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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

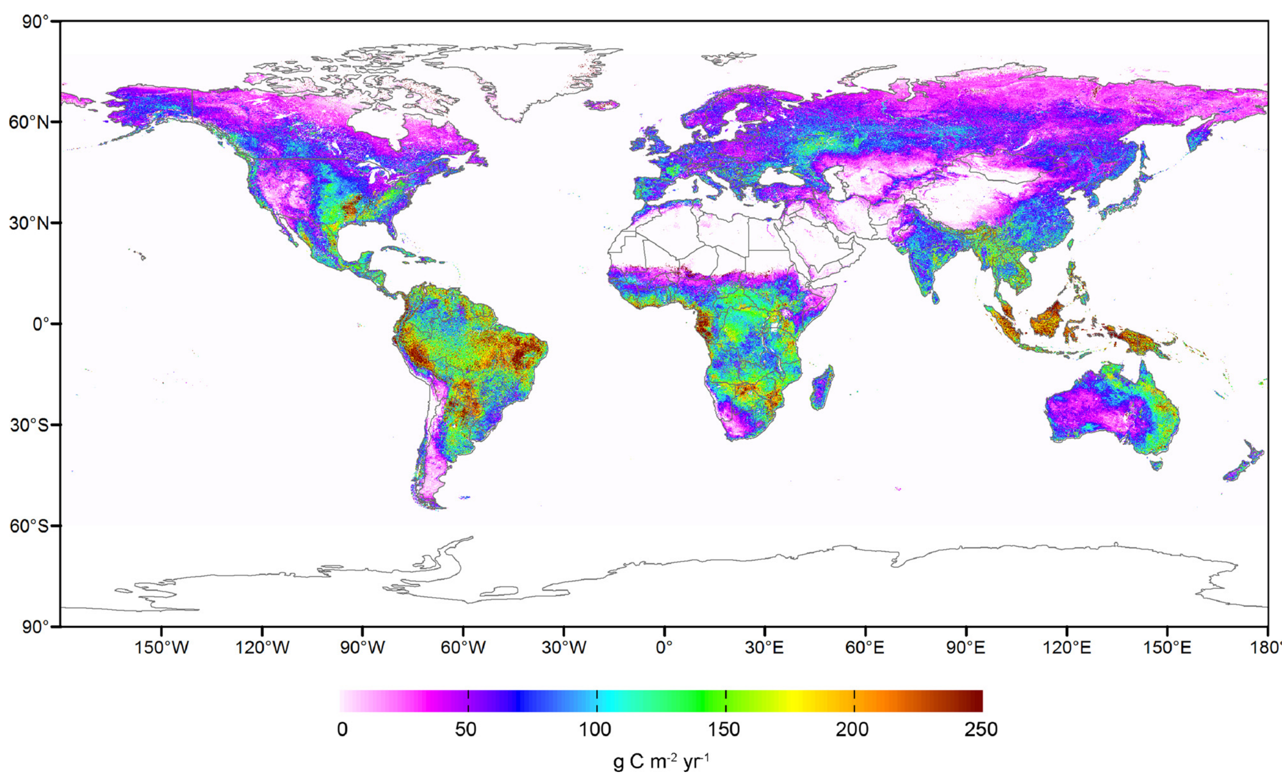


**Fig. 1.** The standard deviation of annual gross ecosystem productivity (GEP) from MODIS (MOD17A3) for the period.2000–2015. (For interpretation of the references to color in the figure the reader is referred to the web version of this article.)