Global patterns of forest autotrophic carbon fluxes

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 1,319 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 continuously with absolute latitude -- a finding that confirms multiple previous studies but contradicts the idea that net primary productivity of temperate forests rivals that of tropical forests. C flux variables generally displayed similar trends across latitude and multiple climate variables, with no differences in allocation detected at this global scale. Temperature variables in general, and mean annual temperature and temperature seasonality in particular, were the best univariate predictors of C flux, explaining 19 - 71% of variation in the C fluxes analyzed. 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 increased with growing season length, but this was never the best univariate 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, this improved understanding of the fundamental climatic controls on forest C cycling sets a foundation for understanding patterns of change.

1 **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 1,319 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 continuously with absolute latitude – a finding that confirms multiple previous studies but contradicts the idea that net primary productivity of temperate forests rivals that of tropical forests. C flux variables generally displayed similar trends across latitude and multiple climate variables, with no differences in allocation detected at this global scale. Temperature variables in general, and mean annual temperature and temperature seasonality in particular, were the best univariate predictors of C flux, explaining 19 - 71% of variation in the C fluxes analyzed. 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 increased with growing season length, but this was never the best univariate 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, this improved understanding of the fundamental climatic controls on forest C cycling sets a foundation for understanding patterns of change.

Keywords: carbon fluxes; carbon dioxide (CO_2); climate; forest; global; productivity; respiration; latitude

Introduction

Carbon (C) cycling in Earth's forests provides the energetic basis for sustaining the majority of Earth's terrestrial biodiversity and many human populations (Millennium Ecosystem 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 (Niedziałkowska et al., 2010; Zak et al., 1994) and possibly diversity (Chu et al., 2018; Waide et al., 1999). They are linked to cycling of energy, water, and nutrients and, critically, influence all 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 than 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 understanding of the climate dependence of forest C cycling on a global scale has been limited by analyses typically considering only one or a few variables at a time, insufficient parsing of related variables, and the mixing of data from forests that vary in stand age, disturbance history, and management status, all of which affect C cycling (Gillman et al., 2015; Litton et al., 2007; Šímová & Storch, 2017).

Forest C fluxes decrease with latitude (e.g., Luyssaert et al., 2007; Gillman et al., 2015; Li & Xiao, 2019). However, studies have differed in their conclusions regarding the shape of this relationship – quite possibly because of lack of standardization with respect to methodology and stand history. For instance, studies agree that gross primary productivity (GPP) increases continuously with decreasing latitude and is indisputably highest in tropical forests (Badgley et al., 2019; Beer et al., 2010; Jung et al., 2011; Li & Xiao, 2019; Luyssaert et al., 2007). In contrast, some studies have suggested that net primary productivity (NPP), or its aboveground portion ($ANPP$), exhibits a less distinct increase from temperate to tropical forests (Luyssaert et al., 2007) – or even a decrease (Huston & Wolverton, 2009, but see @gillman_latitude_2015). A shallower increase in NPP than in GPP with decreasing latitude would align with the suggestion that tropical forests tend to have low carbon use efficiency ($CUE= NPP/GPP$; DeLucia et al., 2007; Anderson-Teixeira et al., 2016; Malhi, 2012). Such differences among C fluxes their relationship to latitude could have profound implications for our understanding of the C cycle and its climate sensitivity. However, until recently the potential to compare latitudinal trends across C fluxes has been limited by lack of a large database with standardization for methodology, stand history, and management (Anderson-Teixeira et al., 2018).

The latitudinal gradient in forest C flux rates, along with altitudinal gradients (Girardin et al., 2010; Malhi

[73] et al., 2017), is driven primarily by climate, which is a significant driver of C fluxes across broad spatial

[74] scales (Cleveland et al., 2011; Luyssaert et al., 2007; Wei et al., 2010). However, there is little consensus as to

[75] the shapes of these relationships or the best predictor variables. The majority of studies have focused on

[76] exploring the relationships of C fluxes to mean annual temperature (MAT) and mean annual precipitation

[77] (MAP), as the most commonly reported site-level climate variables. C fluxes increase strongly with MAT on

[78] the global scale, but whether they saturate or potentially decrease at higher temperatures remains disputed.

[79] Some studies have detected no deceleration or decline in GPP (Luyssaert et al., 2007), NPP (Schuur, 2003),

[80] or root respiration (R_{root}; Piao et al., 2010; Wei et al., 2010) with increasing MAT. In contrast, others have

[81] found evidence of saturation or decline of C flux in the warmest climates; Luyssaert et al. (2007) found

[82] NPP saturating at around $10°C$ MAT; Larjavaara & Muller-Landau (2012) found that increases in GPP

[83] saturate at approximately $25°C$ MAT, and Sullivan et al. (2020) found that, within the tropics, $ANPP_{stem}$

[84] decreases at the highest maximum temperatures. C fluxes generally saturate at high levels of MAP, though

[85] the saturation points identified vary from MAP of ~1000 mm for R_{root} (Wei et al., 2010) up to 2,445 mm for

[86] NPP (Schuur, 2003). Interactions between MAT and MAP are also possible; within the tropics, there is a

[87] positive interaction between MAT and MAP in shaping $ANPP$, such that high rainfall has a negative effect

[88] on productivity in cooler climates, compared to a positive effect in warmer climates (Taylor et al., 2017).

[89] There is also evidence that C fluxes also respond to climate variables such as temperature and precipitation

[90] seasonality (Wagner et al., 2016), cloud cover (Taylor et al., 2017), solar radiation (Beer et al., 2010; Fyllas et

[91] al., 2017), and potential evapotranspiration (Kerkhoff et al., 2005); however, these are not typically assessed

[92] in global-scale analyses of annual forest C flux.

[93] As metrics of annual climate, MAT and MAP fail to capture variation in climate on an intra-annual scale,

[94] including temperature and precipitation seasonality and growing season length. Some studies have suggested

[95] that the apparently strong relationship between MAT and C fluxes is actually a consequence of the correlation

[96] between MAT and growing season length (Kerkhoff et al., 2005; Michaletz et al., 2018, 2014). Kerkhoff et al.

[97] (2005) and Michaletz et al. (2014) found no significant relationship between growing season temperature

[98] and $ANPP$ or NPP standardized to growing season length (but see Chu et al., 2016). While this suggests

[99] that the influence of temperature may be limited to determining the length of the frost-free growing season,

[100] analysis with carefully standardized variables and forest ages would be necessary to test the the veracity and

[101] generality of this hypothesis.

[102] The recent development of the Global Forest Carbon database (ForC), which synthesizes multiple variables

[103] and includes records of stand history (Anderson-Teixeira et al., 2016, 2018), opens up the possibility for

[104] 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 predictions (Table 1). First, we ask how nine forest autotrophic carbon
fluxes in ForC vary with latitude ($Q1$). We then test how these fluxes relate to MAT and MAP ($Q2$), and
additionally how they respond to other, less well-studied, climate variables ($Q3$). Finally, we consider the
relationship between C flux and seasonality, considering the role of seasonality in explaining variation in
carbon fluxes ($Q4$), and the influence of climate on C flux standardized by growing season length ($Q5$).

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.

Questions and hypotheses	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?											
C fluxes decrease continuously with latitude.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Fig. 2
Q2. How do C fluxes vary with mean annual temperature (MAT) and precipitation (MAP)?											
C fluxes increase continuously with MAT.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 3, 4, S4, S5
C fluxes increase with precipitation up to at least 2000 mm yr^{-1}.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S4, S5
Temperature and precipitation jointly shape C fluxes.	(yes)	yes	yes	yes	yes	-	-	-	yes	-	Fig. 3, Table S3
Q3. How are C fluxes related to other annual climate variables?											
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
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
C fluxes increase with solar radiation.	(yes)	yes	yes	yes	yes	yes	yes	yes	yes	-	Figs. S4, S5
Q4. How does seasonality influence annual C fluxes?											
C fluxes decrease with temperature seasonality.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S6, S7
C fluxes decrease with precipitation seasonality.	-	-	-	-	no	-	-	-	-	-	Figs. S6, S7
C fluxes increase with growing season length.	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	Figs. 4, S6, S7
Growing season length is a better predictor of C fluxes than MAT.	(no)	no	no	no	-	no	no	no	no	no	Table S4
Q5. When standardised by growing season length, how do annual C fluxes vary with climate?											
Growing season-standardized C fluxes increase with growing season temperature.	(yes)	-	-	yes	-	yes	-	-	-	-	Figs. S8, S9
Growing season-standardized C fluxes increase with growing season PET.	(yes)	yes	yes	-	yes	-	yes	yes	-	-	Figs. S8, S9
Growing season-standardized C fluxes increase with growing season precipitation.	(yes)	-	-	yes	-	yes	-	-	-	-	Figs. S8, S9
Growing season-standardized C fluxes increase with growing season solar radiation.	(yes)	-	-	-	-	-	yes	yes	-	-	Figs. S8, S9

Forest autotrophic carbon fluxes

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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 & 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. From this, we drew 1,319 records that met our criteria, as outlined below (Fig. 1).

This analysis focused on mature forests with no known history of significant 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 (DeLucia 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 & Storch, 2017), sites were excluded from analysis if they were managed, defined as plots that were planted, managed as plantations, irrigated, fertilised or included 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.

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}.

Variable	Definition	Components included	Methodologies	Sample size	
				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 ≤ 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
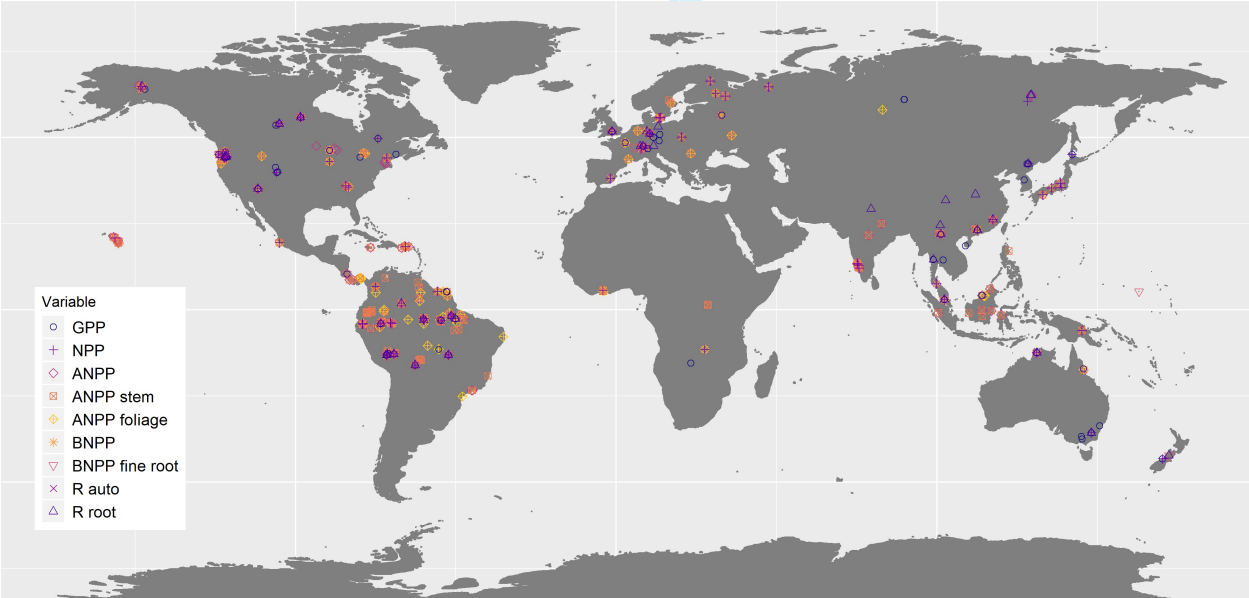

Figure 1: Map showing all data used in the analysis, coded by variable. Variables are plotted individually in Fig. S1.

Climate data

ForC contains geographic coordinates associated with each measurement record and, when available, MAT and 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 & 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 & 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 dataset.

Following the previous studies whose hypothesis we were evaluating (Kerkhoff et al., 2005; Michaletz et al., 2014), 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 for the sites included here, 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 & Hijmans, 2017) were used to calculate mean monthly PET, precipitation, temperature and solar radiation during the growing season.

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 (R Core Team, 2018). 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–were 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 $\Delta AIC < 2$). Effects were considered significant when inclusion of the fixed effect of interest resulted in p ≤ 0.05 and ΔAIC

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165 ≥ 2.0 relative to a corresponding null model. All R^2 values presented here are marginal R^2 values, and refer

166 to the proportion of variation explained by only the fixed effects. Specific analyses are as described below.

167 We first examined the relationship between latitude and C fluxes ($Q1$; Table 1). We tested models with

168 latitude as a first-order linear, second-order polynomial, and logarithmic term. For brevity, we henceforth refer

169 to first-order linear models as "linear" and second-order polynomial models as "polynomial". We selected as

170 the best model that with the highest Δ AIC relative to a null model with no fixed term, with the qualification

171 that a polynomial model was considered an improvement over a linear model only if it reduced the AIC value

172 by 2.0 or more. In addition, pairwise comparisons of R^2 values were carried out for a selection of pairs of C

173 fluxes to test for differences among variables in the proportion of variation explained by latitude and climate.

174 Models were run on data from sets of sites that were common to each pair, in order to account for variation

175 in the number of data points included.

176 To test whether trends in component fluxes across latitude sum to match those of larger fluxes, regression lines

177 for smaller component fluxes were summed to generate new estimates of larger fluxes. Because no fluxes were

178 significantly better predicted by a logarithmic or polynomial fit than by a linear fit, we used linear fits for all

179 fluxes in this analysis. We then determined whether these summed predictions fell within the 95% CI for the

180 larger flux across the entire latitudinal range. Confidence intervals for the line of best fit for the larger flux were

181 estimated using the 'bootMer' function, a parametric bootstrapping method for mixed models (Bates et al.,

182 2015). This function carried out 2000 simulations estimating the line of best fit, using quantiles at 0.025 and

183 0.975 to estimate 95% CIs. This analysis was applied to the following sets of fluxes: (1) $GPP = NPP + R_{auto}$,

184 (2) $NPP = ANPP + BNPP$, and (3) $ANPP = ANPP_{foliage} + ANPP_{stem}$. In addition, we estimated total

185 belowground C flux (TBCF, not analyzed due to limited data) as $TBCF = BNPP + R_{root}$.

186 Variation in allocation to component carbon fluxes was explored for three groupings: (1) $GPP = NPP + R_{auto}$,

187 (2) $NPP = ANPP + BNPP$, and (3) $ANPP = ANPP_{foliage} + ANPP_{stem}$. For each group, measurements

188 taken at the same site and plot, and in the same year, were grouped together. For groups (1) and (2), where

189 2 of the 3 flux measurements were available for a given site, plot, and year, these measurements were used

190 to calculate the third. The ratio of each pair of component fluxes was calculated. The log of these ratios

191 were regressed against latitude and climate variables, using the linear model specified above. Cook's distance

192 analyses were carried out for each of the models, and extreme outliers removed.

193 We next examined the relationships of C fluxes to climate variables ($Q2$-$Q4$; Table 1). We tested first-order

194 linear, second-order polynomial, and logarithmic fits for each climate variable. Again, polynomial fits were

195 considered superior to first-order linear fits only if inclusion of a second-order polynomial term resulted in

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196 ΔAIC $\geq$ 2.0 relative to a first-order linear model. We tested relationships of each C flux (Table 2) against each

197 climate variable (Table S1). Variables which were not significant explanatory variables or which explained

198 <20% of variation in C fluxes are only presented in SI.

199 Multivariate models were used to investigate the potential joint and interactive effects of MAT and MAP on

200 carbon fluxes. An additive model including MAP in addition to MAT was accepted when ΔAIC >2 relative

201 to a null including only MAT as a fixed effect. An interactive model including an MAT x MAP interaction

202 was accepted when ΔAIC >2 relative to a null including MAT and MAP as fixed effects.

203 To test whether and how C fluxes varied with climate when standardised by growing season length ($Q5$;

204 Table 1), we first standardized all annual C fluxes by dividing by growing season length (as defined above).

205 We then derived four variables to describe growing season climate, specifically growing season temperature,

206 precipitation, solar radiation, and PET (Table S1). We tested for correlations between these standardised

207 fluxes and growing season climate variables, using only first-order linear models.

208 All analyses were conducted in R v.3.5.1 (R Core Team, 2018). Code and data necessary to reproduce all

209 results are available through GitHub (https://github.com/forc-db/Global_Productivity) and archived in

210 Zenodo (DOI: TBD).

Results

212 In total, we analyzed 1,319 records from nine forest autotrophic C flux variables taken from forests that had

213 experienced no major anthropogenic disturbances within the past 100 years. These records represented a

214 total of 255 plots in 154 distinct geographic areas across all forested biogeographic and climate zones (Figs. 1,

215 S1; Table 2).

216 *Q1. How does C flux vary with latitude?*

217 All major carbon fluxes decreased with latitude (Fig. 2; Table S2). Latitude was a strong predictor for

218 many of the carbon fluxes, particularly the larger fluxes (Table S2, S6). Specifically, latitude explained 64%

219 of variation in GPP (n = 243, p<0.0001), 50% in NPP (n = 161, p<0.0001) and 44% in ANPP (n = 278,

220 p<0.0001). The C fluxes that were most poorly predicted by latitude were $BNPP_{fine.root}$ (R^2=0.17) and

221 $ANPP_{stem}$ (R^2=0.18). The relationship with latitude was best fit by the first-order linear model, with the

222 exception of NPP and R_{root}, for which a logarithmic model was a slightly – but not significantly – better fit.
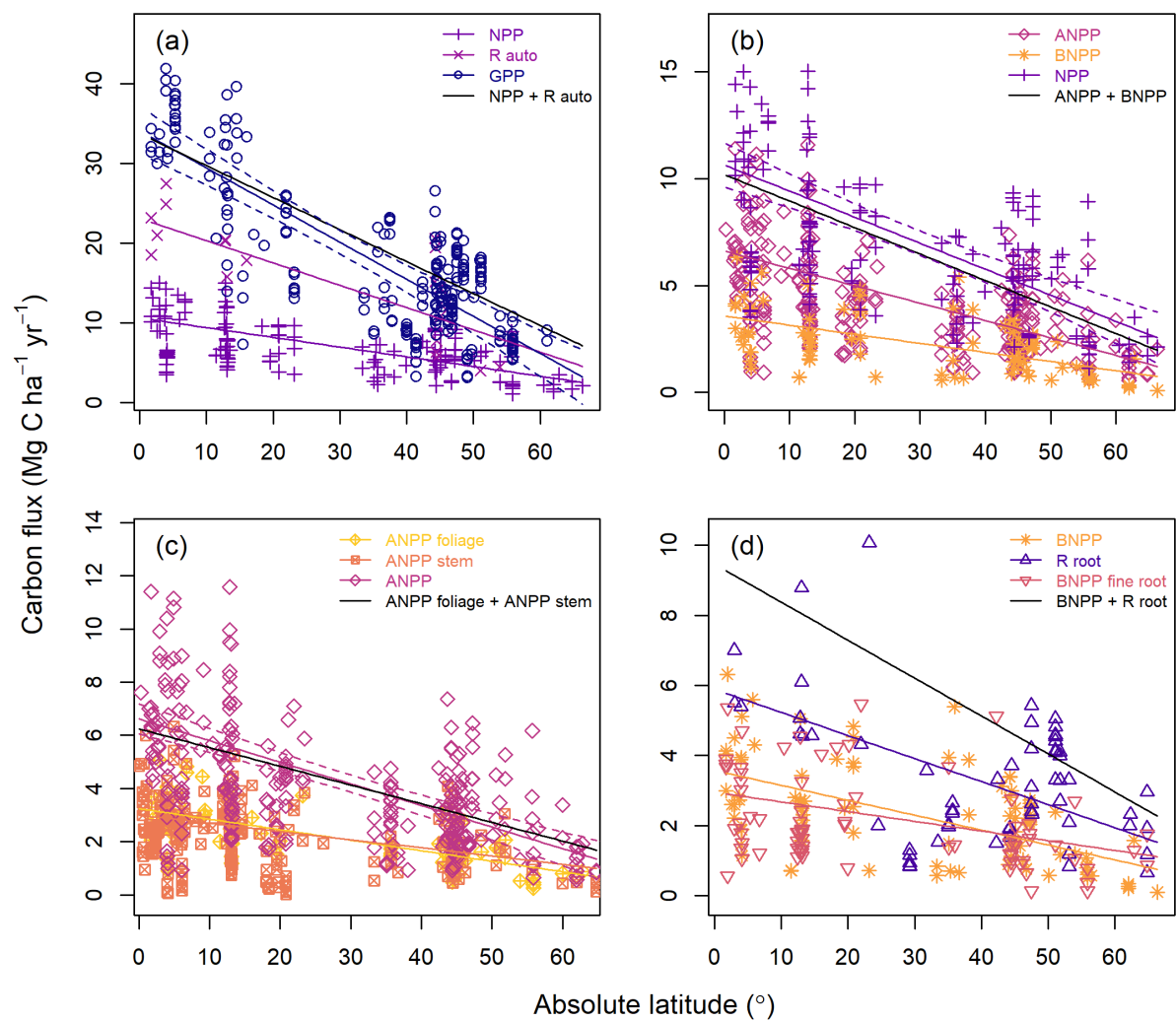
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Figure 2: Latitudinal trends in forest autotropic carbon flux. Plotted are linear models, all of which were significant ($p < 0.05$) and had AIC values within 2.0 of the best model (for two fluxes, logarithmic fits were marginally better; Table S2). 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

223   Smaller component fluxes summed approximately to larger fluxes across the latitudinal gradient (Fig. 2).

224   That is, modeled estimates of GPP, generated from the sum of NPP and R_{auto}; NPP, generated from

225   the sum of $ANPP$ and $BNPP$; and $ANPP$, generated from the sum of $ANPP_{foliage}$ and $ANPP_{stem}$, fell

226   almost completely within the confidence intervals of the regressions of field estimates of GPP, NPP, and

227    $ANPP$, respectively.

228   We found no evidence of systematic variation in C allocation with latitude or climate (Fig. S3). Of 12

229   relationships tested (3 ratios among C flux variables regressed against latitude, MAT, MAP and temperature

230   seasonality), none were significant.

231   *Q2. How does C flux relate to MAT and MAP?*

232   All fluxes increased with MAT (all p<0.05; Figs. 3-4, S4-S5, Table S2). For eight of the nine fluxes, this

233   relationship was linear. For only one variable, $BNPP$, did a lognormal fit provide an improvement over a

234   first-order linear relationship, though this was not significant (ΔAIC <2). As with latitude, MAT tended

235   to explain more variation in the larger fluxes (GPP, NPP, $ANPP$, R_{auto}) and $ANPP_{foliage}$ (all $R^2 > 0.4$)

236   than in subsidiary and belowground fluxes ($ANPP_{stem}$, R_{root}, $BNPP_{fine.root}$; all $R^2 < 0.25$; Table S6).

237   MAP was a significant (p<0.05) predictor of all fluxes (Figs. 4a, S4-S5; Table S2). However, it explained

238   little variation: with the exception of R_{auto}, MAP explained at most 25% of variation in C flux. All fluxes

239   increased with MAP up to at least 2000 mm, above which responses were variable (Figs. 4, S4-S5).

240   There was a significant additive effect of MAT and MAP on GPP, $ANPP$ and R_{auto} (Fig. 3, Table S3), and

241   a significant interactive effect between MAT and MAP for NPP and $ANPP_{stem}$ (Fig. 3, Table S3). The

242   interaction was negative for NPP and positive for $ANPP_{stem}$. For $ANPP_{foliage}$, $BNPP$, $BNPP_{fine.root}$,

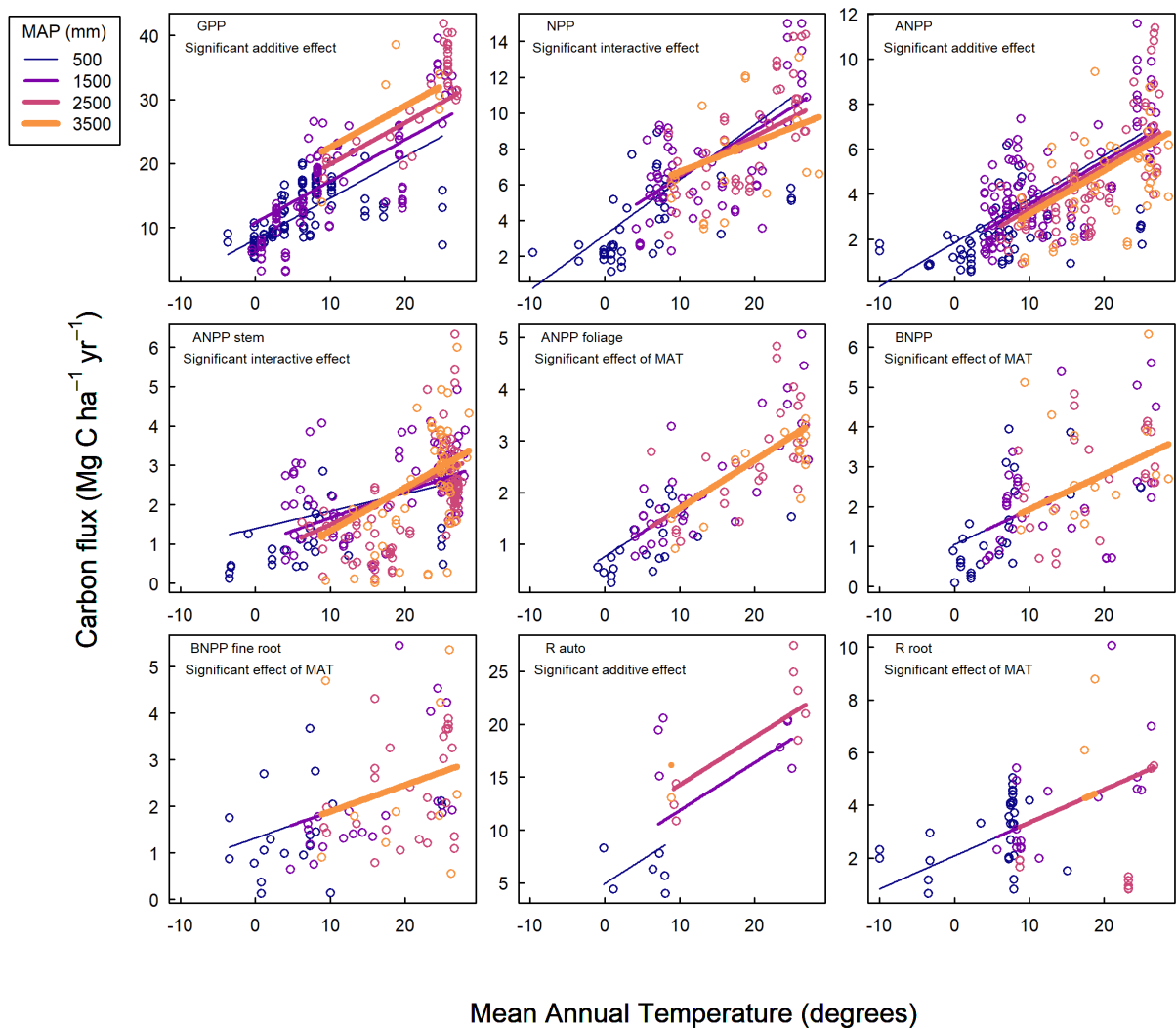243   and R_{root}, MAP did not have a significant effect when accounting for MAT (Fig. 3, Table S3).

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 ($p < 0.05$).

244   *Q3. How does C flux relate to other annual climate variables?*

245   All C flux variables showed a significant relationship with annual PET. The relationship was logarithmic for

246    $ANPP_{foliage}$, $BNPP_{fine.root}$ and R_{root}, and polynomial for all other fluxes (Fig. 4c, S4-5; Table S2). We

247   found strong evidence for a saturation point or peak with PET: C fluxes tended to increase at values below

248   1000mm, before saturating between 1200 and 1700mm. There was also evidence that some C fluxes begin to

249   decrease at values above 1800mm PET.

250   Mean annual VPD was a significant predictor of all C fluxes. $ANPP_{foliage}$, $BNPP_{fine.root}$ and R_{root} showed

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251 a logarithmic relationship with VPD, but all other fluxes showed a polynomial relationship (Figs. 4d, S4-5;

252 Table S2). C fluxes initially increased with VPD, before saturating at around 0.8 kPa, after which point

253 they began to decrease.

254 All fluxes, with the exception of R_{root}, showed a significant positive relationship with solar radiation (Figs.

255 S4-S5, Table S2). Solar radiation explained a low proportion of variability ($<30\%$) in all C fluxes.

256 Annual wet days, cloud cover, and aridity were poor or non-significant predictors of variation in C fluxes,

257 explaining less than 20% of the variation in each of the carbon fluxes (Figs. S4-S5; Table S2).
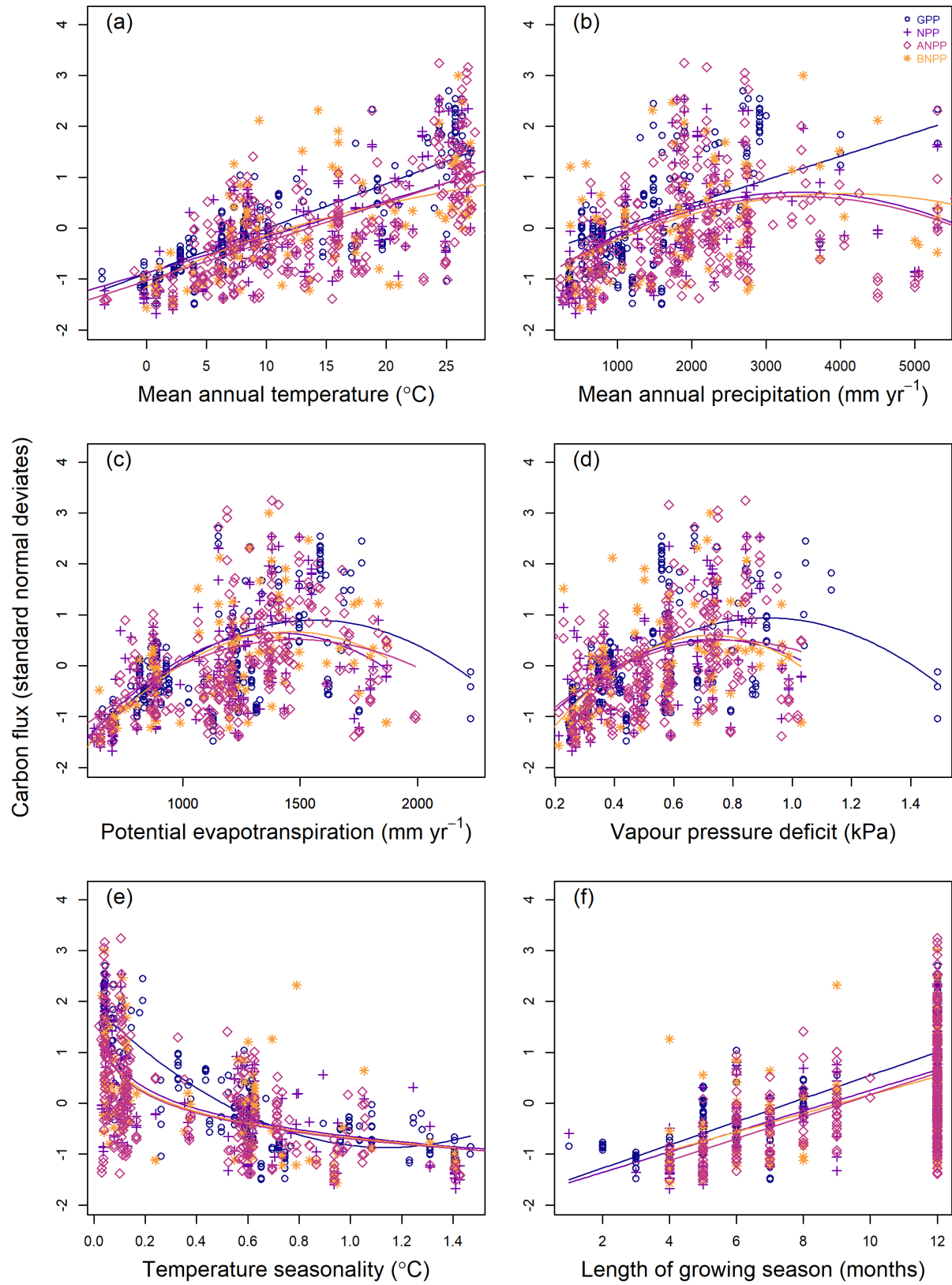
Figure 4: Plots of carbon fluxes against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration, (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. For visualization purposes, data for each flux was rescaled with a mean of 0 and standard deviation of 1. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$).

258 *Q4. What is the role of seasonality in explaining C fluxes?*

259 Variables describing temperature seasonality – temperature seasonality, annual temperature range, annual

260 frost days, and length of growing season – were strongly correlated with both latitude and MAT (all r$\geq$ 0.2;

261 Fig. S2), and were consistently identified as strong univariate predictors of C fluxes (Figs. 4, S4-S7).

262 All fluxes decrease with increasing temperature seasonality, though the shape of this relationship varies (all

263 p<0.05; Figs. 4e, S6-7; Table S2). Temperature seasonality was strongly correlated with annual temperature

264 range, which was likewise a similarly strong predictor of C fluxes (Table S2). C fluxes were highest where

265 temperature seasonality $= 0$, and at an annual temperature range of 15°C or lower (*i.e.*, in the tropics).

266 In contrast, there was no significant effect of precipitation seasonality on C fluxes at this global scale. Both

267 maximum vapour pressure deficit and water stress months were poor or non-significant predictors of variation

268 in C fluxes (Figs. S6-S7; Table S2).

269 We found a significant relationship between length of growing season and C fluxes, with all fluxes showing a

270 positive relationship with length of growing season (Figs. 4e, S6-S7; Table S2). Length of growing season was

271 a strong predictor of C fluxes, explaining 53% of variation in GPP, 38% of variation in NPP, and 34% of

272 variation in ANPP (all p<0.05; Table S2), but it was a weaker predictor than MAT for all fluxes analysed

273 (Table S4).

274 *Q5. Within the growing season, how do C fluxes vary with climate?*

275 When annual C fluxes were standardized by growing season length (in monthly increments), correlations with

276 growing season climate were generally weak (Figs. S8-S9). $ANPP$ increased with growing season temperature

277 ($R^2 = 0.09$, p<0.001) and precipitation ($R^2 = 0.04$, p<0.05). Similarly, $ANPP_{foliage}$ increased slightly with

278 growing season temperature ($R^2 = 0.16$, p<0.01) and precipitation ($R^2 = 0.09$, p<0.05). Growing season

279 solar radiation was positively correlated with on $BNPP$ ($R^2 = 0.17$, p<0.001) and $BNPP_{fine.root}$ ($R^2 = $

280 0.13, p<0.01). Growing season PET had a positive influence on GPP ($R^2 = 0.15$, p<0.01), NPP ($R^2 = $

281 0.07, p<0.01), $BNPP$ ($R^2 = 0.23$, p<0.0001), $BNPP_{fine.root}$ ($R^2 = 0.10$, p<0.05), and $ANPP_{stem}$ ($R^2 = $

282 0.06, p<0.05). All other relationships were non-significant.

283 **Discussion**

284 Our analysis of a large global database (ForC) clarifies how autotrophic C fluxes in mature forests vary

285 with latitude and climate on a global scale. We show that, across all nine variables analyzed, annual C

286 flux decreases continually with latitude (Fig. 2), a finding that confirms multiple previous studies but

287 contradicts the idea that productivity of temperate forests rivals or even exceeds that of tropical forests

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288 (Huston & Wolverton, 2009; Luyssaert et al., 2007). At this global scale, C fluxes increase approximately in

289 proportion to one another, with component fluxes summing appropriately to larger fluxes and no detectable

290 differences in allocation across latitude or climates (Figs. 2, 4, S3). Similarly, we show broad - *albeit* not

291 complete - consistency of climate responses across C fluxes, with the observed latitudinal variation primarily

292 attributable to temperature and its seasonality (Figs. 3-4). Water availability is also influential, but of

293 secondary importance across the climate space occupied by forests (Figs. 3-4). Contrary to prior suggestions

294 that the majority of variation in C cycling is driven primarily by the length of the growing season (Enquist et

295 al., 2007; Kerkhoff et al., 2005; Michaletz et al., 2014), we find modest explanatory power of growing season

296 length and small but sometimes significant influence of climate within the growing season (Figs. 4f,S6-S9).

297 Together, these findings yield a unified understanding of climate's influence on forest C cycling.

298 Our findings indicate that, among mature, undisturbed stands, forest C fluxes are unambiguously highest

299 in the tropical regions, and the relationship with both latitude and MAT is approximately linear (Table 1,

300 $Q1,Q2$; Figs. 2, 4). This contrasts with the suggestion that C fluxes (e.g., NPP, $ANPP$, $ANPP_{stem}$) of

301 temperate forests are similar to or even greater than that of tropical forests (Huston & Wolverton, 2009;

302 Luyssaert et al., 2007). Previous indications of such a pattern may have been an artifact of differences in

303 stand age across biomes. Compared to tropical forests, the temperate forest biome has experienced more

304 widespread anthropogenic disturbance and has a larger fraction of secondary stands (Potapov et al., 2008;

305 Poulter et al., 2018), so analyses comparing across latitudinal gradients without controlling for stand age risk

306 confounding age with biome effects. Because carbon allocation varies with stand age (Anderson-Teixeira et

307 al., 2013; DeLucia et al., 2007; Doughty et al., 2018), age differences may introduce systematic biases into

308 analyses of C fluxes across latitude or global climatic gradients. For example, woody productivity tends to

309 be higher in rapidly aggrading secondary stands than in old-growth forests, where proportionally more C is

310 allocated to respiration and non-woody productivity (DeLucia et al., 2007; Doughty et al., 2018; Kunert et

311 al., 2019; Piao et al., 2010). Thus, findings that temperate forest productivity rivals that of tropical forests

312 are likely an artifact of different forest ages across biomes.

313 We show that C fluxes are broadly consistent in their responses to climate drivers on the global scale, with

314 no trends in C allocation among the variable pairs tested (Figs. 2, 4, S3). This parallels the observation that

315 C allocation across multiple C fluxes varies little with respect to climate along a steep tropical elevational

316 gradient (Malhi et al., 2017; but see Moser et al., 2011), and is not surprising given that carbon allocation

317 within forest ecosystems is relatively constrained (Enquist & Niklas, 2002; Litton et al., 2007; Malhi et al.,

318 2011). We find no trend in the allocation of GPP between production and respiration across latitude or climate

319 (NPP:R_{auto}; Fig. S3), refuting the idea that tropical forests have anomalously low CUE (Anderson-Teixeira

320 et al., 2016; DeLucia et al., 2007; Malhi, 2012). Rather, differences in CUE between old-growth tropical

321 forests relative to (mostly younger) extratropical forests are likely an artifact of comparing stands of different

322 age, as CUE is known to decline with forest age (Collalti & Prentice, 2019; DeLucia et al., 2007; Piao et al.,

323 2010). Another previously observed pattern for which we find no support is a tendency for belowground C

324 allocation to decrease with increasing temperature (Gill & Finzi, 2016; Moser et al., 2011); rather, we observe

325 no trends in allocation between $ANPP$ and $BNPP$ across latitudes. Failure to detect significant tends in C

326 allocation with respect to climate in this analysis does not imply that none exist; rather, it suggests that, at

327 this global scale, differences are subtle and/or that more careful methodological standardization is required

328 to detect them.

329 Despite the broad consistency of climate responses across C fluxes, climate explains lower proportions of

330 variability among some of the subsidiary C fluxes (*e.g.*, $ANPP_{stem}$, $BNPP$, $BNPP_{fine.root}$; Fig. 2; Tables

331 S2, S6). There are two, non-exclusive, potential explanations for this. First, it may be that methodological

332 variation is larger relative to flux magnitude for some of the subsidiary fluxes. Belowground fluxes in particular

333 are difficult to quantify, and measurement methods for the belowground fluxes considered here may use

334 fundamentally different approaches in different sites (*e.g.*, minirhizotrons, ingrowth cores, or sequential coring

335 for $BNPP_{fine.root}$; root exclusion, stable isotope tracking, or gas exchange of excised roots for R_{root}), and

336 sampling depth is variable and often insufficient to capture the full soil profile. $ANPP_{stem}$, which is also

337 poorly explained by latitude or climate, is more straightforward to measure but is subject to variability

338 introduced by differences such as biomass allometries applied and minimum plant size sampled (Clark et al.,

339 2001). However, methodological variation and uncertainty affect all of fluxes considered here, and some of

340 the larger fluxes that vary more strongly with respect to climate ($ANPP$, NPP) are estimated by summing

341 uncertain component fluxes. Second, differences among variables in the proportion of variation explained

342 by climate may be attributable to more direct climatic control over GPP than subsidiary fluxes. That is,

343 subsidiary fluxes may be shaped by climate both indirectly through its influence on GPP and respiration

344 and directly through any climatic influence on C allocation, as well as many other local- and regional-scale

345 factors (e.g., Moser et al., 2011).

346 Temperature and its seasonality were the primary drivers of C fluxes on the global scale (Table 1, *Q2*,*Q4*;

347 Figs. 2-4), consistent with a long legacy of research identifying temperature as a primary driver of forest

348 ecosystem C cycling (e.g., Lieth, 1973; Luyssaert et al., 2007; Wei et al., 2010). We find little evidence of any

349 non-linearity in temperature's influence on C fluxes. The relationship of all fluxes to MAT as an individual

350 driver were best described by a linear function (Table S2) – with the exception of $BNPP$, whose response

351 to MAT was close to linear (Fig. 4a). This result contrasts with the idea that fluxes saturate with MAT

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352 below approximately 25°C MAT (Huston & Wolverton, 2009; Luyssaert et al., 2007). It remains possible

353 that fluxes decline above this threshold (Larjavaara & Muller-Landau, 2012; Sullivan et al., 2020), as is also

354 consistent with tree-ring records indicating that tropical tree growth declines at high temperatures (e.g.,

355 Vlam et al., 2014). However, these higher temperatures also tend to be associated with high PET and VPD,

356 both of which are associated with reduced C fluxes (Figs. 4c-d, S4-S5).

357 Indeed, while temperature responses dominate at this global scale and within the climate space occupied

358 by forests, the effects of temperature are moderated by moisture availability (Table 1, $Q2,Q3$; Figs 3-4).

359 Specifically, C fluxes are reduced under relatively dry conditions (*i.e.*, low MAP; high VPD) and sometimes

360 under very high precipitation (Figs. 3-4). The observed positive interaction between MAT and MAP for

361 $ANPP_{stem}$ on the global scale (Fig. 3) is consistent with an analysis showing a similar interaction for $ANPP$

362 in tropical forests, also with a cross-over point at ~20ˆ∘C (Taylor et al., 2017).

363 However, we detect no such interaction for $ANPP$ or most other C fluxes, and we find a contrasting negative

364 interaction for NPP (Fig. 3), suggesting that more data are required to sort out potential differences in the

365 interactive effects of MAT and MAP on C fluxes in the tropics.

366 Forest C fluxes decline with temperature seasonality (Table 1, $Q4$; Fig. 4e), and are minimal during cold- or

367 dry- dormant seasons. To account for this, a number of analyses seeking to characterize global-scale effects of

368 climate on productivity have examined the relationship of C flux per month of the growing season with growing

369 season climatic conditions (Table 1, $Q5$; Kerkhoff et al., 2005; Anderson et al., 2006; Enquist et al., 2007;

370 Michaletz et al., 2014). The sort of simple metric that has been used to define growing season at a global scale

371 (Kerkhoff et al., 2005) is coarse with respect to temperature because it is calculated on a monthly timescale

372 and problematic with respect to moisture because it doesn't capture temporal lags between precipitation

373 and plant water use caused by storage in soil or snow. We found that a temperature-defined growing season

374 length had strong positive correlation with C fluxes (Fig. 4f), but was never the best univariate predictor.

375 Dividing annual fluxes by growing season length to yield average flux per growing season month removed

376 the majority of climate-related variation, supporting the idea that the latitudinal gradient in carbon flux is

377 attributable more to shorter growing seasons at high latitudes than to inherently lower rates of photosynthesis

378 or respiration by high-latitude forests (Enquist et al., 2007). However, there remained a number of significant

379 correlations with growing season climatic conditions, indicating that climatic conditions remain influential

380 within the growing season (Figs. S8-S9). We conclude that while correcting for growing season length takes

381 analyses a step closer to mechanistic linkage of instantaneous C flux rates to environmental conditions, it

382 remains crude relative to the timescales on which climate affects plant metabolism, and does not advance

383 statistical predictive power. Rather, mechanistic accounting for climatic effects on global forest carbon flux

384 patterns requires models representing physiologically meaningful timescales (e.g., Medvigy et al., 2009; Longo
385 et al., 2019).

386 Our analysis clarifies how annual forest autotrophic C fluxes vary with latitude and climate on a global scale,
387 with some important implications for how forest C cycling relates to climate and, by extension, how it is
388 likely to respond to climatic warming. To the extent that patterns across broad scale climatic gradients
389 can foretell how ecosystem responses to climate change, our findings suggest that higher temperatures with
390 similar moisture availability would result in a generalized acceleration of forest C cycling (Figs. 2-3). This is
391 consistent with observations of continental- to global-scale increases over time in GPP (Li & Xiao, 2019) and
392 $ANPP_{stem}$ (Brienen et al., 2015; Hubau et al., 2020), along with some C cycle components not considered
393 here–tree mortality (Brienen et al., 2015; McDowell et al., 2018), soil respiration (Bond-Lamberty & Thomson,
394 2010), and heterotrophic soil respiration (Bond-Lamberty et al., 2018). However, increasing C flux rates are
395 by no means universal (e.g., Rutishauser et al., 2020; Hubau et al., 2020), likely because other factors are
396 at play, including changes to other aspects of climate, atmospheric pollution (CO_2, SO_2, NO_x), and local
397 disturbances.

398 Moreover, forest ecosystem responses to climatic changes outside the temperature range to which forest
399 communities are adapted and acclimatized will not necessarily parallel responses across geographic gradients
400 in climate. Indeed, tree-ring studies from forests around the world indicate that tree growth rates – along
401 with $ANPP_{stem}$ and possibly other ecosystem C fluxes – respond negatively to temperature (Helcoski et
402 al., 2019; Sniderhan & Baltzer, 2016). Furthermore, in the tropics, climate change will push forests beyond
403 any contemporary climate, and there are some indications that this could reduce C flux rates (Mau et al.,
404 2018; Sullivan et al., 2020). Further research is required to understand the extent to which forest responses
405 to climate change will track the observed global gradients, and the time scale on which they will do so. In
406 the meantime, understanding the fundamental climatic controls on annual C cycling in Earth's forests sets a
407 firmer foundation for understanding forest C cycle responses to accelerating climate change.

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