Title: Global patterns of forest autotrophic carbon fluxes

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###Abstract Carbon (C) fixation, allocation, and metabolism by trees set the basis for energy and material flows in forest ecosystems and define their interactions with Earth's changing climate. However, we lack a cohesive synthesis on how forest carbon fluxes vary globally with respect to climate and one another. Here, we draw upon # records from the Global Forest Carbon Database (ForC), representing all major forest types and the nine most significant autotrophic carbon fluxes, to comprehensively explore how C cycling in mature, undisturbed forests varies with latitude and climate on a global scale. We show that, across all flux variables analyzed, C cycling decreases linearly with absolute latitude – a finding that confirms multiple previous studies but contradicts the idea that net primary productivity (NPP) of temperate forests rivals that of tropical forests. C flux variables generally displayed similar trends across latitude and multiple climate variables, with few differences in allocation detectable at this global scale. **Climate explained a significant proportion (#-#%) of variation in all C fluxes analyzed**, with temperature variables in general and mean annual temperature (MAT) in particular being the best predictors of C flux on this global scale. The effects of temperature were modified by moisture availability, with C flux reduced under hot and dry conditions and sometimes under very high precipitation. C fluxes declined with temperature seasonality, but growing season length did not improve upon MAT as a predictor.

Within the growing season, the influence of climate on C cycling was small but significant for a number of flux variables. These findings clarify how forest C flux varies with latitude and climate on a global scale. In a period of accelerating climatic change, understanding of the fundamental climatic controls on forest C cycling sets a foundation for understanding patterns of change.

Introduction

Carbon cycling in Earth's forests provides the energetic basis for sustaining the majority of Earth's terrestrial biodiversity and many human populations (Assessment, 2005), while strongly influencing atmospheric carbon dioxide (CO_2) and climate (Bonan, 2008). Forests' autotrophic carbon fluxes–that is, carbon fixation, allocation, and metabolism by trees and other primary producers–sets the energy ultimately available to heterotrophic organisms (including microbes), in turn influencing their abundance (Zak et al., 1994; Niedziałkowska et al., 2010) and possibly diversity (Waide et al., 1999; Chu et al., 2018). They are linked to cycling of energy, water, and nutrients, and, critically, influence all carbon (C) stocks and define forest interactions with Earth's changing climate. Each year, over 69 Gt of C cycle through Earth's forests (Badgley et al., 2019)– a flux more than seven times greater that of recent anthropogenic fossil fuel emissions (9.5 Gt C yr^{-1}; Friedlingstein et al., 2019). As atmospheric CO_2 continues to rise, driving climate change, forests will play a critical role in shaping the future of Earth's climate (Cavaleri et al., 2015; Rogelj et al., 2018). However, our ability to draw general macroscopic conclusions regarding global variation in C cycling with respect to climate has been limited in that analyses have typically considered only one or a few variables at a time, have not always sufficiently parse related variables, and have often mixed forests that vary in stand age, disturbance history, and/or management status, all of which affect C cycling (Litton et al., 2007; Gillman et al., 2015; Šímová and Storch, 2017).

Forest C fluxes decrease with latitude, but it remains unclear whether and how the shape of this relationship varies between fluxes. Fluxes are lowest in the boreal regions, and increase into the temperate regions (Luyssaert et al., 2007; Huston and Wolverton, 2009; Beer et al., 2010; Piao et al., 2010; Jung et al., 2011). However, evidence is inconclusive on whether primary productivity continues to increase into the tropics–a question complicated by the fact that different studies use different measures of productivity to explore these relationships. Gross primary productivity (GPP) is highest in tropical forests (Beer et al., 2010; Jung et al., 2011; Badgley et al., 2019; Li and Xiao, 2019). In contrast, some studies suggest that the highest values of net primary productivity (NPP) may be found in temperate forests (Luyssaert et al., 2007; Huston and Wolverton, 2009), while others find NPP highest in the tropics and decreasing with latitude (Šímová and Storch, 2017). Other studies have found that aboveground net primary productivity ($ANPP$) decreases weakly with latitude (Huston and Wolverton, 2009; Gillman et al., 2015).

The latitudinal gradient in C flux rates, along with altitudinal gradients (Girardin et al., 2010; Malhi et al., 2017), is driven primarily by climate, which is a significant driver of C fluxes across broad spatial scales (Luyssaert et al., 2007; Cleveland et al., 2011; Hursh et al., 2017). The majority of studies have focused on exploring the relationships of C fluxes to mean annual temperature (MAT) and mean annual precipitation (MAP), as the most commonly reported site-level climate variables. There is strong evidence that both MAT and MAP show significant positive relationships with C fluxes (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 C flux variables across studies. 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) finds that NPP increases linearly with temperature. Taylor et al. (2017) showed a positive interaction between MAT and MAP in shaping tropical forest productivity, such that high rainfall had a negative effect on productivity in cooler climates, compared to a positive effect in warmer climates. Such complicated dynamics play out with belowground fluxes as well, with typically dominant soil temperature mediated by moisture and carbon supply (Hursh et al., 2017; Xu and Shang, 2016). There is evidence that C fluxes also respond to variables such as cloud cover (Taylor et al., 2017), solar radiation (Fyllas et al., 2017), and potential evapotranspiration (Kerkhoff et al., 2005).

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 C fluxes is actually a consequence of the correlation between MAT and growing season length (Kerkhoff et al., 2005; 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 net primary productivity (loosely defined to include a mix of **VARIABLES**) and MAT, suggesting that the influence of temperature may be limited to determining the length of the frost-free growing season.

The recent development of the Global Forest Carbon database (ForC), which synthesizes multiple variables and including records of stand history (Anderson-Teixeira et al., 2016, 2018), opens up the possibility for a standardized analysis of global scale variation in multiple C fluxes and the principle climatic drivers of these patterns. In order to approach this broad topic, we simplify the major gaps in our knowledge to five broad questions and corresponding hypotheses (Table 1). First, we ask how nine forest autotropic carbon fluxes in ForC 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. Finally, we consider the relationship between C flux and seasonality, considering the role of seasonality in explaining variation in carbon fluxes, and the influence of climate on C flux standardized by growing season length.

Table 1: Summary of research questions, corresponding hypotheses, and results. Statistically signficant support for/ rejection of hypotheses is indicated with 'yes'/'no', and '-' indicates no significant relationship. Parentheses indicate partial overall support or rejection of hypotheses across all fluxes considered.

		Forest autotrophic carbon fluxes									
Questions and hypotheses (with related references)	Overall	GPP	NPP	$ANPP$	$ANPP_{stem}$	$ANPP_{foliage}$	$BNPP$	$BNPP_{fine.root}$	R_{auto}	R_{root}	Support
Q1. How do C fluxes vary with latitude?											
H1.1. C fluxes decrease linearly with latitude.[1,2,3,10]	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Fig. 2
Q2. How do C fluxes vary with MAT and MAP?											
H2.1. C fluxes increase with MAT.[1,4,9]	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S4, S5
H2.2. C fluxes increase with precipitation up to at least 2000 mm yr^{-1}.[1,4]	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S4, S5
H2.3. Temperature and precipitation interactively shape C fluxes.[5]	(yes)	yes	yes	-	yes	-	yes	yes	yes	-	Fig. 3
Q3. How are C fluxes related to other climate variables?											
H3.1. C fluxes display a decelerating increase or unimodal relationship with PET.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S4, S5
H3.2. C fluxes display a decelerating increase or unimodal relationship with vapour pressure deficit.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S4, S5
H3.3. C fluxes increase with solar radiation.	(yes)	yes	yes	yes	yes	yes	yes	yes	yes	-	Figs. S4, S5
Q4. How does seasonality influence C fluxes?											
H4.1. C fluxes decrease with temperature seasonality.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S6, S7
H4.2. C fluxes decrease with precipitation seasonality.	-	-	-	-	-	-	-	-	-	-	Figs. S6, S7
H4.3. C fluxes increase with growing season length.[6,7,8]	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S6, S7
H4.4. Growing season length is a better predictor of C fluxes than MAT.[7,8]	(no)	no	no	no	no	no	no	-	no	no	Table S4
Q5. When standardised by growing season length, how do C fluxes vary with climate?											
H5.1. Growing season C fluxes increase with temperature.[8]	(yes)	-	-	yes	-	yes	-	-	-	-	Figs. S8, S9
H5.2. Growing season C fluxes increase with PET.	(yes)	yes	yes	-	yes	-	yes	yes	-	-	Figs. S8, S9
H5.3. Growing season C fluxes increase with precipitation.	(yes)	-	-	yes	-	yes	-	-	-	-	Figs. S8, S9
H5.4. Growing season C fluxes increase with solar radiation.	(yes)	yes	yes	-	-	-	yes	yes	-	-	Figs. S8, S9

[1] Luyssaert et al. (2007) [2] Gillman et al. (2015) [3] Simova and Storch (2017) [4] Schuur (2003) [5] Taylor et al. (2016) [6] Malhi (2012) [7] Michaletz et al. (2014) [8] Chu et al. (2016) [9] Piao et al. (2010) [10] Huston & Wolverton (2009)

Materials and Methods

Forest carbon flux data

This analysis focused on nine C flux variables included in the open-access ForC database (Table 2) (Anderson-Teixeira et al., 2016, 2018). ForC 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 Soil Respiration Database (Bond-Lamberty and Thomson, 2010). Additional targeted literature searches were conducted to identify further available data on the fluxes analyzed here, with particular focus on mature forests in temperate and boreal regions, which were not included in the review of Anderson-Teixeira et al. (2016). We used ForC v3.0, archived on Zenodo with DOI 10.5281/zenodo.3403855. This version contained 29,730 records from 4,979 plots, representing 20 distinct ecozones across all forested biogeographic and climate zones.

This analysis focused on mature forests with no known history of signficant disturbance or management. There is evidence that stand age influences patterns of C flux and 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, we included only stands of known age $\geq$ 100 years and those described by terms such as “mature”, “intact”, or “old-growth”. Since management can alter observed patterns of C cycling (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 within the past 100 years were also excluded. Disturbances that qualified sites for exclusion included major cutting or harvesting, burning, flooding, drought and storm events with site mortality >10% of trees. Grazed sites were retained.

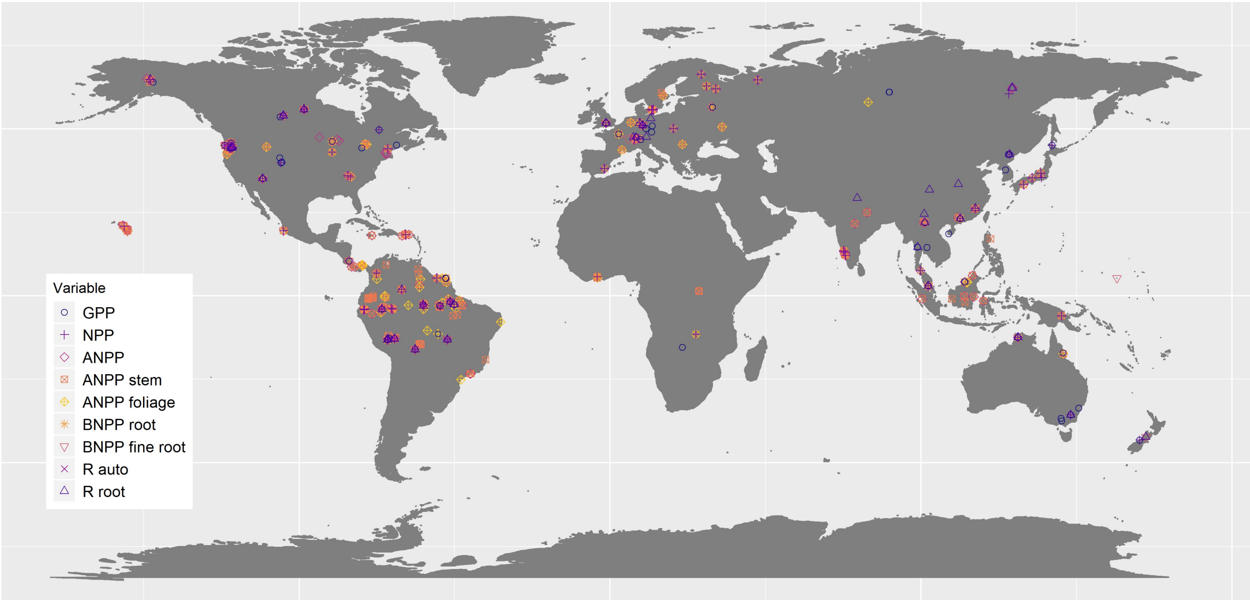

Figure 1: Map showing all data used in the analysis, coded by variable. Variables are plotted individually in Fig. S1.

Climate data

Table 2: Definitions and sample sizes of carbon flux variables used in analysis. All variables are in units of Mg C ha^{-1} yr^{-1}.

				Sample size	
Variable	Definition	Components included	Methodologies	records	geographic areas*
GPP	Gross Primary Production	full ecosystem	flux partitioning of eddy-covariance; NPP+R_{auto}	243	49
NPP	Net Primary Production	stem, foliage, coarse root, fine root, optionally others (e.g., branch, reproductive, understory)	$ANPP$ + $BNPP$ (majority); GPP-R_{auto}	161	56
$ANPP$	Aboveground NPP	stem, foliage, optionally others (e.g., branch, reproductive, understory)	$ANPP_{stem}$ + $ANPP_{foliage}$ (+ others)	278	86
$ANPP_{stem}$	Stem growth component of $ANPP$	woody stems down to DBH $\leq$ 10cm (no branch turnover)	stem growth measurements scaled to biomass using allometries	264	96
$ANPP_{foliage}$	Foliage component of $ANPP$	foliage	litterfall collection, with separation into components	98	49
$BNPP$	Belowground NPP	coarse and fine roots	coarse roots estimated indirectly using allometries based on aboveground stem increment measures ; fine roots as below	101	48
$BNPP_{fine.root}$	Fine root component of $BNPP$	fine roots	measurements combined one or more of the following: soil cores, minirhizotrons, turnover estimates, root ingrowth cores	88	41
R_{auto}	Autotrophic respiration	foliage, stem, and root	chamber measurements of foliage and stem gas exchange + R_{root} (as below)	22	13
R_{root}	Root respiration	(coarse and) fine roots	partitioning of total soil respiration (e.g., through root exclusion), scaling of root gas exchange; excluded alkali absoption and soda lime methods for measuring soil respiration	64	26

* Geographic areas group geographically proximate sites, defined using a hierarchical cluster analysis on the distance matrix of the sites, and a cutoff of 25km

ForC contains geographic coordinates associated with each measurement record and, when available, mean annual temperature (MAT) and mean annual precipitation (MAP) as reported in the primary literature (Anderson-Teixeira et al., 2018). Based on the geographic co-ordinates for each site, data on twelve climate variables–including MAT, MAP, temperature and precipitation seasonality, annual temperature range, solar radiation, cloud cover, annual frost and wet days, potential evapotranspiration (PET), aridity (MAP/PET), and vapor pressure deficit (VPD)–were extracted from five open-access climate datasets: WorldClim (Hijmans et al., 2005), WorldClim2 (Fick and Hijmans, 2017), the Climate Research Unit time-series dataset (CRU TS v4.03 (Harris et al., 2014), the Global Aridity Index and Potential Evapotranspiration Climate Database (Trabucco and Zomer, 2019), and TerraClimate (Abatzoglou et al., 2018) (Table S1). From these data, we derived maximum VPD, defined as the VPD of the month with the largest deficit, and the number of water stress months, defined as the number of months annually where precipitation was lower than PET. Where site-level data was missing for MAT or MAP, we used values from the WorldClim (**2?**) dataset.

For consistency with previous studies (Table 1, *H5*), length of the growing season was estimated to the nearest month, where growing season months were defined as months with mean minimum temperature > 0.5°C. We experimented with a definition of growing season months including a moisture index, defined as (MAT - PET)/PET, > -0.95 (Kerkhoff et al., 2005; see also Michaletz et al., 2014). However, we found that including a moisture index had minimal effect on the estimates of growing season length, and so chose to exclude it. Monthly data for PET, precipitation, and temperature from CRU v 4.03 (Harris et al., 2014) and solar radiation from WorldClim2 (Fick and Hijmans, 2017) were 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.

Analyses

The effects of latitude and climate on C fluxes were analysed using mixed effects models using the package 'lme4' (Bates et al., 2015) in R v.3.5.1 (**?**). The basic model for all analyses included a fixed effect of latitude or climate and a random effect of plot nested within geographic area. Geographic areas–*i.e.*, spatially clustered sites–are defined within ForC using a hierarchical cluster analysis on the distance matrix of the sites and a cutoff of 25km (Anderson-Teixeira et al., 2018). We experimented with inclusion of altitude as a fixed effect, but excluded it from the final models because it added very little explanatory power–that is, the difference in AIC (ΔAIC) relative to models excluding altitude was generally small (often ΔAIC<2). Effects were considered signficant when inclusion of the term of interest resulted in $\Delta AIC \geq 2.0$ relative to a corresponding null 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. Specific analyses are as described below.

We first examined the relationship between latitude and C fluxes (Q1; Table 1). We tested models with latitude as a first-order linear term (corresponding null: model without latitude) and as a second-order polynomial or logarithmic term (corresponding null: model with latitude as a first-order linear term). We selected as the best model that with the highest ΔAIC relative to a null model with no fixed term.

To test whether trends in component fluxes across latitude sum to match those of larger fluxes, regression lines for smaller component fluxes were summed to generate new estimates of larger fluxes. We then determined whether these summed predictions fell within the **95%** CI for the larger flux across the entire range included latitude. **(Becky, is 95% the correct number)** Confidence intervals for the larger flux were calculated using the 'bootMer' function from the lme4 package (Bates et al., 2015). **(Helene asks for more details here: what does the function do? are CIs just based on uncertainty in regression?)** This analysis was applied to the following sets of fluxes: (1) $GPP = NPP + R_{auto}$, (2) $NPP = ANPP + BNPP$, and (3) $ANPP = ANPP_{foliage} + ANPP_{stem}$. In addition, we estimated total belowground C flux (TBCF, not analyzed due to limited data) as $TBCF = BNPP + R_{root}$.

Variation in allocation to component carbon fluxes along latitudinal gradients was explored for the following pairings: $NPP : GPP$, $ANPP : BNPP$, $ANPP_{foliage} : ANPP_{stem}$, $ANPP_{foliage} : NPP$, $ANPP_{stem} : NPP$, $ANPP : NPP$, and $BNPP : NPP$. **issue 91** 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. Thus, models were re-run using only data from sites $\leq$ 1000m.

We next examined the relationships of C fluxes to climate variables (Q2-Q4; Table 1). As with latitude, we tested both linear and polynomial fits for each climate variable. We tested relationships of each C flux (Table 2) against each climate variable (Table S1), but focus presentation–including focal hypotheses (Table 1)–on climate variables that explained >20% of variation in C fluxes. **Becky, please make this more specific. I drafted this based on the results, but its not very clear. BBL: I agree, not clear and might trigger reviewer concerns about tailoring hypotheses to significance.**

Multivariate models were used to investigate the potential joint and interactive effects of MAT and MAP on carbon fluxes. An additive model including MAP in addition to MAT was accepted when ΔAIC >2 relative to a null including only MAT as a fixed effect. An interactive model including an MAT x MAP interaction was accepted when ΔAIC >2 relative to a null including MAT and MAP as fixed effects.

To test whether and how C flux varied with climate when standardised by growing season length (Q5), we first standardized annual C flux by dividing by growing season length (as defined above). We then tested for correlations between these standardised fluxes and growing season climate variables, using only first-order linear models.

All analyses were conducted in R (Version**). Code and data necessary to reproduce all results are archived on GitHub. . . .**

###Results

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

How does C flux vary with latitude?

All major carbon fluxes decreased linearly with latitude (Fig. 2; Table S2). Latitude was a strong predictor for many of the carbon fluxes–particularly the larger fluxes (Table S2). Specifically, latitude explained 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). The C fluxes that were most poorly predicted by latitude were $BNPP_{fine.root}$ (R^2=0.17) and $ANPP_{stem}$ (R^2=0.18). For all C fluxes, the relationship with latitude was better fit by the first-order linear model than by second-order polynomial or logarithmic models.

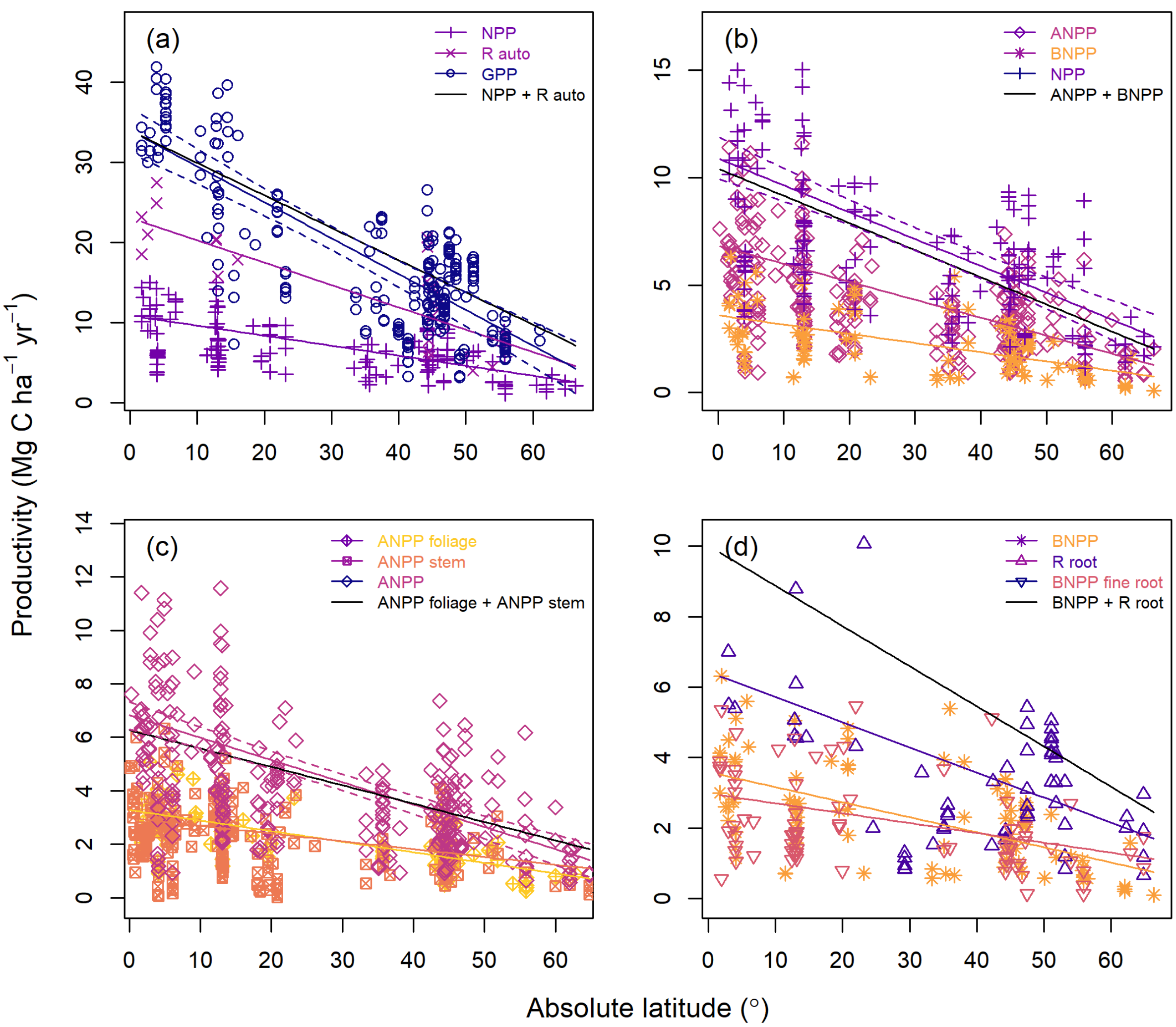

Figure 2: Latitudinal trends in forest autotropic carbon flux. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$). Each panel shows major C fluxes together with component fluxes. Also plotted are predicted trends in the major C fluxes based on the sum of component fluxes. 95% confidence intervals are plotted for the major flux for comparison with predicted trends. In (d), which shows three belowground fluxes, the major flux, total belowground carbon flux, has insufficient data (n=9) to support a regression

In general, smaller component fluxes summed approximately to larger fluxes across the latitudinal gradient (Fig. 2). That is, modelled estimates of GPP, generated from the sum of NPP and R_{auto}; NPP, generated from the sum of $ANPP$ and $BNPP$; and $ANPP$, generated from the sum of $ANPP_{foliage}$ and $ANPP_{stem}$, fell completely within the confidence intervals of the regressions of field estimates of GPP, NPP, and $ANPP$, respectively.

There was little evidence of systematic variation in C allocation with latitude or climate (Fig. S3). Of 28 relationships tested (7 ratios among C flux variables regressed against latitude, MAT, MAP, and temperature seasonality), there were only five significant relationships, all with $R^2 \leq 0.4$ (Fig. S3). **The proportion of NPP allocated to $ANPP_{foliage}$ decreased with latitude ($R^2 = 0.32$) and increased with MAT ($R^2 = 0.37$). The proportion of NPP allocated aboveground ($ANPP$) decreased weakly with**

latitude ($R^2 = 0.11$) and temperature seasonality ($R^2 = 0.17$), while increasing with MAT ($R^2 = 0.11$).

How does C flux relate to MAT and MAP?

All fluxes increased with MAT (all p<0.05; Figs. 3-4, S4-S5, Table S2). For eight of the nine fluxes, this relationship was linear. For only one variable, $BNPP$, did a lognormal fit provide signficant improvement over a first-order linear relatinship. *As with latitude, MAT tended to explain more variation in the larger flux (GPP, NPP, $ANPP$, R_{auto}) and $ANPP_{foliage}$ (all $R^2 > 0.4$) than in subsidiary and belowground fluxes ($ANPP_{stem}$, R_{root}, $BNPP_{fine.root}$; all $R^2 < 0.25$).* **update this**

MAP was a significant (p<0.05) predictor of all fluxes (Figs. 4a, S4-S5; Table S2). However, it explained little variation: with the exception of R_{auto}, MAP explained at most 25% of variation in C flux. For five of the nine fluxes, a second-order polynomial model provided the best fit, while first-order linear and lognormal relationships provided each provided the best fit for two flxues. All fluxes increased with MAP up to at least 2000 mm, above which responses were variable (Figs. 4, S4-S5).

There was a significant additive effect of MAT and MAP on GPP, $ANPP$ and R_{auto} (Fig. 3, Table S3). Accounting for MAT, MAP had a substantial positive effect on GPP and R_{auto} and a small negative effect on $ANPP$. There was a significant interaction between MAT and MAP for NPP and $ANPP_{stem}$ (Fig. 3, Table S3). The interaction was negative for NPP and positive for $ANPP_{stem}$. For $ANPP_{foliage}$, $BNPP$, $BNPP_{fine.root}$, and R_{root}, MAP did not have a signficant effect when accounting for MAT (Fig. 3, Table S3). 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. {**need to confirm this given changes in MAT MAP results (or you could just drop the sentence.)**} **BBL: this paragraph is pretty dense. Perhaps distill to a summary sentence and move rest to SI?**

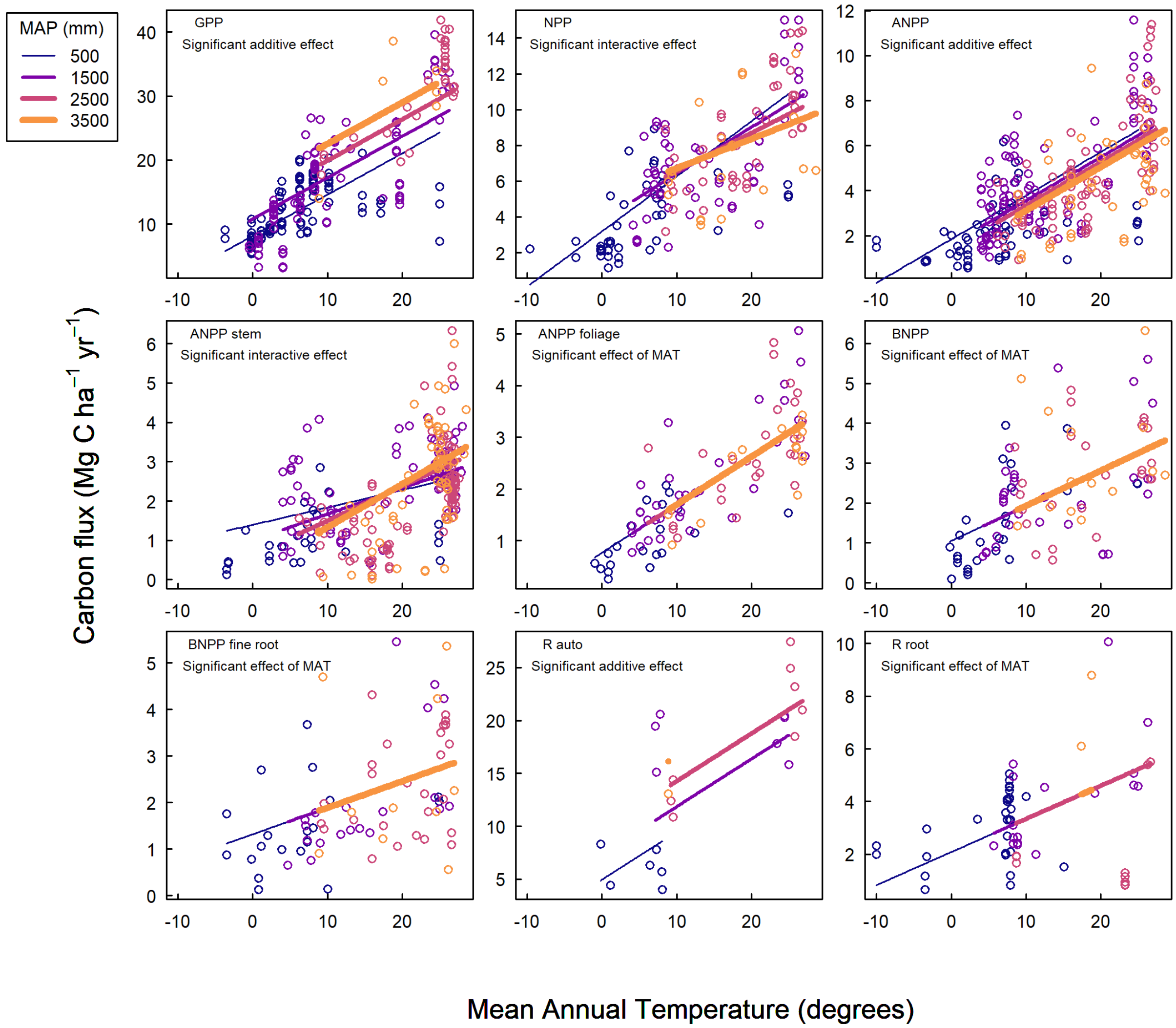

Figure 3: Interactive effects of mean annual temperature and precipitation on annual forest carbon fluxes. For visualization purposes, data points are grouped into bins of 0 - 1000, 1001 - 2000, 2001 - 3000, and >3000mm mean annual precipitation, and lines of best fit models are plotted for mean annual precipitation values of 500, 1500, 2500, and 3500mm. All regressions are significant ($p < 0.05$).

How does C flux relate to other climate variables?

Our results indicated that annual forest C fluxes were most strongly explained by temperature at the global scale, with temperature-related climate variables coming out as strong predictors of C fluxes. In addition to MAT, several of its correlates (Fig. S2) were consistently identified as strong univariate predictors of C fluxes: temperature seasonality, annual temperature range, annual frost days, PET, and length of growing season (Figs. 4, S4-S7).

All C flux variables were signficantly related to potential evapotranspiration. $ANPP_{foliage}$, $BNPP_{fine.root}$ and R_{root} increased linearly with PET; however, all other fluxes showed a polynomial relationship with PET (Fig. 4c, S4-5; Table S2). We found strong evidence for a saturation point or peak with PET: C fluxes tended to increase at values below 1000mm, before saturating between 1200 and 1700mm. There was also evidence that some C fluxes begin to decrease at values above 1800mm PET.

Vapour pressure deficit was a significant predictor of all C fluxes. $BNPP_{fine.root}$ showed a linear relationship with vapour pressure deficit ($R^2 = 0.07$, p<0.05), but all other fluxes showed a polynomial relationship (Figs. 4d, S4-5; Table S2). C fluxes initially increased with vapour pressure deficit, before saturating at around 0.8 kPa, after which point they began to decrease.

All fluxes, with the exception of R_{root}, showed a positive linear relationship with solar radiation (Figs. S4-S5, Table S2). Solar radiation explained a low proportion of variability in all C fluxes, explaining less than 20% of the variation in each flux, with the exception of R_{auto} ($R^2 = 0.26$, p<0.05).

Annual wet days, cloud cover, and aridity were poor or non-significant explainers of variation in C fluxes, explaining less than 20% of the variation in each of the carbon fluxes (Figs. S4-S5; Table S2).

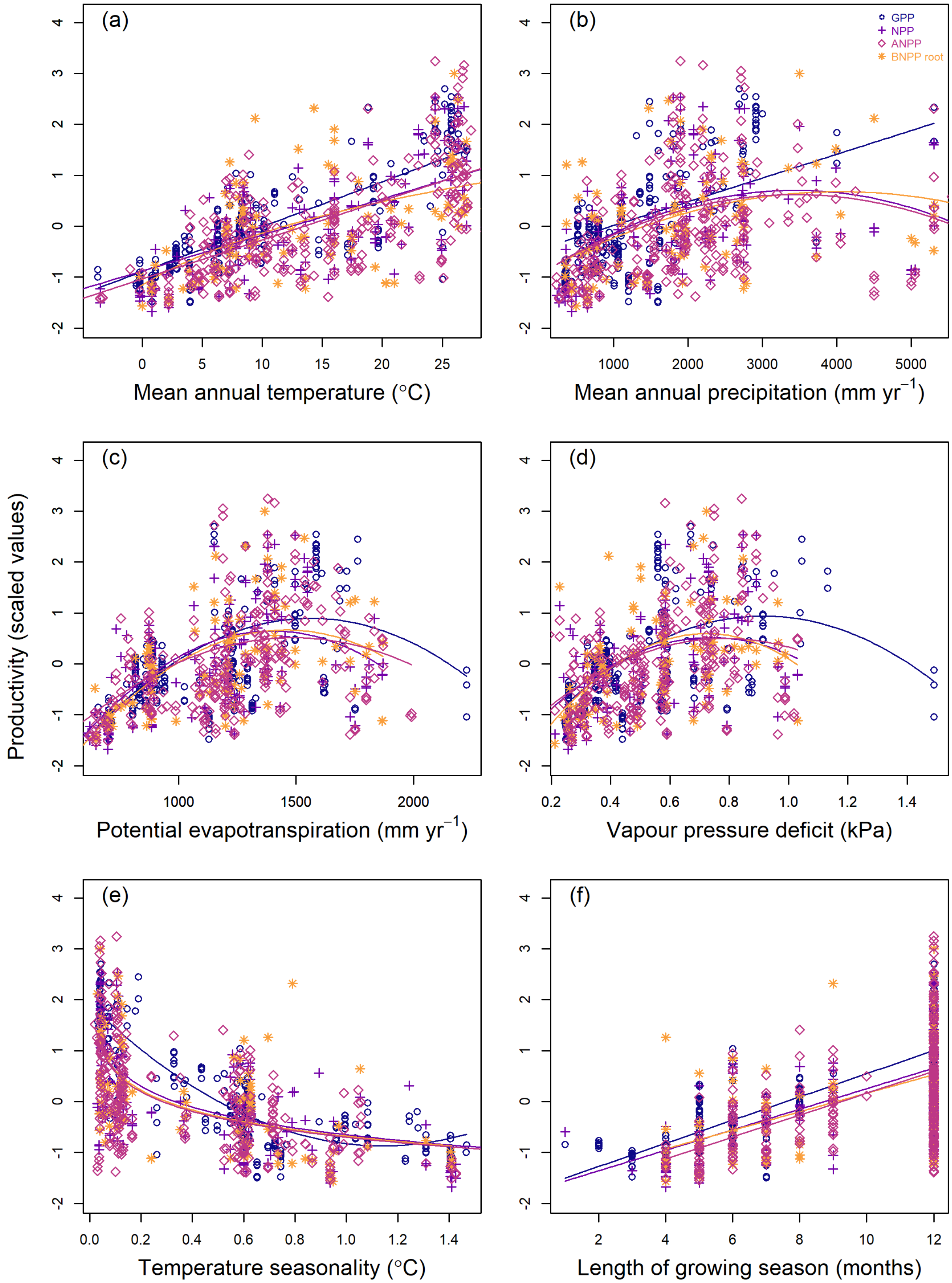

Figure 4: Plots of carbon fluxes against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration, (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. For visualization purposes, data for each flux was rescaled with a mean of 0 and standard deviation of 1. Lines of best fit are plotted according to the best model selected during analysis (**see issue 47**). All regressions are significant ($p < 0.05$).

What is the role of seasonality in explaining C fluxes?

Temperature seasonality was, overall, the best predictor of annual C fluxes. **(update this paragraph based on new results)** GPP, NPP, $ANPP$, and R_{root} exhibited a polynomial relationship with seasonality (all p<0.05; Figs. 4e, S6-7; Table S2). $ANPP_{foliage}$, $ANPP_{stem}$ and R_{auto} decreased linearly with temperature seasonality (all p<0.05; Figs. 4e, S6-S7; Table S2). Temperature seasonality was strongly correlated with annual temperature range, which was likewise a similarly strong predictor of C fluxes (Table S2). C fluxes were highest where temperature seasonality = 0, and at an annual temperature range of 15°C or lower. **BBL: perhaps put this into an ecosystem context; what are these? Aseasonal subtropical places?**

In contrast, there was no significant effect of precipitation seasonality on C fluxes, and both maximum vapour pressure deficit, and water stress months were poor or non-significant predictors of variation in C fluxes (Figs. S6-S7; Table S2).

We found a significant relationship between length of growing season and C fluxes, with all fluxes showing a linear increase with length of growing season (Figs. 4e, S6-S7; Table S2). Length of growing season was a strong predictor of C fluxes, explaining 51% of variation in GPP, 39% of variation in NPP, and 34% of variation in ANPP, but it was a weaker predictor than MAT for all fluxes analysed (Table S4).

Within the growing season, how do C fluxes vary with climate?

When annual C fluxes were standardized by growing season length (in monthly increments), correlations with growing season climate–including temperature, precipitation, solar radiation, and PET–were generally weak (Figs. S8-S9). Specifically, $ANPP$ increased with growing season temperature ($R^2 = 0.10$, p<0.001) and precipitation ($R^2 = 0.04$, p<0.05). Similarly, $ANPP_{foliage}$ increased slightly with growing season temperature ($R^2 = 0.16$, p<0.01) and precipitation ($R^2 = 0.09$, p<0.05). Growing season solar radiation had a positive influence on 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). Growing season PET had a positive influence on 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 $ANPP_{stem}$ ($R^2 = 0.06$, p<0.05). {**Becky, please verify/ edit the following:** There were no other signifcant correlations between growing season length-standardized C fluxes (9 variables in Table 2) and growing season climate (**which variables?**)}.

###Discussion

Our analysis of a large global database (ForC) reveals how autotrophic carbon fluxes in mature forests vary with latitude and climate on a global scale. We show that, across all nine forest autotrophic C fluxes analyzed, C cycling decreases continually with latitude (*H1.1*; Fig. 2)–a finding that confirms multiple previous studies but contradicts the idea that productivity of temperate forests rivals that of tropical forests (Huston and Wolverton, 2009). C fluxes generally increase in proportion to one another (*H1.2*), with few differences in allocation detectable at this global scale (Fig. S2) and with component fluxes summing appropriately to larger fluxes (Fig. 2), indicating no major, systematic omissions or overestimations of flux components. However, climate explained lower proportions of variability among subsidiary C fluxes (*e.g.*, $ANPP_{stem}$, $BNPP_{fine.root}$, R_{root}; Fig. 2; Table S2).

Latitudinal variation in C fluxes is primarily attributable to temperature-related variables (*H3, H4*), particularly MAT (Figs. 3-4). Water availability is also influential, but generally of secondary importance across the climate space occupied by forests (Figs. 3-4). Temperature seasonality and growing season length are closely correlated with MAT and are strong predictors of C fluxes (*H4*; Figs. 4e-f, S2, S6-S7), though growing season length did not 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 C fluxes (*H5*; Fig. S9; Table S4).

These findings clarify how forest C fluxes vary with latitude and climate on a global scale. Past studies have differed in their conclusions regarding the relationship between C fluxes and latitude or its correlates (Table 1, *H1*)–quite possibly because of lack of standardization with respect to stand age and disturbance history. Our findings indicate that, among mature, undisturbed stands, forest C fluxes are unambiguously highest in the tropical regions, and the relationship with latitude is approximately linear (Fig. 2). This contrasts with the suggestion that productivity of temperate forests is similar to that of tropical forests (Huston and Wolverton, 2009). Compared to tropical forests, the temperate forest biome has experienced more widespread anthropogenic disturbance and has a larger fraction of secondary stands (Potapov et al., 2008; Poulter et al., 2018), so analyses comparing across latitudinal gradients without controlling for stand age risk confounding age with biome effects. In addition, because carbon allocation varies with stand age (De Lucia et al., 2007; Anderson-Teixeira et al., 2013; Doughty et al., 2018), age differences may introduce systematic biases into analyses of C fluxes 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 (De Lucia et al., 2007; Piao et al., 2010; Doughty et al., 2018; Kunert et al., 2019).

We show that C fluxes are broadly consistent in their responses to climate drivers on the global scale, with at most modest trends in C allocation among the variable pairs tested (Figs. 2, S3). This parallels the observation that C allocation across multiple C fluxes varies little with respect to climate along a steep tropical elevational gradient (Malhi et al., 2017; but see Moser et al., 2011), and is not surprising given that trees face universal constraints in carbon allocation (**REFS**). The one trend in allocation that emerged from our analysis was a tendency for greater C allocation aboveground–and to foliage in particular–in warm tropical climates (Fig. S3). This is consistent with observations of increasing allocation to roots with declining temperature across a tropical elevational gradient (Moser et al., 2011), and with observations and theory predicting relatively higher belowground carbon allocation at higher latitudes (Gill and Finzi, 2016). It is also consistent with findings that as forest productivity increases, proportionaly more carbon is allocated to $ANPP_{foliage}$ relative to $BNPP_{fine.root}$ (Chen et al., 2019) or $ANPP_{stem}$ (Hofhansl et al., 2015). **(check / comment on Litton et al. (2007))**

One previously hypothesized trend that was not supported by our analysis was that tropical forests tend to have low carbon use efficiency (CUE= NPP/GPP=(GPP-R_{auto}/GPP), which is 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). Our analysis, limited to mature forests, shows no such trend (Fig. S3). CUE is known to decline with forest age (De Lucia et al., 2007; Piao et al., 2010; Collalti and Prentice, 2019), but appears to be roughly independent of GPP (Litton et al., 2007). (*This finding may have some important implications for modeling and our broader understanding. I'm not sure offhand how much theory has been built on the idea of low CUE in tropical forests because of warm temperatures... Helene is not aware of any.*)

update this paragraph (issue 78) One interesting observation was that climate tends to explain more variation in the major fluxes (GPP, NPP, R_{auto}) than in subsidiary fluxes ($BNPP_{fine.root}$, R_{root}, $ANPP_{stem}$) as quantified by R^2 (Fig. 2; Table S2). 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 use fundamentally different approaches in different sites (*e.g.*, minirhizotrons, ingrowth cores, or sequential coring for $BNPP_{fine.root}$; root exclusion, stable isotope tracking, or gas exchange of excised roots for R_{root}), and sampling depth is variable and often insufficient to capture the full soil profile. $ANPP_{stem}$, 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 (Clark et al., 2001). However, methodological variation and uncertainty affect all of fluxes considered here, 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 direct climatic control over GPP than subsidiary fluxes. That is, subsidiary fluxes may be shaped by climate both indirectly through its influence on GPP and respiration and directly through any climatic influence on C allocation, as well as many other local- and regional-scale factors (**REFS**).

The latitudinal gradient in forest C flux (Fig. 2) is driven primarily by temperature-related climate variables, the effects of which are moderated by moisture availability (Table 1, *H2-H3*; Figs. 3-4). MAT and MAP have long been identified as primary global-scale drivers of C fluxes (Lieth, 1973; **REFS**; Taylor et al., 2017). It is not appropriate to attempt to identify individual mean annual climate variables as mechanistic drivers of C fluxes because many climate variables co-vary across the latitudinal gradient (Fig. S2), 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. However, it remains informative to consider these relationships. Among the temperature-related climate variables, MAT is generally the most strongly correlated with C fluxes (Table S2)–perhaps in part because site-specific MAT is recorded for the majority of sites in ForC, whereas other variables were extracted from global gridded data products, introducing spatial scaling errors.

This finding supports the continued focus on MAT as a primary–*albiet* not mechanistic–correlate of C fluxes. The effects of MAT are modified by moisture availability, with reduced C fluxes under relatively dry conditions (*i.e.*, low precipitation; high vapour pressure deficit) and sometimes under very high precipitation (Figs. 3-4). **BBL: I feel like this is pretty repetitive of previous paragraph.** The observed positive interaction between MAT and MAP for $ANPP_{stem}$ on the global scale (Fig. 3) is consistent with an analysis showing a similar interaction for $ANPP$ in tropical forests, also with a cross-over point at ~20∘C (Taylor et al., 2017). However, we detect no such interaction for $ANPP$ or most other C fluxes, and we find a contrasting negative interaction for NPP (Fig. 3), suggesting that more data are required to sort out potential differences in the interactive effects of MAT and MAP on C fluxes in the tropics.

Forest autotrophic C fluxes decline with temperature seasonality (Table 1, *H4*; Fig. 4e), and are minimal 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 C flux per month of the growing season with growing season climatic conditions (Table 1, *H5*; Kerkhoff et al., 2005; Anderson et al., 2006; Enquist et al., 2007; Michaletz et al., 2014). The sort of simple metric needed to define growing season at a global scale (Kerkhoff et al., 2005) is coarse with respect to temperature because it's calculated on a monthly timescale and problematic with respect to moisture because it doesn't capture temporal lags between precipitation and plant water use caused by storage in soil or snow. We found that a temperature-defined growing season length had strong positive correlation with C fluxes (Fig. 4f), but explained less variation than MAT. Dividing annual fluxes by growing season length to yield average flux per growing season month removed the majority of climate-related variation, supporting the idea that the latitudinal gradient in carbon flux is attributable more to shorter growing seasons at high latitudes than to inherently lower rates of photosynthesis or respiration by high-latitude forests (Enquist et al., 2007). However, there remained a number of significant correlations with growing season climatic conditions, indicating 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 crude relative to the timescales on which climate affects plant metabolism, and does not advance statistical predictive power. Mechanistic accounting for climatic effects on global forest carbon flux patterns instead requires models representing physiologically meaningful timescales (e.g., **REFS**; Longo et al., 2019).

Our analysis clarifies how forest autotrophic carbon fluxes vary 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. Our findings show that higher temperatures with similar moisture availability result in a generalized acceleration of forest C cycling (Figs. 2-3). This is consistent with observations of continental- to global-scale increases over time in GPP (Li and Xiao, 2019) and $ANPP_{stem}$ (Brienen et al., 2015; Hubau et al., 2020), along with some C cycle components not considered here–tree mortality (Brienen et al., 2015; McDowell et al., 2018), soil respiration (Bond-Lamberty and Thomson, 2010), and heterotrophic soil respiration (Bond-Lamberty et al., 2018). **DISCUSS/CITE [Wu et al. 2020]** (Wu et al., 2020) However, increasing C flux rates are by no means universal (Rutishauser et al., 2020) (**MORE REFS**), likely because other factors are at play, including changes to other aspects of climate, atmospheric pollution (CO_2, SO_2, NO_x), and local disturbances. **(discuss new Sullivan paper that finds higher max temperatures associated to lower ANPP_stem)** Moreover, forest ecosystem responses to climatic changes outside the temperature range to which forest communities are adapated and acclimatized will not necessarily parallel responses across geographic gradients in climate. Nevertheless, as we enter a period of accelerating climatic change, understanding of the fundamental climatic controls on C cycling sets a foundation for understanding patterns of change.

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