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

2 **A data-model intercomparison**

3

4 **Running head:** Seasonal C-flux simulations at Amazon forests

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27

28

## Abstract

29 To predict forest response to long-term climate change with confidence requires that land surface  
30 models (LSMs) first be successfully tested against ecosystem response to short-term variations in  
31 environmental drivers, including regular seasonal patterns. Here, we use an integrated dataset from  
32 four forests in the Brasil flux network, spanning a range of dry season intensities and lengths, to test  
33 how well four state-of-the-art models (IBIS, ED2, JULES, and CLM3.5) simulate the seasonality of  
34 carbon exchanges in Amazonian tropical forests. We found that most LSMs poorly represent the  
35 annual cycle of gross primary productivity (*GPP*), photosynthetic capacity (*P<sub>c</sub>*, a proxy for  
36 phenology), and other fluxes and pools. Specifically, our analysis shows that models simulated  
37 consistent dry season declines in *GPP* in the equatorial Amazon (Manaus K34, Santarem K67, and  
38 Caxiuana CAX); however, observed *GPP* increased. Model predicted *GPP* reductions are driven  
39 by “soil water stress” and in some cases a constant or decreasing photosynthetic infrastructure (e.g.  
40 *P<sub>c</sub>*, and leaf area index (*LAI*)). Nevertheless, at this rainforests, observed dry-season increasing  
41 incoming radiation, leaf-flush and abscission, and/or *P<sub>c</sub>* result in higher uptake. Similarly, we  
42 report divergences between model-observed seasonal net ecosystem exchange (*NEE*) and  
43 respiration (*Re*) at equatorial locations. By contrast, at the southern Amazon forest (Jarú RJA)  
44 observed declines in *GPP* and *Re* as the dry season progresses are well represented by most LSMs.  
45 While the (1) water-limitation mechanism is described in models and the primary driver of seasonal  
46 photosynthesis in southern Amazonia, we identify other biophysical processes: (2) light harvesting  
47 adaptations (e.g. *LAI* and/or leaf-level assimilation rate increases related to leaf demography); and  
48 (3) allocation schemes (e.g. lags between leaf and wood production) that are poor or absent in  
49 current model formulations. All three mechanisms dominate equatorial Amazon carbon flux  
50 dynamics and are critical for correctly simulating flux seasonality at tropical forests.

51

52 **1. Introduction**

53 Land surface models (LSMs) are the most widely used and appropriate tool for predicting large-  
54 scale responses of vegetation to future climate scenarios. However, to forecast the future of  
55 Amazonia under climate change remains a challenge. The previous generation of LSMs produced  
56 projections of Amazonia's future that diverged widely, with outcomes ranging from large-scale  
57 forest die-back to forest resilience (Betts *et al.*, 2004, 2004; Friedlingstein *et al.*, 2006; Baker *et al.*,  
58 2008). More recent LSMs simulations showed the large-scale die-off scenario to be unlikely (Cox  
59 *et al.*, 2013), given (1) an improved model understanding of forest response to the negative effects  
60 of temperature -previously overestimated and now constrained (Cox *et al.*, 2013); and (2) current  
61 models being forced with updated climate projections (temperature and precipitation) bounded by  
62 observations that no longer demonstrate drastic climate changes in response to rising CO<sub>2</sub> in the  
63 tropics (Cox *et al.*, 2013; Huntingford *et al.*, 2013). Yet tropical forest response to climate change  
64 remains uncertain as models produce varying outcomes (Shao *et al.*, 2013) even without die-off.  
65 Some cutting-edge LSMs projected forest degradation due to future deforestation and increasing  
66 temperature, with catastrophic consequences for the global climate based on climate-carbon cycle  
67 feedbacks (Wang *et al.*, 2013, 2014; Friend *et al.*, 2014), while other LSMs foresaw strong carbon  
68 sinks in these forests due to CO<sub>2</sub> fertilization of photosynthesis (Rammig *et al.*, 2010; Ahlström *et al.*,  
69 2012; Huntingford *et al.*, 2013; Friend *et al.*, 2014). Although the effects of temperature, water  
70 limitation and CO<sub>2</sub> fertilization mechanisms remain uncertain, all LSMs continue to agree that  
71 Amazonian forests play an important role in regulating the global carbon and water cycle (Eltahir &  
72 Bras, 1994; Werth & Avissar, 2002; Wang *et al.*, 2013, 2014; Ahlström *et al.*, 2015).

73

74 Key to reducing uncertainty in LSMs is their systematic evaluation against observational datasets.

75 This exercise enables the identification of model deficiencies through comparison with observed  
76 patterns in ecosystem processes, as well as the mechanisms underpinning such processes (Baker *et*  
77 *al.*, 2008; Christoffersen *et al.*, 2014). Recent model-data evaluations in tropical forests have  
78 focused on the cascade of ecosystem responses to long term droughts (Powell *et al.*, 2013) and the  
79 definition of spatial patterns in productivity and biomass (Delbart *et al.*, 2010; Castanho *et al.*,  
80 2013). However, one important context for model assessment in tropical forests is in the  
81 seasonality of ecosystem water and carbon exchange, as observational datasets reveal axes of  
82 variation in productivity, biomass and/or forest function across space (da Rocha *et al.*, 2009;  
83 Restrepo-Coupe *et al.*, 2013) and/or through time (Saleska *et al.*, 2003; von Randow *et al.*, 2004;  
84 Hutrya *et al.*, 2007; Brando *et al.*, 2010). The most consistent temporal variation in tropical forests  
85 is the seasonality of water, energy, and carbon exchange, since all tropical ecosystems are seasonal  
86 in terms of insolation and a majority experience recurrent changes in precipitation, temperature  
87 and/or day length. Evaluation with respect to seasonality has typically focused on  
88 evapotranspiration (*ET*) (Shuttleworth, 1988; Werth & Avissar, 2002; Christoffersen *et al.*, 2014)  
89 and on net carbon exchange (*NEE*) (Baker *et al.*, 2008; von Randow *et al.*, 2013; Melton *et al.*,  
90 2015). Where models compensated misrepresentations of gross primary productivity (*GPP*) in the  
91 *NEE* balance, by improving or adjusting the efflux term represented by heterotrophic (Melton *et al.*,  
92 2015) or ecosystem respiration (Baker *et al.*, 2008) to available moisture among other strategies.  
93 Only recently have the seasonal dynamics of *GPP* drawn the attention of different groups (De  
94 Weirdt *et al.*, 2012; Kim *et al.*, 2012) and where Kim *et al.* (2012) demonstrated that a consequence  
95 of its incorrect derivation was to overestimate the vulnerability of tropical forests to climate  
96 extremes. Therefore, identifying discrepancies in observed *versus* modeled seasonality in carbon  
97 flux even when seasonal amplitudes are not large -as can be the case for evergreen tropical forests  
98 (see Albert *et al.* (in preparation) for cryptic phenology), can lead to important model developments

99 with significant consequences -to obtain better projections of the fate of tropical ecosystems under  
100 present and future climate scenarios.

101

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

116

117 If the improved representation of the dynamics of leaves and other carbon pools, translates into  
118 more accurate simulations of seasonal *GPP*, *NEE* and/or the long-term carbon budget (De Weirdt  
119 *et al.*, 2012; Kim *et al.*, 2012; Melton *et al.*, 2015), then comparisons between observations and  
120 model derived seasonality of carbon allocation, could provide insight into the mechanistic response  
121 of vegetation to climate and strategies to incorporate them into LSMs. For example, critically  
122 evaluating the seasonality of net primary production of leaves ( $NPP_{leaf}$ ) and wood ( $NPP_{wood}$ ) in

123 tandem with *GPP*, will inform deficiencies in model allocation schemes and carbon pool residence  
124 times. Model net primary production (*NPP*) typically arises from the allocation of photosynthate to  
125 main organs, either as a constant fraction of *GPP* (Kucharik *et al.*, 2006), or according to fixed  
126 allometric rules (Sitch *et al.*, 2003). However, such a view of supply-limited growth has come into  
127 question recently (Würth *et al.*, 2005; Fatichi *et al.*, 2014). Thus as water, temperature, and  
128 nutrients can all impact cell expansion, there may be a temporary imbalance between carbon used  
129 for tissue growth and maintenance respiration *versus* carbon supplied by assimilation  
130 (photosynthesis) (Fatichi *et al.*, 2014). Patterns in seasonality of *GPP*, *NPP<sub>leaf</sub>* and *NPP<sub>wood</sub>*,  
131 therefore, potentially reveal the degree of coupling (or lack thereof) of these two carbon sinks  
132 (*NPP<sub>wood</sub>* and *NPP<sub>leaf</sub>*) with photosynthetic activity (*GPP*). Indeed, Doughty *et al.* (2014) used  
133 bottom-up estimates of the ecosystem carbon-budget at a forest in southwest Amazonia and showed  
134 that components of *NPP* varied independently of photosynthetic supply, which they interpreted in  
135 terms of theories of optimal allocation patterns. While an alternative interpretation of such patterns  
136 could simply refer to biophysical limitations on growth, which vary seasonally (Fatichi *et al.*, 2014),  
137 both studies suggest that modeling allocation as a function of *GPP* will likely fail to capture  
138 observed seasonality. Ground-based bottom-up estimates of primary productivity at a temporal  
139 resolution greater than a year (i.e., seasonal) are difficult if not impossible, principally because there  
140 is no accepted method for estimating whole-tree non-structural carbon (*NSC*) and its variation with  
141 seasons (Würth *et al.*, 2005; Richardson *et al.*, 2015). We proposed coupling co-located top-down  
142 eddy flux estimates of *GPP* with bottom-up *NPP* estimates (*NPP<sub>wood</sub>*, *NPP<sub>leaf</sub>* and *NPP<sub>litter-fall</sub>*) to  
143 circumvent this problem and to obtain a better informed view of the mechanisms (e.g. allocation  
144 schemes) models may incorporate or test against, to improve seasonal simulations of carbon fluxes  
145 and pools.

146

147 The focus of this study was to evaluate, for the first time, modeled seasonal cycles of different  
148 carbon pools and fluxes, including leaf area index (*LAI*), *GPP*, leaf fall, leaf flush, and wood  
149 production, with high resolution eddy flux estimates of *GPP* and ground-based surveys. We  
150 centered our study on a comparison between forests located in the equatorial Amazon (radiation-  
151 and phenology-driven) to a southern forest (driven by water availability) and explored the different  
152 model strategies to incorporate and simulate physical and ecological drivers. Here, we assessed  
153 four state-of-the-art LSMs in active development for use in coupled climate-carbon cycle  
154 simulations in terms of whether they could simultaneously determine patterns of growth and  
155 photosynthesis, thereby getting the ‘right answer for the right reason’. We conclude by proposing  
156 several approaches for improving model formulations and highlight the need for model-informed  
157 field campaigns and future experimental designs.

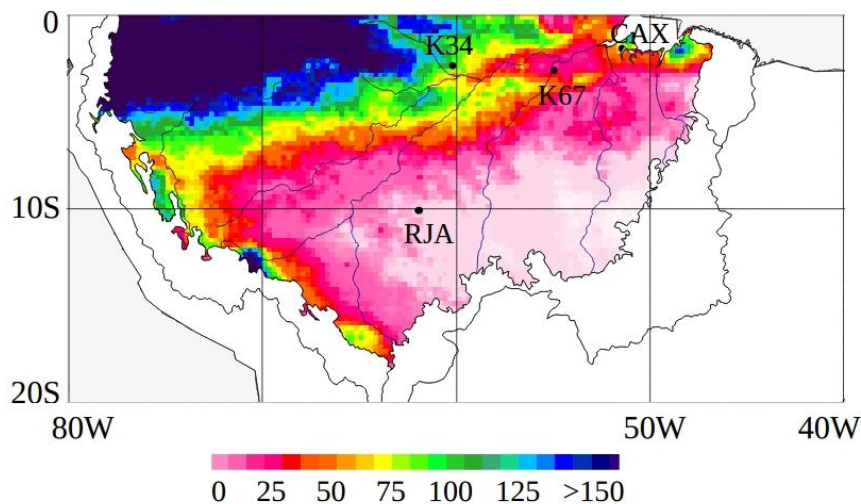
158

## 159 **2. Methods**

### 160 **2.1. Site descriptions**

161 We analyzed data from the Brazil flux network for four tropical forests represented by the southern  
162 site of Reserva Jarú (RJA), and three central Amazonia forests ( $\sim 3^\circ\text{S}$ ) from west to east: the Reserva  
163 Cuieiras near Manaus (K34), the Tapajós National forest, near Santarém (K67), and the Caxiuana  
164 National forest near Belém (CAX) (Fig. 1). For detailed site information see previous works by  
165 Restrepo-Coupe et al. (2013), and de Goncalves et al. (2009; 2013) and individual site publications  
166 (Araújo et al., 2002; Carswell et al., 2002; Malhi et al., 2002; Saleska et al., 2003; Kruijt et al.,  
167 2004; von Randow et al., 2004; Hutryra et al., 2007; da Costa et al., 2010).





168

169 Figure 1. Locations eddy covariance tower study sites at the Amazon Basin *sensu-stricto* (Eva &  
 170 Huber (eds), 2005). Monthly minimum precipitation from the Tropical Rainfall Measuring Mission  
 171 (TRMM) (NASA, 2014) based on an annual composite for the years 1998 to 2014.

172

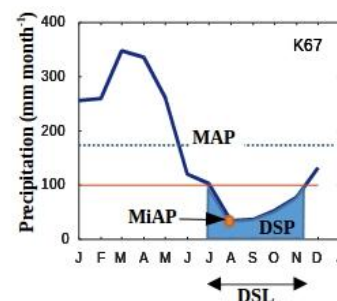
173 All study sites had mean annual precipitation (*MAP*) above 2000 mm year<sup>-1</sup> (Supplement Fig. 1),  
 174 based on the satellite-derived precipitation from the Tropical Rainfall Measuring Mission (TRMM)  
 175 (Huffman *et al.*, 2007; NASA, 2014) 1998-2013 (Table 1). CAX and K34 have *MAP* over 2500  
 176 mm year<sup>-1</sup> (2572 and 2674mm year<sup>-1</sup>, respectively). By contrast, at the southern forest of RJA and  
 177 the equatorial forest of K67 *MAP* was ~2030 mm year<sup>-1</sup>. Moreover, RJA has a 5-month dry season  
 178 length (*DSL*) analogous to two of the central Amazon sites of CAX and K67 (4-month); however,  
 179 longer than K34 site (2-months). Where the dry season was defined as those periods where  
 180 precipitation is less than ~100 mm month<sup>-1</sup>, this threshold corresponded to 80% of the average  
 181 monthly *ET* observed at tropical forests (Sombroek, 2001; da Rocha *et al.*, 2004; Restrepo-Coupe *et*  
 182 *al.*, 2013). RJA and K67 showed similar mean dry-season precipitation (47 mm month<sup>-1</sup> at RJA and  
 183 54 mm month<sup>-1</sup> at K67). However, the annual minimum averaged across the years 1998-2014  
 184 (*MiAP*) at RJA was 14 mm month<sup>-1</sup> compared to a more benign dry season minimum of 37 mm  
 185 month<sup>-1</sup> at K67 (Fig. 1 and Table 1). Despite being located at a latitude further from the equator

186 (10°S) incoming photosynthetic active radiation (*PAR*) at the southern forest of Jarú, was less  
 187 seasonal (low amplitude) if compared to the central Amazon forests (latitude ~3°S) (Fig. 2). At  
 188 RJA, peak top of the atmosphere radiation (*TOA*) was synchronous to the wet season—where we  
 189 expected higher reflectance by clouds decreasing the surface available *PAR* (Fig. 2). All equatorial  
 190 sites sat on highly weathered deep clay soils ( $\geq 10$  m), whereas RJA sat on a lower water storage  
 191 capacity loamy sandy soil and a more shallow and variable profile, with depth to bedrock as  
 192 shallow as 2-3 m (Hodnett *et al.*, 1996; Christoffersen *et al.*, 2014).

193

Site	Latitude	Longitude	Mean annual precipitation <i>MAP</i> [mm/month]	Dry season precipitation <i>DSP</i> [mm/month]	Dry season length <i>DSL</i> [months]	Minimum annual precipitation <i>MiAP</i> [mm/month]
K34	-2.61	-60.21	2674	105	2**	103
CAX	-1.72	-51.53	2572	78	4	60
K67	-2.86	-54.96	2035	54	4	37
RJA	-10.08	-61.93	2031	47	5	14

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



194

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

197

## 198 2.2. Eddy covariance methods

199 At the above-mentioned forests, climate, carbon, energy, water and momentum fluxes were  
 200 measured by the eddy covariance (EC) method. Starting with half-hourly CO<sub>2</sub>-flux data provided  
 201 from each site's operator, we calculated net ecosystem exchange (*NEE* in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), with  
 202 fluxes to the atmosphere defined as positive. *NEE* was then filtered it for low turbulence periods  
 203 ( $u^*_{\text{thresh}}$ ). For a detailed description of instrumentation, applied corrections, quality control  
 204 procedures, and methods for data processing refer to Restrepo-Coupe *et al.* (2013). Gross  
 205 ecosystem exchange (*GEE*) was derived from tower measurements of daytime *NEE* by subtracting

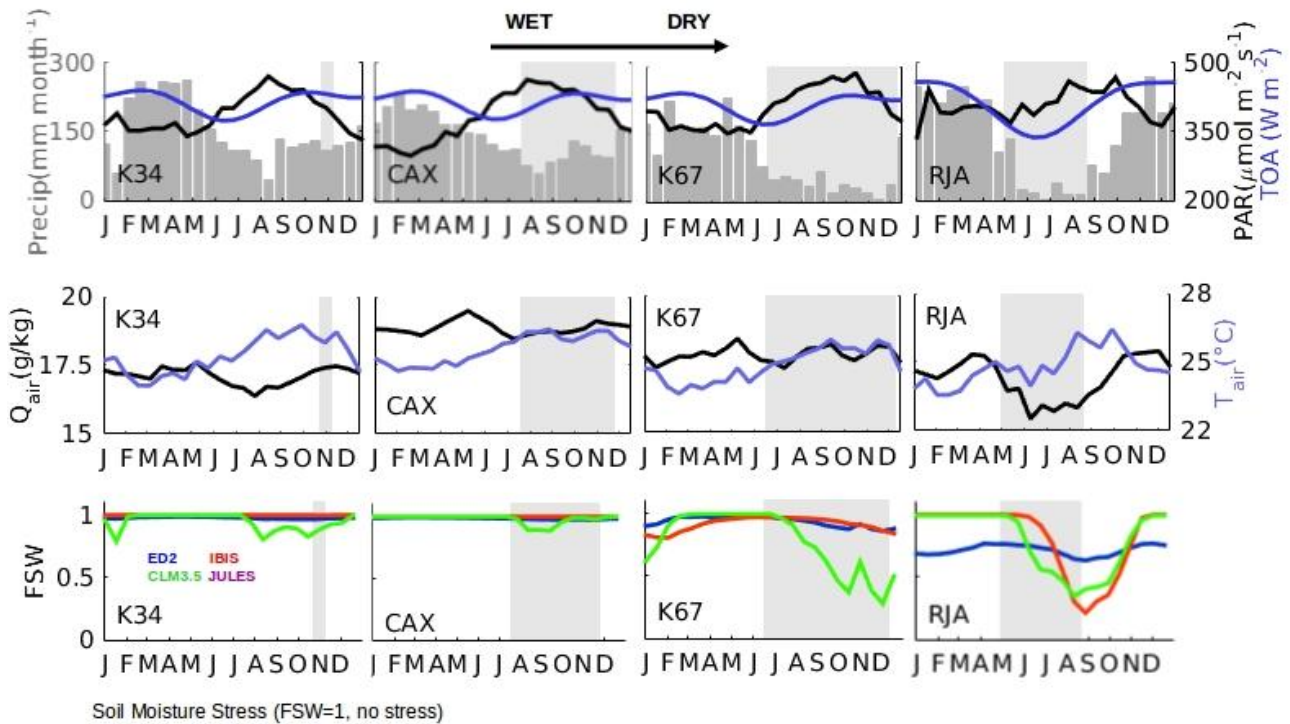
206 estimates of ecosystem respiration ( $R_{eco}$ ), which in turn we derived from the nighttime  $NEE$ . We  
207 assumed daytime  $R_{eco}$  was the same as nighttime  $R_{eco}$ .  $GEE$  is a negative value ( $GEE = NEE - R_{eco}$ )  
208 as generally  $NEE$  is negative in the daytime, and  $R_{eco}$  is positive (meteorological convention). We  
209 expressed ecosystem-scale photosynthesis, or gross ecosystem productivity ( $GEP$ ), as negative  $GEE$   
210 and assumed negligible re-assimilation of metabolic respiration  $CO_2$  within the leaf and  
211 insignificant  $CO_2$  recirculation below the EC system (Stoy *et al.*, 2006). For comparison with  
212 model output, we assumed negligible seasonal changes in photorespiration and used  $GEP$   
213 interchangeably with gross primary productivity ( $GPP$ ).

214

215 We defined ecosystem photosynthetic capacity ( $P_c$ ,  $gC\ m^{-2}\ d^{-1}$ ) as the 16-day average  $GPP$  at a  
216 fixed photosynthetically active radiation ( $PAR$ ) range (site specific daytime mean  $PAR$ ,  $PAR_{avg} \pm$   
217  $100\ \mu mol\ m^{-2}\ s^{-1}$ ) (Supplement Table 1); thus, to remove the effect of day-to-day changes in  
218 available light (e.g. cloudy *versus* clear days), photoperiod, and any other effect of non-optimum  
219  $PAR$  levels. Similarly we used vapor pressure deficit ( $VPD$ ), air temperature ( $T_a$ ) to remove  $GPP$   
220 measures obtained during non-optimum conditions by restricting  $P_c$  calculations to mean daytime  
221  $VPD$  ( $VPD_{avg}$ ) and  $T_a$  ( $T_{a\ avg} \pm$  one standard deviation from their respective time series.  $P_c$   
222 represents the vegetation built capacity to do photosynthesis ( $P_c$  as biophysical driver of  $GPP$ ).  
223 Where at the four study sites, it has been shown that the seasonal pattern of  $P_c$  was independent of  
224 and other climatic variables (Restrepo-Coupe *et al.*, 2013).

225

226 We looked at evapotranspiration ( $ET$ ,  $mm\ d^{-1}$ ) calculated as the latent heat flux ( $LE$ ,  $W\ m^{-2}$ )  
227 measured at the tower multiplied by the latent heat of vaporization ( $\lambda$ ,  $kJ\ kg^{-1}$ ). We developed a  
228 Type II linear model between surface incident short wave radiation ( $SW_{down}$ ,  $W\ m^{-2}$ ) and the  
229 dependent variable,  $ET$ .



231

232 Figure 2. From top to bottom annual cycle of daily average observed climatic variables: incoming  
 233 photosynthetic active radiation ( $PAR$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , black line right y-axis) and precipitation ( $Precip$ ;  
 234  $\text{mm month}^{-1}$ , dark gray bars left y-axis), top of the atmosphere incoming radiation ( $TOA$ ;  $\text{W m}^{-2}$ ,  
 235 blue line right y-axis) (not a driver). From left to right study sites (from wet to dry forest) near  
 236 Manaus forest (K34), Caxiuana forest (CAX), Santarém forest (K67), and Reserva Jarú southern  
 237 forest (RJA). Gray shaded area is dry season as defined using satellite derived measures of  
 238 precipitation (TRMM: 1998-2014). Second row LSM drivers: near surface specific humidity ( $Q_{air}$ ;  
 239  $\text{kg kg}^{-1}$ , black line left y-axis) and temperature ( $T_{air}$ ;  $^{\circ}\text{C}$ , blue line right y-axis). Lower panel depicts  
 240 model ecosystem-scale of model soil moisture “stress” ( $FSW$ , where 1=no stress). Simulations  
 241 from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple).

242

243 From the standard suite of climatic variables available for periods between 1999 and 2006 measured

244 at each EC tower, meteorological drivers for the models were generated. Variables included:  
245  $SW_{down}$ ; air temperature ( $T_{air}$ , °K); near surface specific humidity ( $Q_{air}$ , g kg<sup>-1</sup>); rainfall ( $Precip$ , mm  
246 month<sup>-1</sup>); magnitude of near surface wind ( $WS$ , m s<sup>-1</sup>), surface atmospheric pressure ( $Pa$ , hPa);  
247 surface incident longwave radiation ( $LW_{down}$ , W m<sup>-2</sup>); and a fixed CO<sub>2</sub> concentration ( $CO2_{air}$  at 375  
248 ppm) (de Goncalves *et al.*, 2009) (Fig. 2). Drivers were created for consecutive years where gaps  
249 were no greater than two months. The data was subject to quality control and filled using other  
250 tower measurements (e.g. from a temperature profile), near-by sites and the variables mean monthly  
251 diurnal cycle. We analyzed data for 2000-2005 for K34, 2002-2004 for K67, 2000-2002 for RJA  
252 and 1999-2003 for CAX. We restricted flux and meteorological observations and the calculation of  
253 seasonality to the above-mentioned dates in order to match model drivers and output.

254

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

258

### 259 **2.3.Field measurements**

260 The following vegetation infrastructure descriptors and carbon pools were included on the analysis:  
261 Leaf Area Index ( $LAI$ ): model output was compared to  $LAI$  observations for Caxiuana, CAX as  
262 reported by Metcalfe *et al.* (2007)), and for Santarem, K67 as by Brando *et al.* (2010).  $LAI$  was  
263 normalized from 0 to 1 ( $LAI_{normalized}$ ) for purposes of presentation. Thus, in order to visualize any  
264 changes in  $LAI$ , independent of the observed or modeled absolute value, using Equation 1, where at  
265 time  $i$ ,  $LAI_i$  was adjusted by  $LAI_{min}$  and  $LAI_{max}$  that corresponded to the minimum and maximum  
266 seasonal  $LAI$ , respectively:

$$LAI_{normalized(i)} = \frac{LAI_i - LAI_{min}}{LAI_{max} - LAI_{min}}$$

Equation 1

267

268

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

272

273 Modeled  $NPP_{leaf}$  followed a basic leaf balance model proposed by Restrepo-Coupe et al. (2013).  
 274 Assuming the change in ecosystem  $Pc$  ( $dPc/dt$ ) to be driven by 1) the loss or gain of leaves,  
 275  $NPP_{litter-fall}$  and  $NPP_{leaf}$ , respectively (quantity); and 2) the changes in leaf-level carbon assimilation  
 276 at saturating light ( $SLA \times A_{max}$ ) related to age (quality). Therefore, solving for leaf production we  
 277 obtained:

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

Equation 2

278

279

280 where specific leaf area ( $SLA$ ) values were set to 0.0140 for K67 and CAX (Domingues *et al.*, 2005),  
 281 0.0164  $m^2/gC$  for K34 (Carswell *et al.*, 2002). The  $A_{max}$  was reduced to reach 40% of the mean  
 282 value at the time when leaf-fall reached its maximum (2-month linear gradient). Maximum  $A_{max}$   
 283 was set to 8.66  $gC\ m^{-2}\ d^{-1}$  at K67 (Domingues *et al.*, 2005), and to 7.36  $gC\ m^{-2}\ d^{-1}$  at K34 (Carswell  
 284 *et al.*, 2000) and CAX.

285

286 Wood net primary productivity ( $NPP_{wood}$ ) was based on stem wood increment measurements  
 287 (diameter at breast height, DBH) as reported by Rice et al. (2004) at K67, Chambers et al. (2013) at  
 288 K34, and da Costa et al. (2010) at CAX. No data was available for RJA.

289

## 290           **2.4.Land system models (LSMs)**

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

296

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

304

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

309

310 The Community Land Model-Dynamic Global Vegetation Model version 3.5 (CLM3.5): Is the  
311 predecessor to the current CLM4-CNDV model (Gotangco Castillo *et al.*, 2012), which is the land  
312 component of the Community Earth System Model (CESM). CLM3.5 runs were set using a  
313 prognostic phenology, which incorporated recent improvements to its canopy interception scheme,

314 new parameterizations for canopy integration, a TOPMODEL-based model for runoff, canopy  
315 interception, soil water availability, soil evaporation, water table depth determination by the  
316 inclusion of a groundwater model, and nitrogen constraints on plant productivity (without explicit  
317 nitrogen cycling) (Oleson *et al.*, 2008). The model treated the canopy as a weighted average (by  
318 their respective *LAI*s) of sun and shaded leaves. The leaf phenology subroutine of this model for  
319 tropical forests applied only to the Broadleaf Deciduous Tree (BDT) PFT fraction (“raingreen”  
320 PFT), but all CLM3.5 simulations reported here were >95% tropical Broadleaf Evergreen Tree  
321 (BET) fractional PFT cover. The allocation scheme for this model dictated that leaf turnover for the  
322 tropical BET (at a rate of  $0.5 \text{ yr}^{-1}$ ) be replaced instantaneously with new leaf production to maintain  
323 fixed allometric relationships (Sitch *et al.*, 2003); therefore, seasonality of *LAI* was not possible for  
324 these simulations.

325

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

332

333 Model output followed the LBA-Data Model Intercomparison Project (LBA-DMIP) protocol (de  
334 Goncalves *et al.*, 2009); however, it includes some additional variables related to water limitation  
335 (e.g. soil water availability factor or soil water “stress”), land use change (e.g. additional carbon  
336 pools), and disturbance (e.g. mortality) (Powell *et al.*, 2013). Here, we present soil water “stress”  
337 (*FSW*) values, calculated following Ju *et al.* (2006). By definition *FSW* ranging from 0 to 1 is a



338 measure of the water available to roots, where  $FSW=1$ , is no stress.

339

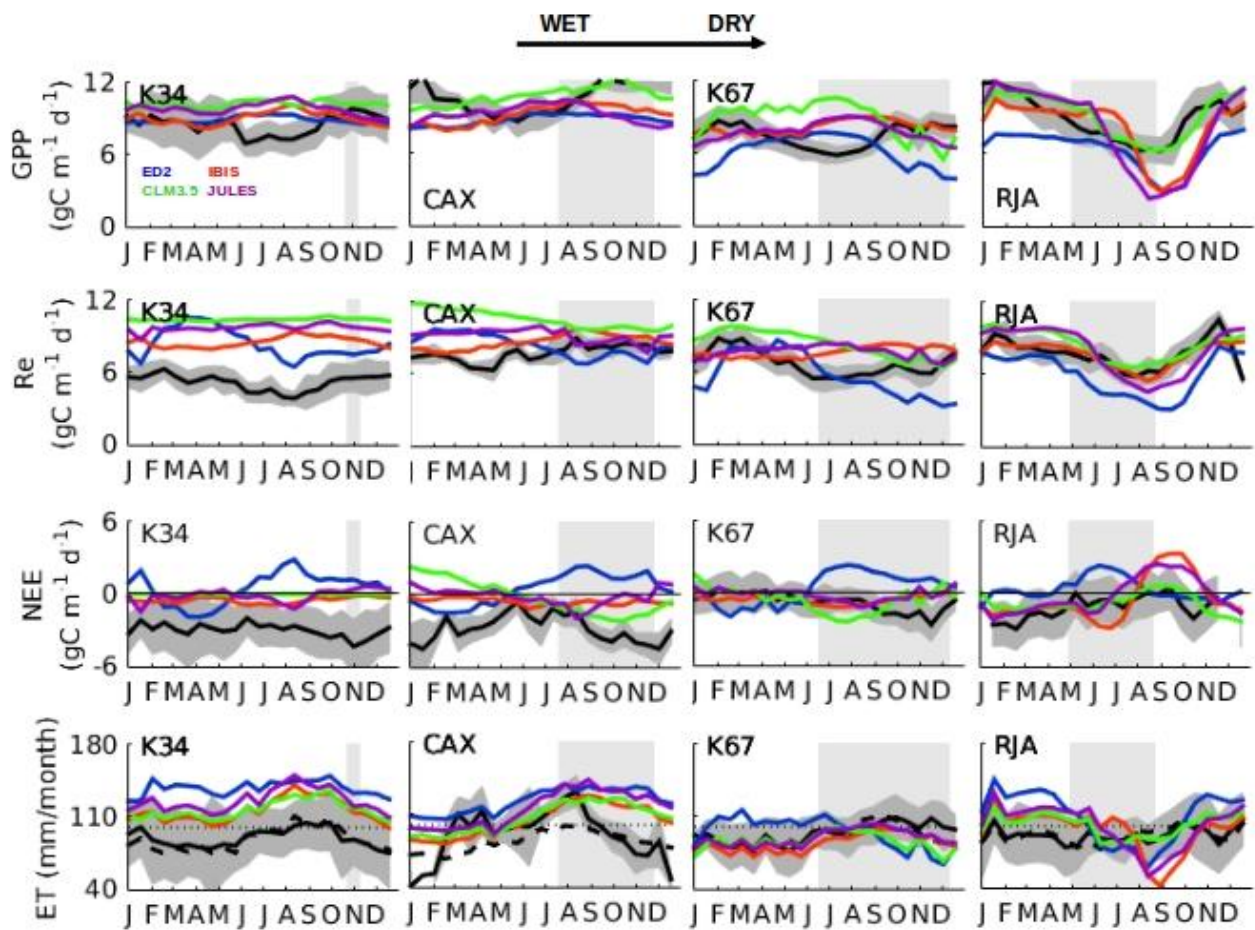
### 340 3. Results

#### 341 3.1. Gross primary productivity (*GPP*) and ecosystem photosynthetic capacity (*Pc*)

342 The observed annual cycle of ecosystem-scale *GPP* showed two divergent patterns: (1) increasing  
343 levels of photosynthetic activity (*GPP*) as the dry season progresses in the equatorial Amazon (K34,  
344 K67 and CAX) where *MiAP* was 60 and 36 mm month<sup>-1</sup>, respectively, and maximum radiation was  
345 synchronous with low precipitation; and (2) declining productivity as the dry-season advanced in  
346 the southern forests (RJA) where radiation was somewhat aseasonal and *MiAP* was less than half its  
347 central Amazon counterparts (14 mm month<sup>-1</sup>) (Fig. 1). By contrast, at all sites, model simulations  
348 showed peak *GPP* seasonality at the end of wet season with declining *GPP* during the dry season  
349 (Fig. 3). The reduced dry season *GPP* observed at the southern Amazon forest of Jarú (RJA) was  
350 consistent with increasing degrees of water limitation. At the sites in the equatorial Amazon (K34,  
351 K67 and CAX), modeled soil water “stress” (*FSW*; Fig. 2) (where  $FSW=1$ , no stress) acted to  
352 reduce model *GPP* during the dry season, even as observed *Pc* increased following higher levels of  
353 incoming solar radiation (*PAR*; Fig. 2 and *Pc*; Fig. 4). Similar to *GPP*, models tended to achieve  
354 good *Pc* representation at RJA. However, simulated *Pc* at the equatorial Amazon forest sites  
355 remained unchanged (IBIS and JULES) or decreasing gradually from the middle of the wet season  
356 to the end of the dry period at K67 (ED2 and CLM3.5) (Fig. 4).

357

358



359

360 Figure 3: Annual cycle of daily average ecosystem-scale photosynthesis ( $GPP$ ;  $gC\ m^{-2}\ d^{-1}$ ),  
 361 ecosystem respiration ( $R_e$ ;  $gC\ m^{-2}\ d^{-1}$ ) net ecosystem exchange ( $NEE$ ;  $gC\ m^{-2}\ d^{-1}$ ) and  
 362 evapotranspiration ( $ET$ ;  $mm\ d^{-1}$ ) near Manaus forest (K34), Caxiuaná forest (CAX), Santarém forest  
 363 (K67), and Reserva Jarú southern forest (RJA). Observed (black + dark gray uncertainty) and  
 364 simulated by models (colors). Dashed black line at ET panels corresponds to a linear model where  
 365 the independent variable is incoming radiation ( $SW_{down}$ ). Gray shaded area is dry season as defined  
 366 using satellite derived measures of precipitation (TRMM: 1998-2014). Simulations from ED2  
 367 (blue), IBIS (red), CLM3.5 (green), and JULES (purple). Observations from the Brasil flux network.  
 368  
 369  $FSW$  reached an all-site minimum at RJA by the end of the dry season (Fig. 2) and corresponded  
 370 with a decrease in model  $ET$  not seen on the EC measurements (Fig. 3). With the exception of CAX,

371 seasonal observations of  $ET$  at all of the sites showed very little seasonality and remained close to  
372  $120 \text{ mm month}^{-1}$  ( $4 \text{ mm d}^{-1}$ ). In general, models were able to capture the seasonality of  $ET$ ;  
373 however, they overestimated the dry-period reduction in water exchange at RJA and in the case of  
374 K34 and CAX overestimated  $ET$  absolute values. By contrast, a very simple linear regression  
375 driven by  $SW_{down}$  was able to represent  $\sim 83\%$  of the seasonality of  $ET$  (Fig. 3).

376

### 377 **3.2 Carbon allocation**

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

383

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

390

391 In the field, leaf litter-fall plays an important role in determining the seasonality of  $LAI$ ,  $P_c$  (as per  
392 Equation 2), heterotrophic respiration and soil carbon pools. Data for the central Amazon forests  
393 showed a highly seasonal leaf-fall cycle (Chave *et al.*, 2010), with an  $LAI$  maximum at the  
394 beginning of the dry season at CAX and in the middle of the dry period at K67 (Fig. 4). At

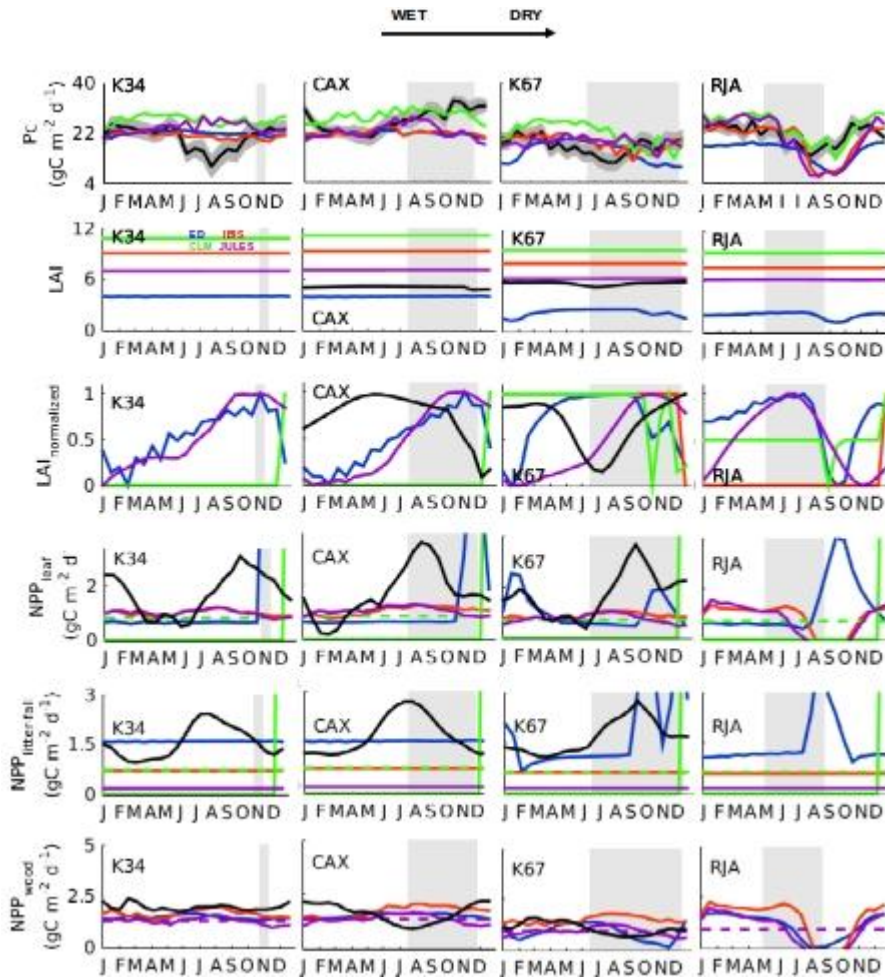
395 equatorial sites, peak litter-fall corresponded to a maximum in  $SW_{down}$ , where we observed a  
396 statistically significant linear regression between  $SW_{down}$  and  $NPP_{litter-fall}$  with a coefficient of  
397 determination,  $R^2$  equal to 0.34 at K34, 0.21 at K67, and 0.6 at CAX ( $p < 0.01$ ) (Supplement Fig. 2).  
398 With the exception of ED2, which included a drought-deciduous phenology and consequentially  
399 seasonal variations in leaf abscission, seasonality in  $NPP_{litter-fall}$  was not resolved in most LSMs (Fig.  
400 4).

401

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

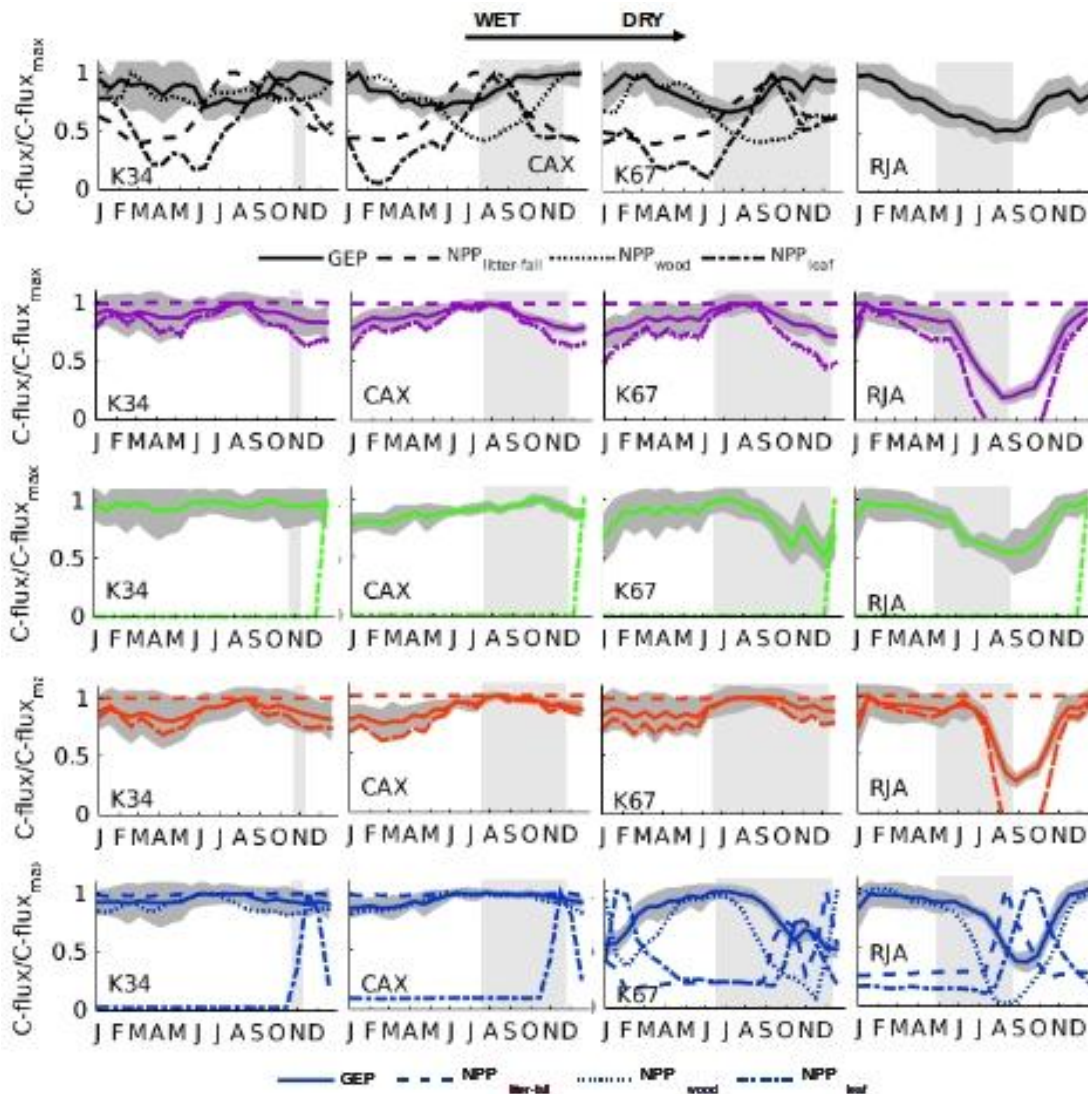
408

409 In contrast to  $NPP_{leaf}$ ,  $NPP$  allocation to wood growth ( $NPP_{wood}$ ) was aseasonal at K34; however at  
410 K67 peaked during the wet season, displaying opposite seasonality and being out-of-phase with  
411  $NPP_{leaf}$ . This pattern seemed to be different at CAX, with both  $NPP_{leaf}$  and  $NPP_{wood}$  maximum  
412 during the dry season, at this site precipitation was significantly seasonal (wet season was the  
413 rainiest of all equatorial sites) and the amplitude of the seasonal cycle of  $SW_{down}$  was the highest of  
414 all Brasil flux central Amazon locations. By contrast, models simulated a peak in  $NPP_{wood}$  at CAX  
415 and K67 that corresponded to the beginning of the dry season. The seasonality of model  $NPP_{wood}$   
416 was absent at the three equatorial forests and only significant differences between the wet and dry  
417 periods were observed at RJA, where all simulations showed minimum  $NPP_{wood}$  at the end of the  
418 dry season.



419

420 Figure 4. From top to bottom annual cycle of daily average ecosystem photosynthetic capacity ( $P_c$ ,  
 421  $GPP$  at a fixed  $PAR$  range  $725-875 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Leaf Area Index ( $LAI$ ;  $\text{m}^2 \text{m}^{-2}$ ), normalized  $LAI$  (its  
 422 value constrained between 0 and 1 in order to better track its changes), net primary productivity  
 423 ( $NPP$ ;  $\text{m}^{-2} \text{d}^{-1}$ ) allocated to leaves -leaf flush ( $NPP_{leaf}$ ;  $\text{m}^{-2} \text{d}^{-1}$ ),  $NPP$  allocated to litter-fall ( $NPP_{litter-}$   
 424  $fall$ ;  $\text{gC m}^{-2} \text{d}^{-1}$ ). Gray shaded area is dry season as defined using satellite derived measures of  
 425 precipitation (TRMM: 1998-2014). Lower row  $NPP$  allocated to wood ( $NPP_{wood}$ ;  $\text{gC m}^{-2} \text{d}^{-1}$ ).  
 426 From left to right study sites (from wet to dry forest) near Manaus forest (K34), Caxiuaná forest  
 427 (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). Observed (black) versus  
 428 simulated by models (colors). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and  
 429 JULES (purple). Dashed green lines (CLM3.5) at  $NPP_{litter-fall}$  and  $NPP_{leaf}$ , indicate average values  
 430 for comparison purposes (models allocated at the end of the year as indicated by continuous line).



431

432 Figure 5. From left to right study sites (from wet to dry forest) near Manaus forest (K34), Caxiuanã  
 433 forest (CAX), Santarém forest (K67), and Reserva Jarú southern forest (RJA). From top to bottom,  
 434 annual cycle observed (black) and model simulations from JULES (purple), CLM3.5 (green), IBIS  
 435 (red), and ED2 (blue). Normalized (by its seasonal maximum) annual cycle of daily average  
 436 ecosystem-scale photosynthesis ( $GPP/GPP_{max}$ ) (continuous line), net primary productivity ( $NPP$ )  
 437 allocated to leaves -leaf flush ( $NPP_{leaf}/NPP_{leaf,max}$ ),  $NPP$  allocated to litter-fall ( $NPP_{litter-fall}/NPP_{litter-  
 438 fall,max}$ ), and  $NPP$  allocated to wood ( $NPP_{wood}/NPP_{wood,max}$ ). Gray shaded area is dry season as  
 439 defined using satellite derived measures of precipitation (TRMM: 1998-2014).

440

441

442 Our analysis shows a statistically significant negative linear regression between  $SW_{down}$  and  $NPP_{wood}$   
443 with a coefficient of determination,  $R^2$  equal to 0.45 at K67 and 0.62 at CAX ( $p < 0.01$ ) (Supplement  
444 Fig. 3). Non-significant correlation was found between  $SW_{down}$  and  $NPP_{wood}$  or precipitation and  
445  $NPP_{wood}$  at K34 -the wettest and least seasonal of the four studied forests.

446

447 Seasonal observations of the different  $NPP$  components and  $GPP$  showed a lack of temporal  
448 synchrony between them, neither a shared allocation pattern among forests –each exhibiting  
449 different phenology (Fig. 5). At some sites (CAX and K67), there was a statistically significant  
450 correlation ( $\sim 1$  to 2-month lag,  $NPP_{leaf}$  ahead) between  $GPP$  and  $NPP_{leaf}$  (Supplement Fig. 5).  
451 However, there was no temporal correspondence between  $GPP$  and  $NPP_{wood}$ . By comparison,  
452 model allocation ( $NPP_{leaf}$ ,  $NPP_{litter-fall}$  and  $NPP_{wood}$ ) and  $GPP$  was coupled at most models (Fig. 5).

453

### 454 **3.2 Ecosystem respiration ( $R_e$ ) and net ecosystem exchange ( $NEE$ )**

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

464

#### 465           4.       **Discussion**

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

477

#### 478 **4.1 Seasonality of gross primary productivity ( $GPP$ ), and other carbon fluxes**

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

487

488 Satellite phenology studies have shown annual precipitation values and the length of the dry season



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

503

#### 504 **4.2 Carbon allocation strategies**

505 Models include *LAI* in the vegetation dynamics module using a variety of strategies: (1) prescribed  
506 *LAI* values from remote sensing sources; (2) dynamic calculation of daily *LAI*; and (3) *LAI* is fixed  
507 and the model later allocating any changes at the end of the year, thus only to calculate changes in  
508 the carbon balance and next year *LAI* values. This last approach may need to be re-evaluated given  
509 the importance of phenology as an ecosystem productivity driver. Models that dynamically  
510 calculate *LAI* generally rely in defining *LAI* range values for each PFT (Clark *et al.*, 2011), where  
511 the actual value will depend mostly on the phenological status of the vegetation type – a function of  
512 temperature. Although some evergreen ecosystems do respond to temperature thresholds (e.g.

513 positive correlation between  $T_{air}$  and  $LAI$  and a threshold at  $T_{air}>0$  has been identified for conifer  
514 forests at temperate areas (Khomik *et al.*, 2010)),  $LAI$  and  $P_c$  at tropical ecosystems do exhibited a  
515 negative or no correlation with  $T_{air}$ . Moreover, model  $LAI$  values were unreasonably 2+ units above  
516 observed values (Baldocchi *et al.*, 1988; Gower *et al.*, 1999; Asner *et al.*, 2003; Sakaguchi *et al.*,  
517 2011). Some models assumed  $LAI$  value above six, the theoretical limit of  $LAI$  (assuming no  
518 clumping and planar leaf angle distribution) according to Beer's law. Similar to previous findings  
519 by Christoffersen *et al.* (2014) regarding model performance when simulating water fluxes, some of  
520 the model deficiencies could be resolved by changing the parameterization of each PFT, such as the  
521 case of maximum and minimum  $LAI$  values. However, a true improvement will only come if we  
522 increase the frequency and coverage of our measurements, and a better understanding of the carbon  
523 allocation, mechanisms that control the change in  $LAI$ , and the balance between loss due to  
524 abscission, leaf production, and other ecosystem processes.

525

526 In the observations,  $P_c$  values increased during the dry season at all central Amazon sites. Elevated  
527  $P_c$  can be achieved through leaf flush, as younger leaves have higher leaf carbon assimilation at  
528 saturating light ( $A_{max}$ ) compared to old leaves (Wu *et al.*, submitted; Sobrado, 1994), or by changes  
529 in leaf herbivory, *epiphyllous* growth, and stress, among other factors. Alternatively,  $P_c$  can be  
530 increased through a surge in canopy infrastructure (quantity of leaves) measured as leaf area index  
531 ( $LAI$ ) (Doughty & Goulden, 2008). Our observations suggested a combination of these two  
532 processes or  $P_c$  mostly driven by the presence of younger leaves, as we observed a small increase in  
533  $LAI$  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,  
534 respectively. In order to address the relationship between leaf demography (leaf age distribution)  
535 and carbon fluxes, we presented the seasonality of *in situ* observations of  $NPP_{leaf}$  and compared it to  
536 model estimates. We have shown that, at the equatorial Amazon estimated  $NPP_{leaf}$  was

537 synchronous with the seasonality of  $SW_{down}$ . Thus, increasing light may trigger new leaf production  
538 as part of a light-based growth strategy missed by the models evaluated here. Some vegetation  
539 schemes have introduced a time-dynamic carbon allocation: to leaves, generic roots, coarse and fine  
540 roots, etc. However, even if models assign  $NPP_{leaf}$  varying turnover time from 243 days to a  
541 maximum of 2.7 years, the timing of leaf production seems to be missed. The counterintuitive  
542 mechanism observed at some central Amazon forests where all or most of the leaf-demography  
543 processes (leaf-fall, leaf-flush and  $LAI$ ) increase during the dry season, constitutes an important  
544 challenge for modelers and plant physiologists. An appropriate model representation and further  
545 studies are required of: (1) the leaf lifespan, (2) the seasonality of leaf age distribution (e.g. sun and  
546 shade leaf cohorts: young, mature, old), (3) the effect of leaf-fall on increasing light levels at lower  
547 layers of the canopy, and (4) the relationship between leaf age and physiology (Albert *et al.*, in  
548 preparation), to properly characterize Amazon basin leaf phenology and associated changes in  
549 productivity. Thus, as a homogeneous age cohort where all leaves have similar ability to assimilate  
550 carbon can contribute to the model simulated aseasonal  $P_c$  and  $GEP$  seasonality driven only by  
551 water availability.

552

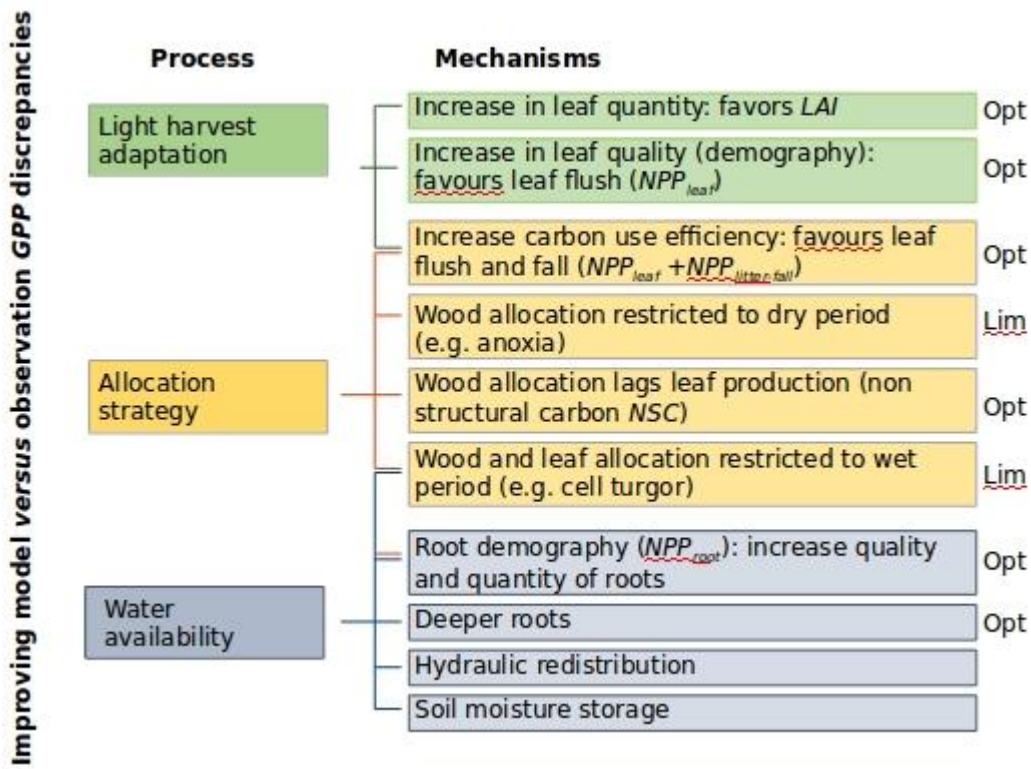
553 Previous studies have linked the robustness of models predictions of the terrestrial ecosystem  
554 carbon response to climate change projections to the uncertainty of the different carbon pools within  
555 the models (Ahlström *et al.*, 2012). Observations show that the seasonality of allocation (e.g.  
556  $NPP_{litter-fall}$ ) and leaf-demography (e.g.  $NPP_{leaf}$ ) are closely related to the fast and slow soil carbon  
557 pools (input) and ecosystem respiration. Decomposition of  $NPP_{litter-fall}$  initiates the transfer of  
558 carbon to the soil microbial and the slow and passive pools in many models and determines  
559 heterotrophic respiration. Similarly, autotrophic respiration (maintenance and growth) also will be  
560 driven by live tissue allocation ( $NPP_{wood}$ ,  $NPP_{leaf}$ , and  $NPP_{roots}$ ). Therefore,  $R_{eco}$  will depend on a

561 well-characterized phenological response of litter and woody debris, wood and leaf accumulation,  
562 and the soil carbon pools. Still, in some models and according to a set of prescribed allometric  
563 relationships for each PFT where leaves, fine roots and stems  $NPP$  are allocated at the end of each  
564 simulated year. Thus, to improve simulation-data agreement and to generate reliable projections for  
565 ecosystem response to climate perturbations, the next generation of models must include a basic  
566 mechanistic understanding of the environmental controls on ecosystem metabolism that goes  
567 beyond correlations (e.g.  $NPP_{leaf}$  versus  $SW_{down}$ ,  $NPP_{litter\ fall}$  versus  $Precip$ ) and addresses the long  
568 time adaptation to climate and their seasonality. We highlight the need for extended EC  
569 measurements accompanied by seasonal based biophysical inventories, as both datasets  
570 complement and inform each other.

571

572 The seasonal patterns in seasonal  $GPP$  and  $NPP$  (leaf and wood); show to be (1) aseasonal at K34;  
573 (2) synchronous at CAX; and (3) out-of-phase at K67. The  $GPP$ ,  $NPP_{leaf}$  and  $NPP_{wood}$  dry-season  
574 maxima at CAX may be interpreted in terms of a combination of mechanisms: (1) optimal  
575 allocation patterns (Doughty *et al.*, 2014) -- in sync photosynthetic activity and carbon allocation  
576 driven by dry-season light increases; and (2) reflect biophysical limitations (Fatichi *et al.*, 2014) --  
577 wet season anoxia, drive both leaves and wood to be produced during the dry season. Similar to  
578 CAX, observations of a simultaneous increase in  $NPP_{leaf}$  and  $NPP_{wood}$  during the dry season have  
579 been reported at seasonally inundated floodplain tropical forests, where anoxia limits respiratory  
580 requirements of  $NPP_{wood}$  and show peak  $NPP_{wood}$  shifted into the dry season (Dezzeb *et al.*, 2003).  
581 Consistently, seasonal observations at flooded forests showed reduced production of new leaves and  
582 lower photosynthetic assimilation during the inundation period (Parolin, 2000). By comparison, the  
583  $NPP_{wood}$  patterns observed at K67 where dry-season  $MiAP$  is  $\sim 50\%$  of mean annual  $ET$  may reflect  
584 biophysical limitations on the sink tissue (e.g. cell turgor and cell division in cambial tissues) --

585 water availability as a driver (Wagner *et al.*, 2012; Rowland *et al.*, 2013), or/and an allocation  
 586 strategy that favors  $NPP_{leaf}$  to  $NPP_{wood}$ . At K67 and K34 forests, the timing of  $GPP$  versus  $NPP_{wood}$   
 587 highlights the importance of  $NSC$  (Fatichi *et al.*, 2014) and difficulties faced by more mechanistic  
 588 LSMs.



589  
 590 Figure 6. Ecosystem response to climate seasonality □ selection of biological adaptive mechanisms:  
 591 light harvest adaptations (green tones), allocation strategies (orange tones), and water limitation  
 592 (blue tones). Mechanisms classified when possible into resource optimization (Opt) and biophysical  
 593 limitations (Lim).

594  
 595 **4.3 Final considerations for model improvement**

596 This study identified three main tropical forest responses to climatic drivers that if understood could  
 597 reduce the model – observation  $GPP$  discrepancies. These are (1) light harvest adaptation schemes;  
 598 (2) response to water availability; and (3) other allocation strategies (Fig. 6). We propose thorough

599 (1) optimization patterns and (2) thresholds (limitation) to obtain the seasonality of the different  
600 carbon pools. For example, models could incorporate some of the recent findings: (1) leaf  
601 demography as a function of light environment as in Wu et al. (submitted), and (2) leaf phenology  
602 (greenness) seasonal patterns driven by soil moisture availability as a function of *MAP* threshold as  
603 in Guan et al. (2015). However, less has been reported about other processes and reservoirs  
604 different than  $NPP_{leaf}$ . In particular, our study lacks belowground information, as data that explores  
605 the seasonality of root allocation at tropical sites is scarce and difficult to interpret. Future work  
606 should address this important carbon-pool and the correspondent model ability to simulate the  
607 seasonality of belowground processes.

608

609 Climate models have come a long way, from the 1970 when the first land surface scheme was  
610 introduced in order to represent the atmosphere-biosphere interaction by partitioning ocean from  
611 dry land (Manabe & Bryan, 1969). Simulations of water, energy and carbon fluxes based on the  
612 response of different plant functional types to climate drivers and disturbance signifies a great step  
613 forward on weather prediction and the study of future climates under the effect of land cover  
614 changes and atmospheric CO<sub>2</sub> enrichment (Pitman, 2003; Niu & Zeng, 2012). Models are  
615 constrained in their development given the high computational needs and the multiple processes  
616 that need to be accounted for on a three dimensional grid from *LAI* seasonality, to ground water flux,  
617 to leaf level parameterization, there is a tradeoff and a “priority list”. This study highlights some of  
618 the advances in tropical forest simulations of carbon and water fluxes and aims to identify future  
619 opportunities, as the inclusion of light harvesting and allocation strategies in an attempt to improve  
620 *GPP* and *NPP* predictions.

621

## 622 5. Conclusions

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

636  
637 We explore different ESM approaches to track the phenology of carbon allocation, in particular  
638 measures of plant metabolism ( $P_c$  as proxy), standing biomass (wood increment and leaf-flush) and  
639 additions to soil organic matter (leaf-fall) in an attempt to understand the model-data discrepancies  
640 on the estimates of  $GPP$  and  $NEE$ . We are able to identify the seasonality of net primary  
641 productivity allocated to litter-fall ( $NPP_{litter-fall}$ ) and leaf production ( $NPP_{leaf}$ ) and the total balance  
642 (leaf area index,  $LAI$ ) as key biological drivers, which if understood (mechanisms and vegetation  
643 response) and properly implemented, could improve model predictions. In particular, *in situ*  
644 observations show that at the central Amazon estimated  $NPP_{leaf}$  is synchronous with the seasonality  
645 of incoming solar radiation, a light-based growth strategy missed by most of models. Similarly, the

646 seasonality of *LAI* at tropical forests seems underestimated and the mechanisms that control the  
647 change in *LAI* and the balance between loss of capacity due to  $NPP_{litter-fall}$  and increase of capacity  
648 from  $NPP_{leaf}$ , not well understood. The counterintuitive leaf-demography process observed at some  
649 equatorial Amazon sites ( $NPP_{litter-fall}$  versus  $NPP_{leaf}$ ) where *Pc* and/or *LAI* increased during the dry  
650 season, and the here reported lags between *GPP* and  $NPP_{wood}$ , challenge Amazon basin model  
651 phenology representations. As fluxes are not exclusively driven by meteorology, incorporating this  
652 key biological adaptive mechanisms into ESMs is an important task in order to advance our  
653 understanding of tropical vegetation-climate feedbacks.

654

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666

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