

¹ **Title:** Global patterns of forest autotrophic carbon fluxes

² **Running head:** Global patterns of forest carbon fluxes

³ **Authors:**

⁴ Rebecca Banbury Morgan^{1,2}

⁵ Valentine Herrmann¹

⁶ Norbert Kunert^{1,3}

⁷ Ben Bond-Lamberty⁴

⁸ Helene C. Muller-Landau³

⁹ Kristina J. Anderson-Teixeira^{1,3*}

¹⁰ **Institutional Affiliations:**

¹¹ 1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; Front Royal, VA, USA

¹² 2. School of Geography, University of Leeds, Leeds, UK

¹³ 3. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research
¹⁴ Institute; Panama, Republic of Panama

¹⁵ 4. Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park Maryland
¹⁶ 20740 USA

¹⁷ *Corresponding Author:

¹⁸ phone: 1-540-635-6546

¹⁹ fax: 1-540-635-6506

²⁰ email: teixeirak@si.edu

21 **Abstract**

22 Carbon (C) fixation, allocation, and metabolism by trees set the basis for energy and material flows in forest
23 ecosystems and define their interactions with Earth's changing climate. However, we lack a cohesive synthesis
24 on how forest carbon fluxes vary globally with respect to climate and one another. Here, we draw upon 1,319
25 records from the Global Forest Carbon Database (ForC), representing all major forest types and the nine
26 most significant autotrophic carbon fluxes, to comprehensively explore how C cycling in mature, undisturbed
27 forests varies with latitude and climate on a global scale. We show that, across all flux variables analyzed, C
28 cycling decreases continuously with absolute latitude – a finding that confirms multiple previous studies ~~but~~ ~~and~~
29 contradicts the idea that net primary productivity of temperate forests rivals that of tropical forests. C flux
30 variables generally displayed similar trends across latitude and multiple climate variables, with no differences
31 in allocation detected at this global scale. Temperature variables in general, and mean annual temperature
32 and temperature seasonality in particular, were the best univariate predictors of C flux, explaining 19 - 71%
33 of variation in the C fluxes analyzed. The effects of temperature were modified by moisture availability,
34 with C flux reduced under hot and dry conditions and sometimes under very high precipitation. C fluxes
35 increased with growing season length, but this was never the best univariate predictor. Within the growing
36 season, the influence of climate on C cycling was small but significant for a number of flux variables. These
37 findings clarify how forest C flux varies with latitude and climate on a global scale. In a period of accelerating
38 climatic change, this improved understanding of the fundamental climatic controls on forest C cycling sets a
39 foundation for understanding patterns of change.

40 **Keywords:** carbon fluxes; carbon dioxide (CO₂); climate; forest; global; productivity; respiration; latitude

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41 **Introduction**

42 Carbon (C) cycling in Earth's forests provides the energetic basis for sustaining the majority of Earth's ter-
43 restrial biodiversity and many human populations (Assessment, 2005), while strongly influencing atmospheric
44 carbon dioxide (CO_2) and climate (Bonan, 2008). Forests' autotrophic carbon fluxes – that is, carbon fixation,
45 allocation, and metabolism by trees and other primary producers – sets the energy ultimately available to
46 heterotrophic organisms (including microbes), in turn influencing their abundance (Niedziałkowska et al.,
47 2010; Zak et al., 1994) and possibly diversity (Chu et al., 2018; Waide et al., 1999). They are linked to
48 cycling of energy, water, and nutrients and, critically, influence all C stocks and define forest interactions with
49 Earth's changing climate. Each year, over 69 Gt of C cycle through Earth's forests (Badgley et al., 2019) – a
50 flux more than seven times greater than that of recent anthropogenic fossil fuel emissions (9.5 Gt C yr^{-1} ;
51 Friedlingstein et al., 2019). As atmospheric CO_2 continues to rise, driving climate change, forests will play a
52 critical role in shaping the future of Earth's climate (Cavaleri et al., 2015; Rogelj et al., 2018). However, our
53 understanding of the climate dependence of forest C cycling on a global scale has been limited by analyses
54 typically considering only one or a few variables at a time, insufficient parsing of related variables, and the
55 mixing of data from forests that vary in stand age, disturbance history, and management status, all of which
56 affect C cycling (Gillman et al., 2015; Litton et al., 2007; Šimová & Storch, 2017).

57 Forest C fluxes decrease with latitude (e.g., Luyssaert et al., 2007; Gillman et al., 2015; Li & Xiao, 2019).
58 However, studies have differed in their conclusions regarding the shape of this relationship – quite possibly
59 because of lack of standardization with respect to methodology and stand history. *Productivity may vary with*
60 *stand age, disturbance, and management (De Lucia et al., 2007; Šimová & Storch, 2017; Yu et al., 2014),*
61 *making clear latitudinal patterns difficult to discern without standardization of the dataset.* [???] For instance,
62 studies agree that gross primary productivity (*GPP*) increases continuously with decreasing latitude and is
63 indisputably highest in tropical forests (Badgley et al., 2019; Beer et al., 2010; Jung et al., 2011; Li & Xiao,
64 2019; Luyssaert et al., 2007). In contrast, some studies have suggested that net primary productivity (*NPP*),
65 or its aboveground portion (*ANPP*), exhibits a less distinct increase from temperate to tropical forests
66 (Luyssaert et al., 2007) – or even a decrease (Huston & Wolverton, 2009, but see @gillman_latitude_2015). A
67 shallower increase in *NPP* than in *GPP* with decreasing latitude would align with the suggestion that tropical
68 forests tend to have low carbon use efficiency ($CUE = NPP/GPP$; De Lucia et al., 2007; Anderson-Teixeira
69 et al., 2016; Malhi, 2012). Such differences among C fluxes ~~their~~ relationship to latitude could have profound
70 implications for our understanding of the C cycle and its climate sensitivity. However, until recently the
71 potential to compare latitudinal trends across C fluxes has been limited by lack of a large database with
72 standardization for methodology, stand history, and management (Anderson-Teixeira et al., 2018).

Wording

73 The latitudinal gradient in forest C flux rates, along with altitudinal gradients (Girardin et al., 2010; Malhi
74 et al., 2017), is driven primarily by climate, which is a significant driver of C fluxes across broad spatial
75 scales (Cleveland et al., 2011; Luyssaert et al., 2007; Wei et al., 2010). However, there is little consensus as to
76 the shapes of these relationships or the best predictor variables. The majority of studies have focused on
77 exploring the relationships of C fluxes to mean annual temperature (*MAT*) and mean annual precipitation
78 (*MAP*), as the most commonly reported site-level climate variables. C fluxes increase strongly with *MAT* on
79 the global scale, but whether they saturate or potentially decrease at higher temperatures remains disputed.
80 Some studies have detected no deceleration or decline in *GPP* (Luyssaert et al., 2007), *NPP* (Schuur, 2003),
81 or root respiration (R_{root} ; Piao et al., 2010; Wei et al., 2010) with increasing *MAT*. In contrast, others have
82 found evidence of saturation or decline of C flux in the warmest climates; Luyssaert et al. (2007) found
83 *NPP* saturating at around 10°C *MAT*; Larjavaara & Muller-Landau (2012) found that increases in *GPP*
84 saturate at approximately 25°C *MAT*, and Sullivan et al. (2020) found that, within the tropics, *ANPP_{stem}*
decreases at the highest maximum temperatures. C fluxes generally saturate at high levels of *MAP*, though
the saturation points identified vary from *MAP* of ~1000 mm for R_{root} (Wei et al., 2010) up to 2,445 mm
for *NPP* (Schuur, 2003). Interactions between *MAT* and *MAP* may also influence productivity (Yu et al.,
87 2014); within the tropics, there is a positive interaction between *MAT* and *MAP* in shaping *ANPP*, such
88 that high rainfall has a negative effect on productivity in cooler climates, compared to a positive effect in
89 warmer climates (Taylor et al., 2017). There is also evidence that C fluxes also respond to climate variables
90 such as temperature and precipitation *seasonality* (Wagner et al., 2016), cloud cover (Taylor et al., 2017),
91 solar radiation (Beer et al., 2010; Fyllas et al., 2017), and potential evapotranspiration (Kerkhoff et al., 2005);
92 however, these are not typically assessed 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. Most forests—even tropical*
95 *evergreen—exhibit some seasonality in both climate and C flux (e.g., Wagner et al., 2014), and this seasonality*
96 *influences annual C fluxes (Churkina et al., 2005; Fu et al., 2019; Keenan et al., 2014). In particular, growing*
97 *season length has been linked to ANPP, NPP, GPP, and net ecosystem exchange of CO₂ (NEE, or the*
98 *difference between GPP and ecosystem respiration; Kerkhoff et al., 2005; Churkina et al., 2005; Keenan*
99 *et al., 2014; Michaletz et al., 2014; Zhou et al., 2016). However, the relative importance of growing season*
100 *length, as opposed to climate within the growing season, remains debated. On one end of the spectrum,*
101 *some studies have suggested that the influence of temperature on C fluxes may be limited to determining the*
102 *length of the frost-free growing season, and that climate within the growing season has little influence on C*
103 *fluxes because of plant adaptation and acclimatization to local climates (Enquist et al., 2007; Kerkhoff et al.,*

105 2005; Michaletz et al., 2018, 2014). In support of this, Kerkhoff et al. (2005) and Michaletz et al. (2014)
106 found no significant relationship between growing season temperature and *ANPP* or *NPP* standardized
107 to a climate-defined growing season length (but see Chu et al., 2016). The idea that growing season length
108 is an important determinant of annual C flux also aligns with evidence that cross-site variation in *NEE* is
109 strongly correlated with growing season length (Churkina et al., 2005) and that warming-induced increases
110 in growing season length are enhancing forest *GPP* and C sequestration (Keenan et al., 2014; Zhou et al.,
111 2016). On the other end of the spectrum, climatic conditions within the growing season may exert a stronger
112 influence on annual C fluxes than the length of the growing season. This aligns with observations that in
113 forests, *NEE* tends to be more closely tied to the maximum rate of CO₂ uptake than to the carbon uptake
114 period (Fu et al., 2019; Zhou et al., 2016), and with numerous tree-ring analyses finding that annual growth is
115 more closely controlled by peak growing season climate than by spring or fall conditions (e.g., Helcoski et al.,
116 2019). Thus, the extent to which growing season length controls global-scale variation in forest autotrophic C
117 fluxes remains unclear.

118 The recent development of the Global Forest Carbon database (ForC), which synthesizes multiple variables
119 and includes records of stand history (Anderson-Teixeira et al., 2016, 2018), opens up the possibility for a
120 standardized analysis of global scale variation in multiple C fluxes and the principle climatic drivers of these
121 patterns. The most comprehensive analysis of this type was Luyssaert et al. (2007), which was based on a
122 database <25% the size of the ForC version used here, did not control for effects of stand age, and examined
123 global climatic trends in only three variables. In order to approach this broad topic, we simplify the major
124 gaps in our knowledge to five broad questions and corresponding predictions (Table 1). First, we ask how
125 nine forest autotrophic carbon fluxes in ForC vary with latitude (*Q1*). We then test how these fluxes relate
126 to *MAT* and *MAP* (*Q2*), and additionally how they respond to other, less well-studied, climate variables
127 (*Q3*). Finally, we consider the relationship between C flux and seasonality, considering the role of seasonality
128 in explaining variation in carbon fluxes (*Q4*), and the influence of climate on C flux standardized by growing
129 season length (*Q5*).

*Our analyses represent a major step forward
in relation to previous work.*

~~Units need to be defined. Reference Table 2 from caption here.~~

Table 1: Summary of research questions, corresponding hypotheses, and results. Statistically significant 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	Forest autotrophic carbon fluxes										Support
		GPP	NPP	ANPP	ANPP _{stem}	ANPP _{foliage}	BNPP	BNPP _{fine.root}	R _{auto}	R _{root}		
Q1. How do C fluxes vary with latitude?												
C fluxes decrease continuously with latitude.	yes	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	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	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	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	yes	Figs. 4, S4, S5
C fluxes increase with solar radiation.	(yes)	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	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	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	no	Table S4
Q5. When standardised by growing season length, how do annual C fluxes still 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

130 **Materials and Methods**

131 *Forest carbon flux data*

132 This analysis focused on nine C flux variables included in the open-access ForC database (Table 2; Anderson-
133 Teixeira et al., 2016, 2018). ForC contains records of field-based measurements of forest carbon stocks and
134 annual fluxes, compiled from original publications and existing data compilations and databases. Associated
135 data, such as stand age, measurement methodologies, and disturbance history, are also included. The database
136 was significantly expanded since the publication of Anderson-Teixeira et al. (2018) through integration with
137 the Global Soil Respiration Database (Bond-Lamberty & Thomson, 2010). Additional targeted literature
138 searches were conducted to identify further available data on the fluxes analyzed here, with particular focus on
139 mature forests in temperate and boreal regions, which were not included in the review of Anderson-Teixeira
140 et al. (2016). We used ForC v3.0, archived on Zenodo with DOI 10.5281/zenodo.3403855. This version
141 contained 29,730 records from 4,979 plots, representing 20 distinct ecozones across all forested biogeographic
142 and climate zones. From this, we drew 1,319 records that met our criteria, as outlined below (Fig. 1).

143 This analysis focused on mature forests with no known history of significant disturbance or management.
144 There is evidence that stand age influences patterns of C flux and allocation in forest ecosystems, and can
145 confound relationships between latitude and primary productivity (De Lucia et al., 2007; Gillman et al.,
146 2015). To reduce any biasing effects of stand age, we included only stands of known age ≥ 100 years and
147 those described by terms such as “mature”, “intact”, or “old-growth”. Since management can alter observed
148 patterns of C cycling (Šímová & Storch, 2017), sites were excluded from analysis if they were managed,
149 defined as plots that were planted, managed as plantations, irrigated, fertilised or included the term “managed”
150 in their site description. Sites that had experienced significant disturbance within the past 100 years were
151 also excluded. Disturbances that qualified sites for exclusion included major cutting or harvesting, burning,
152 flooding, drought and storm events with site mortality $>10\%$ of trees. Grazed sites were retained.

should this table be first, considering it includes variable definitions?

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

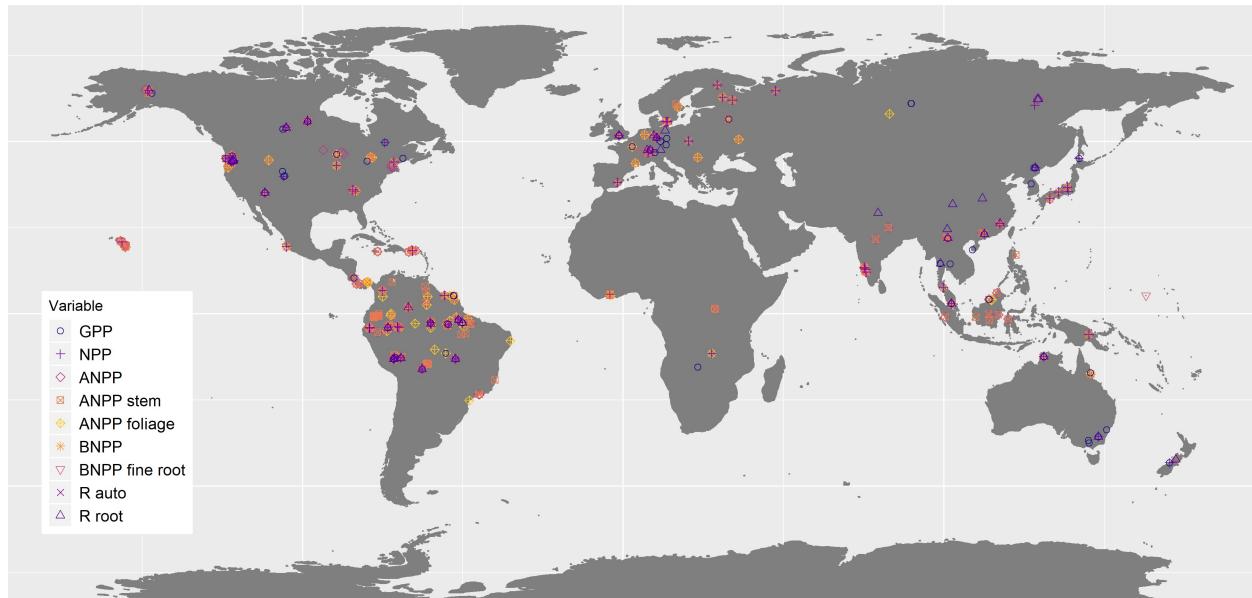


Figure 1: Map showing all data used in the analysis, coded by variable. Variables are plotted individually in Fig. S1.

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Can't really see overlaid points well in this version.

153 Climate data

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154 ForC contains geographic coordinates associated with each measurement record and, when available, *MAT*
 155 and *MAP* as reported in the primary literature (Anderson-Teixeira et al., 2018). Based on the geographic
 156 co-ordinates for each site, data on twelve climate variables – including *MAT*, *MAP*, temperature seasonality
 157 (*i.e.*, standard deviation across months), precipitation seasonality (*i.e.*, coefficient of variation across months),
 158 annual temperature range, solar radiation, cloud cover, annual frost and wet days, potential evapotranspiration
 159 (*PET*), aridity (*MAP/PET*), and vapor pressure deficit (*VPD*) – were extracted from five open-access
 160 climate datasets: WorldClim (Hijmans et al., 2005), WorldClim2 (Fick & Hijmans, 2017), the Climate
 161 Research Unit time-series dataset (CRU TS v4.03 (Harris et al., 2014), the Global Aridity Index and Potential
 162 Evapotranspiration Climate Database (Trabucco & Zomer, 2019), and TerraClimate (Abatzoglou et al., 2018)
 163 (Table S1). Definitions and methods used to calculate each variable are included in Table S1. From these
 164 data, we derived maximum *VPD*, defined as the *VPD* of the month with the largest deficit, and the number
 165 of water stress months, defined as the number of months annually where precipitation was lower than *PET*.

166 Where site-level data was missing for *MAT* or *MAP*, we used values from the WorldClim dataset.

This is consistent with

167 Following the previous studies whose hypothesis we were evaluating (Kerkhoff et al., 2005; Michaletz et al.,

168 2014), length of the growing season was estimated to the nearest month, where growing season months were

169 defined as months with mean minimum temperature $> 0.5^{\circ}\text{C}$. We experimented with a definition of growing
 170 season months including a moisture index, defined as $(\text{MAT} - \text{PET})/\text{PET} > -0.95$ (Kerkhoff et al., 2005;
 171 see also Michaletz et al., 2014). However, we found that including a moisture index had minimal effect on
 172 the estimates of growing season length for the sites included here, and so chose to exclude it. Monthly data
 173 for *PET*, precipitation, and temperature from CRU v 4.03 (Harris et al., 2014) and solar radiation from
 174 WorldClim2 (Fick & Hijmans, 2017) were used to calculate mean monthly *PET*, precipitation, temperature
 175 and solar radiation during the growing season.

176 Analyses — Perhaps reference the questions here (from Table 1)
 ↳ put in that order for easier readability?
 177 The effects of latitude and climate on C fluxes were analysed using mixed effects models using the package
 178 ‘lme4’ (Bates et al., 2015) in R v.3.5.1 (???). The basic model for all analyses included a fixed effect of
 179 latitude or climate and a random effect of plot nested within geographic area. Geographic areas—*i.e.*, spatially
 180 clustered sites—were defined within ForC using a hierarchical cluster analysis on the distance matrix of the
 181 sites and a cutoff of 25km (Anderson-Teixeira et al., 2018). We experimented with inclusion of altitude as a
 182 fixed effect, but excluded it from the final models because it added very little explanatory power – that is, the
 183 difference in AIC (ΔAIC) relative to models excluding altitude was generally small (often $\Delta\text{AIC} < 2$). Effects

for what years?
 This matters (considering global warming...)

184 were considered significant when inclusion of the fixed effect of interest resulted in $p \leq 0.05$ and $\Delta AIC \geq 2.0$
185 relative to a corresponding null model. All R^2 values presented here are marginal R^2 values, and refer to the
186 proportion of variation explained by only the fixed effects. Specific analyses are as described below.

187 We first examined the relationship between latitude and C fluxes ($Q1$; Table 1). We tested models with
188 latitude as a first-order linear, second-order polynomial, and logarithmic term. For brevity, we henceforth refer
189 to first-order linear models as “linear” and second-order polynomial models as “polynomial”. We selected as
190 the best model that with the highest ΔAIC relative to a null model with no fixed term, with the qualification
191 that a polynomial model was considered an improvement over a linear model only if it reduced the AIC value
192 by 2.0 or more. In addition, pairwise comparisons of R^2 values were carried out for a selection of pairs of C
193 fluxes to test for differences among variables in the proportion of variation explained by latitude and climate.
194 Models were run on data from sets of sites that were common to each pair, in order to account for variation
195 in the number of data points included.

196 To test whether trends in component fluxes across latitude sum to match those of larger fluxes, regression lines
197 for smaller component fluxes were summed to generate new estimates of larger fluxes. Because no fluxes were
198 significantly better predicted by a logarithmic or polynomial fit than by a linear fit, we used linear fits for all
199 fluxes in this analysis. We then determined whether these summed predictions fell within the 95% CI for the
200 larger flux across the entire latitudinal range. Confidence intervals for the line of best fit for the larger flux were
201 estimated using the ‘bootMer’ function, a parametric bootstrapping method for mixed models (Bates et al.,
202 2015). This function carried out 2000 simulations estimating the line of best fit, using quantiles at 0.025 and
203 0.975 to estimate 95% CIs. This analysis was applied to the following sets of fluxes: (1) $GPP = NPP + R_{auto}$,
204 (2) $NPP = ANPP + BNPP$, and (3) $ANPP = ANPP_{foliage} + ANPP_{stem}$. In addition, we estimated total
205 belowground C flux (TBCF, not analyzed due to limited data) as $TBCF = BNPP + R_{root}$.

206 Variation in allocation to component carbon fluxes was explored for three groupings: (1) $GPP = NPP + R_{auto}$,
207 (2) $NPP = ANPP + BNPP$, and (3) $ANPP = ANPP_{foliage} + ANPP_{stem}$. For each group, measurements
208 taken at the same site and plot, and in the same year, were grouped together. For groups (1) and (2), where
209 2 of the 3 flux measurements were available for a given site, plot, and year, these measurements were used
210 to calculate the third. The ratio of each pair of component fluxes was calculated. The log of these ratios
211 were regressed against latitude and climate variables, using the linear model specified above. Cook’s distance
212 analyses were carried out for each of the models, and extreme outliers removed.

213 We next examined the relationships of C fluxes to climate variables ($Q2-Q4$; Table 1). We tested first-order
214 linear, second-order polynomial, and logarithmic fits for each climate variable. Again, polynomial fits were

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we then calculated

($NPP : R_{auto}$, $ANPP : BNPP$, $ANPP_{foli} : ANPP_{stem}$)

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215 considered superior to first-order linear fits only if inclusion of a second-order polynomial term resulted in
216 $\Delta\text{AIC} \geq 2.0$ relative to a first-order linear model. We tested relationships of each C flux (Table 2) against each
217 climate variable (Table S1). Variables which were not significant explanatory variables or which explained
218 <20% of variation in C fluxes are only presented in SI.

219 Linear models were used to investigate the potential joint and interactive effects of *MAT* and *MAP* on
220 carbon fluxes. An additive model including *MAP* in addition to *MAT* was accepted when $\Delta\text{AIC} > 2$ relative
221 to a null including only *MAT* as a fixed effect. An interactive model containing a *MAT* x *MAP* interaction
222 was accepted when $\Delta\text{AIC} > 2$ relative to a null including *MAT* and *MAP* as fixed effects.

223 To test whether and how C fluxes varied with climate when standardised by growing season length (*Q5*;
224 Table 1), we first standardized all annual C fluxes by dividing by growing season length (as defined above).
225 We then derived four variables to describe growing season climate, specifically growing season temperature,
226 precipitation, solar radiation, and PET (Table S1). We tested for correlations between these standardised
227 fluxes and growing season climate variables, using only first-order linear models.

228 All analyses were conducted in R v.3.5.1 (???). Code and data necessary to reproduce all results are available
229 through GitHub (https://github.com/forc-db/Global_Productivity) and archived in Zenodo (DOI: TBD).

230 Results

231 In total, we analyzed 1,319 records from nine forest autotrophic C flux variables taken from forests that had
232 experienced no major anthropogenic disturbances within the past 100 years. These records represented a
233 total of 255 *sites*  distinct geographic areas across all forested biogeographic and climate zones (Figs. 1,
234 S1; Table 2).

235 *Q1. How do C flux vary with latitude?* 

236 All major carbon fluxes decreased with latitude (Fig. 2; Table S2). Latitude was a strong predictor for
237 many of the carbon fluxes, particularly the larger fluxes (Table S2, S6). Specifically,  latitude explained 64%
238 of variation in GPP ($n = 243$, $p < 0.0001$), 50% in NPP ($n = 161$, $p < 0.0001$) and 44% in ANPP ($n = 278$,
239 $p < 0.0001$). The C fluxes that were most poorly predicted by latitude were *BNPP_{fine.root}* ($R^2 = 0.17$) and
240 *ANPP_{stem}* ($R^2 = 0.18$). The relationship with latitude was best fit by the first-order linear model, with the
241 exception of *NPP* and *R_{root}*, for which a logarithmic model was a slightly – but not significantly – better fit.

include in. That is very useful context.

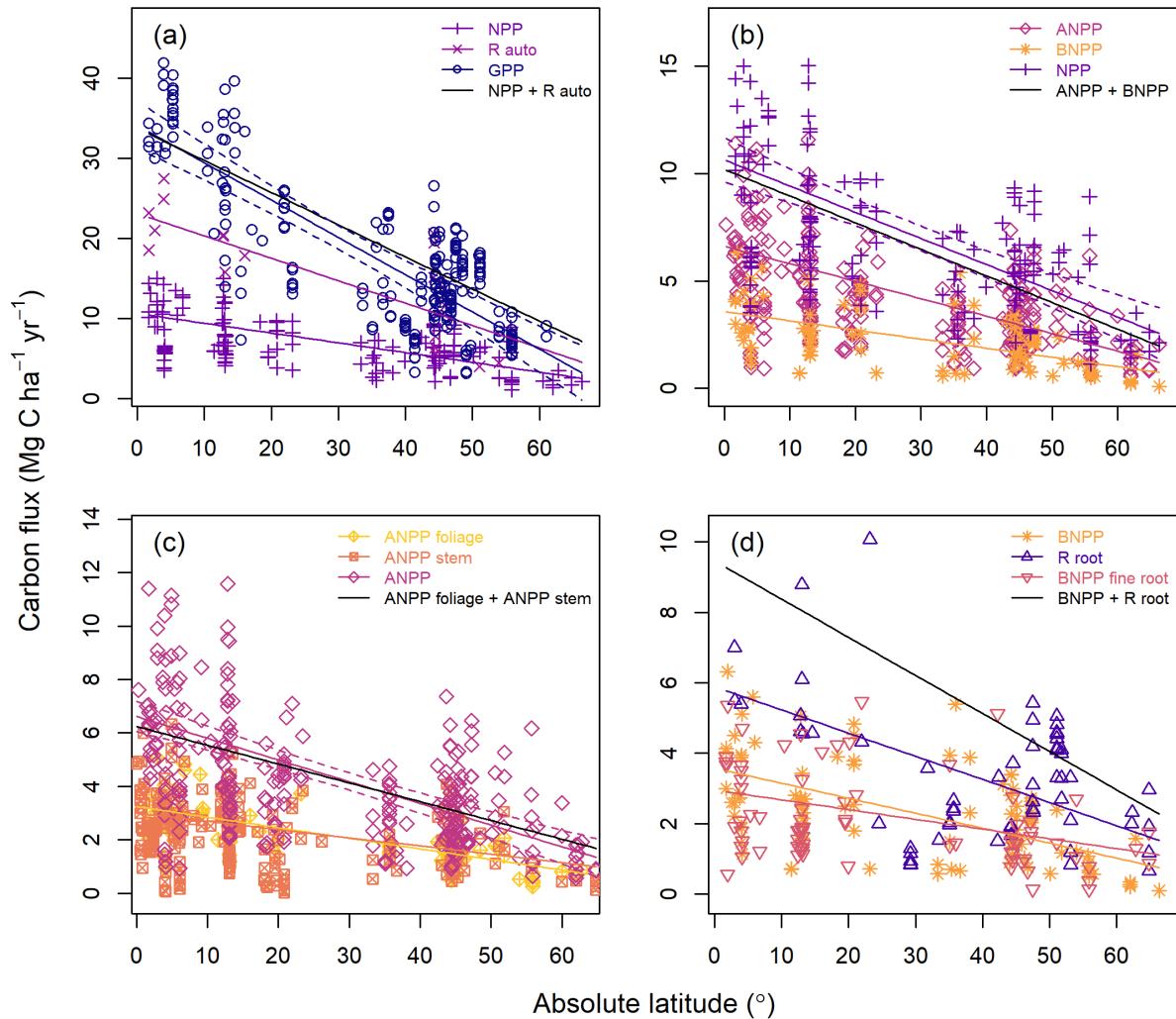


Figure 2: Latitudinal trends in forest autotrophic carbon flux. Plotted are linear models, all of which were significant ($p < 0.05$) and had AIC values within 2.0 of the best model (for two fluxes, logarithmic fits were marginally better; Table S2). Each panel shows major C fluxes together with component 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

242 Smaller component fluxes summed approximately to larger fluxes across the latitudinal gradient (Fig. 2).
 243 That is, modeled estimates of GPP , generated from the sum of NPP and R_{auto} ; NPP , generated from
 244 the sum of $ANPP$ and $BNPP$; and $ANPP$, generated from the sum of $ANPP_{foliage}$ and $ANPP_{stem}$, fell
 245 almost completely within the confidence intervals of the regressions of field estimates of GPP , NPP , and
 246 $ANPP$, respectively.
 247 We found no evidence of systematic variation in C allocation with latitude or climate (Fig. S3). Of 16
 248 relationships tested (4 ratios among C flux variables regressed against latitude, MAT , MAP and temperature

? only 3 ratios evident in methods

249 seasonality), none were significant.

250 Q2. How do ~~C~~ C flux relate to MAT and MAP?

251 All fluxes increased with *MAT* (all $p < 0.05$; Figs. 3-4, S4-S5, Table S2). For eight of the nine fluxes, this
252 relationship was linear. For only one variable, *BNPP*, did a lognormal fit provide an improvement over a
253 first-order linear relationship, though this was not significant ($\Delta AIC < 2$). As with latitude, *MAT* tended
254 to explain more variation in the larger fluxes (*GPP*, *NPP*, *ANPP*, *R_{auto}*) and *ANPP_{foliage}* (all $R^2 > 0.4$)
255 than in subsidiary and belowground fluxes (*ANPP_{stem}*, *R_{root}*, *BNPP_{fine.root}*; all $R^2 < 0.25$; Table S6).

256 *MAP* was a significant ($p < 0.05$) predictor of all fluxes (Figs. 4a, S4-S5; Table S2). However, it explained
257 little variation: with the exception of *R_{auto}*, *MAP* explained at most 25% of variation in C flux. All fluxes
258 increased with *MAP* up to at least 2000 mm, above which responses were variable (Figs. 4, S4-S5).

259 There was a significant additive effect of *MAT* and *MAP* on *GPP*, *ANPP* and *R_{auto}* (Fig. 3, Table S3), and
260 a significant interactive effect between *MAT* and *MAP* for *NPP* and *ANPP_{stem}* (Fig. 3, Table S3). The
261 interaction was negative for *NPP* and positive for *ANPP_{stem}*. For *ANPP_{foliage}*, *BNPP*, *BNPP_{fine.root}*,
262 and *R_{root}*, *MAP* did not have a significant effect when accounting for *MAT* (Fig. 3, Table S3).

word. may
awkward

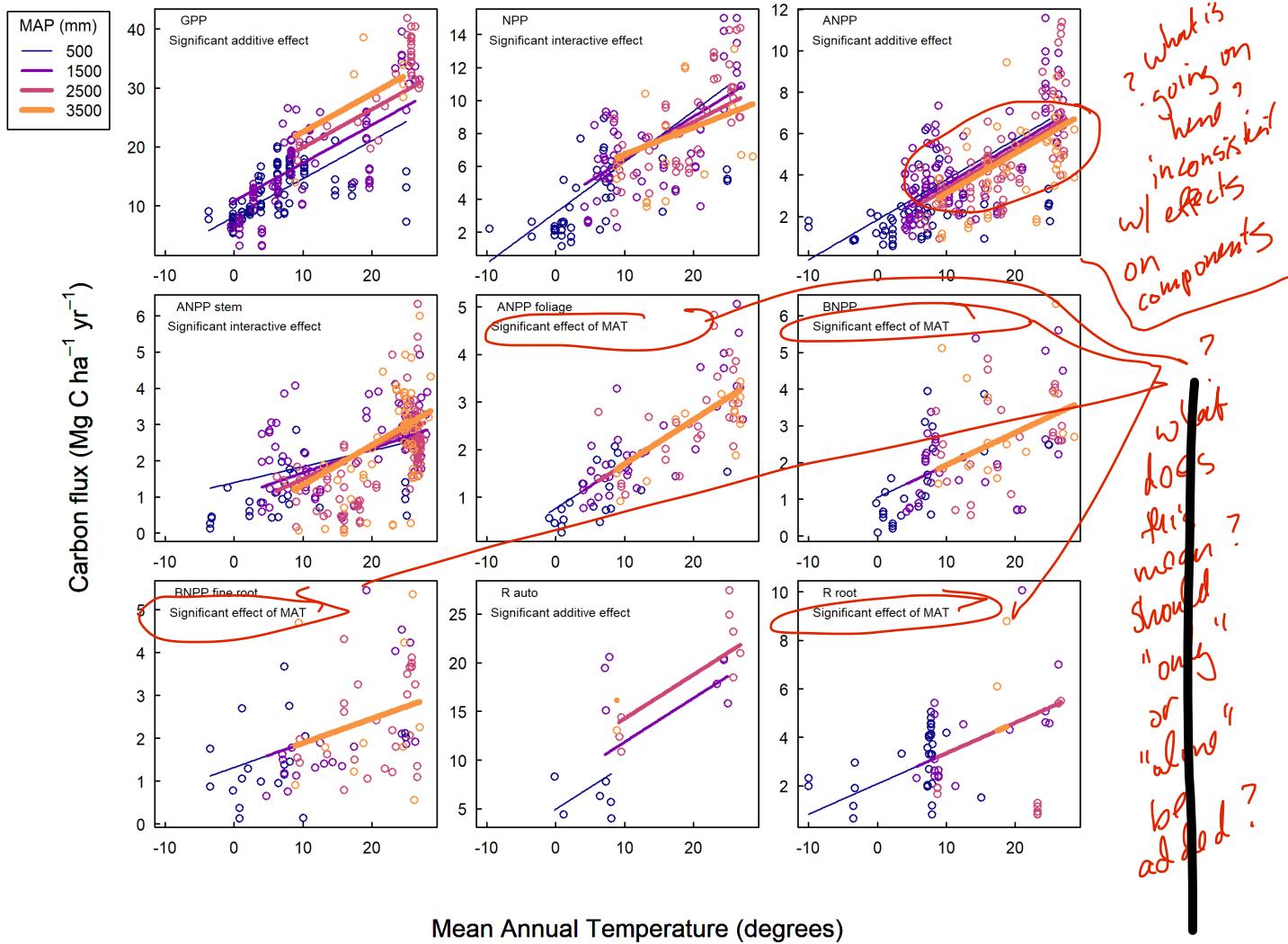


Figure 3: Interactive effects of mean annual temperature and precipitation on annual forest carbon fluxes. For visualization purposes, data points are grouped into bins of 0 - 1000, 1001 - 2000, 2001 - 3000, and >3000mm mean annual precipitation, and lines of best fit models are plotted for mean annual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

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

264 All C flux variables showed a significant relationship with annual PET. The relationship was logarithmic for
 265 $ANPP_{foliage}$, $BNPP_{fine.root}$ and R_{root} , and polynomial for all other fluxes (Fig. 4c, S4-5; Table S2). We
 266 found strong evidence for a saturation point or peak with PET: C fluxes tended to increase at values below
 267 1000mm, before saturating between 1200 and 1700mm. There was also evidence that some C fluxes begin to
 268 decrease at values above 1800mm PET.

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

is that simply because those sites generally experience water limitation for part of the year?
 14

²⁷⁰ a logarithmic relationship with *VPD*, but all other fluxes showed a polynomial relationship (Figs. 4d, S4-5;
²⁷¹ Table S2). C fluxes initially increased with *VPD*, before saturating at around 0.8 kPa, after which point
²⁷² they began to decrease.

²⁷³ All fluxes, with the exception of R_{root} , showed a significant positive relationship with solar radiation (Figs.
²⁷⁴ S4-S5, Table S2). Solar radiation explained a low proportion of variability (<30%) in all C fluxes.

²⁷⁵ Annual wet days, cloud cover, and aridity were poor or non-significant predictors of variation in C fluxes,
²⁷⁶ explaining less than 20% of the variation in each of the carbon fluxes (Figs. S4-S5; Table S2).

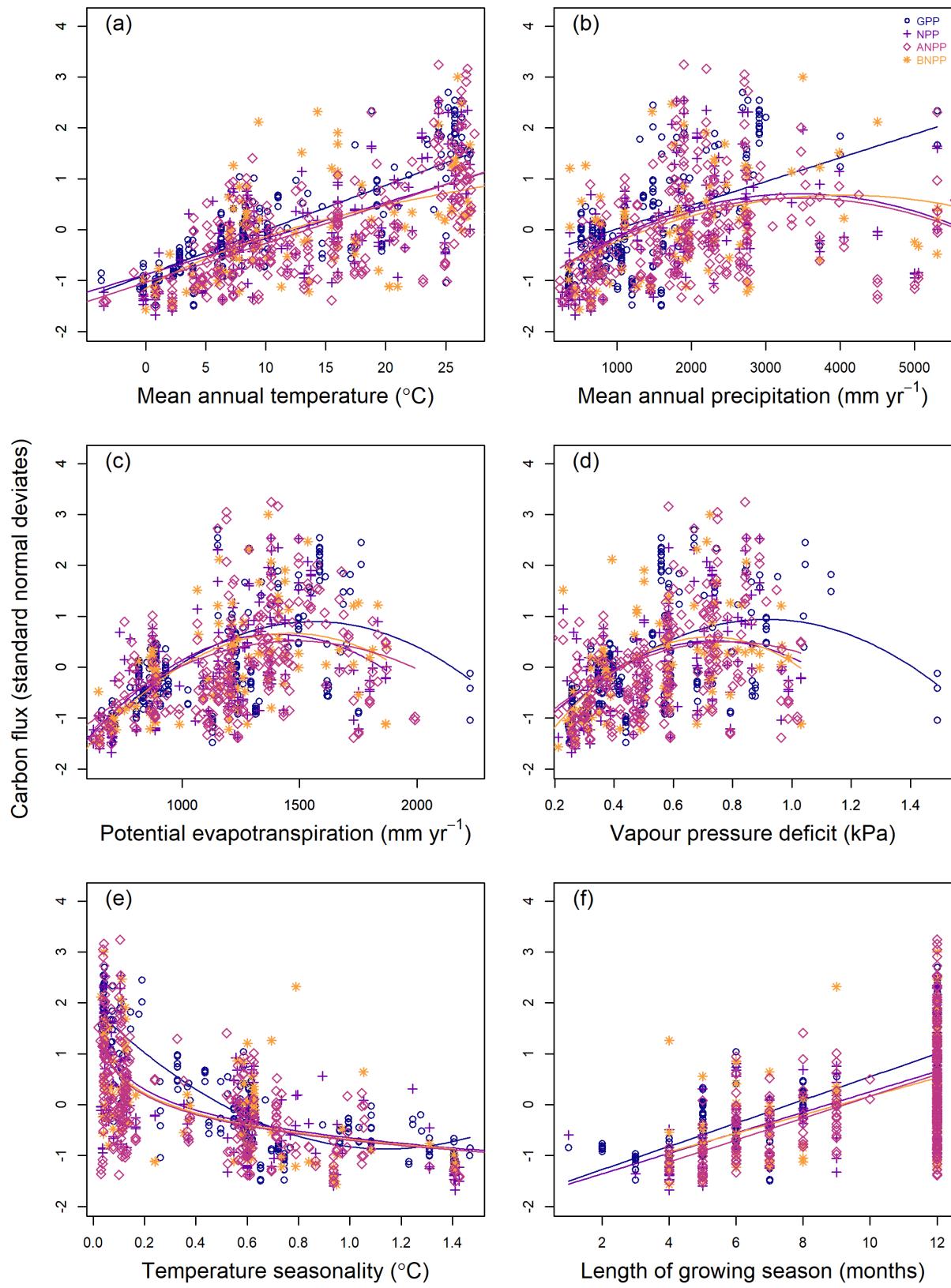


Figure 4: Plots of carbon fluxes against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration; (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. For visualization purposes, data for each flux was rescaled with a mean of 0 and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

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

278 Variables describing temperature seasonality – temperature seasonality, annual temperature range, annual
279 frost days, and length of growing season – were strongly correlated with both latitude and *MAT* (all $r \geq 0.2$;
280 Fig. S2), and were consistently identified as strong univariate predictors of C fluxes (Figs. 4, S4-S7).

281 All fluxes decrease with increasing temperature seasonality, though the shape of this relationship varies (all
282 $p < 0.05$; Figs. 4e, S6-7; Table S2). Temperature seasonality was strongly correlated with annual temperature
283 range, which was likewise a similarly strong predictor of C fluxes (Table S2). C fluxes were highest where
284 temperature seasonality = 0, and at an annual temperature range of 15°C or lower (*i.e.*, in the tropics).

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

288 We found a significant relationship between length of growing season and C fluxes, with all fluxes showing a
289 positive relationship with length of growing season (Figs. 4e, S6-S7; Table S2). Length of growing season was
290 a strong predictor of C fluxes, explaining 53% of variation in GPP, 38% of variation in NPP, and 34% of
291 variation in ANPP (all $p < 0.05$; Table S2), but it was a weaker predictor than *MAT* for all fluxes analysed
292 (Table S4).

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

294 When annual C fluxes were standardized by growing season length (in monthly increments), correlations with
295 growing season climate were generally weak (Figs. S8-S9). *ANPP* increased with growing season temperature
296 ($R^2 = 0.09$, $p < 0.001$) and precipitation ($R^2 = 0.04$, $p < 0.05$). Similarly, *ANPP_{foliage}* increased slightly with
297 growing season temperature ($R^2 = 0.16$, $p < 0.01$) and precipitation ($R^2 = 0.09$, $p < 0.05$). Growing season
298 solar radiation was positively correlated with ~~BNPP~~ ($R^2 = 0.17$, $p < 0.001$) and *BNPP_{fine.root}* ($R^2 =$
299 0.13, $p < 0.01$). Growing season PET had a positive influence on *GPP* ($R^2 = 0.15$, $p < 0.01$), *NPP* ($R^2 =$
300 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}* ($R^2 =$
301 0.06, $p < 0.05$). All other relationships were non-significant.

302 Discussion

303 Our analysis of a large global database (ForC) clarifies how autotrophic C fluxes in mature forests vary
304 with latitude and climate on a global scale. We show that, across all nine variables analyzed, ~~annual~~ C
305 flux decreases continually with latitude (Fig. 2), a finding that confirms multiple previous studies ~~but and~~
306 contradicts the idea that productivity of temperate forests rivals or even exceeds that of tropical forests

307 (Huston & Wolverton, 2009; Luyssaert et al., 2007). At this global scale, C fluxes increase approximately in
308 proportion to one another, with component fluxes summing appropriately to larger fluxes and no detectable
309 differences in allocation across latitude or climates (Figs. 2, 4, S3). Similarly, we show broad - *albeit* not
310 complete - consistency of climate responses across C fluxes, with the observed latitudinal variation primarily
311 attributable to temperature and its seasonality (Figs. 3-4). Water availability is also influential, but of
312 secondary importance across the climate space occupied by forests (Figs. 3-4). Contrary to prior suggestions
313 that the majority of variation in C cycling is driven primarily by the length of the growing season (Enquist et
314 al., 2007; Kerkhoff et al., 2005; Michaletz et al., 2014), we find modest explanatory power of growing season
315 length and ~~at most weak~~
~~small but sometimes~~ significant influence of climate within the growing season (Figs. 4f, S6-S9).
316 Together, these findings yield a unified understanding of climate's influence on forest C cycling.

317 Our findings indicate that, among mature, undisturbed stands, forest C fluxes are unambiguously highest
318 in the tropical regions, and the relationship with both latitude and *MAT* is approximately linear (Table 1,
319 *Q1, Q2*; Figs. 2, 4). This contrasts with the suggestion that C fluxes (e.g., *NPP*, *ANPP*, *ANPP_{stem}*) of
320 temperate forests are similar to or even greater than that of tropical forests (Huston & Wolverton, 2009;
321 Luyssaert et al., 2007). Previous indications of such a pattern may have been an artifact of differences in
322 stand age across biomes. Compared to tropical forests, the temperate forest biome has experienced more
323 widespread anthropogenic disturbance and has a larger fraction of secondary stands (Potapov et al., 2008;
324 Poulter et al., 2018; Yu et al., 2014), so analyses comparing across latitudinal gradients without controlling
325 for stand age risk confounding age with biome effects. Because carbon allocation varies with stand age
326 (Anderson-Teixeira et al., 2013; De Lucia et al., 2007; Doughty et al., 2018; Yu et al., 2014), age differences
327 may introduce systematic biases into analyses of C fluxes across latitude or global climatic gradients. For
328 example, woody productivity tends to be higher in rapidly aggrading secondary stands than in old-growth
329 forests, where proportionally more C is allocated to respiration and non-woody productivity (De Lucia et
330 al., 2007; Doughty et al., 2018; Kunert et al., 2019; Piao et al., 2010). Thus, findings that temperate forest
331 productivity rivals that of tropical forests are likely an artifact of different forest ages across biomes.

332 We show that C fluxes are broadly consistent in their responses to climate drivers on the global scale, with
333 no trends in C allocation among the variable pairs tested (Figs. 2, S3). This parallels the observation that
334 C allocation across multiple C fluxes varies little with respect to climate along a steep tropical elevational
335 gradient (Malhi et al., 2017; but see Moser et al., 2011), and is not surprising given that carbon allocation
336 within forest ecosystems is relatively constrained (Enquist & Niklas, 2002; Litton et al., 2007; Malhi et al.,
337 2011). We find no trend in the allocation of *GPP* between production and respiration across latitude or climate
338 (*NPP:R_{auto}*; Fig. S3), refuting the idea that tropical forests have anomalously low *CUE* (Anderson-Teixeira
339 *signifiant*
340 *counter to*

*Careful in interpretation.
Failure to reject the null hypothesis
can simply indicate lack of statistical
power. Not a lot of data points.*

339 et al., 2016; De Lucia et al., 2007; Malhi, 2012). Rather, differences in *CUE* between old-growth tropical
340 forests relative to (mostly younger) extratropical forests are likely an artifact of comparing stands of different
341 age, as *CUE* is known to decline with forest age (Collalti et al., 2020; De Lucia et al., 2007; Piao et al., 2010).
342 Another previously observed pattern for which we find no support is a tendency for belowground C allocation
343 to decrease with increasing temperature (Gill & Finzi, 2016; Moser et al., 2011); rather, we observe no trends
344 in allocation between *ANPP* and *BNPP* across latitudes. Failure to detect significant tends in C allocation
345 with respect to climate in this analysis does not imply that none exist; rather, it suggests that, at this global
346 scale, differences are subtle and/or that more careful methodological standardization is required to detect
347 them.

↑ and for more data

348 in the paragraph above, discuss/ cite Collalti et al. (2020)

349 Despite the broad consistency of climate responses across C fluxes, climate explains lower proportions of
350 variability among some of the subsidiary C fluxes (e.g., *ANPP_{stem}*, *BNPP*, *BNPP_{fine.root}*; Fig. 2; Tables
351 S2, S6). There are two, non-exclusive, potential explanations for this. First, it may be that methodological
352 variation is larger relative to flux magnitude for some of the subsidiary fluxes. Belowground fluxes in particular
353 are difficult to quantify, and measurement methods for the belowground fluxes considered here may use
354 fundamentally different approaches in different sites (e.g., minirhizotrons, ingrowth cores, or sequential coring
355 for *BNPP_{fine.root}*; root exclusion, stable isotope tracking, or gas exchange of excised roots for *R_{root}*), and
356 sampling depth is variable and often insufficient to capture the full soil profile. *ANPP_{stem}*, which is also
357 poorly explained by latitude or climate, is more straightforward to measure but is subject to variability
358 introduced by differences such as biomass allometries applied and minimum plant size sampled (Clark et al.,
359 2001). However, methodological variation and uncertainty affect all of fluxes considered here, and some of
360 the larger fluxes that vary more strongly with respect to climate (*ANPP*, *NPP*) are estimated by summing
361 uncertain component fluxes. Second, differences among variables in the proportion of variation explained
362 by climate may be attributable to more direct climatic control over *GPP* than subsidiary fluxes. That is,
363 subsidiary fluxes may be shaped by climate both indirectly through its influence on *GPP* and respiration
364 and directly through any climatic influence on C allocation, as well as many other local- and regional-scale
365 factors (e.g., Moser et al., 2011).

366 Temperature and its seasonality were the primary drivers of C fluxes on the global scale (Table 1, Q2, Q4;
367 Figs. 2-4), consistent with a long legacy of research identifying temperature as a primary driver of forest
368 ecosystem C cycling (e.g., Lieth, 1973; Luyssaert et al., 2007; Wei et al., 2010). We find little evidence of any
369 non-linearity in temperature's influence on C fluxes. The relationship of all fluxes to *MAT* as an individual
370 driver were best described by a linear function (Table S2) – with the exception of *BNPP*, whose response

working
this
doesnt
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start
well

as well as
through climatic influence on
CUE and
C allocation

hypothesis

371 to MAT was close to linear (Fig. 4a). This result contrasts with the idea that fluxes saturate with MAT
372 below approximately 25°C MAT (Huston & Wolverton, 2009; Luyssaert et al., 2007). It remains possible
373 that fluxes decline above this threshold (Larjavaara & Muller-Landau, 2012; Sullivan et al., 2020), as is also
374 consistent with tree-ring records indicating that tropical tree growth declines at high temperatures (e.g.,
375 Vlam et al., 2014). However, these higher temperatures also tend to be associated with high PET and VPD ,
376 both of which are associated with reduced C fluxes (Figs. 4c-d, S4-S5).

377 Indeed, while temperature responses dominate at this global scale and within the climate space occupied
378 by forests, the effects of temperature are moderated by moisture availability (Table 1, Q2, Q3; Figs 3-4).
379 Specifically, C fluxes are reduced under relatively dry conditions (*i.e.*, low MAP ; high VPD) and sometimes
380 under very high precipitation (Figs. 3-4). The observed positive interaction between MAT and MAP for
381 $ANPP_{stem}$ on the global scale (Fig. 3) is consistent with an analysis showing a similar interaction for $ANPP$
382 in tropical forests, also with a cross-over point at $\sim 20^{\circ}\text{C}$ (Taylor et al., 2017).
383 However, we detect no such interaction for $ANPP$ or most other C fluxes, and we find a contrasting negative
384 interaction for NPP (Fig. 3), suggesting that more data are required to sort out potential differences in the
385 interactive effects of MAT and MAP on C fluxes in the tropics.

386 Forest C fluxes decline with temperature seasonality (Table 1, Q4; Fig. 4e), indicating that fluxes during the
387 growing season are not large enough to compensate for minimal flux during winters. A temperature-defined
388 growing season length correlated strongly with global-scale variation in annual C flux (Table 1, Q5; Fig.
389 4f; see also Churkina et al., 2005), consistent with the idea that the latitudinal gradient in carbon flux is
390 attributable more to shorter growing seasons at high latitudes than to inherently lower rates of photosynthesis
391 or respiration by high-latitude forests (Enquist et al., 2007; Fu et al., 2019). While there is evidence that
392 trees in high-latitude forests have adaptations to maximize photosynthesis at low temperatures (Helliker &
393 Richter, 2008; Huang et al., 2019), this is not sufficient to yield growing season fluxes comparable to those of
394 tropical forests, as indicated by a number of positive correlations between monthly mean flux during the
395 growing season and growing season temperature, solar radiation, and PET (Table 1, Figs. S8-S9). Thus, we
396 reject the hypothesis that growing season length alone accounts for global-scale variation in productivity—*i.e.*,
397 that there is no relationship between C flux per month of the growing season and growing season climatic
398 conditions (Table 1, Q5; Kerkhoff et al., 2005; Enquist et al., 2007; Michaletz et al., 2014). Rather, annual C
399 flux is shaped by both growing season length and the climate of peak growing season months (Chu et al.,
400 2016; Fu et al., 2019). Given strong co-variation between growing season length and MAT (Fig. S2; Chu et
401 al., 2016), accurately partitioning this variation will require data on intra-annual variation in C flux coupled
402 with a more refined metric of growing season length than used here (e.g., based on leaf phenology or C

This avoids/fails to mention that our analysis of growing season is constrained by quantifying only to 20 integer months. Need to say this!

AND controls a higher precision measure of growing season length!

403 exchange, *sensu* Fu et al., 2019). Fu et al. (2019) find that global-scale geographic variation in annual NEE
404 is driven more strongly by growing season length than by carbon uptake rates within the growing season,
405 whereas interannual variation in NEE and GPP at any given site appears to be driven predominantly by
406 the maximum rate of C uptake, as opposed to growing season length (Fu et al., 2019; Zhou et al., 2016).
407 Further analysis of interannual variation in C fluxes in relation to climate will be valuable to disentangling
408 how seasonality shapes broad geographic patterns in forest C flux.

409 Our analysis clarifies how annual forest autotrophic C fluxes vary with latitude and climate on a global scale,
410 with some important implications for how forest C cycling relates to climate and, by extension, how it is
411 likely to respond to climatic warming. To the extent that patterns across broad scale climatic gradients
412 can foretell ~~how~~ ecosystem responses to climate change, our findings suggest that higher temperatures with
413 similar moisture availability would result in a generalized acceleration of forest C cycling (Figs. 2-3). This is
414 consistent with observations of continental- to global-scale increases over time in GPP (Li & Xiao, 2019) and
415 ANPP_{stem} (Brienen et al., 2015; Hubau et al., 2020), along with some C cycle components not considered
416 here: tree mortality (Brienen et al., 2015; McDowell et al., 2018), soil respiration (Bond-Lamberty & Thomson,
417 2010), and heterotrophic soil respiration (Bond-Lamberty et al., 2018). However, increasing C flux rates are by
418 no means universal (e.g., Rutishauser et al., 2020; Hubau et al., 2020), likely because other factors are at play,
419 including changes to other aspects of climate, atmospheric pollution (CO₂, SO₂, NO_x), and local disturbances.
420 Moreover, forest ecosystem responses to climatic changes outside the temperature range to which forest
421 communities are adapted and acclimatized will not necessarily parallel responses across geographic gradients
422 in climate. Indeed, tree-ring studies from forests around the world indicate that tree growth rates – along
423 with ANPP_{stem} and possibly other ecosystem C fluxes – respond negatively to temperature (Helcoski et
424 al., 2019; Sniderhan & Baltzer, 2016). Furthermore, in the tropics, climate change will push forests beyond
425 any contemporary climate, and there are some indications that this could reduce C flux rates (Mau et al.,
426 2018; Sullivan et al., 2020). Further research is required to understand the extent to which forest responses
427 to climate change will track the observed global gradients, and the time scale on which they will do so. In
428 the meantime, understanding the fundamental climatic controls on annual C cycling in Earth's forests sets a
429 firmer foundation for understanding forest C cycle responses to accelerating climate change.

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