

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

² **Running head:**

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 **Author Affiliations:**

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

¹² 2. *Becky-* current

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 **Keywords:**

²² **Paper type:** Primary Research Article

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.
wording: 'growing season is then'

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	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.

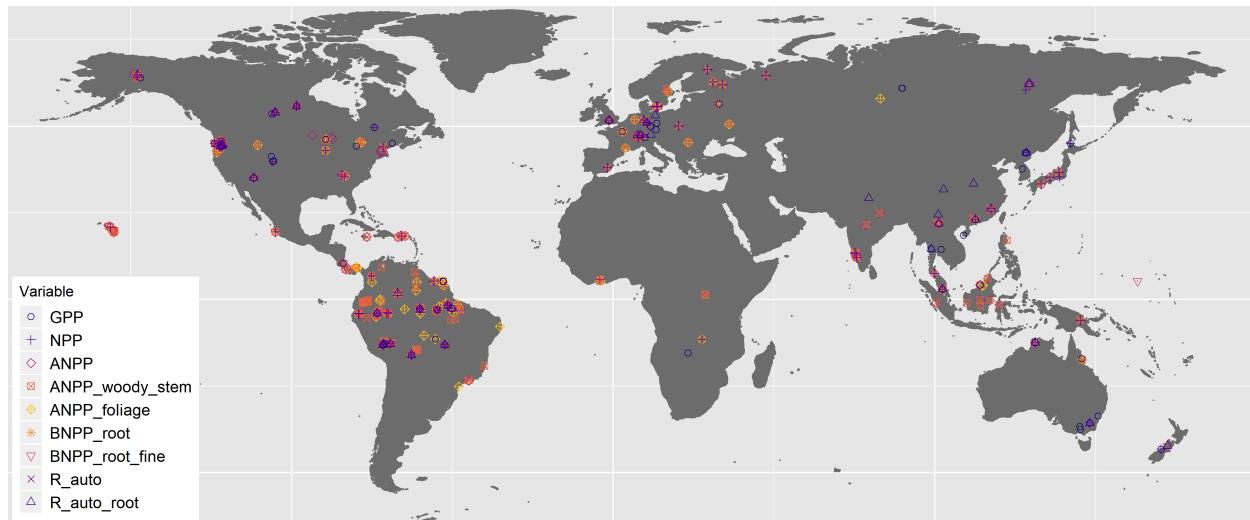


Figure 1: Map showing all data used in the analysis, coded by variable. Variables are plotted individually in Fig. S1.

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 litterfall collection, separated into components	98	49
$BNPP$	Belowground NPP	coarse and fine roots	in the fig. , 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

not WorldClim?
 v. 2?

doesn't
 WorldClim
 replace
 WorldClim?
 why are
 they all
 in one
 series

is this
 usually
 referred to
 as a
 climate
 dataset?

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 (Δ AIC) relative to models excluding altitude was generally small (often Δ AIC < 2). Hypotheses were
170 accepted if the Δ AIC 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 Δ 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 ≤ 1000 m.
This word

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

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

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

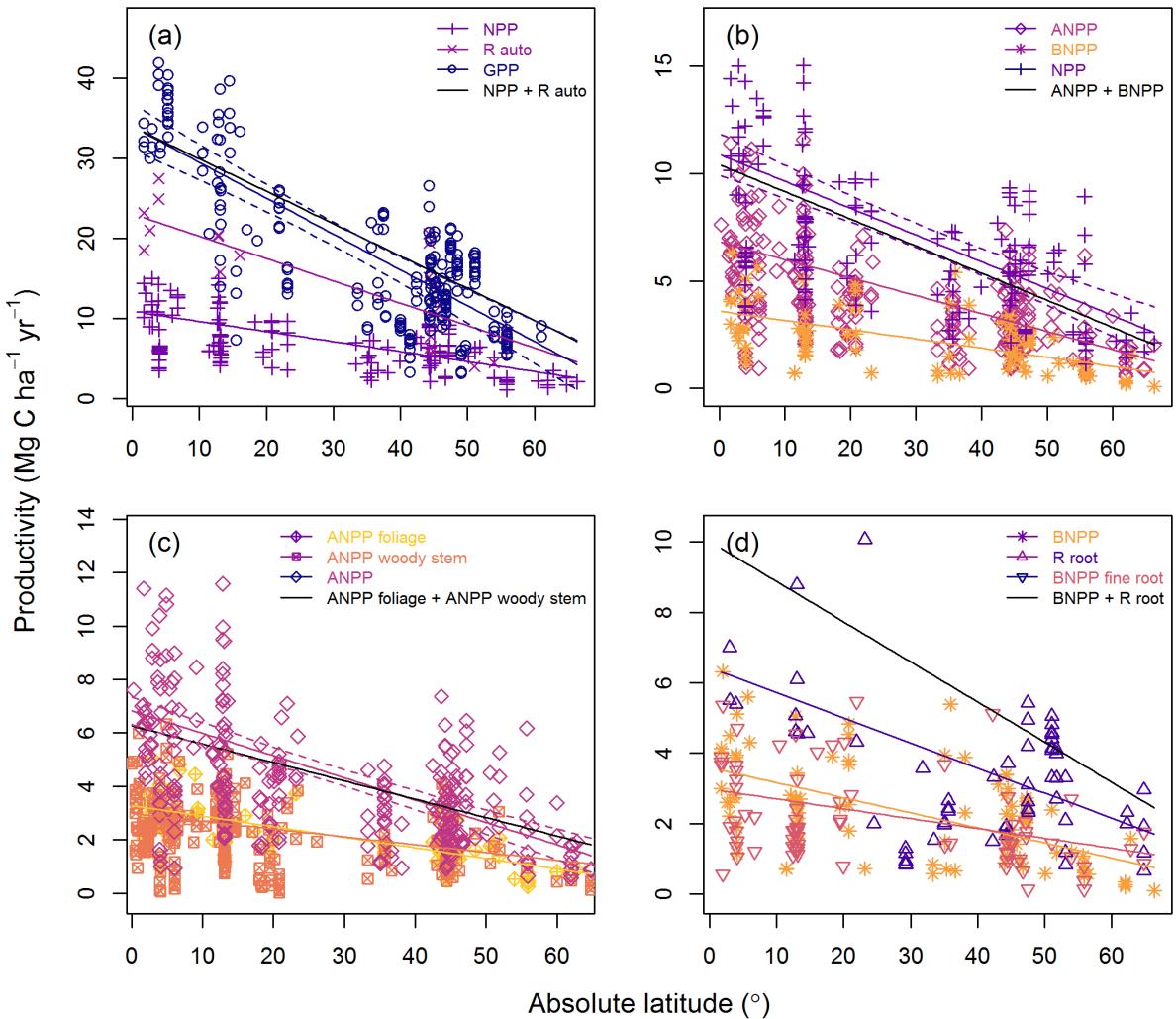


Figure 2: Latitudinal trends in forest autotrophic carbon flux. Lines of best fit are plotted according to the best model selected during analysis. All regressions are significant ($p < 0.05$). Each panel shows major C fluxes together with component fluxes. Also plotted are predicted trends in the major 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 $R^2 < 0.25$).

245 MAP was a significant ($p < 0.05$) predictor of all FACF ~~but~~ ^{except} ~~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 ~~measures 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 ^{**} 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.)}

but is there really a
significant decrease, or
is this just an artefact
of fitting a polynomial model?

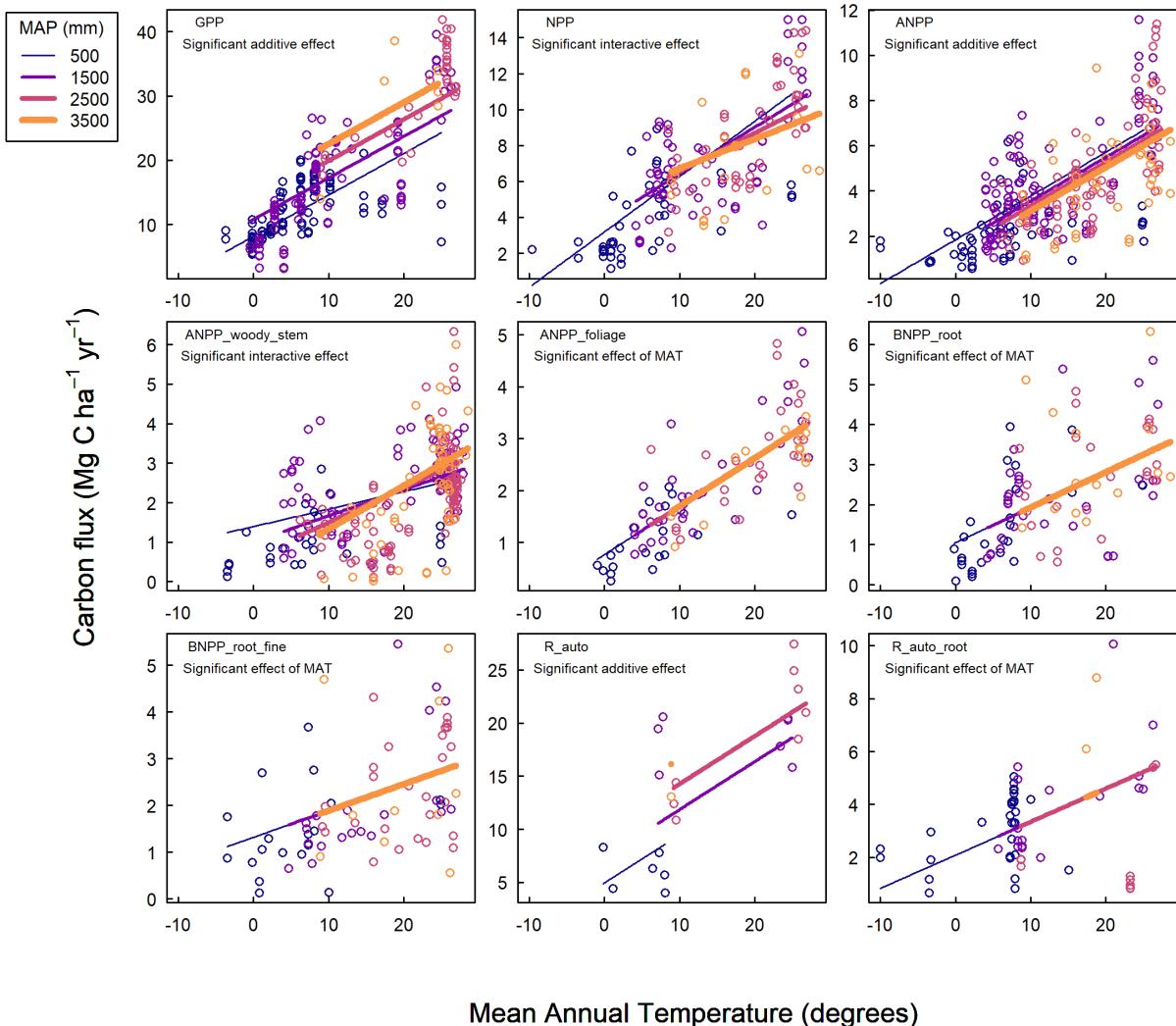


Figure 3: Interactive effects of mean annual temperature and mean annual precipitation on FACF. For visualization purposes, data points are grouped into bins of 0 - 1000, 1001 - 2000, 2001 - 3000, and >3000mm mean annual precipitation, and lines of best fit models are plotted for mean annual precipitation 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.

but always more weakly than MAT?

weak, though!

I suspect

Saturation would be 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 FAF, 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 FAF,
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 FAF simply because it
is correlated with MAT + MAT is a good predictor?
Carefully consider wording + interpretation. What variable
is the single best predictor?

→ agree with Ben that results section
become kind of a slogan. Make it
more concise.

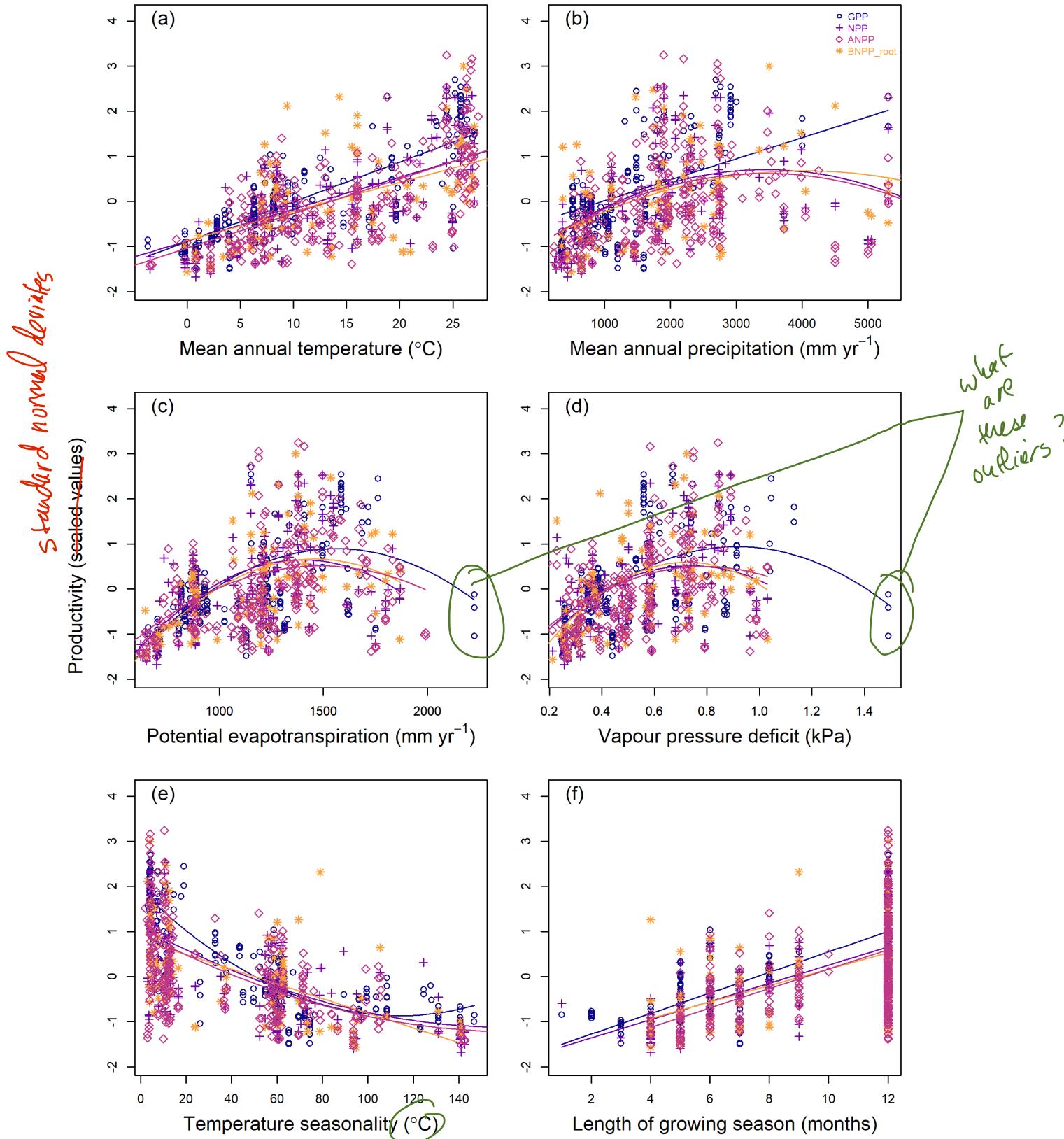


Figure 4: Plots of carbon fluxes against (a) mean annual temperature; (b) mean annual precipitation; (c) potential evapotranspiration; (d) vapour pressure deficit; (e) temperature seasonality; (f) length of growing season. For visualization purposes, data for each flux was rescaled with a mean of 0 and 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 ($p < 0.05$).

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.

lodes 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), indicating no major, systematic omissions or overestimations of flux components. However, climate explained lower proportions of variability among subsidiary C fluxes (e.g., $ANPP_{woody}$, $BNPP_{fine.root}$, $R_{auto-root}$; 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 importance across the climate space occupied by forests (Figs. 3-4). Temperature seasonality and growing season length are closely correlated with MAT and are strong predictors of FACF (H4; Figs. 4e-f, S2, S6-S7), 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 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 relationship³²⁸ 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**³⁴⁸ (?), 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 $BNPP_{root-fine}$ (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 ,

now
to my
knowledge

for
allocation
see
Hofhansl
et al.
2015
New phys.

what about differences in sites included? In general, r^2 increases for lower range of independent variable as quantified by r^2

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 ~~use~~
367 through fundamentally different approaches ^{in different sites} (e.g., minirhizotrons, ingrowth cores, or sequential coring for
368 $BNPP_{root-fine}$; root exclusion, stable isotope tracking, or gas exchange of excised roots for $R_{auto-root}$), and
369 sampling depth is variable and often insufficient to capture the full soil profile. $ANPP_{woody-stem}$, which is
370 also poorly explained by latitude or climate, is more straightforward to measure but is subject to variability
371 introduced by differences such as biomass allometries applied and minimum plant size sampled (Clark et
372 al. 2001 *Ecological Applications*). However, methodological variation and uncertainty affect all of fluxes
373 considered here—not necessarily any less than the aforementioned, and some of the larger fluxes that vary
374 more strongly with respect to climate ($ANPP, NPP$) are estimated by summing uncertain component fluxes.
375 Second, differences among variables in the proportion of variation explained by climate may be attributable
376 to more direct climatic control over GPP than subsidiary fluxes. That is, subsidiary fluxes may be shaped
377 by climate both indirectly through its influence on GPP and respiration and directly through any climatic
378 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 frost ^{free} days, 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 $\sim 20^\circ\text{C}$ (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

wording
in $H1$ is still
that from
these types
of data &
analysis
can't...
not that it
is "not
appropriate"
in general

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)
427 (**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.

433 Acknowledgements

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

435 References

- 436 Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., and Hegewisch, K. C. (2018). TerraClimate, a high-
437 resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*,
438 5(1):170191.
- 439 Anderson-Teixeira, K. J., Wang, M. M. H., McGarvey, J. C., Herrmann, V., Tepley, A. J., Bond-Lamberty,
440 B., and LeBauer, D. S. (2018). ForC: a global database of forest carbon stocks and fluxes. *Ecology*,
441 99(6):1507–1507.
- 442 Anderson-Teixeira, K. J., Wang, M. M. H., McGarvey, J. C., and LeBauer, D. S. (2016). Carbon dynamics of

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

are

- 443 mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Global Change*
444 *Biology*, 22(5):1690–1709.
- 445 Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jimenez, E., Navarrete, D., Almeida,
446 S., Costa, A. C. L., Salinas, N., Phillips, O. L., Anderson, L. O., Alvarez, C., Baker, T. R., Goncalvez,
447 P. H., Huaman-Ovalle, J., Mamani, M., Meir, P., Monteagudo, A., Patino, S., Penuela, M. C., Prieto, A.,
448 Quesada, C. A., Rozas-Davila, A., Rudas, A., Silva, J. A., and Vasquez, R. (2009). Above and belowground
449 net primary productivity across Amazonian forests on contrasting soils. *Biogeosciences*, (6):2759–2778.
- 450 Badgley, G., Anderegg, L. D. L., Berry, J. A., and Field, C. B. (2019). Terrestrial gross primary production:
451 Using NIR ν to scale from site to globe. *Global Change Biology*, 25(11):3731–3740.
- 452 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**.
453 *Journal of Statistical Software*, 67(1).
- 454 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M. A.,
455 Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert,
456 S., Margolis, H., Oleson, K. W., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I.,
457 and Papale, D. (2010). Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation
458 with Climate. *Science*, 329(5993):834–838.
- 459 Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests.
460 *Science*, 320(5882):1444–1449.
- 461 Bond-Lamberty, B., Bailey, V. L., Chen, M., Gough, C. M., and Vargas, R. (2018). Globally rising soil
462 heterotrophic respiration over recent decades. *Nature*, 560(7716):80–83.
- 463 Bond-Lamberty, B. and Thomson, A. (2010). A global database of soil respiration data. *Biogeosciences*,
464 7(6):1915–1926.
- 465 Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., Lopez-Gonzalez, G.,
466 Monteagudo-Mendoza, A., Malhi, Y., Lewis, S. L., Vásquez Martinez, R., Alexiades, M., Álvarez Dávila, E.,
467 Alvarez-Loayza, P., Andrade, A., Aragão, L. E. O. C., Araujo-Murakami, A., Arellano, E. J. M. M., Arroyo,
468 L., Aymard C., G. A., Bánki, O. S., Baraloto, C., Barroso, J., Bonal, D., Boot, R. G. A., Camargo, J.
469 L. C., Castilho, C. V., Chama, V., Chao, K. J., Chave, J., Comiskey, J. A., Cornejo Valverde, F., da Costa,
470 L., de Oliveira, E. A., Di Fiore, A., Erwin, T. L., Fauset, S., Forsthofer, M., Galbraith, D. R., Grahame,
471 E. S., Groot, N., Héault, B., Higuchi, N., Honorio Coronado, E. N., Keeling, H., Killeen, T. J., Laurance,
472 W. F., Laurance, S., Licona, J., Magnussen, W. E., Marimon, B. S., Marimon-Junior, B. H., Mendoza, C.,
473 Neill, D. A., Nogueira, E. M., Núñez, P., Pallqui Camacho, N. C., Parada, A., Pardo-Molina, G., Peacock,
474 J., Peña-Claros, M., Pickavance, G. C., Pitman, N. C. A., Poorter, L., Prieto, A., Quesada, C. A., Ramírez,
475 F., Ramírez-Angulo, H., Restrepo, Z., Roopsind, A., Rudas, A., Salomão, R. P., Schwarz, M., Silva, N.,
476 Silva-Espejo, J. E., Silveira, M., Stropp, J., Talbot, J., ter Steege, H., Teran-Aguilar, J., Terborgh, J.,
477 Thomas-Caesar, R., Toledo, M., Torello-Raventos, M., Umetsu, R. K., van der Heijden, G. M. F., van der
478 Hout, P., Guimarães Vieira, I. C., Vieira, S. A., Vilanova, E., Vos, V. A., and Zagt, R. J. (2015). Long-term
479 decline of the Amazon carbon sink. *Nature*, 519(7543):344–348.
- 480 Cavalieri, M. A., Reed, S. C., Smith, W. K., and Wood, T. E. (2015). Urgent need for warming experiments
481 in tropical forests. *Global Change Biology*, 21(6):2111–2121.

- 482 Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., and Sack, L. (2016). Does climate directly
483 influence NPP globally? *Global Change Biology*, 22(1):12–24.
- 484 Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M. M. C., Chuyong, G.,
485 Dobrowski, S. Z., Grierson, P., Harms, K. E., Houlton, B. Z., Marklein, A., Parton, W., Porder, S., Reed,
486 S. C., Sierra, C. A., Silver, W. L., Tanner, E. V. J., and Wieder, W. R. (2011). Relationships among
487 net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis: Nutrients,
488 climate and tropical NPP. *Ecology Letters*, 14(9):939–947.
- 489 Collatti, A. and Prentice, I. C. (2019). Is NPP proportional to GPP? Waring's hypothesis 20 years on. *Tree
490 Physiology*, 39(8):1473–1483.
- 491 DeLUCIA, E. H., Drake, J. E., Thomas, R. B., and Gonzalez-Meler, M. (2007). Forest carbon use efficiency:
492 is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6):1157–1167.
- 493 Fick, S. E. and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for
494 global land areas: NEW CLIMATE SURFACES FOR GLOBAL LAND AREAS. *International Journal of
495 Climatology*, 37(12):4302–4315.
- 496 Fyllas, N. M., Bentley, L. P., Shenkin, A., Asner, G. P., Atkin, O. K., Díaz, S., Enquist, B. J., Farfan-Rios,
497 W., Gloor, E., Guerrieri, R., Huasco, W. H., Ishida, Y., Martin, R. E., Meir, P., Phillips, O., Salinas, N.,
498 Silman, M., Weerasinghe, L. K., Zaragoza-Castells, J., and Malhi, Y. (2017). Solar radiation and functional
499 traits explain the decline of forest primary productivity along a tropical elevation gradient. *Ecology Letters*,
500 20(6):730–740.
- 501 Gill, A. L. and Finzi, A. C. (2016). Belowground carbon flux links biogeochemical cycles and resource-use
502 efficiency at the global scale. *Ecology Letters*, 19(12):1419–1428.
- 503 Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., and Whittaker, R. J. (2015). Latitude,
504 productivity and species richness: Latitude and productivity. *Global Ecology and Biogeography*, 24(1):107–
505 117.
- 506 Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley,
507 K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., and Whittaker, R. J. (2010). Net primary
508 productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian
509 Andes: NET PRIMARY PRODUCTIVITY FROM ANDES TO AMAZON. *Global Change Biology*,
510 16(12):3176–3192.
- 511 Harris, I., Jones, P., Osborn, T., and Lister, D. (2014). Updated high-resolution grids of monthly climatic
512 observations - the CRU TS3.10 Dataset: UPDATED HIGH-RESOLUTION GRIDS OF MONTHLY
513 CLIMATIC OBSERVATIONS. *International Journal of Climatology*, 34(3):623–642.
- 514 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A. (2005). Very high resolution
515 interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15):1965–1978.
- 516 Hofhansl, F., Schnecker, J., Singer, G., and Wanek, W. (2015). New insights into mechanisms driving carbon
517 allocation in tropical forests. *New Phytologist*, 205(1):137–146.

- 518 Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sánchez, A., Daniels, A. K.,
519 Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T.
520 C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., Amani, C. A.,
521 Baker, T. R., Banin, L. F., Baya, F., Begne, S. K., Bennett, A. C., Benedet, F., Bitariho, R., Bocko, Y. E.,
522 Boeckx, P., Boundja, P., Brienen, R. J. W., Brncic, T., Chezeaux, E., Chuyong, G. B., Clark, C. J., Collins,
523 M., Comiskey, J. A., Coomes, D. A., Dargie, G. C., de Haulleville, T., Kamdem, M. N. D., Doucet, J.-L.,
524 Esquivel-Muelbert, A., Feldpausch, T. R., Fofanah, A., Foli, E. G., Gilpin, M., Gloor, E., Gonmadje, C.,
525 Gourlet-Fleury, S., Hall, J. S., Hamilton, A. C., Harris, D. J., Hart, T. B., Hockemba, M. B. N., Hladik,
526 A., Ifo, S. A., Jeffery, K. J., Jucker, T., Yakusu, E. K., Kearsley, E., Kenfack, D., Koch, A., Leal, M. E.,
527 Levesley, A., Lindsell, J. A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J. C., Makana, J.-R., Malhi, Y.,
528 Marshall, A. R., Martin, J., Martin, E. H., Mbayu, F. M., Medjibe, V. P., Mihindou, V., Mitchard, E.
529 T. A., Moore, S., Munishi, P. K. T., Bengone, N. N., Ojo, L., Ondo, F. E., Peh, K. S.-H., Pickavance, G. C.,
530 Poulsen, A. D., Poulsen, J. R., Qie, L., Reitsma, J., Rovero, F., Swaine, M. D., Talbot, J., Taplin, J., Taylor,
531 D. M., Thomas, D. W., Toirambe, B., Mukendi, J. T., Tuagben, D., Umunay, P. M., van der Heijden,
532 G. M. F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J. T., and Zemagho, L. (2020).
533 Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, 579(7797):80–87.
- 534 Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J., and Watts, J. (2017). The sensitivity of soil
535 respiration to soil temperature, moisture, and carbon supply at the global scale. *Global Change Biology*,
536 23(5):2090–2103.
- 537 Huston, M. A. and Wolverton, S. (2009). The global distribution of net primary production: resolving the
538 paradox. *Ecological Monographs*, 79(3):343–377.
- 539 Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., Arneth, A.,
540 Bernhofer, C., Bonal, D., Chen, J., Gianelle, D., Gobron, N., Kiely, G., Kutsch, W., Lasslop, G., Law,
541 B. E., Lindroth, A., Merbold, L., Montagnani, L., Moors, E. J., Papale, D., Sottocornola, M., Vaccari,
542 F., and Williams, C. (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat,
543 and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of
544 Geophysical Research*, 116:G00J07.
- 545 Kerkhoff, A. J., Enquist, B. J., Elser, J. J., and Fagan, W. F. (2005). Plant allometry, stoichiometry and the
546 temperature-dependence of primary productivity: Plant allometry, stoichiometry and productivity. *Global
547 Ecology and Biogeography*, 14(6):585–598.
- 548 Kunert, N., El-Madany, T. S., Aparecido, L. M. T., Wolf, S., and Potvin, C. (2019). Understanding the
549 controls over forest carbon use efficiency on small spatial scales: Effects of forest disturbance and tree
550 diversity. *Agricultural and Forest Meteorology*, 269-270:136–144.
- 551 Larjavaara, M. and Muller-Landau, H. C. (2012). Temperature explains global variation in biomass among
552 humid old-growth forests: Temperature and old-growth forest biomass. *Global Ecology and Biogeography*,
553 21(10):998–1006.
- 554 Li and Xiao (2019). Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A Global,
555 Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2. *Remote Sensing*, 11(21):2563.
- 556 Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D.,
557 Bozzato, F., Pretzsch, H., de Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C. B.,

- 558 Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A. C., Ammer, C., Schall,
559 P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H. Y. H., Lei, X., Schelhaas, M.-J.,
560 Lu, H., Gianelle, D., Parfenova, E. I., Salas, C., Lee, E., Lee, B., Kim, H. S., Bruelheide, H., Coomes,
561 D. A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonke, B., Tavani, R., Zhu, J., Brandl,
562 S., Vayreda, J., Kitahara, F., Searle, E. B., Neldner, V. J., Ngugi, M. R., Baraloto, C., Frizzera, L., Ba azy,
563 R., Oleksyn, J., Zawi a-Nied wiecki, T., Bouriaud, O., Bussotti, F., Finer, L., Jaroszewicz, B., Jucker, T.,
564 Valladares, F., Jagodzinski, A. M., Peri, P. L., Gonmadje, C., Marthy, W., OBrien, T., Martin, E. H.,
565 Marshall, A. R., Rovero, F., Bitariho, R., Niklaus, P. A., Alvarez-Loayza, P., Chamuya, N., Valencia,
566 R., Mortier, F., Wortel, V., Engone-Obiang, N. L., Ferreira, L. V., Odeke, D. E., Vasquez, R. M., Lewis,
567 S. L., and Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests.
568 *Science*, 354(6309):aaf8957–aaf8957.
- 569 Litton, C. M., Raich, J. W., and Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change
570 Biology*, 13(10):2089–2109.
- 571 Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D.,
572 Wingate, L., Matteucci, G., Aragão, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D.,
573 Bonnefond, J. M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M.,
574 Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R.,
575 Hollinger, D. Y., Hutyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E.,
576 Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L.,
577 Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard,
578 O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M. L., Tang, J., Valentini, R., Vesala, T.,
579 and Janssens, I. A. (2007). CO₂ balance of boreal, temperate, and tropical forests derived from a global
580 database. *Global Change Biology*, 13(12):2509–2537.
- 581 Malhi, Y. (2012). The productivity, metabolism and carbon cycle of tropical forest vegetation: Carbon cycle
582 of tropical forests. *Journal of Ecology*, 100(1):65–75.
- 583 Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco,
584 W., Silva-Espejo, J. E., del Aguilla-Pasquell, J., Farfán Amézquita, F., Aragão, L. E. O. C., Guerrieri, R.,
585 Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O. L., Meir, P., and Silman, M. (2017). The
586 variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget
587 perspective. *New Phytologist*, 214(3):1019–1032.
- 588 McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B.,
589 Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C. G., Galbraith, D., Goodsman,
590 D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D. J., Kassim, A. R., Keller, M., Koven, C., Kueppers,
591 L., Kumagai, T., Malhi, Y., McMahon, S. M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau,
592 H. C., Phillips, O. L., Powell, T., Sierra, C. A., Sperry, J., Warren, J., Xu, C., and Xu, X. (2018). Drivers
593 and mechanisms of tree mortality in moist tropical forests. *New Phytologist*, 219(3):851–869.
- 594 Michaletz, S. T., Cheng, D., Kerkhoff, A. J., and Enquist, B. J. (2014). Convergence of terrestrial plant
595 production across global climate gradients. *Nature*, 512(7512):39–43.
- 596 Michaletz, S. T., Kerkhoff, A. J., and Enquist, B. J. (2018). Drivers of terrestrial plant production across
597 broad geographical gradients. *Global Ecology and Biogeography*, 27(2):166–174.

- 598 Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., and Iost, S. (2011). Elevation effects on the carbon
599 budget of tropical mountain forests (S Ecuador): the role of the belowground compartment: ELEVATION
600 EFFECTS ON FOREST CARBON CYCLING. *Global Change Biology*, 17(6):2211–2226. Former
- 601 Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A.,
602 Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen,
603 A., Sitch, S., and Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*,
604 333(6045):988–993.
- 605 Piao, S., Luysaert, S., Ciais, P., Janssens, I. A., Chen, A., Cao, C., Fang, J., Friedlingstein, P., Luo, Y., and
606 Wang, S. (2010). Forest annual carbon cost: a global-scale analysis of autotrophic respiration. *Ecology*,
607 91(3):652–661.
- 608 Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D., Egorov, A.,
609 Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., and Zhuravleva, I.
610 (2008). Mapping the World's Intact Forest Landscapes by Remote Sensing. *Ecology and Society*, 13(2):art51.
- 611 Poulter, B., Aragão, L., Andela, N., Bellassen, V., Ciais, P., Kato, T., Lin, X., Nachin, B., Luysaert, S.,
612 Pederson, N., Peylin, P., Piao, S., Saatchi, S., Schepaschenko, D., Schelhaas, M., and Shvidenko, A. (2018).
613 The global forest age dataset (GFADv1.0), link to NetCDF file.
- 614 Rogelj, J., Shindell, D., Jiang, K., Fifita, S., Forster, P., Ginzburg, V., Handa, C., Kobayashi, S., Kriegler,
615 Mundaca, L., Séférian, R., Vilariño, M. V., Calvin, K., Emmerling, J., Fuss, S., Gillett, N., He, C.,
616 Hertwich, E., Höglund-Isaksson, L., Huppmann, D., Luderer, G., McCollum, D. L., Meinshausen, M.,
617 Millar, R., Popp, A., Purohit, P., Riahi, K., Ribes, A., Saunders, H., Schädel, C., Smith, P., Trutnevyyte, E.,
618 Xiu, Y., Zhou, W., Zickfeld, K., Flato, G., Fuglestvedt, J., Mrabet, R., and Schaeffer, R. (2018). Mitigation
619 Pathways Compatible with 1.5°C in the Context of Sustainable Development. page 82.
- 620 Rutishauser, E., Wright, S. J., Condit, R., Hubbell, S. P., Davies, S. J., and Muller-Landau, H. C. (2020).
621 Testing for changes in biomass dynamics in large-scale forest datasets. *Global Change Biology*, 26(3):1485–
622 1498.
- 623 Schuur, E. A. G. (2003). PRODUCTIVITY AND GLOBAL CLIMATE REVISITED: THE SENSITIVITY Former
624 OF TROPICAL FOREST GROWTH TO PRECIPITATION. *Ecology*, 84(5):1165–1170.
- 625 Taylor, P. G., Cleveland, C. C., Wieder, W. R., Sullivan, B. W., Doughty, C. E., Dobrowski, S. Z., and
626 Townsend, A. R. (2017). Temperature and rainfall interact to control carbon cycling in tropical forests.
627 *Ecology Letters*, 20(6):779–788.
- 628 Trabucco, A. and Zomer, R. J. (2019). Global Aridity Index and Potential Evapo-Transpiration (ET0)
629 Climate Database v2. page 10.
- 630 Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., and
631 Parmenter, R. (1999). The Relationship Between Productivity and Species Richness. *Annual Review of
632 Ecology and Systematics*, 30(1):257–300.
- 633 Šimová, I. and Storch, D. (2017). The enigma of terrestrial primary productivity: measurements, models,
634 scales and the diversity-productivity relationship. *Ecography*, 40(2):239–252.