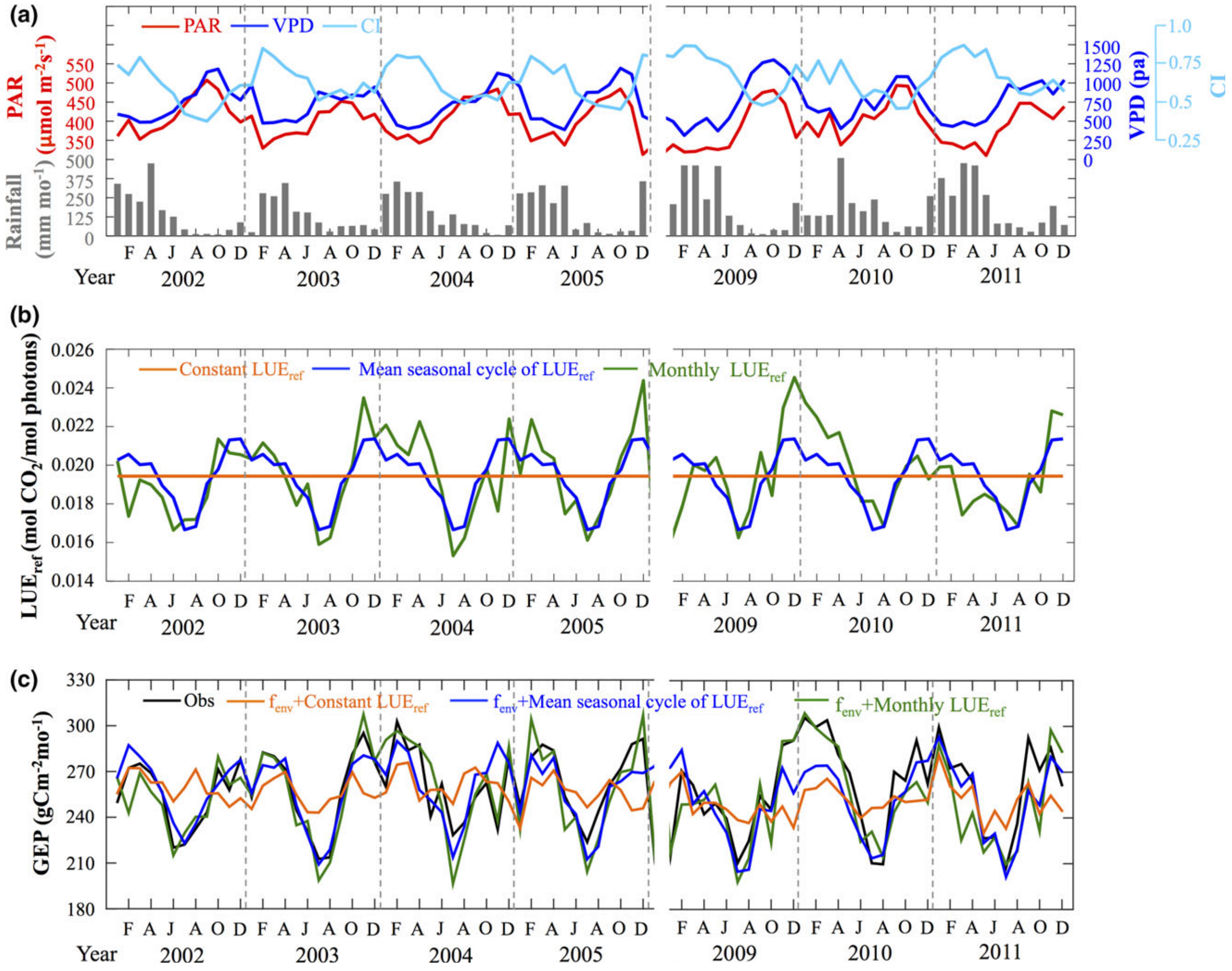

Fig. 4 Interannual variation of monthly environmental variables, biotic factor (LUE_{ref}), eddy covariance (EC) derived GEP, and LUE-based model simulated GEP. (a) Interannual variation of four monthly environmental drivers: satellite TRMM-based Rainfall (gray bar) and EC-derived PAR (red), VPD (blue), and CI (light blue); (b) interannual variation in biotic factor represented by three temporal resolutions of LUE_{ref} (monthly in green, to a mean seasonal cycle (one data point for each month of the year) in blue, to a constant LUE_{ref} derived as the mean of the entire monthly time series in orange) at k67 site; (c) interannual variation in EC-derived GEP (black), explained by LUE-based model simulated GEP driven by time-varying environmental drivers and a constant LUE_{ref} (orange; $R^2 = 0.14$; $P < 10^{-5}$), driven by time-varying environmental drivers and a mean seasonal cycle of LUE_{ref} (blue; $R^2 = 0.61$; $P < 10^{-5}$), and driven by time-varying environmental drivers and monthly LUE_{ref} (green; $R^2 = 0.74$; $P < 10^{-5}$).

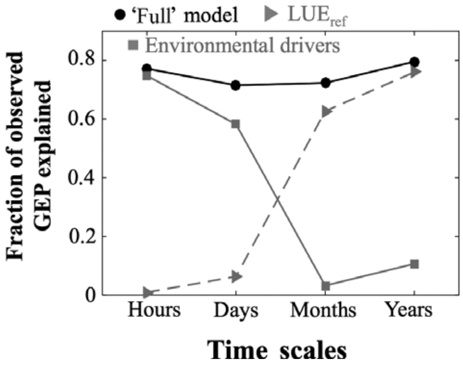

Fig. 5 Fraction of EC-derived GEP explained by environmental drivers (gray squares), by the biotic factor (LUE$_{\mathrm{ref}}$, gray triangles), and by a full LUE-based model that includes both components (black circles), as a function of timescale of observation. Partitioning among model components used a sum-of-squares approach, as given by Eqns (19–21).

PAR and CI led to a concave photosynthetic response, with the maximum photosynthesis at the moderate CI and (ii) the combined effect of PAR, CI, and VPD also led to a concave response, but with increased curvature and with the maximum photosynthesis reached when CI is around 0.42. This optimal CI value differentiated a 'light-limited regime' from a 'stomatal-limited regime' (Fig. 6b).

The hump-shaped relationship of Fig. 6b has important implications for the environmental sensitivity of tropical forest physiological response in wet vs. dry seasons. Relative to current seven-year environmental conditions, we simulated how the k67 forest GEP$_{\mathrm{norm}}$ responded to a reduction in CI (typically associated with more sunlight, less rainfall, and higher VPD; Table S3), generally seen during atmospheric drought conditions in the Amazon basin. Our results showed that with CI reduction and associated increase in PAR, VPD, and Ta (Fig. S6), the integrated environmental effect led to an initial increase and then a decrease in wet season modeled GEP$_{\mathrm{norm}}$ and a continuous decrease in dry-season modeled GEP$_{\mathrm{norm}}$ (Fig. 6d). This is because wet-season environmental conditions tend to be cool, humid, and less bright, while the dry-season

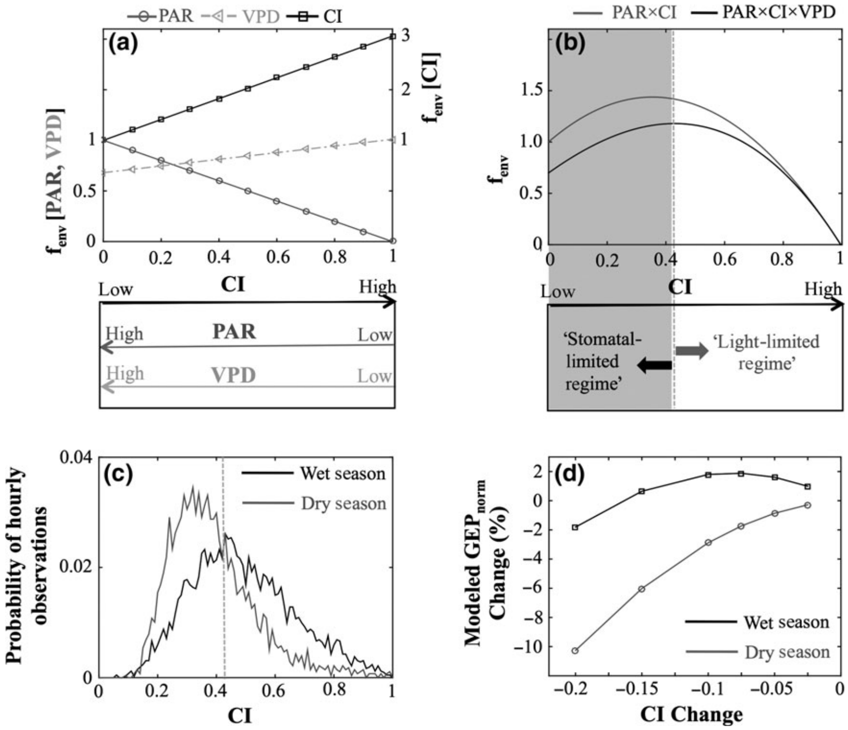

Fig. 6 Model simulated photosynthetic response to environmental drivers (f_{env}) under given biotic control (i.e., a fixed LUE$_{\mathrm{ref}}$) based on the reference LUE-based photosynthesis model (Eqn 22; coefficients from Table S2) and correlations among environmental drivers (Table S1), expressed as a function of CI (with PAR and VPD being expressed as a linear function of CI; see Table S1). (a) Model simulated environmental response to each environmental driver [CI in black squares (CI$_{\mathrm{scalar}}$; Eqn 14); PAR in gray circles (L_{scalar}×PAR; Eqn 11); VPD in gray triangles (W_{scalar}; Eqn 12)]; (b) model simulated environmental response to joint environmental effects [total light effect in gray line (CI$_{\mathrm{scalar}}$×L_{scalar}×PAR); joint light and water effect in black line CI$_{\mathrm{scalar}}$×L_{scalar}×PAR× W_{scalar})]; (c) probability distribution of hourly CI observations for a given SZA bin (20° SZA ≤40°) for the wet season (black) and the dry season (gray) under current seven-year conditions; (d) modeled GEP$_{\mathrm{norm}}$ response to CI reduction (corresponding to the increase in PAR and VPD; Fig. S6) relative to current seven-year conditions, for the wet season (black) and the dry season (gray). The gray dashed lines in (b) and (c) indicate the optimal CI where GEP$_{\mathrm{norm}}$ is at its maximum.

conditions are already hotter, less humid, and brighter (Fig. 6c). In addition, our results also indicated that modeled GEP_{norm} at k67 had small sensitivity to moderate fluctuations in CI: a reduction in CI by 0.1 (a ~20% change in CI), associated with an increase in midday PAR of ~220 μmol m^{-2} s^{-1} and an increase in midday VPD of ~170 Pa (Fig. S6), causing absolute changes of <3% in modeled GEP_{norm} in both wet and dry seasons (Fig. 6d and Table S3).

As modeled GEP_{norm} of this forest had small sensitivity to environmental variability (Fig. 6d), and dry season of this forest is more likely to be within its 'stomatal-limited regime' (Fig. 6b, c), we found, as expected, that the mean seasonality of modeled GEP driven by environment alone showed inadequate seasonal variation (Fig. 7), accounting for only ~15% of mean seasonality of observed GEP. By contrast, the model driven by biotically controlled LUE_{ref} alone well tracked the mean seasonality of observed GEP ($R^2 = 0.90$; Fig. 7), due to a strong dry-season increase in canopy photosynthetic infrastructure, not captured by the environment-only model. The main deviation for biotic-only model was late in the dry season (October to December), when observed GEP fell significantly below that predicted by LUE_{ref}, consistent with environment-driven stomatal limitation that prevented the canopy's full photosynthetic efficiency from being utilized (Fig. 6b, c). This late dry-season suppression of GEP by stomatal limitation was captured by both models which included environmental drivers (the environment-only model and the full model).

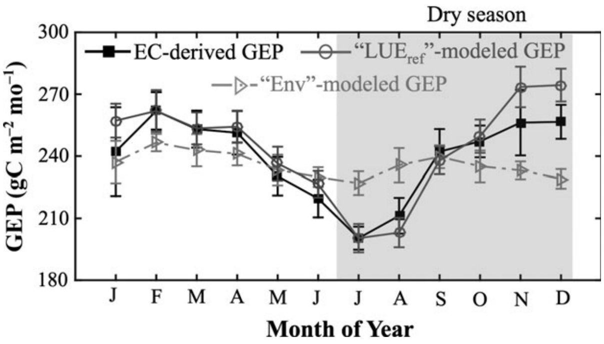

Fig. 7 Seven-year mean annual cycles of monthly EC-derived GEP (black squares, named as 'EC-derived GEP'), modeled GEP with a constant LUE_{ref} and varying environmental drivers (gray triangles, named as 'Env-modeled GEP'), and modeled GEP with monthly LUE_{ref} and constant environmental drivers (gray circles, named as 'LUE_{ref}-modeled GEP'). The dry-season increase in LUE_{ref} (gray circles) is evidently not prevented by water limitation, but consistent with leaf/canopy physiological response (e.g., dry-season stomatal closure), the realized GEP is lower, relative to LUE_{ref} in the dry season than in the wet season. Error bars are for 95% confidence intervals; dry season is shaded in gray.

Decoupling the effects of Ta and VPD on GEP_{norm}

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

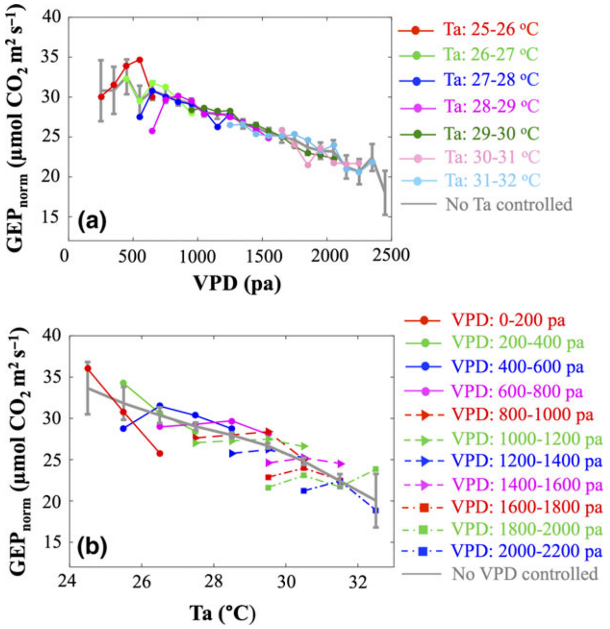

Fig. 8 Relationships between canopy photosynthetic efficiency-normalized GEP (GEP_{norm}, filtered by PAR≥1500 μmol CO_2 m^{-2} s^{-1}) and VPD in (a) and GEP_{norm} and Ta in (b). All the hourly measurements at k67 site (years 2002–2005, 2009–2011) were used. Different colored lines in (a) represent different temperature (Ta) bins (1 °C bin). Different colored lines and symbols in (b) represent different VPD bins (200 pa bin). The central gray line indicates the overall bivariate relationship between GEP_{norm} and VPD (a) and Ta (b), without being conditioned by Ta in (a), or VPD in (b). Uncertainty bars indicate 95% confidence interval. The mean of all GEP_{norm} vs. VPD slopes in (a), each from a separate Ta bin, is significantly negative (*t*-test, $P = 0.0251$), while the mean of all GEP_{norm} vs. Ta slopes in (b), each from a separate VPD bin, is statistically indistinguishable from 0 (*t*-test, $P = 0.0875$).

Environmental controls on interannual variability of monthly LUE_{ref}

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

Discussion

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

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

Our analysis confirms that variation of environmental drivers is the dominant control on the variation of tropical forest GEP at hourly to daily timescales (through direct plant physiological response), as suggested by previous studies (Goulden *et al.*, 2004; Hutyra *et al.*, 2007; Oliveira *et al.*, 2007; Doughty & Goulden, 2008a; Cirino *et al.*, 2014). This shorter-timescale physiological response follows a positive response to variations in light availability (PAR and CI) and a negative response to atmospheric water deficit (VPD) (Figs 2 and 6). We are also able to model these responses by a parsimonious LUE-based photosynthesis model (Eqn 22; explaining $R^2 = 77\%$ of EC-derived GEP; Fig. 3a).

This analysis allows us to investigate the cause for previously reported observations (at a nearby evergreen forest site) that at given PAR, hourly GEP is higher in the morning than in the afternoon (Doughty *et al.*, 2006). It had been suggested that a combination of increased evapotranspiration demand and plant endogenous circadian rhythms might explain the afternoon decline in light sensitivity of GEP in this tropical forest (Goulden *et al.*, 2004; Doughty *et al.*, 2006). Our LUE-based photosynthesis model, by including environmental variables beyond PAR, can well simulate the diel patterns of GEP (Fig. 3a and Fig. S7), confirming that physiological response to higher afternoon evaporative demand is sufficient to account for observed diel patterns in GEP. In addition, our analysis confirms the positive effect of moderate cloudiness on GEP as reported by earlier studies (Gu *et al.*, 2002, 2003b; Oliveira *et al.*, 2007; Mercado *et al.*, 2009; Cirino *et al.*, 2014).

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

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

Our finding that environmental variation alone explains progressively less GEP variability at longer and longer timescales is consistent with similar findings in temperate biomes (Hui *et al.*, 2003; Richardson *et al.*, 2007; Urbanski *et al.*, 2007; Teklemariam *et al.*, 2010; Marcolla *et al.*, 2011; Wu *et al.*, 2012). However, this trend is much more pronounced at this tropical site, with environmental variation accounting for only ~10% or less of GEP at longer timescales (i.e., monthly and yearly), as compared to ~30% or more in a temperate forest (Richardson *et al.*, 2007; Urbanski *et al.*, 2007). This difference might be attributed to much smaller environmental variability in the tropics and to canopy photosynthetic efficiency in the tropics being less tightly synchronized with environmental variability (Table 1). Our seven-year dataset is not long enough to draw strong inferences about the controls on interannual GEP variability and so the pattern found in this study remains to be tested with a longer data record and more tropical forest sites in future. However, this work shows that the environmental responses that

Table 1 Environmental controls on interannual variation of monthly LUE_{ref} over seven years at k67 site. Two metrics, R^2 (coefficient of determination), and P (significant level) were used for measuring the correlations between environmental drivers and LUE_{ref}. Four environmental variables were analyzed including EC-derived PAR, VPD, and CI, and satellite TRMM-derived Rainfall. Time lapse i that refers to the variation in environmental drivers is the ith month preceding the variation on LUE_{ref}

	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	($R^2 = 0.03$; $P = 0.14$)	($R^2 = 0.01$; $P = 0.40$)	($R^2 = 0.14$; $P = 0.0005$)	($R^2 = 0.30$; $P < 10^{-5}$)	($R^2 = 0.42$; $P < 10^{-5}$)	($R^2 = 0.34$; $P < 10^{-5}$)	($R^2 = 0.05$; $P = 0.06$)

explain most of the hourly variability in GEP do not explain its seasonal or interannual variability, highlighting that understanding and modeling the long-term dynamics of GEP in response to environmental drivers may be especially challenging in the tropics.

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

However, understanding and quantitative representation of the biological mechanisms underlying this demographically induced LUE_{ref} seasonality and interannual variability are still largely lacking. Our analysis showed that there is no direct instantaneous environmental control on interannual variability of monthly LUE_{ref} (Table 1). Instead, LUE_{ref} well tracked preceding environmental drivers (i.e., PAR with $R^2 = 0.38$) of 3 months at k67 site (Table 1). This preceding environmental control on LUE_{ref} interannual variability might be as a consequence of leaf maturation time to transfer from newly flushing leaves of low photosynthetic efficiency to mature leaves with maximum photosynthetic efficiency (Wu *et al.*, 2016). In addition, leaf demography may also arise from other biological mechanisms, including adaptations to avoid herbivores or pathogens (Lieberei, 2007) or for optimal carbon acquisition under seasonally and interannually varying resource availability (Kikuzawa, 1991, 1995; Wright & van Schaik, 1994; Wright, 1996; Brienen *et al.*, 2015; Guan *et al.*, 2015). To empirically test environmental control on LUE_{ref} variability and also to reconcile different mechanisms of leaf demography (and demography induced LUE_{ref}) thus require an interdisciplinary approach to expand our observation skills across time, space, and spatial resolutions and will be critical to understanding the long-term response and resiliency of tropical forests to changing climate.

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

Can canopy photosynthetic efficiency-normalized GEP help to resolve long-standing debates about environmental limitations and sensitivity to temperature in tropical evergreen forests?

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

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

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

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

Possible caveats and limitations

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

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

Implications

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

The method used here to partition environmental and biotic controls on photosynthesis could also be used to tackle a range of questions about tropical forest function. For example, it may be applicable to the study of ecosystem respiration and transpiration, and processes also subject to these controls (Hutyra *et al.*, 2007; Phillips *et al.*, 2009; Brienen *et al.*, 2015). In addition, this partitioning approach might provide insight into whether there are systematic differences between temperate and tropical zones in the relative importance of environmental and biotic controls on ecosystem metabolism — the biotic control in temperate biomes (i.e., leaf phenology) being more tightly synchronized with environmental seasonality than in tropical biomes (Cleland *et al.*, 2007). Finally, our results also suggest that failing to account for biotically regulated variations in canopy photosynthetic light-use efficiency (i.e., $\mathrm{LUE_{ref}}$), risks inaccurate model predictions of tropical forest GEP at longer timescales. We have shown that the variation in monthly $\mathrm{LUE_{ref}}$ –arising from phenology of leaf quality (Wu *et al.*, 2016) and possibly from biological responses to climate extremes (Doughty *et al.*, 2015) and disturbance (Anderegg *et al.*, 2015) – is a key driver of seasonal and interannual changes in tropical evergreen forest GEP. Therefore, models that accurately simulate seasonal and interannual changes in biotically regulated functions like $\mathrm{LUE_{ref}}$ will be critical to predicting future tropical forest carbon dynamics.

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Author contributions

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., A.C.A., R.C.O., and P.B.C. contributed to installation, maintenance, or processing of eddy covariance data. J.W. performed the data analysis. J.W. drafted the manuscript, and S.R.S., K.G., 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 final version of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Correlations among environmental variables for seven years hourly observations (years: 2002–2005, 2009–2011) within a fixed SZA bin (20–40°) at k67 site.

Table S2. Model coefficients (mean ± 95% confidence interval) of the reference LUE-based photosynthesis models (Eqn 22) driven by hourly environmental drivers and monthly $\mathrm{LUE}_{\mathrm{ref}}$, using the training data of 4-year eddy covariance measurements (2003, 2005, 2009, and 2011) at k67 site.

Table S3. Sensitivity analysis on modeled $\mathrm{GEP}_{\mathrm{norm}}$ response to a reduction in CI relative to current seven-year condition by using the reference LUE model (Eqn 22) under the scenario of a constrained SZA bin ($20° \le \mathrm{SZA} \le 40°$), which accounts for environmental correlations (Table S1).

Figure S1. The derivation, distribution and validation of CI at k67 site: (a) scatterplot of theoretical PAR and observed PAR; (b) diel pattern of CI; (c) correlation between CI and diffuse fraction (the ratio between diffuse and total PAR; from a BF5 Sunshine Sensor at k67 site).

Figure S2. Modeled FAPAR seasonality based on Leaf area Index (LAI) and changing solar zenith angles (SZA) at k67 site (driven exclusively by average annual cycle of monthly ground-based LAI measurements).

Figure S3. Relationships among the four major environmental variables (VPD, Ta, PAR, and Cloudiness Index, CI) under a given SZA bin (20–40°).

Figure S4. Relationships among the four major environmental variables (VPD, Ta, PAR, and CI) for all the daytime measurements.

Figure S5. Path diagrams illustrate environmental controls on (a) the logarithm of light-use-efficiency, or Log (ε), and (b) GEP.
Figure S6. Sensitivity analysis of environmental change under a reduction in CI relative to current seven-year condition when accounting for environmental correlations (Table S1), under the scenario of a given SZA bin ($20° \leq \text{SZA} \leq 40°$).
Figure S7. Mean diel patterns of modeled and EC-derived GEP: (a) training data (years 2003, 2005, 2009, and 2011), and (b) testing data (years 2002, 2004, and 2010).