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Do land surface models capture the seasonality of carbon fluxes in the Amazon basin?

A data-model intercomparison

Running head: Seasonal C-flux simulations at Amazon forests

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Abstract

To predict forest response to long-term climate change with confidence requires that land surface models (LSMs) first be successfully tested against ecosystem response to short-term variations in environmental drivers, including regular seasonal patterns. Here, we use an integrated dataset from four forests in the Brasil flux network, spanning a range of dry season intensities and lengths, to test how well four state-of-the-art models (IBIS, ED2, JULES, and CLM3.5) simulate the seasonality of carbon exchanges in Amazonian tropical forests. We found that most LSMS poorly represent the annual cycle of gross primary productivity (GPP), photosynthetic capacity (Pc, a proxy for phenology), and other fluxes and pools. Specifically, our analysis shows that models simulated consistent dry season declines in GPP in the equatorial Amazon (Manaus K34, Santarem K67, and Caxiuanã CAX); however, observed GPP increased. Model predicted GPP reductions are driven by “soil water stress” and in some cases a constant or decreasing photosynthetic infrastructure (e.g. Pc, and leaf area index (LAI)). Nevertheless, at this rainforests, observed dry-season increasing incoming radiation, leaf-flush and abscission, and/or Pc result in higher uptake. Similarly, we report divergences between model-observed seasonal net ecosystem exchange (NEE) and respiration (Re) at equatorial locations. By contrast, at the southern Amazon forest (Jari RJA) observed declines in GPP and Re as the dry season progresses are well represented by most LSMS.

While the (1) water-limitation mechanism is described in models and the primary driver of seasonal photosynthesis in southern Amazonia, we identify other biophysical processes: (2) light harvesting adaptations (e.g., LAI and/or leaf-level assimilation rate increases related to leaf demography); and (3) allocation schemes (e.g. lags between leaf and wood production) that are poor or absent in current model formulations. All three mechanisms dominate equatorial Amazon carbon flux dynamics and are critical for correctly simulating flux seasonality at tropical forests.
1. Introduction

Land surface models (LSMs) are the most widely used and appropriate tool for predicting large-scale responses of vegetation to future climate scenarios. However, to forecast the future of Amazonia under climate change remains a challenge. The previous generation of LSMs produced projections of Amazonia’s future that diverged widely, with outcomes ranging from large-scale forest die-back to forest resilience (Betts et al., 2004, 2004; Friedlingstein et al., 2006; Baker et al., 2008). More recent LSMs simulations showed the large-scale die-off scenario to be unlikely (Cox et al., 2013), given (1) an improved model understanding of forest response to the negative effects of temperature—previously overestimated and now constrained (Cox et al., 2013); and (2) current models being forced with updated climate projections (temperature and precipitation) bounded by observations that no longer demonstrate drastic climate changes in response to rising CO$_2$ in the tropics (Cox et al., 2013; Huntingford et al., 2013). Yet tropical forest response to climate change remains uncertain as models produce varying outcomes (Shao et al., 2013) even without die-off. Some cutting-edge LSMs projected forest degradation due to future deforestation and increasing temperature, with catastrophic consequences for the global climate based on climate-carbon cycle feedbacks (Wang et al., 2013, 2014; Friend et al., 2014), while other LSMs foresaw strong carbon sinks in these forests due to CO$_2$ fertilization of photosynthesis (Rammig et al., 2010; Ahlström et al., 2012; Huntingford et al., 2013; Friend et al., 2014). Although the effects of temperature, water limitation and CO$_2$ fertilization mechanisms remain uncertain, all LSMs continue to agree that Amazonian forests play an important role in regulating the global carbon and water cycle (Eltahir & Bras, 1994; Werth & Avissar, 2002; Wang et al., 2013, 2014; Ahlström et al., 2015).

Key to reducing uncertainty in LSMs is their systematic evaluation against observational datasets.
This exercise enables the identification of model deficiencies through comparison with observed patterns in ecosystem processes, as well as the mechanisms underpinning such processes (Baker et al., 2008; Christoffersen et al., 2014). Recent model-data evaluations in tropical forests have focused on the cascade of ecosystem responses to long term droughts (Powell et al., 2013) and the definition of spatial patterns in productivity and biomass (Delbart et al., 2010; Castanho et al., 2013). However, one important context for model assessment in tropical forests is in the seasonality of ecosystem water and carbon exchange, as observational datasets reveal axes of variation in productivity, biomass and/or forest function across space (da Rocha et al., 2009; Restrepo-Coupe et al., 2013) and/or through time (Saleska et al., 2003; von Randow et al., 2004; Hutyra et al., 2007; Brando et al., 2010). The most consistent temporal variation in tropical forests is the seasonality of water, energy, and carbon exchange, since all tropical ecosystems are seasonal in terms of insolation and a majority experience recurrent changes in precipitation, temperature and/or day length. Evaluation with respect to seasonality has typically focused on evapotranspiration (ET) (Shuttleworth, 1988; Werth & Avissar, 2002; Christoffersen et al., 2014) and on net carbon exchange (NEE) (Baker et al., 2008; von Randow et al., 2013; Melton et al., 2015). Where models compensated misrepresentations of gross primary productivity (GPP) in the NEE balance, by improving or adjusting the efflux term represented by heterotrophic (Melton et al., 2015) or ecosystem respiration (Baker et al., 2008) to available moisture among other strategies. Only recently have the seasonal dynamics of GPP drawn the attention of different groups (De Weirdt et al., 2012; Kim et al., 2012) and where Kim et al. (2012) demonstrated that a consequence of its incorrect derivation was to overestimate the vulnerability of tropical forests to climate extremes. Therefore, identifying discrepancies in observed versus modeled seasonality in carbon flux even when seasonal amplitudes are not large-as can be the case for evergreen tropical forests (see Albert et al. (in preparation) for cryptic phenology), can lead to important model developments
with significant consequences to obtain better projections of the fate of tropical ecosystems under present and future climate scenarios.

Analysis of eddy covariance datasets have shown that in non-water limited forests of Amazonia, the observed seasonality of GPP was not exclusively controlled by seasonal variations in light quantity (as has been demonstrated for ET) or water availability. Instead GPP was driven by a combination of incoming radiation and phenological rhythms influencing leaf quantity (measured as leaf area index, LAI) and quality (leaf-level photosynthetic capacity as a function of time since leaf flush) (Wu et al., submitted; Restrepo-Coupe et al., 2013). The lack of a direct correlation between GPP and climate suggests that ecosystem models that are missing sufficient detail of canopy leaf phenology will likely not capture seasonal productivity patterns. Accordingly, recent studies showed model simulations (ED2 and ORCHIDEE) to be deficient in terms of predicted seasonality in GPP and litterfall, if missing leaf-demography and turnover as in Kim et al. (2012) and in De Weirdt et al. (2012), respectively. Between the two studies, only two sites (eastern (K67) and northeastern (CAX)) were represented, both of which experience very similar precipitation and light regimes. This further highlights the need for expanded evaluation of modeled seasonality of GPP across a range of sites spanning a broader range of climates and phenologies.

If the improved representation of the dynamics of leaves and other carbon pools, translates into more accurate simulations of seasonal GPP, NEE and/or the long-term carbon budget (De Weirdt et al., 2012; Kim et al., 2012; Melton et al., 2015), then comparisons between observations and model derived seasonality of carbon allocation, could provide insight into the mechanistic response of vegetation to climate and strategies to incorporate them into LSMS. For example, critically evaluating the seasonality of net primary production of leaves (NPP_{leaf}) and wood (NPP_{wood}) in
tandem with GPP, will inform deficiencies in model allocation schemes and carbon pool residence times. Model net primary production (NPP) typically arises from the allocation of photosynthate to main organs, either as a constant fraction of GPP (Kucharik et al., 2006), or according to fixed allometric rules (Sitch et al., 2003). However, such a view of supply-limited growth has come into question recently (Würth et al., 2005; Fatichi et al., 2014). Thus as water, temperature, and nutrients can all impact cell expansion, there may be a temporary imbalance between carbon used for tissue growth and maintenance respiration versus carbon supplied by assimilation (photosynthesis)(Fatichi et al., 2014). Patterns in seasonality of GPP, NPP\textsubscript{leaf} and NPP\textsubscript{wood}, therefore, potentially reveal the degree of coupling (or lack thereof) of these two carbon sinks (NPP\textsubscript{wood} and NPP\textsubscript{leaf}) with photosynthetic activity (GPP). Indeed, Doughty et al. (2014) used bottom-up estimates of the ecosystem carbon-budget at a forest in southwest Amazonia and showed that components of NPP varied independently of photosynthetic supply, which they interpreted in terms of theories of optimal allocation patterns. While an alternative interpretation of such patterns could simply refer to biophysical limitations on growth, which vary seasonally (Fatichi et al., 2014), both studies suggest that modeling allocation as a function of GPP will likely fail to capture observed seasonality. Ground-based bottom-up estimates of primary productivity at a temporal resolution greater than a year (i.e., seasonal) are difficult if not impossible, principally because there is no accepted method for estimating whole-tree non-structural carbon (NSC) and its variation with seasons (Würth et al., 2005; Richardson et al., 2015). We proposed coupling co-located top-down eddy flux estimates of GPP with bottom-up NPP estimates (NPP\textsubscript{wood}, NPP\textsubscript{leaf} and NPP\textsubscript{litterfall}) to circumvent this problem and to obtain a better informed view of the mechanisms (e.g. allocation schemes) models may incorporate or test against, to improve seasonal simulations of carbon fluxes and pools.
The focus of this study was to evaluate, for the first time, modeled seasonal cycles of different carbon pools and fluxes, including leaf area index (LAI), GPP, leaf fall, leaf flush, and wood production, with high resolution eddy flux estimates of GPP and ground-based surveys. We centered our study on a comparison between forests located in the equatorial Amazon (radiation- and phenology-driven) to a southern forest (driven by water availability) and explored the different model strategies to incorporate and simulate physical and ecological drivers. Here, we assessed four state-of-the-art LSMS in active development for use in coupled climate-carbon cycle simulations in terms of whether they could simultaneously determine patterns of growth and photosynthesis, thereby getting the ‘right answer for the right reason’. We conclude by proposing several approaches for improving model formulations and highlight the need for model-informed field campaigns and future experimental designs.

2. Methods

2.1. Site descriptions

We analyzed data from the Brazil flux network for four tropical forests represented by the southern site of Reserva Jarú (RJA), and three central Amazonia forests (~3°S) from west to east: the Reserva Cuieiras near Manaus (K34), the Tapajós National forest, near Santarém (K67), and the Caxiuanã National forest near Belém (CAX) (Fig. 1). For detailed site information see previous works by Restrepo-Coupe et al. (2013), and de Goncalves et al. (2009; 2013) and individual site publications (Araújo et al., 2002; Carswell et al., 2002; Malhi et al., 2002; Saleska et al., 2003; Kruijt et al., 2004; von Randow et al., 2004; Hutyra et al., 2007; da Costa et al., 2010).
Figure 1. Locations eddy covariance tower study sites at the Amazon Basin sensu-stricto (Eva & Huber (eds), 2005). Monthly minimum precipitation from the Tropical Rainfall Measuring Mission (TRMM) (NASA, 2014) based on an annual composite for the years 1998 to 2014.

All study sites had mean annual precipitation (MAP) above 2000 mm year\(^{-1}\) (Supplement Fig. 1), based on the satellite-derived precipitation from the Tropical Rainfall Measuring Mission (TRMM) (Huffman et al., 2007; NASA, 2014) 1998-2013 (Table 1). CAX and K34 have MAP over 2500 mm year\(^{-1}\) (2572 and 2674 mm year\(^{-1}\), respectively). By contrast, at the southern forest of RJA and the equatorial forest of K67 MAP was \(~\)2030 mm year\(^{-1}\). Moreover, RJA has a 5-month dry season length (DSL) analogous to two of the central Amazon sites of CAX and K67 (4-month); however, longer than K34 site (2-months). Where the dry season was defined as those periods where precipitation is less than \(~\)100 mm month\(^{-1}\), this threshold corresponded to 80% of the average monthly ET observed at tropical forests (Sombroek, 2001; da Rocha et al., 2004; Restrepo-Coupe et al., 2013). RJA and K67 showed similar mean dry-season precipitation (47 mm month\(^{-1}\) at RJA and 54 mm month\(^{-1}\) at K67). However, the annual minimum averaged across the years 1998-2014 (MiAP) at RJA was 14 mm month\(^{-1}\) compared to a more benign dry season minimum of 37 mm month\(^{-1}\) at K67 (Fig. 1 and Table 1). Despite being located at a latitude further from the equator
(10°S) incoming photosynthetic active radiation (PAR) at the southern forest of Jaru, was less seasonal (low amplitude) if compared to the central Amazon forests (latitude ~3°S) (Fig. 2). At RJA, peak top of the atmosphere radiation (TOA) was synchronous to the wet season—where we expected higher reflectance by clouds decreasing the surface available PAR (Fig. 2). All equatorial sites sat on highly weathered deep clay soils (≥ 10 m), whereas RJA sat on a lower water storage capacity loamy sandy soil and a more shallow and variable profile, with depth to bedrock as shallow as 2-3 m (Hodnett et al., 1996; Christoffersen et al., 2014).

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Mean annual precipitation [mm/month]</th>
<th>Dry season precipitation [mm/month]</th>
<th>Dry season length [months]</th>
<th>Minimum annual precipitation [mm/month]</th>
</tr>
</thead>
<tbody>
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<td>-2.61</td>
<td>-60.21</td>
<td>2674</td>
<td>105</td>
<td>2**</td>
<td>193</td>
</tr>
<tr>
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<td>78</td>
<td>4</td>
<td>60</td>
</tr>
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<td>-54.96</td>
<td>2035</td>
<td>54</td>
<td>4</td>
<td>37</td>
</tr>
<tr>
<td>RJA</td>
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<td>-61.93</td>
<td>2031</td>
<td>47</td>
<td>5</td>
<td>14</td>
</tr>
</tbody>
</table>

**Defined as Rain<110 mm/month, 100 mm/month at other sites

Table 1. Precipitation at Amazon basin study sites. Based on the Tropical Rainfall Measuring Mission (TRMM) (NASA, 2014) for the years 1998 to 2014.

2.2 Eddy covariance methods

At the above-mentioned forests, climate, carbon, energy, water and momentum fluxes were measured by the eddy covariance (EC) method. Starting with half-hourly CO₂-flux data provided from each site's operator, we calculated net ecosystem exchange (NEE in μmol CO₂ m⁻² s⁻¹), with fluxes to the atmosphere defined as positive. NEE was then filtered for low turbulence periods (u*thresh). For a detailed description of instrumentation, applied corrections, quality control procedures, and methods for data processing refer to Restrepo-Coupe et al. (2013). Gross ecosystem exchange (GEE) was derived from tower measurements of daytime NEE by subtracting
estimates of ecosystem respiration \( (R_{eco}) \), which in turn we derived from the nighttime NEE. We assumed daytime \( R_{eco} \) was the same as nighttime \( R_{eco} \). GEE is a negative value \( (GEE = NEE - R_{eco}) \) as generally NEE is negative in the daytime, and \( R_{eco} \) is positive (meteorological convention). We expressed ecosystem-scale photosynthesis, or gross ecosystem productivity \( (GEP) \), as negative GEE and assumed negligible re-assimilation of metabolic respiration \( CO_2 \) within the leaf and insignificant \( CO_2 \) recirculation below the EC system (Stoy et al., 2006). For comparison with model output, we assumed negligible seasonal changes in photorespiration and used \( GEP \) interchangeably with gross primary productivity \( (GPP) \).

We defined ecosystem photosynthetic capacity \( (Pc, gC m^{-2} d^{-1}) \) as the 16-day average \( GPP \) at a fixed photosynthetically active radiation \( (PAR) \) range (site specific daytime mean \( PAR, PAR_{avg} \pm 100 \ \mu mol \ m^{-2} \ s^{-1} \) (Supplement Table 1); thus, to remove the effect of day-to-day changes in available light (e.g. cloudy versus clear days), photoperiod, and any other effect of non-optimum \( PAR \) levels. Similarly, we used vapor pressure deficit \( (VPD) \), air temperature \( (T_a) \) to remove \( GPP \) measures obtained during non-optimum conditions by restricting \( Pc \) calculations to mean daytime \( VPD(VPD_{avg}) \) and \( T_a (T_{a,avg}) \pm \) one standard deviation from their respective time series. \( Pc \) represents the vegetation built capacity to do photosynthesis \( (Pc \) as biophysical driver of \( GPP) \).

Where at the four study sites, it has been shown that the seasonal pattern of \( Pc \) was independent of and other climatic variables (Restrepo-Coupe et al., 2013).

We looked at evapotranspiration \( (ET, \ mm \ d^{-1}) \) calculated as the latent heat flux \( (LE, \ W \ m^{-2}) \) measured at the tower multiplied by the latent heat of vaporization \( (\lambda, \ kJ \ kg^{-1}) \). We developed a Type II linear model between surface incident short wave radiation \( (SW_{down}, \ W \ m^{-2}) \) and the dependent variable, \( ET \).
Figure 2. From top to bottom annual cycle of daily average observed climatic variables: incoming photosynthetic active radiation (PAR, μmol m⁻² s⁻¹, black line right y-axis) and precipitation (Precip, mm month⁻¹, dark gray bars left y-axis), top of the atmosphere incoming radiation (TOA; W m⁻², blue line right y-axis) (not a driver). From left to right study sites (from wet to dry forest) near Manaus forest (K34), Caxiuana forest (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). Second row LSM drivers: near surface specific humidity (Q₉₀₀; kg kg⁻¹, black line left y-axis) and temperature (T₉₀₀; °C, blue line right y-axis). Lower panel depicts model ecosystem-scale of model soil moisture “stress” (FSW, where 1=no stress). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple).

From the standard suite of climatic variables available for periods between 1999 and 2006 measured
at each EC tower, meteorological drivers for the models were generated. Variables included:

SW\textsubscript{down}; air temperature (T\textsubscript{air}, °K); near surface specific humidity (Q\textsubscript{air}, g kg\textsuperscript{-1}); rainfall (Precip, mm month\textsuperscript{-1}); magnitude of near surface wind (WS, m s\textsuperscript{-1}), surface atmospheric pressure (Pa, hPa);

surface incident longwave radiation (LW\textsubscript{down}, W m\textsuperscript{-2}); and a fixed CO\textsubscript{2} concentration (CO\textsubscript{2_{air}} at 375 ppm) (de Goncalves et al., 2009) (Fig. 2). Drivers were created for consecutive years where gaps were no greater than two months. The data was subject to quality control and filled using other tower measurements (e.g. from a temperature profile), near-by sites and the variables mean monthly diurnal cycle. We analyzed data for 2000-2005 for K34, 2002-2004 for K67, 2000-2002 for RJA and 1999-2003 for CAX. We restricted flux and meteorological observations and the calculation of seasonality to the above-mentioned dates in order to match model drivers and output.

Hourly fluxes (GPP, NEE, R\textsubscript{eco}, and ET) and meteorology were aggregated to 16-day time periods, assuming that at least 4 days were available with at least 21 hours of observations each. Gaps were not filled further and mean annual cycles were then calculated.

2.3. Field measurements

The following vegetation infrastructure descriptors and carbon pools were included on the analysis:

Leaf Area Index (LAI): model output was compared to LAI observations for Caxiuan, CAX as reported by Metcalfe et al. (2007), and for Santarem, K67 as by Brando et al. (2010). LAI was normalized from 0 to 1 (LAI\textsubscript{normalized}) for purposes of presentation. Thus, in order to visualize any changes in LAI, independent of the observed or modeled absolute value, using Equation 1, where at time \( i \), LAI\textsubscript{i} was adjusted by LAI\textsubscript{min} and LAI\textsubscript{max} that corresponded to the minimum and maximum seasonal LAI, respectively:
\[ LAI_{\text{normalized}}(i) = \frac{LAI_i - LAI_{\text{min}}}{LAI_{\text{max}} - LAI_{\text{min}}} \]  

Equation 1

Leaf litter-fall or net primary productivity allocated to litter-fall (\(NPP_{\text{litter-fall}}\) g C m\(^{-2}\) d\(^{-1}\)): values corresponded to monthly litter-bed measurements at Manaus, K34 (here presented for the first time), and to those reported by Rice et al. (2004) for K67 and by Fisher et al. (2007) for CAX.

Modeled \(NPP_{\text{leaf}}\) followed a basic leaf balance model proposed by Restrepo-Coupe et al. (2013).

Assuming the change in ecosystem \(Pc\) (\(dPc/dt\)) to be driven by 1) the loss or gain of leaves, \(NPP_{\text{litter-fall}}\) and \(NPP_{\text{leaf}}\) respectively (quantity); and 2) the changes in leaf-level carbon assimilation at saturating light (SLA x \(A_{\text{max}}\)) related to age (quality). Therefore, solving for leaf production we obtained:

\[ NPP_{\text{leaf}} = NPP_{\text{litter-fall}} + \frac{1}{A_{\text{max}} \times SLA} \times \frac{dPc}{dt} \]  

Equation 2

where specific leaf area (SLA) values were set to 0.0140 for K67 and CAX (Domingues et al., 2005), 0.0164 m\(^2\)/g C for K34 (Carswell et al., 2002). The \(A_{\text{max}}\) was reduced to reach 40\% of the mean value at the time when leaf-fall reached its maximum (2-month linear gradient). Maximum \(A_{\text{max}}\) was set to 8.66 g C m\(^{-2}\) d\(^{-1}\) at K67 (Domingues et al., 2005), and to 7.36 g C m\(^{-2}\) d\(^{-1}\) at K34 (Carswell et al., 2000) and CAX.

Wood net primary productivity (\(NPP_{\text{wood}}\)) was based on stemwood increment measurements (diameter at breast height, DBH) as reported by Rice et al. (2004) at K67, Chambers et al. (2013) at K34, and da Costa et al. (2010) at CAX. No data was available for RJA.
2.4. Land system models (LSMs)

We presented output from four state-of-the-art terrestrial biosphere models. All LSMS were process based (e.g., photosynthesis, respiration, and evapotranspiration) and able to simulate the fluxes of carbon, water, and energy between the atmosphere and the land surface. The model simulations were run as part of the Interactions between Climate, Forests, and Land Use in the Amazon Basin: Modeling and Mitigating Large Scale Savannization project (Powell et al., 2013).

The Ecosystem Demography model version 2 (ED2): The model explicitly tracked the dynamics of fine-scale ecosystem structure and function, including net ecosystem productivity (NEP), carbon partitioning, and growth and mortality dynamics (Medvigy et al., 2009). It used four PFTs for the tropics, 10-minute time step for the dynamic global vegetation model (DGVM) and LAI on a daily basis. The number of canopy layers varied per number of plant cohorts and had three different soil carbon pools for each layer (fast, slow and structural), water extraction depth varies according to plant functional types (PFTs); however, the model did not included hydraulic redistribution.

The Integrated Biosphere Simulator (IBIS): The model simulated hourly carbon fluxes. LAI was allocated annually and biomass was integrated over the year (Foley et al., 1996). IBIS required 76 parameters to be specified, of those 14 were related to soil, 12 were specific to each of the nine PFTs, and 50 were related to morphological and biophysical characteristics of vegetation.

The Community Land Model-Dynamic Global Vegetation Model version 3.5 (CLM3.5): Is the predecessor to the current CLM4-CNDV model (Gotangco Castillo et al., 2012), which is the land component of the Community Earth System Model (CESM). CLM3.5 runs were set using a prognostic phenology, which incorporated recent improvements to its canopy interception scheme,
new parameterizations for canopy integration, a TOPMODEL-based model for runoff, canopy
interception, soil water availability, soil evaporation, water table depth determination by the
inclusion of a groundwater model, and nitrogen constraints on plant productivity (without explicit
nitrogen cycling) (Oleson et al., 2008). The model treated the canopy as a weighted average (by
their respective LAIs) of sun and shaded leaves. The leaf phenology subroutine of this model for
tropical forests applied only to the Broadleaf Deciduous Tree (BDT) PFT fraction (“raingreen”
PFT), but all CLM3.5 simulations reported here were >95% tropical Broadleaf Evergreen Tree
(BET) fractional PFT cover. The allocation scheme for this model dictated that leaf turnover for the
tropical BET (at a rate of 0.5 yr⁻¹) be replaced instantaneously with new leaf production to maintain
fixed allometric relationships (Sitch et al., 2003); therefore, seasonality of LAI was not possible for
these simulations.

The Joint UK Land Environment Simulator (JULES): Included a multi-layer canopy scheme for
light interception (built-in a sun fleck penetration scheme), a coupled scheme of leaf photosynthesis
and stomatal conductance, and the representation of the effects of ozone on leaf physiology. The
version of JULES shown here represented the carbon allocation, growth and population dynamics
of five plant functional types. The turnover of carbon from living plant tissues was fed into a four-
pool soil carbon model (Clark et al., 2011).

Model output followed the LBA-Data Model Intercomparison Project (LBA-DMIP) protocol (de
Goncalves et al., 2009); however, it includes some additional variables related to water limitation
(e.g. soil water availability factor or soil water “stress”), land use change (e.g. additional carbon
pools), and disturbance (e.g. mortality) (Powell et al., 2013). Here, we present soil water “stress”
(FSW) values, calculated following Ju et al. (2006). By definition FSW ranging from 0 to 1 is a
measure of the water available to roots, where $FSW=1$, is no stress.

3. Results

3.1. Gross primary productivity ($GPP$) and ecosystem photosynthetic capacity ($Pc$)

The observed annual cycle of ecosystem-scale $GPP$ showed two divergent patterns: (1) increasing levels of photosynthetic activity ($GPP$) as the dry season progresses in the equatorial Amazon (K34, K67 and CAX) where MiAP was 60 and 36 mm month$^{-1}$, respectively, and maximum radiation was synchronous with low precipitation; and (2) declining productivity as the dry-season advanced in the southern forests (RJA) where radiation was somewhat aseasonal and MiAP was less than half its central Amazon counterparts (14 mm month$^{-1}$) (Fig. 1). By contrast, at all sites, model simulations showed peak $GPP$ seasonality at the end of wet season with declining $GPP$ during the dry season (Fig. 3). The reduced dry season $GPP$ observed at the southern Amazon forest of Jarú (RJA) was consistent with increasing degrees of water limitation. At the sites in the equatorial Amazon (K34, K67 and CAX), modeled soil water “stress” ($FSW$; Fig. 2) (where $FSW=1$, no stress) acted to reduce model $GPP$ during the dry season, even as observed $Pc$ increased following higher levels of incoming solar radiation ($PAR$; Fig. 2 and $Pc$; Fig. 4). Similar to $GPP$, models tended to achieve good $Pc$ representation at RJA. However, simulated $Pc$ at the equatorial Amazon forest sites remained unchanged (IBIS and JULES) or decreasing gradually from the middle of the wet season to the end of the dry period at K67 (ED2 and CLM3.5) (Fig. 4).
Figure 3: Annual cycle of daily average ecosystem-scale photosynthesis (GPP; gC m⁻² d⁻¹), ecosystem respiration (Re; gC m⁻² d⁻¹) net ecosystem exchange (NEE; gC m⁻² d⁻¹) and evapotranspiration (ET; mm d⁻¹) near Manaus forest (K34), Caxiuanã forest (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). Observed (black + dark gray uncertainty) and simulated by models (colors). Dashed black line at ET panels corresponds to a linear model where the independent variable is incoming radiation (SW_{down}). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple). Observations from the Brasil flux network.

FSW reached an all-site minimum at RJA by the end of the dry season (Fig. 2) and corresponded with a decrease in model ET not seen on the EC measurements (Fig. 3). With the exception of CAX,
seasonal observations of $ET$ at all of the sites showed very little seasonality and remained close to 
120 mm month$^{-1}$ (4 mm d$^{-1}$). In general, models were able to capture the seasonality of $ET$; 
however, they overestimated the dry-period reduction in water exchange at RJA and in the case of 
K34 and CAX overestimated $ET$ absolute values. By contrast, a very simple linear regression 
driven by $SW_{\text{down}}$ was able to represent ~83% of the seasonality of $ET$ (Fig. 3).

3.2 Carbon allocation

We explored different model approaches to simulate the phenology of carbon allocation, in 
particular measures of plant metabolism (ecosystem photosynthetic capacity, $Pc$ as proxy), standing 
biomass (wood increment, leaf-production and the balance of gain and loss of leaves), and additions 
to soil organic matter (leaf-fall), in an attempt to understand the model-data discrepancies on the 
estimates of GPP and NEE.

Our results indicated that none of the models was able to capture or replicate the observed dry- 
season LAI changes at our equatorial Amazon forests EC locations (Fig. 4). In addition, with the 
exception of ED2, the annual mean LAI values were unrealistically high (Baldocchi et al., 1988; 
Gower et al., 1999; Asner et al., 2003; Sakaguchi et al., 2011). In contrast, with some model 
phenology schemes that assumed LAI and $T_{\text{air}}$ to be positively correlated, we observed a negative o 
no correlation (non-statistically significant; p-value >0.1) (Supplement Fig. 6).

In the field, leaf litter-fall plays an important role in determining the seasonality of LAI, $Pc$ (as per 
Equation 2), heterotrophic respiration and soil carbon pools. Data for the central Amazon forests 
showed a highly seasonal leaf-fall cycle (Chave et al., 2010), with an LAI maximum at the 
beginning of the dry season at CAX and in the middle of the dry period at K67 (Fig. 4). At
equatorial sites, peak litter-fall corresponded to a maximum in $SW_{down}$, where we observed a statistically significant linear regression between $SW_{down}$ and $NPP_{litter-fall}$ with a coefficient of determination, $R^2$ equal to 0.34 at K34, 0.21 at K67, and 0.6 at CAX ($p<0.01$) (Supplement Fig. 2). With the exception of ED2, which included a drought-deciduous phenology and consequentially seasonal variations in leaf abscission, seasonality in $NPP_{litter-fall}$ was not resolved in most LSMs (Fig. 4).

Estimates of leaf-production (increase in the amount of young-high photosynthetic capacity leaves) from the observations at K67 forest showed peak $NPP_{leaf}$ in the dry season in contrast to most simulations. In general, $NPP_{leaf}$ was: (1) constant in most models; (2) allocated at the end of the year, similar to $NPP_{litter-fall}$ or (3) declining, in particular during the strong K67 dry season (Fig. 2). Even if counterintuitive, at some of the equatorial Amazon sites key leaf-demography processes (e.g. leaf-fall and leaf-flush) and/or LAI, increased in tandem during the dry season.

In contrast to $NPP_{leaf}$, $NPP$ allocation to wood growth ($NPP_{wood}$) was aseasonal at K34; however at K67 peaked during the wet season, displaying opposite seasonality and being out-of-phase with $NPP_{leaf}$. This pattern seemed to be different at CAX, with both $NPP_{leaf}$ and $NPP_{wood}$ maximum during the dry season, at this site precipitation was significantly seasonal (wet season was the rainiest of all equatorial sites) and the amplitude of the seasonal cycle of $SW_{down}$ was the highest of all Brasil flux central Amazon locations. By contrast, models simulated a peak in $NPP_{wood}$ at CAX and K67 that corresponded to the beginning of the dry season. The seasonality of model $NPP_{wood}$ was absent at the three equatorial forests and only significant differences between the wet and dry periods were observed at RJA, where all simulations showed minimum $NPP_{wood}$ at the end of the dry season.
Figure 4. From top to bottom annual cycle of daily average ecosystem photosynthetic capacity ($P_c$, GPP at a fixed PAR range 725-875 µmol m$^{-2}$ s$^{-1}$), Leaf Area Index (LAI; m$^2$ m$^{-1}$), normalized LAI (its value constrained between 0 and 1 in order to better track its changes), net primary productivity ($NPP_{\text{leaf}}, m^2 d^{-1}$) allocated to leaves -leaf flush ($NPP_{\text{leaf}}, m^2 d^{-1}$), NPP allocated to litter-fall ($NPP_{\text{litter-fall}}, g C m^2 d^{-1}$). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). Lower row NPP allocated to wood ($NPP_{\text{wood}}, g C m^2 d^{-1}$).

From left to right study sites (from wet to dry forest) near Manaus forest (K34), Caxiuanã forest (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). Observed (black) versus simulated by models (colors). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple). Dashed green lines (CLM3.5) at NPP$_{\text{litter-fall}}$ and NPP$_{\text{leaf}}$ indicate average values for comparison purposes (models allocated at the end of the year as indicated by continuous line).
Figure 5. From left to right study sites (from wet to dry forest) near Manaus forest (K34), Caxiuanã forest (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). From top to bottom, annual cycle observed (black) and model simulations from JULES (purple), CLM3.5 (green), IBIS (red), and ED2 (blue). Normalized (by its seasonal maximum) annual cycle of daily average ecosystem-scale photosynthesis ($GPP/GPP_{max}$) (continuous line), net primary productivity ($NPP$) allocated to leaves - leaf flush ($NPP_{leaf}/NPP_{leaf_{max}}$), $NPP$ allocated to litter-fall ($NPP_{litter-fall}/NPP_{litter-fall_{max}}$), and $NPP$ allocated to wood ($NPP_{wood}/NPP_{wood_{max}}$). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014).
Our analysis shows a statistically significant negative linear regression between $SW_{down}$ and $NPP_{wood}$ with a coefficient of determination, $R^2$ equal to 0.45 at K67 and 0.62 at CAX ($p<0.01$) (Supplement Fig. 3). Non-significant correlation was found between $SW_{down}$ and $NPP_{wood}$ or precipitation and $NPP_{wood}$ at K34 - the wettest and least seasonal of the four studied forests.

Seasonal observations of the different NPP components and GPP showed a lack of temporal synchrony between them, neither a shared allocation pattern among forests - each exhibiting different phenology (Fig. 5). At some sites (CAX and K67), there was a statistically significant correlation (~1 to 2-month lag, $NPP_{leaf}$ ahead) between GPP and $NPP_{leaf}$ (Supplement Fig. 5).

However, there was no temporal correspondence between GPP and $NPP_{wood}$. By comparison, model allocation ($NPP_{leaf}$, $NPP_{litter-fall}$ and $NPP_{wood}$) and GPP was coupled at most models (Fig. 5).

3.2 Ecosystem respiration ($R_e$) and net ecosystem exchange (NEE)

Similar to GPP, the timing and amplitude of ecosystem respiration ($R_e$) seasonality at RJA was well captured by most models; however, all simulations at equatorial Amazon sites overestimated $R_e$. In particular, during the months for which $R_e$ reached a minimum - the wet season at CAX and the dry season at K67, model $R_e$ showed opposite seasonality to observations. The imbalance between predicted $R_e$ and GPP translated into an underestimation of the observed net ecosystem uptake (negative NEE), with the models predicting a positive NEE (strong carbon source), in particular, at K34 and CAX. More importantly, the seasonality of NEE in the equatorial forests (K34, K67 and CAX) was missed, with the LSMs foreseeing a greater carbon loss during the dry season, as opposed to those observed during the September-December losses (Fig. 3).
4. Discussion

In this study, we found that land surface models poorly represented the annual cycle of carbon flux dynamics for the Amazon evergreen tropical forest sites with eddy covariance towers. In particular, at equatorial Amazonia, observations showed an increase in GPP, Pc, and/or LAI during the dry season. In contrast, models simulated constant or declining GPP and Pc, and in general, assumed no seasonal cycling in LAI (Fig. 4). The disparity between model and in situ measurements of GPP indicated that there is a bias in the modeled ecosystem response to climate and a lack of understanding of which drivers, meteorological (e.g. light or water) or phenological (e.g. leaf demography) or a combination thereof, control ecosystem carbon flux. Moreover, a mismatch between seasonal observations of carbon pools and allocation strategies ($\text{NPP}_{\text{leaf}}$, $\text{NPP}_{\text{wood}}$, $\text{NPP}_{\text{litter-fall}}$) and model results, highlights the importance of phenology as an essential tool for understanding productivity within the tropical forest of the Amazon.

4.1 Seasonality of gross primary productivity (GPP), and other carbon fluxes

We observed the greatest discrepancies between measured and model predicted GPP, $R_s$, and NEE at central Amazon sites, where productivity is hypothesized to be primarily controlled by a combination of light availability and phenology (Wu et al., submitted; Restrepo-Coupe et al., 2013). By contrast, models were able to capture the “correct” seasonality at the southern forest of RJA, a site that shows significant signs of water limitation. However, at RJA the amplitude of the annual cycle were overestimated by most models, which assume lower than expected GPP during the dry season. Our results suggest that, while models have improved their ability to simulate water stress; their ability to simulate light-based growth strategies is still an issue.

Satellite phenology studies have shown annual precipitation values and the length of the dry season
to be important factors when determining ecosystem response (Guan et al., 2015). Nevertheless, K67 and RJA share similar rainfall values, with MAP of 2030 mm year\(^{-1}\), dry season precipitation (DSP) of 50 mm month\(^{-1}\), and a 4 to 5 month dry period, only the minimum annual precipitation differs, having RJA MiAP of 14 compared to 37 mm month\(^{-1}\) measured at K67. Moreover, increasing levels of incoming light at K67 and other equatorial sites during the dry season provided an opportunity for vegetation to increase productivity under the existent precipitation regime, as rainfall delivered more than 50% of ecosystem water needs assuming a monthly ~120 mm requirement. For central Amazon tropical forests, observed increases in GPP, vegetation photosynthetic potential (Pc as a proxy), and allocation patterns, linked to light harvesting strategies, were concurrent with the reported incoming in solar radiation increase (Huete et al., 2006; Brando et al., 2010; Restrepo-Coupe et al., 2013). By comparison, at RJA, there was no tradeoff between light, precipitation and atmospheric demand, as solar radiation was somewhat aseasonal (with a maximum at the beginning of the wet season) and dry season rainfall values (MiAP) reached less than 10% of mean tropical forest ET.

4.2 Carbon allocation strategies

Models include LAI in the vegetation dynamics module using a variety of strategies: (1) prescribed LAI values from remote sensing sources; (2) dynamic calculation of daily LAI; and (3) LAI is fixed and the model later allocating any changes at the end of the year, thus only to calculate changes in the carbon balance and next year LAI values. This last approach may need to be re-evaluated given the importance of phenology as an ecosystem productivity driver. Models that dynamically calculate LAI generally rely in defining LAI range values for each PFT (Clark et al., 2011), where the actual value will depend mostly on the phenological status of the vegetation type—a function of temperature. Although some evergreen ecosystems do respond to temperature thresholds (e.g.
positive correlation between $T_{\text{air}}$ and $\text{LAI}$ and a threshold at $T_{\text{air}}>0$ has been identified for conifer forests at temperate areas (Khomik et al., 2010). $\text{LAI}$ and $P_c$ at tropical ecosystems do exhibited a negative or no correlation with $T_{\text{air}}$. Moreover, model $\text{LAI}$ values were unreasonably 2+ units above observed values (Baldocchi et al., 1988; Gower et al., 1999; Asner et al., 2003; Sakaguchi et al., 2011). Some models assumed $\text{LAI}$ value above six, the theoretical limit of $\text{LAI}$ (assuming no clumping and planar leaf angle distribution) according to Beer’s law. Similar to previous findings by Christoffersen et al. (2014) regarding model performance when simulating water fluxes, some of the model deficiencies could be resolved by changing the parameterization of each PFT, such as the case of maximum and minimum $\text{LAI}$ values. However, a true improvement will only come if we increase the frequency and coverage of our measurements, and a better understanding of the carbon allocation, mechanisms that control the change in $\text{LAI}$, and the balance between loss due to abscission, leaf production, and other ecosystem processes.

In the observations, $P_c$ values increased during the dry season at all central Amazon sites. Elevated $P_c$ can be achieved through leaf flush, as younger leaves have higher leaf carbon assimilation at saturating light ($A_{\text{max}}$) compared to old leaves (Wu et al., submitted; Sobrado, 1994), or by changes in leaf herbivory, epiphyllous growth, and stress, among other factors. Alternatively, $P_c$ can be increased through a surge in canopy infrastructure (quantity of leaves) measured as leaf area index ($\text{LAI}$) (Doughty & Goulden, 2008). Our observations suggested a combination of these two processes or $P_c$ mostly driven by the presence of younger leaves, as we observed a small increase in $\text{LAI}$ at K67 during the dry season ($0.7 \text{ m}^2/\text{m}^2 \sim 10\%$ of annual mean) and a gradual decline at CAX, respectively. In order to address the relationship between leaf demography (leaf age distribution) and carbon fluxes, we presented the seasonality of in situ observations of $\text{NPP}_{\text{leaf}}$ and compared it to model estimates. We have shown that, at the equatorial Amazon estimated $\text{NPP}_{\text{leaf}}$ was
synchronous with the seasonality of $SW_{down}$. Thus, increasing light may trigger new leaf production as part of a light-based growth strategy missed by the models evaluated here. Some vegetation schemes have introduced a time-dynamic carbon allocation to leaves, generic roots, coarse and fine roots, etc. However, even if models assign $NPP_{leaf}$ varying turnover time from 243 days to a maximum of 2.7 years, the timing of leaf production seems to be missed. The counterintuitive mechanism observed at some central Amazon forests where all or most of the leaf-demography processes (leaf-fall, leaf-flush and $LAI$) increase during the dry season, constitutes an important challenge for modelers and plant physiologists. An appropriate model representation and further studies are required of: (1) the leaf lifespan, (2) the seasonality of leaf age distribution (e.g. sun and shade leaf cohorts: young, mature, old), (3) the effect of leaf-fall on increasing light levels at lower layers of the canopy, and (4) the relationship between leaf age and physiology (Albert et al., in preparation), to properly characterize Amazon basin leaf phenology and associated changes in productivity. Thus, as a homogeneous age cohort where all leaves have similar ability to assimilate carbon can contribute to the model simulated aseasonal $Pc$ and $GEP$ seasonality driven only by water availability.

Previous studies have linked the robustness of models predictions of the terrestrial ecosystem carbon response to climate change projections to the uncertainty of the different carbon pools within the models (Ahlström et al., 2012). Observations show that the seasonality of allocation (e.g. $NPP_{litter-fall}$) and leaf-demography (e.g. $NPP_{leaf}$) are closely related to the fast and slow soil carbon pools (input) and ecosystem respiration. Decomposition of $NPP_{litter-fall}$ initiates the transfer of carbon to the soil microbial and the slow and passive pools in many models and determines heterotrophic respiration. Similarly, autotrophic respiration (maintenance and growth) also will be driven by live tissue allocation ($NPP_{wood}$, $NPP_{leaf}$ and $NPP_{roots}$). Therefore, $R_{eco}$ will depend on a
well-characterized phenological response of litter and woody debris, wood and leaf accumulation, and the soil carbon pools. Still, in some models and according to a set of prescribed allometric relationships for each PFT where leaves, fine roots and stems NPP are allocated at the end of each simulated year. Thus, to improve simulation-data agreement and to generate reliable projections for ecosystem response to climate perturbations, the next generation of models must include a basic mechanistic understanding of the environmental controls on ecosystem metabolism that goes beyond correlations (e.g. NPP_{leaf} versus SW_{down}, NPP_{literfall} versus Precip) and addresses the long time adaptation to climate and their seasonality. We highlight the need for extended EC measurements accompanied by seasonal based biophysical inventories, as both datasets complement and inform each other.

The seasonal patterns in seasonal GPP and NPP (leaf and wood); show to be (1) aseasonal at K34; (2) synchronous at CAX; and (3) out-of-phase at K67. The GPP, NPP_{leaf} and NPP_{wood dry-season maxima at CAX may be interpreted in terms of a combination of mechanisms: (1) optimal allocation patterns (Doughty et al., 2014) -- in sync photosynthetic activity and carbon allocation driven by dry-season light increases; and (2) reflect biophysical limitations (Fatichiet al., 2014) -- wet season anoxia, drive both leaves and wood to be produced during the dry season. Similar to CAX, observations of a simultaneous increase in NPP_{leaf} and NPP_{wood} during the dry season have been reported at seasonally inundated floodplain tropical forests, where anoxia limits respiratory requirements of NPP_{wood} and show peak NPP_{wood} shifted into the dry season (Dezzeo et al., 2003). Consistently, seasonal observations at flooded forests showed reduced production of new leaves and lower photosynthetic assimilation during the inundation period (Parolin, 2000). By comparison, the NPP_{wood} patterns observed at K67 where dry-season MiAP is ~50% of mean annual ET may reflect biophysical limitations on the sink tissue (e.g. cell turgor and cell division in cambial tissues) --
water availability as a driver (Wagner et al., 2012; Rowland et al., 2013), or/and an allocation strategy that favors \( \text{NPP}_{\text{leaf}} \) to \( \text{NPP}_{\text{wood}} \). At K67 and K34 forests, the timing of \( \text{GPP} \) versus \( \text{NPP}_{\text{wood}} \) highlights the importance of NSC (Fatichi et al., 2014) and difficulties faced by more mechanistic LSMs.

Figure 6. Ecosystem response to climate seasonality [selection of biological adaptive mechanisms: light harvest adaptations (green tones), allocation strategies (orange tones), and water limitation (blue tones). Mechanisms classified when possible into resource optimization (Opt) and biophysical limitations (Lim).

4.3 Final considerations for model improvement

This study identified three main tropical forest responses to climatic drivers that if understood could reduce the model–observation \( \text{GPP} \) discrepancies. These are (1) light harvest adaptation schemes; (2) response to water availability; and (3) other allocation strategies (Fig. 6). We propose thorough
(1) optimization patterns and (2) thresholds (limitation) to obtain the seasonality of the different carbon pools. For example, models could incorporate some of the recent findings: (1) leaf demography as a function of light environment as in Wu et al. (submitted), and (2) leaf phenology (greenness) seasonal patterns driven by soil moisture availability as a function of MAP threshold as in Guan et al. (2015). However, less has been reported about other processes and reservoirs different than $NPP_{leaf}$. In particular, our study lacks belowground information, as data that explores the seasonality of root allocation at tropical sites is scarce and difficult to interpret. Future work should address this important carbon-pool and the correspondent model ability to simulate the seasonality of belowground processes.

Climate models have come a long way, from the 1970 when the first land surface scheme was introduced in order to represent the atmosphere-biosphere interaction by partitioning ocean from dry land (Manabe & Bryan, 1969). Simulations of water, energy and carbon fluxes based on the response of different plant functional types to climate drivers and disturbance signifies a great step forward on weather prediction and the study of future climates under the effect of land cover changes and atmospheric CO$_2$ enrichment (Pitman, 2003; Niu & Zeng, 2012). Models are constrained in their development given the high computational needs and the multiple processes that need to be accounted for on a three dimensional grid from LAI seasonality, to ground water flux, to leaf level parameterization, there is a tradeoff and a “priority list”. This study highlights some of the advances in tropical forest simulations of carbon and water fluxes and aims to identify future opportunities, as the inclusion of light harvesting and allocation strategies in an attempt to improve GPP and NPP predictions.
5. **Conclusions**

At central Amazon tropical forests, four land surface models (LSMs) simulated gross primary productivity (GPP) peaks at the end of wet season, and then declines along with the progress of the dry season, thus in contrast to eddy covariance observations, which reach a minimum GPP at end of wet season and then increase in the dry season. Similarly, the modeled annual cycle of daily average ecosystem-scale respiration (R_e) and net exchange (NEE) was out-of-phase and their absolute values were overestimated for R_e and underestimated for NEE. The above-mentioned discrepancies between predicted and observed carbon fluxes indicate that some models may be missing important processes. Our work highlights phenology, allocation strategies, and plant physiological responses to seasonal climatic constraints (i.e. low light and water availability) as important descriptors of ecosystem photosynthetic capacity (Pc), and thus, key drivers of ecosystem productivity and other metabolic processes (e.g. heterotrophic respiration). Interestingly, water limitation issues previously reported seem to be resolved by most models, as seen by improvements on the simulation of ecosystem ET.

We explore different ESM approaches to track the phenology of carbon allocation, in particular measures of plant metabolism (Pc as proxy), standing biomass (wood increment and leaf-flush) and additions to soil organic matter (leaf-fall) in an attempt to understand the model-data discrepancies on the estimates of GPP and NEE. We are able to identify the seasonality of net primary productivity allocated to litter-fall (NPP_{litter-fall}) and leaf production (NPP_{leaf}) and the total balance (leaf area index, LAI) as key biological drivers, which if understood (mechanisms and vegetation response) and properly implemented, could improve model predictions. In particular, *in situ* observations show that at the central Amazon estimated NPP_{leaf} is synchronous with the seasonality of incoming solar radiation, a light-based growth strategy missed by most of models. Similarly, the
seasonality of LAI at tropical forests seems underestimated and the mechanisms that control the change in LAI and the balance between loss of capacity due to \( NPP_{\text{liter-fall}} \) and increase of capacity from \( NPP_{\text{leaf}} \) are not well understood. The counterintuitive leaf-demography process observed at some equatorial Amazon sites (\( NPP_{\text{liter-fall}} \) versus \( NPP_{\text{leaf}} \)) where \( P_c \) and/or LAI increased during the dry season, and the here reported lags between \( GPP \) and \( NPP_{\text{wood}} \) challenge Amazon basin model phenology representations. As fluxes are not exclusively driven by meteorology, incorporating this key biological adaptive mechanisms into ESMs is an important task in order to advance our understanding of tropical vegetation-climate feedbacks.

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