5-25-2015

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Recommended Citation

Cleveland, C. C., P. Taylor, K. D. Chadwick, K. Dahlin, C. E. Doughty, Y. Malhi, W. K. Smith, B. W. Sullivan, W. R. Wieder, and A. R. Townsend (2015), A comparison of plot-based satellite and Earth system model estimates of tropical forest net primary production, Global Biogeochem.Cycles, 29, 626-644, doi:10.1002/2014GB005022.

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RESEARCH ARTICLE

Special Section:
Trends and Determinants of the Amazon Rainforests in a Changing World, A Carbon Cycle Perspective

Key Points:
- Rates of NPP in tropical forests using three approaches are compared
- Different methods produce similar NPP estimates but inconsistent patterns
- A strategy for improving tropical NPP estimates is described

Supporting Information:
- Figures and Tables S1 and S2

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A comparison of plot-based satellite and Earth system model estimates of tropical forest net primary production

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Abstract Net primary production (NPP) by plants represents the largest annual flux of carbon dioxide (CO_2) from the atmosphere to the terrestrial biosphere, playing a critical role in the global carbon (C) cycle and the Earth's climate. Rates of NPP in tropical forests are thought to be among the highest on Earth, but debates about the magnitude, patterns, and controls of NPP in the tropics highlight uncertainty in our understanding of how tropical forests may respond to environmental change. Here, we compared tropical NPP estimates generated using three common approaches: (1) field-based methods scaled from plot-level measurements of plant biomass, (2) radiation-based methods that model NPP from satellite-derived radiation absorption by plants, (3) and biogeochemical model-based methods. For undisturbed tropical forests as a whole, the three methods produced similar NPP estimates (i.e., ~ 10 Pg C yr^{-1}). However, the three different approaches produced vastly different patterns of NPP both in space and through time, suggesting that our understanding of tropical NPP is poor and that our ability to predict the response of NPP in the tropics to environmental change is limited. To address this shortcoming, we suggest the development of an expanded, high-density, permanent network of sites where NPP is continuously evaluated using multiple approaches. Well-designed NPP megatransects that include a high-density plot network would significantly increase the accuracy and certainty in the observed rates and patterns of tropical NPP and improve the reliability of Earth system models used to predict NPP–carbon cycle–climate interactions into the future.

1. Introduction

Net primary production (NPP) represents the largest flux of carbon dioxide (CO_2) from the atmosphere to the terrestrial biosphere, marks the initial step in the terrestrial carbon (C) cycle and C storage, and strongly regulates global climate [*Chapin et al.*, 2011; *Schlesinger and Bernhardt*, 2013]. From a societal perspective, NPP is also the source of all the food, fuel, and fiber on the planet and sustains all other life, including humans [*Haberl et al.*, 2007; *Smith et al.*, 2012]. Owing to its central importance for ecological and social systems, there has been considerable effort to produce accurate, high-resolution estimates of terrestrial NPP across space and through time [*Lieth*, 1978; *Field et al.*, 1998; *Nemani et al.*, 2003; *Zhao and Running*, 2010]. As a result, estimates of global terrestrial NPP are plentiful, with a recent synthesis indicating that global NPP rates are converging at ~60 Pg C yr^{-1} [*Ito*, 2011]. Of this total, the largest fraction (30–40%) is thought to occur in the tropical forest biome [*Field et al.*, 1998; *Phillips et al.*, 1998; *Malhi and Grace*, 2000; *Grace et al.*, 2001; *Cleveland et al.*, 2013].

Given such high rates of NPP in tropical forest, even small variations in plant production can profoundly influence the terrestrial C cycle [e.g., *Schimel*, 1995]. For example, multiple studies have linked large, interannual variations in atmospheric CO_2 accumulation to climate-induced variations in NPP and biomass in the tropics [*Townsend et al.*, 2002; *Phillips et al.*, 2009; *Lewis et al.*, 2011; *Clark et al.*, 2013; *Zhou et al.*, 2014].

Similarly, *Zhao and Running* [2010] argued that global-scale NPP anomalies most strongly reflect interannual variations in tropical forest NPP, implying that the long-term trajectory of tropical NPP has a disproportionate influence on future global terrestrial C storage. Unfortunately, high structural, functional, and environmental diversity of tropical forests have challenged our ability to accurately measure NPP in this heterogeneous biome [e.g., *Gillman et al.*, 2014]. While it is indisputable that variations in tropical NPP have important consequences for the global C cycle, the spatial and temporal magnitude of that variation remains poorly understood. The recent debate over the climate sensitivity of forest C cycling, particularly to drought conditions [*Malhi and Grace*, 2000; *Saleska et al.*, 2007; *Samanta et al.*, 2010, 2011; *Medlyn*, 2011; *Wright*, 2013; *Phillips and Lewis*, 2014; *Doughty et al.*, 2015], further underscores the need for robust, high-resolution estimates of NPP across the tropics to better understand and predict how changing environmental conditions will influence their role in the global C cycle [*Clark*, 2004; *Cox et al.*, 2013].

Estimates of tropical NPP have been generated using multiple approaches, from plot-scale extrapolations to satellite- and model-derived estimates, among others. On the one hand, it is promising that such different methods seem to be converging on a global mean NPP value [*Ito*, 2011]. Yet, despite convergence at the global scale, estimates of tropical NPP generated using different approaches have yielded different pictures of the climate sensitivity of the biome and its response to environmental change [*Booth et al.*, 2012; *Cox et al.*, 2013; *Huntingford et al.*, 2013]. For example, some plot-based estimates suggest significant, multidecadal increases in tropical NPP and C storage in the Amazon Basin—by far the largest remaining tropical forest area—that could reflect enhanced plant production driven by rising atmospheric CO_2 concentrations [e.g., *Phillips et al.*, 1998; *Lewis et al.*, 2006; *Phillips et al.*, 2009; *Brienen et al.*, 2015]. However, others have questioned this result [*Wright*, 2013]. For example, a recent analysis of long-term, biomass growth rates of selected species in Costa Rica concluded that plant productivity has not increased concurrently with CO_2 over the past decade and that possible stimulatory effects of rising CO_2 have been countered by climate-driven declines in production [*Clark et al.*, 2013]. Similarly, using remote sensing approaches, *Zhou et al.* [2014] reported a decline in Congo rainforest greenness over roughly the same period, though the mechanistic links between canopy greenness and forest CO_2 uptake and storage are still unresolved [*Samanta et al.*, 2012; *Morton et al.*, 2014].

Inconsistent patterns of tropical NPP reported in the literature highlight considerable uncertainty in our understanding of the spatial and temporal dynamics of tropical forest productivity. Such inconsistencies are not surprising and likely reflect differences in the ways that current methodological approaches estimate NPP. It is also important to note that regardless of the approach used, all large-scale NPP estimates are *modeled*—either explicitly or implicitly. For example, radiation-based approaches include satellite measurements of canopy "greenness," but actual NPP estimates are modeled using a suite of biophysical and biogeochemical data. Field-based estimates may be considered more robust in that they are based on actual small-scale measurements of plant growth [but see *Clark et al.*, 2001]. Nonetheless, to generate large-scale estimates, plot-based NPP measurements must be scaled using allometric relationships and approximations of belowground C allocation, both of which represent significant sources of possible error and uncertainty [*Clark and Clark*, 2000; *Chave et al.*, 2004]. Field-based estimates in tropical forests are also quite rare, and NPP estimates have not been adequately validated or calibrated in tropical forests [e.g., *Marvin et al.*, 2014]. Yet, with the advent of several new large-scale forest monitoring networks, field data on NPP are becoming increasingly available, creating new opportunities to compare the magnitude and patterns of tropical NPP using different approaches [*Doughty et al.*, 2015; *Malhi et al.*, 2015]. Still, given their limited spatial and temporal coverage, field-based NPP estimates must be extrapolated over broad geographic regions (e.g., using empirical relationships between NPP and climate) [*Del Grosso et al.*, 2008; *Schuur*, 2003] to generate larger-scale (but uncertain) estimates of NPP.

Here we ask, how do estimates of tropical NPP generated using different approaches vary across space and through time? To address this question, we compared tropical NPP estimates generated using three commonly used approaches: field-, radiation-, and biogeochemical-based methods (Figure 1). Our goal was not to exhaustively review and integrate results from various fields of research but rather to enhance our understanding of the drivers and potential biases in each approach to aid in the interpretation, comparison, and detection of NPP responses to climatic variation. We begin by summarizing these methods, how they are used to generate large-scale NPP estimates, and some of the strengths and limitations of each approach. We then compare large-scale estimates generated using the different approaches and explore the
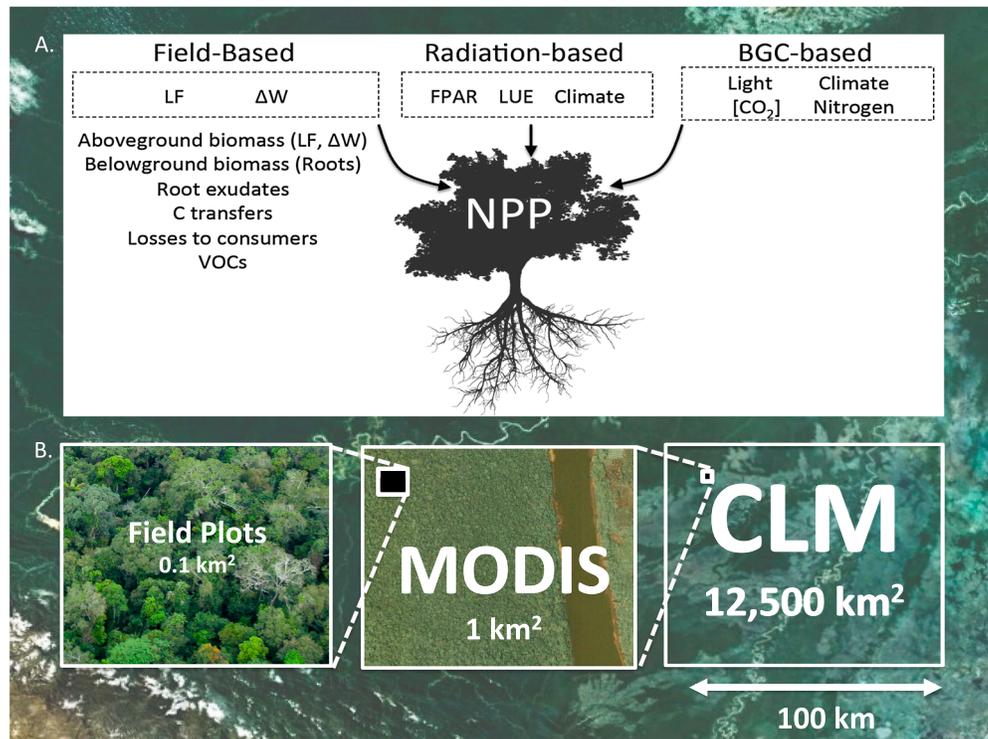
Figure 1. Conceptual figure illustrating the different approaches used to estimate NPP in tropical forests and the vastly different scales at which they operate. (a) Accurate field-based NPP estimates require measuring multiple biomass and C flux components (e.g., root growth, rhizosphere C deposition, volatile organic C [VOC] emissions, and others), but NPP is most commonly estimated from litterfall (LF) and stem (wood) growth (ΔW) alone. Radiation-based NPP estimates are typically generated using remotely sensed data, where estimates of APAR (PAR * fPAR) are derived from satellite measurements of fPAR. In the radiation-based approaches, light use efficiency (LUE) is parameterized and meteorological data are based on climate reanalysis products. Biogeochemical model-based estimates of NPP using, e.g., CLM are typically generated using climate reanalysis data (temperature and precipitation), light and atmospheric CO_2 are prescribed, and nitrogen availability is modeled. (b) A visual comparison of the scales at which the different approaches operate. Field-based measurements are typically made at very small scales (e.g., one ha plots; 0.1 km^2), satellite-based approaches typically generate NPP estimates with a 1 km^2 pixel size (resolution), and model-based approaches generate estimates with pixel sizes of thousands of square kilometers.

patterns of NPP across space and through time, highlighting where there is convergence and where there is disagreement, and we discuss possible reasons for inconsistencies among estimates. Next, as a case study, we consider decadal-scale NPP patterns in the Amazon Basin and compare radiation- and biogeochemical model-based NPP estimates with actual NPP measurements from three specific sites in the region where detailed, long-term plot-level NPP data are available. Regardless of the approach used, however, we note that the challenges of measuring NPP in tropical forests are perhaps greater than in any other major terrestrial biome [*Townsend et al.*, 2008; *Cleveland et al.*, 2011; *Malhi et al.*, 2011, 2015]. As such, we conclude with an overview of some of the gaps in our understanding of NPP and discuss some critical next steps that would improve our ability to generate more reliable estimates in this globally important biome.

1.1. Approaches Commonly Used to Estimate NPP in Tropical Forests

Terrestrial NPP has been estimated in many ways [*Cramer et al.*, 1999; *Schloss et al.*, 1999; *Scurlock et al.*, 2002; *Schuur*, 2003; *Running et al.*, 2004; *Sala and Austin*, 2000; *Thornton et al.*, 2007; *Del Grosso et al.*, 2008; *Zhao and Running*, 2011; *Castanho et al.*, 2013]. In this paper, we compare field-, radiation-, and biogeochemical model-based methods (Figure 1a). It is also important to note that the concepts, logic, and the specific metrics used, as well as the uncertainties associated with each of the different methods, are in many ways distinct, and they all operate at vastly different scales (Figure 1b). For example, plot-level estimates of NPP are typically based on detailed measurements of biomass growth in small (~1 ha) and widely dispersed plot networks and offer limited insight about the effects of spatial environmental heterogeneity (e.g., in climate, topography,

and soils) that can influence NPP over relatively small scales [*Quesada et al.*, 2009; *Rapp and Silman*, 2012; *Quesada et al.*, 2012]. Radiation-based approaches typically operate at relatively larger scales (~1 km^2) but are limited by the resolution of the analytical instrument being used (250 m for the moderate-resolution imaging spectroradiometer [MODIS]), the climate data products used to convert satellite observations into NPP (~111 km^2 or 1° for the MODIS algorithm), and assumptions about biome-level parameterization of vegetation photosynthetic capacity that determine the relationship between satellite-derived indices and biomass production rates, among others. Finally, biogeochemical models simulate C cycling processes at the global scale and generate relatively coarse spatial resolution estimates (>1° in the Community Land Model [CLM]) [*Lawrence et al.*, 2011; *Oleson et al.*, 2013] and also use approximations that apply mean biome-level photosynthesis and C allocation schemes. However, because the three approaches produce NPP estimates in different ways (Figure 1a), they offer a unique and valuable opportunity to assess patterns of tropical NPP via intercomparison.

1.2. Field-Based Estimates of NPP

Field-based estimates of NPP are typically based on assessments of biomass production through time [*Woodwell and Whittaker*, 1968; *Baker et al.*, 2004; *Ito*, 2011] and are generated from repeated (e.g., annual) measurements of aboveground plant growth in relatively small (~1 ha) plots (Figure 1). Most field-based NPP estimates are based on measurements of litterfall (leaf fall and/or twigs) as an estimate of canopy growth [*Clark et al.*, 2001; *Chave et al.*, 2010]. In some cases, stem growth is also measured to estimate aboveground wood productivity [*Malhi et al.*, 2004, 2011], a technique that relies on forest-type or regionally specific allometric equations that incorporate measures of tree height, wood density, and basal area to estimate biomass accumulation [*Malhi et al.*, 2006; *Feldspauch et al.*, 2012]. Far less frequently, field-based estimates of NPP also include belowground biomass growth measurement. Such measurements usually focus on fine root production (the most important belowground NPP component); coarse root production is almost always estimated as a fixed proportion of aboveground production. Estimates of total NPP (the sum of aboveground and belowground NPP) are often based on assumptions about C partitioning to aboveground versus belowground growth. New research that aims to comprehensively measure all major components of forest NPP is underway [*Malhi et al.*, 2011] and suggests that belowground NPP averages ~24% of aboveground NPP. Such efforts represent a very important next step in more accurate tropical C monitoring and include measurements of other NPP components such as branch fall or herbivory and estimates of autotrophic respiration by roots (coarse and fine), leaves, and wood [*Malhi et al.*, 2009; *Doughty et al.*, 2014a; *Malhi et al.*, 2014].

Field-based NPP estimates are based on actual measurements of biomass and hence provide a benchmark for validating estimates using other, more synthetic approaches. However, several sources of error in field-based measurement techniques can introduce considerable uncertainty and biases into NPP estimates akin to those that are thought to affect biomass estimation [e.g., *Marvin et al.*, 2014], and evaluations between field-based, radiation-based, and satellite-derived NPP estimates reflect errors associated with both approaches. For example, most total NPP measurements, including the field-based data used in this analysis, are modified to account for unmeasured portions of aboveground (e.g., using litterfall to estimate wood growth, or vice versa) and belowground NPP (e.g., using a single scaling factor; see below). Second, field-based methods have not been applied consistently across studies, though several plot networks have strived to implement standardized inventory measurement techniques. For example, choice of allometric scaling [*Feldspauch et al.*, 2012], collection interval [*Clark et al.*, 2001], and field plot size can all affect biomass and NPP estimates [*Lewis et al.*, 2004]. Third, most direct NPP measurements are prone to underestimation because of missing components including litter that is trapped in the canopy or that decays prior to collection, fine root mortality, and decay prior to collection, losses as root exudates and VOCs, and C transfers to symbionts, among others [*Clark et al.*, 2001; *Malhi et al.*, 2009, *Vicca et al.*, 2012; *Malhi et al.*, 2015]. Fourth, field-based NPP estimates are labor and resource intensive, with limited spatial and temporal coverage. Most available field-based NPP estimates have only captured short-term (3–5 years) dynamics and are conducted in plots of 1 ha or less, providing only a snapshot of natural variability, which may or may not be representative of the regional NPP. Thus, while the sources of uncertainty discussed here are not comprehensive, they highlight the potential for error in field estimates of NPP. For these reasons field data should not be viewed as an independent and wholly accurate measure of NPP, especially when upscaled, but should rather be carefully interpreted in light of known limitations.

1.3. Radiation-Based NPP Estimates

Radiation-based NPP estimates have been widely used since *Monteith* [1972] first showed that NPP is directly related to intercepted solar radiation, the first-order limit to productivity. In the late 1990s, this logic was combined with emerging satellite measurements of vegetation radiation absorption to generate the first spatially and temporally continuous estimates of total ecosystem (i.e., above and below ground) NPP [*Field et al.*, 1995, 1998; *Running et al.*, 2004]. Present day radiation-based NPP estimates are calculated according to the general equation:

$$NPP = APAR \times LUE - RA \qquad (1)$$

where *APAR* represents the amount of absorbed photosynthetically active solar radiation (PAR), generally estimated as the product of the satellite-derived fraction of PAR absorbed at the vegetation surface (FPAR: unitless), and the meteorologically derived total incoming PAR (IPAR; MJ m^{-2}). *LUE* represents light use efficiency, generally estimated as the product of a biome-level parameterized maximum light use efficiency (LUE$_{MAX}$; g C MJ^{-1}) and meteorologically derived biophysical constraints (e.g., temperature and water availability). *RA* represent autotrophic respiration, which is generally estimated as a fixed reduction scalar or using a temperature sensitive respiration function.

The main strength of the radiation-based approach is its compatibility with high spatiotemporal resolution satellite data. However, there are key challenges to generating radiation-based NPP estimates in tropical ecosystems. First, radiation-based approaches rely on satellite indices to estimate the total solar radiation absorbed by a given vegetated area (i.e., FPAR). Yet, satellite FPAR data have the potential to saturate in areas with high vegetation density like those that often occur in the tropics [*Lee et al.*, 2013; *Zhou et al.*, 2014]. Second, most radiation-based approaches are partially based on meteorological data, which is currently only available in the tropics at relatively coarse spatial scales (0.5° to > 2° resolution), significantly limiting the spatial resolution of radiation-based NPP estimates [*Zhao et al.*, 2006; *Samanta et al.*, 2011]. Third, most current radiation-based approaches use biome-level model parameterization schemes to define LUE$_{MAX}$ and meteorologically derived temperature and moisture constraints [*Madani et al.*, 2014]. These parameterizations depend on field-scale estimates, often derived from daily flux measurements and meteorological data collected at eddy covariance ("flux") towers. However, there are currently few active flux towers in the tropics, and parameters derived from these towers are likely not representative of the tropical forest biome [*Malhi and Grace*, 2000]. Further, high species diversity may equate to substantial variation in LUE across the tropical forest biome, and such variation is not captured using coarse (biome-level) parameterizations [*Townsend et al.*, 2008] which represents a major source of uncertainty in the radiation-based approach [*Madani et al.*, 2014]. Fourth, cloud cover often limits ground observation by optical remote sensing instruments such as the MODIS sensor and can significantly limit the temporal resolution of satellite indices [*Zhao and Running*, 2010; *Samanta et al.*, 2011; *Zhao and Running*, 2011].

1.4. Biogeochemical Model-Based NPP Estimates

Biogeochemical model-based estimates of NPP are typically generated from a larger set of simulated C fluxes between the atmosphere and terrestrial ecosystems [*Farquhar et al.*, 1980; *Randerson et al.*, 2009; *Ito*, 2011]. Within an overall C cycle framework, NPP is calculated according to the equation:

$$NPP = GPP - RA \qquad (2)$$

where *GPP* represents gross primary productivity, or C fixed via photosynthesis, and *RA* represents autotrophic respiration for a given vegetated area. Most uncoupled terrestrial biogeochemistry models are forced with solar radiation, precipitation, atmospheric conditions, atmospheric [CO_2], soil properties, and biome-level vegetation characteristics (Figure 1). GPP calculations in biogeochemical models are typically based on the Farquhar photosynthesis model [*Farquhar et al.*, 1980] and a stomatal conductance model that calculates leaf- and canopy-level water, energy, and CO_2 fluxes [*Ball et al.*, 1987; *Bonan*, 2008]. Global NPP estimates generated using biogeochemical models are usually relatively coarse spatially, with most operating at a resolution of > 0.5°.

The strength of the biogeochemical model-based approach comes from the fact that models often include mechanistic representations of processes such as water and energy balance, photosynthesis, plant growth, nutrient dynamics, decomposition, and disturbance [*Randerson et al.*, 2009; *Lawrence et al.*, 2011]. As such, biogeochemical models are valuable tools for investigating feedbacks between changing climate, [CO_2],

land cover and land use. The models, however, are constrained by their underlying logic, which is an oversimplification of real-world biogeochemical dynamics. Similarly, the low resolution and fidelity of input data and the computational expense of model simulations limit estimates of tropical forest NPP to relatively coarse resolutions (Figure 1b). Finally, model parameterizations and assumptions about critical variables such as plant physiological and phylogenetic diversity, plant C allocation schemes, and soil characteristics, among others, result in single value estimates of NPP being applied across large regions of this heterogeneous biome [*Townsend et al.*, 2008].

2. Methods

2.1. Field-Based NPP Estimates

In our NPP model comparison, we recognize three interrelated classes of field-based data and compare estimates using all three to radiation- and biogeochemical model-based NPP. The first class of field-based data represents plot-based NPP data from several sites in the Amazon Basin. Hereafter, we refer these data as *field plot-based NPP*. Next, we assembled a set of field-based data from a large data set compiled in the Ecosystem Model-Data Intercomparison (EMDI) project, which has been used to explore climate controls on ecosystem productivity [e.g., *Del Grosso et al.*, 2008; *Zaks et al.*, 2007]. From the EMDI database [http://daac.ornl.gov/NPP/guides/NPP_EMDI.html], we extracted data from field sites where aboveground and belowground NPP measurements were available (i.e., class A and class B measurements) from deciduous and broadleaf evergreen forests, excluding data from other biome types. The modified EMDI database was subsequently expanded with field plot-based data from several large-scale tropical forest NPP monitoring networks, including the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) [*Avissar et al.*, 2002; http://lba.inpa.gov.br/lba/], the Amazon Forest Inventory Network (RAINFOR) [*Malhi et al.*, 2002; *Phillips et al.*, 2009; http://www.geog.leeds.ac.uk/projects/rainfor/], the Andes Biodiversity and Ecosystem Research Group (ABERG) [*Malhi*, 2010; http://www.andesconservation.org/], the Global Ecosystem Monitoring Network (GEM) [http://gem.tropicalforests.ox.ac.uk/], and other published studies. These additional data mainly consisted of aboveground NPP measurements, including litterfall from more than 500 tropical sites, wood growth estimates from more than 275 tropical sites, and more than 150 sites from which both litterfall and wood (stem) growth rates were available.

Comprehensive assessments of tropical NPP are uncommon because measuring all components of NPP is resource intensive and difficult to execute in remote regions. Most studies have prioritized measurements of canopy growth, whereas measurements of aboveground and belowground wood growth are less common. The paucity of comprehensive studies of field NPP limits the ability to compare field-based NPP measures to NPP estimates generated using other approaches. However, a recent synthesis of available data suggests roughly equal allocation of NPP between canopy, wood, and fine root growth, with predictable and linear scaling across these components as overall NPP increases [*Malhi et al.*, 2011], allowing us to use scaling factors to estimate unmeasured NPP components in various studies. Specifically, for sites where only litterfall or stem growth NPP was available, we estimated aboveground NPP using empirical relationships between litterfall and wood growth [in the sense of *Clark et al.*, 2001; *Malhi et al.*, 2004, 2011]. This approach yielded ~650 estimates of tropical ANPP with 24% and 19% relative error (95% confidence interval; CI) when wood growth or litterfall were used, respectively. Next, to compare field-based ANPP estimates with total NPP estimates generated using radiation- and model-based approaches, we used a 37% scaling factor to increase the field-based ANPP estimates to account for fine root belowground NPP, calculated as the average belowground allocation from 40 studies across the tropics where litterfall, wood, and root growth were simultaneously measured [in the sense of *Malhi et al.*, 2011]. In addition, we used an additional 20% scaling factor to increase the field-based ANPP estimates to account for components of NPP not measured in most field campaigns [*Clark et al.*, 2001; *Malhi*, 2010]. Finally, most field-based NPP data are reported in units of dry mass, which we converted to units of C, assuming that the C content of dry biomass is 50%, as in *Malhi et al.* [2004]. In this paper, all NPP values are expressed as units of C/area/time. Hereafter, we refer to the aggregated plot-based data from the EMDI project and additional data sources as *aggregated field-based NPP*.

Finally, many studies have examined correlations between climatological factors and ecosystem productivity [*Lieth*, 1975; *Clark et al.*, 2001; *Schuur*, 2003; *Zaks et al.*, 2007; *Del Grosso et al.*, 2008]. In many cases, empirical

relationships between major climate factors, such as mean annual temperature and rainfall, and plot-based measurements of NPP have been used to model NPP across broad gradients and scales. Generally, rates of forest productivity increase with rainfall, with the greatest rates of annual NPP observed in areas where warm and wet climate conditions favor plant growth [*Del Grosso et al.*, 2008]. In very wet regions, rainforest growth is thought to decline because excess soil moisture may slow feedbacks between plant and soil nutrient recycling [*Schuur*, 2003]. Across the Amazon Basin, however, recent studies find only weak correlations between average precipitation and litterfall [*Chave et al.*, 2010] or wood growth [*Quesada et al.*, 2012], suggesting more complicated controls related to regional variation in floristic composition and/or soil fertility. While the underlying mechanisms linking patterns of forest NPP to long-term average climate conditions remains poorly resolved, many studies have used simple empirical models to describe the generally positive correlation between NPP and rainfall. Given the limited spatial coverage of inventory plots, these empirical models have been used, in turn, to broadly map the potential spatial distribution of tropical rainforest NPP. Building on past studies, we developed an empirical model to extrapolate tropical NPP using the correlation between field data and rainfall measurements. Ideally, an empirical model for gridding NPP would also include other state factor variables like topography, geology, soil type, and altitude, in order to better capture the combinatorial effects of soil fertility, temperature, and disturbance on NPP. However, significant relationships among tropical forest NPP and these controls at the pantropical scale remain elusive, although state factor control at more regional scales certainly exist [*ter Steege et al.*, 2006; *Quesada et al.*, 2012; *Girardin et al.*, 2013]. Thus, we extrapolated NPP as a function of mean annual rainfall (see Figure S1 in the supporting information).

Recent studies investigating the relationship between average rainfall and NPP find that forest NPP increases with greater average rainfall levels up to about 2500 mm/yr of rainfall [e.g., *Del Grosso et al.*, 2008]. As part of a working group at the National Center for Ecological Analysis and Synthesis, *Del Grosso et al.* [2008] found that the relationship between ANPP and rainfall could be best described by the empirical function,

$$ANPP = \frac{A \times MAP^B}{e^{(C \times MAP)}} \tag{3}$$

(see Figure S1 for more details). Using this equation, we refit the relationship between aggregated field-based NPP and actual measurements of rainfall from nearby monitoring stations to characterize the relationship for tropical rainforests. The model parameters were optimized by minimizing the root mean square error for modeled and observed ANPP using a full Newton-type method for reducing the sum of squares (Figure S1). After we modeled ANPP as a function of rainfall, a scaling factor of 24% was applied to capture belowground NPP, as discussed above. Using this approach, we used the CRU 2.0 database at 2° spatial resolution for pantropical mapping of NPP based on mean annual rainfall. Modeling NPP on annual rainfall rates is rudimentary because other environmental factors control rates of NPP, such as soil fertility [*Cleveland et al.*, 2011], drought [*Doughty et al.*, 2015] and temperature [*Girardin et al.*, 2013], disturbance regime, and potentially biogeographical differences in species composition across continents [*Banin et al.*, 2014]. To date however, we do not understand well enough how hydroclimatological and landscape control NPP to map NPP rates pantropically using spatially explicit environmental data sets, such as terrain, climate, and soil type. Nevertheless, the straightforward correlation between rainfall and NPP has guided our understanding of tropical C cycling [*Clark et al.*, 2001; *Schuur*, 2003; *Del Grosso et al.*, 2008], and hereafter, we refer to these empirically modeled estimates of NPP as the National Center for Ecological Analysis and Synthesis Tropical database, or *NCEAS-T extrapolated NPP*.

2.2. Radiation-Based NPP: MODIS and the MODIS NPP Algorithm

We used data generated by the MODIS NPP algorithm to represent radiation-based NPP for the tropical forest biome for the period 2000–2010 [*Zhao et al.*, 2005, 2006; *Zhao and Running*, 2010], downloadable from http://www.ntsg.umt.edu/project/mod17#data-product. The MODIS NPP algorithm estimated NPP according to the below equation, which is expanded from equation (1).

$$NPP = \sum_{i=0}^{n} [FPAR_i \times IPAR_i \times LUE_{MAX} \times fTMIN_i \times fVPD_i - RA_i] \tag{4}$$

In the MODIS algorithm, absorbed photosynthetically active radiation (*APAR*), as described in equation (1), was estimated as the product of the fraction of photosynthetically active radiation absorbed by the vegetation (*FPAR*) and the total photosynthetically active radiation incident at the vegetation surface

(*IPAR*). Light use efficiency (*LUE*) was calculated using a biome-specific maximum light use efficiency value (*LUE*$_{MAX}$; 1.268 g C MJ^{-1} for tropical forests) multiplied by water stress (high daily vapor pressure deficit; *VPD*) and low temperature stress (low daily minimum temperature; *TMIN*) reduction scalars [*Zhao and Running*, 2010]. Autotrophic respiration (*RA*) was calculated using a maintenance respiration index sensitive to average daily temperature (*TAVG*) and a growth respiration reduction scalar [*Zhao and Running*, 2010]. All biome-level parameters used in the MODIS NPP algorithm were calibrated using global flux tower data and are reported in the biome properties look-up table in *Zhao and Running*, 2010.

Satellite-derived *FPAR* data used in the MODIS algorithm were from the MODIS C5 FPAR/LAI data product [*Myneni et al.*, 2002] available at https://lpdaac.usgs.gov/. Temporal gaps in FPAR data caused by cloudiness and/or heavy aerosols were filled using a simple linear interpolation, in which unreliable or missing data were filled based on the quality assessment field that accompanies the MODIS C5 FPAR/LAI data product [*Zhao et al.*, 2005]. Daily meteorological data, including *PAR*, *VPD*, *TMIN*, and *TAVG*, were derived from the NCEP/DOE II reanalysis data set [*Kanamitsu et al.*, 2002]. NCEP/DOE II data have been previously shown to capture large-scale surface climate anomalies [*Betts et al.*, 2006; *Zhao et al.*, 2006]. However, due to their relative coarseness (>1° resolution), meteorological inputs were smoothed to the one km^2 MODIS pixel resolution using a simple nonlinear spatial interpolation function [*Zhao et al.*, 2005]. While various methods exist for across-scale comparison, we chose to aggregate MODIS NPP data to the CLM pixel resolution of ~1° using bilinear interpolation. For more MODIS NPP algorithm details, please refer to *Zhao et al.* [2005, 2006], and *Zhao and Running* [2010].

2.3. Biogeochemical Model-Based Estimates: CLM 4.5 BGC

The Community Land Model (CLM) is the terrestrial component of the Community Earth System Model [*Lawrence et al.*, 2011] and represents many of the biophysical and biogeochemical processes that are critical to ecosystem function. Here, we used an uncoupled run of CLM v. 4.5 BGC [*Oleson et al.*, 2013; *Koven et al.*, 2013] where historical precipitation, solar radiation, atmospheric conditions (CRUNCEP version 3.1 1901–2009) [*Viovy*, 2011], transient land cover change [*Lawrence and Chase*, 2007; *Lawrence et al.*, 2012; *Oleson et al.*, 2013], and CO$_2$ concentrations were provided to the model, and CLM estimated all water, C, and nitrogen (N) components of the global terrestrial ecosystem at ~1° resolution. In CLM, each grid cell is divided into land units that include vegetation, lakes, urban areas, glaciers, and crops. Vegetated land units are further divided into one of 15 plant functional types (PFTs) (e.g., broadleaved evergreen tropical trees). Importantly, within a grid cell, all PFTs share the same soil resources and access the same pool of water. PFT fractions within grid cells change over time, particularly with changes in land use. Nutrient constraints beyond N (e.g., from phosphorus) are not currently included in CLM. NPP is calculated instantaneously, as the difference between gross primary productivity and autotrophic respiration using a 30 min time step.

2.4. Spatial and Temporal Comparisons of Tropical NPP

To facilitate spatial comparisons between the various NPP estimates used in this study, we upscaled the aggregated field-based NPP data by averaging when two or more plots fell within a CLM grid cell and aggregated MODIS NPP data to the CLM pixel resolution of 1°. All methods for comparing data across scales have drawbacks. Here we chose to aggregate in part because the native resolution of the meteorological data used in the MODIS algorithm is comparable to the resolution of CLM (>1°) and in part because it is a commonly used method to evaluate both MODIS [*Mao et al.*, 2012] and Earth system model output [*Beer et al.*, 2010; *Todd-Brown et al.*, 2013; *Wieder et al.*, 2015]. The alternative approach, keeping data in its native resolution then replicating coarser values, would more effectively capture small-scale (subgridcell) variation in the finer scale data sets but artificially raises sample sizes for statistical tests. Since our focus was on regional to pantropical comparisons, we chose to aggregate.

We restricted our analysis to include only tropical forests dominated by evergreen trees by using the CLM PFT distribution in the year 2000 [*Lawrence et al.*, 2012] and extracting grid cells with > 60% cover of tropical broadleaf evergreen trees. To avoid the possibly confounding effects of human land use, we excluded grid cells with > 10% of the crop PFT in the analysis. Spatial NPP patterns from MODIS and CLM represent average NPP values from 2000 to 2010. Patterns in aggregated field-based data reflect NPP data collected

over a wide range of study dates (1960–2013), though most were collected in the past 20 years. By contrast, NCEAS-T extrapolated NPP reflects the long-term influence of moisture availability on tropical productivity.

Next, we examined temporal variation in tropical NPP across two timeframes. First, we examined decadal average NPP estimates for MODIS and CLM from 2000 to 2010. We are aware of only one plot-based estimate of total NPP in the tropics that spanned this entire period [*Clark et al.*, 2013]. Therefore, we limited the temporal comparison to the modeled estimates from radiation- and biogeochemistry-based approaches; the NCEAS-T extrapolated NPP data were excluded from both temporal analyses because the empirical model of rainfall-NPP relationship reflects long-term ecosystem responses to mean climate conditions more so than short-term controls on forest NPP by interannual rainfall variation.

Finally, we compared short-term patterns of NPP modeled using radiation- and biogeochemistry model-based approaches to actual one ha plot-based field NPP data obtained in three regions of the Amazon Basin from 2009 to 2010. To do so, we divided the Amazon into three ecoclimatic zones comprising the *East*, *West*, and *South* Amazon. These broadly defined regions contain lowland tropical forest and comprise a broad east-to-west gradient in climate and forest structure and dynamics across the Basin [*Malhi et al.*, 2004; *Baker et al.*, 2004; *ter Steege et al.*, 2006; *Quesada et al.*, 2012]. The field data were collected on a monthly (canopy and wood) to trimonthly (root ingrowth cores) basis in seven one-hectare plots that are part of the GEM field inventory network. These include four plots in Caxiuanã National Forest Reserve (1°43′S, 51°27′W) [*Da Costa et al.*, 2010; *Doughty et al.*, 2014a], two plots in Tambopata-Candamo Reserve in the Madre de Dios region of Peru (12°49′S, 69°16′W) [*Malhi et al.*, 2014], and one plot in the southern Amazon in Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (16.0158°S, 62.7301°W) [*Araujo-Murakami et al.*, 2014]. NPP measurements were made using a consistent field methodology and include direct measurements of canopy, wood and fine root growth, which reduces uncertainties imparted by varying field techniques and correction factors to estimate aboveground and belowground productivity. Within each Amazon region, we averaged field data from these plots to obtain a mean temporal response regionally (Figure S2), and compared them to the mean regional monthly values of all the pixels (i.e., from CLM and MODIS) within each region. The 2009–2010 period covers two wet-dry season cycles and includes a major drought event that began in November 2010.

3. Results and Discussion

3.1. Rates of Tropical NPP Using Different Approaches

Annual estimates of NPP at the biome scale were similar using NCEAS-T extrapolated- (9.5 Pg C yr^{-1}), radiation- (9.4 Pg C yr^{-1}) and biogeochemistry-based approaches (10.8 Pg C yr^{-1}) (Figure 2a). Such convergence is noteworthy because the three approaches estimate NPP in very different ways [e.g., *Zhao et al.*, 2006; *Betts et al.*, 2006]. It is important to note that the biome-scale NPP estimates presented here are all substantially lower than most other estimates of tropical NPP [e.g., *Cleveland et al.*, 2013]. This discrepancy likely reflects the fact that, at the course resolution of CLM 4.5, the spatial extent of grid cells meeting the >60% forest cover and <10% agriculture land criteria we required for a cell to be identified as intact tropical rainforest is greatly reduced (8.7×10^6 km^2 of grid cell area) when compared with the amount of land area that has been included in other studies (e.g., 16.2×10^6 km^2 of evergreen broadleaf forest area in *Cleveland et al.* [2013]). Yet, annual NPP rates calculated on a per area basis are similar to mean annual rates (~1200 g C m^{-2} yr^{-1}) reported in past studies [e.g., *Aragão et al.*, 2009; *Malhi et al.*, 2011] and were similar among the different approaches examined here, varying from 1090 ± 106, 1082 ± 299, and 1253 ± 148 g C m^{-2} yr^{-1} for field-, radiation-, and biogeochemical model-based estimates, respectively (Figure 2a). NPP estimates from CLM 4.5 are consistently higher than those from MODIS (Figure 2b) and reflect changes to canopy photosynthesis and soil biogeochemical aspects of the model [*Bonan et al.*, 2011, 2012; *Koven et al.*, 2013].

3.2. Spatial Variation in Tropical NPP

While total NPP estimates using the three methods showed reasonably good agreement (Figure 2a), the inconsistent spatial patterns that emerged using the different approaches (Figure 3) imply that the total NPP values are being achieved for different reasons, or perhaps even coincidentally. By nature, the NCEAS-T extrapolated (i.e., empirically modeled) NPP estimates showed no temporal variability and the least spatial
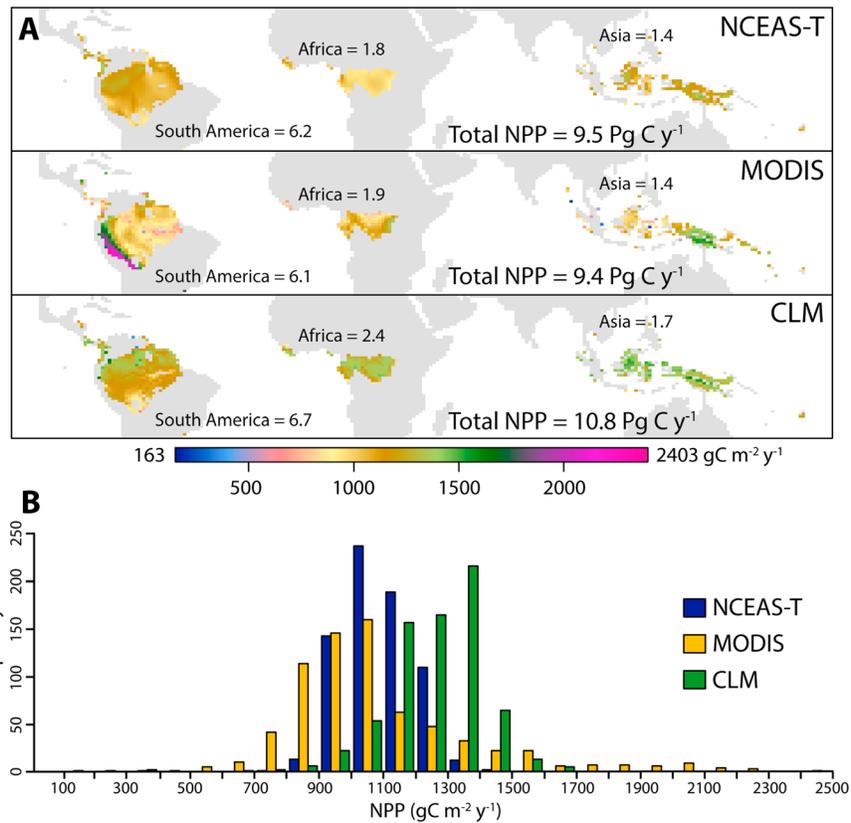
Figure 2. (a) Average rates of NPP (colors) for each grid cell included in the analysis averaged from 2000 to 2010. Inset values depict the sum of both regional and total global NPP estimates over the 2000–2010 period using the different approaches. (b) Histograms of NPP values using the three different approaches for the 2000–2010 period.

heterogeneity (Figure 2a), highlighting a significant weakness in scaling plot-level NPP estimates to climate drivers. The NCEAS-T extrapolations cannot provide information about how tropical NPP may change in response to environmental perturbations. In addition to climate constraints, NPP is limited by multiple interacting factors, especially across complex tropical forest ecosystems [e.g., *Townsend et al.*, 2008], variability which simple, empirically based climate extrapolations cannot resolve.
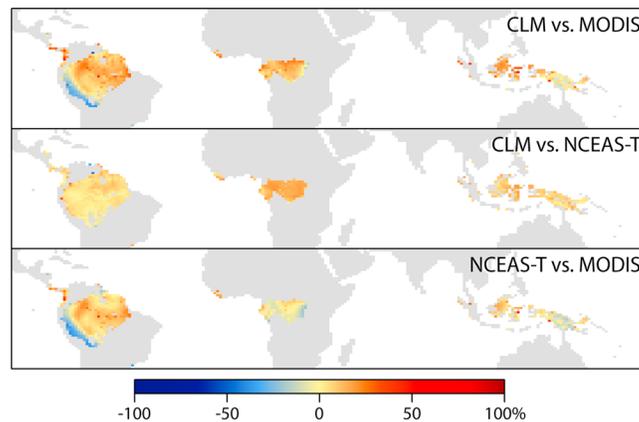
Figure 3. Normalized differences in NPP using the different approaches, where values represent the difference in NPP using the different approached divided by sum × 100 (e.g., [CLM − MODIS] / [CLM + MODIS] * 100).

Radiation-based NPP estimates showed the largest variability (Figure 2b). Satellite-derived NPP estimates show a strong gradient across the Amazon Basin, with higher rates in western Amazon compared to the east (Figure 2a). While this pattern is broadly consistent with field-based observations [*Castanho et al.*, 2013], it is only weakly driven by variability in satellite observations of FPAR ($R = 0.26$, $P < 0.05$). Instead, patterns of radiation-based NPP largely reflect responses to climate data, particularly daily minimum temperature ($R = -0.66$, $P < 0.01$) (Table S1). The relatively subtle effect of satellite-measured indices on the spatial pattern of NPP highlights a number of limitations

with radiation-based approaches in the tropics. First, tropical forests are dominated by evergreen species, and the sensitivity of canopy foliage (i.e., FPAR) to changes in biophysical factors is not well understood [*Lee et al.*, 2013; *Zhao et al.*, 2014]. Next, the biome-level parameterization approach applies single vegetation photosynthetic capacity, temperature sensitivity, and moisture sensitivity values to the entire tropical biome. Given the well-known high biological, biogeochemical, and environmental diversity of tropical forests [*Townsend et al.*, 2008], this is a gross simplification and a major source of uncertainty in the radiation-based approach [*Madani et al.*, 2014]. More, satellite-derived indices (including FPAR) saturate in areas of dense vegetation, providing limited information on changes in photosynthetic capacity across dense tropical forests [*Lee et al.*, 2013; *Zhao et al.*, 2014]. Finally, tropical forests experience cloud cover for up to 70% of the year, limiting the frequency of satellite observations and biasing the spatial pattern more toward dry season dynamics, when clouds are not as prevalent [*Zhao and Running*, 2010; *Samanta et al.*, 2011; *Zhao and Running*, 2011]. These limitations to satellite remote sensing in the tropics result in NPP estimates that more strongly track patterns in meteorological inputs, such as minimum temperature (photosynthetic active radiation), which decreases (increases) with elevation (as in the western Amazon) more strongly than real ecoregional differences in canopy greenness and productivity (Figure 3). Together, these factors contribute to radiation-based NPP patterns that largely reflect the spatial pattern of the meteorological inputs to the satellite algorithm, especially TMIN and IPAR (Table S1). Since these coarse-scale meteorological data have been shown to carry high uncertainty and potential bias [*Zhao et al.*, 2006; *Samanta et al.*, 2011], radiation-based NPP estimates in the tropics should be interpreted carefully.

Biogeochemical model-based NPP patterns were generally similar to field-based estimates, likely reflecting the fact that NPP using both approaches is strongly influenced by precipitation (Table S1). However, biogeochemical model-based NPP estimates showed more spatial variability (Figure 2a), as multiple factors interact to influence productivity. These constraints are applied using PFT parameterizations that are most often derived from detailed field measurement data [*Bonan et al.*, 2011, 2012]. A key challenge of the biogeochemical modeling approach is that most models use a single PFT to represent all broadleaf evergreen trees pantropically despite high environmental heterogeneity [*Townsend et al.*, 2008; *Castanho et al.*, 2013]. Developing multiple tropical evergreen forest PFT parameterizations would require coordinated, long-term field efforts to provide the full range of parameter information required by biogeochemical models but would likely substantially improve the spatial representation in biogeochemical model-based estimates and may improve the accuracy and certainty of projected tropical forest response to climate change and elevated atmospheric CO_2 concentrations.

Comparing the three large-scale spatial estimates of NPP reveals our limited ability to quantify spatial variability in the tropics using current estimation techniques (Figure 3). For example, field observations indicate that NPP declines from west to east in the Amazon Basin, though none of the spatial NPP estimates considered in this study reproduces this general NPP gradient. Relatively low NPP rates in eastern and central Amazon forests are thought to reflect nutrient constraints of highly weathered and infertile soils relative to the younger and less infertile soils more typical of western Amazonia [*Quesada et al.*, 2010; *Castanho et al.*, 2013] and also perhaps reduced forest dynamism on deep and structurally stable eastern Amazonian soils compared to shallow or weaker western Amazonian soils [*Quesada et al.*, 2012]. Other factors may also contribute to reduced tree growth rates in the eastern and southern realms of the Amazon Basin, which, in general, experience lower annual rainfall, longer dry seasons, and higher levels of solar radiation [*Malhi et al.*, 2011]. Floristic composition, which strongly shifts across the wide edaphic and climate gradients within the Amazon Basin [*ter Steege et al.*, 2006; *Fyllas et al.*, 2009], may also regulate the spatial NPP patterns. In relatively dry and low fertility regions, plants often display life-history traits that favor longevity (e.g., greater wood density and thick, long-lived leaves) over growth (e.g., maximizing leaf area index) [*Baker et al.*, 2004; *Malhi et al.*, 2004]. While this productivity gradient has been suggested by multiple previous field-based analyses [*Castanho et al.*, 2013], the relative importance of climate, soil properties, and species distribution as control factors remains unclear. Yet, because most field-based NPP measurements offer only a glimpse into the C cycle of tropical forests, they too should also be treated with caution. For instance, field estimates often only measure aboveground NPP, which is then converted to total NPP using conversion factors. This simplification can lead to bias in total NPP estimates, especially since C allocation between aboveground and belowground NPP can vary substantially across tropical forest ecosystems [*Aragão et al.*, 2009; *Malhi et al.*, 2011]. Similar rules for C partitioning are also present in
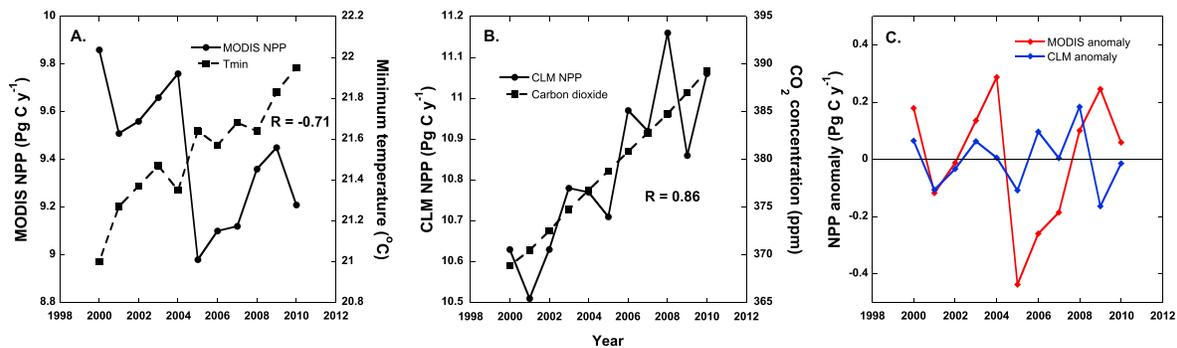
Figure 4. (a) Pantropical NPP (MODIS) and annual minimum temperature (T_{min}) for the 2000–2010 period. (b) Pantropical NPP (CLM) and atmospheric CO_2 concentrations for the 2000–2010 period. (c) Pantropical NPP anomalies from MODIS and CLM for the 2000–2010 period.

both the MODIS and CLM algorithms. Ultimately, all of these methods have limitations that prevent them from capturing the complex spatial distribution of NPP in the tropics, highlighting the need for better integration that leverages the strengths of each of these approaches if we are to more accurately reproduce spatial variability of NPP in the tropics.

3.3. Temporal Variations in Tropical NPP: 2000–2010

From 2000 to 2010, mean annual NPP estimated by the radiation-based approach was roughly ~1.5 Pg C yr^{-1} lower than those generated using a biogeochemical model-based approach. More importantly, over this time period, radiation-based data indicate a 7% decline in NPP, whereas CLM estimates increased by ~4%. Declines in MODIS NPP were significantly negatively correlated with average annual minimum temperature (T_{min}), which increased by 1 °C (Figure 4a and Table S2). However, it is important to note that this decline likely reflects the sensitivity of autotrophic respiration in the MODIS algorithm more than it does observed responses of satellite-measured variables (e.g., FPAR; Table S1) to changing temperature. Moreover, these findings are generally consistent with recent site-level observations linking increased temperature to greater rates of autotrophic respiration [*Clark et al.*, 2003; *Clark et al.*, 2013]. In the MODIS algorithm, increasing temperature also increases vapor pressure deficit, thereby enhancing plant moisture stress [e.g., *Zhao and Running*, 2010], though the accuracy of the temperature-based assumptions in the algorithm remain a subject of considerable debate [*Medlyn*, 2011; *Samanta et al.*, 2011].

The increase in CLM NPP was most strongly correlated with rising atmospheric CO_2 concentrations over the period (Figure 4b). Similar CO_2 fertilization effects on terrestrial productivity are common in Earth system models [*Stocker et al.*, 2013]. Yet, CO_2 stimulation of NPP in such models may be unrealistically high, as most models fail to capture the effects of other constraints on NPP that would attenuate CO_2 fertilization effects (e.g., nutrient limitation) [*Cleveland et al.*, 2013; *Wieder et al.*, 2015; *Zaehle et al.*, 2015]. To date, there is some evidence that rising atmospheric CO_2 concentrations stimulate NPP in field plots [*Phillips et al.*, 2009; *Lewis et al.*, 2009], with other studies suggesting a stronger and counteractive role for temperature-associated declines in NPP [*Clark et al.*, 2013]. A recent study suggests that the Amazon biomass carbon sink has shown a steady decline over time as wood production (a proxy for NPP) has flattened out but mortality rates continue to increase [*Brienen et al.*, 2015].

To compare interannual variability without strong trends dominating the comparison, we detrended the CLM and MODIS NPP data. The detrended data show that CLM- and radiation-based NPP are coarsely synchronous from 2000 to 2008, but in antiphase from 2009 to 2011 (Figure 4c). In 2005 and 2010, severe drought conditions occurred across the Amazon Basin [*Lewis et al.*, 2011] and both data sets show a drop in NPP in these years (except CLM in 2010), yet understanding how temperature, moisture, cloudiness and radiation directly and interactively influence forest NPP is unresolved and an area of active debate.

3.4. Short-Term Patterns of Field-, Radiation-, and Biogeochemical-Based NPP Across the Amazon Basin

We compared the patterns in NPP among the approaches from 2009 to 2010 in three regions of the Amazon where comprehensive and standardized field measurements provide temporal resolution of field NPP
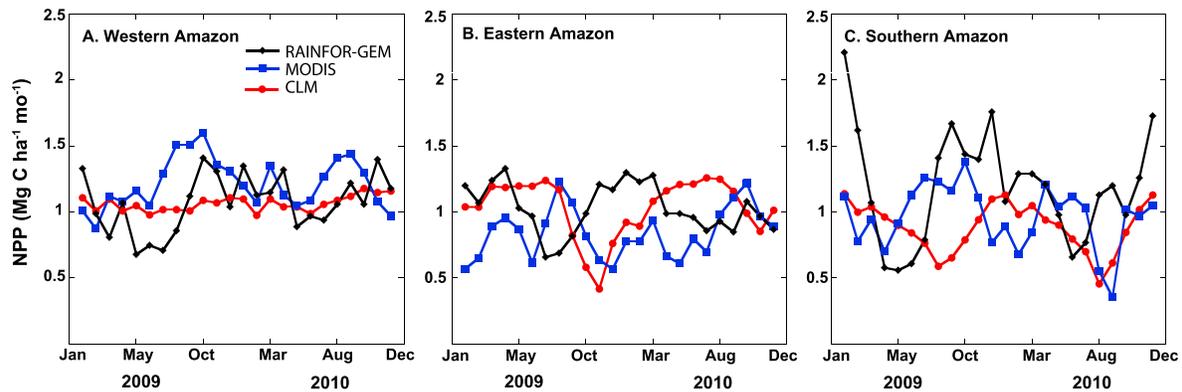
Figure 5. Field- (RAINFOR-GEM), MODIS-, and CLM-based NPP estimates for the (a) Western Amazon, (b) Eastern Amazon, and (c) Southern Amazon for the January 2009 to December 2010 period.

(RAINFOR and GEM projects). Here, we compare NPP estimates from the western, eastern and southern Amazon regions, which represent end-member ecosystems across the wide floristic, edaphic, and climatic gradients that unfold in the Amazon Basin [*Baker et al.*, 2004; *Malhi et al.*, 2011; *Quesada et al.*, 2012]. In these regions, all approaches show seasonal variation in NPP, yet the temporal patterns in NPP are rarely synchronous (Figure 5). The lack of harmony between NPP estimates raises questions about the comparability, accuracy, and ultimately, the utility of each method for monitoring tropical forest C dynamics. Direct comparison is complicated by differences in what NPP measurements represent biologically. For example, MODIS and CLM instantaneously quantify NPP as CO_2 leaving the atmosphere that is assimilated into vegetation. By contrast, field-based observations of NPP quantify the expression of that C assimilation into leaf, wood, or root growth; thus, introducing a time-lag between assimilation and growth that may be buffered at seasonal timescales by poorly understood reservoirs of nonstructural carbohydrate storage within the trees [*Doughty et al.*, 2015]. Moreover, leaf litterfall collected in the field represents an aspect of the seasonal cycle of leaf production; temporal changes in litterfall could reflect shifts in phenology, like the timing of bud break, as much as differences in photosynthetic rates, though recent research suggests that leaf production and loss are balanced in their temporal timing in most lowland Amazonian forests [*Malhi et al.*, 2014].

Perhaps more concerning is the sensitivity of each approach to different environmental drivers (Table S2), and our inability to distinguish which results from the three approaches are real. During the 2010 drought, which began in July 2010 and strongly affected the southern Amazon (Figure 5), both CLM and MODIS showed a sharp decline in NPP, a parallel decline that reflects the temperature and precipitation sensitivity of the MODIS and CLM algorithms, respectively. At the same time, data from field plots suggest that forest NPP may be resilient to drought conditions [*Doughty et al.*, 2015] or that NPP may even increase during drought [*Saleska et al.*, 2007]. However, this does not mean tropical forests are insensitive to drought; the same network of sites found decreased total GPP and autotrophic respiration during the drought period but relatively constant NPP, suggesting a shift in carbon use efficiency during the drought period. This decline in autotrophic respiration came at the expense of maintenance respiration and led to increased tree mortality in the plots [*Doughty et al.*, 2015]. Intensive field measurements of aboveground and belowground forest function both suggest that rates of tropical forest NPP may not be as sensitive to moisture constraints as previously thought [*Doughty et al.*, 2014b], as many trees appear to adaptively shift C allocation in response to seasonal shifts in moisture availability. For example, *Doughty et al.* [2014a] found that trees tend to allocate NPP to canopy and root growth in the dry season, and prioritize wood growth in the wet season. The ability of trees to partition nonstructural carbohydrates appears to be an important mechanism that helps forests adjust to climate variability [*Poorter and Kitajima*, 2007]. In regions with stronger seasonality—like the southern and eastern Amazon—it is possible that trees have developed strategies to adjust investments to manage seasonal shifts in resource availability [*Malhi et al.*, 2014]. Such flexible C allocation should impact canopy greenness and satellite FPAR measurements, resulting in radiation-based NPP estimates that at least partially capture this dynamic. However, given the limitations of satellite indices to accurately measure changes in FPAR as well as the unresolved

nature of greenness-productivity relationships in evergreen systems, these mechanisms are likely missed in radiation-based NPP estimates. In the case of biogeochemical model-based NPP estimates, these mechanisms are not currently represented, but increasing the number of tropical PFTs could help address this issue.

MODIS and CLM also do not account for community level processes because their algorithms are built on ecophysiological principles of individual plant function. Therefore, these approaches cannot capture potential important ecosystem-scale dynamics that influence NPP. For example, the mortality of large trees during drought may have the strongest effects on tropical forest C cycling [*Phillips et al.*, 2009, 2010]. Experimental manipulations of rainfall rates in the Amazon [*Nepstad et al.*, 2007; *da Costa et al.*, 2010; *Metcalfe et al.*, 2010] suggest that this could be the primary threat from droughts, which could increase in severity and frequency, yet the turnover and loss of trees is absent from MODIS and current Earth system models. In theory, turnover and loss of trees should impact satellite measures of greenness and could be contributing to temporal trends in the radiation-based NPP estimates, however, the shortcomings of satellite measures of greenness discussed previously (i.e., saturation and cloud contamination) result in NPP trends mainly influenced by a parameterized response to climate drivers. While our comparison suggests that the utility of MODIS and CLM approaches for examining tropical NPP patterns remains in question, there may be ways to reconfigure these approaches to benefit from the high temporal and spatial resolution of both approaches, which we believe is needed to develop a more mechanistic understanding of tropical forest function from field data across broad scales.

3.5. Conclusions and Recommendations

The C cycle in tropical forest may represent the biggest gap in our current understanding of the terrestrial C cycle, and understanding NPP is a critical first step toward assessing the tropical C cycle as a whole. At the scale of the tropical rainforest biome, the NPP intercomparison shows that the three methods produce three very similar large-scale NPP estimates, both in terms of total C fixed (9.9 ± 0.8 Pg C yr^{-1}) and average NPP rate (1108 ± 120 g C m^{-2} yr^{-1}). Unfortunately, the three methods show tremendous divergence in the patterns and rates of NPP in space and through time. Such variation suggests that our understanding of tropical NPP is incomplete, limiting our ability to accurately predict future variations in NPP and responses to environmental change. To address these shortcomings, we argue that a combination of field-, radiation-, and model-based approaches is needed to monitor and more completely understand controls on tropical NPP, especially given the importance of tropical forest NPP to the global C cycle, the climate system, and society. Below, we offer a framework that could improve our understanding of tropical NPP; one that combines these different approaches and builds on a previously established and growing infrastructure network.

To enhance our understanding of local C dynamics, a well-integrated, long-term, pantropical network that assesses NPP using multiple approaches is urgently needed. Previous work has underscored the value and importance of an integrated, global-scale C monitoring network [e.g., *Running et al.*, 1999]. In the U.S., the National Science Foundation has invested significantly in the National Ecological Observatory Network (NEON), a national network of sites with the goal of establishing the impacts of environmental change on the ecology of the U.S. While costly, a similar approach for tropical forest dynamics and C cycling is both practical and necessary. What would such a network look like? We suggest a series of tropical megatransects with nested plots spanning important climatic gradients and soil nutrient gradients across the tropical forest biome, with an emphasis on understanding C cycle dynamics in the Amazon Basin, the largest remaining tract of largely undisturbed rainforest in the world. Megatransects could include replicated, large-scale field plots that include local meteorological stations. The foundation for such a network already exists: the RAINFOR and GEM plot networks across the Amazon Basin and the GEM transects in the African and Asian tropics could serve as a starting point for a widespread and standardized monitoring network of tropical forest function. However, this emerging network lacks several key elements. For example, few studies have adequately addressed belowground production and C cycle processes, although the plots in the GEM/ABERG networks include regular assessments of fine root NPP [e.g., *Girardin et al.*, 2013; *Malhi et al.*, 2015]. Similarly, despite the tremendous C cycle insight provided by flux tower sites and studies in temperate ecosystems, there are very few flux towers currently operating in tropical forests, and only a handful in the Amazon Basin. The establishment of a tropical

flux network across climatic gradients would significantly reduce uncertain across methods given the utility of flux data for model parameterization and calibration. Finally, while a growing number of plot-based studies have been conducted in the past few decades, inconsistent methods used across studies challenge efforts to synthesize and interpret NPP rates and patterns. Thus, we argue that field-based methods for monitoring NPP should be standardized, and measurements of belowground NPP should emphasized. The NPP protocol developed by GEM (http://gem.tropicaforests.ox.ac.uk) may be a useful basis for a standardized pantropical measurement protocol.

A challenge to implementing such a network is to design it in such a way that the plots are representative of NPP across the landscape. One recent study showed that plot-based estimates of forest structure and biomass metrics may not be representative of the metrics across the landscape they are designed to characterize [*Marvin et al.*, 2014], raising some questions about the ability to accurately extrapolate from field plot studies. The *Marvin et al.* [2014] analysis was conducted using emerging airborne remote sensing technologies that are improving our ability to consider forests at landscape scales [*Asner et al.*, 2012]. While tremendous advances in several airborne remote sensing platforms (e.g., lidar) have greatly enhanced our ability to assess plant biomass with high resolution and at multiple scales [e.g., *Asner et al.*, 2007; *Mascaro et al.*, 2014; *Féret and Asner*, 2014], at present, it is impractical to use them with the high frequency necessary to assess short-term (e.g., annual) changes in plant productivity. In addition, assessment of woody biomass is only weakly related to assessment of NPP, because patterns in biomass are strongly driven by tree mortality, and woody production is only a small component of NPP [*Malhi et al.*, 2015]. In the U.S. one potential application of the NEON Airborne Observation Platform (AOP, [*Kampe et al.*, 2010]) will be to incorporate remotely sensed vegetation data into a framework like NCAR' Data Assimilation Research Testbed (DART) [*Zhang et al.*, 2014] to help constrain estimates of NPP in biogeochemical models like CLM. However, these applications of airborne remote sensing are years away in the U.S. and presumably even more distant in the tropics. In the meantime, designing a nested plot network using airborne remote sensing data to select sites that have roughly representative mean canopy structural characteristics and biomass could increase confidence in the applicability of these data to large scales. Similarly, preliminary analysis using satellite data could help to determine representativeness of the topographic and land cover characteristics of the plots [e.g., *Anderson et al.*, 2009], which would further reduce uncertainty in extrapolating plot-based NPP estimates.

In addition, since radiation-based approaches are currently the most widely used methods for assessing long-term, large-scale global NPP and C dynamics, advances in satellite-based technology are critically needed to overcome the many limitations of remote sensing techniques in the tropics. Fortunately, many of the previously identified shortcomings of remote sensing in tropical forests could be addressed with either currently available or soon to be available novel satellite observation platforms. For instance, rapid progress is being made in the satellite-based measurement of solar-induced chlorophyll fluorescence (SiF), a measurement that studies have found to correlate strongly with stomatal conductance even during periods of vegetation stress from drought [*Coops et al.*, 2010; *Parazoo et al.*, 2013, 2014]. Thus, SiF measurements could be used to estimate LUE, which could greatly improve radiation-based NPP estimates by removing the need for biome-level parameterization and coarse, meteorologically derived, temperature and water stress reduction scalars (see equation (1)). Currently, the Japanese Global Greenhouse Gas Observation by Satellite (GoSat) launched in January 2009 and the new NASA Orbiting Carbon Observatory (OCO-2) mission (launched in 2014) are both capable of measuring SiF. In addition, the European Space Agency Fluorescence Explorer (FLEX) mission (proposed) could improve SiF data availability my more than 100-fold [*Frankenberg et al.*, 2013]. Progress in microwave remote sensing is resulting in increasingly accurate measurement of soil moisture and water content in aboveground biomass (vegetation optical depth, VOD), which studies have shown to correlate strongly with other independent satellite indices including FPAR [*Jones et al.*, 2011; *Zhou et al.*, 2014]. Microwave remote sensing of VOD can penetrate cloud cover and thus represents a way to overcome temporal gaps in satellite measures of vegetation dynamic caused by cloud contamination, an issue of central importance in tropical forest ecosystem. Soil moisture and VOD data are currently available from the Advanced Microwave Scanning Radiometer (AMSR-E) aboard NASA's Earth Observing System (EOS) Aqua satellite, but these observation records will be greatly enhance by the launch of NASA's Soil Moisture Active Passive (SMAP) mission (launched in January 2015) [*Entekhabi et al.*, 2010]. Nevertheless, the fundamental trade-off

between spatial and temporal resolution in satellite data collection means that at present we must either rely on frequent, coarse data (e.g., MODIS) to estimate vegetation properties, which will miss small-scale changes (e.g., partial logging) or less frequent, fine-scale data (e.g., LandSat, airborne) that will miss some temporal variability (e.g., vegetation responses to short dry spells).

A number of pressing challenges remain. For example, understanding, translating, and distilling the information in these various satellite data streams into usable information on ecosystem C flux remains a challenge, as does an approach for combining new forms of satellite data into an integrated C dynamic assessment tool. Increased focus around these research areas will be critical for improving radiation-based NPP estimates and the utility of satellite observations to C dynamics monitoring in complex tropical forest ecosystem. Modeling efforts need to build in ecosystem level dynamics, trait-based plant function, flexible C allocation, and spatial variation in biomass turnover times that can capture legacy effects of past disturbances [*Moorcroft et al.*, 2001]. Similarly, biogeochemical models may better capture regional trends, like gradients in productivity across the Amazon, by including more information on soil fertility [*Vicca et al.*, 2012] and additional nutrient constraints on plant productivity [*Wang et al.*, 2010; *Yang et al.*, 2014]. Dynamic vegetation models could also be used as a scaling tool to bridge between the improved satellite data that will become available and the proposed field plot network by using spectral information in process-based algorithms developed and calibrated against information collected in the field. Such models may be the best bridge from field data to fully coupled climate models and would provide an improved understanding of tropical ecosystems both now and into the future.

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