

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

² **Running head:**

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23 **Abstract**

24 Carbon fixation, allocation, and metabolism by trees set the basis for energy and material flows in forest
25 ecosystems and define their interactions with Earth's changing climate. Yet, we lack a cohesive synthesis on
26 how forest autotrophic carbon fluxes (FACF) vary globally with respect to climate and one another. Here,
27 we draw upon # records from the Global Forest Carbon Database (ForC), representing all major forest types
28 and the nine most significant FACF, to comprehensively explore how C cycling in mature, undisturbed forests
29 varies with latitude and climate on a global scale. We show that, across all FACF variables analyzed, C
30 cycling decreases linearly with latitude – a finding that confirms multiple previous studies but contradicts
31 the idea that net primary productivity (*NPP*) of temperate forests rivals that of tropical forests. FACF
32 generally displayed similar trends across latitude and multiple climate variables, with few differences in
33 allocation detectable at this global scale, but differed in that latitude explained a lower proportion of variation
34 among subsidiary fluxes (in particular, woody aboveground *NPP* and belowground *NPP*, *BNPP*). Climate
35 explained a significant proportion (#-%) of variation in all C fluxes analyzed, with temperature variables in
36 general and mean annual temperature (MAT) in particular being the best predictors of FACF on this global
37 scale. The effects of temperature were modified by moisture availability, with FACF reduced under hot and
38 dry conditions and sometimes under very high precipitation. FACF declined with temperature seasonality,
39 but growing season length did not improve upon MAT as a predictor.
40 Within the growing season, the influence of climate on C cycling was small but significant for a number of
41 FACF. These findings clarify the big picture of how FACF varies with latitude and climate on a global scale.
42 As we enter a period of accelerating climatic change, understanding of the fundamental climatic controls on
43 FACF sets a foundation for understanding patterns of change.

variables

Do we really need the (novel)
abbreviation FACF?
It's not makes this abstract
harder to read. I suggest trying
to avoid its use at least in
the abstract.

44 Introduction

45 Carbon cycling in forests worldwide provides the energetic basis for sustaining the majority of Earth's
46 terrestrial biodiversity and many human populations (**REF**), while strongly influencing atmospheric CO₂
47 and climate (Bonan, 2008). Forests' autotrophic carbon fluxes (FACF)—that is, carbon fixation, allocation,
48 and metabolism by trees and other primary producers—sets the energy ultimately available to heterotrophic
49 organisms (including microbes), in turn influencing their abundance (e.g., Zak et al. 1994; Niedzialkowska
50 et al. 2010) and possibly diversity [Waide et al. (1999); Chu et al. 2019 (DOI: 10.1111/ele.13175)]. FACF
51 influences all organic matter stocks in forest ecosystems and is linked to cycling of energy, water, and nutrients.
52 Critically, FACF also define forest interactions with Earth's changing climate. Over 69 Gt of CO₂ cycle
53 through Earth's forests each year (Badgley et al., 2019), and in recent decades their net C sequestration
54 (~2.4 Gt C yr⁻¹) offset roughly 30% of anthropogenic fossil fuel emissions (Pan et al., 2011). As atmospheric
55 carbon dioxide levels continue to rise, driving climate change, forests will play a critical role in shaping the
56 future of Earth's climate (Cavaleri et al., 2015; Rogelj et al., 2018). However, our ability to draw general
57 macroscopic conclusions regarding global variation in FACF with respect to climate has been limited in that
58 these analyses often mix forests that vary in stand age, disturbance history, and/or management status; do
59 not always sufficiently parse related variables; and typically consider only one or a few variables at a time.

60 FACF decrease with latitude, but it remains unclear whether and how the shape of this relationship varies
61 across fluxes. Studies agree that FACF are lowest in the boreal regions, and increase into the temperate
62 regions (Luyssaert et al., 2007; Huston and Wolverton, 2009; Beer et al., 2010; Piao et al., 2010; Jung et al.,
63 2011). However, evidence is inconclusive on whether primary productivity continues to increase into the
64 tropics, or whether it plateaus in temperate regions. Evidence for this is further complicated by the fact that
65 different studies use different measures of productivity to explore these relationships. For example, modelling
66 of global terrestrial ecosystem gross primary productivity (*GPP*) through upscaling and calibration of eddy
67 flux measurements indicates that *GPP* peaks in tropical forests (Beer et al., 2010; Jung et al., 2011; Badgley
68 et al., 2019; Li and Xiao, 2019). In contrast, some studies suggest that the highest values of net primary
69 productivity (*NPP*) may be found in temperate forests (Luyssaert et al., 2007; Huston and Wolverton, 2009),
70 while others find *NPP* highest in the tropics and decreasing with latitude (Šimová and Storch, 2017). Other
71 studies have chosen to focus exclusively on above-ground net primary productivity (*ANPP*), finding evidence
72 of a weak negative relationship between *ANPP* and latitude (Huston and Wolverton, 2009; Gilman et al.,
73 2015). *decreases weakly with latitude* *I have found that*

74 The latitudinal gradient in FACF is primarily driven by climate, which is a significant driver of FACF across
75 broad spatial scales (Luyssaert et al., 2007; Cleveland et al., 2011; Hursh et al., 2017). The majority of studies
76 have focused on exploring the relationships of FACF to mean annual temperature (MAT) and mean annual
77 precipitation (MAP), as the most commonly reported site-level climate variables. While these fail to capture
78 some important aspects of climate such as seasonality, they do describe broad trends in temperature and water
79 availability, and therefore capture a substantial portion of global-scale variation in climate. There is strong
80 evidence that both MAT and MAP show significant positive relationships with FACF (Chu et al., 2016).
81 However, as with latitude, the shape of those relationships is not always clear, and, again, is complicated by
82 the use of different measures of FACF across studies. Various measures of primary productivity {FACF?} are
83 saturate at high levels of MAP, though the saturation points identified vary from 1500mm (Luyssaert et al.,
84 2007) up to 2445mm MAP (Schuur, 2003). Studies of the influence of MAT on productivity {FACF?} are
85 less conclusive. Luyssaert et al. (2007) examined GPP and NPP and found that, while *GPP* increases

86 linearly with MAT, NPP saturates at around 10°C MAT. In contrast, Larjavaara and Mullen-Landau (2012),
87 find that increases in GPP saturate at approximately 25°C MAT, while Schuur (2003) shows that NPP
88 increases linearly with temperature. Taylor et al. (2017) showed a positive interaction between MAT and
89 MAP in shaping tropical forest productivity, such that high rainfall had a negative effect on productivity in
90 cooler climates, compared to a positive effect in warmer climates. {It would be good to add some more
91 citations on soil respiration. I'm sure BBL can help.}

92 FACF can be influenced by many other factors as well, which often act across a range of scales, and may
93 show interactive effects with each other (Cleveland et al., 2011). On a local scale, stand age (Litton et al.,
94 2007; Gillman et al., 2015), biodiversity (Liang et al., 2016), management (Šimová and Storch, 2017), nutrient
95 availability (Aragão et al., 2009), and altitude (Girardin et al., 2010; Malhi et al., 2017) all impact FACF.
96 On a global scale, we expect that FACF are most strongly influenced by broad climatic gradients. There
97 is evidence that FACFs also respond to variables such as cloud cover (Taylor et al., 2017), solar radiation
98 (Fyllas et al., 2017), and potential evapotranspiration (Kerkhoff et al., 2005) in potentially significant ways.
99 Furthermore, MAT and MAP are very coarse measures of climate, and so fail to capture much variation
100 in climate on an intra-annual scale, including the effects of factors such as growing season length, number
101 of frost-free days, temperature seasonality, and dry season length. Some studies have suggested that the
102 apparently strong relationship between MAT and FACFs is actually a consequence of the correlation between
103 MAT and growing season length (Kerkhoff et al., 2005; Malhi, 2012; Michaletz et al., 2014, 2018). Kerkhoff et
104 al. (2005) and Michaletz et al. (2014) find that, within the growing season, there is no significant relationship
105 between primary productivity and MAT, suggesting that the effect of temperature is due to increased length
106 of growing season, rather than an inherent influence of temperature on FACF.

107 The recent development of the Global Forest Carbon database (ForC), which synthesizes multiple variables
108 and including records of stand history (Anderson-Teixeira et al., 2016, 2018), opens up the possibility for a
109 standardized analysis of global scale variation in multiple FACF and the principle climatic drivers of these
110 patterns. In order to approach this broad topic, we simplify the major gaps in our knowledge to five broad
111 questions and corresponding hypotheses (Table 1). First, we ask how FACF vary with latitude. We then test
112 how these fluxes relate to MAT and MAP, and additionally how they respond to other, less well-studied,
113 climate variables. Finally, we consider the relationship between FACF and seasonality, considering the role of
114 seasonality in explaining variation in carbon fluxes, and the influence of climate on FACF standardized by
115 growing season length. We address the above questions for nine carbon fluxes contained in ForC, allowing for
116 an in-depth exploration of the effect of climate on FACF globally.

which variables?
GPP, NPP, Woody KNPP?

IF growing season is defined by temperature, then temperature effect, point would be that temperature doesn't matter except for frost or not.

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

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

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

Perhaps define 4 options:
 works for everyting except 2,3.
 yes = right direction, + sig
 (yes) = " , not sig
 (no) = wrong " , not sig
 no = wrong dir, sig

117 **Materials and Methods**

118 *Forest carbon flux data*

119 This analysis focused on nine FACF included in the open-access ForC database (Table 2) (Anderson-Teixeira
120 et al., 2016, 2018). ForC contains records of field-based measurements of forest carbon stocks and annual
121 fluxes, compiled from original publications and existing data compilations and databases. Associated data,
122 such as stand age, measurement methodologies, and disturbance history, are also included. The database
123 was significantly expanded since the publication of Anderson-Teixeira et al. (2018) through integration
124 with the Global Soil Respiration Database (Bond-Lamberty and Thomson, 2010). Additional targeted
125 literature searches were conducted to identify any further available data on the FACF analyzed here, with
126 particular focus on mature forests in temperate and boreal regions, which were not included in the review of
127 Anderson-Teixeira et al. (2016). We used ForC v3.0, archived on Zenodo with DOI 10.5281/zenodo.3403855.
128 This version contained 29,730 records from 4,979 plots, representing 20 distinct ecozones across all forested
129 biogeographic and climate zones.

130 This analysis focused on mature forests with no known history of significant disturbance or management.
131 There is evidence that stand age influences patterns of FACF and carbon allocation in forest ecosystems, and
132 can confound relationships between latitude and primary productivity (DeLUCIA et al., 2007; Gillman et al.,
133 2015). To reduce any biasing effects of stand age, we included only stands of known age ≥ 100 years and
134 those described by terms such as “mature”, “intact”, or “old-growth”. Since management can alter observed
135 patterns of FACF (Šimová and Storch, 2017), sites were excluded from analysis if they were managed, defined
136 as plots that were planted, managed as plantations, irrigated, fertilised or including the term “managed”
137 in their site description. Sites that had experienced significant disturbance within the past 100 years were
138 also excluded. Disturbances that qualified sites for exclusion included major cutting or harvesting, burning,
139 flooding, drought and storm events with site mortality $>10\%$ of trees. Grazed sites were retained.

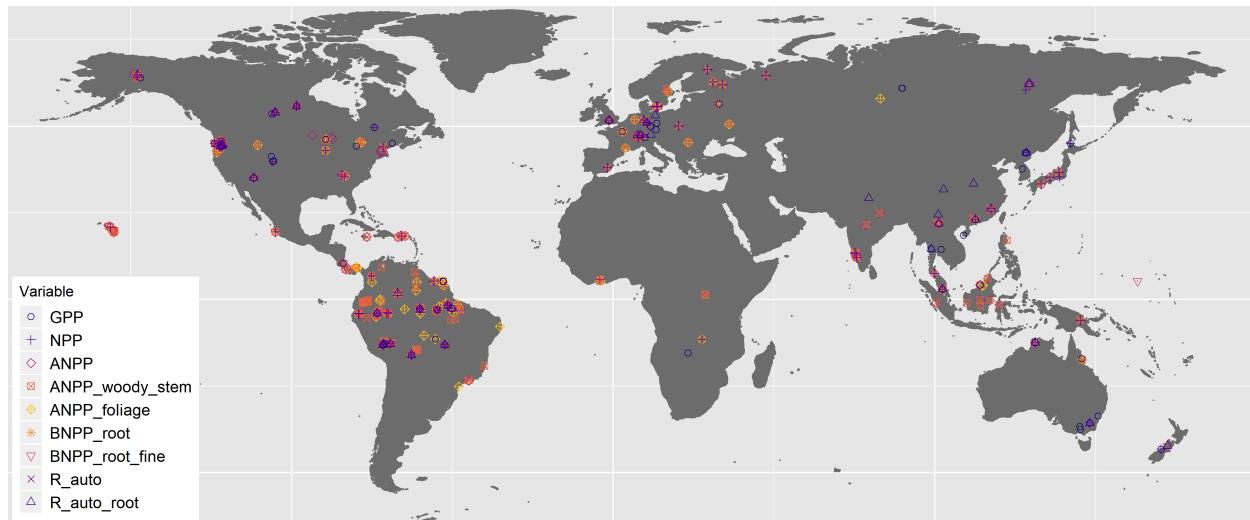


Figure 1: Map showing all data used in the analysis, coded by variable. Variables are plotted individually in Fig. S1.

140 *Climate data*

141 ForC contains geographic coordinates associated with each measurement record and, when available, mean

Table 2: Definitions and sample sizes of FAF 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)	$ANPP_{woody-stem} + ANPP_{foliage}$ (+ others)	278	86
$ANPP_{woody.stem}$	Woody stem growth component of ANPP	woody stems down to DBH $\leq 10\text{cm}$ (no branch turnover)	stem growth measurement scaled to biomass using allometries	264	96
$ANPP_{foliage}$	Foliage component of ANPP	foliage	litterfall collection, with separation separated into components	98	49
$BNPP$	Belowground NPP	coarse and fine roots	in fig 2, I prefer BNPP 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 + $R_{auto-root}$ (as below)	22	13
$R_{auto-root}$	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

142 annual temperature (MAT) and mean annual precipitation (MAP) as reported in the primary literature
143 (Anderson-Teixeira et al., 2018). Based on the geographic co-ordinates for each site, data on twelve climate
144 variables—including MAT, MAP, temperature and precipitation seasonality, annual temperature range, solar
145 radiation, cloud cover, annual frost and wet days, potential evapotranspiration (PET), aridity (MAP/PET),
146 and vapor pressure deficit (VPD)—were extracted from five open-access climate datasets: WorldClim (Hijmans
147 et al., 2005), WorldClim2 (Fick and Hijmans, 2017), the Climate Research Unit (CRU) time-series dataset
148 v. 4.03 (Harris et al., 2014), the Global Aridity Index and Potential Evapotranspiration Climate Database
149 (Trabucco and Zomer, 2019), and TerraClimate (Abatzoglou et al. 2018) (Table S1). From these data, we
150 derived maximum VPD, defined as the VPD of the month with the largest deficit, and the number of water
151 stress months, defined as the number of months annually where precipitation was lower than PET. Where
152 site-level data was missing for MAT or MAP, we used values from the WorldClim dataset.

153 Length of the growing season was estimated to the nearest month, where growing season months were defined
154 as months with mean minimum temperature $> 0.5^\circ\text{C}$. We experimented with a definition of growing season
155 months including a moisture index, defined as $(\text{MAT} - \text{PET})/\text{PET}$, > -0.95 (Kerkhoff et al., 2005; see also
156 Michaletz et al., 2014). However, we found that including a moisture index had no effect on the estimates
157 of growing season length, and so chose to exclude it. (Becky, was it really no effect? or minimal?)
158 Monthly data for PET, precipitation, and temperature from the CRU dataset v 4.03 (Harris et al., 2014),
159 and solar radiation from WorldClim2 (Fick and Hijmans, 2017) were used to calculate mean monthly PET,
160 precipitation, temperature and solar radiation during the growing season. Total growing season precipitation

161 and solar radiation were also calculated.

162 *Analyses*

163 The effects of latitude and climate on FACF were analysed using mixed effects models using the package 'lme4'
164 (Bates et al., 2015) in R v.3.5.1 (?). The basic model for all analyses included a fixed effect of latitude or
165 climate and a random effect of plot nested within geographic area. Geographic areas—*i.e.*, spatially clustered
166 sites—are defined within ForC using a hierarchical cluster analysis on the distance matrix of the sites and a
167 cutoff of 25km (Anderson-Teixeira et al., 2018). We experimented with inclusion of altitude as a fixed effect,
168 but excluded it from the final models because it added very little explanatory power—that is, the difference in
169 AIC (ΔAIC) relative to models excluding altitude was generally small (often $\Delta\text{AIC} < 2$). Hypotheses were
170 accepted if the ΔAIC between a model including the fixed effect of interest and a corresponding null model
171 excluding that fixed effect exceeded 2.0. All R^2 values presented here are marginal R^2 values, and refer to
172 the proportion of variation explained by only the fixed effects. Specific analyses are as described below.

173 We first examined the relationship between latitude and FACF (Q1; Table 1). We tested models with
174 latitude as a linear term (corresponding null: model without latitude) and as a second-order polynomial term
175 (corresponding null: model with latitude as a linear term), and calculated AIC values to determine the best
176 model. Models were accepted as the best model if $\Delta\text{AIC} > 2$ with respect to the corresponding null, and
177 were significant with respect to a null model with no fixed term. We also examined relationships among
178 fluxes across latitude, testing whether sums of component fluxes matched the larger fluxes and whether C
179 allocation varied with latitude, as specified below.

180 To test whether trends in component fluxes across latitude sum to match those of larger fluxes, regression
181 lines for smaller component fluxes were summed to generate new estimates of larger fluxes, which were
182 then compared against the latitudinal regression of the larger flux. Confidence intervals for the larger flux
183 were calculated using the `bootMer` function from the lme4 package (Bates et al., 2015). This analysis
184 was applied to following sets of fluxes: (1) $GPP = NPP + R_{auto}$, (2) $NPP = ANPP + BNPP$, and (3)
185 $ANPP = ANPP_{foliage} + ANPP_{woody.stem}$. In addition, we estimated total belowground C flux (TBCF, not
186 analyzed due to limited data) as $TBCF = BNPP + R_{root}$.

187 Variation in allocation to component carbon fluxes along latitudinal gradients was explored for the fol-
188 lowing pairings: $GPP : NPP$, $ANPP : BNPP$, $ANPP_{foliage} : ANPP_{woody.stem}$, $ANPP_{foliage} : NPP$,
189 $ANPP_{woody.stem} : NPP$, $ANPP : NPP$, and $BNPP : NPP$. For each set of paired fluxes, measurements
190 taken at the same site and plot, and in the same year, were paired together, and the ratio of each pair of
191 measurements calculated. The ratios were regressed against latitude and climate variables, using the linear
192 model specified above. Cook's distance analyses were carried out for each of the models, and indicated that
193 data from a few high-elevation sites were having a disproportionate influence on the regressions. To account
194 for this, models were re-run using only data from sites $\leq 1000\text{m}$.

195 *This* →
196 We next examined the relationships of FACF to climate variables (Q2-Q4; Table 1). As with latitude, we
197 tested both linear and polynomial fits for each climate variable. We tested relationships of each FACF (Table
198 2) against each climate variable (Table S1), but focus presentation—including focal hypotheses (Table 1)—on
199 climate variables that explained $>20\%$ of variation in FACF. **Becky, please make this more specific. I**
200 **drafted this based on the results, but its not very clear.**

To investigate the potential joint and interactive effects of climate variables on carbon fluxes, multivariate

See us
relevant
to look at
ANPP:NPP
ANPP:NPP
and ANPP:BNPP

if no other variable
then this is the best,
simply "among" the best.

suggest new
explanations were

give number of
climate variables
selected

models were also specified. We explored a large range of climate variable combinations and ultimately decided to focus on MAT and MAP. We favored these over variables with similar explanatory power because they are the most commonly reported climate variables and are recorded in ForC. MAT was consistently among the best individual predictors of FACF (Table S2), although it was occasionally out-performed by closely correlated climate variables (Fig. S2). In combination with MAT as a primary climate variable, MAP was consistently among the best secondary climate variables. Specifically, compared again a model including MAT x MAP, there were no other variables that, in interaction with MAT, improved AIC by >2.0 and R^2 by >0.05. In examining the joint and interactive effects of climate variables, an additive model including MAT and MAP as fixed effects was accepted when $\Delta\text{AIC} > 2$ relative to a null including only MAT as a fixed effect. An interactive model including an MAT x MAP interaction was accepted when $\Delta\text{AIC} > 2$ relative to a null including MAT and MAP as fixed effects.

To test whether and how FACF varied with climate when standardised by growing season length (Q5), we first standardized FACF by dividing by growing season length (as defined above). We then tested for correlations between growing season length-standardised FACF against growing season climate variables. For analyses on data within the growing season, only linear models were specified.

All analyses were conducted in R (Version). Code and results are archived on GitHub....

Results

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

How do FACF vary with latitude?

All major carbon fluxes decreased linearly with latitude (Fig. 2; Table S2). Latitude was a strong predictor for many of the carbon fluxes—particularly the larger fluxes (Table S2). Specifically, latitude explained 64% of variation in GPP ($n = 254$, $p < 0.0001$), 50% in NPP ($n = 114$, $p < 0.0001$) and 45% in ANPP ($n = 259$, $p < 0.0001$). The FACF that were most poorly predicted by latitude were $BNPP_{root-fine}$ ($R^2 = 0.17$) and $ANPP_{woody.stem}$ ($R^2 = 0.18$). For all FACF, the relationship with latitude was better fit by the linear model.

rather than the 2nd order polynomial model).

better fit

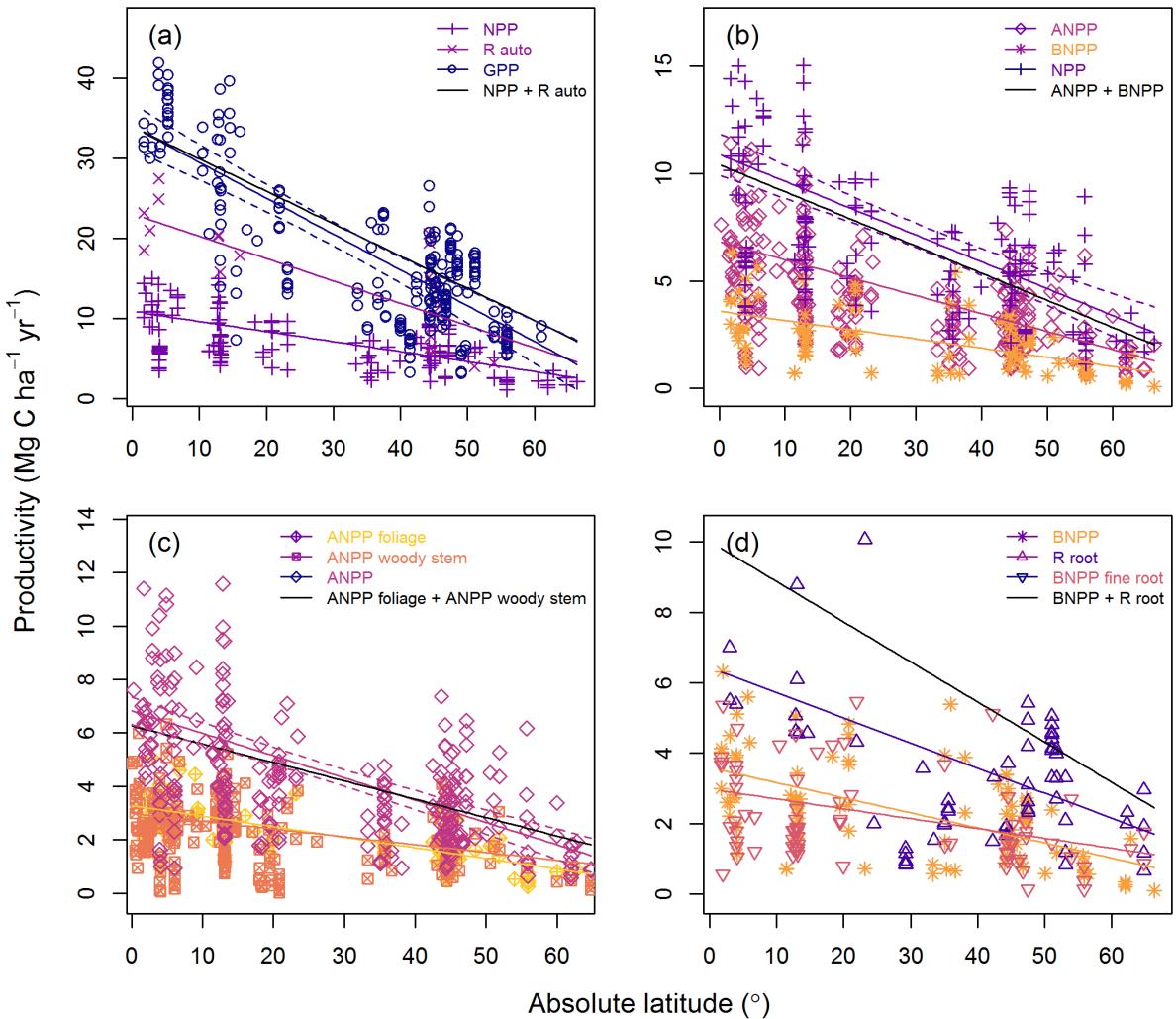


Figure 2: Latitudinal trends in forest autotrophic carbon flux. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$). Each panel shows major C fluxes together with component fluxes. Also plotted are predicted trends in the major C fluxes based on the sum of component fluxes. 95% confidence intervals are plotted for the major flux for comparison with predicted trends. In (d), which shows three belowground fluxes, the major flux, total belowground carbon flux, is one for which we have no data

so no sites report BNPP and R root?

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

systematic

with

28% cut off

233 There was little evidence of ~~substantial~~ variation in C allocation across latitude or climate (Fig. S3). Of the
 234 7 FACP ratios regressed against latitude and three climate variables (MAT, MAP, temperature seasonality),
 235 there were only five significant relationships, all with $R^2 \leq 0.4$ (Fig. S3). Specifically, the proportion of NPP
 236 allocated to $ANPP_{foliage}$ decreased with latitude ($R^2 = 0.32$) and increased with MAT ($R^2 = -0.37$), and
 237 the proportion of NPP allocated aboveground ($ANPP$) decreased weakly with latitude ($R^2 = 0.11$) and
 238 $=$

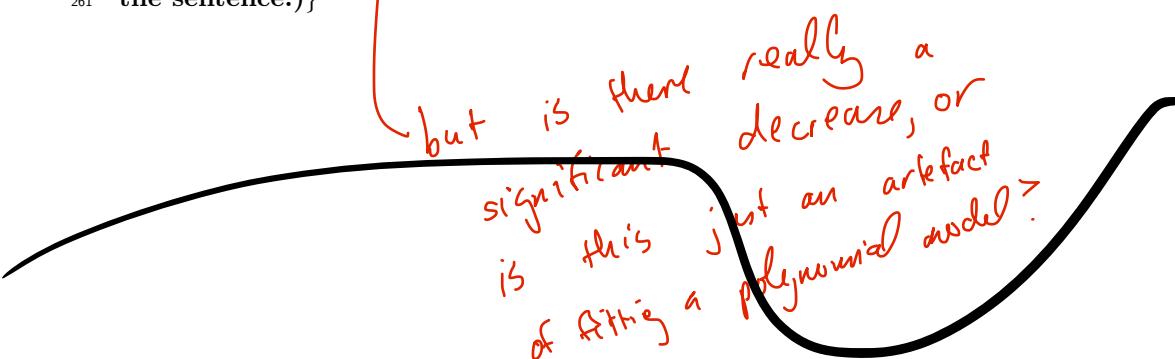
238 temperature seasonality ($R^2 = 0.17$), while increasing with MAT ($R^2 = 0.11$). ~~The remaining 23 relationships~~
239 examined were non significant.

240 How do FACF relate to MAT and MAP?

241 All FACF increased linearly with MAT, and we found no support for a saturation point of FACF with MAT
242 (all $p < 0.05$; Figs. 3-4, S4-S5, Table S2). As with latitude, MAT tended to explain more variation in the larger
243 FACF (*GPP*, *NPP*, *ANPP*, *R_{auto}*) and *ANPP_{foliage}* (all $R^2 > 0.4$) than in subsidiary and belowground
244 fluxes (*ANPP_{woody-stem}*, *R_{root}*, *BNPP_{root-fine}*; all $R^2 < 0.25$). *k*

245 MAP was a significant ($p < 0.05$) predictor of all FACF ~~but ANPP_{woody-stem}~~ (Figs. 4a, S4-S5; Table S2).
246 However, it explained little variation: with the exception of *R_{auto}*, MAP explained at most 37% of variation
247 in FACF. For the majority of FACF, a polynomial model was the best fit. FACF generally increased with
248 precipitation, up until a saturation point at between 3000 and 4000mm annual precipitation, above which
249 they started to decrease (Figs. 4, S4-S5). The notable exception to this was GPP: the model indicated that
250 GPP continued to increase with precipitation up to ~~precipitation of at least 5000mm annually~~ ($p < 0.0001$, $R^2 =$
251 0.33). Data above this point were not available, but the model trend indicated that the saturation point for
252 this model would be around 5000mm MAP. *#*

253 There was a significant additive effect of MAT and MAP on *GPP*, *ANPP* and *R_{auto}* (Fig. 3, Table S3).
254 Accounting for MAT, MAP had a substantial positive effect on *GPP* and *R_{auto}* and a small negative effect on
255 *ANPP*. There was a significant interactive ^o~~o~~ effect between MAT and MAP for *NPP* and *ANPP_{woody-stem}*
256 (Fig. 3, Table S3). The interaction was negative for *NPP* and positive for *ANPP_{woody-stem}*. For
257 *ANPP_{foliage}*, *BNPP*, *BNPP_{root-fine}*, and *R_{auto-root}*, MAP did not have a significant effect when ac-
258 counting for MAT (Fig. 3, Table S3). For the variables which showed a significant interactive or additive
259 effect between MAT and MAP, no other climate variable, in combination with MAT, significantly improved on
260 that model. {need to confirm this given changes in MAT MAP results (or you could just drop
261 the sentence.)}



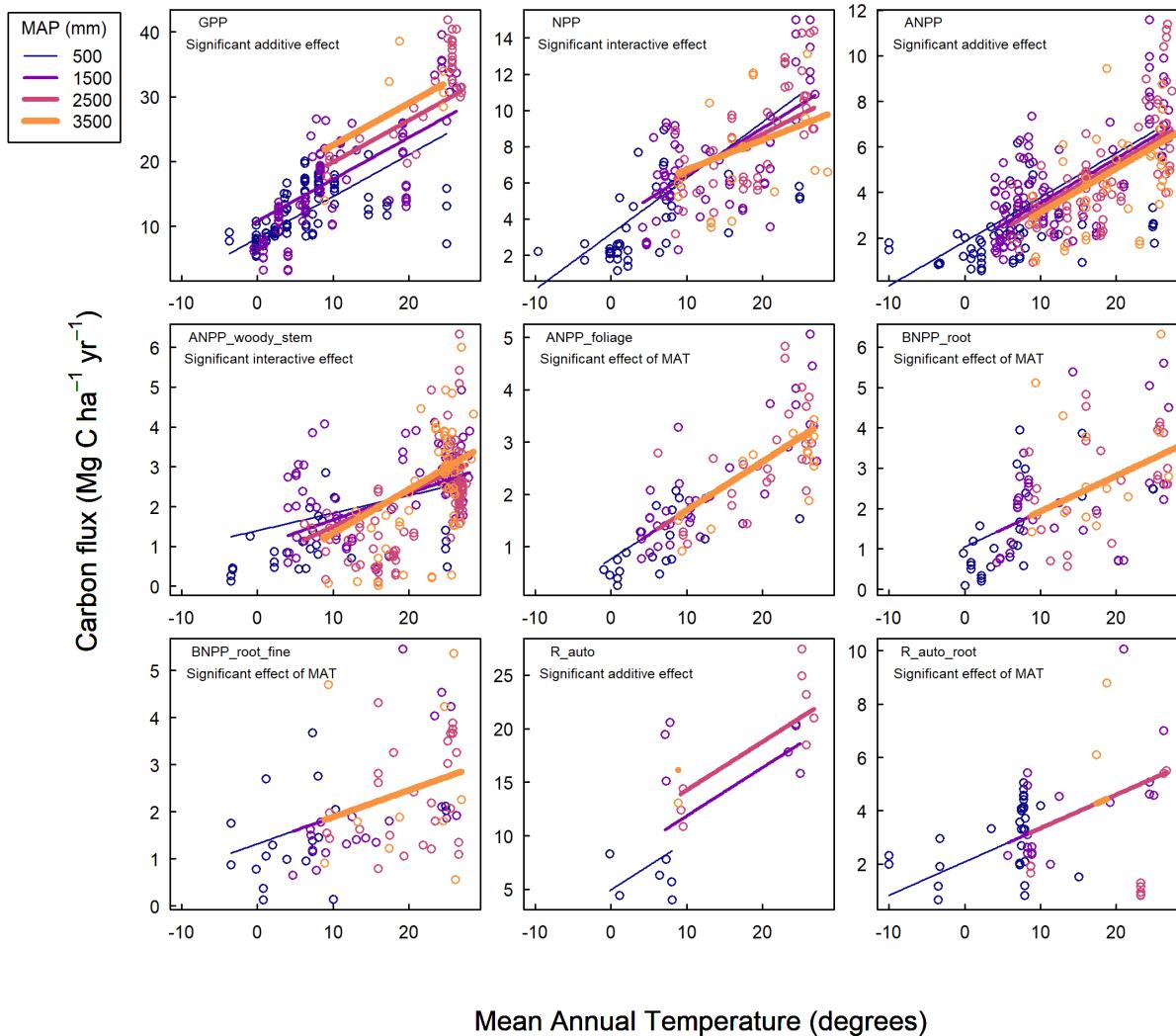


Figure 3: Interactive effects of mean annual temperature and mean annual precipitation on FACF. For visualization purposes, data points are grouped into bins of 0 - 1000, 1001 - 2000, 2001 - 3000, and >3000mm mean annual precipitation, and lines of best fit models are plotted for mean annual precipitation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

262 How do FACF relate to other climate variables?

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

267 We found a significant relationship between C flux and potential evapotranspiration for all FACF. $ANPP_{foliage}$,
 268 $BNPP_{root-fine}$ and R_{root} increased linearly with PET; however, all other fluxes showed a polynomial
 269 relationship with PET (Fig. 4c, S4-5; Table S2). We found strong evidence for a saturation point or peak
 270 with PET: FACF tended to increase at values below 1000mm, before saturating between 1200 and 1700mm.

271 There was also evidence that FACF begin to decrease at values above 1800mm PET.

Some

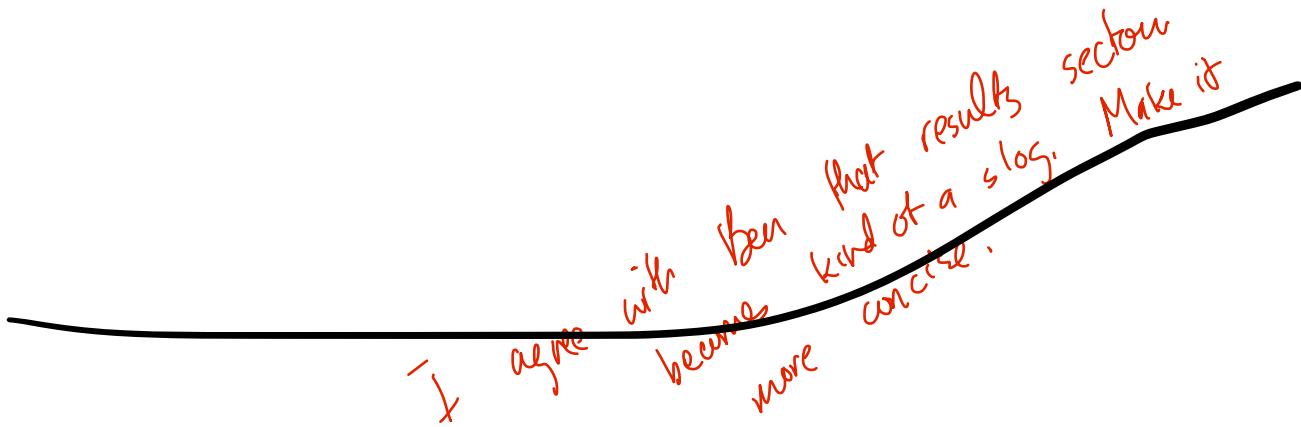
But always
more weakly
than
MAT?
weak, though!
I suspect
saturation would do
as well in most
cases

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

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

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

So... is PET a good predictor of FACF simply because it
is correlated with MAT + MAT is a good predictor?
Carefully consider wording + interpretation. What variable
is the single best predictor?



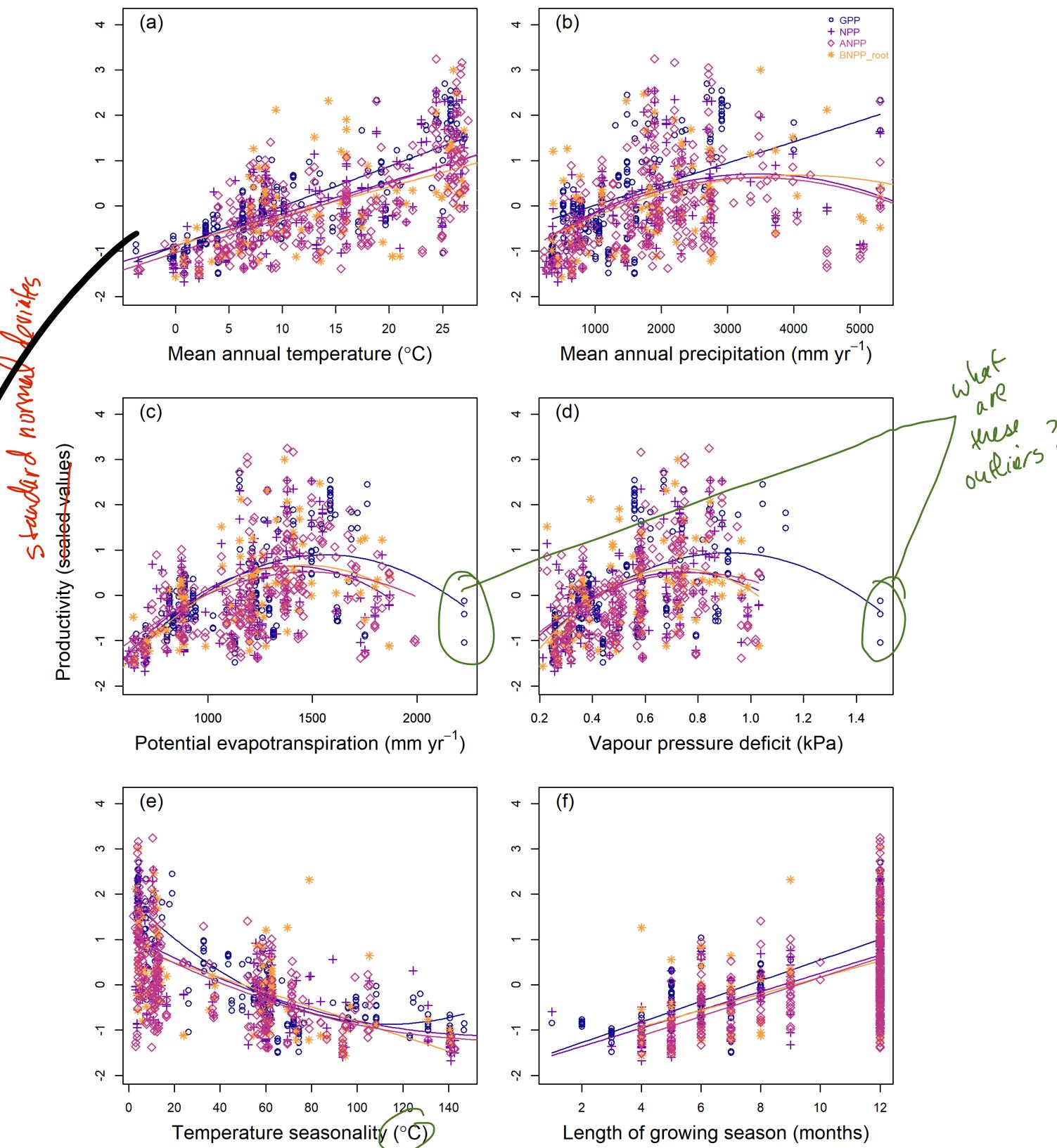


Figure 4: Plots of carbon fluxes against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration; (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. For visualization purposes, data for each flux was rescaled with a mean of 0 and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

14
No - units are 100 x % (which does not make sense to me)

281 What is the role of seasonality in explaining FACF?

well, it's strongly negatively correlated with MAT, so if MAT is a predictor, Tseas has to be as well! Careful of wording.

looks like it is actually asymptotic

282 Temperature seasonality was a significant predictor of FACF. GPP, NPP, ANPP, and R_{root} exhibited a polynomial relationship with seasonality (all $p < 0.05$; Figs. 4e, S6-7; Table S2). ANPP_{foliage}, ANPP_{woody-stem} and R_{auto} decreased linearly with temperature seasonality (all $p < 0.05$; Figs. 4e, S6-S7; Table S2). Temperature seasonality was strongly correlated with annual temperature range, which was likewise a similarly strong predictor of FACF (Table S2). FACF were highest where temperature seasonality = 0, and at an annual temperature range of 15°C or lower.

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

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

295 Within the growing season, how do FACF vary with climate?

using what months?

296 When FACF were standardized by growing season length, correlations with growing season climate—including temperature, precipitation, solar radiation, and PET—were generally weak (Figs. S8-S9). Specifically, ANPP increased with growing season temperature ($R^2 = 0.10$, $p < 0.001$) and precipitation ($R^2 = 0.04$, $p < 0.05$). Similarly, ANPP_{foliage} increased slightly with growing season temperature ($R^2 = 0.16$, $p < 0.01$) and precipitation ($R^2 = 0.09$, $p < 0.05$). Growing season solar radiation had a positive influence on GPP ($R^2 = 0.21$, $p < 0.001$), NPP ($R^2 = 0.21$, $p < 0.001$), BNPP ($R^2 = 0.16$, $p < 0.001$) and BNPP_{fine.root} ($R^2 = 0.12$, $p < 0.01$). Growing season PET had a positive influence on GPP ($R^2 = 0.15$, $p < 0.01$), NPP ($R^2 = 0.18$, $p < 0.01$), BNPP ($R^2 = 0.23$, $p < 0.0001$), BNPP_{fine.root} ($R^2 = 0.11$, $p < 0.05$), and ANPP_{woody-stem} ($R^2 = 0.06$, $p < 0.05$). {Becky, please verify/ edit the following: There were no other significant correlations between growing season length-standardized FACF (9 variables in Table 2) and growing season climate (which variables?)}.

307 Discussion

308 Our analysis of a large global database (ForC) reveals how autotrophic carbon fluxes in mature forests vary with latitude and climate on a global scale. We show that, across all nine FACF analyzed, C cycling decreases continually with latitude (H1.1; Fig. 2)—a finding that confirms multiple previous studies but contradicts the idea that productivity of temperate forests rivals that of tropical forests (Huston and Wolverton, 2009). 312 FACF generally increase in proportion to one another (H1.2), with few differences in allocation detectable at this global scale (Fig. S2) and with component fluxes summing appropriately to larger fluxes (Fig. 2), 314 indicating no major, systematic omissions or overestimations of flux components. However, climate explained lower proportions of variability among subsidiary C fluxes (e.g., ANPP_{woody}, BNPP_{fine.root}, $R_{auto-root}$; 316 Fig. 2; Table S2). Latitudinal variation in FACF is primarily attributable to temperature-related variables (H3, H4), particularly MAT (Figs. 3-4). Water availability is also influential, but generally of secondary 318 importance across the climate space occupied by forests (Figs. 3-4). Temperature seasonality and growing 319 season length are closely correlated with MAT and are strong predictors of FACF (H4; Figs. 4e-f, S2, S6-S7), 320 though growing season length doesn't improve upon MAT as a predictor. Within the growing season,

To what degree are differences in results among fluxes due to different sites included? If only sites with data for all explanatory variables are analyzed, how do ranking of explanatory variables change?

321 influence of climate on C cycling is smaller but still significant for a number of FACF (*H5*; Fig. S9; Table
322 S4). These findings resolve a number of open debates and clarify the big picture of how FACF vary with
323 latitude and climate on a global scale.

324 Past studies have differed in their conclusions regarding the relationship between FACF and latitude or its
325 correlates (Table 1, *H1*)—quite possibly because of lack of standardization with respect to stand age and
326 disturbance history. Our findings indicate that, among mature, undisturbed stands, FACF are unambiguously
327 highest in the tropical regions, and the relationship^{is approximately linear (Fig. 2)} This contrasts with
328 the suggestion that productivity of temperate forests is similar to that of tropical forests (Huston and
329 Wolverton, 2009). Compared to tropical forests, the temperate forest biome has experienced more widespread
330 anthropogenic disturbance and has a larger fraction of secondary stands (Potapov et al., 2008; Poulter
331 et al., 2018), so analyses comparing across latitudinal gradients without controlling for stand age risk
332 confounding age with biome effects. In addition, because carbon allocation varies with stand age (DeLUCIA
333 et al., 2007) (Doughty et al. 2018: DOI: 10.1111/btp.12504; Anderson-Teixeira et al. 2013:
334 doi: 10.1111/gcb.12194), age differences may introduce systematic biases into analyses of FACF across
335 latitude or global climatic gradients. For example, woody productivity tends to be higher in rapidly aggrading
336 secondary stands than in old-growth forests, where proportionally more C is allocated to respiration (Doughty
337 et al. 2018: DOI: 10.1111/btp.12504);(DeLUCIA et al., 2007; Piao et al., 2010; Kunert et al., 2019).
338 By constraining our analysis to stands \geq 100 years old with no record of major recent disturbance, we have
339 clarified the shape of the relationship between FACF and latitude.

340 We show that FACF are broadly consistent in their responses to climate drivers on the global scale, with
341 at most modest trends in C allocation among the variable pairs tested (Figs. 2, S3). This parallels the
342 observation that C allocation across multiple FACF varies little with respect to climate along a steep tropical
343 elevational gradient (Malhi et al., 2017; but see Moser et al., 2011), and is not surprising given that trees face
344 some universal constraints in carbon allocation (REFS). The one trend in allocation that emerged from our
345 analysis was a tendency for greater C allocation aboveground—and to foliage in particular—in warm tropical
346 climates (Fig. S3). This is consistent with observations of increasing allocation to roots with declining
347 temperature across a tropical elevational gradient^{s(?)}, and with observations and theory predicting relatively
348 higher belowground carbon allocation at higher latitudes (Gill and Finzi, 2016). It is also consistent with
349 findings that as forest productivity increases, proportionally more carbon is allocated to $ANPP_{foliage}$ relative
350 to $ANPP_{root-fine}$ (Chen et al. 2019; doi: 10.1111/ele.13193) or $ANPP_{woody}$ (Hofhansl et al., 2015). (check / comment on Litton et al. (2007)) One previously hypothesized trend that was not supported
351 by our analysis was that tropical forests tend to have low carbon use efficiency ($CUE = NPP/GPP = (GPP -$
352 $R_{auto})/GPP$), which are based on observations of low CUE in old-growth tropical forests relative to (mostly
353 younger) extratropical forests (DeLUCIA et al., 2007; Malhi, 2012; Anderson-Teixeira et al., 2016). Limiting
354 the analysis to mature forests, our analysis shows no such trend (Fig. S3), suggesting that the relatively
355 low CUE of intact tropical forests is more appropriately attributed to the fact that these forests are old
356 than to their tropical climate. Indeed, CUE is known to decline with forest age (DeLUCIA et al., 2007;
357 Piao et al., 2010; Collalti and Prentice, 2019), but appears to be roughly independent of GPP (Litton et al.,
358 2007). (This finding may have some important implications for modeling and our broader understanding. I'm
359 not sure offhand how much theory has been built on the idea of low CUE in tropical forests because of warm
360 temperatures...)

362 One interesting observation was that climate tends to explain more variation in the major fluxes (GPP ,

none
to
my
knowledge

for
allocation
size
scale
H. Malhi
et al.
2015
New phys.
check

what about differences in sites included? In general, it increases for lower range of independent variable as quantified by r²

363 NPP , R_{auto}) than in subsidiary fluxes ($BNPP_{fine.root}$, $R_{auto-root}$, $ANPP_{woody-stem}$) (Fig. 2; Table S2).
364 There are two non-exclusive, potential explanations for this. First, it may be that methodological variation
365 is larger relative to flux magnitude for some of the subsidiary fluxes. Belowground fluxes in particular are
366 difficult to quantify, and measurement methods for the belowground fluxes considered here may be measured through fundamentally different approaches (e.g., minirhizotrons, ingrowth cores, or sequential coring for
367 $BNPP_{root-fine}$; root exclusion, stable isotope tracking, or gas exchange of excised roots for $R_{auto-root}$), and
368 sampling depth is variable and often insufficient to capture the full soil profile. $ANPP_{woody-stem}$, which is
369 also poorly explained by latitude or climate, is more straightforward to measure but is subject to variability
370 introduced by differences such as biomass allometries applied and minimum plant size sampled (Clark et
371 al. 2001 *Ecological Applications*). However, methodological variation and uncertainty affect all of fluxes
372 considered here—not necessarily any less than the aforementioned, and some of the larger fluxes that vary
373 more strongly with respect to climate ($ANPP$, NPP) are estimated by summing uncertain component fluxes.
374 Second, differences among variables in the proportion of variation explained by climate may be attributable
375 to more direct climatic control over GPP than subsidiary fluxes. That is, subsidiary fluxes may be shaped
376 by climate both indirectly through its influence on GPP and respiration and directly through any climatic
377 influence on C allocation, as well as many other local- and regional-scale factors (REFS).

379 The latitudinal gradient in FACF (Fig. 2) is driven primarily by temperature-related climate variables, the
380 effects of which are moderated by moisture availability (Table 1, H2-H3; Figs. 3-4). Indeed, MAT and MAP
381 have long been identified as primary global-scale drivers of FACF (Lieth 1973: doi 10.1007/BF01536729;
382 REFS; Taylor et al., 2017). It is not appropriate to attempt to identify individual mean annual climate
383 variables as mechanistic drivers of FACF because many climate variables co-vary across the latitudinal
384 gradient (Fig. S2), because climatic drivers affect forest carbon flux on much shorter time scales than can
385 be captured by annual climate summary variables, and because both climatic conditions and C flux vary
386 intra- and inter-annually around the long-term means. However, it remains informative to consider these
387 relationships. Among the temperature-related climate variables (MAT, temperature seasonality, annual
388 temperature range, annual frostdays, length of growing season, and PET; Table S1), MAT is generally the
389 most strongly correlated with FACF (Table S2)—perhaps in part because site-specific MAT is recorded for the
390 majority of sites in ForC, whereas other variables were extracted from global gridded data products. This
391 finding supports the continued focus on MAT as a primary—albeit not mechanistic—correlate of FACF. The
392 effects of MAT are modified by moisture availability, with reduced FACF under relatively dry conditions
393 (i.e., low precipitation; high vapour pressure deficit) and sometimes under very high precipitation (Figs. 3-4).
394 The observed positive interaction between MAT and MAP for $ANPP_{woody.stem}$ on the global scale (Fig. 3) is
395 consistent with an analysis showing a similar interaction for $ANPP$ in tropical forests, also with a cross-over
396 point at ~20°C (Taylor et al., 2017). However, we detect no such interaction for $ANPP$ or most other FACF,
397 and we find a contrasting negative interaction for NPP (Fig. 3), suggesting that more data are required to
398 sort out potential differences in the interactive effects of MAT and MAP on FACF in the tropics.

399 FACF are negatively correlated with temperature seasonality (Table 1, H4; Fig. 4e), and are minimal
400 during cold- or dry-dormant seasons. To account for this, a number of analyses seeking to characterize
401 global-scale effects of climate on productivity have examined the relationship of C flux per month of the
402 growing season with growing season climatic conditions (Table 1, H5; Kerkhoff et al., 2005; Anderson et al.
403 2006: doi:10.1111/j.1461-0248.2006.00914.x ; Enquist et al. 2007: doi: 10.1111/j.1365-2486.2006.01222.x;
404 Michaletz et al., 2014). We found that the sort of simple metric needed to define growing season at a

how robust are variable rankings if Worldclim data used
for all?

405 global scale (Kerkhoff et al., 2005) was rough with respect to temperature and problematic with respect
406 to moisture because it doesn't capture temporal lags between precipitation and plant water use caused by
407 storage in soil or snow. A temperature-defined growing season length had strong positive correlation with
408 FACF (Fig. 4f), but explained less variation than *MAT*. Dividing FACFs by growing season length to
409 yield FACF per growing season month removed the majority of climate-related variation, supporting the
410 idea that the latitudinal gradient in FACF is attributable more to shorter growing seasons at high latitudes
411 than to inherently lower rates of photosynthesis or respiration by high-latitude forests (*Enquist et al. 2007:*
412 doi: 10.1111/j.1365-2486.2006.01222.x). However, there remained a number of significant correlations with
413 growing season climatic conditions, suggesting that climatic conditions remain influential within the growing
414 season. We conclude that while correcting for growing season length takes analyses a step closer to mechanistic
415 linkage of instantaneous C flux rates to environmental conditions, it remains very crude relative to the ~~the~~
416 timescales on which climate affects plant metabolism and does not advance statistical predictive power.
417 Rather, mechanistic accounting for climatic effects on global FACF patterns requires models representing
418 physiologically meaningful timescales (e.g., refs).

do you mean over time? clarify wording

419 Our analysis clarifies how FACF vary with latitude and climate on a global scale, with some important
420 implications for how forest carbon cycling relates to climate and, by extension, how it is likely to respond
421 to climatic warming. Our findings show that higher temperatures with similar moisture availability result
422 in a generalized acceleration of FACF (Figs. 2–3). This is consistent with observations of continental- to
423 global-scale increases in *GPP* (Li and Xiao, 2019) and *ANPP_{woodystem}* (Brienen et al., 2015; Hubau et al.,
424 2020), along with some C cycle components not considered here—tree mortality (Brienen et al., 2015; McDowell
425 et al., 2018), soil respiration (Bond-Lamberty and Thomson, 2010), and heterotrophic soil respiration (Bond-
426 Lamberty et al., 2018). However, increasing C flux rates by no means universal (Rutishauser et al., 2020)
(MORE REFS). This is likely because factors other than rising temperatures are at play, including changes
428 to other aspects of climate, atmospheric pollution (CO₂, SO₂, NO_x), and local disturbances. Moreover,
429 forest ecosystem responses to climatic changes outside the temperature range to which forest communities
430 are adapted and acclimatized will not necessarily parallel responses ~~across~~ across geographic gradients in
431 climate. Nevertheless, as we enter a period of accelerating climatic change, understanding of the fundamental
432 climatic controls on FACF sets a foundation for understanding patterns of change.

are

Need to discuss now
Sullivan paper that finds
higher max temperatures
associated with lower
ANPP stem.

433 Acknowledgements

434 Scholarly Studies ForestGEO Compilation of the ForC database was originally funded by DOE

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