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The surface-atmosphere exchange of carbon dioxide in tropical rainforests: Sensitivity to environmental drivers and flux measurement methodology

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ABSTRACT

Tropical rainforests play a central role in the Earth system by regulating climate, maintaining biodiversity, and sequestering carbon. They are under threat by direct anthropogenic impacts like deforestation and the indirect anthropogenic impacts of climate change. A synthesis of the factors that determine the net ecosystem exchange of carbon dioxide (NEE) at the site scale across different forests in the tropical rainforest biome has not been undertaken to date. Here, we study NEE and its components, gross ecosystem productivity (GEP) and ecosystem respiration (RE), across thirteen natural and managed forests within the tropical rainforest biome with 63 total site-years of eddy covariance data. Our results reveal that the five ecosystems with the largest annual gross carbon uptake by photosynthesis (i.e. GEP $>$ 3000 g C $m^{-2} y^{-1}$) have the lowest net carbon uptake – or even carbon losses – *versus* other study ecosystems because RE is of a similar magnitude. Sites that provided sub-canopy CO_2 storage observations had higher average magnitudes of GEP and RE and lower average magnitudes of NEE, highlighting the importance of measurement methodology for understanding carbon dynamics in ecosystems with characteristically tall and dense vegetation. A path analysis revealed that vapor pressure deficit (VPD) played a greater role than soil moisture or air temperature in constraining GEP under light saturated conditions across most study sites, but to differing degrees from -0.31 to -0.87 μmol CO_2 m^{-2} s^{-1} hPa^{-1}. Climate projections from 13 general circulation models (CMIP5) under the representative concentration pathway that

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generates 8.5 W m^{-2} of radiative forcing suggest that many current tropical rainforest sites on the lower end of the current temperature range are likely to reach a climate space similar to present-day warmer sites by the year 2050, warmer sites will reach a climate not currently experienced, and all forests are likely to experience higher VPD. Results demonstrate the need to quantify if and how mature tropical trees acclimate to heat and water stress, and to further develop flux-partitioning and gap-filling algorithms for defensible estimates of carbon exchange in tropical rainforests.

1. Introduction

Tropical rainforests regulate the amount of heat and moisture that enters the atmosphere in the tropics (Avissar and Werth, 2005), act as a critical reservoir for biodiversity (Gibson et al., 2011), and serve as a globally important stock of carbon (Dixon et al., 1994; Phillips et al., 1998). They may be turning into a net source of carbon to the atmosphere due largely to degradation and disturbance (Baccini et al., 2017). Such threats to tropical rainforests affect not only their carbon dynamics, but also the other ecosystem and Earth system services that rainforests provide (Foley et al., 2005; Kim et al., 2015; Mitchard, 2018), and emphasize the need to understand the functional diversity of rainforests for a deeper understanding of the Earth system (Asner et al., 2017; Levine et al., 2016; Pavlick et al., 2013).

Inverse and forward modeling approaches demonstrate that tropical forests contribute ~20% of the interannual variability of global net biome production (net carbon flux including fire emissions) (Ahlström et al., 2015), but up to 1/3 of the interannual variability of biosphere-atmosphere carbon dioxide (CO_2) flux in the southern hemisphere (Fu et al., 2017). Satellite observations demonstrate diverse patterns of carbon fluxes within the tropical rainforest biome; for example, the standard deviation of gross ecosystem productivity (GEP) estimated from Moderate Resolution Imaging Spectroradiometer (MODIS) is higher across some tropical rainforest areas - especially in southeast Asia, coastal Africa, and the western Amazon - than many other global ecosystems (Fig. 1, Xiao et al., (2016)). Such observations motivate the need to study the controls over carbon fluxes in the natural and increasingly managed ecosystems of the tropical rainforest biome (Hall et al., 1995).

Much has been learned about the net surface-atmosphere exchange (NEE) of CO_2 since the first eddy covariance measurements of *terra firme* tropical rainforests demonstrated a substantial carbon sink on daily timescales (Grace et al., 1996, 1995; Malhi et al., 1998; Oberbauer et al., 2000). Tropical rainforests tend to have lower carbon use efficiency than temperate forests (Chambers et al., 2004), emphasizing the critical role of ecosystem respiration (RE) to the tropical carbon balance. Counterintuitive seasonal CO_2 flux patterns are now resolved; tropical rainforest GEP is often greater in the dry season due to leaf emergence (Aguilos et al., 2018; Huete et al., 2008, 2006; Hutyra et al., 2007; Lopes et al., 2016; Saleska et al., 2016, 2007, 2003) despite strong limitations to GEP when water is limiting (Kiew et al., 2018; Wu et al., 2017) and a "brown down" due to water limitation toward drier regions (Saleska et al., 2009). Some studies find that tropical rainforest trees tend to be isohydric (Fisher et al., 2006; Konings and Gentine, 2016), suggesting that they tightly regulate stomatal conductance under conditions of water stress including when the vapor pressure deficit (VPD) is high. However, tropical trees exhibit a range of hydraulic behavior (Braga et al., 2016; Giardina et al., 2018; Klein, 2014; Powell et al., 2017; Siddiq et al., 2017) and modeling studies suggest that anisohydric strategies may be preferred in tropical systems with little risk of water stress (Inoue et al., 2016; Kumagai and Porporato, 2012). These climate and hydrologic stresses are coupled with

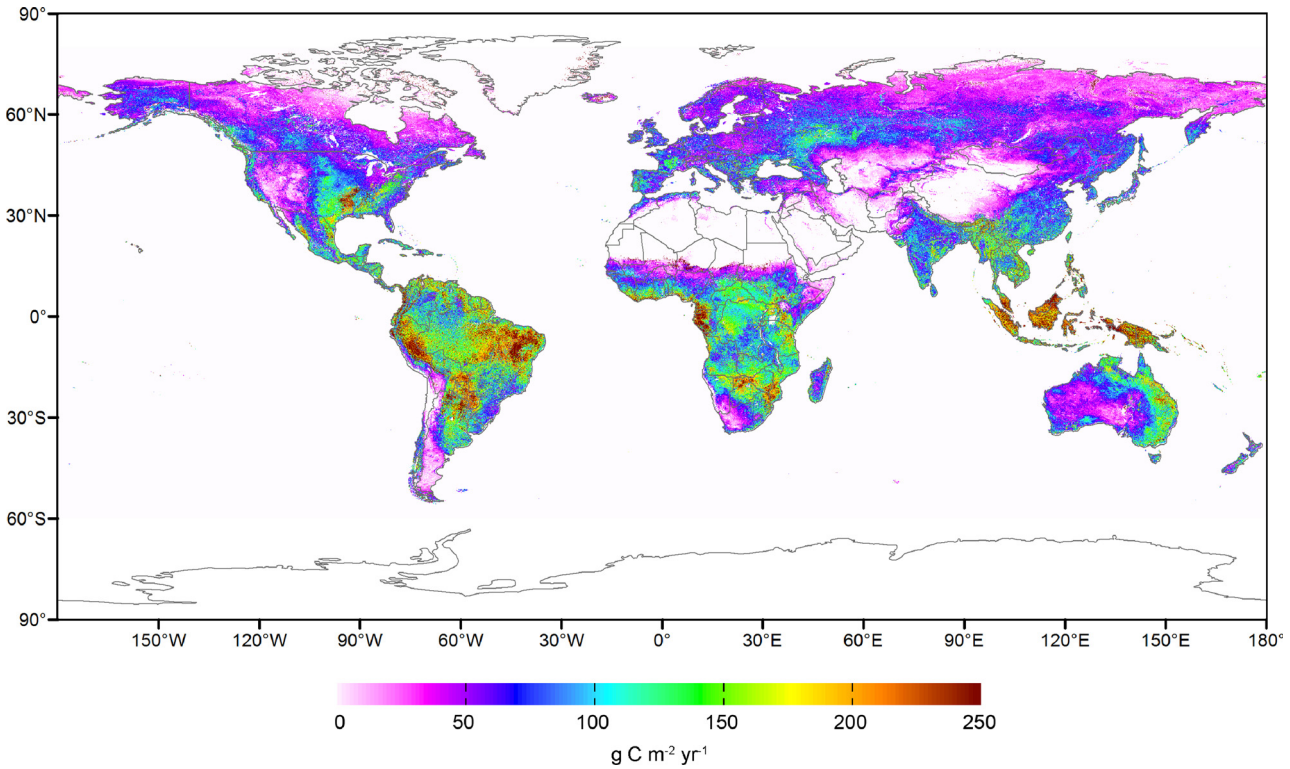

Fig. 1. The standard deviation of annual gross ecosystem productivity (GEP) from MODIS (MOD17A3) for the period.2000–2015. (For interpretation of the references to color in the figure the reader is referred to the web version of this article.)

management pressures that impact carbon fluxes in tropical ecosystems.

Forests in the tropical rainforest biome are increasingly managed, and managed ecosystems must also be studied for a comprehensive understanding of carbon metabolism in the tropics. Reforestation tends to increase carbon sequestration (Wolf et al., 2011b, 2011c), but responses of tropical rainforests to other anthropogenic and natural disturbances, such as deforestation (Pan et al., 2011), fire (van Marle et al., 2017) and drought (Bonal et al., 2008; Phillips et al., 2009) are diverse and interactive. For example, a tropical peat forest near Palangkaraya, Indonesian Borneo (ID-Pag; see Table 1) was a net source of CO_2 to the atmosphere over multiple years due to constraints on GEP by VPD, radiative perturbations due to peat fire smoke, and perturbation of the water table (Hirano et al., 2012; 2008; 2007). These and other factors create large interannual variability in tropical rainforest NEE (e.g. Fig. 1) that remains poorly understood at the ecosystem scale.

Studying the annual and interannual variability in tropical rainforest carbon exchange at the ecosystem scale is challenging due to the unique difficulties that they present to the eddy covariance methodology (Kruijt et al., 2004; Miller et al., 2004). Intact tropical forests tend to be at remote sites away from line power sources, which creates logistical challenges for making quasi-continuous long-term measurements. Tropical rainforest canopies are characteristically tall and dense, resulting in complex within-canopy atmospheric transport (Fuentes et al., 2016; Gerken et al., 2017; Tóta et al., 2012) that makes standard approaches for measuring and modeling nighttime ecosystem respiration difficult to apply (Dargie et al., 2017; de Araújo et al., 2010; Grace et al., 2016; Loescher et al., 2003; Pan et al., 2011; Santos et al., 2016). Alternate approaches for estimating nighttime RE based on daytime flux measurements (e.g. Lasslop et al., (2010)) may represent an improvement, but the sensitivity of tropical rainforest carbon fluxes to flux partitioning methods across different ecosystems has not been studied to date.

Despite these and other challenges, there is a pressing need to quantify surface-atmosphere carbon exchange across managed and (quasi-) unmanaged ecosystems in the tropical rainforest biome to further understand their role in the Earth system. As a critical step in this process, the impacts of methodological approaches and environmental drivers on carbon exchange need to be investigated. Here, we study NEE and its components, GEP and RE, across thirteen natural and managed tropical forest ecosystems in seven countries in all five continents where tropical rainforests exist. We place particular emphasis on the relationship between surface-atmosphere carbon exchange and environmental drivers and critique different eddy covariance data processing approaches with an eye toward methodological improvements. The goal of this paper is to synthesize observations of NEE and its components in managed and unmanaged tropical rainforests and to highlight important current and future directions for studying tropical rainforest carbon metabolism in a changing climate.

2. Materials and methods

2.1. Study sites

For the purposes of this study we define tropical rainforests as comprising characteristic evergreen broadleaf vegetation (Fig. 2) rather than inhabiting a climate zone with the absence of a dry season, given that severe droughts can and do occur in tropical rainforests (Lewis et al., 2011). We also include managed ecosystems given their increasing importance to the carbon cycle of the tropical rainforest biome (Tyukavina et al., 2015). By this definition we include the site BR-Ban (Table 1) on the tropical rainforest – cerrado ecotone (Borma et al., 2009; da Rocha et al., 2009) as well as reforested (PA-SPn) and managed (VU-Coc) tropical rainforests (Table 1). We exclude sites with characteristic savanna, subtropical, or tropical dry forest vegetation, noting some subjectivity in the definition of what constitutes a tropical

Table 1
Tropical rainforest eddy covariance sites explored in the present study. Observations come from both the LaThuile and FLUXNET2015 databases. Sites indicated by + were available only for the LaThuile database. [#] indicates managed ecosystems. 'System' indicates the use of open (OP) or closed path (CP) eddy covariance systems. 'Unk' indicates unknown.

Site ID	Lat.	Long.	Observation period	Forest age (year)	Canopy height (m)	Leaf area index ($m^2 m^{-2}$)	Soil depth (m)	Water table depth (m)	Carbon storage	System	Gap-filling (%)	References
AU-Rob	−17.1175	145.6301	2014-2014	Unk	28	3.2	> 8	~ 6	No	OP	61%	(Beringer et al., 2016; Bradford et al., 2014)
BR-Ban[+]	−9.8244	−50.1591	2003-2006	Unk	18	3.5-4.5	3	3.7-4.5	No	OP	46%	(Borma et al., 2009; da Rocha et al., 2009; Restrepo-Coupe et al., 2013)
BR-Cax[+]	−1.7197	−51.4590	1999-2003	Unk	30-35	5.1	3-4	~ 10 (wet season)	No	CP	79%	(Carswell et al., 2002; Restrepo-Coupe et al., 2013)
BR-Ji2[+]	−10.0832	−61.9309	2000-2002	Unk	30	5.5	1.2-4	Unk	No	CP	36%	(Andreae et al., 2002; Kruijt et al., 2004; Meir et al., 2001)
BR-Ma2[+]	−2.6091	−60.2093	1999-2006	Unk	30-35	4.7	> 15	35	No	CP	45%	(Araújo et al., 2002; Restrepo-Coupe et al., 2013)
BR-Sa1	−2.8567	−54.9589	2002-2011	Unk	35-40	6.0	> 12	> 100	Yes	CP	63%	(Martens et al., 2004; Nepstad et al., 2002; Restrepo-Coupe et al., 2013)
BR-Sa3	−3.0180	−54.9714	2000-2004	> 100	35-40	4.9	> 12	> 100	Yes	CP	62%	(Goulden et al., 2006; Restrepo-Coupe et al., 2013)
GF-Guy	5.2777	−52.9288	2004-2014	Unk	35-40	7.0	> 5	1-30	Yes	OP	55%	(Bonal et al., 2008)
GH-Ank	5.2685	−2.6942	2011-2014	Unk	25-30	5.9	≥ 1	≥ 1	Yes	CP	72%	(Belelli Marchesini et al., 2008; Chiti et al., 2010)
ID-Pag[+]	−2.3450	114.0360	2002-2003	> 50	26	5.6	4 (Peat depth)	0.2-1.7	Yes	OP	65%	(Hirano et al., 2007)
MY-PSO	2.9730	102.3062	2003-2009	Unk	35	6.5	Unk	Unk	Yes	OP	69%	(Kosugi et al., 2008, 2012)
PA-SPn[#]	9.3181	−79.6346	2007-2009	6-8	8-12	3.0–5.4	> 1	Unk	Yes	OP	75%	(Wolf et al., 2011a,b,c)
VU-Coc[+, #]	−15.4427	167.1920	2001-2004	> 20	16	5.6	Unk	Unk	No	OP	47%	(Navarro et al., 2008; Roupsard et al., 2006)

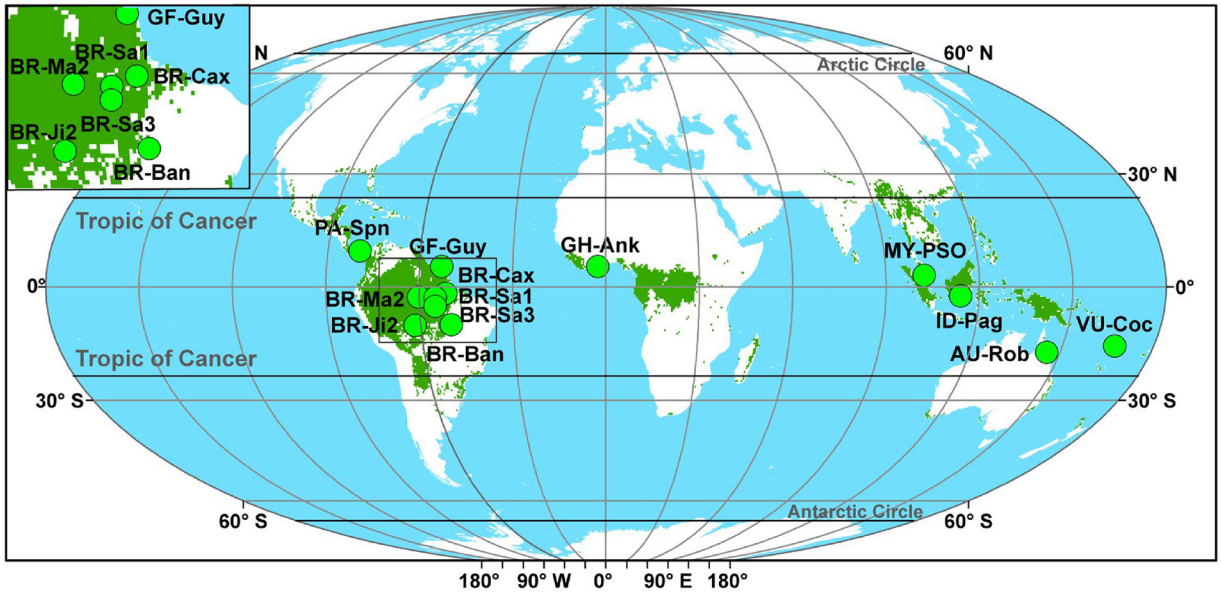

Fig. 2. A map of global tropical rainforest area (in green) based on the MODI MCD12C1 land cover classification with the location and distribution of the 13 tropical rainforest eddy covariance sites used in this study (see Table 1).

rainforest. We analyze surface-atmosphere exchange observations obtained from the LaThuile and FLUXNET2015 databases for 13 tropical rainforests located in Australia, Brazil, French Guiana, Ghana, Malaysia, Panama, and Vanuatu (Fig. 2) and summarize key variables in Table 1, which also lists respective publications in which additional site information is available. We use the conventions that GEP and RE are positive quantities and that NEE = RE – GEP such that net C uptake by the biosphere is denoted as negative per the atmospheric convention.

2.2. The LaThuile and FLUXNET2015 databases

We explored data from both the LaThuile and FLUXNET2015 databases. Both databases harmonize, standardize, and gap-fill half-hourly or hourly observations of NEE submitted by Principal Investigators from regional flux networks. The LaThuile database standardizes flux observations following Papale et al., (2006) and Reichstein et al., (2005), and uses nighttime RE observations under conditions of sufficient friction velocity (u_*) to model RE during daytime and thus estimate GEP by the difference between modeled RE and measured NEE. The FLUXNET2015 database uses additional daytime flux partitioning approaches (Lasslop et al., 2010) to estimate GEP and RE, and includes multiple uncertainty estimates about each approach. For sites included in both databases, we focus on the longer FLUXNET2015 records and compare flux estimates from both databases for completeness. We note that subcanopy CO_2 storage is required for the calculation of NEE in the FLUXNET2015 dataset but not the LaThuille dataset, and that carbon flux estimates from FLUXNET processing algorithms may differ from those determined by Principal Investigators. Additional information with regards to flux processing in the FLUXNET2015 dataset is provided in Appendix A.

2.3. Data analysis

We analyze the sensitivity of NEE, GEP, and RE to flux methodology amongst the 13 study sites and characterize differences in the response of tropical canopies to atmospheric water stress via the VPD (Kiew et al., 2018; Wu et al., 2017) given the intermittent availability of soil moisture measurements and to account for recent arguments that VPD will increasingly constrain canopy conductance and thereby GEP (Novick et al., 2016; Sulman et al., 2016). We critique the notion that VPD is responsible for the decline in light-saturated GEP and NEE using a path analysis that also includes soil water content (SWC) and air temperature (T_a) and their interactions to account for soil hydraulic limitations to productivity and the role of high temperatures in enzyme denaturation. We first designed the path diagrams for their correlations as in Fig. A1; T_a, VPD and SWC affect GEP or NEE under light-saturated conditions, and all micrometeorological variables are directly related (as is the case with T_a and VPD) or correlated. To derive the final path diagram, we ran the path analysis multiple times, removing insignificant paths with P-values > 0.05 on each iteration, until all remaining paths were statistically significant. The path value (PV, arrow thickness in Fig. A1) was derived from the standardized partial regression coefficients, representing the relative strength of a given relationship. The PV was designed to quantitatively compare the relative influence of T_a, VPD and SWC on GEP and NEE under light-saturated conditions. The path model was fitted using the 'lavaan' package in R3.0.2 for Mac and we use the convention that carbon uptake by the biosphere is denoted as positive (i.e. –NEE) in the path analysis to use the same sign convention as GEP to simplify comparison.

2.4. General circulation models

To ascertain the projected climate state of the study sites, monthly averages of T_a and VPD from 13 General Circulation Models (GCMs) were obtained from the Coupled Model Intercomparison Project - Phase 5 archive (CMIP5, Table A2) (Taylor et al., 2012) for Representative Concentration Pathway 8.5 (high emissions scenario). These models were previously downscaled to 0.5° grid using the Bias Correction – Spatial Downscaling method (Wood et al., 2004). Thirteen different models comprised the ensemble and were averaged together to create a single monthly time series for the model grid cells that contain the sites for each variable from 1950 to 2050. Annual averages and standard deviations were calculated from the monthly means. Atmospheric vapor pressure (e_a) was estimated by assuming that when T_a is close to its daily minimum it is saturated with water vapor such that relative humidity is close to 100% (i.e. the dewpoint temperature was assumed to be near the daily minimum temperature) following Roderick and Farquhar (2002).

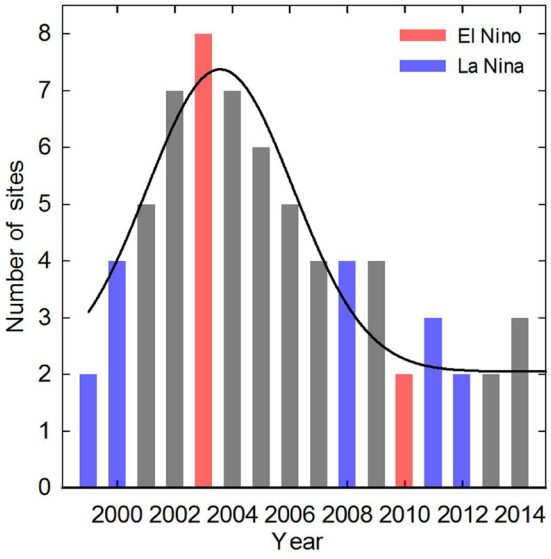

Fig. 3. The number of tropical rainforest eddy covariance research sites per year with data archived in the LaThuile and/or FLUXNET2015 databases as of March 2017.

3. Results

3.1. Data availability

More tropical forest eddy covariance sites provided data to FLUXNET in the past, (e.g. data from eight sites from the year 2003 are available for analysis) than in more recent years; as of 2018 only two sites are available for the El Niño year of 2010 and the La Niña year of 2012 (Fig. 3). While there were more La Niña years than El Niño years in the available period (Fig. 3), more sites were affected by the 2003 El Niño. Our results are subject to this asymmetry of data availability among years.

3.2. Meteorological variability

We used daily mean meteorological data to compare mean monthly meteorological characteristics among sites. Mean T_a was approximately 26 °C at BR-Ban, BR-Cax, BR-Sa1, BR-Ma2, BR-Sa3, GF-Guy and MY-PSO and approximately 25 °C in BR-Ji2, GH-Ank, VU-Coc, and PA-SPn (Fig. 4a). AU-Rob experienced cooler conditions and was more seasonal with a mean monthly (± standard deviation) T_a of 21.7 ± 2.6 °C, while ID-Pag was the hottest and the least seasonal with a mean monthly T_a of 26.6 ± 0.4 °C (Fig. 4a). Similarly, the highest monthly soil temperature (T_s) was found at ID-Pag (27.4 ± 0.4 °C, Fig. 4e) and the lowest at AU-Rob (18.9 ± 2.6 °C). BR-Ban had the highest monthly mean and standard deviation of VPD (12.2 ± 5.6 hPa, Fig. 4d). BR-Sa3 (9.0 ± 2.2 hPa) and ID-Pag (8.1 ± 1.3 hPa) had a larger monthly VPD than MY-PSO, BR-Ma2, GF-Guy, BR-Sa1 (all ~ 6.0 ± 1.2 hPa, Fig. 4d), while GH-Ank (3.0 ± 1.4 hPa) and AU-Rob (4.4 ± 1.6 hPa) had the lowest monthly mean VPD (Fig. 4d). Monthly mean precipitation and PPFD were both highly variable at all 13 sites, on average 5.6 ± 4.0 mm/day and 402.6 ± 63.4 umol m^{-2} s^{-1}, respectively (Fig. 4b, c). BR-Ban had the highest monthly mean PPFD (488.1 ± 64.5 umol m^{-2} s^{-1}) while monthly mean PPFD at GH-Ank was the lowest amongst the 13 sites (297.4 ± 65.3 umol m^{-2} s^{-1}, Fig. 4c). Monthly mean soil water content in VU-Coc (44.7 ± 5.8%), MY-PSO (41.6 ± 2.7%), PA-SPn (39.1 ± 9.9%), and BR-Cax (38.6 ± 4.5%) was higher than that of GF-Guy and GH-Ank (18.9 ± 3.3%, Fig. 4f), noting that not all sites were able to provide VPD, PPFD, T_s and soil water content observations.

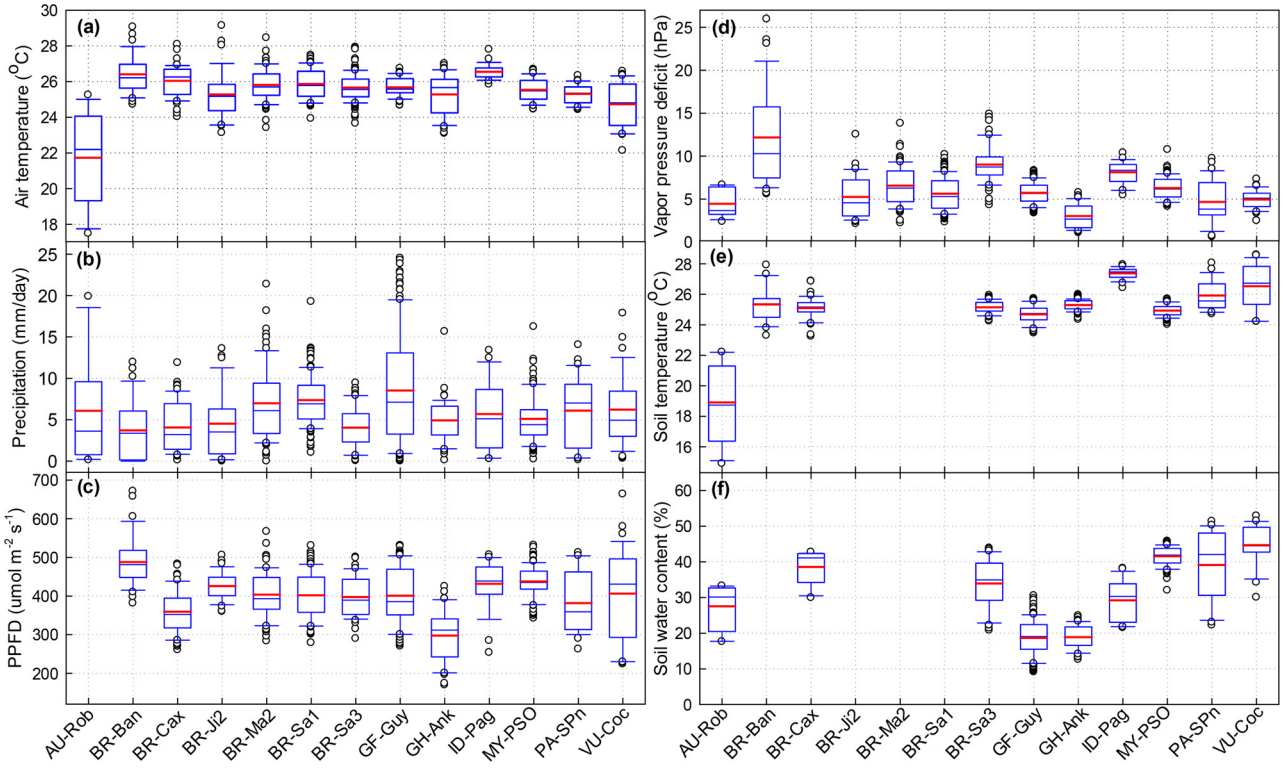

Fig. 4. Median (blue) and average (red) monthly above-canopy air temperature (a), precipitation (b), photosynthetic photon flux density (PPFD, c), vapor pressure deficit (d), soil temperature (e), and soil water content (f) from daily mean observations with boxes representing, from top to bottom, 95th, 75th, 50th, 25th, and 5th percentiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Carbon fluxes in tropical rainforests: trends and sensitivity to flux methodology

We compare carbon flux values obtained using nighttime partitioning methods from both the LaThuile and FLUXNET2015 databases, and then discuss differences between daytime and nighttime partitioning methods from the FLUXNET2015 database. The cumulative sum of NEE using nighttime partitioning methods (Fig. A2) exhibits differences in magnitude and sometimes sign amongst sites during the observation periods (Table 1). At ID-Pag, approximately 700 g C m^{-2} of carbon (or ~ 350 g C m^{-2} y^{-1}) was released to the atmosphere over two years (Fig. A2). MY-PSO took up 7000 g C m^{-2} during the seven-year available observation period or ~ 1000 g C m^{-2} y^{-1} (Fig. A2a and Table 2). BR-Ban, BR-Ma2, and BR-Cax were also measured to be net carbon sinks (i.e. negative NEE) on the order of -1000 g C m^{-2} y^{-1}, but the carbon sinks at BR-Sa1, GF-Guy and BR-Sa3 were weaker, approximately −200 g C m^{-2} y^{-1} on average (Table 2, Fig. A2a).

The cumulative sum of RE (Fig. A2c) using nighttime partitioning techniques showed large differences while the cumulative sum of GEP (Fig. A2b) was less variable during the available observation periods. Mean annual RE ranged from 1430 g C m^{-2} y^{-1} (BR-Ban) to 3580 g C m^{-2} y^{-1} (ID-Pag) across the 13 sites while mean annual GEP ranged from 2330 g C m^{-2} y^{-1} at PA-SPn to 3720 g C m^{-2} y^{-1} at GF-Guy (Table 2, Fig. A2).

RE estimated from daytime partitioning approaches tended to be larger than those derived from nighttime partitioning approaches; for example, RE at BR-Sa1 estimated from daytime partitioning approaches was larger than that of nighttime partitioning approaches by 560 g C m^{-2} y^{-1} on average ($P < 0.05$, Tables 2 and A3). We proceed with our analysis by comparing GEP and RE derived from nighttime partitioning approaches simply because more data are available to analyze (Table 2) while noting important differences in C flux estimates that result from differences in partitioning methodology.

An ANOVA coupled to a least-significant difference test for multiple comparisons (Rice, 1989) demonstrated that the 13 sites (using nighttime partitioning approaches) can be separated at the $P < 0.05$ level into the five sites that represent a relatively weak mean annual C sink with a NEE less negative than -400 g C m^{-2} y^{-1} (GF-Guy, VU-Coc, BR-Sa3, BR-Sa1) or even a C source (ID-Pag), the four sites (BR-Ma2, MY-PSO, BR-Cax and BR-Ban) that represented a stronger C sink of less than −900 g C m^{-2} y^{-1}, and the remaining four sites with NEE between -400 and −900 g C m^{-2} y^{-1} (Table 2, Fig. 5). Perhaps counter-intuitively, the sites that represented a weaker net ecosystem C uptake (i.e. those with NEE values closer to zero, Fig. A2) had higher GEP (greater than 3000 g C m^{-2} y^{-1} for all sites) and higher RE (greater than 3000 g C m^{-2} y^{-1} for all sites, Fig. 5). Four of these five sites with the exception of VU-Coc provided subcanopy carbon storage observations to the FLUXNET database (Table 1). In contrast, the sites that represented a stronger net ecosystem C uptake had lower GEP (less than 2800 g C m^{-2} y^{-1} for all sites, Fig. 5b) and RE (less than 1800 g C m^{-2} y^{-1} for all sites, Fig. 5c). Three of these four sites with the exception of MY-PSO were unable to provide subcanopy C storage observations to the FLUXNET database (Table 1).

3.4. Responses of tropical rainforest carbon flux to environmental variability

There was a strong relationship between half-hourly or hourly GEP and VPD during periods of high PPFD which was rather insensitive when thresholding observations to include PPFD values greater than 1300 μmol m^{-2} s^{-1} (Fig. 6). For a conservative interpretation of light saturated conditions, we chose PPFD values greater than 1500 μmol m^{-2} s^{-1} following Wu et al. (2017) to explore the relationship between VPD and GEP (Fig. 7), which demonstrates a variety of slopes ranging from -0.31 μmol CO_2 m^{-2} s^{-1} hPa^{-1} (AU-Rob) to -0.87 μmol CO_2 m^{-2} s^{-1} hPa^{-1} (PA-SPn).

Relationships between VPD and GEP alone are not necessarily indicative that VPD is the primary control over the decrease in GEP at high light levels because VPD is correlated with T_a and SWC, each of which exert independent controls over GEP (Fig. A1), which itself is subject to the assumptions of the partitioning routine used to estimate it from NEE observations. VPD, T_a, and SWC are related under light saturated conditions in most instances, as expected, at the seven ecosystems in which T_a, VPD and SWC observations were available (Table A4). The path analyses for GEP demonstrates that VPD (-0.54) and SWC (-0.31) have direct negative effects on GEP under light saturated conditions across these seven sites, but the response of T_a is on average positive (0.28, Table 3). A similar pattern holds for the constraints on NEE at high PPFD (Table 4), but the effect of VPD (-0.45) is even stronger in relative terms than that of SWC (-0.08) and T_a again has a positive effect (0.13). The total effect of VPD on GEP (-0.51) and NEE (-0.44) under light saturated conditions is stronger than the other

Table 2
The annual mean and standard deviation of net ecosystem exchange (NEE), gross ecosystem productivity (GEP), and ecosystem respiration (RE) in units of g C m^{-2} y^{-1} from tropical forest eddy covariance sites in the LaThuile and FLUXNET2015 eddy covariance databases. * indicates that measurements of subcanopy CO_2 storage were included in the NEE calculation in the LaThuile or FLUXNET2015 databases. Note that AU-Rob only includes one year of data and standard deviation could not be calculated. Values refer to measurement from the FLUXNET2015 when observations were available from both databases, i.e. we study the FLUXNET2015 values when data are available from both datasets because the time series are longer.

Sites	LaThuile			FLUXNET2015				
	NEE	Nighttime flux partitioning approaches		NEE	Nighttime flux partitioning approaches		Daytime flux partitioning approaches	
		GEP	RE		GEP	RE	GEP	RE
AU-Rob	–	–	–	−744	1994	1250	2112	1547
BR-Ban	−1190 ± 172	2623 ± 202	1433 ± 374	–	–	–	–	–
BR-Cax	−1002 ± 88	2791 ± 360	1788 ± 419	–	–	–	–	–
BR-Ji2	−733 ± 124	2990 ± 154	2257 ± 278	–	–	–	–	–
BR-Ma2	−953 ± 151	2515 ± 604	1578 ± 487	–	–	–	–	–
BR-Sa1*	–	–	–	−57 ± 197	3425 ± 365	3391 ± 227	3634 ± 599	3953 ± 649
BR-Sa3*	–	–	–	−171 ± 328	3234 ± 505	3033 ± 745	3348 ± 239	3483 ± 504
GF-Guy*	–	–	–	−157 ± 86	3720 ± 223	3560 ± 222	3637 ± 222	3426 ± 269
GH-Ank*	–	–	–	-768 ± 223	2825 ± 715	2009 ± 508	2776 ± 475	2250 ± 286
ID-Pag*	375 ± 179	3209 ± 177	3584 ± 2	–	–	–	–	–
MY-PSO*	–	–	–	−999 ± 110	2495 ± 120	1510 ± 76	2608 ± 169	1629 ± 188
PA-SPn*	–	–	–	−600 ± 248	2328 ± 376	1679 ± 128	2215 ± 22	1667 ± 39
VU-Coc	−367 ± 264	3505 ± 74	3138 ± 338	–	–	–	–	–

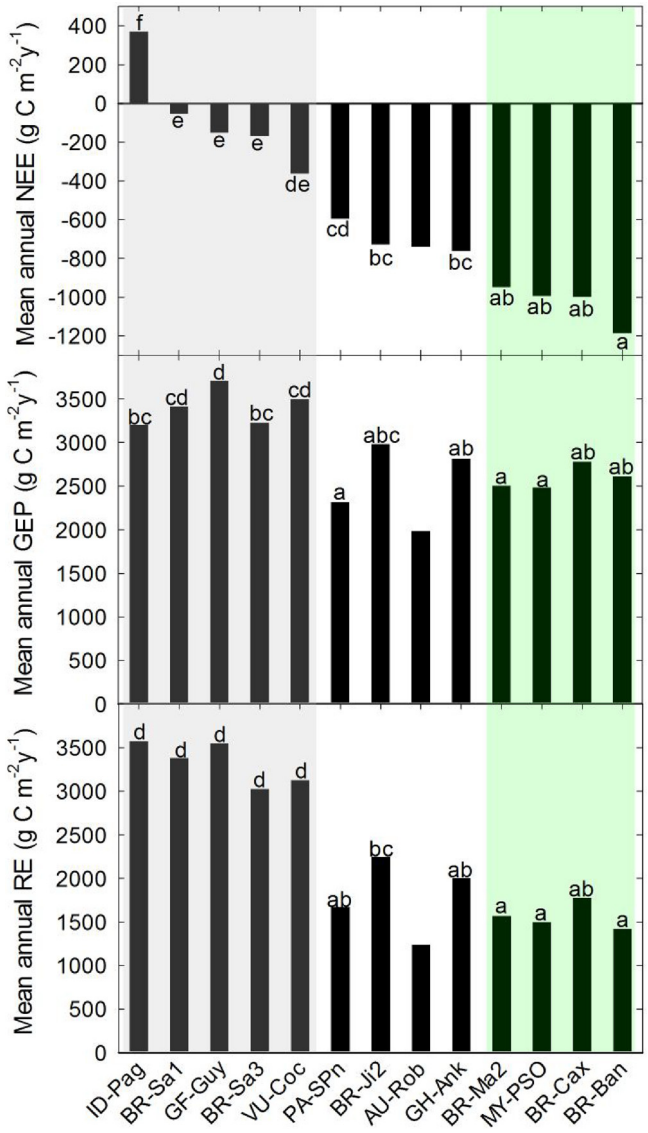

Fig. 5. Mean annual net ecosystem exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (RE) during the available observation period for the eddy covariance research sites described in Table 1 (see also Table 2). Gray shading represents the sites identified by the least-significant difference test ($P < 0.05$) for multiple comparisons as having a net C sink of greater than -400 g C m^{-2} y^{-1}; green shading represents sites with a NEE of less than −900 g C m^{-2} y^{-1}, while white represents sites with NEE between -400 and −900 g C m^{-2} y^{-1}. The different lowercase letters indicate the significant difference ($P < 0.05$) between carbon flux at different sites and are marked as a, b, c, d, e and f, successively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicators (Tables 3 & 4). The path analysis also indicates that T_a has a strong indirect effect on GEP (-0.36, Table 3) and NEE (-0.29, Table 4) due to its impact on VPD.

Path values from individual sites point to differences in the relationship between micrometeorological variables and carbon fluxes under light saturated conditions. AU-Rob, near the tropical/subtropical forest ecotone, has positive direct and total effects on GEP and NEE by SWC (0.31 and greater) that balances the negative effect of VPD (-0.37 to -0.38). T_a has no significant direct effect on GEP at 3 of the seven sites (4 sites for NEE) that measured both SWC and VPD, but T_a had a total effect on GEP that exceeded that of VPD at BR-Sa3 and ID-Pag (and a larger total effect on NEE at BR-Sa3). The strong relationships between T_a and VPD (0.83-0.87, Table A4) lead to large indirect effects on GEP and NEE. SWC exerted a strong positive influence on GEP (0.71) and NEE (0.67) in the regrowing tropical forest PA-SPn.

3.5. Projected future climate conditions

Climate projections from 13 general circulation models (CMIP5) under RCP 8.5 suggest that many current tropical rainforest sites on the cooler end of the current temperature range are likely to reach a climate space similar to present-day warmer sites by the year 2050, and warmer sites will reach a climate space not currently experienced (Fig. 8). T_a and VPD have increased from the 1950s until the present at the study sites and are projected to increase further by the year 2050 (Fig. 8). The cooler AU-Rob ecosystem is projected to have a mean T_a on the order of 24.5 °C by 2050, approaching the mean annual T_a of many study sites at the present (approximately 25–26 °C, Fig. 4a). Many other ecosystems are projected to reach mean annual T_a values of 30 °C or greater, which is not observed across any study sites at the present (Fig. 4a). Most sites are projected to have annual average VPD of > 10 hPa, the point at which stomatal conductance often responds to VPD (Körner, 1995; Lasslop et al., 2010; Oren et al., 1999), noting that some of the drier ecosystems (e.g. BR-Ban on the tropical rainforest/cerrado ecotone) currently experience such conditions on an annual or monthly basis (Fig. 4d) and that GEP appears to respond to VPD at values below 10 hPa across the study ecosystems under light-saturated conditions (Figs. 6 and 7).

4. Discussion

4.1. Surface-atmosphere carbon dioxide flux in tropical rainforests

The broad definition of tropical rainforests applied in this study – including both managed and unmanaged ecosystems – leads to a large diversity of ecosystems with diverse ecosystem-atmosphere exchange of CO_2, but with largely consistent patterns with respect to micrometeorological variability and measurement methodology. The five ecosystems that are estimated to have greater carbon uptake (with the magnitude of GEP greater than 3000 g C m^{-2} y^{-1}) sequester less carbon – or even lose it – on an annual basis because RE likewise tends to be large (Fig. 5). This apparent negative relationship between GEP and NEE should be critically examined against the observation that tower sites which were able to calculate NEE as the combination of subcanopy storage and eddy flux had higher magnitudes of GEP and RE and lower magnitudes of NEE (Table 1, Fig. 5). These findings may have implications for approaches that seek to upscale tower-based observations to larger regions given that the inclusion of subcanopy storage was related to a decrease in the magnitude of the measured C sink.

Carbon dioxide storage can dominate surface-atmosphere CO_2 exchange over parts of the diurnal cycle (Malhi et al., 1998), particularly during the early morning, late evening and night (i.e. often during periods in which the NEE fluxes are used for gapfilling and partitioning algorithms). Given the importance of subcanopy CO_2 storage measurements to net surface-atmosphere CO_2 exchange in tropical rainforests (Araújo et al., 2002; Hayek et al., 2018; Hutyra et al., 2008), methodological differences among sites should be investigated to reduce uncertainties associated with NEE, GEP, and RE estimates. Additionally, careful consideration should be taken by users of tropical flux data to ensure robustness of results in the face of these uncertainties. Note that due to the small number of sites considered here (13 total), which limits statistical analysis and the diversity of ecosystems in question, we caution against making categorical statements about the cause of the finding that sites with high GEP have less net CO_2 uptake. To illustrate this point, VU-Coc showed high GEP and RE, leading to a relatively weak net C sink, and was unable to provide subcanopy storage measurements. This can be attributed in part to the fact that seasonal cycles of net primary productivity of this coconut palm canopy are driven by fruit development; fruits accounted for 46%

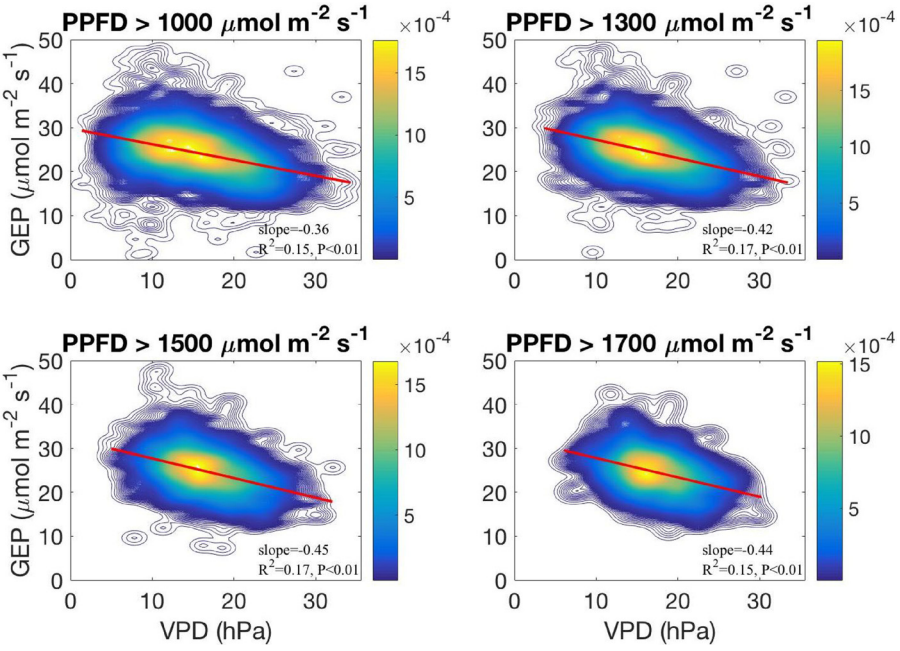

Fig. 6. The relationship between vapor pressure deficit (VPD) and gross ecosystem productivity (GEP) as represented by a two-dimensional kernel density estimate ("heat map") for all half-hourly observations that passed FLUXNET quality control tests under different PPFD thresholds for the Indonesia-Palangkaraya (ID-Pag) tropical peat forest ecosystem, taken as an example for all other sites. The color bar denotes the probability of finding a value within a given pixel and slopes are in units of μmol CO_2 m^{-2} s^{-1} hPa^{-1} from regression lines (red) calculated using ordinary least squares regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

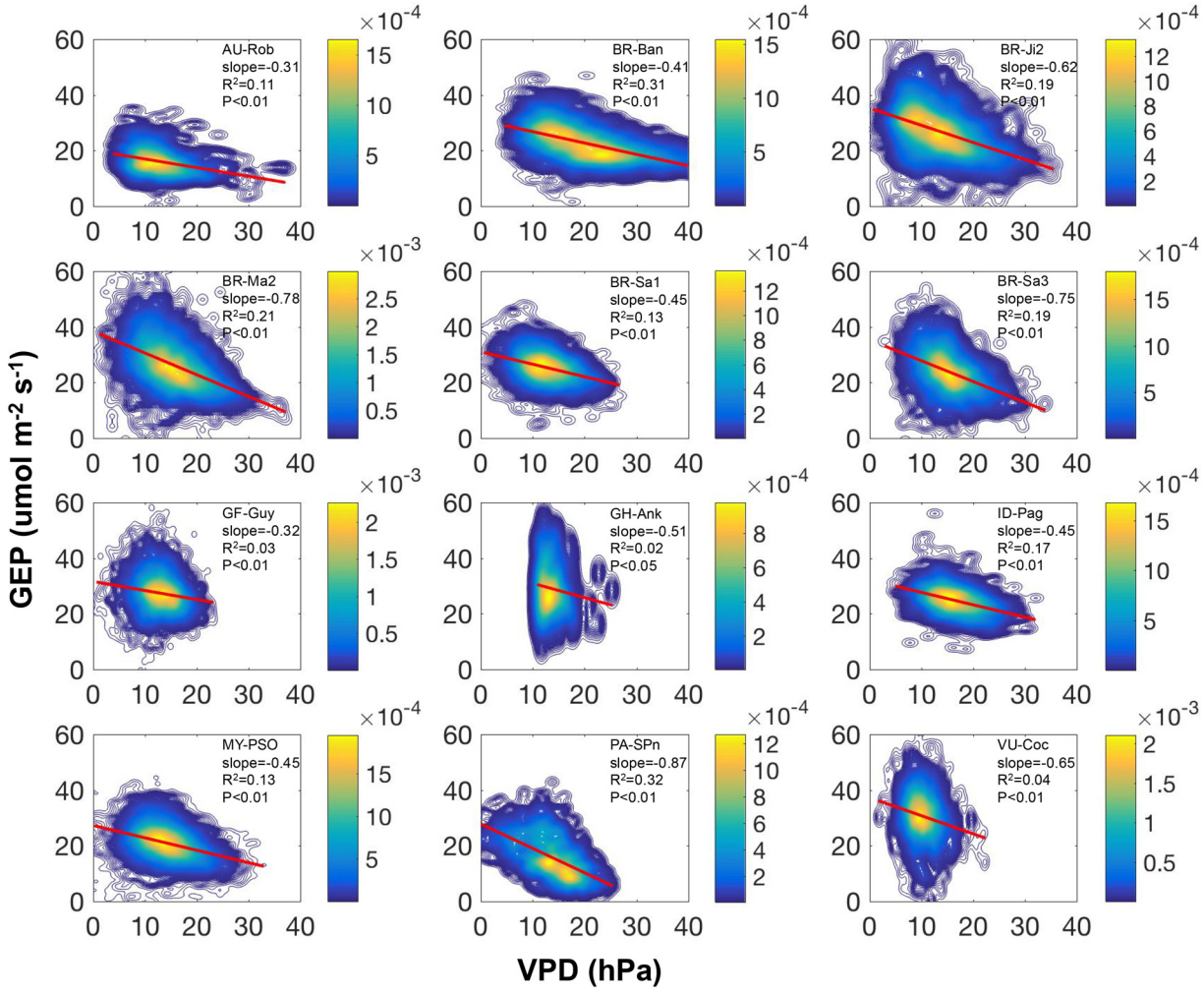

Fig. 7. The relationship between vapor pressure deficit (VPD) and gross ecosystem productivity (GEP) as represented by a two-dimensional kernel density estimate ("heat map") for all half-hourly observations that passed FLUXNET quality control thresholds for different sites, choosing also values for which PPFD > 1500 μmol m^{-2} s^{-1} following Wu et al., (2017) to include only periods with light-saturated conditions (Fig. 6). The color bar denotes the probability of finding a value within a given pixel and slopes are in units of μmol CO_2 m^{-2} s^{-1} hPa^{-1}.

Table 3
Standardized effect of air temperate (T_a), vapor pressure deficit (VPD) and soil water content (SWC) on gross ecosystem productivity (GEP) from the path analysis (Fig. A1) for all half-hourly observations that passed FLUXNET quality control thresholds for different sites, choosing also values for which PPFD > 1500 μmol m^{-2} s^{-1} to include only periods with light-saturated conditions. ns means insignificant paths (P > 0.05).

Site	Direct effect on GEP			Indirect effect on GEP			Total effect on GEP		
	Ta	VPD	SWC	Ta	VPD	SWC	Ta	VPD	SWC
AU-Rob	0.28	−0.38	0.37	−0.36	−0.04	−0.08	−0.08	−0.42	0.41
BR-Sa3	−0.12	−0.35	ns	−0.29	ns	0.11	−0.41	−0.35	0.08
GF-Guy	ns	−0.22	0.06	−0.21	−0.01	0.02	−0.21	−0.22	0.08
ID-Pag	ns	−0.50	−0.31	−0.42	0.16	0.26	−0.42	−0.35	−0.05
MY-PSO	0.27	−0.57	0.09	−0.51	−0.02	0.09	−0.24	−0.59	0.25
PA-SPn	ns	−0.15	0.61	−0.03	−0.43	0.11	−0.03	−0.58	0.71
VU-Coc	0.14	−0.18	0.05	−0.02	−0.02	0.10	0.11	−0.20	0.12
All	0.28	−0.54	−0.31	−0.36	0.03	0.05	−0.08	−0.51	−0.25

Table 4
Standardized effect of air temperate (T_a), vapor pressure deficit (VPD) and soil water content (SWC) on net ecosystem exchange (NEE) from the path analysis (Fig. A1) for all half-hourly observations that passed FLUXNET quality control thresholds for different sites, choosing also values for which PPFD > 1500 μmol m^{-2} s^{-1} to include only periods with light-saturated conditions. ns means insignificant paths (P-value > 0.05).

Sites	Direct effect on -NEE			Indirect effect on -NEE			Total effect on -NEE		
	Ta	VPD	SWC	Ta	VPD	SWC	Ta	VPD	SWC
AU-Rob	ns	−0.37	0.31	−0.33	−0.04	0.04	−0.33	−0.40	0.35
BR-Sa3	−0.12	−0.27	ns	−0.23	ns	0.09	−0.34	−0.27	0.09
GF-Guy	−0.18	−0.15	−0.03	−0.11	ns	0.10	−0.29	−0.15	0.07
ID-Pag	ns	−0.58	−0.17	−0.49	0.09	0.30	−0.49	−0.49	0.12
MY-PSO	0.22	−0.56	ns	−0.48	ns	0.10	−0.27	−0.56	0.10
PA-SPn	ns	−0.25	0.49	−0.08	−0.35	0.18	−0.08	−0.60	0.67
VU-Coc	ns	−0.19	−0.08	−0.06	0.03	0.07	−0.06	−0.16	−0.01
All	0.13	−0.45	−0.08	−0.29	0.01	0.04	−0.16	−0.44	−0.04

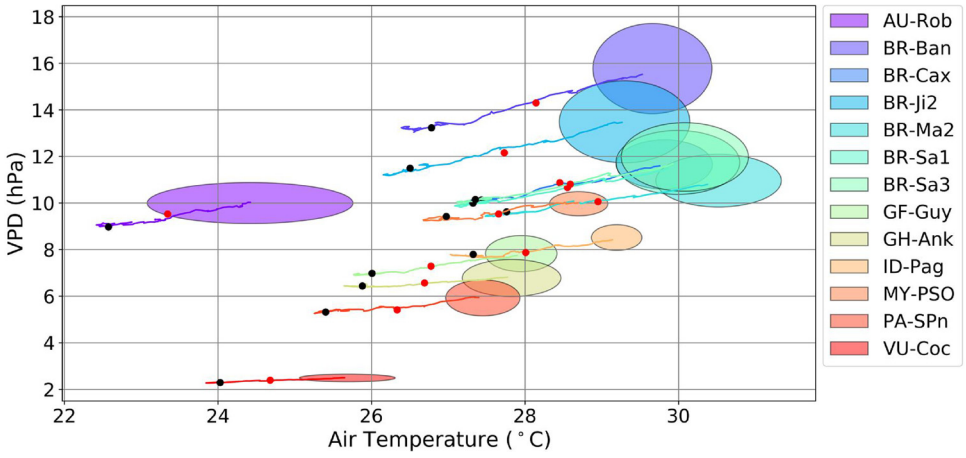

Fig. 8. Future climate projections from the ensemble mean of 13 CMIP5 models for vapor pressure deficit (VPD) and air temperature (T_a) for the representative concentration pathway (RCP) 8.5. The black dots represent the 1950 average; the red dots represent the 2017 average while the lines represent the time series from 1950 to 2050, smoothed with a five-year moving average. As a consequence, dots that reflect individual years may not perfectly align with lines. The oval shadings indicate the standard deviation of the 2050 projected climate regime. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of tree net primary productivity at Vu-Coc (Navarro et al., 2008). Conversely, some non-agricultural sites that provided subcanopy C storage measurements (e.g. GH-Ank and PA-SPn) did not have high magnitudes of GEP and RE compared to other study ecosystems, leading to a relatively weak net C sink (Table 1, Fig. 5). In other words, methodological differences alone cannot fully explain the pattern of NEE across sites, highlighting the role of environmental and ecological controls on NEE. Other unmeasured state factors such as soil fertility, forest composition, topography and disturbance history, can also strongly influence tropical rainforest C cycling (e.g. Aiba and Kitayama, (1999); Asner et al., (2015); Cleveland et al., (2011); Fuentes et al., (2016); Paoli et al., (2008); Raich et al., (1997)). Resolving other controls on rates of ecosystem C exchange will require more holistic biogeochemical research alongside field inventories of tropical rainforest C budgets for an improved understanding of the mechanisms that result in different surface-atmosphere C fluxes amongst tropical rainforests.

This study also found that RE at BR-Sa1 estimated from daytime partitioning approaches was larger than that of nighttime partitioning approaches by 560 g C m^{-2} y^{-1} on average ($P < 0.05$). Previous work

at this site demonstrated that the choice of u_* threshold can change inferred NEE from a C sink to a C source (Hayek et al., 2018; Miller et al., 2004; Saleska et al., 2003). Nighttime partitioning approaches use nighttime RE observations under conditions of sufficient u_* to model RE during daytime and thus estimate GEP by the difference between modeled RE and measured NEE while daytime flux partitioning approaches is based on daytime data, which are used to parameterize a model to estimate GEP and RE. If we assume RE based on daytime flux measurements represent an improvement (Lasslop et al., 2010), both RE and GEP estimated from nighttime partitioning approaches may be underestimated. Small changes in the approach used to derive component fluxes has a substantial impact on their estimates, especially in tropical rainforests where GEP and RE are characteristically of large magnitude.

4.2. Responses of tropical rainforest carbon flux to environmental drivers

High rainfall and warm temperatures consistently enhance both aboveground net primary productivity and decomposition at tropical rainforest sites (Cusack et al., 2009; Salinas et al., 2011; Taylor et al., 2017) by maximizing decomposer activity and promoting physical leaching of forest floor material (Cleveland et al., 2010; Wieder et al., 2009). Further increases in T_a translate into an increase in VPD if atmospheric humidity remains constant, and VPD serves as a strong control over GEP (Kiew et al., 2018; Wu et al., 2017). As a consequence, the ability of tropical rainforest trees to acclimate to both T_a and VPD should be investigated to understand how they may (or may not) adapt to projected global changes over the coming decades. Recent studies have also emphasized the important role of canopy surface temperature in constraining GEP in tropical forests (Pau et al., 2018). Five of the study ecosystems provided outgoing longwave radiation flux observations by which radiometric surface temperature can be estimated using the Stefan-Boltzmann law, but it is difficult to distinguish canopy surface temperature from the temperature of other elements in the ecosystem that tend to be warmer than leaves during the day (like tree bark) or cooler like soil. Integrating phenological cameras that can observe the thermal (Pau et al., 2018), visible (Lopes et al., 2016; Richardson et al., 2009), and near infra-red bands (Richardson et al., 2009) with existing eddy covariance measurements is a logical way forward for understanding spatial and temporal processes that are important for flux dynamics.

To the extent that the response of GEP to VPD reflects canopy isohydricity through its relationship to leaf water potential (Martinez-Vilalta et al., 2014; Matheny et al., 2017), our results suggest that the trees at different sites may have varying degrees of isohydricity that may influence their response to predicted increases in VPD (Fig. 8). Isohydricity is strongly related to canopy height (Giardina et al., 2018; Konings and Gentine, 2016), as is reference canopy conductance (conductance when VPD = 10 hPa, Novick et al., (2009)). From the observations, it is unclear why the 13 different tropical rainforest canopies exhibited different responses of GEP to increases in VPD (Fig. 7) as the slope of the relationships were unrelated to other aspects of the soil-vegetation-atmosphere hydraulic transport system including rooting depth and SWC (data not shown). Path analysis indicated that VPD tended to have a stronger total (negative) effect on GEP and NEE under light-saturated conditions than did T_a or SWC across most study ecosystems (Tables 3 and 4), in agreement with the findings of Wu et al., (2017) and Kiew et al., (2018). The negative relationship between flux and T_a is mainly because T_a is closely related with VPD (Table A4), which led to large indirect (negative) effects on GEP or NEE. In other words, VPD is mainly responsible for the decline in light-saturated GEP and NEE based on the path analysis, but this does not preclude the importance of T_a (especially via its relationship to VPD and surface temperature) and SWC on controlling carbon fluxes in tropical rainforest ecosystems, noting also that we were able to study the interplay between hydraulic variables and carbon fluxes at only seven of the thirteen study sites due to data availability constraints (Tables 3 and 4).

4.3. Future directions

Future studies should continue research on tropical tree sensitivity to hydrologic stress both through decreases in SWC and increases VPD, and study whether and how tropical trees may acclimate to VPD as well as canopy surface temperature (Pau et al., 2018), which may limit responses to future climate increases (Kutsch et al., 2001; Marchin et al., 2016). Models consistently estimate future increases in T_a and VPD at the study sites (Fig. 8), albeit with a considerable uncertainty range across the CMIP5 models. Ecosystems with already higher VPD are expected to experience the strongest VPD increase. No such agreement is found for SWC given the challenges of estimating future precipitation (Novick et al., 2016), highlighting the importance to measure and study both VPD and soil moisture trends in concert to understand how tree physiology is impacted by water supply (via SWC) and demand (via VPD). Moreover, increasing CO_2 levels will also impact stomatal aperture and thus GEP (Swann et al., 2016), highlighting the need to study all climate change effects on GEP in concert.

Results also demonstrate that flux measurement methodology in tropical rainforest ecosystems is an important avenue of future research (Hayek et al., 2018). The impact of nighttime gapfilling on carbon fluxes partitioning (as discussed in Section 4.1) is further exacerbated by tropical rainforests' characteristically large plant area indices and the presence of large within-canopy air spaces that result in decoupling between above and below-canopy flows. Recent studies have demonstrated the utility of using the variance of vertical wind velocity (σ_w) rather than u_* as an improved criterion for approximating the coupling between the within and above-canopy air space in forested canopies for determining the quality of flux measurements (Santana et al., 2018), especially at night (Acevedo et al., 2009; Jocher et al., 2017; Thomas et al., 2013). Hayek et al., (2018) reiterated the importance of subcanopy drainage and introduced approaches to account for potential "missing" CO_2 storage. Results in the present manuscript agree with the argument that alternative flux partitioning and eddy covariance processing techniques should be explored across different tropical forests to better-constrain their role in the regional and global C cycle.

5. Conclusions

Eddy covariance measurements suggest that tropical rainforest canopies exhibit a wide range of NEE values that range from carbon source to sink, but these estimates are sensitive to flux measurement methodology. Sites that included subcanopy CO_2 storage values reported characteristically higher magnitudes of GEP (greater than 3000 g C m^{-2} y^{-1}) and RE, and consequently lower NEE, characteristicaly between approximately 400 g C m^{-2} y^{-1} (i.e. a CO_2 source to the atmosphere) and about -400 g C m^{-2} y^{-1}. This highlights the importance of standardized processing of biosphere-atmosphere flux measurements, which is particularly challenging in tropical forests given logistical considerations. Such estimates will serve to increase the confidence in studies that assess ecosystem and environmental variability as drivers for variations in NEE, GEP, and RE. That being said, CO_2 storage measurements alone cannot fully explain the differences in NEE, GEP,

and RE amongst sites, demonstrating the importance of ecological differences amongst tropical forest ecosystems. Our results emphasize the importance and diversity of tropical rainforest carbon flux responses to atmospheric water deficit, and future studies should investigate the acclimation of mature tropical trees to increases in VPD in addition to T_a. Combined, our results highlight the importance of continued research into the biosphere-atmosphere exchange of CO_2 in tropical forests, especially as fewer observations are available in more recent years than in the past.

Logistical challenges of making ecosystem-scale measurements on a quasi-continuous basis at remote research sites with tall canopies that require considerable infrastructure and reliable power systems persist. Recent and forthcoming research initiatives including the Amazon Tall Tower Observatory (ATTO, see Andreae et al., (2015)), Next Generation Ecosystem Experiments—Tropics (NGEE-Tropics, Chambers et al., (2014)) and associated Amazon Free Atmosphere Carbon Enrichment facility (AmazonFACE, Norby et al. (2015)) suggest that more eddy covariance and model estimates of tropical rainforest GEP and RE will be available in the future if funding is sustained. Such investments will help stem the decline in tropical rainforest flux data availability (Fig. 3), but global initiatives must be undertaken to improve our ability to observe the carbon dynamics of tropical ecosystems across different regions.

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Appendix A

A1 Notes on the FLUXNET2015 C flux calculation

It is noteworthy that NEE is only approximately equal to RE minus GEP for daily data although NEE is equal to RE minus GEP for half-hourly data in FLUXNET 2015. In FLUXNET 2015, a reference NEE was selected on the basis of the Model Efficiency (identified with "_REF" in the variable name). The extraction of NEE_REF is done separately for each time aggregation and for this reason the u* threshold associated to the NEE_REF can change across time. The Model Efficiency calculation (which determines _REF variables) is performed independently using variable u* thresholds (NEE_VUT_REF, Table A1) and for each temporal aggregation. Therefore, percentile variables are re-ranked at each temporal aggregation, and reference values (_REF) are recomputed, and should not be considered the same variable. For instance, NEE_VUT_REF at half-hourly resolution might have been generated using a different u* threshold than NEE_VUT_REF at daily resolution. In this way, NEE is approximately but not exactly equal to RE minus GEP for yearly data in Table 3 because annual NEE, RE and GEP were taken from the sum from daily data.

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Table A1
A list of variables and their description and units, including the name of each variable in the LaThuile and FLUXNET2015 databases.

Variable	LaThuile	FLUXNET2015	Units	Description
NEE	NEE_f	NEE_VUT_REF	μmol CO_2 m^{-2} s^{-1} or g C m^{-2} y^{-1}	Net ecosystem exchange
GEP	GEP_f	GEP_NT_VUT_REF	μmol CO_2 m^{-2} s^{-1} or g C m^{-2} y^{-1}	Gross ecosystem productivity
RE	Reco	RECO_NT_VUT_REF	μmol CO_2 m^{-2} s^{-1} or g C m^{-2} y^{-1}	Ecosystem respiration
T_a	Ta_f	TA_F	°C	Air temperature
VPD	VPD_f	VPD_F	hPa	Vapor pressure deficit
Precipitation	Precip_f	P_F	mm	Precipitation
T_s	Ts1_f	TS_F_MDS_1	°C	Soil temperature (upper layer) *
SWC	SWC1_f	SWC_F_MDS_1	%	Soil water content (upper layer) *
PPFD	PPFD_f	PPFD_IN	umol m^{-2} s^{-1}	Photosynthetic photon flux density

* Soil measurement depths vary.

Table A2
The 13 General Circulation Models (GCMs) from the Coupled Model Intercomparison Project - Phase 5 archive (CMIP5) used in the present analysis.

Model Name	Model Country	Developed by
ACCESS1.0	Australia	Commonwealth Scientific and Industrial Research Organisation, Australia (CSIRO), and Bureau of Meteorology, Australia (BOM)
BNU-ESM	China	College of Global Change and Earth System Science, Beijing Normal University, China
CNRM-CM5	France	National Centre of Meteorological Research, France
CSIRO-Mk3-6-0	Australia	Commonwealth Scientific and Industrial Research Organization/Queensland Climate Change Centre of Excellence, Australia
CanESM2	Canada	Canadian Centre for Climate Modeling and Analysis
GFDL-CM3	United States	National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory
GISS-E2-R	United States	NASA Goddard Institute for Space Studies
IPSL-CM5A-LR	France	Institut Pierre Simon Laplace, France
MIROC-ESM	Japan	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MIROC5	Japan	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies and Japan Agency for Marine-Earth Science and Technology
MPI-ESM-LR	Germany	Max Planck Institute for Meteorology (MPI-M)
MRI-CGCM3	Japan	Meteorological Research Institute, Japan
inmcm4	Russia	Institute for Numerical Mathematics, Russia

Table A3
Results of a one-way analysis of variance (ANOVA) for mean comparisons of annual RE and GEP at BR-Sa1 using nighttime and daytime partitioning approaches. NT_DT means nighttime partitioning approaches versus daytime partitioning approaches. Please see Table A1 for abbreviations.

		Sum of Squares	df	Mean Square	F	Sig.
RE × NT_DT	Between Groups	1,423,608.758	1	1,423,608.758	6.026	0.026
	Within Groups	3780046.637	16	236252.915		
	Total	5203655.395	17			
GEP × NT_DT	Between Groups	196,991.091	1	196,991.091	0.801	0.384
	Within Groups	3932744.559	16	245796.535		
	Total	4129735.650	17			

Table A4
The covariance between air temperature (T_a), vapor pressure deficit (VPD), and soil water content (SWC) at the study ecosystems during the measurement period as determined by path analysis (Fig. A1).

Site	Covariance		
	Ta-SWC	Ta-VPD	VPD-SWC
AU-Rob	−0.43	0.53	−0.11
BR-Sa3	−0.27	0.84	−0.23
GF-Guy	−0.49	0.83	−0.09
ID-Pag	−0.06	0.87	−0.51
MY-PSO	−0.24	0.86	−0.27
PA-SPn	0.04	0.33	−0.72
VU-Coc	0.24	0.2	−0.37
All	ns	0.66	−0.1

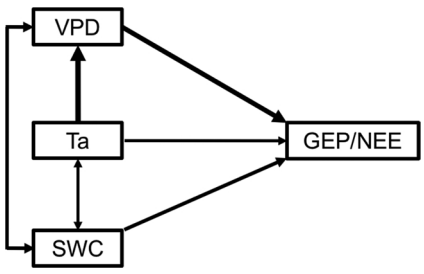

Fig. A1. A path diagram illustrating interactions between the micrometeorological variables T_a, VPD and SWC and their controls on GEP and NEE. We use half-hourly observations that passed FLUXNET quality control thresholds for different sites, choosing also values for which PPFD $>$ 1500 μmol m^{-2} s^{-1} to include only periods with light-saturated conditions for the analysis. The thickness of each arrow indicates standardized correlation coefficients (path value) described in Tables 3 and 4.

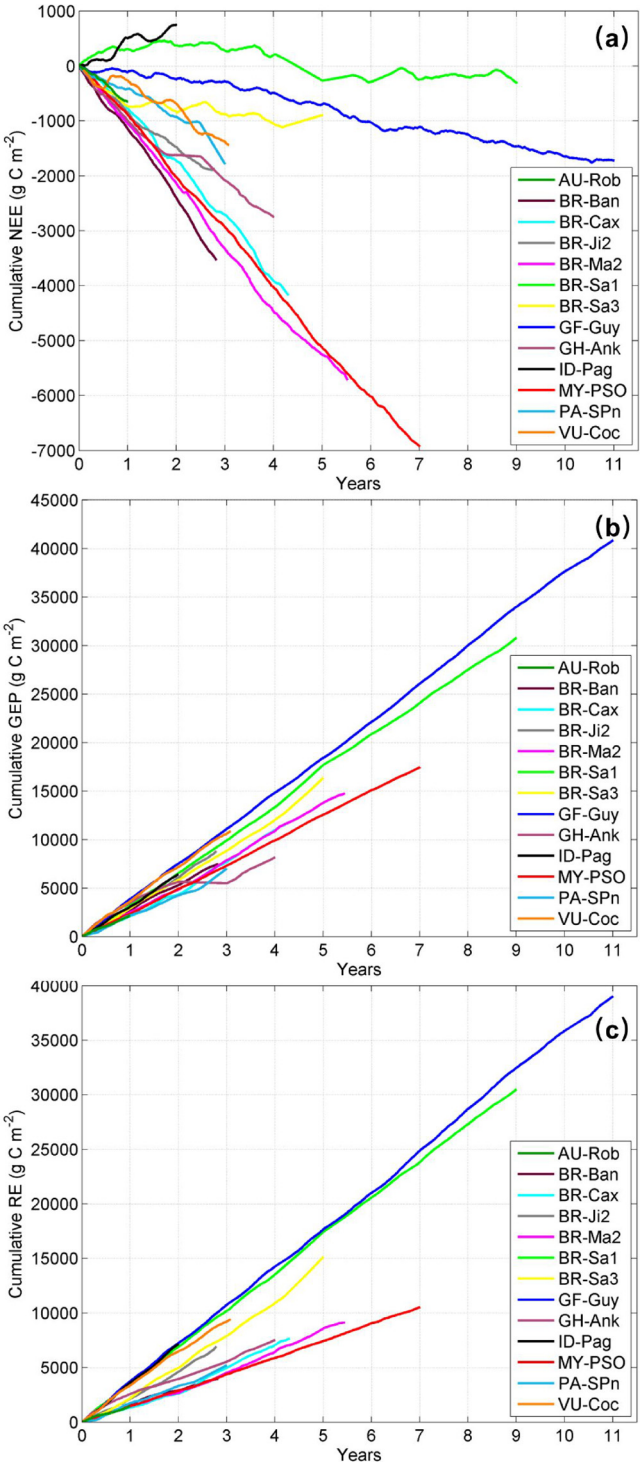

Fig. A2. The cumulative sum of net ecosystem exchange (NEE, a), gross ecosystem productivity (GEP, b) and ecosystem respiration (RE, c) using nighttime partitioning methods since the beginning of the measurements at the tropical forest eddy covariance research sites (see Table 1) using observations from the FLUXNET2015 database when possible and the LaThuile database when data were not available in FLUXNET2015 (Table 2).

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