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**The Importance of Physiological, Structural and Trait**

**Responses to Drought Stress in Driving Spatial and Temporal**

**Variation in GPP across Amazon Forests Leaf Area Index**

**Changes Explain GPP Variation across an Amazon Drought**

**Stress Gradient**

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**Commented [FS1]:** R1 AR3. In response to the reviewers comment “The title Leaf Area Index Changes Explain GPP variations across an Amazon Drought Stress Gradient is not surprising as LAI generally scales well with GPP, and hence you would expect the changes to do so as well. Moreover, as also stated in the manuscript, the changes of LAI are affected by drought stress, and thus it is indirectly the drought stress that is causing the variation in GPP. Lastly, the title does not fully cover all three research questions made by the authors in the manuscript, although it points towards your most interesting finding. However, I would suggest that you reconsider the title.”

The authors put forward an alternative title ‘The importance of physiological, structural and trait responses to drought stress in driving spatial and temporal variation in GPP across Amazon forests’. Or simplified to ‘The mechanisms driving spatial and temporal variation in GPP across an Amazon drought stress gradient’.

## Abstract

The capacity of Amazon forests to sequester carbon is threatened by climate change-induced shifts in precipitation patterns. However, the relative importance of plant physiology, ecosystem structure, and trait composition responses in determining variation in ~~gross primary productivity (GPP)~~, remain largely unquantified, and vary among models. We evaluate the relative importance of key climate constraints to ~~gross primary productivity (GPP)~~, comparing direct plant physiological responses to water availability and indirect structural and trait responses (via changes to leaf area index (LAI), roots and photosynthetic capacity). To separate these factors we combined the Soil-Plant-Atmosphere model with forcing and observational data from seven intensively studied forest plots along an Amazon drought stress gradient. We also used machine learning to evaluate the relative importance of individual climate factors across sites. Our model experiments showed that variation in LAI was the principal driver of differences in GPP across the gradient, accounting for 33% of observed variation. Differences in photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ) accounted for 21% of variance, and climate (which included physiological responses) accounted for 16%. Sensitivity to differences in climate was highest where shallow rooting depth was coupled with high LAI. On sub-annual timescales, the relative importance of LAI in driving GPP increased with drought stress ( $R^2=0.72$ ), ~~coincident with decreased whilst the~~ importance of solar radiation ~~decreased~~ ( $R^2=0.90$ ). Given the role of LAI in driving GPP across Amazon forests, improved mapping of canopy dynamics is critical, opportunities for which are offered by new satellite-based remote sensing missions such as GEDI, Sentinel and FLEX.

Keywords: Canopy Dynamics, Leaf Traits, Tropical Rainforests, Precipitation, Gross Primary Productivity

**Commented [FS2]:** R1 AR32. In response to reviewer comment "Line 32 Abbreviate GPP in line 32, not line 34"

**Commented [FS3]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

## 1. Introduction

As the entry point for carbon into the biosphere, gross primary productivity (GPP) is central to the global carbon cycle. Tropical rainforests alone account for one third of total terrestrial ~~photosynthesis~~ GPP, assimilating ~41 Pg of carbon each year (Beer et al., 2010). Carbon fluxes across the tropics are tightly coupled to climate, and water availability is a principal driver of spatial and temporal variation in ~~photosynthesis-GPP~~ (Fisher et al., 2007, Von Randow et al., 2013, Beer et al., 2010, Malhi et al., 2015, Guan et al., 2015). Across Amazon forests, GPP decreases linearly with increasing seasonal water deficit (Malhi et al., 2015). Shifts in precipitation patterns as a result of anthropogenic climate change are predicted to have a major impact on Amazon GPP (Phillips et al., 2009, Malhi et al., 2008, Meir and Woodward, 2010, Zhang et al., 2015, Meir et al., 2015a). Longer and more intense dry seasons are projected, together with an increased frequency and severity of drought events (Joetzjer et al., 2013, Boisier et al., 2015, Duffy et al., 2015). Given the biogeochemical influence of Amazon forests at regional and global scales (Liu et al., 2017), accurately predicting GPP response to drought stress is critical.

Dynamic global vegetation models (DGVMs) disagree on the effects of projected precipitation change on Amazon carbon dynamics. Galbraith et al. (2010) found future shifts in precipitation patterns had little effect on model estimates of biomass change (for two of the three models tested), reflecting poorly the observed sensitivity of Amazon forests to water availability illustrated by through-fall exclusion experiments and natural drought events (Rowland et al., 2015a, Nepstad et al., 2007, Phillips et al., 2009). Substantial progress has been made in model development to capture the impact of drought stress on plant physiology. By coupling stomatal conductance and plant hydraulic theory, models have proved better able to predict ecosystem functioning and mortality (Eller et al., 2018, Fisher et al., 2018, Fisher et al., 2006, Fisher et al., 2007, Bonan et al., 2014). However, the interactions between drought stress, ecosystem structure (e.g. canopy dynamics and rooting depth) and trait composition (e.g.  $V_{cmax}$ ,  $J_{max}$ , leaf lifespan and leaf mass per unit area (LMA)), are typically absent from models, despite having a

**Commented [FS4]:** R2 AR1. In response to the reviewers comment “- In a few instances, which I will describe below, I found the formulation of sentences vague.” Edited in accordance with specific comments

**Commented [FS5]:** R1 AR2. In response to the reviewers comment “Throughout the manuscripts, your hypothesis/conclusions are repeated (abstract, introduction, discussion, and conclusion). This takes up a lot of space that could otherwise have been used elsewhere in the manuscript. Therefore, I urge you to delete several of these repeated paragraphs. Please see the specific comments below for my suggestions.”

The repetition of hypotheses and conclusions has been revised as per the specific comments (see AR7, AR8, AR13 and AR17).

major impact on simulated GPP (Fauset et al., 2012, Sakschewski et al., 2016, Lee et al., 2013).  
Furthermore, changes in canopy dynamics have been identified as a likely cause for the disparity  
85 between field observations and model predictions (Restrepo-Coupe et al., 2017, Powell et al., 2013).

The relative importance of plant physiology, ecosystem structure, and trait composition responses in  
determining variation in GPP, remain largely unquantified in data-constrained analysis (Meir et al.,  
2015b). Plant physiological responses to drought stress include stomatal conductance, which is limited  
by water availability and atmospheric demand. Stomatal conductance constrains GPP via changes in  
90 CO<sub>2</sub> supply, but is considered a short (varying on sub-hourly timescales), rather than long-term response

to climate forcings (Sperry et al., 2002). ~~Changes to both ecosystem structure and traits, such as leaf  
area index (LAI), rooting depth and carboxylation capacity, are expected to be more  
longstanding~~ ~~Changes to ecosystem structure and traits, such as LAI, rooting depth and carboxylation  
capacity, are expected to be more longstanding~~ (Meir et al., 2015a).

95 Extensive evidence links spatial and temporal variation in drought stress with ecosystem structure  
~~(across sub-annual and annual timescales). Leaf area index (LAI) typically decreases with increasing  
drought stress (Iio et al., 2014, Meir et al., 2015b, Brando et al., 2008, Grier and Running, 1977, Wright  
et al., 2013). LAI determines the surface area for GPP, impacting light capture capacity. Across the  
wet-dry tropical forest transition, LAI declines on average ~1.4 m<sup>2</sup>m<sup>-2</sup> (Iio et al., 2014). Brando et al.  
100 (2008) report a 21-26% decline in LAI following five years of drought onset at the Amazon throughfall  
exclusion experiment at Tapajós National Forest, Pará, Brazil. Growth of nNear surface root mass,  
length and surface area decline with seasonal drought stress (and increase during periods of high soil  
water availability to exploit available resources), whilst deep roots can support water supply during dry  
periods (Nepstad et al., 1994, Metcalfe et al., 2008). Root depth, mass and traits influence hydraulic  
105 supply and consequently stomatal conductance.~~

Leaf traits similarly exhibit spatial and temporal variation with changing water availability. Leaf  
nitrogen content (per unit mass), light- and CO<sub>2</sub>-saturated photosynthetic rates (per unit mass) increase  
with drought stress across tropical precipitation gradients, ~~whilst as p<sub>ψ</sub>50~~ (the water potential at which  
50% of hydraulic conductivity is lost) declines (Wright et al., 2004, Santiago et al., 2004, Anderegg,

**Commented [FS6]:** R1 AR6. In response to reviewer comment "Line 88 can be read as if you say LAI is a trait. Conventionally, LAI is not considered a trait (you could use max LAI), but rather relates to the ecosystem structure. Thus, for clarification could you please consider rephrasing the sentence to e.g.: Changes to both ecosystem structure and traits, such as LAI, rooting depth and carboxylation capacity, are expected to be more longstanding (Meir et al., 2015a)."  
Corrected as suggested

**Commented [FS7]:** R2 AR5. In response to reviewer comment "Line 90. Please explain on what time scale this evidence is valid."  
We have now included detail on the relevant timescale. Evidence exists across sub-annual (Araujo-Murakami et al., 2014, Xu et al., 2016) and annual timescales (Brando et al., 2008, Meir et al., 2009).

**Commented [FS8]:** R1 AR33. In response to reviewer comment "Line 88 Abbreviate LAI in line 88, not line 90"

**Commented [FS9]:** R2 AR6. In response to reviewer comment "Line 90. This paragraph is rather qualitative, therefore vague. Please explain how strong the responses are."  
Quantitative details have now been added to this section.

With respect to near surface root mass, length and surface area growth declines with seasonal water deficit, the paper referenced (Metcalfe et al., 2008) does not provide estimates on the strength of the response, only that is it significant (p<0.001). However, from the figure presented we can estimate that root mass, length and surface area growth decline by up to 75%, 65% and 25% respectively (approximated using figure data retrieval software)."

**Commented [FS10]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious."  
Adjustments throughout

**Commented [FS11]:** R1 AR34. In response to reviewer comment "Line 100 Please change p50 to ψ50"  
Corrected

110 2015). Leaf traits affect GPP via photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ) (Bahar et al., 2017, Fyllas et al., 2017), and through their influence on canopy carbon economics, via leaf growth and maintenance costs (Bloom et al., 1985). ~~However, understanding the interactions between photosynthetic drivers across different spatial and temporal scales is limited.~~

Field observations show variation in Amazon GPP is correlated with physiological, ecosystem structure and trait composition responses to climate (Restrepo-Coupe et al., 2013, Goulden et al., 2004, Hutyrá et al., 2007, Wu et al., 2017, Wagner et al., 2017). Modelling approaches have similarly highlighted the role of canopy dynamics and leaf traits in driving spatial and temporal variation in GPP (Mercado et al., 2011, Castanho et al., 2013, Restrepo-Coupe et al., 2013, Rodig et al., 2018), however their relative effects have not been explicitly isolated and quantified. Quantifying the direct effect of discrete photosynthetic drivers has been limited by the need for detailed field measurements of carbon fluxes, canopy dynamics and traits. ~~Furthermore, whilst Aa~~ deserved research effort has focused on the importance of nutrient availability in driving spatial variation in GPP (Mercado et al., 2011, Castanho et al., 2013), however the role of ecosystem responses to water availability has received less attention (Green et al., 2019). In light of projected changes in rainfall patterns across the basin, capturing responses to water availability in ecosystem models is critical to reducing current uncertainty around Amazon climate-vegetation feedbacks. We aim to reduce the uncertainty by assessing the relative effects of physiological, structural and trait responses to water availability on GPP across monthly to annual timescales.

We apply ~~a validated ecosystem~~ ecosystem model to plots across the Amazon, spanning a large drought stress gradient (~~herein, the term drought stress refers to seasonal water deficit~~), and a range in forest types from moist equatorial to seasonally dry tropical forests. Process modelling allows the links between climate, ecosystem structure and leaf traits to be quantified explicitly, and separated, across timescales (Figure 1). The soil plant atmosphere model (SPA) (Williams et al., 1996, Williams et al., 1998, Fisher et al., 2006, Fisher et al., 2007, Rowland et al., 2015b) is well suited to this investigation given its prior use in accurately simulating carbon and water fluxes in Amazon tropical forests. ~~We link the modelling to calibrate and validate the model using field data gathered over multiple years (2009-~~

**Commented [FS12]:** R2 AR7. In response to the reviewer comment "Line 104: understanding is limited. This is quite an empty sentence. Please make it more concrete by stating what understanding is missing exactly." On reflection this sentence repeated (but with less specifics) the earlier statement of "The relative importance of plant physiology, ecosystem structure, and trait composition responses in determining variation in GPP, remain largely unquantified in data-constrained analysis (Meir et al., 2015b)." We have therefore removed it.

**Commented [FS13]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

**Commented [FS14]:** R2 AR3. In response to the reviewer comment "I miss a discussion on the temporal scale of the responses. The authors use 'multiple' (2) years of forcing data. They find that indirect responses dominate. I understand that the paper describes equilibrium responses to an existing drought stress gradient. Still indirect responses probably need some time to develop, while droughts are often intermittent. If I do not fully understand how the authors see this, it may indicate the need to discuss this issue explicitly." We thank the reviewer for highlighting an important issue around the definition of drought stress. In the presented study we focused on seasonal drought stress, and compared GPP drivers across seasons and across a gradient in seasonal drought stress. In the original version of the manuscript a clear distinction between seasonal drought stress (our focus) and drought events (not addressed in the manuscript) was not made. By defining drought stress in the context of our study early on we hope to ensure our references to drought stress are not ambiguous. The temporal scale of responses can then be discussed by comparing model experiments 1 and 3. We appreciate that the comparison was somewhat limited in the original version of the manuscript and as such have expanded the discussion (on from line 516).

2010) on permanent sample plots from the Global Ecosystems Monitoring (GEM) network (Doughty et al., 2015a, Malhi et al., 2015). The datasets comprise detailed measurements of carbon fluxes, carbon stocks and leaf traits, ~~and were used to constrain the SPA model~~. We simulate the effect of forest structure and leaf trait distributions along the drought stress gradient, and explore the covariation of observed leaf traits (leaf N content (a proxy for photosynthetic capacity) and LMA) and those derived from model calibrations (leaf lifespan), before using SPA to address the following questions:

1. Is spatial variation in GPP across the drought stress gradient principally driven by the direct effects of climate and soils, which include physiological responses to water availability via hydraulic transport and stomatal conductance? Alternatively, are indirect effects of climate, via structural and trait responses to water availability (LAI, rooting biomass, root depth and photosynthetic capacity i.e  $V_{cmax}$  and  $J_{max}$ ), more important?
2. Does the sensitivity of GPP to differences in climate, LAI, photosynthetic capacity ( $V_{cmax}$  and  $J_{max}$ ) and rooting depth vary across the drought stress gradient?
3. ~~What drives seasonal variation in GPP across an Amazon forest drought stress gradient?~~

Linked to question one, we hypothesise that indirect effects of climate via structural and trait responses are more important than the direct effects (via physiological responses), in explaining spatial variation in GPP across the drought stress gradient (Figure 1). We further posit that LAI is the principal driver of differences in GPP among Amazon forests, effected through the observed increase in leaf area with decreasing drought stress.

For question two, we predict that the sensitivity of GPP to differences in climate, LAI, photosynthetic capacity ( $V_{cmax}$  and  $J_{max}$ ) and rooting depth will vary dependent on water demand (via LAI and stomatal conductance) and supply (climate and root depth and biomass; Figure 1). We expect that forests under lower drought stress will be most sensitive to differences in LAI and photosynthetic capacity within the bounds of observations across ~~the gradient~~the gradient. We predict that forests under higher drought stress will be more sensitive to differences in rooting depth. We expect forests with high LAI but shallow rooting depth will be most sensitive to differences in climate, due to their higher transpiration demand but low capacity for water supply.

**Commented [FS15]:** R2 AR8. In response to reviewer comment "Line 127. We link . . . Vague sentence. Additionally, 2 years is really the minimal number of multiple years. Couldn't you use a longer data set? This is relevant to how fast ecosystems respond to and recover from drought. How do you capture transient responses and how do you know those 2 years are representative for average (or not extreme) conditions?"  
Sentence edited.  
With respect to the reviewers comment on drought response and recovery please see AR 3. In response to the reviewers question about using a longer data set. We were limited by the length of the timeseries available across plots of different data streams.

**Commented [FS16]:** R2 AR2. In response to the reviewers comment "- In my opinion research question 3 adds little value to the paper and the corresponding results are relatively shallow relative to the existing literature. The results are quite obvious. I suggest removing this rq and the corresponding results. It will make the paper sharper and more to the point."  
We take on board the reviewer's point with regards to RQ3. However, the reviewer's subsequent comment regarding discussion on the temporal scale of responses prompted additions to the manuscript which we feel highlights the importance of RQ3s inclusion (see AR 3).

For question three, we hypothesise that on monthly timescales, climate will be more important than canopy dynamics in driving GPP. Across the drought stress gradient, we expect that solar radiation will be relatively more important during the wet season, ~~whilst~~ VPD will be more important during the dry season, reflecting seasonal shifts in light and water availability. Due to differences in dry season length, we predict that for forests experiencing lower drought stress, solar radiation will be most important in driving sub-annual variation in GPP, ~~whilst for GPP. For~~ forests under higher drought stress, VPD will be the dominant driver.

**Commented [FS17]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

By combining detailed plot-level timeseries data with a hydrodynamic terrestrial ecosystem model, we are able to use an innovative model experimentation approach to understand the drivers of spatial variation in GPP, beyond correlative effects. We are able to apportion variation in GPP to the direct and indirect effects of climate (Figure 1), across sub-annual and annual timescales (Q1 and Q3). Furthermore, by performing a sensitivity analysis within the context of observed variation in parameters across the Amazon (Q2) we identify areas potentially more vulnerable to changes in precipitation regime.

## 2. Methods

~~We parameterised and validated the ecosystem model SPA to permanent sample plots along an Amazon mean Maximum Climatological Water Deficit (MCWD) gradient (–85 to –498 mm yr<sup>-1</sup>) for the years 2009–2010. Plot characteristics are summarised in Table 1, and detailed in full in the supplementary material. MCWD is a measure of peak seasonal water deficit, where more negative MCWD indicate higher drought stress. We used characterise plot water status using mean Maximum Climatological Water Deficit (MCWD) MCWD instead of and not annual precipitation, as water deficit is more closely linked to the mechanisms constraining GPP, than total water input. MCWD is the maximum cumulative water deficit reached within a year. A water deficit estimate for each month is calculated as the difference between precipitation and transpiration (which ground measurements estimate at ~100 mm month<sup>-1</sup>, see Aragao et al. (2007)). Therefore, the forest is in water deficit if monthly precipitation falls below 100mm. Maximum cumulative water deficit is calculated as the sum of sequential monthly water~~

190 deficits (for equations see supplementary material). More negative MCWD values indicate higher drought stress.

195 We analysed the distribution of LAI and leaf traits across the MCWD gradient. We then undertook a series of model experiments to: (i) apportion spatial variation in GPP to drivers (climate, soils, LAI, rooting biomass and depth and photosynthetic capacity); (ii) investigate how the sensitivity of GPP to differences in drivers varies across the MCWD gradient; and (iii) quantify the importance of LAI, VPD, solar radiation, precipitation and air temperature in driving sub-annual variation in GPP using the random forest machine learning technique (Breiman, 2001).

### 2.1 The Soil Plant Atmosphere model (SPA)

200 The Soil-Plant-Atmosphere model (SPA) is a hydrodynamic terrestrial ecosystem model, which has been calibrated and evaluated for moist tropical forests in Manaus and Caxiuanã (Williams et al., 1996, Williams et al., 1998, Fisher et al., 2007). In SPA, carbon and water fluxes are estimated through process-based modelling of radiative transfer, boundary layer and stomatal conductance, plant and leaf ecophysiology and soil-plant energy and water balance (Smallman et al., 2013, Williams et al., 1996). Plant physiological responses to water availability are well represented in SPA due to the stomatal conductance algorithm being coupled directly to plant water use (Fisher et al., 2006). As a result, higher evaporative demand under increased LAI drives increased root water uptake and consequently a depletion in soil moisture. Within SPA, C allocation between structural tissue and the non-structural C (NSC) pool is executed via the sub model DALEC<sub>canopy</sub> (Bloom and Williams, 2015) (Figure 2).

210 DALEC<sub>canopy</sub> was updated on daily timesteps and in this study, forced using LAI observation data. Constraining simulated LAI was integral to the model experiments conducted. It allowed the quantification of direct effects of different LAI timeseries on GPP under different plot conditions. However, the capacity of SPA to accurately simulate canopy dynamics is demonstrated by both López-Blanco et al. (2018) and Sus et al. (2010). To force modelled LAI, LMA (gC m<sup>-2</sup>) and daily LAI estimates were used to calculate the foliar C stock. Leaf NPP was calculated as the difference between the foliar C stock of the current and previous timestep. Leaf NPP was allocated prior to other

**Commented [FS18]:** R2 AR9. In response to reviewer comment “- Line 171. Please define MCWD precisely.” Also see supplementary material.

**Commented [FS19]:** R1 AR7&8. In response to reviewer comments “Line 142-162 As the introduction is already very long, and much of your hypothesis is repeated later in the manuscript, I would highly recommend deleting these paragraphs.” And “Line 175-181 These lines are almost identical to your scientific research questions listed in the introduction. Please consider deleting one or the other.” Removed as suggested

**Commented [FS20]:** R1 AR4. In response to the reviewer comment “Several times you state that changes in LAI is an indirect structural effect from changes in soil moisture. From there, it follows that it is LAI which drives the GPP across the MCWD gradient. A strong emphasis is throughout the manuscript put on LAI and LAI as a driver of GPP, while LAI is strongly impacted by drought stress. However, the model is forced with LAI from hemispherical photographs, but the authors do not explain how the forced LAI is linked to and impact the simulated soil moisture content. From Fig. 2 it follows that LAI impacts the foliage carbon pool, and this pool together with carbon pool of fine roots and soil moisture impacts GPP, but the link between the forced LAI and soil moisture is not well explained for your model setup. Please clarify this in the manuscript.”

The link between LAI and soil moisture within the model is now described in the ‘2.1 The Soil Plant Atmosphere model (SPA)’ subsection.

**Formatted:** Subscript

**Commented [FS21]:** R1 AR9. In response to the reviewer comment “Line 232-234 You state that the mapping of canopy dynamics is critical, and that changes in canopy dynamics cause disparity between field observations and model predictions – how well is canopy dynamics simulated by SPA? How is the LAI forced over the canopy layers in SPA? Please elaborate on these aspects in the manuscript and explain how your study improve these shortcomings.”

See insertion for performance of SPA.

On the subject of how the presented study improves current shortcomings in LAI modelling: The authors outline a need for model development around structural and trait responses to drought stress. An exploration of the model structures which would more accurately simulate LAI was outside the scope of the manuscript, but is the subject of ongoing research by the authors. In addition see other AR9 responses.



plant components, and if the leaf NPP requirement exceeded total NPP for the given timestep, the non-structural C pool was drawn upon (where total NPP was calculated as the difference between simulated GPP and autotrophic respiration) (see supplementary material). [The NSC pool serves functions additional to the seasonal redistribution of C (e.g. phloem transport and osmoregulation; Dietze et al., 2014). As such, we assume the NSC pool is stable over time. If the NSC pool becomes depleted, a fraction of NPP is redirected towards NSC storage. Allocation towards NSC storage is executed in subsequent time steps when leaf NPP does not exceed total NPP. Root and wood NPP were calculated from the NPP remaining after leaf allocation.] Leaf maintenance respiration was calculated as a function of leaf N content (Reich et al., 2008) and total leaf C stock (see supplementary material). Within SPA, wood and fine root maintenance respiration were simulated as a function of component C stock and a plot specific respiration coefficient. Growth respiration was calculated as fixed fraction of net primary productivity (NPP; -0.28) (Waring and Schlesinger, 1985). Model inputs and outputs are listed in Table 2.

## 2.2 Model Calibration

Following data collation to parameterise SPA, the model was calibrated and validated for each plot prior to conducting model experiments. Measurements used to parameterise SPA include: soil texture, soil C stock, leaf N content, LMA, photosynthetic capacity, the fraction of NPP allocated to fine roots and wood, root depth, and foliar, wood and fine root C stocks (Table 2). Soil, wood and fine root C stocks (single point measurements, not timeseries) were initial model inputs and allowed to vary thereafter dependent on simulated C dynamics. Plot specific field measurements of leaf N content are presented in Fyllas et al. (2009), or where absent were retrieved from trait databases using plot species composition (Kattge et al., 2011; Poorter and Bongers, 2006). Photosynthetic capacity estimates ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ) were derived from leaf N content (Walker et al., 2014), or field measurements (Caxiuanã only). Wood and root respiration measurements were used together with component C stocks to estimate plot specific wood and root respiration coefficients.

The model was driven using hourly meteorological data, retrieved from local weather stations. [The number of missing hourly field meteorological measurements across the timeseries varied from 2-40%

**Commented [FS22]:** R1 AR11. In response to the reviewer comment "Line 239 This sentence is not clear." Edited and expanded to detail additional functions of the NSC pool such as phloem transport and osmoregulation.

**Commented [FS23]:** R1 AR5. In response to the reviewer comment "Several times you briefly mention the C allocation (line 232 to 241, Fig. 2 and Supplement material). In the text you state that allocation to NPPLeaf occurs first. Normally NPP is considered a flux, and normally you would allocate to a pool. Thus, do you mean that allocation to the foliar stock occurs first? If assimilation does not provide the C need for allocation to support the LAI, you take from the labile/non-structural carbon pool. However, in the supplement material in the last three equations, you state that if the labile pool has been depleted you allocate from the total NPP. Surely this must only be the case when you have enough NPP to sustain the foliar stock as required by the LAI. Please clarify this in the manuscript." The reviewer is correct in their summation of the C allocation scheme. Allocation towards NSC storage is executed in subsequent time steps when the NPPLeaf requirement does not exceed total NPP. This is now clarified in the manuscript. Also see supplementary material.

**Commented [FS24]:** R1 AR1. In response to the reviewer comment "The authors investigate the importance of different drivers (LAI, leaf traits, climate) for GPP at both temporal and spatial scale across a drought stress gradient in the amazonian region using the Soil-Plant-Atmosphere (SPA) ecosystem model. The SPA model is applied at 7 sites, using sites specific parameters and is forced with LAI observed from hemispherical photographs. Simulation experiments and machine learning techniques are used to investigate their scientific questions. They find that indirect effects via plant traits and ecosystem structural changes, here expressed as LAI, are found to be the main driver of GPP across a spatial drought gradient, but the sensitivity of GPP to changes in these drivers varied with the gradient. On a sub-annual timescale climatic drivers were found to be more important for GPP. The authors discuss how these direct physiological and indirect mechanism affect GPP but fail to explain the added value of forcing their model with observed LAI and to explain in detail how this forced LAI propagates down the modelling structure of SPA. The manuscript is well written and well structured, however, with many repetitions that should be deleted to make space for more details on your methods. As explained in detail in the comments below, I would like the authors to consider my questions and comments, before I recommend the publication of this manuscript."

AR 1. The brief summary of how LAI is forced within the model (lines 232-237) has been expanded to provide a more in-depth description, and instead included in the '2.1 The Soil Plant Atmosphere model (SPA)' subsection (also see comments AR 5, 9 and 10). In addition, as suggested, we outline the value of using LAI data to force the model.

**Commented [FS25]:** R1 AR35. In response to reviewer comment "Line 195 Please Abbreviate NPP here"

245 ~~across sites, whilst the frequency of gaps varied from 2-99 yr<sup>-1</sup>. Gaps less than 6 hours in length~~

~~accounted for between 20-100% of total gaps across plots.~~ Short gaps in air temperature, wind speed,

shortwave radiation and vapour pressure deficit measurements (<6 hours), were filled by spline interpolation between existing data. Where local meteorological data was unavailable for a longer period of time, or for gaps in precipitation measurements, hourly spline-interpolated ERA-Interim data were used (Dee et al., 2011). The interpolation of solar radiation estimates accounted for the solar zenith

250 angle. MCWD was calculated for the years 2009-2010, ~~and as the minimum monthly water deficit reached within the year, where monthly water deficit is equal to the previous month's water deficit, plus precipitation, minus evapotranspiration (Aragao et al., 2007).~~ Calculated MCWD was consistent with

previously published estimates for all plots excluding Caxiuanã, which were calculated across different years (Malhi et al., (2015), Caxiuanã -203mm, Tambopata -259mm, Kenia -386mm, Tanguro -482mm;

255 this study, Caxiuanã -85±65mm, Tambopata -265±59mm, Kenia 342±146mm, Tanguro 451±73mm).

The simulation of soil water drainage in SPA was calibrated against timeseries of field measurements of soil moisture. Initial investigations comparing modelled soil moisture to monthly field data highlighted an overestimation by SPA. ~~Pre-calibration, SPA soil moisture estimates were on average~~

260 ~~11-68% higher than field measurements across plots. The difference between model and field soil moisture estimates increased significantly with MCWD (R<sup>2</sup>=0.69, p=0.04).~~ The empirical model used

in SPA to relate soil texture to water retention (Saxton et al., 1986, eqn. 10) was then calibrated by adjusting the slope of the interaction to better represent soil moisture across tropical soils (to within standard error estimates of mean annual soil moisture).

265 Leaf litterfall parameters (day of peak leaf fall, leaf fall period and leaf lifespan) were calibrated against field data to accurately simulate litterfall period and amplitude (within standard error estimates of annual litterfall). Wood and fine root biomass turnover rates were ~~estimated assumed proportional ing each forest ecosystem was at steady state to NPP.~~ given the maturity of stands and their disturbance history:

$$\text{turnover rate}_i \propto \frac{NPP_i}{C \text{ stock}_i}$$

**Commented [FS26]:** R2 AR10. In response to the reviewer comment “- Line 208. How frequent were data gaps?” Statistics on the frequency of data gaps has now been added to the manuscript.

**Commented [FS27]:** R2 AR11. In response to the reviewers comment “- Line 222. . . .overestimation. . . please quantify.”

270 Where  $i$  is wood or fine roots.

Local, monthly LAI estimates derived from hemispherical photographs were scaled to daily estimates via linear interpolation, and used to force simulated LAI. The vertical distribution of leaf area is kept constant, as current field data is insufficient to provide an accurate depiction of how vertical distributions change with canopy density across the MCWD gradient.

275 Leaf NPP was calculated as the difference between the foliar C stock of the previous timestep and that which would equate to field measured LAI. Leaf NPP was allocated prior to other plant components, and if the leaf NPP requirement exceeded total NPP for the given timestep, the non-structural C pool was drawn upon (where total NPP was calculated as the difference between simulated GPP and autotrophic respiration) (see supplementary material). Under the assumption that allocation to NSC is

280 an active process and that the pool serves functions additional to the seasonal redistribution of C (Dietze et al., 2014), depletions in the NSC pool induce redirection of a fraction of NPP towards NSC storage to maintain a stable NSC pool. Root and wood NPP were calculated from the NPP remaining after leaf allocation. We calculate model uncertainty as a result of input parameters. SPA was forced with the

285 observed LAI timeseries plus and minus the standard error for each plot. Model uncertainty estimates were limited to that derived from LAI as the availability of uncertainty estimates for leaf traits, root depth and root biomass were variable and plot dependent, and there were no uncertainty estimates for hourly meteorological data or soil properties. Model structural uncertainty was not calculated and we recognise that the model error estimates presented are therefore underestimated. |With respect to model

290 structural uncertainty, we highlight that the stomatal conductance algorithm embedded within SPA is consistent with leaf and canopy scale observations, and surpasses the performance of the Ball-Berry model where soils experience moisture-stress (Bonan et al., 2014). However, model (and empirical) uncertainty remains around the role of non-structural carbon in regulating water-transport in large trees during drought periods (O'Brien et al., 2014) Furthermore, SPA does not account for hydraulic lift and redistribution of water through the soil profile, which is known to impact water fluxes across the soil-

295 plant-atmosphere continuum in Amazon trees (Oliveira et al, 2005; Wang et al., 2011).

**Commented [FS28]:** R1 AR10. In response to the reviewers comment "NPPLeaf was calculated as the difference between the foliar C stock of the previous time step and that which would equate to field measured LAI. The field measured LAI has a monthly resolution. In principle you would have foliar C stock that could change at every model time step. But if the foliar C stock already equates to the field measured LAI, because the resolution of the forced LAI is monthly, NPPLeaf would just be zero." This is now clarified in the manuscript.

**Commented [FS29]:** R1 AR9. In response to the reviewer comment "Line 232-234 You state that the mapping of canopy dynamics is critical, and that changes in canopy dynamics cause disparity between field observations and model predictions – how well is canopy dynamics simulated by SPA? How is the LAI forced over the canopy layers in SPA? Please elaborate on these aspects in the manuscript and explain how your study improve these shortcomings." In addition see other AR9 responses.

**Commented [FS30]:** R1 AR12 & AR16. In response to reviewer comments "Line 243 How was the SPA model calibration constraint by an upper and lower sample error of LAI? Please add clarification to the text."

The model was forced using the observed LAI timeseries plus and minus the standard error for each plot. This is now clarified in the text.

"Line 326 Please explain why the GPPSPA variance is calculated under the LAI standard error."

LAI upper and lower standard error were used to calculate an estimate of SPA uncertainty based on model input data. With regards to other model inputs, the availability of trait uncertainty estimates was variable and plot dependent, and there were no uncertainty estimates for hourly meteorological data. We were consequently limited to LAI estimates.

**Commented [FS31]:** R1 AR23. In response to the reviewers comment "Line 517 In this section, or possible add another section to the discussion, you will also have to address the uncertainties from the intrinsic model behaviour. You recognised already in line 245 that the model uncertainty is underestimated due to the lack of intrinsic model error. However, during your discussion this is not assessed at all. Please assess these uncertainties in particular in relation to the moisture stress and how the plant hydraulics is modelled in SPA and acknowledge its limitations."

### 2.3 Model Validation

300 ~~For each plot, SPA calibrations were constrained by the upper and lower sample error of LAI measurements to produce an estimate of model uncertainty. However, given we do not quantify intrinsic model error beyond that associated with parameter estimates, we recognise that the model error estimates presented are underestimated.~~ Observation constrained SPA simulations were then validated against biometric field measurements of C fluxes (i.e. from infra-red gas analysers, dendrometers, root ingrowth cores litterfall traps etc.). Linear regression models were constructed to compare modelled estimates and independent field measurements of GPP, autotrophic respiration and total NPP. A comprehensive comparison of model estimates and independent field measurements of component NPP and respiration were also made. Validation of the SPA model against biometric data lent confidence to 305 subsequent analyses, where the model was used to explore C fluxes under non-observed conditions.

### 2.4 Model Experiments

310 ~~Our aim was to isolate the direct effects of climate and soils (via physiological responses), and the indirect effects via ecosystem structure, and leaf traits, on simulated GPP. Our aim was to isolate the direct effects of climate and soils (via physiological responses), ecosystem structure, and leaf traits on simulated GPP.~~ To avoid capturing the feedback effects of changing photosynthate supply (i.e. as a result of changes in climate, soils, ecosystem structure or traits) on ecosystem structure, model experiments were conducted in the absence of C cycle feedbacks. Thus, within model experiments, C stocks for each component (leaves, wood, fine root, coarse root) were constrained to observations unless 315 otherwise stated.

#### 2.4.1 Experiment 1. Drivers of Spatial Variation in GPP

320 Through a series of model input alternations, we used SPA to quantify the effects of (i) climate, (ii) soil properties, (iii) LAI, (iv) root biomass and (v) rooting depth, and (vi) trait responses driven by photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ), on simulated GPP. Model inputs for each driver were alternated at each plot, to that of all other plots, and annual GPP values for each of the two years retrieved. For example, plot CAX04 was simulated with the climate, soil properties, LAI, root biomass, root depth and photosynthetic capacity of CAX06, TAM05, TAM06, KEN01, KEN02, and Tanguero

**Commented [FS32]:** R2 AR12. In response to the reviewers comment "- Line 254. This sentence confused me initially, it sounds like you are only focussed on direct effects. Please rephrase."  
Rephrased.

etc. (Figure S1). SPA simulated GPP for a total of 462 combinations (for climate, 7 plots  $\times$  3 alternations  $\times$  2 years, plus for the remaining drivers, 5 drivers  $\times$  7 plots  $\times$  6 alternations  $\times$  2 years) were combined with 14 annual GPP estimates from observation constrained (control) runs (7 plots  $\times$  2 years). A factorial ANOVA was applied to the difference between GPP from each model run and its control simulation (n=476, i.e. 462 +14) (Galbraith et al., 2010). The proportions of variation in GPP explained by climate, soil properties, LAI, photosynthetic capacity, root biomass and rooting depth, were then calculated as the conditional sum of square divided by the total sum of squares.

#### 2.4.2 Experiment 2. Variation in Forest Sensitivity to Drivers of GPP

We quantified how the relative sensitivity of GPP to differences in LAI, climate, photosynthetic capacity and rooting depth varied across the MCWD gradient. For example, we tested whether forests occupying lower drought stress zones were more sensitive to differences in LAI than forests in higher drought stress zones, etc. We used model outputs generated in *Experiment 1* to calculate the sensitivity of GPP to drivers at each plot, within the bounds of observations across the MCWD gradient. Root biomass and soil properties were not included in the analysis as across the MCWD gradient they explained little variation in GPP (*Experiment 1*, Table 6). The sensitivity of GPP to drivers at each plot was calculated as the absolute range in simulated GPP values under each driver alternation i.e. the sensitivity of CAX04 to variation in LAI was calculated as the maximum GPP minus the minimum GPP simulated by alternating LAI to that of all other plots etc. Plots were grouped by location (Caxiuanã, Tambopata, Kenia and Tanguro) to compare how the sensitivity of GPP to LAI, climate, photosynthetic capacity and rooting depth varies across the MCWD gradient.

#### 2.4.3 Experiment 3. Drivers of Sub-Annual Variation in GPP

We quantified the role of climate and LAI in explaining variation in sub-annual GPP. We used the random forest technique to compute the relative importance of LAI, VPD, solar radiation, precipitation and air temperature driving variation in monthly GPP (n=168; 7 plots  $\times$  24 months), where GPP estimates were derived from SPA simulations. To quantify the effects of LAI and climate variables on monthly GPP we used the random forest machine learning technique applied by means of the Python Scikit-Learn module (Breiman, 2001, Pedregosa et al., 2011). The approach uses multiple mathematical

350 decision tree predictors to describe a dependent variable as a function of selected independent variables. An importance value between 0 and 100 was assigned to each driver based on a tree-wise comparison of explanatory power (Moore et al., 2018, López-Blanco et al., 2017). We calculated the average relative importance of drivers at each plot to determine the principal drivers of variation in sub-annual GPP and investigated the seasonality of driver importance.

### 355 3. Results

~~Following model calibration, validation and an investigation into the distribution of LAI and leaf traits across the MCWD gradient, we (i) quantify the drivers of spatial variation in GPP, (ii) compute the variation in forest sensitivity to drivers of GPP, and (iii) calculate the relative importance of drivers of sub-annual variation in GPP.~~

**Commented [FS33]:** R1 AR13. N response to reviewer comment "Line 301-302 These lines are repetitions, and not needed. Please consider deleting."  
Deleted as suggested

#### 360 3.1 Model Calibration

Calibrated SPA soil water content corresponded well to field measurements from the GEM network (Figure 3). Simulated mean annual soil moisture estimates were within field measurement standard error for all plots. ~~The timing of observed peak soil moisture was captured by SPA simulations ( $R^2=0.98$ ,  $p<0.001$ ,  $RMSE=1$  month). A positive, but non-significant, correlation existed between model and field estimates of seasonal soil moisture range ( $R^2=0.35$ ,  $p=0.21$ ,  $RMSE=5\%$ ). SPA simulated seasonal soil moisture range exhibited a non-significant, positive correlation with field measurements ( $R^2=0.35$ ,  $p=0.21$ ,  $RMSE=5\%$ ). Notably, for some plots such as Kenia, the magnitudes of seasonal peak soil water fluxes were not captured by SPA simulations (up to 39% lower than field estimates), whilst~~ ~~For Tanguro, peak soil water lasted 3 months longer in SPA simulations than was measured in the~~ field.

**Commented [FS34]:** R1 AR36. In response to reviewer comment "Line 307 Add a space between the two sentences."

**Commented [FS35]:** R1 AR14. In response to reviewer comment "Line 308 There is something wrong with the structure of this sentence." Reworked as suggested

**Commented [FS36]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

SPA was also successfully calibrated to simulate local leaf litterfall accurately. The calibration of leaf fall cycle parameters in SPA using GEM leaf litterfall timeseries (Table 4), resulted in the magnitude and timing of leaf litterfall being well represented by the model for all plots (monthly leaf litterfall range for GEM measurements and SPA simulations  $R^2=0.54$ ,  $p=0.009$ ,  $RMSE=11.2$  gC m<sup>2</sup> yr<sup>-1</sup>; timing of

375 leaf litterfall peak  $R^2=0.96$ ,  $p<0.001$ ,  $RMSE=1.1$  months) (Figure 4). SPA-simulated mean annual leaf  
litterfall correlated significantly with GEM estimates ( $R^2=0.99$ ,  $p<0.001$ ,  $RMSE=9.0$   $gC\ m^{-2}\ yr^{-1}$ ).

### 3.2 Model Validation

Estimates of ecosystem-scale C fluxes from SPA model runs were validated against biometrically  
derived estimates from the GEM network.  $GPP_{SPA}$  and  $GPP_{GEM}$  estimates were correlated across plots,  
380 though not significantly ( $R^2=0.36$ ,  $p=0.15$ ; Figure 5a). Along the MCWD gradient,  $GPP_{SPA}$  estimates  
varied across plots by  $1137\ gC\ m^{-2}\ yr^{-1}$ , whilst in line with  $GPP_{GEM}$  estimates which varied by  $1202\ gC$   
 $m^{-2}\ yr^{-1}$ . Error bars overlap between  $GPP_{SPA}$  and  $GPP_{GEM}$  estimates for all plots except KEN01 and  
TAM06, though marginally (difference KEN01  $115\ gC\ m^{-2}\ yr^{-1}$ , TAM06  $50\ gC\ m^{-2}\ yr^{-1}$ ).  $GPP_{GEM}$  error  
bars are field estimate standard error, and  $GPP_{SPA}$  error bars represent simulated GPP variance under  
385 LAI standard error. Across plots,  $GPP_{SPA}$  estimates were 0.57% higher than  $GPP_{GEM}$  estimates. The  
correlation between GPP and MCWD was similar for  $GPP_{SPA}$  ( $R^2=0.64$ ,  $p=0.03$ , slope=2.4) and  $GPP_{GEM}$   
estimates ( $R^2=0.52$ ,  $p=0.07$ , slope=2.00).

$NPP_{SPA}$  estimates (the sum of model simulated root and wood NPP and data-constrained leaf NPP) were  
also correlated with  $NPP_{GEM}$  measurements across plots ( $R^2=0.38$ ,  $p=0.14$ ), though not significantly due  
390 to differences in Kenia plots (on exclusion of Kenia plots  $R^2=0.92$ ,  $p=0.01$ ,  $RMSE=42\ gC\ m^{-2}\ yr^{-1}$ )  
(Figure 5b).  $NPP_{SPA}$  estimates were 7.9% lower than field measurements across plots on average.  $Ra_{SPA}$   
(the sum of predicted leaf respiration, and parameterised root and wood respiration) were significantly  
correlated with biometric measurements ( $Ra_{GEM}$ ) across plots ( $R^2=0.59$ ,  $p=0.04$ ; Figure 5c), though  
were on average 5.3% higher.

395 Leaf respiration estimates simulated as a function of leaf nitrogen content were correlated with field  
measurements, though not significantly ( $R^2=0.47$ ,  $p=0.09$ ; Table 5). Parameterised wood and fine root  
respiration, together with fine root NPP, correlated significantly with field measurements. SPA  
estimates of wood NPP did not correlate significantly with GEM measurements due to underestimation  
at KEN01 (on exclusion  $R^2=0.78$ ,  $p=0.02$ ,  $RMSE=7.5\ gC\ m^{-2}\ yr^{-1}$ ). Further comparisons of SPA  
400 estimates and GEM measurements of component NPP and respiration are presented in Table 5.

**Commented [FS37]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

### 3.4 LAI and Leaf Traits Trends along the MCWD gradient

Field estimated mean annual LAI ranged from 2.2 to 5.2 m<sup>2</sup> m<sup>-2</sup>, and increased (though not significantly) with MCWD across plots (R<sup>2</sup>=0.35, p=0.16; [Table 3](#)). A negative, non-significant correlation existed between calibrated leaf lifespan and MCWD (R<sup>2</sup>=0.50, p=0.08). Photosynthetic capacity (V<sub>cmax</sub> and J<sub>max</sub>) estimates derived from measured leaf N content similarly exhibited a negative non-significant correlation with MCWD (R<sup>2</sup>=0.51, p=0.07 and R<sup>2</sup>=0.53, p=0.06 respectively). A positive non-significant correlation existed between model-calibrated leaf lifespan, measured LMA (log-log R<sup>2</sup>=0.39, p=0.14), and LAI (R<sup>2</sup>=0.28, p=0.22). Model-calibrated leaf lifespan exhibited a negative, non-significant correlation with photosynthetic capacity estimates (V<sub>cmax</sub> R<sup>2</sup>=0.46, p=0.09; J<sub>max</sub> R<sup>2</sup>=0.47, p=0.09). A significant positive correlation existed between mean annual LAI and LMA (R<sup>2</sup>=0.85, p=0.003).

### 3.5 Model Experiments

#### 3.5.1 Experiment 1. Drivers of Spatial Variation in GPP

Structural and trait responses to water availability explained more variation in GPP across the MCWD gradient than did climate. LAI accounted for the largest proportion of variance in mean annual GPP across plots (32.8%, [Table 6](#)), whilst Differences in photosynthetic capacity explained 21.3% of variance was explained by differences in photosynthetic capacity ([Table 6](#)). Photosynthetic capacity increased with decreasing MCWD ([Table 3](#)); this relationship partially offset the decrease in GPP linked to declining LAI. The direct effects of climate on GPP (which included physiological responses to water availability including stomatal conductance) accounted for 16.2% of plot variation in mean annual GPP. Rooting depth did not vary directionally with MCWD and consequently only had a small effect on GPP (4.1%). Soil properties and root biomass accounted for a very small fraction of variance (<2%).

#### 3.5.2 Experiment 2. Variation in Forest Sensitivity to Drivers of GPP

The relative sensitivity of GPP to drivers varied across the MCWD gradient (Figure 6). GPP was most sensitive to changes in LAI (per unit m<sup>2</sup> leaf area) for plots located at Caxiuanã, which experience the least negative MCWD and have large rooting depth (Caxiuanã LAI sensitivity Δ 537 gC m<sup>-2</sup> yr<sup>-1</sup> vs

**Commented [FS38]:** R1 AR31. In response to the reviewers comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

**Commented [FS39]:** R2 AR13. In response to the reviewers comment "- Line 359. Please clarify how this can be seen in table 3." This was an error and should have referenced the preceding section ('3.4 LAI and Leaf Trait Trends along the MCWD gradient'). Now corrected.



430 ~~overall mean LAI sensitivity  $\Delta 380 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ . The sensitivity of GPP to LAI exhibited a positive, non-significant correlation with MCWD ( $R^2=0.88$ ,  $p=0.06$ ; ~~Tanguro LAI sensitivity  $\Delta 286 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Kenia  $\Delta 345 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Tambopata  $\Delta 353 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ). Reflecting LAI trends, the sensitivity of GPP to differences in photosynthetic capacity (per unit  $\mu\text{mol C g s}^{-1}$ ) was similarly highest at Caxiuanã (~~Caxiuanã photosynthetic capacity sensitivity  $\Delta 27 \text{ gC m}^{-2} \text{ yr}^{-1}$ , mean photosynthetic capacity sensitivity  $\Delta 20 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Table 3~~), and decreased linearly (though not significantly) across the MCWD gradient ( $R^2=0.83$ ,  $p=0.09$ ; ~~Tanguro photosynthetic capacity sensitivity  $\Delta 16 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Kenia  $\Delta 18 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Tambopata  $\Delta 18 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ). Tambopata plots, which have high LAI but shallow rooting depth, were 435 most sensitive to differences in climate (per unit MCWD mm) ( ~~$3.44 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ), whilst Kenia plots, which have similarly shallow rooting depth but low LAI, were the least sensitive (~~Kenia climate sensitivity  $\Delta 1.64 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Tanguro  $\Delta 2.77 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Caxiuanã  $\Delta 1.78 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ). The sensitivity of GPP to differences in rooting depth (per m rooting depth) was highest at Tanguro and Tambopata (~~Tanguro rooting depth sensitivity  $\Delta 114 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Tambopata  $\Delta 79 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ), and lowest at 440 Caxiuanã and Kenia (~~Caxiuanã rooting depth sensitivity  $\Delta 28 \text{ gC m}^{-2} \text{ yr}^{-1}$ ; Kenia  $\Delta 20 \text{ gC m}^{-2} \text{ yr}^{-1}$~~ ).

### 3.5.3 Experiment 3. Drivers of Sub-Annual Variation in GPP

In contrast to drivers of spatial variation in GPP, on a sub-annual timescale LAI had less explanatory power than climate (Tables 6 and 7). The relative importance of solar radiation in driving monthly GPP increased significantly with MCWD ( $R^2 = 0.90$ ,  $p < 0.001$ ), whilst as the relative importance of LAI 445 declined ( $R^2=0.72$ ,  $p=0.015$ ). The relative importance of VPD did not vary directionally across the MCWD gradient ( $R^2=0.10$ ,  $p=0.49$ ). Both precipitation and air temperature had little effect on monthly GPP, though it is noted that a significant interaction existed between both precipitation and VPD ( $p < 0.001$ ) and air temperature and shortwave radiation ( $p < 0.001$ ). Furthermore, temperature varied least across plots in comparison to other climate forcings (standard deviation as a percentage of the mean; 450 temperature 9.8%, VPD 73%, precipitation 192%, shortwave radiation 34%). As such, seasonal changes in the relative importance of temperature and precipitation were not investigated further. The relative importance of LAI, VPD and solar radiation shifted seasonally, reflecting changes in the availability of light and water. Solar radiation was typically the most important driver of monthly GPP during the wet

**Commented [FS40]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

**Commented [FS41]:** R2 AR14. In response to the reviewers comment "- Section 3.5.2. This section is difficult to read because of the many numbers. Is presenting them in a table of figure an option?" The authors have moved the site specific  $\Delta$  values to Figure 6.

**Commented [FS42]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

season, whilst VPD was more important during the dry season (Figure 7). The relative importance of  
455 LAI forcings peaked before dry season onset for forests under lower drought stress (Caxiuanã and  
Tambopata), and during the dry season for forests under higher drought stress (Kenia and Tanguro).  
Notably, LAI was also more important during the dry season at KEN02, which occupies shallow soil  
(<1m) in comparison to KEN01.

## 4. Discussion

460 ~~Our aim was to better understand the mechanisms coupling GPP and drought stress across Amazon  
forests. We found that, leaf traits (both modelled and observed) and LAI co-varied along the MCWD  
gradient. Across observed ranges in key variables, LAI was the principal driver of spatial variation in  
GPP, followed by photosynthetic capacity (Q1). Forest sensitivity to differences in LAI and  
465 photosynthetic capacity decreased with increasing drought stress (Q2). Forests with higher evaporative  
potential (high LAI) relative to water supply were most sensitive to differences in climate and rooting  
depth. Solar radiation was a key driver of sub-annual variation in GPP, the relative effect of which  
increased with decreasing drought stress, coincident with declines in the relative importance of LAI,  
consistent with the evaluation from the sensitivity analysis (Q3).~~

### 4.1 LAI and Leaf Traits along the MCWD gradient

470 Leaf trait parameters retrieved from SPA litterfall calibrations suggest a wide range of potential leaf  
lifespans across the MCWD gradient (~1-3 years), and are in accordance with estimates for Amazon  
tree species, reported by Reich et al. (1991) of between two months and four years (Table 4). Leaf trait  
estimates co-varied across the MCWD gradient, in line with leaf economic theory (Wright et al., 2004).  
However, the interactions were often not significant. We suggest that in instances where  $R^2$  values  
475 indicate a large proportion of variation is explained, high p-values may have occurred as a result of a  
small sample size (i.e. 7 plots). As drought stress increased, a shift towards deciduous strategies resulted  
in reduced leaf lifespan, but higher photosynthetic capacity. The co-variation of leaf traits along the  
MCWD gradient shapes both the rate of carbon assimilation (via photosynthetic capacity), and the  
carbon economics of canopy dynamics (via LMA, leaf lifespan and metabolic rate). Coincident with

**Commented [FS43]:** R1 AR17. In response to reviewer comment "Line 401-410 This paragraph sounds like a conclusion, and since you have a Conclusion section, where this is also stated, I would suggest you delete this paragraph." Deleted as suggested

480 changes in leaf traits, mean annual LAI increased with decreasing drought stress. ~~Whilst~~ ~~Research~~  
efforts have focused on mapping LAI (Iio et al., 2014) and leaf trait (Kattge et al., 2011, Asner et al.,  
2015) distributions across climatic gradients, ~~however~~ their covariance has not yet been explored. Given  
the role of leaf traits in shaping canopy carbon economics, the mechanisms underpinning LAI and leaf  
trait distributions across the resource availability gradient could prove important in understanding the  
485 effect of changes in precipitation regime on future Amazon carbon dynamics.

**Commented [FS44]:** R1 AR31. In response to reviewer comment “In general, Please reconsider the usage of the word whilst – it reads a little pretentious.”  
Adjustments throughout

#### 4.2 Drivers of Spatial Variation in GPP

Indirect effects of climate via ecosystem structure and long-term trait responses to water availability accounted for 54% of variation in GPP (Q1; Figure 1). Direct effects of climate (which included physiological responses to water availability) accounted for only 16% of observed variance (Table 6).

490 Our results are consistent with previous reports on the importance of ecosystem structure and traits in determining spatial variation in GPP (Rodig et al., 2018, van de Weg et al., 2013, Reichstein et al., 2014), but go further to quantify the direct contribution of discrete drivers to observed variation in carbon assimilation. LAI explained the greatest proportion of variation in GPP, followed by photosynthetic capacity, ~~whilst~~ ~~Root~~ and soil properties had little explanatory power.

**Commented [FS45]:** R1 AR31. In response to reviewer comment “In general, Please reconsider the usage of the word whilst – it reads a little pretentious.”  
Adjustments throughout

495 Evidence of changes in LAI in response to precipitation regime has been presented across multiple ecosystems and over time (Grier and Running, 1977, Schleppi et al., 2011, Iio et al., 2014, Dobbertin et al., 2010, Wright et al., 2013). Amazonian forest throughfall exclusion experiments identified a decline in LAI with the onset of reduced soil water (Fisher et al., 2007, Meir et al., 2008, Brando et al., 2008). At Caxiuanã, over a 4-year period, observed leaf area was 20-30% lower than the control stand  
500 (Meir et al., 2009), with long-term reductions estimated at between 10-15% (Rowland et al., 2015a). Investigations show that declines in LAI are not caused by increased leaf turnover due to drought stress, but instead are the result of lower leaf production (Nepstad et al., 2002, Schuldt et al., 2011), suggesting an active response of plant allocation strategy to water availability. Concurrently, after 15 years under throughfall exclusion, Rowland et al. (2018) found that leaf litterfall still remained consistently lower.

**Commented [FS46]:** R1 AR18. In response to the reviewer comment

“Line 437-449 You mention how changes in LAI is a response to precipitations regimes, and even call it a key response mechanism. Then, one could infer that it is just as much changes in precipitation that explains the changes in GPP as it is LAI. You state that changes in LAI is an indirect effect from climate — although the impact might be somewhat delayed, but did you investigate lagged correlations and variances between precipitation and GPP?”

With respect to annual timescales the field data used were across 2 years only, limiting the scope to test for lag effects. However, this could certainly prove an interesting investigation for the future. Across sub-annual timescales we are unable to compare field estimates of GPP (due to the nature of biometric estimates), however model experiment 3 found that the effect of moisture stress was better captured via VPD (line 392).

505 Reported trends in canopy dynamics are therefore in accordance with our findings, and indicate that LAI is a key response mechanism to precipitation regime. ~~Whilst~~ ~~Other~~ studies such as da Costa et al.

(2018) have similarly pointed towards structural responses as the principal determinant of variation in GPP, however, they identify changes in sapwood area as the main driver, rather than LAI. We suggest that whilst sapwood area may be more important in shaping the response to temporal short term changes in precipitation, for forests at steady state, over longer timescales emergent canopy properties (LAI) drive GPP trends.

**Commented [FS47]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

Photosynthetic capacity also proved an important driver of spatial variation in GPP across the MCWD gradient. Our results are consistent with a number of Amazon-based studies linking leaf traits to productivity (Aragao et al., 2009, Cleveland et al., 2011, Castanho et al., 2013). Interestingly, the observed shifts in photosynthetic capacity along the gradient had a compensatory effect on the GPP-MCWD interaction. Reductions in GPP under high drought stress were alleviated by higher photosynthetic capacitance. Similarly, shifts in photosynthetic capacity in response to temperature have been reported to reduce spatial variation in GPP across a tropical elevation gradient (Bahar et al., 2017, van de Weg et al., 2013). Consistent with Fyllas et al. (2017), our results also show that the effect of climatic forcings on carbon fluxes can be successfully captured through spatial variation in canopy dynamics and leaf traits. However, as we have focused on the role of leaf traits in the absence of carbon cycle feedbacks, we do not take into account the effect of concurrent shifts in LMA and leaf lifespan, which together influence canopy carbon economics (Wright et al., 2004, Osnas et al., 2013, McMurtrie and Dewar, 2011). Furthermore, as nutrient dynamics are not directly accounted for in SPA, we are

**Commented [FS48]:** R1 AR19. In response to the reviewer comment "Line 452 You do not have a forest at steady state, if it is changing and experiencing trends. Please explain what you mean by a steady state forest – is it continuous cover, constant number of trees etc.? Or better yet refrain from using the term." Term omitted

unable to quantify the impact of soil nutrients on the GPP-MCWD interaction, beyond its manifestation in leaf traits. Nevertheless, the interaction between photosynthetic capacity and LAI proved important in driving variation in GPP across the MCWD gradient.

**Commented [FS49]:** Moved to limitations section.

Root depth, root biomass and soil properties had little direct effect on spatial variation in GPP. Whilst We recognise that the difficulty in measuring root depth and biomass (Metcalf et al., 2007) adds uncertainty to our results, however, the findings do not reflect the importance of belowground functioning highlighted by other studies (Fisher et al., 2007, Metcalfe et al., 2008, Baker et al., 2008, Phillips et al., 2009, Ichii et al., 2007). Notably, a number of GEM plots had hard pan layers (Quesada et al., 2012) so they may be acclimated to operate in shallow rooting zones, and are therefore not

**Commented [FS50]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

**Commented [FS51]:** R1 AR37. In response to reviewer comment "Line 473-774 Add they to the sentence: . . . so they may be acclimated. . ."

necessarily representative of other Amazon forests under the same precipitation regime. Differences in root depth and biomass can alleviate water constraints to photosynthesis via the direct physiological pathway (i.e stomatal conductance). But in the absence of C cycle feedbacks, changes in root depth and biomass do not drive changes in emergent canopy properties (i.e. LAI) which proved most important in determining GPP. However, it is therefore likely that given these drivers are largely associated with the acquisition of water, rather than carbon, if feedbacks were enabled within analyses, root and soil properties would prove to have a stronger effect.

### 4.3 Variation in Forest Sensitivity to Drivers of GPP

The sensitivity of GPP to differences in LAI, climate, photosynthetic capacity and rooting depth varied across the MCWD gradient with evaporative potential and water uptake capacity (Q2; Figure 6). As the model experiment was conducted in the absence of carbon cycle feedbacks, sensitivities reflect shorter rather than long-term effects of changes in forcings. The sensitivity of GPP to differences in LAI and photosynthetic capacity was greatest for forests occupying the lowest drought stress zone and declined with increasing drought stress. Our results are in agreement with findings from Wright et al. (2013), who reported that GPP was most sensitive to decreases in leaf area when water availability was highest. Forests with a high LAI (and therefore high evaporative potential) but shallow rooting depth were most sensitive to differences in climate. Our results suggest that where rooting depth is relatively shallow, and unable to ameliorate the effects of drought stress as seen elsewhere (Nepstad et al., 2007, Malhi et al., 2009a), forests with a high LAI could be more vulnerable to reduced precipitation. Investigations into the vulnerability of Amazon forests to drought have put a deservedly large emphasis on the role of physiological responses (Choat et al., 2012, Phillips et al., 2009, Bennett et al., 2015, Corlett, 2016). However, our results indicate that the role of ecosystem structure could also prove important, and that forests with a high evaporative potential (high LAI) but low water uptake capacity (shallow rooting depth) should be a focus for future studies.

**Commented [F552]:** R1 AR21. In response to reviewer comment "Line 477 It is unclear which analysis this sentence is referring to. Your analysis or the work by Quesada et al 2012 mentioned in the previous sentence? Please clarify and elaborate on this statement." This statement refers to the presented analysis (Experiment 1). Differences in root depth and biomass can alleviate water constraints to photosynthesis via the direct physiological pathway (i.e stomatal conductance). But in the absence of C cycle feedbacks, changes in root depth and biomass do not drive changes in emergent canopy properties (i.e. LAI) which proved most important in determining GPP. This is now clarified in the text.

#### 4.4 Drivers of Sub-Annual Variation in GPP

Seasonal (*i.e.* sub-annual) variation in GPP was driven by changes in solar radiation, VPD and LAI.

560 The relative importance of ~~which, these factors~~ was dependent on MCWD (Q3; Figure 7). Shortwave radiation was the dominant driver of sub-annual variation in GPP across plots, ~~and but~~ its relative ~~effect importance was greater for moister forests increased with decreasing drought stress~~ (Table 7). The relative importance of LAI in driving sub-annual GPP increased with drought stress. ~~In accordance with our findings, a~~ number of studies report that for Amazon forests ~~subject to significantly low annual rainfall, GPP declines with increased VPD, and in accordance with our findings,~~ in higher rainfall zones, 565 GPP increases in line with solar radiation, ~~and for forests subject to significantly low annual rainfall GPP declines with increased VPD~~ (Von Randow et al., 2013, Goulden et al., 2004, Hutrya et al., 2007, Saleska et al., 2003, Rowland et al., 2014, Carswell et al., 2002). Our results suggest that LAI is not the principal driver of sub-annual ~~variation~~ in GPP, in contrast to its role in driving spatial variation 570 across the MCWD gradient. However, ~~while~~ other studies agree that leaf area alone does not drive variation in sub-annual GPP (Wu et al., 2017, Wu et al., 2016, Brando et al., 2010, Restrepo-Coupe et al., 2013, Bi et al., 2015), we ~~fail do notto~~ account for potential shifts in photosynthetic capacity with leaf age. The coordination of leaf age (via leaf flushing and new leaf emergence) with climatic drivers such as solar radiation is thought to exceed the effects of LAI in non-water limited forests (Myneni et al., 2007). We further recognise the uncertainty introduced through using leaf N content to derive 575 photosynthetic capacity estimates (for five of the seven plots), given the distribution of leaf N between photosynthetic and non-photosynthetic proteins is not fixed (Onoda et al., 2017). However, notwithstanding ~~the effects of~~ temporal variation in photosynthetic capacity, we demonstrate that the relative importance of ~~canopy-LAI~~ dynamics and climatic forcing driving variation in GPP, shift with 580 light and water availability.

Our results indicate that with respect to drought stress, annual GPP is constrained via indirect pathways (i.e. ecosystem structure and traits) across spatial scales, but is limited via direct pathways (i.e. physiology) across sub-annual timescales (Figure 1). [In a study on net ecosystem exchange (NEE), Richardson et al., (2007) found that indirect pathways became progressively more important in driving

585 NEE as the period of integration was lengthened (for a spruce-dominated forest in Maine, USA). The  
authors reasoned that the shift from direct to indirect pathways (as the period of integration transitions  
through day-week-month-seasonal-annual), reflected the timescales over which these processes  
operate. Stomata vary at hourly time scales with meteorology and soil conditions. The shift in direct to  
indirect pathways driving GPP variance reported here can similarly be explained by the difference in  
590 timescales over which responses to drought stress operate. LAI varies over monthly timescales,  
constrained by C and nutrient investment requirements over years. As a result, over monthly timescales,  
up to one third of variation in GPP was explained by indirect effects of climate (i.e. LAI; Table 7), but  
direct effects (via physiological responses) remained the dominant driver (consistent with Richardson  
et al., 2007). Across the drought stress gradient, structural and trait responses to water availability  
595 (across annual to decadal timescales) result in indirect pathways dominating the GPP response, and the  
direct effects of climate are less important. Our results indicate that with respect to soil moisture, GPP  
is demand limited across spatial scales, but is supply limited across sub-annual timescales.

#### 4.5 Limitations and Opportunities

600 As nutrient dynamics are not directly accounted for in SPA, we are unable to quantify the impact of soil  
nutrients on the GPP-MCWD interaction. Soil nutrient availability varied widely across plots (Table 1).  
We recognise that nutrient limitation likely impacts GPP across the MCWD gradient, effected through  
both nutrient availability and plants acquisition capacity (which is dependent on moisture-stress).  
However, there was no significant interaction between GPP and soil phosphorous (GEM  $R^2=0.1$ ,  
605  $p=0.48$ ; SPA  $R^2=0.01$ ,  $p=0.81$ ) or soil nitrogen (GEM  $R^2=0.37$ ,  $p=0.14$ ; SPA  $R^2=0.31$ ,  $p=0.19$ ).  
Furthermore, we expect to capture soil nutrient effects via the inclusion of site specific leaf nutrient  
estimates as a model inputs (which influence simulated photosynthetic and metabolic rate).

We recognise that the lack of significant correlation between SPA and GEM GPP estimates could  
impact the interpretation of our results. However, we argue that five of the seven plot estimates were  
within the error bounds of field measurements, and that the inferential statistics used were limited by  
610 our small sample size ( $n=7$ ). We also note that GEM GPP error estimates (calculated as the propagated  
standard error of component NPP and respiration measurements) do not account for assumptions used

**Commented [FS53]:** R1 AR22 In response to the reviewer comment "Line 515 What do you mean by GPP is demand limited across spatial scale? Is it the atmospheric transpirational demand? And how does this relate to your already conducted analysis of you results? According to your own analysis, LAI is explaining most of the variation across the spatial scale (sec. 3.5.1, sec. 3.5.2, and 4.2). You must elaborate on the statement."  
This statement referred to the role of ecosystem structure and traits (i.e. demand) in determining spatial variation in GPP, in comparison to the supply limit observed across sub-annual timescales. However we recognise that the statement was unclear and have amended it.

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**Commented [FS54]:** R1 AR20. In response to reviewer comment "Line 465-468 With the SPA model you are not able to quantify the impact of soil nutrient on the GPP-MCWD interactions because you lack nutrient cycling in the SPA model. However, according to Table 1 there is a huge P gradient across your sites, therefore please discuss how this could possible affect your results."  
Discussion on nutrient limitation is now included.

**Commented [FS55]:** Moved from section 4.4

in scaling biometric measurements to plot level (e.g. uncertainty in using estimated total woody surface area to scale stem CO<sub>2</sub> efflux measurements).

615 Given the importance of LAI in driving variation in GPP, data on canopy dynamics is critical to  
constrain carbon flux estimates across the Amazon basin. Our approach utilised field estimates of LAI  
620 from hemispherical photographs to constrain model simulations. The accuracy and spatial validity of  
indirect estimates of LAI has been questioned at higher leaf areas (Bréda, 2003, Jonckheere et al., 2004,  
Weiss et al., 2004). In this study, we expect that if field measurements of LAI were underestimated at  
higher leaf areas, the proportion of spatial variation in GPP explained by LAI would increase, as a result  
625 of increased variation in both field-measured and model simulated GPP. Yet, our highest estimates of  
LAI (Caxiuanã  $5.11 \pm 1.41 \text{ m}^2\text{m}^{-2}$ ) align with destructive sampling measurements from a terra-firme  
Amazon forest (McWilliam et al. (1993)  $5.7 \pm 0.5 \text{ m}^2\text{m}^{-2}$ ). Furthermore, a comparison of LAI estimation  
approaches (Asner et al., 2003) suggested that indirect methods were appropriate for broadleaved  
forests, and presented no statistical difference between destructive harvesting and indirect methods.  
630 However, the use of ground measurements is limited to smaller spatial scales, and LAI estimates across  
the basin are needed to constrain carbon flux estimates. ~~Whilst-Though~~ the interpretation of forest  
responses to drought stress through remote sensing approaches have caused controversy (Asner and  
Alencar, 2010, Saleska et al., 2007, Samanta et al., 2010), an increase in canopy mapping through  
satellite missions could be instrumental to efforts aiming to better understand LAI dynamics. Current  
635 and upcoming satellite missions including FLEX (FLuorescence EXplorer), GEDI (Global Ecosystem  
Dynamics Investigation) and Sentinel will offer opportunity for new insights into changes in leaves *in-  
situ*, vertical canopy structure, and temporal variability via repeat measurements (Morton, 2016, Drusch  
et al., 2017, Pettorelli et al., 2018). Efforts to map trait distributions will also prove important (Kattge  
et al., 2011, Asner et al., 2015) given their role in driving variation in GPP.

## 635 5. Conclusion

We show that indirect effects of climate (via ecosystem structure and trait responses) exceed direct  
effects (via physiological responses) in driving spatial variation in GPP across an Amazon MCWD  
gradient (Q1). Conversely, across sub-annual timescales, the reverse was true (Q3). The relative

**Commented [FS56]:** R1 AR15. In response to the reviewers comment "Line 320-325 The correlation between GEM estimated and SPA simulation GPP are non-significant and moderate. As GPP is imperative for your analysis, have you considered the impact it might have on you results? Have you investigated how the GEM estimated GPP relates to the LAI from the hemispherical photographs?" Discussion on the GEM-SPA GPP comparison and its potential impact is now included in the limitation sections. In response to the reviewers question, GPP estimates are not significantly correlated with LAI ( $R^2=0.18$ ,  $p=0.33$ ), likely due to concurrent shift towards higher photosynthetic capacity at drier sites.

**Commented [FS57]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout



sensitivity of GPP to changes in direct and indirect forcings shifted across the MCWD gradient and was  
640 dependent on water availability, demand and acquisition potential (Q2). We identify the potential  
vulnerability of forests with a high evaporative potential (i.e. high LAI), but low water uptake capacity  
(i.e. shallow rooting depth), to changes in precipitation regime. Given the role of LAI in driving GPP  
across the drought stress gradient, we highlight a requisite for improved mapping of canopy dynamics  
(via remote sensing). We propose that ecosystem model development should focus on the integration  
645 of structural and trait responses to drought stress (alongside physiological responses). The inclusion of  
both direct and indirect effects of climate in ecosystem models, would reduce current uncertainty in  
predicted annual and sub-annual GPP for tropical forests.

**Commented [FS58]:** R1 AR24 In response to the reviewer comment "Line 544-546 Something is wrong with this part of sentences. Please rephrase." Rephrased.

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#### **Supplementary Material**

Supplementary material is included in a separate document.

**Authorship Contributions** Sophie Flack-Prain, Mathew Williams and Patrick Meir conceived the  
research questions. Data used in model calibration and validation was collected by Yadvinder Malhi  
655 and associates. Model experiments were designed and conducted by Sophie Flack-Prain with  
contributions from Mathew Williams and Thomas L. Smallman. Sophie Flack-Prain and Mathew  
Williams prepared the manuscript with active contributions from all co-authors.

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**Commented [FS62]:** R1 AR25. In response to the reviewers comment "Line 576 According to the manuscript preparation guidelines for authors for Biogeoscience, Journal names are to be abbreviated according to the Journal Title Abbreviations by Caltech Library (see [https://www.biogeosciences.net/for\\_authors/manuscript\\_preparation.html](https://www.biogeosciences.net/for_authors/manuscript_preparation.html) )."

Now corrected

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## Tables

1480 Table 1. Amazonian Forest Inventory Network (RAINFOR) site code and Environmental characteristics of GEM network Amazon permanent sample plots across the MCWD gradient. Meteorological data is from local weather stations, gap filled with ERA interim data for the years 2009-2010 (Dee et al., 2011).

Plot name	Caxiuanã Control	Caxiuanã Tower	Tambopata V	Tambopata VI	Kenia Wet	Kenia Dry	Tanguro Control
<b>RAINFOR site code</b>	CAX04	CAX06	TAM05	TAM06	KEN01	KEN02	---
Latitude	-1.716	-1.737	-12.831	-12.839	-16.016	-16.016	-13.077
Longitude	-51.457	-51.462	-69.271	-69.296	-62.73	-62.73	-52.386
Elevation (m.a.s.l)	47		223		384		385
Mean Maximum Climatological Water Deficit (mm)	-85.5		-256		-342		-498

**Commented [FS63]:** R1 AR46. In response to reviewer comment "Would it be possible to add species composition or just dominant species at each site to the table?" This could be added. However, species richness varies between 65 and 195 across plots, with the most common species typically accounting for less than 20% of stems.

**Commented [FS64]:** R1 AR42. In response to reviewer comment "Line 996-999 Table 1: Please include the abbreviation of RAINFOR in the Table 1 text."

**Commented [FS66]:** R1 AR44. In response to reviewer comment "Is there no site code for Tanguro?" No, it is not on the RAINFOR database (though RAINFOR does hold data on other Tanguro plots).

**Commented [FS65]:** R1 AR43. In response to reviewer comment "Should RAINFOR be above the second horizontal line?" No, the row name should read 'RAINFOR site code'. This has been resolved by adding a hyphen.

Mean annual air temperature (°C)	26.1	24.6	23.4	25.4			
Soil Type	Vetic	Ferralsol	Cambisol	Alisol	Cambisol	Cambisol	Ferralsol
	Acrisol						
Soil N (%)	0.06	0.13	0.16	0.17	0.22	0.17	0.16
Soil P <sub>total</sub> (mg kg <sup>-1</sup> )	37.4	178.5	256.3	528.8	447.1	244.7	147

**Commented [FS67]:** R1 AR45. In response to reviewer comment "Please use correct degree symbol for the unit of Mean annual air temperature" Now corrected.

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Table 2. Summary of the relationship between model variables and field data. Values are either a SPA model parameter (input) or output. Model parameters may be initial conditions ~~subsequently allowed to fluctuate~~, a fixed value, or a time-series, whereby the parameter value at each time point is prescribed to the model. Model outputs are generated on either an hourly or daily time-step and are presented in the text as the mean annual sum (2009-2010), unless otherwise stated. Model outputs are calibrated or evaluated using field data. Values are specific to each of the seven GEM Amazonian permanent sample plots.

**Commented [FS68]:** R1 AR26. In response to reviewer comment "Line 1010 Table 2, delete 'subsequently allowed to fluctuate'. This is already implied by being initial conditions." Deleted as suggested

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Value	Model Parameter or Output	Source of Value or Calibration/Validation Data
LMA	parameter (single fixed)	GEM plot-measured value or literature-based estimate from plot species list
V <sub>max</sub>	parameter (single fixed)	(estimate from) GEM plot-measured value or TRY database estimate from plot species list

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<b>J<sub>max</sub></b>	parameter (single fixed)	(estimate from) GEM plot-measured value or TRY database estimate from plot species list
<b>Leaf N content</b>	parameter (single fixed)	GEM plot-measured value or TRY database estimate from plot species list
<b>LAI</b>	parameter (timeseries fixed)	GEM monthly plot-measured value
<b>Leaf NPP</b>	output	model calibration to GEM plot-measured leaf litterfall and LAI
<b>Wood NPP</b>		
<i>fraction of total NPP</i>	parameter (single fixed)	GEM plot-measured value
<i>total wood NPP</i>	output	simulated value validated against GEM field-measured total wood NPP
<b>Root NPP</b>		
<i>fraction of total NPP</i>	parameter (single fixed)	GEM plot-measured value
<i>total root NPP</i>	output	simulated value validated against GEM field-measured total root NPP

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<b>Leaf turnover</b>	parameter (single fixed; function of three individual fixed parameters relating to the leaf litterfall cycle)	model calibration to GEM plot-measured leaf litterfall
<b>Root turnover</b>	parameter (single fixed)	estimated using root NPP assuming steady state conditions
<b>Wood turnover</b>	parameter (single fixed)	estimated using wood NPP assuming steady state conditions
<b>Foliar C stock</b>	parameter (timeseries fixed)	product of LAI and LMA
<b>Wood C stock</b>	parameter initial condition; thereafter output	initial condition uses GEM plot-measured DBH values converted to C stock using allometric equation output calculated in SPA as simulated wood C stock plus NPP minus turnover
<b>Root C stock</b>	parameter initial condition; thereafter output	initial condition used GEM plot-measured root stock values or literature-based estimate output calculated in SPA as simulated root C stock plus NPP minus turnover

<b>Leaf respiration</b>	output	sum of leaf maintenance and growth respiration; maintenance respiration generated using measured leaf N content, foliar C stock and the Reich <i>et al.</i> , (2008) leaf respiration model, validated against GEM estimates; growth respiration calculated in SPA as leaf NPP $\times$ 0.28
<b>Wood respiration</b>	output	sum of wood maintenance and growth respiration; maintenance respiration calculated as a function of wood C stock, the coefficient being derived from GEM estimates; growth respiration calculated in SPA as wood NPP $\times$ 0.28
<b>Root respiration</b>	output	sum of root maintenance and growth respiration; maintenance respiration calculated as a function of root C stock, the coefficient being derived from GEM estimates; growth respiration calculated in SPA as root NPP $\times$ 0.28
<b>Respiration</b>	output	sum of simulated leaf, wood and root respiration, evaluated against GEM data
<b>GPP</b>	output	generated through SPA process-based modelling of GPP using detailed parameters, evaluated against GEM data

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**NPP**                      output                      calculated in SPA as GPP minus autotrophic  
respiration, evaluated against GEM data

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1505 Table 3. Field estimated mean annual leaf area index (LAI), leaf traits, maximum rooting depth and fine root biomass for Amazon permanent sample plots along a MCWD gradient. LAI estimates were derived from monthly hemispherical photographs. LAI, leaf trait and rooting depth estimates were used to constrain SPA model runs. Estimate standard errors are presented in brackets. Fine root C stock estimates were absent for Tanguro plots.

	<b>LAI</b> (m <sup>2</sup> m <sup>-2</sup> )	<b>LMA</b> (g m <sup>-2</sup> )	<b>leaf N content</b> (g m <sup>-2</sup> )	<b>Maximum</b> <b>Rooting</b> <b>Depth (m)</b>	<b>Fine Root</b> <b>C Stock</b> (g C m <sup>-2</sup> )
<b>CAX04</b>	4.99 (± 1.07)	93 (± 17)	1.82 (± 0.43)	8	345
<b>CAX06</b>	5.23 (± 0.92)	87 (± 54)	2.12 (± 0.7)	10	433
<b>TAM05</b>	4.85 (± 0.81)	101 (± 24)	2.38 (± 0.56)	1	770



<b>TAM06</b>	4.64 ( $\pm$ 0.77)	96 ( $\pm$ 21)	2.51 ( $\pm$ 0.64)	1	500
<b>KEN01</b>	2.77 ( $\pm$ 0.17)	53 ( $\pm$ 13)	2.12 ( $\pm$ 0.25)	2	818
<b>KEN02</b>	2.22 ( $\pm$ 0.14)	42 ( $\pm$ 13)	2.31 ( $\pm$ 0.31)	1	607
<b>Tanguro</b>	4.13 ( $\pm$ 1.01)	64 ( $\pm$ 13)	2.01 ( $\pm$ 0.52)	<10	-

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Table 4. SPA calibrated leaf litterfall parameters for plots across an Amazon MCWD gradient. Peak leaf fall is the day of year leaf litterfall reaches its maximum, leaf lifespan reflects maximum lifespan of leaves and leaf fall period is the number of days over which systematic increases in leaf fall occur. Leaf litterfall parameters were calibrated against GEM field estimates to capture leaf litterfall and timing.

	<b>Peak Leaf Fall</b> (day of year)	<b>Leaf Lifespan</b> (years)	<b>Leaf Fall Period</b> (days)
<b>CAX04</b>	210	3.00	150
<b>CAX06</b>	190	1.45	100
<b>TAM05</b>	220	1.30	130
<b>TAM06</b>	230	1.42	100

<b>KEN01</b>	200	1.05	100
<b>KEN02</b>	180	1.01	100
<b>Tanguro</b>	180	1.04	120

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Table 5. A comparison of GEM field measurements and SPA process-based modelling estimates of component autotrophic respiration and NPP. We present the  $R^2$ , p-value, and root mean square error (RMSE) of the interaction between SPA and GEM annual estimates, together with the range in GEM biometrically derived estimates across seven sample plots at four locations in the Amazon basin.

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<b>Component</b>	<b><math>R^2</math></b>	<b>p-value</b>	<b>RMSE</b>	<b>Range in Field Estimates (<math>\text{gC m}^{-2} \text{yr}^{-1}</math>)</b>
<b>Respiration</b>				
Foliage	0.47	0.09	92.0	454-830
Wood	0.75	0.01	100.5	411-1054
Fine Root	0.91	<0.001	74.1	232-1041
<b>NPP</b>				
Foliage	0.99	<0.001	9.0	150-491

Wood	0.21	0.30	25.3	189-292
Fine Root	0.59	0.04	49.5	189-418

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Table 6. The proportion of variation in GPP across seven GEM Amazonian permanent sample plots explained by photosynthetic drivers in SPA. Model drivers were alternated individually at each plot to that of all other plots and the resultant change in GPP retrieved. Proportion of variance explained was calculated as conditional sum of squares divided by the total sum of squares (n=476; where the conditions were LAI, photosynthetic capacity, rooting depth, root biomass, climate and soil).

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<b>Driver</b>	<b>Percentage of Variation Explained (%)</b>
LAI	32.8
Photosynthetic capacity	21.3
Climate	16.2
Root depth	4.1
Soil	1.2
Root biomass	0.7

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Table 7. The relative importance of LAI, VPD, solar radiation, precipitation and air temperature ( $T_{\text{air}}$ ) in driving monthly variation in GPP (%). Monthly GPP estimates are derived from calibrated SPA simulations for seven permanent sample plots across an Amazon MCWD gradient, constrained using monthly field LAI measurements. Relative importance values were derived from analyses using the random forest technique (n=168).

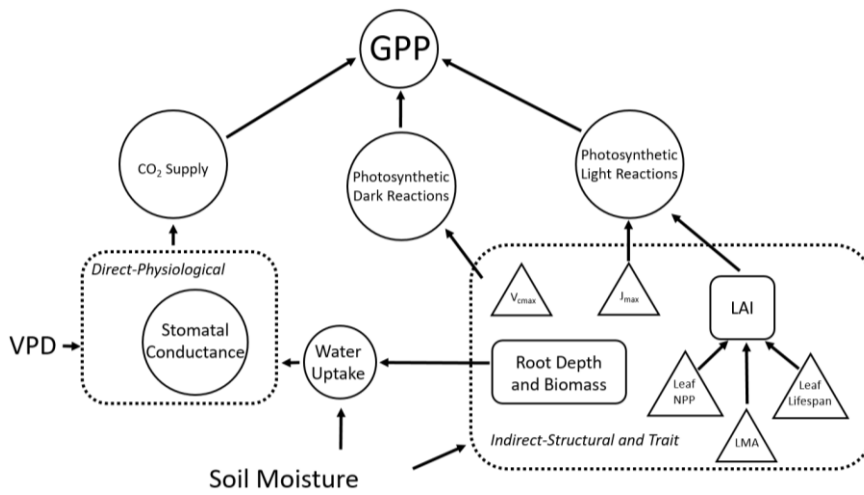
<b>Plot</b>	<b>LAI</b>	<b>VPD</b>	<b>Solar Radiation</b>	<b>Precipitation</b>	<b>T<sub>air</sub></b>
CAX04	13	17	58	8	5
CAX06	6	16	64	8	5
TAM05	17	22	53	3	5
TAM06	17	21	53	3	7
KEN01	16	21	45	10	8

KEN02	32	14	42	4	8
Tanguro	33	20	24	6	10

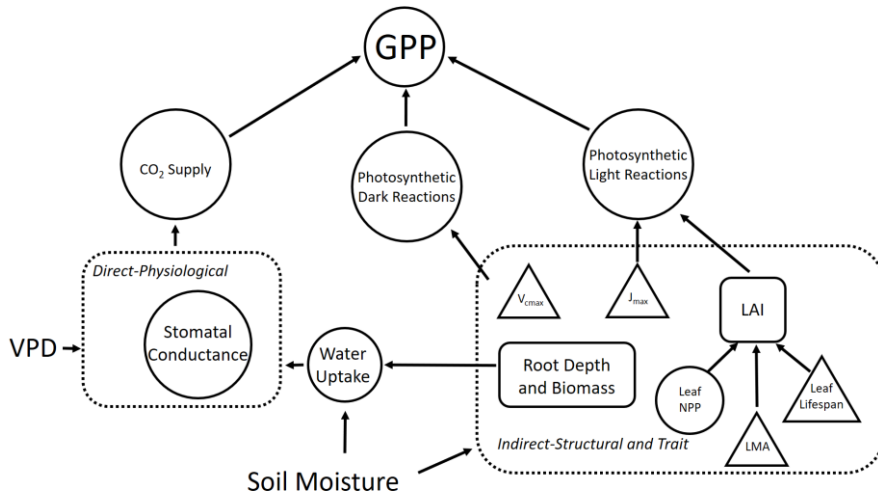
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### Figures



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**Commented [FS69]:** R1 AR27. In response to reviewer comment "Line 1095 Figure 1, NPLeaf does not classify as a trait. Please correct the figure accordingly." Corrected

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Figure 1. A schematic of the direct and indirect effects of drought stress ~~(~~via soil moisture and VPD on GPP. Drought stress affects GPP directly via stomatal conductance, and indirectly through its determinant effect on plant traits and structural properties. Plant processes are represented by circles, traits are represented by triangles and vegetation properties (i.e. ecosystem structure) are represented by rectangles. Dashed boxes identify interactions driving the direct and indirect pathways through which drought stress impacts GPP. We note that other climate forcings (e.g. shortwave radiation and temperature) impact GPP but are not included here.

**Commented [FS70]:** R1 AR47. In response to reviewer comment "Line 1095 Please delete the single parenthesis in this line."

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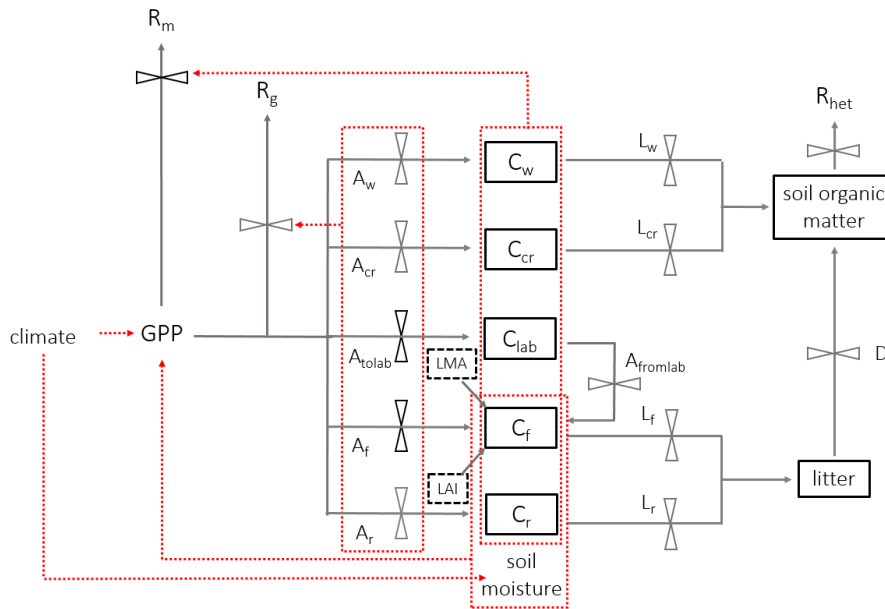


Figure 2. A schematic of DALECCanopy, the carbon allocation sub-model integrated within the soil-plant-atmosphere model. Carbon moves between pools (solid boxes) via fluxes (solid arrows). Leaf carbon fluxes are constrained by field measurements (black dashed boxes). An effect of climate, carbon pools or fluxes on another carbon flux is shown by a red dashed arrow, whereby red dotted boxes indicate a collective impact of the contained carbon pools or fluxes. Black flux bars indicate that the carbon pathway is prioritised within the model above pathways from the same **node**. Climate is a model input, **whilst and** soil moisture is simulated within SPA. Carbon pools (C), allocation (A) and litterfall (L) are separated by component: w = wood, cr = coarse roots, r = fine roots, f = foliage, lab = labile (or non-structural carbon), with to and from used for labile carbon.

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**Commented [FS71]:** R1 AR48. In response to reviewer comment "Line 1112 Please correct nodule to module." This was supposed to refer to 'nodule' however as this does not read well we have changed it to node.

**Commented [FS72]:** R1 AR31. In response to reviewer comment "In general, Please reconsider the usage of the word whilst – it reads a little pretentious." Adjustments throughout

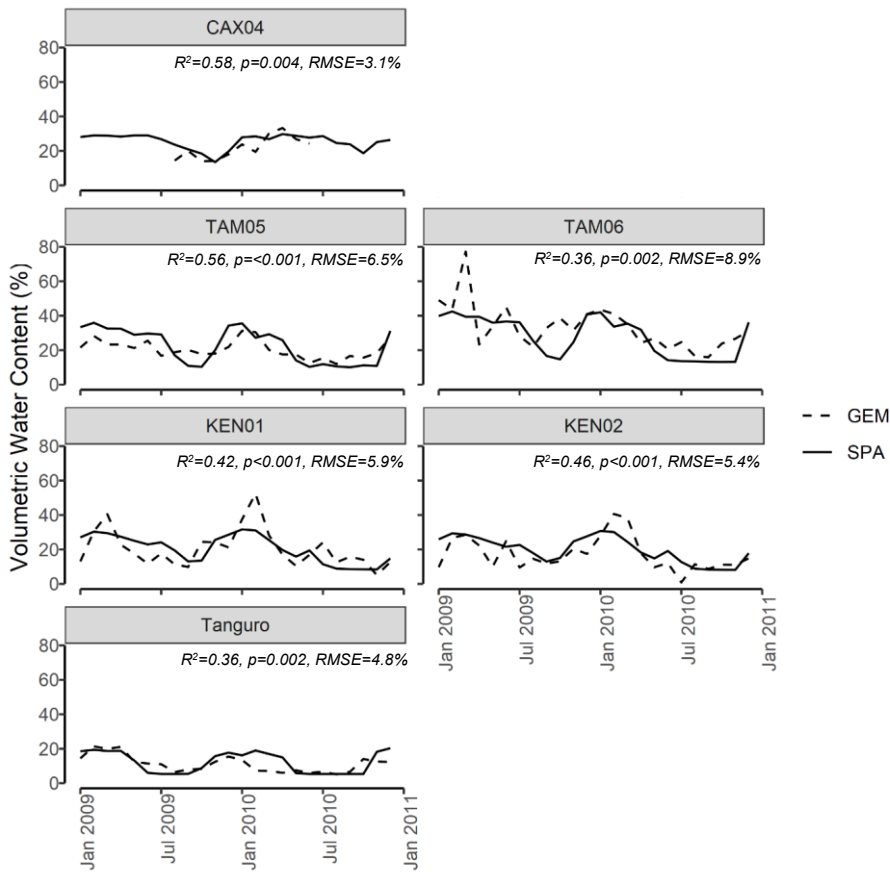
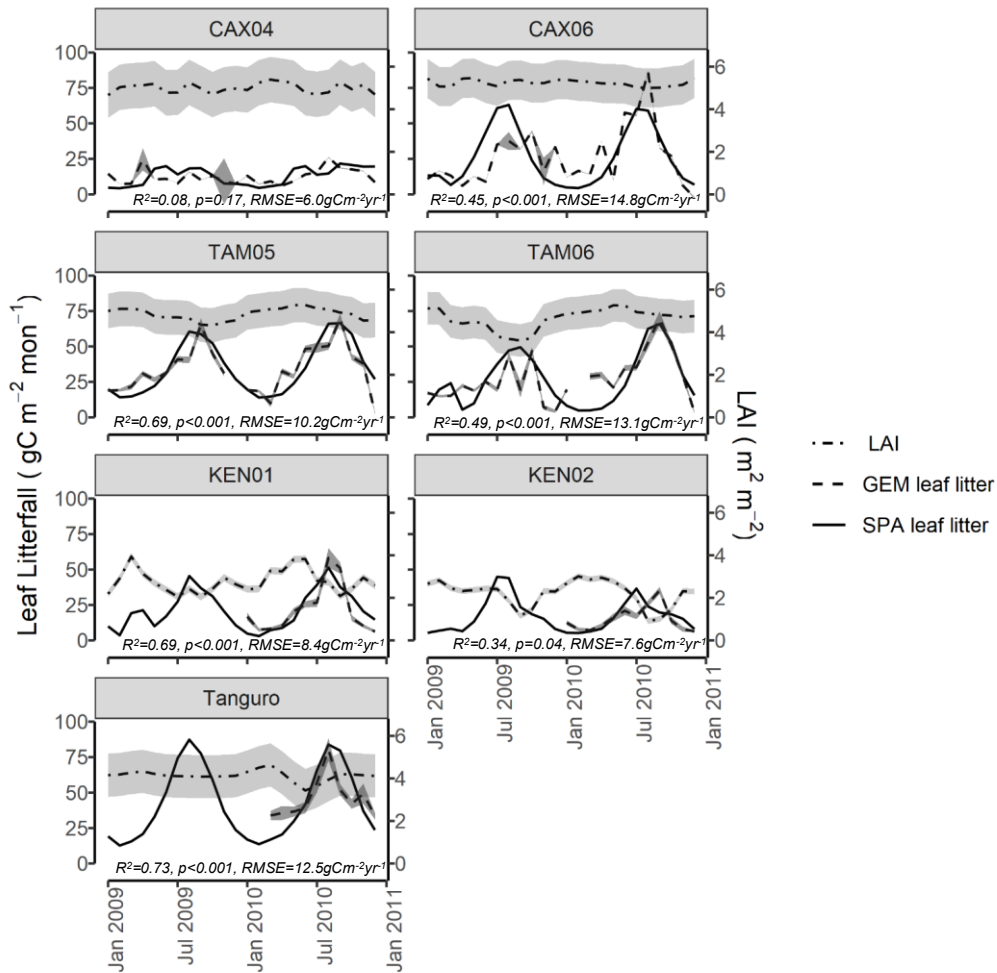


Figure 3. SPA estimated soil volumetric water content compared to GEM measured values for six of the seven sample plots at four locations across the Amazon basin. Data presented is for the time period 2009-2010. Field data for CAX04 was limited to a shorter time period and for CAX06 was unavailable.  $R^2$ , p-value and RMSE estimates presented are derived from linear regressions between monthly GEM measurements and SPA simulations.

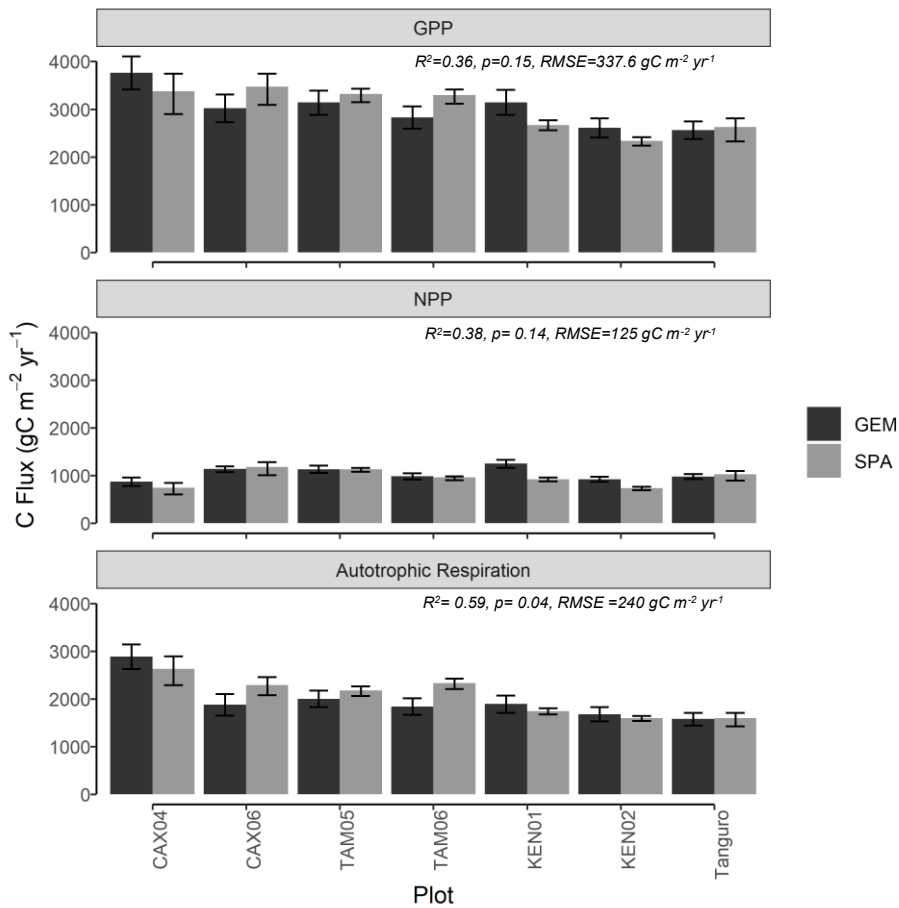




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Figure 4. Field estimated monthly LAI, leaf litterfall (GEM), and standard error, compared with SPA simulated leaf litterfall for seven plots at four locations across the Amazon basin. SPA leaf litterfall was calibrated against GEM estimates to derive three fixed model drivers relating to the leaf cycle (peak leaf fall timing, leaf fall period and leaf lifespan). GEM leaf litterfall data was available for 2009-2010 for CAX04, CAX06, TAM05, TAM06 and for 2010 only for KEN01, KEN02 and Tanguro. R<sup>2</sup>, p-value and RMSE estimates presented are derived from linear regressions between monthly GEM measurements and SPA simulations.

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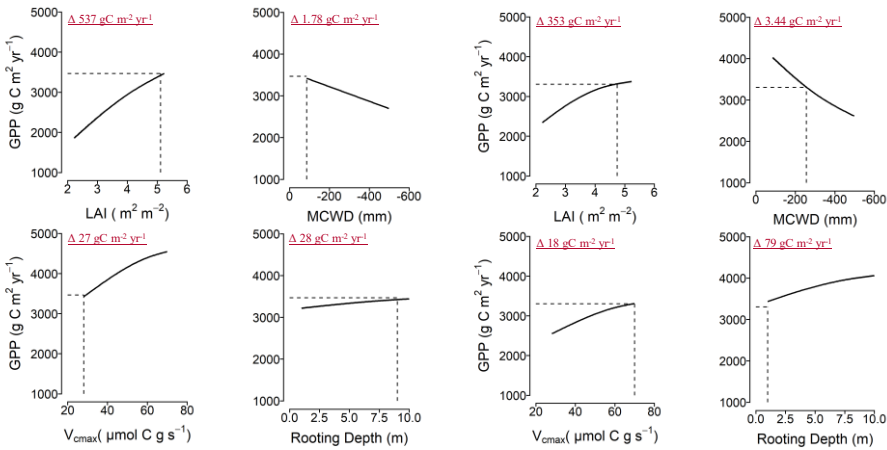


1620 Figure 5. Carbon flux estimates ( $\text{gC m}^{-2} \text{yr}^{-1}$ ) of (a) GPP, (b) NPP and (c) autotrophic respiration, derived  
 from process-based modelling (SPA) and biometric methods (GEM) for seven permanent sample plots  
 at four locations across the Amazon basin. Estimates are mean annual values representative of the years  
 2009-2010. GEM error bars represent standard error from field carbon flux measurements. SPA error  
 bars represent simulated C fluxes under the upper and lower field LAI standard error.  $R^2$ , p values and  
 1625 RMSE represent the interaction between SPA and GEM C flux estimates.

Caxiuană

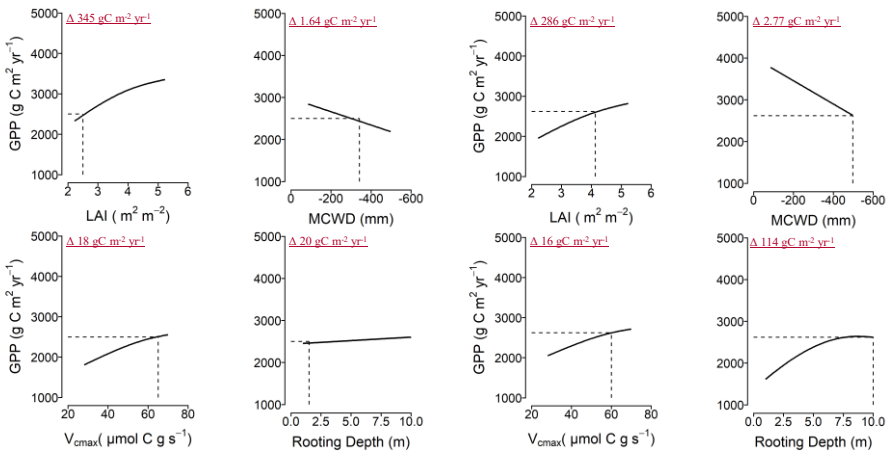
Tambopata

**Commented [FS73]:** R2 AR14. In response to the reviewers comment “- Section 3.5.2. This section is difficult to read because of the many numbers. Is presenting them in a table of figure an option?”  
The authors have moved the site specific  $\Delta$  values to Figure 6.



Kenia

Tanguro



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Figure 6. The sensitivity of GPP to model driver alternations in SPA at each location. Model drivers LAI, climate (characterised by MCWD), photosynthetic capacity (characterised by  $V_{\text{cmax}}$ ) and rooting depth, derived from field observations, were alternated individually at each plot to that of all other plots and the resultant GPP retrieved. Solid lines represent SPA simulated GPP under the named driver alternations, whilst the dashed line represents the simulated value under observed conditions. SPA

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**Commented [FS74]:** R1 AR31. In response to reviewer comment “In general, Please reconsider the usage of the word whilst – it reads a little pretentious.”  
Adjustments throughout

GPP estimates presented are location averages. Climate and LAI were input to the model as timeseries, ~~while~~ P photosynthetic capacity and rooting depth were fixed values. Plots are ordered to reflect soil moisture-stress which increases from Caxiuanã >Tambopata>Kenia>Tanguro. The range in GPP estimates under each set of driver alternations, for each location is presented (i.e.  $\Delta$  values).

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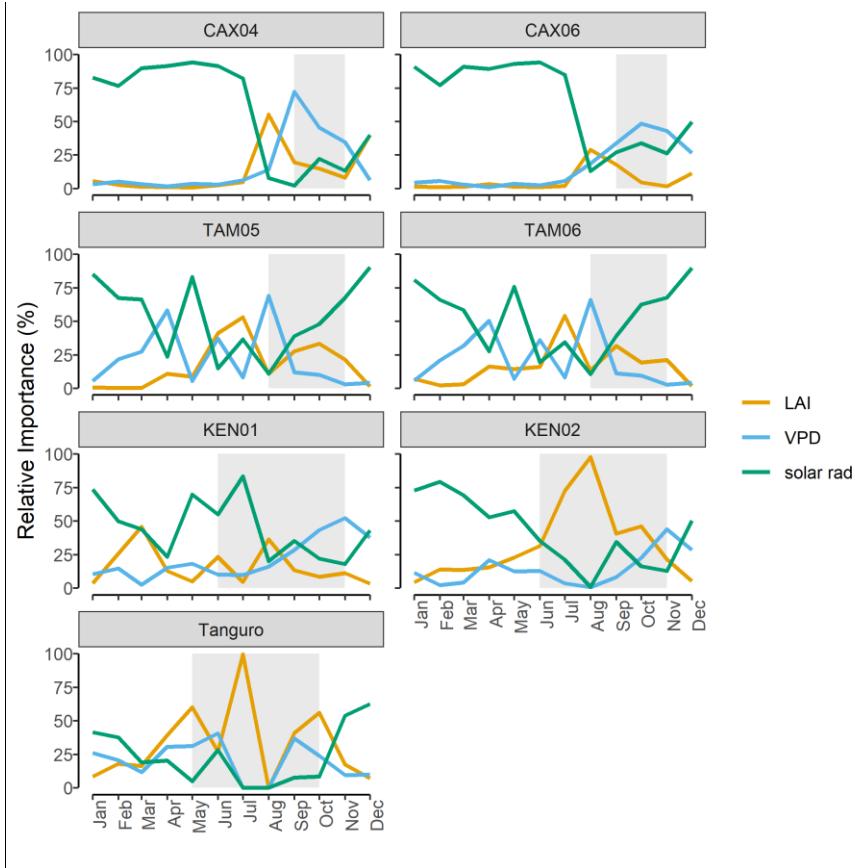


Figure 7. The relative importance (%) of LAI, vapour pressure deficit (VPD) and solar radiation (solar rad) in driving SPA estimated monthly photosynthesis at permanent sample plots across an Amazon MCWD gradient. Relative importance was calculated using random forest machine learning. Shaded regions represent the dry season, where monthly precipitation was below 100mm. Plots are ordered to reflect drought stress which increased from Caxiuana> Tambopata> Kenia> Tanguro.

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## Supplementary Material

### Plot Characteristics

1670 Data from the Global Ecosystem Monitoring (GEM) network were used from seven one-hectare  
permanent sample plots at four locations across the east and west Amazon (Table 1). Differences  
between soil and species composition at each location were sufficient to avoid significant  
pseudoreplication effects (1, 2). The two north eastern plots (CAX04 and CAX06) are located in the  
Caxiuanã National Forest in Pará State, Brazil. These relatively infertile, slow-growing but high  
1675 biomass plots (~ 200 MgC ha<sup>-1</sup>) are typical of the eastern Amazon. Plots typically experience a long but  
modest intensity dry season from July to December, when rainfall does not exceed 100mm mon<sup>-1</sup> (3,  
4). CAX04 is located on sandy loam, vetic Acrisol soil (all soil classifications applied here are World  
Reference Base Classification (FAO 2014)), whereas CAX06 occupies a clay-rich Ferralsol, causing  
species composition to differ between plots (2, 5). The south western Peruvian plots (TAM05 and  
1680 TAM06) of the Tambopata Biological Reserve in the Madre de Dios region are subject to a moderate  
dry season from May to September (6). The region's geomorphology is a result of it being situated on  
old floodplains of the Tambopata River (7). TAM05 is located on a Pleistocene terrace (7), whilst the  
palm rich forest of TAM06 is located on a Holocene floodplain (6). Soils at TAM05 are relatively  
infertile Cambisols compared to the more fertile Alisols found at TAM06 (8). The Bolivian plots (KEN01  
1685 and KEN02) located in the Hacienda Kenia in Guarayos Province, Santa Cruz, experience a strong dry  
season between April and September and occupy the transition zone between humid Amazonian forests  
and *chiquitano* dry forests (9). Both plots are situated on relatively fertile sandy loam Cambisols (2),  
though soil depth varies, with KEN01 positioned on deeper soil in a slight topographic depression  
(Table 3), whilst KEN02 occupies more shallow soil over Precambrian rock (7), leading to a difference  
1690 in species composition between plots (9). The south eastern plot of the Fazenda Tanguro, Mato Grosso  
State was subject to an intense dry season between May and September. The old growth forest plot sits  
close to the dry forest- savannah transition zone (2) and occupies relatively infertile sandy Ferralsol soil  
(7).

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### SPA Leaf Respiration Model

The Reich, Tjoelker (10) model predicting leaf respiration as a function of leaf N content was integrated into SPA. In align with the approach taken by Atkin, Bloomfield (11), we also adjust the baseline respiration rate as a function of the temperature during the warmest quarter:

$$b = 1.025 - 0.036 \text{ WQ} \quad (1)$$

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$$\text{leaf}_{\text{resp}} = 10^b N_{\text{leaf}}^{1.411} \quad (2)$$

$$\text{leaf}_{\text{resp}_t} = 2.0^{0.1(T_{\text{air}}-20)} \text{leaf}_{\text{resp}} \quad (3)$$

$$\text{leaf}_{\text{resp}_{\text{total}}} = C_{\text{leaf}} \times 2 \times \text{leaf}_{\text{resp}_t} \quad (4)$$

Where:

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$b$  is a nitrogen scalar to account for differences in WQ, WQ is the temperature ( $^{\circ}\text{C}$ ) during the warmest quarter,  $\text{leaf}_{\text{resp}}$  is the respiration rate of leaves ( $\text{nmol g}^{-1}$  leaf mass  $\text{s}^{-1}$ ),  $N_{\text{leaf}}$  is the nitrogen content of the leaf ( $\text{mmol g}^{-1}$  leaf mass),  $\text{leaf}_{\text{resp}_t}$  is the temperature adjusted respiration rate ( $\text{nmol g}^{-1}$  leaf mass  $\text{s}^{-1}$ ),  $T_{\text{air}}$  is air temperature ( $^{\circ}\text{C}$ ),  $\text{leaf}_{\text{resp}_{\text{total}}}$  is the total leaf respiration ( $\text{nmol g}^{-1}$   $\text{s}^{-1}$ ), and  $C_{\text{leaf}}$  is the foliar C stock ( $\text{gC m}^{-2}$ ).

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### SPA Non-Structural Carbon Pool

For the purpose of the presented study, LAI was forced in model runs. Where leaf NPP requirements could not be met by daily C assimilated, leaf growth was supplemented by the labile carbon pool as follows:

$$\text{NPP}_i = \text{GPP}_i - \text{Ra}_i \quad (5)$$

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$$\text{NPP}_{\text{leaf}_i} = (\text{LAI}_i - \text{LAI}_{i-1}) \times \text{LCA} \quad (6)$$

$$\text{If } \text{NPP}_{\text{leaf}_i} > \text{NPP}_i \Rightarrow \quad (7)$$

**Commented [FS75]:** R1 AR29. In response to reviewer comment "Please consider numerating your equations if the LAI is forced using monthly time series, then how does the LAI change between the daily time steps in the calculations for NPPLeaf i? Is it because you nudge the LAI, and hence not force it at every time step? Please clarify." Numbering added. See AR 10 for clarification on LAI change at each timestep.

**Commented [FS76]:** R1 AR30. In response to reviewer comment "As mentioned already, the three latter equations are confusing. If the labile pool is depleted ( $\text{NSCi} < \text{NSCi}-1$ ) then you allocate from the total NPP pool to the labile pool. I assume that this is only the case when  $\text{NPPLeaf}_i$  is met by the daily assimilation? Please clarify and complete your sets of equations for all cases" Please see AR 5.

**Commented [FS77]:** R1 AR28 Corrected

$$\underline{NSC_i = NSC_{i-1} - (NPP_{leaf_i} - NPP_i)} \quad (8)$$

$$\underline{\text{If } NSC_i < NSC_{cap} \text{ AND } NPP_{leaf_i} < NPP_i \Rightarrow} \quad (9)$$

$$\underline{NPP_{i+1} = NPP_{i+1} - NSC_{frac}} \quad (10)$$

$$\underline{NSC_{i+1} = NSC_i + NSC_{frac}} \quad (11)$$

Where:

NPP is modelled net primary productivity, GPP is modelled gross primary productivity, Ra is modelled autotrophic respiration,  $NPP_{leaf}$  is modelled leaf net primary productivity, LAI is the field estimated leaf area index, LCA is the field estimated leaf C content per unit leaf area, NSC is the non-structural carbon pool,  $NSC_{frac}$  is the fraction of NPP redirected towards the NSC pool,  $NSC_{cap}$  is the NSC pool capacitance, and i is the daily timestep.

### Calculation of Maximum Climatological Water Deficit

We calculate maximum climatological water deficit (MCWD) in line with the equations presented in Arago et al. (2007):

$$\underline{\text{If } WD_{n-1} - E + P_n \leq 0 \Rightarrow} \quad (12)$$

$$\underline{WD_n = WD_{n-1} - E + P_n} \quad (13)$$

$$\underline{\text{Else } WD_n = 0} \quad (14)$$

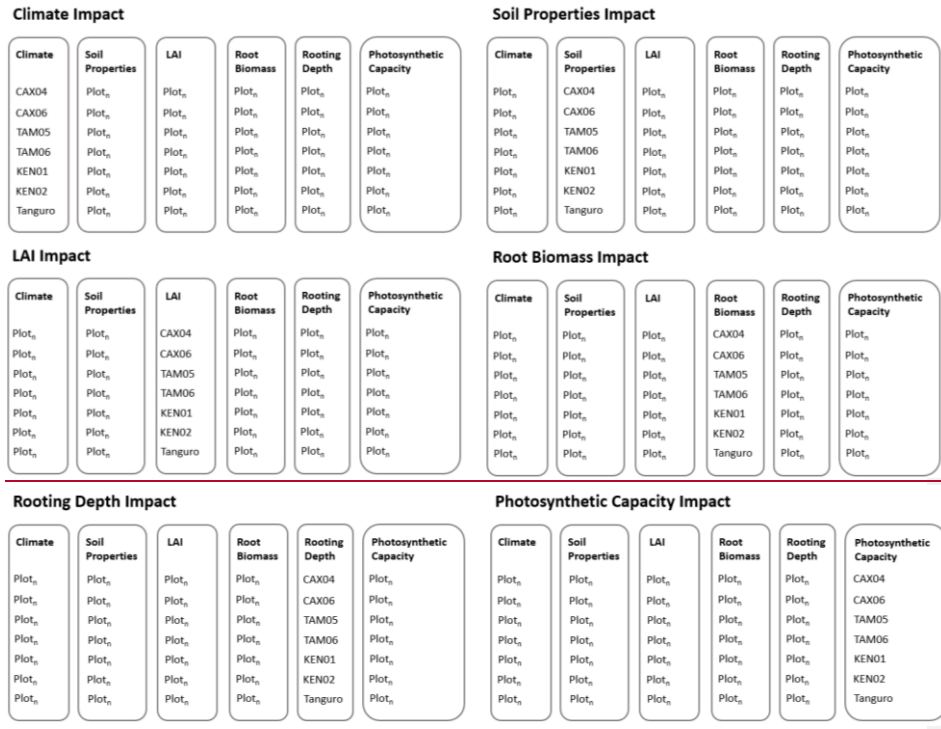
Where:

WD is the water deficit for each month (n), E is evapotranspiration (assumed to be 100 mm month<sup>-1</sup>), and P is precipitation (mm month<sup>-1</sup>).

**Commented [FS78]:** R1 AR5. In response to the reviewer comment "Several times you briefly mention the C allocation (line 232 to 241, Fig. 2 and Supplement material). In the text you state that allocation to  $NPP_{leaf}$  occurs first. Normally NPP is considered a flux, and normally you would allocate to a pool. Thus, do you mean that allocation to the foliar stock occurs first? If assimilation does not provide the C need for allocation to support the LAI, you take from the labile/non-structural carbon pool. However, in the supplement material in the last three equations, you state that if the labile pool has been depleted you allocate from the total NPP. Surely this must only be the case when you have enough NPP to sustain the foliar stock as required by the LAI. Please clarify this in the manuscript."  
The reviewer is correct in their summation of the C allocation scheme. Allocation towards NSC storage is executed in subsequent time steps when the  $NPP_{leaf}$  requirement does not exceed total NPP. This is now clarified in these equations and in the manuscript.



**Experimental Model Runs**



1740 **Figure S1. Model experimental design to apportion variation in simulated GPP to that driven by differences in (i) climate, (ii) soil properties, (iii) LAI, (iv) root biomass and (v) rooting depth, and (vi) trait responses driven by photosynthetic capacity ( $V_{cmax}$  and  $J_{max}$ ). For a given plot i.e. Plot<sub>n</sub>(CAX04, CAX06, TAM05, TAM06, KEN01, KEN02, Tanguro), model inputs (i-vi) were alternated to that of all other plots, and the simulated GPP retrieved.**

1745 **References**

Atkin, O. K., Bloomfield, K. J., Reich, P. B., Tjoelker, M. G., Asner, G. P., Bonal, D., Bönisch, G., Bradford, M. G., Cernusak, L. A., and Cosio, E. G.: Global variability in leaf respiration in relation to climate, plant functional types and leaf traits, *New Phytologist*, 206(2), 614-636, 2015.

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**Commented [FS79]:** R2 AR4. In response to the reviewer comment “The model methodology is explained insufficiently to allow for independent reproducibility of the results and for understanding what the authors really did.”

A new figure has been added to the supplementary material detailing the inputs of each model run used in the analysis. We hope this figure helps sufficiently explain our methodology. However, we would be happy to consider further changes if the reviewer could provide more information on which details they believe to be missing.

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- 1765 [Fisher, R. A., Williams, M., Da Costa, A. L., Malhi, Y., Da Costa, R. F., Almeida, S., and Meir, P.: The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment, \*Global Change Biology\*, 13\(11\), 2361-2378, 2007.](#)
- [Malhi, Y., Amezquita, F. F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., Aragão, L. E. O. C., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora, L., Marthews, T. R., Halladay, K., Quesada, C. A., Robertson, A. L., Fisher, J. B., Zaragoza-Castells, J., Rojas-Villagra, C. M., Pelaez-Tapia, Y., Salinas, N., Meir, P., and Phillips, O. L.: The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru, \*Plant Ecology & Diversity\*, 7\(1-2\), 85-105, 2014.](#)
- 1770 [Malhi, Y., Aragão, L. E., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C., and Meir, P.: Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest, \*Proceedings of the National Academy of Sciences\*, 106\(49\), 20610-20615, 2009.](#)

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