Global patterns of forest autotrophic carbon fluxes

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Abstract

Introduction

Carbon fixation, allocation, and metabolism by trees sets the basis for energy and material flows in forest ecosystems and defines their interactions with Earth's changing climate. Forest autotrophic carbon flux (FACF) influences all organic matter stocks in ecosystems and is linked to cycling of energy, water, and nutrients (**REFS**). Forest productivity sets the energy available to heterotrophic communities, in turn influencing their abundance (**REFS**) and possibly diversity (**REFS**)–but probably not individual metabolic rate (**Anderson & Jetz 2005, but check more recent literature**). On the global scale, forests play a critical role in regulating atmospheric CO_2 and climate (**Bonan**). The total amount of CO_2 cycling through Earth's forests each year (*i.e.*, total gross primary production, *GPP*) is more than five times anthropogenic fossil fuel emissions, and net sequestration (~2.4 $GtCyr^{-1}$) offsetting roughly 30% of these emissions (Pan et al., 2011). As atmospheric carbon dioxide levels continue to rise, with consequences for global climate, there is increasing recognition that proper protection and management of forest resources will have an important role to play in mitigating climate change (** REFS- e.g., IPCC 1.5C and land reports**). Given the importance of understanding broad-scale patterns in forest autotrophic carbon flux (FACF), there have been many meta-analyses on the theme. However, our ability to draw general macroscopic conclusions regarding global variation in multiple productivity variables with respect to climate has been limited in that these analyses often mix forests that vary in stand age, disturbance history, and/or management status; do not always sufficiently parse related variables (*e.g.*, combining net primary productivity records with and without belowground components); and typically consider only one or a few variables at a time. The recent development of a global forest carbon database synthesizing multiple variables and including records of stand history (ForC; (Anderson-Teixeira et al., 2016, 2018)) opens up the possibility for a standardized analysis of global scale variation in multiple components of forest productivity and the principle climatic drivers of these patterns.

On a global scale, the productivity of forests varies with latitude, showing a general trend of decreasing productivity with latitude (Beer et al., 2010; Jung et al., 2011). Studies agree that productivity is lowest in the boreal regions, and increases into the temperate regions (Luyssaert et al., 2007; Huston and Wolverton, 2009; Beer et al., 2010; Jung et al., 2011). However, evidence is inconclusive on whether productivity continues to increase into the tropics, or whether it plateaus in temperate regions. Evidence for this is further complicated by the fact that different studies use different measures of productivity to explore these relationships. For example, modelling of global terrestrial ecosystem gross primary productivity (GPP) through upscaling and calibration of eddy flux measurements indicates that GPP peaks in tropical forests (Beer et al., 2010; Jung et al., 2011);Bagdley et al. 2019). This is corroborated by analysis of site-level GPP measurements, which appear to reach their highest levels in tropical forests (Luyssaert et al., 2007). In contrast, there is evidence that the highest values of net primary productivity (NPP) may be found in temperate forests (Luyssaert et al., 2007; Huston and Wolverton, 2009), although other studies find NPP is highest in the tropics, showing a decrease with latitude (Šímová and Storch, 2017). Other studies have chosen to focus exclusively on above-ground net primary productivity (ANPP), finding evidence of a weak negative relationship between ANPP and latitude (Huston and Wolverton, 2009; Gillman et al., 2015). An understanding of the global patterns of productivity is important; however elucidating the drivers of these patterns will be even more valuable in expanding our understanding of global carbon cycling. Primary productivity can be influenced by many factors, which often act across a range of scales, and may show interactive effects with each other. On a local scale, stand age (Litton et al., 2007; Gillman et al., 2015), management (Šímová and Storch, 2017); nutrient availability (Aragão et al., 2009); and altitude (Girardin et al., 2010; Malhi et al., 2017) all impact forest productivity. On a global scale, we expect that productivity is most strongly influenced by broad climatic gradients.

We know from previous research that climate is a significant driver of productivity across broad spatial scales (Cleveland et al., 2011). The majority of studies have focused on exploring the relationships between productivity and mean annual temperature (MAT) and mean annual precipitation (MAP), as the most commonly reported site-level climate variables. These variables have the advantage that they describe broad trends in temperature and water availability, and therefore capture a lot of global-scale variation in climate. There is strong evidence that both MAT and MAP show significant positive relationships with productivity (Chu et al., 2016). However, as with latitude, the shape of those relationships is not always clear, and, again, is complicated by the use of different measures of productivity across studies. There is support across multiple studies for the hypothesis that various measures of primary productivity saturate at high levels of MAP, though the saturation points identified vary from 1500mm (Luyssaert et al., 2007) up to 2445mm MAP (Schuur, 2003). Studies of the influence of MAT on productivity are less conclusive. Luyssaert et al. (2007) examined GPP and NPP and found that, while GPP increases linearly with MAT, NPP saturates at around 10°C MAT. In contrast, Larjavaara and Muller-Landau (2012), find that increases in GPP saturate at approximately 25°C MAT, while Schuur (2003) shows that NPP increases linearly with temperature. The influence of these climate variables on productivity is further complicated by the possibility of interactive effects occurring between them. Taylor et al. (2017) showed that increased MAP had a negative effect at low MAT, but a positive effect at high levels of MAT, and vice versa, suggesting that both temperature and water availability are important in explaining productivity.

While MAT and MAP are important climate variables, they do not capture all aspects of climate that may influence productivity, and may be insufficient to capture the breadth of climatic effects on productivity (Cleveland et al., 2011). There is evidence that productivity also responds to variables such as cloud cover (Taylor et al., 2017), solar radiation (Fyllas et al., 2017), and potential evapotranspiration (Kerkhoff et al., 2005) in potentially significant ways. Furthermore, MAT and MAP are very coarse measures of climate, and so fail to capture much variation in climate on an intra-annual scale, including the effects of factors such as growing season length, number of frost-free days, temperature seasonality, and dry season length. Some studies have suggested that the apparently strong relationship between MAT and productivity is actually a factor of the correlation between MAT and growing season length (Kerkhoff et al., 2005; Malhi, 2012; Michaletz et al., 2014, 2018). Kerkhoff et al. (2005) and Michaletz et al. (2014) find that, within the growing season, there is no significant relationship between productivity and MAT, indicating that the effect of temperature is due to increased length of growing season, rather than an inherent influence of temperature on productivity.

In order to approach these broad and complex issues, we simplify the major gaps in our knowledge to five key questions and corresponding specific predictions (Table 1). Firstly, we ask how forest autotrophic carbon fluxes (FACF) vary with latitude. We then test how these fluxes relate to MAT and MAP, and additionally how they respond to other, less well studied, climate variables. We finally consider the relationship between FACF and seasonality, considering the role of seasonality in explaining variation in carbon fluxes, and the influence of climate on FACF per month of the growing season.

Resolving these questions requires data which, firstly, control for variables influencing productivity, including stand age, disturbance regime, elevation, and methodology; and secondly includes all major carbon fluxes. Here we use a comprehensive global database of forest carbon fluxes to explore the above questions for nine carbon fluxes, allowing for an in-depth exploration of the effect of climate on global productivity.

Table 1: Hypothesis table

Hypotheses & Specific Predictions	Related references	Overall	Forest autotrophic carbon fluxes (FACF)									Support
			GPP	NPP	ANPP	BNPP	ANPP foliage	ANPP woody stem	BNPP fine root	R auto root	R auto	
H1. FACF decreases linearly with latitude.												
1.1. FACFs decrease linearly with latitude (L-)	Luyssaert et al. (2007)	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Fig. 2-3
1.1.alt. FACFs are similar in tropical and temperate forests, but lower in boreal regions (CD-)	Gillman et al. (2015); Simova and Storch (2017)	no	no	no	no	no	no	no	no	no	no	Fig. 2-3
1.2. Allocation to FACFs varies with latitude	Litton et al. (2007); DeLucia et al. (2007)	no	-	no	no	no	no	no	no	-	-	
H2. FACF increases with MAT, with an interactive effect of MAP.												
2.1. FACFs increase linearly with MAT (L+)	Schuur (2003)	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Fig. 5
2.2. FACFs increase with precipitation but saturate or decrease at very high levels (CD+)	Luyssaert et al. (2007); Schuur (2003)	yes	yes	yes	yes	yes	yes	()	L+	L+	yes	Fig. 5
2.3. There is a postive interaction between temperature and precipitation (I+)	Taylor et al. (2016)	(yes)	yes	L+	yes	I-	L+	yes	I-	yes	yes	Fig. 4
H3. FACF are strongly correlated with other annual climate variables.												
3.1. FACFs increases with PET, but saturates or decreases at high levels (CD+)		(yes)	yes	yes	yes	yes	L+	yes	L+	yes	L+	Fig. 5
3.2. FACFs increase with vapour pressure deficit, but saturate or decrease at high levels (CD+)		(yes)	yes	yes	yes	yes	yes	yes	L+	yes	yes	Fig. 5
3.3. FACFs increase linearly with solar radiation (L+)		(yes)	yes	yes	yes	CD+	yes	CD+	yes	()	yes	
H4. FACF is reduced under seasonal climates.												
4.1. FACFs decrease linearly with temperature seasonality (L-)		yes	CU+	CU+	CU+	yes	yes	yes	yes	CU+	CU+	Fig. 5
4.2. FACFs decrease linearly with precipitation seasonality (L-)		no	()	()	()	()	()	()	()	()	()	
4.3. FACFs increase linearly with growing season length (L+)	Malhi (2012); Michaletz et al. (2014); Chu et al. (2016)	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Fig. 5
4.4. Growing season length is a better predictor of FACFs than MAT	Michaletz et al. (2014); Chu et al. (2016)	no	no	no	no	no	no	no	no	no	no	
H5. Considering only growing season months, FACF correlates with climatic drivers.												
5.1. Increase with temperature (L+)	Michaletz et al. (2014)	(mixed)	()	()	yes	()	yes	()	()	()	()	
5.2. Increase with PET (L+)		(yes)	yes	yes	()	yes	()	yes	yes	()	()	
5.3. Increase with precipitation (L+)		no	()	()	yes	()	yes	()	()	()	()	
5.4. Increase with solar radiation (L+)		(mixed)	yes	yes	()	yes	()	()	yes	()	()	

Materials and Methods

Analyses were conducted on data contained in the open-access ForC database (Anderson-Teixeira et al., 2016, 2018). This database contains records of field-based measurements of forest carbon stocks and annual fluxes, compiled from original publications and existing data compilations and databases. Associated data, such as stand age, measurement methodologies, and disturbance history, are also included. The database was significantly expanded since the publication of (Anderson-Teixeira et al., 2018) through integration with the Global Database of Soil Respiration (Bond-Lamberty and Thomson, 2010). Additional targeted literature searches were conducted to identify any further available data on primary productivity, with particular focus on mature forests in temperate and boreal regions. ForC currently contains 29730 records from 4979 plots, representing 20 distinct ecozones across all forested biogeographic and climate zones. We used ForC v3.0, archived on Zenodo with DOI 10.5281/zenodo.3403855.

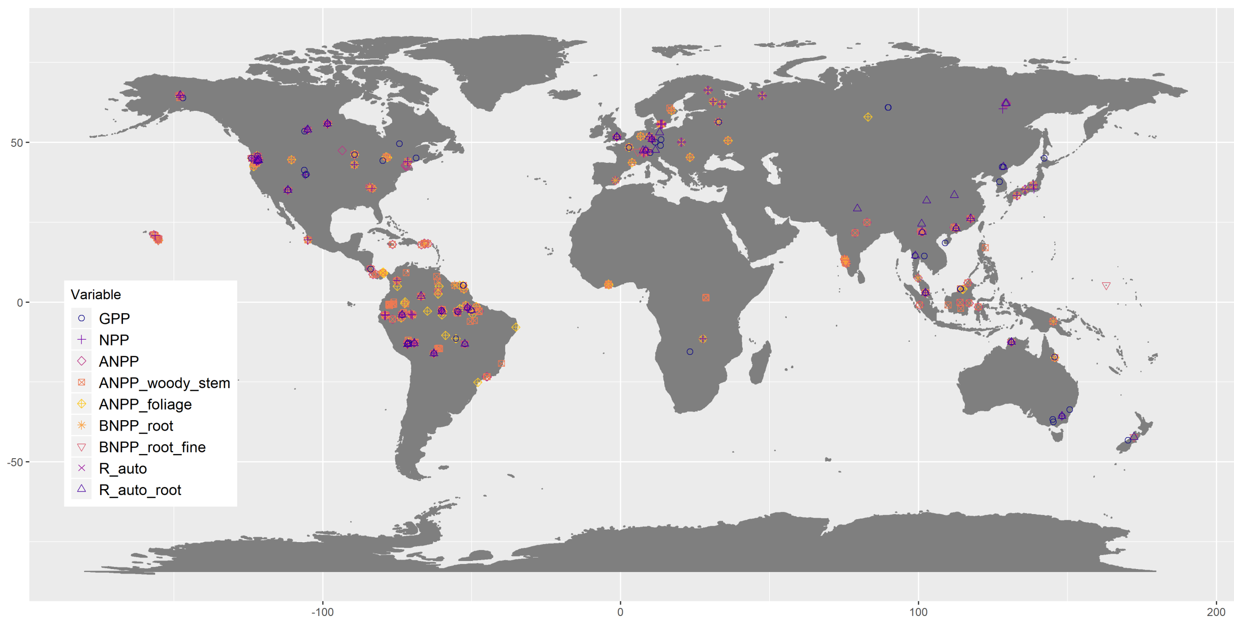

Figure 1: Map showing all data used in the analysis, coded by variable

Data selection. Over 50 variables of forest carbon stocks and annual fluxes are represented in the ForC database; this analysis focussed on measures of primary productivity. Table 1 contains details of the variables selected for analysis.

Table 2: Definitions and sample sizes of variables used in analysis. Geographic areas group geographically proximate sites, defined using a hierarchical cluster analysis on the distance matrix of the sites, and a cutoff of 25km.

Variable	Definition	Components included	Methodologies used	Number of records	Number of geo-graphic areas
GPP	Annual gross primary production; annual uptake of carbon dioxide by an ecosystem	NA	Flux partitioning of eddy covariance	243	49

Variable	Definition	Components included	Methodologies used	Number of records	Number of geographic areas
NPP	Annual net primary production; the component of GPP that is stored in plant tissue; $GPP - R_{auto}$	Foliage, branch, stem, coarse root and fine root	Direct measurement of annual increments of components	92	42
$ANPP$	Aboveground net primary production	Foliage, stem, and optionally branch	Direct measurement of annual increments of components	256	80
$ANPP_{foliage}$	Net primary production of foliage	Foliage	Direct measurement of litterfall, correcting for changes in leaf biomass when measured	98	49
$ANPP_{woody-stem}$	Net primary production of woody stems	Woody stems	Direct measurement of stem growth increment	264	96
$BNPP_{root}$	Belowground net primary production	Coarse and fine roots	Direct measurement of one or more of: fine root turnover, soil cores, root ingrowth cores, minirhizotrons; indirect estimates of coarse roots using allometries based on aboveground stem increment measures	101	48
$BNPP_{fine.root}$	Net primary production of fine roots	Fine roots	Direct measurement of one or more of: minirhizotrons, fine root turnover, soil cores, root ingrowth cores	88	41
R_{auto}	Annual autotrophic respiration, including above- and belowground components	Foliage, stem, and root	Chamber measurements of component gas exchange	22	13
R_{root}	Annual root respiration	Coarse and fine roots	*Measurement of root gas exchange, root exclusion from soil respiration chambers*	64	26

A subset of the ForC database was generated for the purposes of this analysis, in order to control for data quality and remove biasing factors. Since management can alter observed patterns of primary productivity

(Šímová and Storch, 2017), sites were excluded from analysis if they were managed, defined as plots that were planted, managed as plantations, irrigated, fertilised or including the term "managed" in their site description. Sites that had experienced significant disturbance were also excluded. Disturbances that justified site exclusion were major cutting or harvesting, and/or burning, flooding, drought and storm events with site mortality >10% of trees. Grazed sites were retained.
There is evidence that stand age influences patterns of primary productivity and carbon allocation in forest ecosystems, and can confound relationships between latitude and primary productivity (De Lucia et al., 2007; Gillman et al., 2015). To reduce any biasing effects of stand age, stands under 100 years of age were excluded from analysis. Sites for which stand age was unknown were excluded from analysis.

Methodological consistency. The data in ForC is derived from a range of studies, often employing different methods. For this reason, criteria were introduced to standardise for differences in methodology. Where data was based on forest plot census measurements, studies which used a minimum diameter at breast height (DBH) measure of >10cm were excluded from analysis. It would be preferable to standardise by minimum area sampled; however x% of plots in the database are 1 ha or under in size; excluding these plots would place significant constraints on sample size.

As discussed above, estimates of NPP, $ANPP$, and $BNPP$ are generated through summing measurements of their component parts. Since the components included in productivity estimates vary between studies, estimates of productivity were classified within the ForC database according to their components, and then filtered for analysis. Estimates of NPP were selected if they included foliage, branch, stem, coarse root, and fine root. Measures of NPP which included additional components, including understorey, volatile organic compounds (VOCs), exudates, estimates of NPP lost to herbivory, and the NPP of reproductive structures, were excluded. Estimates of ANPP were selected if they included foliage, stem growth and optionally branch turnover. Any measures of primary productivity where components were unknown were excluded from analysis.

Climate datasets. Where site-level data on mean annual temperature, mean annual precipitation, and latitude were available in the primary literature, this data was compiled and entered directly into the ForC database. Based on the geographic co-ordinates for each site, data on a further 11 climate variables was extracted from five open-access climate datasets: WorldClim (Hijmans et al., 2005), WorldClim2 (Fick and Hijmans, 2017), the Climate Research Unit (CRU) time-series dataset v. 4.03 (Harris et al., 2014), the Global Aridity Index and Potential Evapotranspiration Climate Database (Trabucco and Zomer, 2018), and TerraClimate (Abatzoglou et al., 2018) (see Supplementary Information S1 for details of climate variables). Where site-level data was missing for mean annual temperature and/or mean annual precipitation, data was extracted from the WorldClim dataset.

Additionally, two climate variables were derived from the above datasets: maximum vapour pressure deficit, defined as the vapour pressure deficit of the month with the largest deficit; and water stress months, defined as the number of months annually where precipitation was lower than potential evapotranspiration.

Length of growing season. Growing season months were defined as months with mean minimum temperature $> 0.5°$C. Growing season months were initially calculated following methods used by Kerkhoff et al. (2005), which additionally required that growing season months had a moisture index, defined as (MAT - PET)/PET, > -0.95. Michaletz et al. (2014) included an equivalent requirement in their calculation of growing season length. However, we found that including this requirement had no effect on the estimates of growing season length, and so chose to exclude it.

Monthly data for PET, precipitation, and temperature was downloaded from the Climate Research Unit (CRU) time-series dataset v 4.03 (Harris et al., 2014), and for solar radiation from WorldClim2 (Fick and Hijmans, 2017), and used to calculate mean monthly PET, precipitation, temperature and solar radiation during the growing season. Total growing season precipitation and solar radiation were also calculated.

Model specification. The effects of climate and latitude on primary productivity were analysed using mixed effects models using the package 'lme4' (Bates et al., 2015) in R v.3.5.1 (R Core Team, 2018). The effect of each extracted climate variable on each measure of primary productivity was modelled by specifying the climate variable as a fixed effect. For each climate variable, three models were specified: a null model; a model with the climate variable as a linear term; and a model with the climate variable as a polynomial term. AIC values were calculated for the models and used to select the best model. If the best model included a polynomial term, the shape of the polynomial relationship was considered. If the shape of the relationship *made biological sense*, and was a significant improvement on the linear relationship (deltaAIC >2), we accepted the polynomial as the best model. If not, we ran the linear model as the final model. R^2 values were calculated for the best model. All R^2 values presented here are marginal R^2 values, and refer to the proportion of variation explained by only the fixed effects, unless otherwise specified. In addition, slope coefficients were calculated for the linear models.

Because the magnitude of fluxes varies significantly, in order to facilitate comparisons between regression models for each flux, data for each flux was scaled, to give the data a mean of 0 and standard deviation of 1. As each data set was scaled separately, this does not allow for statistical comparisons of slope values, but does assist in visualising the data.

To test for a potential influence of altitude, models were also run with site altitude included as a second fixed effect. These models were compared against models with no altitude term, and AIC values calculated to identify whether inclusion of altitude as a term improved the models. Including altitude had a very small effect on most models, with the difference in AIC values between models including and excluding altitude often being <2, suggesting the models are very similar in their explanatory power. As a result, it was decided to present results only from models do not include altitude as a fixed term.

Within the ForC database, sites within 25km^2 of each other are clustered into geographic areas. To account for correlations in measurements between tightly clustered sites, a random effect was specified as plot nested within geographic area. *Data from the temperate regions was heavily skewed towards studies from the old-growth forests of the Pacific Northwest.* These forests have very high productivity, and so to ensure that results were not unduly influenced by geographic sampling bias, we tried a version of the model where data were weighted according to forested land area within each Koeppen climate zone. Results were similar between the weighted and unweighted model, so, to avoid problems of over-fitting, the weighted model was dropped, and results from this are not presented here.

Models were run for total annual productivity against annual climate variables, and for monthly growing season productivity, defined as total productivity/length of growing season, against growing season climate variables. For analyses on data within the growing season, only linear models were specified.

To investigate the potential interactive effects of climate variables on carbon fluxes, multivariate models were also specified. To ensure that models were biologically meaningful, the terms included in the models tested built on results from the univariate models. Modelling of individual climate variables identified that the best predictors of carbon fluxes were variables related to temperature. We therefore decided to include mean annual temperature as a term in all multivariate models. We first modelled the interaction effect between mean annual temperature and mean annual precipitation, in order to capture climate variation along the axes of temperature and water availability. Models were tested for a significant interactive effect and a significant additive effect. We then explored whether any other climate variable, in combination with mean annual temperature, could significantly improve on the combination of mean annual temperature and mean annual precipitation. In specifying the range of models to test, climate variables which were strongly correlated with temperature were dropped, in order to capture the greatest range of variation in climate. For each possible pairing of climate variables, two models were specified: a model with the two climate variables showing an additive effect; and a model with the two climate variables showing an interactive effect. As before, plot nested within geographic area was included as a random effect. Altitude was not considered. AIC values were calculated for the models, and used to compare models. Models were considered to be significantly better than the baseline MAT*MAP model if:
i) the AIC value of the model was smaller than the AIC value of the baseline model by >2
ii) the r-squared value of the model was larger than the r-squared value of the baseline model by >5

Validating models of component fluxes. Comparison of component fluxes is based on the assumption that components sum accurately to estimates of larger fluxes. To test this, components of larger fluxes were regressed against latitude, and the models used to generate a series of point estimates along lines of best fit for each component. The point estimates for smaller component fluxes were summed to generate new "stacked" estimates of larger fluxes, which were then compared against actual measurements of the larger flux. Confidence intervals for the larger flux were calculated using the 'bootMer' function from the lme4 package (Bates et al., 2015). Stacked plots were generated for:

1. GPP = NPP + R_{auto}
2. NPP = ANPP + BNPP
3. ANPP = $ANPP_{foliage}$ + $ANPP_{woody\ stem}$
4. Total belowground carbon flux = BNPP + R_{root}

Allocation to carbon fluxes along latitudinal gradients. Variation in allocation to component carbon fluxes along latitudinal gradients was explored for a range of pairings: firstly, GPP:NPP, ANPP:BNPP, and $ANPP_{foliage}$:$ANPP_{woody\ stem}$; and secondly, the ratio of NPP to each of ANPP, BNPP, $ANPP_{foliage}$, and $ANPP_{woody\ stem}$. For each set of paired fluxes, measurements taken at the same site and plot, and in the same year, were paired together, and the ratio of each pair of measurements calculated. The ratios were regressed against latitude and climate variables, using the linear model specified above. Cook's distance analyses were carried out for each of the models, and indicated that data from a few high-elevation sites were having a disproportionate influence on the regressions. To account for this, models were re-run using only data from sites $\leq$ 1000m.

Results

In total, we analyzed 1228 records from 9 C flux variables taken from forests that had experienced no major anthropogenic disturbances within the past 100 years. These records represented a total of 154 distinct geographic areas (Fig. 1, Table 2), across all forested biogeographic and climate zones.

How does productivity vary with latitude?

All major carbon fluxes increased linearly with decreasing latitude (fig. 2).

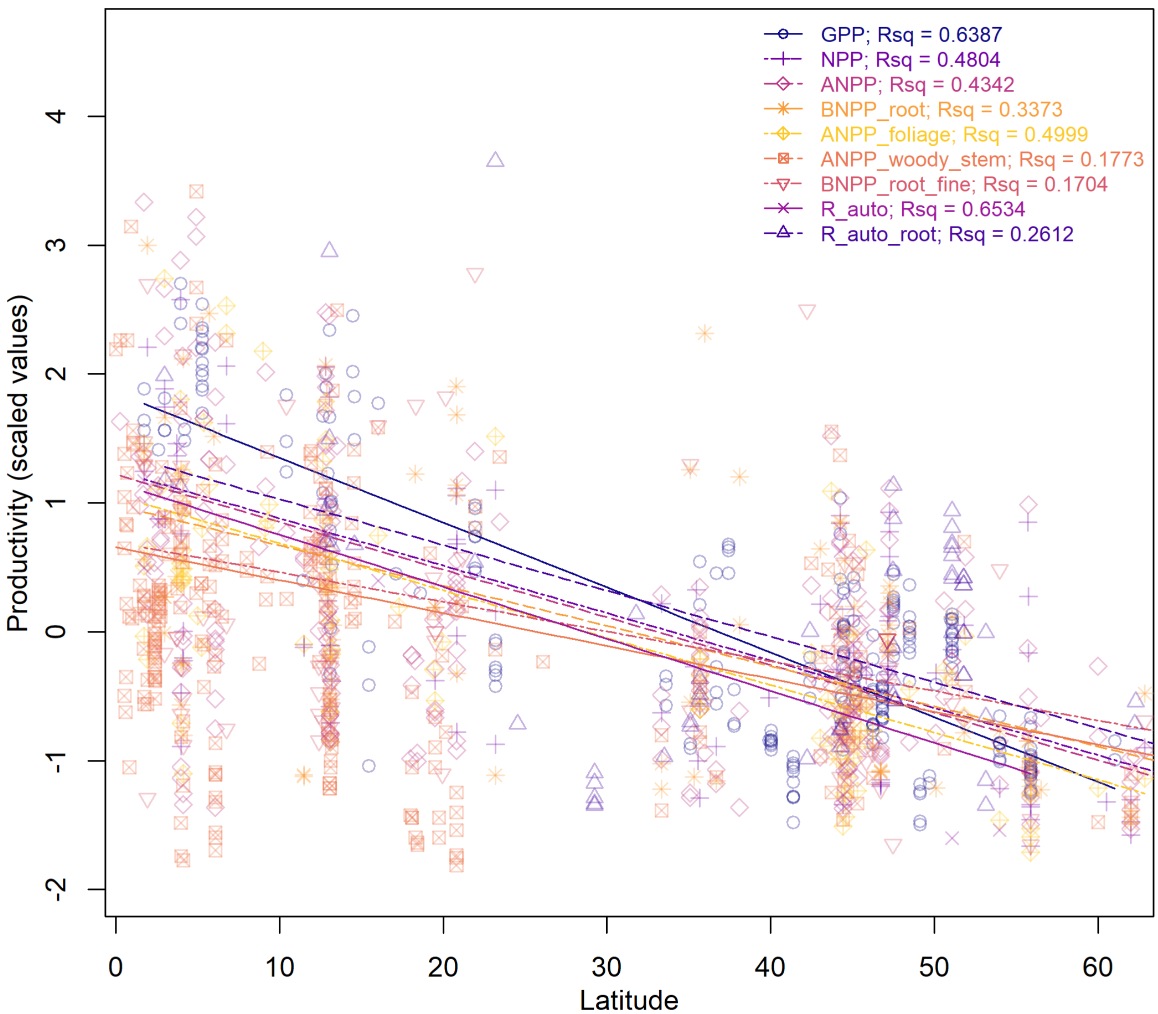

Figure 2: Graphs to show primary productivity ($MgC\ ha^{-}1\ yr^{-}1$) regressed against latitude. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$).

Latitude was a strong predictor for many of the carbon fluxes, explaining 64% of variation in GPP (n = 254, p<0.0001), 50% in NPP (n = 114, p<0.0001) and 45% in ANPP (n = 259, p<0.0001). For all fluxes, their relationship with latitude was best predicted by the linear model.

Relationships and differences among fluxes. In general, smaller component fluxes summed approximately to larger fluxes across the latitudinal gradient (fig. 3). That is, modelled estimates of GPP, generated from the sum of NPP and R auto; NPP, generated from the sum of ANPP and $BNPP_{root}$; and ANPP, generated from the sum of $ANPP_{foliage}$ and $ANPP_{woody\ stem}$, fell completely within the confidence intervals of the regressions of field estimates of GPP, NPP and ANPP respectively.

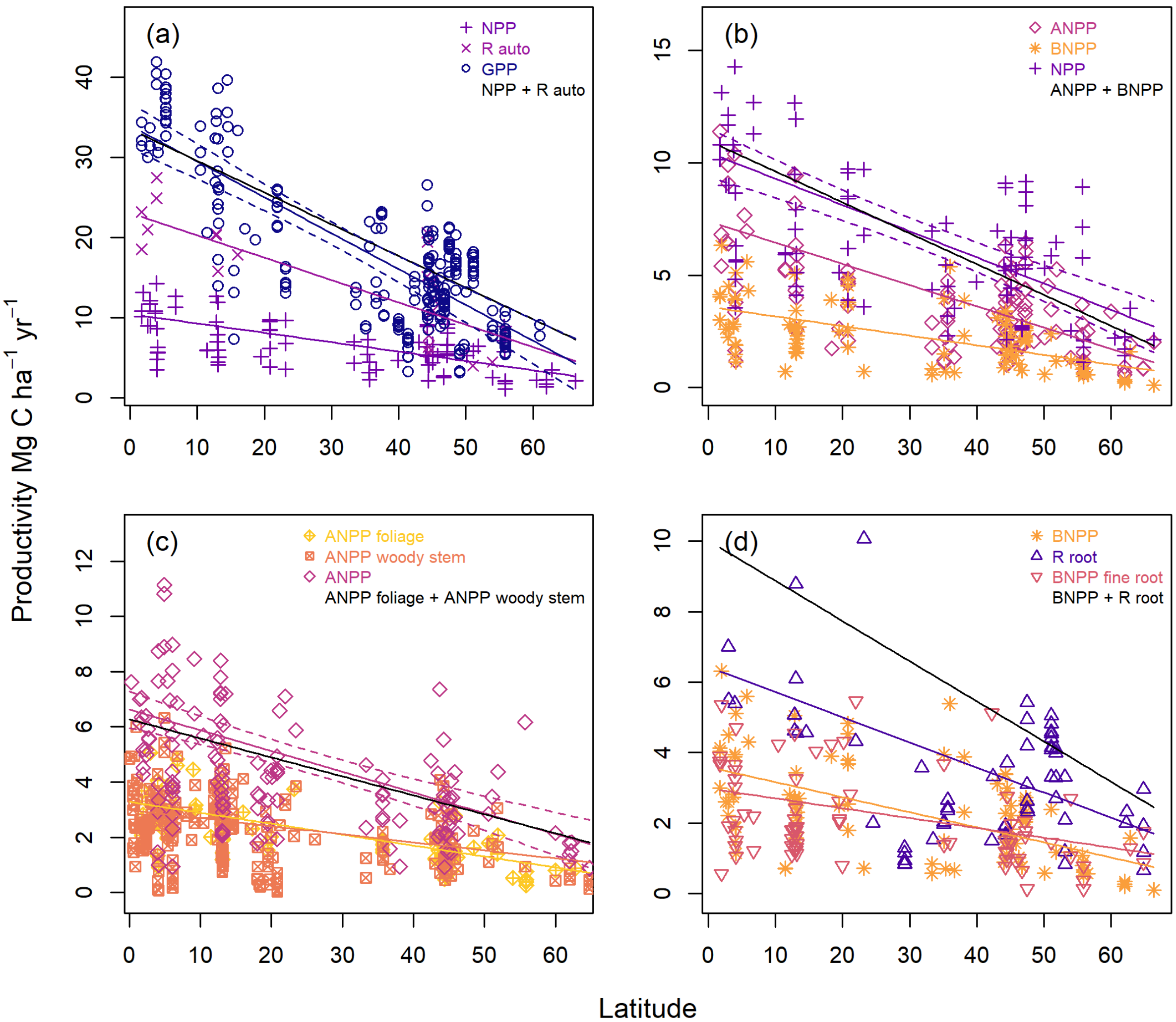

Figure 3: Graphs of primary productivity ($MgC\ ha^{-}1\ yr^{-}1$) regressed against latitude. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$). Plots 1 - 3 show two component fluxes; a larger flux, defined as the combination of the two component fluxes; and a modelled estimate of the sum of the two component fluxes. 95% confidence intervals are plotted for the larger flux. Plot 4 shows three belowground fluxes, and a modelled estimate of the total belowground carbon flux

We found no evidence that allocation between fluxes varied substantially with latitude or climate. There were no significant results from regressing ratios of carbon fluxes against latitude, or against any of the climate variables.

R^2 values were generally highest in the major fluxes, and decreased in subsidiary fluxes (Supporting Information S2). Of the major fluxes, R_{auto} and GPP were the most strongly explained by latitude and climate, with climate explaining at most 71% of variation in GPP, and 65% in R_{auto}. The proportion of variation explained by climate and latitude decreased in NPP and ANPP, with climate explaining at most 51% of variation in NPP and 44% in ANPP. Of the major fluxes, $BNPP_{root}$ was the least well explained by climate and latitude, with climate explaining at most 36% of variation.

With the exception of $ANPP_{foliage}$, the proportion of variation explained by climate and latitude in subsidiary fluxes was much lower. Climate explained at most 24% of variation in $ANPP_{woody\ stem}$, 19% in $BNPP_{fine\ root}$, and 27% in R_{root}. In contrast, climate strongly explained variation in $ANPP_{foliage}$, with mean annual temperature explaining 58% of variation. This pattern was also seen in the R^2 values for multivariate models.

How does productivity relate to MAT and MAP? We focus first on considering the relationship between productivity and MAT and MAP. MAT and MAP are the most commonly reported site-level climate variables, and much previous research into the effect of climate on forest productivity has focused on these as key climate variables. MAT was a significant ($p<0.05$) and strong predictor of productivity for all carbon fluxes tested, with all fluxes showing a linear increase with temperature (fig. 5). We found no support for a saturation point of productivity with temperature.

MAP was found to be a significant ($p<0.05$) but poor predictor of productivity, explaining, with the exception of R_{auto}, at most 37% of variation in carbon flux. For the majority of fluxes productivity was best predicted by a polynomial model. Productivity increased with precipitation, up until a saturation point at between 3000 and 4000mm annual precipitation, above which productivity started to decrease (fig. 5). The notable exception to this was GPP: the model indicated that GPP continued to increase with precipitation up to measures of at least 5000mm annually ($p<0.0001$, $R^2 = 0.33$. Data above this point was not available, but the model trend indicated that the saturation point for this model would be around 5000mm MAP.

There was a significant interactive effect between MAT and MAP for GPP, $BNPP_{root}$, $BNPP_{fine\ root}$, ANPP, $ANPP_{woody\ stem}$, and R_{root} (fig.4). There was a significant additive effect for R_{auto}. NPP and $ANPP_{foliage}$ showed no significant interactive or additive effect: including MAP as a second variable did not improve on the model including only MAT.

For the variables which showed a significant interactive or additive effect between MAT and MAP, no other climate variable, in combination with MAT, significantly improved on that model. For NPP, there was a significant interactive effect between MAT and water stress months, with this model explaining nearly 5% more variation in NPP than MAT alone. However, for $ANPP_{foliage}$, no multivariate model improved on the univariate model including only MAT.

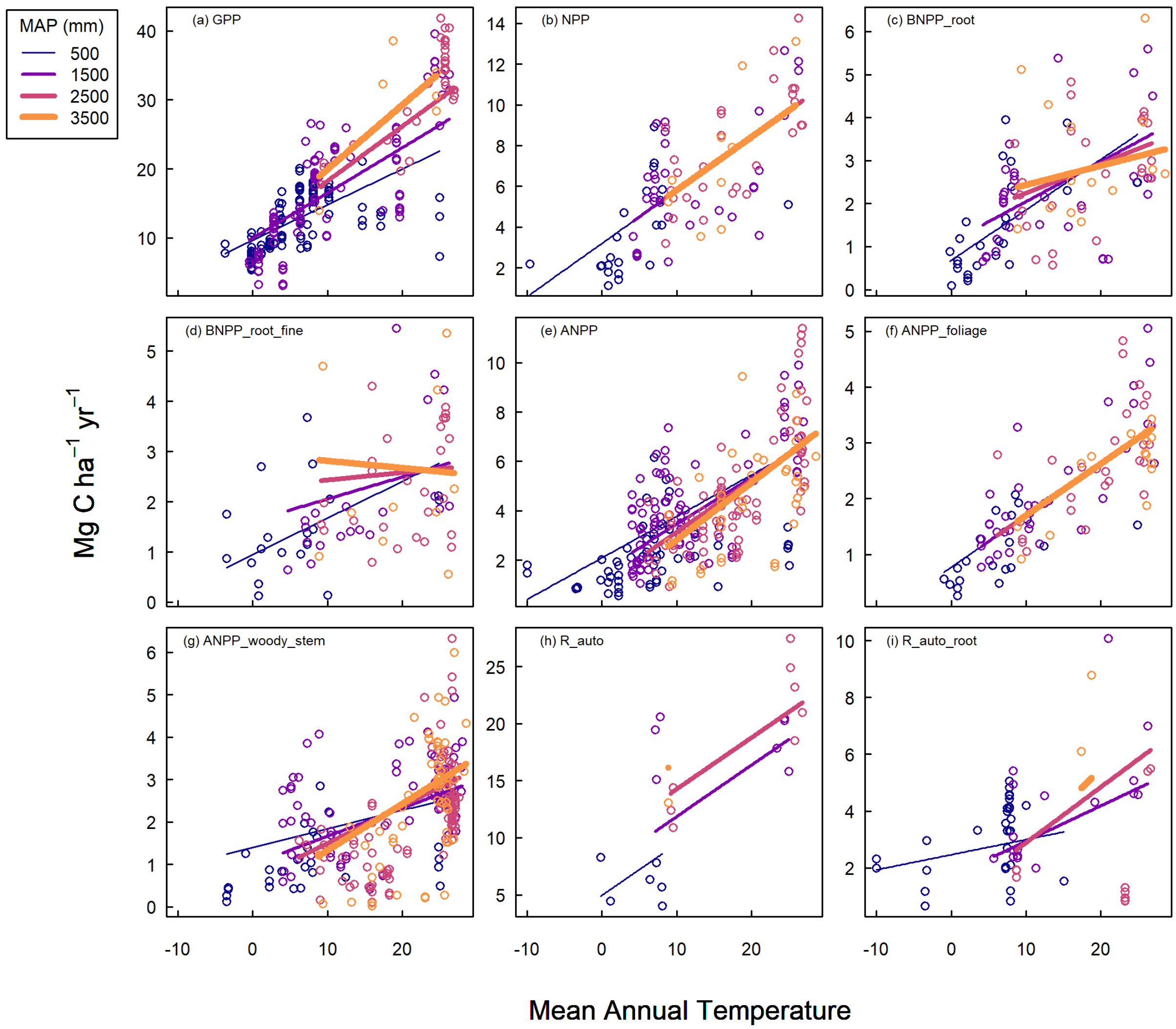

Figure 4: Plots of primary productivity ($MgC\ ha^{-}1\ yr^{-}1$) regressed against mean annual precipitation. Points are grouped into bins of 0 - 1000, 1001 - 2000, 2001 - 3000, and >3000mm mean annual precipitation, and lines of best fit plotted for mean annual precipitation values of 500, 1500, 2500, and 3500mm. All regressions are significant ($p < 0.05$).

How does productivity relate to other climate variables? Our results indicated that productivity was most strongly explained by temperature at the global scale, with temperature-related climate variables coming out as strong predictors of productivity. In addition to MAT, temperature seasonality, annual temperature range, and annual frost days were consistently identified as good predictors of productivity across fluxes.

We found a significant relationship between productivity and potential evapotranspiration for all fluxes. $\mathrm{ANPP}_{\mathrm{foliage}}$, $\mathrm{BNPP}_{\mathrm{fine\ root}}$ and $\mathrm{R}_{\mathrm{root}}$ increased linearly with PET; however, all other fluxes showed a polynomial relationship with PET (fig. 5). We found strong evidence for a saturation point or peak with PET: productivity tended to increase at values below 1000mm, before saturating between 1200 and 1700mm. There was evidence that productivity begins to decrease at values above 1800mm PET.

Vapour pressure deficit was a significant predictor of productivity for all fluxes. $\mathrm{BNPP}_{\mathrm{fine\ root}}$ showed a linear relationship with vapour pressure deficit ($R^2 = 0.07$, p<0.05), but all other fluxes showed a polynomial relationship (fig. 5). Productivity initially increased with vapour pressure deficit, before saturating at around 0.8 kPa. At values above 0.8 kPa, productivity began to decrease.

All fluxes, with the exception of R_{root}, showed a positive linear relationship with solar radiation. Solar radiation explained a low proportion of variability in productivity for all fluxes, explaining less than 20% of the variation in each flux, with the exception of R_{auto} ($R^2 = 0.26$, $p<0.05$).

Of the climate variables tested, annual wet days, aridity, cloud cover, mean diurnal temperature range, precipitation seasonality, maximum vapour pressure deficit and water stress months were poor or non-significant explainers of variation in productivity, explaining less than 20% of the variation in each of the carbon fluxes.

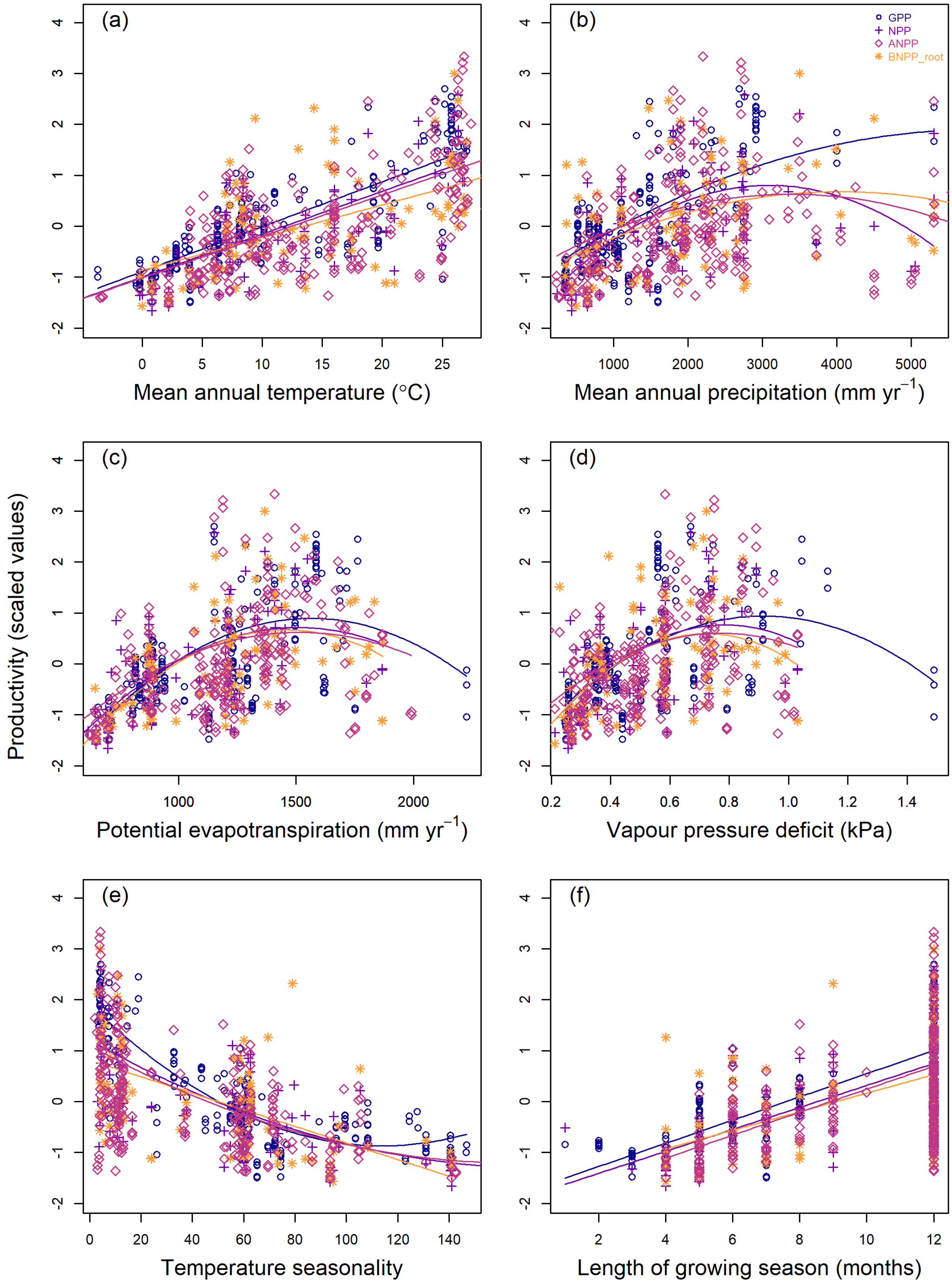

Figure 5: Plots of primary productivity ($MgC\ ha^{-}1\ yr^{-}1$) regressed against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration, (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$).

What is the role of seasonality in explaining productivity? Temperature seasonality was a significant predictor of productivity. We found a polynomial relationship with productivity for GPP, NPP, ANPP, and R_{root}. Productivity decreased rapidly as seasonality increased, with the rate of decrease slowing as seasonality increased (fig. 5). $ANPP_{foliage}$, $ANPP_{woody\ stem}$ and R_{auto} decreased linearly with temperature seasonality. Temperature seasonality was strongly correlated with annual temperature range, and, as expected, all fluxes showed almost identical responses to it. Productivity was highest where temperature seasonality = 0, and at an annual temperature range of 15°C or lower.

In contrast, there was no significant effect of precipitation seasonality on productivity.

We found a significant relationship between length of growing season and productivity, with all fluxes showing a linear increase in productivity with length of growing season (fig. 5). Length of growing season was a strong predictor of productivity, explaining 51% of variation in GPP, 39% of variation in NPP, and 34% of variation in ANPP, but it was not identified as a stronger predictor than MAT for any of the fluxes analysed.

Within the growing season, how does productivity vary with climate? Within growing season months, we found that climate had a much weaker effect on productivity. For each of temperature, precipitation, PET, and solar radiation, we found a small effect of climate for certain carbon fluxes. There was a small increase in productivity with temperature and precipitation for ANPP (with temperature $R^2 = 0.10$, $p<0.001$; with precipitation $R^2 = 0.04$, $p<0.05$) and $ANPP_{foliage}$ (with temperature $R^2 = 0.16$, $p<0.01$; with precipitation $R^2 = 0.09$, $p<0.05$). Productivity increased with solar radiation for GPP ($R^2 = 0.21$, $p<0.001$), NPP ($R^2 = 0.21$, $p<0.001$), BNPP ($R^2 = 0.16$, $p<0.001$) and $BNPP_{fine\ root}$ ($R^2 = 0.12$, $p<0.01$), and with PET for GPP ($R^2 = 0.15$, $p<0.01$), NPP ($R^2 = 0.18$, $p<0.01$), BNPP ($R^2 = 0.23$, $p<0.0001$), $BNPP_{fine\ root}$ ($R^2 = 0.11$, $p<0.05$), and $ANPP_{woody\ stem}$ ($R^2 = 0.06$, $p<0.05$).

Discussion

We used a large global database (ForC), containing an unprecedented amount of data representing all major forest types (Fig. 1) and the nine most significant forest autotrophic carbon flux (FACF) variables (Table 2), to comprehensively explore how C cycling in mature, undisturbed forests varies with latitude and climate on a global scale. We test a suite of hypotheses, including many previously posed (Table 1), with more data and standardisation for factors that have not always been controlled for (*e.g.*, stand age, flux components measured) to gain a stronger understanding of climatic effects on FACF. We show that, across all nine FACF variables analyzed, C cycling decreases linearly with latitude (Figs. 2-3)–a finding that confirms multiple previous studies (**REFS**) but contradicts the idea that productivity of temperate forests rivals that of tropical forests (**REFS**). The FACF variables increase in proportion to one another, with no differences in allocation detectable at this global scale and with component fluxes summing appropriately to larger fluxes (Fig. 3), indicating no major, systematic omissions or overestimations of flux components. However, we did detect a tendency for greater variability among subsidiary C fluxes (e.g., $ANPP_{woody}$, $BNPP_{fineroot}$; Fig. 2; **some SI table?**; **discussed below??**). Climate explains a significant proportion of variation in all C fluxes analyzed (albiet less for subsidiary fluxes), with temperature variables being the best predictors of FACF on this global scale (Figs. 4-5). While other climate variables are significant predictors of FACF, none of them improve on the explanatory power of temperature-related variables in general or MAT specifically (Fig. 5). Water availability is an important factor in explaining FACF on a global scale: we find a positive influence of precipitation at low MAP, with saturation at higher levels of MAP (Fig. 5b) and a significant interaction between MAT and MAP for seven of the nine variables analyzed (Fig. 4). Temperature seasonality and growing season length are closely correlated with MAT and are strong predictors of FACF (Fig. 5e-f), though growing season length doesn't improve upon MAT as a predictor. Within the growing season, the influence of climate on C cycling is smaller but still significant for a number of carbon fluxes (**some SI table?**). These findings clarify the big picture of how FACF varies with latitude and climate on a global scale.

Past studies have differed in their conclusions regarding the relationship between productivity and latitude or its correlates (**REFS**)–quite possibly because of lack of standardization with respect to stand age and disturbance history. Our findings indicate that, among mature, undisturbed stands, FACF is unambiguously highest in the tropical regions, and the relationship is approximately linear (Figs. 2-3). This contrasts with suggestions that productivity of temperate forests is similar to that of tropical forests (**REFS**). Such observations may be attributable to the fact that temperate forests are predominantly secondary and of younger age than tropical forests (**REF**), so analyses comparing across latitudinal gradients without strict control of stand age tend to be comparing younger temperate stands with older tropical (and often boreal) forests (Poulter et al. 2018-DOI:10.1594/PANGAEA.889943). Because C allocation varies with stand age (**REFS (KAT/NOBBY)**), age differences may introduce systematic biases into analyses of FACF across latitude or global climatic gradients. For example, woody productivity tends to be higher in rapidly aggrading secondary stands than in old-growth forests, where proportionally more C is allocated to respiration (**REFS**) [*purpose for respiration/ other compenents (**REFS????- NOBBY?**)]. By constraining our analysis to stands $\geq$ 100 years old with no record of major recent disturbance, we have clarified the shape of the relationship between FACF and latitude.

[**NOBBY, please pay special attention to this paragraph**]. We show that FACF are broadly consistent in their responses to climate drivers on the global scale (with the exception of some differences in MAT-MAP interactions; Fig. 4), with no major trends in C allocation among the variable pairs tested (Fig. 2; **Some SI table**). Although variation in allocation has been observed along gradients of elevation (Moser et al., 2011) and water availability (Newman et al., 2006)–along with non-climatic axes of stand age (Litton et al., 2007), nutrient availability (Litton et al., 2007; Gill and Finzi, 2016), and forest structure (Taylor et al., 2019)–variation in relation to climate is not apparent at the global scale within ForC, which contains the bulk of relevant data. Our conclusion, then, is that hypothesized gradients in allocation along global climate gradients cannot currently be supported for mature forests, although data quantity and standardization is currently insuffcent to rule out the possibility that such trends exist. Of particular interest and significance are the relationships amongst GPP, net primary productivity (NPP and its components, particularly $ANPP_{woody-stem}$), and respiration (R_{auto} and components). There have been suggestions that tropical forests tend to have low carbon use efficiency (CUE= NPP/GPP=(GPP-R_{auto}/GPP), which are based on observations of low CUE in old-growth tropical forests relative to (mostly younger) extratropical forests (De Lucia et al., 2007; Malhi 2012; Anderson-Teixeira et al., 2016), but our analysis suggests that these low values might more appropriately be attributed to the fact that these forests are old than to their tropical climate. Indeed, CUE is known to decline with forest age ((De Lucia et al., 2007);**REFS(NOBBY)**) but appears to be roughly independent of GPP (Litton et al., 2007). Among our sites with relevant data, there is indication in our data that CUE or $ANPP_{woody-stem}/GPP$ increase with latitude (**some SI table**). Careful methodological standardization across a consistent set of mature forest sites will be necessary to determine whether any climate-driven gradients in allocation exist at the global scale.

One interesting observation was that climate tends to explain more variation in the major fluxes (GPP, NPP, R_{auto} - latitude R^2 $\geq$ 48%) than in subsidiary fluxes (latitude R^2 <27% for $BNPP_{fine.root}$, $R_{auto-root}$,$ANPP_{woody-stem}$) (Fig. 2; **some SI table?**). There are two non-exclusive potential explanations for this. First, it may be that methodological variation is larger relative to flux magnitude for some of the subsidiary fluxes. Belowground fluxes in particular are difficult to quantify, and measurement methods for the belowground fluxes considered here may be measured through fundamentally different approaches (*e.g.*, minirhizotrons, ingrowth cores, or sequential coring for $BNPP_{root-fine}$; root exclusion, stable isotope tracking, or gas exchange of excised roots for $R_{auto-root}$), and sampling depth is variable and often insufficient to capture the full soil profile. $ANPP_{woody-stem}$, which is also poorly explained by latitude or climate, is more straightforward to measure but is subject to variability introduced by differences such as biomass allometries applied and minimum plant size sampled. However, methodological variation and uncertainty affect all of fluxes considered here–not necessarily any less than the aforementioned, and some of the larger fluxes that vary more strongly with respect to climate ($ANPP$, NPP) are estimated by summing uncertain component fluxes. Second, differences among variables in the proportion of variation explained by climate may be attributable to more dicrect climatic control over GPP than subsidiary fluxes. That is, subsidiary fluxes may be shaped by climate both indirectly through its influence on GPP and potentially respiration and directly through any climatic influence on C allocation, as well as by many other local- and regional-scale factors (**REFS**).

The latitudinal gradient in FACF (Figs. 2-3) is driven primarily by temperature-related climate variables, and secondarily by moisture availability (Figs. 4-5). Because many climate variables co-vary across the latitudinal gradient, because climatic drivers affect forest carbon flux on much shorter time scales than can be captured by annual climate summary variables, and because both climatic conditions and C flux vary intra- and inter-annually around the long-term means, it is not appropriate to attempt to identify any one mean annual climate variable as a mechanistic driver of FACF. However, it remains informative to consider these relationships. We find that temperature-related climate variables (MAT, temperature seasonality, . . . **LIST**) explain the highest proportion of variability in productivity, and among these, MAT is generally the best predictor–perhaps because site-specific MAT is recorded for the majority of sites in ForC, whereas other variables are extracted from global gridded data products (Table S1**?**). The effects of temperature are modified by moisture availability, with reduced FACF under hot and dry conditions (*i.e.*, high PET, high deficit; Fig. 5c-d) and sometimes under very high precipitaiton (Figs. 4, 5b). Negative effects of very high precipitation on FACF have been previously observed (**REFS**) and are attributable to nutrient and light limitations (**REFS**) Thus, although temperature and water availability jointly and interactively drive global-scale patterns of FACF.

FACF is reduced by climatic seasonality (Fig. 5e), and productivity is shut down during cold- or dry- dormant seasons. To account for this, a number of analyses seeking to characterize global-scale effects of climate on productivity have examined the relationship of FACF per month of the growing season with growing season climatic conditions (**REFS**). We found that the sort of simple metric needed to define growing season at a global scale was uncertain for temperature and problematic for moisture (**WORK ON THIS**). A temperature-defined growing season length had stong positive correlation with FACF (Fig. 5f), but explained less variation than MAT. Dividing FACFs by growing season length to yield FACF per growing season month removed the majority of climate-related variation, supporting the idea that the latitudinal gradient in FACF is attributable more to shorter growing seasons at high latitudes than to inherently lower rates of photosyntheiss or respiration by high-latitude forests (*[Enquist GCB review]*). However, there remained a number of significant correlations with growing season climatic conditions, suggesting that climatic conditions remain influential within the growing season. We conclude that while correcting for growing season length takes analyses a step closer to mechanistic linkage of instantaneous C flux rates to environmental conditions, it remains very crude relative to the the timescales on which climate affects plant metabolism and does not advance statistical predictive power. Rather, mechanistic accounting for climatic effects on global productivity patterns requires models representing physiologically meaningful timescales (*e.g.*, **refs**).

Our analysis clarifies the big picture of how FACF varies with latitude and climate on a global scale, with some important implications for how forest carbon cycling relates to climate and, by extension, how it is likely to respond to climatic warming. Contrary to some previous suggestions, we find no support for non-linear trends in mature forest C cycling with respect to latitude or MAT, and no distinct trends in C allocation across the global scale (Fig. 3). The implication is that under warmer conditions with similar moisture availability–and within the temperature range to which forest communities are adapated and acclimatized–higher temperatures result in a generalized acceleration of FACF, with no major shifts in C allocation among subsidiary fluxes. Of course, actual climatic changes will result in very different sets of conditions than represented across geographic gradients in climate, but our analysis clarifies the big picture as to how carbon cycles through forest ecosystems that have developed under relatively stable climatic conditions. As we enter a period of accelerating climatic change, understanding of the fundamental climatic controls on FACF sets a foundation for understanding patterns of change. [**work on this**]

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References

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., and Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data*, 5:1–12.

Anderson-Teixeira, K. J., Wang, M. M., McGarvey, J. C., Herrmann, V., Tepley, A. J., Bond-Lamberty, B., and LeBauer, D. S. (2018). ForC: a global database of forest carbon stocks and fluxes. *Ecology*, 99(6):1507.

Anderson-Teixeira, K. J., Wang, M. M., Mcgarvey, J. C., and Lebauer, D. S. (2016). Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Global Change Biology*, 22(5):1690–1709.

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., Almeida, S., Costa, A. C. L., Salinas, N., Phillips, O. L., Anderson, L. O. ., Baker, T. R., Goncalvez, P. H., Huamán-Ovalle, J., Mamani-Solórzano, M., Meir, P., Monteagudo, A., Peñuela, M. C., Prieto, A., Quesada, C. A., Rozas-Dávila, A., Rudas, A., Silva Junior, J. A., and Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, 6(1):2441–2488.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, 67(1).

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K. W., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I., and Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, 329(5993):834–838.

Bond-Lamberty, B. and Thomson, A. (2010). A global database of soil respiration data. *Biogeosciences*, 7(6):1915–1926.

Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., and Sack, L. (2016). Does climate directly influence NPP globally? *Global Change Biology*, 22(1):12–24.

Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M. M. C., Chuyong, G., Dobrowski, S. Z., Grierson, P., Harms, K. E., Houlton, B. Z., Marklein, A., Parton, W., Porder, S., Reed, S. C., Sierra, C. A., Silver, W. L., Tanner, E. V. J., and Wieder, W. R. (2011). Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis: Nutrients, climate and tropical NPP. *Ecology Letters*, 14(9):939–947.

De Lucia, E. H., Drake, J. E., Thomas, R. B., and Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6):1157–1167.

Fick, S. E. and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12):4302–4315.

Fyllas, N. M., Bentley, L. P., Shenkin, A., Asner, G. P., Atkin, O. K., Díaz, S., Enquist, B. J., Farfan-Rios, W., Gloor, E., Guerrieri, R., Huasco, W. H., Ishida, Y., Martin, R. E., Meir, P., Phillips, O., Salinas, N., Silman, M., Weerasinghe, L. K., Zaragoza-Castells, J., and Malhi, Y. (2017). Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. *Ecology Letters*, 20(6):730–740.

Gill, A. L. and Finzi, A. C. (2016). Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecology Letters*, 19(12):1419–1428.

Gillman, L. N., Wright, S. D., Cusens, J., Mcbride, P. D., Malhi, Y., and Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, 24(1):107–117.

Girardin, C. A. J., Malhi, Y., Aragão, L. E., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley, K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., and Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, 16(12):3176–3192.

Harris, I., Jones, P. D., Osborn, T. J., and Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3):623–642.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15):1965–1978.

Huston, M. A. and Wolverton, S. (2009). The global distribution of net primary production: resolving the paradox. *Ecological Monographs*, 79(3):343–377.

Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., Arneth, A., Bernhofer, C., Bonal, D., Chen, J., Gianelle, D., Gobron, N., Kiely, G., Kutsch, W., Lasslop, G., Law, B. E., Lindroth, A., Merbold, L., Montagnani, L., Moors, E. J., Papale, D., Sottocornola, M., Vaccari, F., and Williams, C. (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of Geophysical Research: Biogeosciences*, 116(3):1–16.

Kerkhoff, A. J., Enquist, B. J., Elser, J. J., and Fagan, W. F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, 14(6):585–598.

Larjavaara, M. and Muller-Landau, H. C. (2012). Temperature explains global variation in biomass among humid old-growth forests. *Global Ecology and Biogeography*, 21(10):998–1006.

Litton, C. M., Raich, J. W., and Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, 13(10):2089–2109.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M. L., Tang, J., Valentini, R., Vesala, T., and Janssens, I. A. (2007). CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, 13(12):2509–2537.

Malhi, Y. (2012). The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology*, 100(1):65–75.

Malhi, Y., Girardin, C. A., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco, W., Silva-Espejo, J. E., del Aguilla-Pasquell, J., Farfán Amézquita, F., Aragão, L. E., Guerrieri, R., Ishida, F. Y., Bahar, N. H., Farfan-Rios, W., Phillips, O. L., Meir, P., and Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, 214(3):1019–1032.

Michaletz, S. T., Cheng, D., Kerkhoff, A. J., and Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, 512(1):39–43.

Michaletz, S. T., Kerkhoff, A. J., and Enquist, B. J. (2018). Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, 27(2):166–174.

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., and Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*, 17(6):2211–2226.

Newman, G. S., Arthur, M. A., and Muller, R. N. (2006). Above- and Belowground Net Primary Production in a Temperate Mixed Deciduous Forest. *Ecosystems*, 9(3):317–329.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautianen, A., Sitch, S., and Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(August):988 – 993.

R Core Team (2018). *R: A language and environment for statistical computing.*

Schuur, E. A. G. (2003). PRODUCTIVITY AND GLOBAL CLIMATE REVISITED: THE SENSITIVITY OF TROPICAL FOREST GROWTH TO PRECIPITATION. *Ecology*, 84(5):1165–1170.

Taylor, P. G., Cleveland, C. C., Soper, F., Wieder, W. R., Dobrowski, S. Z., Doughty, C. E., and Townsend, A. R. (2019). Greater stem growth, woody allocation, and aboveground biomass in Paleotropical forests than in Neotropical forests. *Ecology*, 100(3):1–9.

Taylor, P. G., Cleveland, C. C., Wieder, W. R., Sullivan, B. W., Doughty, C. E., Dobrowski, S. Z., and Townsend, A. R. (2017). Temperature and rainfall interact to control carbon cycling in tropical forests. *Ecology Letters*, 20(6):779–788.

Trabucco, A. and Zomer, R. J. (2018). Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2. *CGIAR Consortium for Spatial Information (CGIAR-CSI)*, (November):10.

Šímová, I. and Storch, D. (2017). The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship. *Ecography*, 40(2):239–252.