

¹ **Title:** Carbon cycling in mature and regrowth forests globally: a macroecological synthesis based on the
² global Forest Carbon (ForC) database

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²⁶ ## [1] 0

²⁷ **NOTES TO COAUTHORS:**

²⁸ • We're still finalizing the data (and adding some data). Outliers in plots will all be checked/ resolved,
²⁹ and we'll be able to pull in more data (*GROA* needs classification by dominant vegetation before it can
³⁰ be pulled in, and we're working on that)

³¹ • “????” indicates a reference that we have entered in the .Rmd file, but not yet in the bibliography file.
³² Don't worry about those. (However, places with “REF” need references)

³³ • bold/ italic text indicates places where I know we need to go back and revisit/ fill in info

³⁴ **Summary**

³⁵ *Background.* Earth's climate is closely linked to forests, which strongly influence atmospheric carbon dioxide
³⁶ (CO_2) and climate by their impact on the global carbon (C) cycle. However, efforts to incorporate forests
³⁷ into climate models and CO_2 accounting frameworks have been constrained by a lack of accessible,
³⁸ global-scale data on how C cycling varies across forest types and stand ages.

³⁹ *Methods/Design.* Here, we draw from the Global Forest Carbon Database, ForC, to provide a macroscopic
⁴⁰ overview of C cycling in the world's forests, giving special attention to stand age-related variation.

⁴¹ Specifically, we use 14847 *ForC* records from 874 geographic locations representing 34 C cycle variables to
⁴² characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate
⁴³ broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years)
⁴⁴ forests. For regrowth forests, we quantify age trends for all variables.

⁴⁵ *Review Results/ Synthesis.* *ForC v3.0* yielded a fairly comprehensive picture of C cycling in the world's
⁴⁶ major forest biomes, with broad closure of C budgets. The rate of C cycling generally increased from boreal
⁴⁷ to tropical regions in both mature and regrowth forests, whereas C stocks showed less directional variation.
⁴⁸ The majority of flux variables, together with most live biomass pools, increased significantly with stand age,
⁴⁹ and the rate of increase again tended to increase from boreal to tropical regions.

⁵⁰ *Discussion.* NEED TO WRITE THIS!!!

⁵¹ *Key words:* forest ecosystems; carbon cycle; stand age; productivity; respiration; biomass; global

52 **Background**

53 Forest ecosystems are shaping the course of climate change (IPCC1.5) through their influence on atmospheric
54 carbon dioxide (CO₂). Despite the centrality of forest C cycling in regulating atmospheric CO₂, important
55 uncertainties in climate models (???, ???, ???, Krause *et al* 2018) and CO₂ accounting frameworks (Pan *et*
56 *al* 2011) can be traced to lack of accessible, comprehensive data on how C cycling varies across forest types
57 and in relation to stand history. These require large-scale databases with global coverage, which runs
58 contrary to the nature in which forest C stocks and fluxes are measured and published. While remote sensing
59 measurements are increasingly useful for global- or regional-scale estimates of a few critical variables [Li and
60 Xiao (2019); **REFS for biomass, biomass change, net CO2 flux**], measurement of most forest C stocks
61 and fluxes require intensive on-the-ground data collection. Here, we provide a robust and comprehensive
62 analysis of carbon cycling from a stand to global level, and by biome and stand age, using the largest global
63 compilation of forest carbon data, which is available in our open source Global Carbon Forest database
64 (ForC; Fig. 1).

65 (*Abby has offered to update stats in this paragraph:*)

66 A robust understanding of forest impacts on global C cycling is essential. Annual gross CO₂ sequestration in
67 forests (gross primary productivity, *GPP*) is estimated at >69 Gt C yr⁻¹ (???), or >7 times average annual
68 fossil fuel emissions from 2007-2016 (9.4 ± 0.5 Gt C yr⁻¹; Le Quéré *et al* 2017) (**update**). Most of this
69 enormous C sequestration is counterbalanced by CO₂ releases to the atmosphere through ecosystem
70 respiration (*R_{eco}*) or fire, with forests globally dominant as sources of both soil respiration (???) and fire
71 emissions (REF). (**check if deforestation statistic below includes natural fire, exclude here if it**
72 **does.**) In recent years, the remaining CO₂ sink averaged 3.0 ± 0.8 Gt C yr⁻¹ from 2007-2016, offsetting
73 32% of anthropogenic fossil fuel emissions (Le Quéré *et al* 2017) (**update, give range**). Yet, this sink is
74 reduced by *deforestation/ forest losses to anthropogenic and natural disturbances*. Recent net deforestation
75 (*i.e.*, gross deforestation minus regrowth) has been a source of CO₂ emissions, estimated at ~1.1 Gt C yr⁻¹
76 from YEAR-YEAR (Pan *et al* 2011), reducing the net forest sink to ~1.2-1.7 Gt C yr⁻¹ across Earth's forests
77 (Le Quéré *et al* 2017, Schimel *et al* 2015) (**update, give range**).

78 The future of the current forest C sink is dependent both upon forest responses to climate change itself and
79 human land use decisions, which will feedback and strongly influence the course of climate change.
80 Regrowing forests in particular will play an important role (Pugh *et al* 2019), as these represent a large
81 (~#%) and growing proportion of Earth's forests (McDowell *et al* 2020). Understanding, modeling, and
82 managing forest-atmosphere CO₂ exchange is thus central to efforts to mitigate climate change [Grassi *et al*
83 (2017); Griscom *et al* (2017); **Cavaleri et al 2015**].

84 Despite the importance of forests, comprehensive global studies have historically been limited by the scattered
85 and more local nature of research studies. Primary research articles typically cover only a small numbers of
86 sites at a time. The rare exceptions that span regions or continents with rare exceptions spanning regions or
87 continents are typically coordinated through research networks such as ForestGEO (Anderson-Teixeira *et al*
88 2015, e.g., Lutz *et al* 2018) or FLUXNET [Baldocchi *et al* (2001); e.g., **FLUXNET_REF**]. The result of
89 decades of research on forest C cycling is that tens of thousands of records have been distributed across
90 literally thousands of scientific articles –often behind paywalls– along with variation in data formats, units,
91 measurement methods, etc.. In this format, the data are effectively inaccessible for many global-scale
92 analyses, including those attempting to benchmark model performance with global data (Clark *et al* 2017,

93 Luo et al 2012), quantify the the role of forests in the global C cycle (*e.g.*, Pan *et al* 2011), or use
94 book-keeping methods to quantify actual or scenario-based exchanges of CO₂ between forests and the
95 atmosphere [Griscom *et al* (2017); **REFS**]. Scattered data are not conducive for advancing science nor for
96 making decisions about how to best manage our forests as a tool for constraining the climate crisis.

97 To address the need for global-scale analyses of forest C cycling, we recently developed *ForC*
98 (Anderson-Teixeira *et al* 2016, pp @anderson-teixeira_forc_2018). *ForC* contains published estimates of
99 forest ecosystem C stocks and annual fluxes (>50 variables), with the different variables capturing the unique
100 ecosystem pools (*e.g.*, woody, foliage, and root biomass; dead wood) and flux types (*e.g.*, gross and net
101 primary productivity; soil, root, and ecosystem respiration). These data are ground-based measurements,
102 and *ForC* contains associated data required for interpretation (*e.g.*, stand history, measurement methods).
103 These data have been amalgamated from original peer-reviewed publications, either directly or via
104 intermediary data compilations. Since its most recent publication (Anderson-Teixeira *et al* 2018), *ForC*
105 has grown to include two additional large databases: the Global Soil Respiration Database (SRDB;
106 Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database
107 (GROA; Cook-Patton *et al* 2020) that also synthesized published forest C data. Following these additions,
108 *ForC* currently contains 47846 records from 10609 plots and 1532 distinct geographic areas representing all
109 forested biogeographic and climate zones. This represents an 175% increase in records from the prior
110 publication (Anderson-Teixeira *et al* 2018).

111 Here, we analyze the more extensive *ForC* data (Fig. 1) to provide a robust overview of stand-level carbon
112 cycling of the world's major forest biomes and how it varies with stand age. Our primary goal is to provide a
113 data-driven summary of our current state of knowledge on broad trends in forest C cycling. Specifically, we
114 address three broad questions:

- 115 1. How thoroughly can we represent C budgets for each of the world's major forest biomes (*i.e.*, tropical,
116 temperate broadleaf and deciduous, boreal) based on the current *ForC* data?
- 117 2. How do C cycling vary across the world's major forest biomes?
- 118 3. How does C cycling vary with stand age (in interaction with biome)?

119 While components of these questions have been previously addressed (Luyssaert *et al* 2007,
120 Anderson-Teixeira *et al* 2016, Cook-Patton *et al* 2020, Banbury Morgan *et al* n.d.), our analysis represents
121 by far the most comprehensive analysis of C cycling in global forests, and will serve as a foundation for
122 improved understanding of global forest C cycling and highlight where key sources of uncertainty still reside.

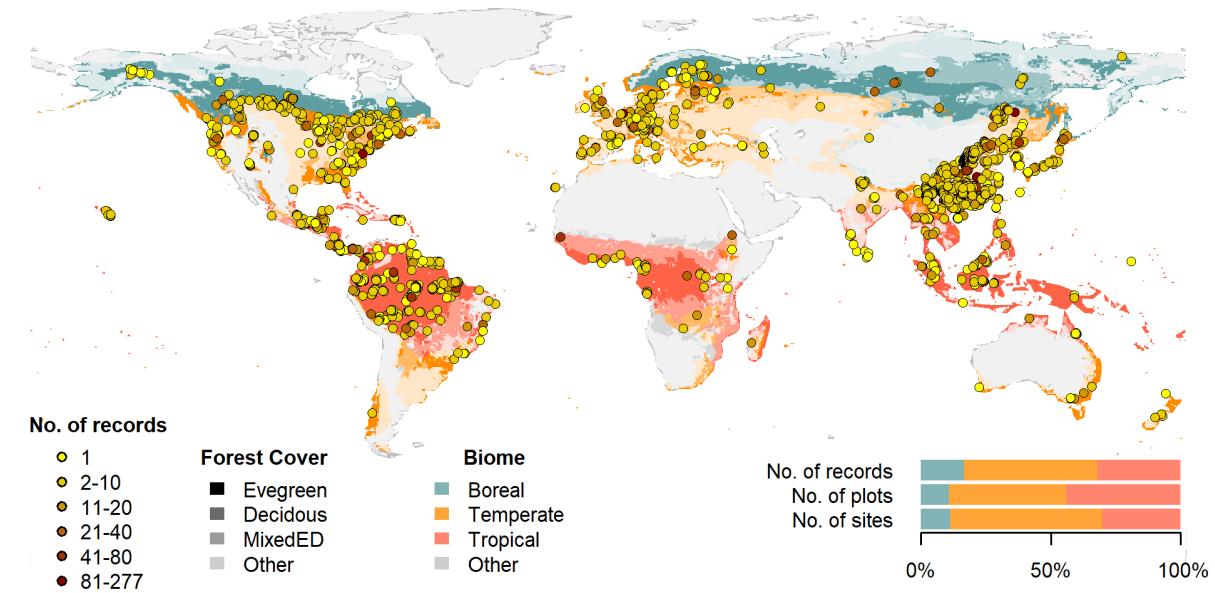


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown in the inset.

123 Methods/ Design

124 This review synthesizes data from the *ForC* database (Fig. 1; <https://github.com/forc-db/ForC>;
 125 Anderson-Teixeira *et al* 2016, pp @anderson-teixeira_forc_2018). *ForC* amalgamates numerous
 126 intermediary data sets (*e.g.*, Luyssaert *et al* 2007, Bond-Lamberty and Thomson 2010, Cook-Patton *et al*
 127 2020) and original studies. Original publications were referenced to check values and obtain information not
 128 contained in intermediary data sets, although this process has not been completed for all records. The
 129 database was developed with goals of understanding how C cycling in forests varies across broad geographic
 130 scales and as a function of stand age. As such, there has been a focus on incorporating data from regrowth
 131 forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age data when
 132 possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention was given to developing
 133 the database for tropical forests (Anderson-Teixeira *et al* 2016), which represented roughly one-third of
 134 records in *ForC* v.2.0* (Anderson-Teixeira *et al* 2018). Since publication of *ForC* v.2.0, we added the
 135 following data to *ForC*: the Global Database of Soil Respiration Database (*SRDB* v.##, 9497 records;
 136 Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment database (*GROA*
 137 v1.0, 18143 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020). We've also added data from
 138 individual publications (detailed list at [https://github.com/forc-
 139 db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv](https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv)), with a particular
 140 focus on productivity (Banbury Morgan *et al* n.d., *e.g.*, Taylor *et al* 2017), dead wood, and ForestGEO sites
 141 (*e.g.*, Lutz *et al* 2018, p @johnson_climate_2018). We note that there remains a significant amount of
 142 relevant data that is not yet included in *ForC*, particularly biomass data from national forest inventories

¹⁴³ (e.g.,; **REFS**). The database version used for this analysis has been tagged as a new release on Github (**XX**)
¹⁴⁴ and assigned a DOI through Zenodo (DOI: TBD).

¹⁴⁵ To facilitate analyses, we created a simplified version of ForC, *ForC-simplified*
¹⁴⁶ (https://github.com/forc-db/ForC/blob/master/ForC_simplified), which we analyzed here. In generating
¹⁴⁷ *ForC-simplified*, all measurements originally expressed in units of dry organic matter (*OM*) were converted
¹⁴⁸ to units of C using the IPCC default of $C = 0.47 * OM$ (IPCC 2006). Duplicate or otherwise conflicting
¹⁴⁹ records were reconciled as described in APPENDIX S1, resulting in a total of 30927 records (64.6% size of
¹⁵⁰ total database). Records were filtered to remove plots that had undergone significant anthropogenic
¹⁵¹ management or major disturbance since the most recent stand initiation event. Specifically, we removed all
¹⁵² plots flagged as managed in ForC-simplified (19%). This included plots with any record of managements
¹⁵³ manipulating CO₂, temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name
¹⁵⁴ contained the terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”. Plots flagged as
¹⁵⁵ disturbed in ForC-simplified (5.9%) included stands that had undergone any notable anthropogenic thinning
¹⁵⁶ or partial harvest. We retained sites that were grazed or had undergone low severity natural disturbances
¹⁵⁷ (<10% mortality) including droughts, major storms, fires, and floods. We removed all plots for which no
¹⁵⁸ stand history information had been retrieved (7.7%). In total, this resulted in 21872 records (45.7% of the
¹⁵⁹ records in the database) being eligible for inclusion in the analysis.

¹⁶⁰ We selected 23 annual flux and 11 C stock variables for inclusion in the analysis. These different flux and
¹⁶¹ stock variables (Table 1) represent different pools (e.g., aboveground biomass, dead wood, ecosystem total)
¹⁶² and levels of combination (e.g., total aboveground net primary productivity (*ANPP*) versus the ANPP of
¹⁶³ individual elements such as foliage, roots, and branches. Note that two flux variables, aboveground
¹⁶⁴ heterotrophic (R_{het-ag}) and total (R_{het}) respiration, were included for conceptual completeness but had no
¹⁶⁵ records in *ForC* (Table 1). Records for these variables represented 89.1% of the total records eligible for
¹⁶⁶ inclusion. For this analysis, we combined some of ForC’s specific variables (e.g., multiple variables for net
¹⁶⁷ primary productivity, such as measurements including or excluding fruit and flower production and herbivory)
¹⁶⁸ into more broadly defined variables. Specifically, net ecosystem exchange (measured by eddy-covariance;
¹⁶⁹ **FLUXNET REF**) and biometric estimates of *NEP* were combined into the single variable *NEP* (Table 1).
¹⁷⁰ Furthermore, for *NPP*, *ANPP*, and *ANPP_{litterfall}*, *ForC* variables specifying inclusion of different
¹⁷¹ components were combined. Throughout ForC, for all measurements drawing from tree census data (e.g.,
¹⁷² biomass, productivity), the minimum diameter breast height (DBH) threshold for tree census was $\leq 10\text{cm}$.
¹⁷³ All records were measured directly or derived from field measurements (as opposed to modeled).

¹⁷⁴ For this analysis, we grouped forests into four broad biome types based on climate zones and dominant
¹⁷⁵ vegetation type (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and
¹⁷⁶ two age classifications (young and mature). Climate zones (Fig. 1) were defined based on site geographic
¹⁷⁷ coordinates according to Köppen-Geiger zones (Rubel and Kottek 2010). We defined the tropical biome as
¹⁷⁸ including all equatorial (A) zones, temperate biomes as including all warm temperate (C) zones and warmer
¹⁷⁹ snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and the boreal biome as including the colder snow
¹⁸⁰ climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones
¹⁸¹ were excluded from the analysis. We defined leaf type (broadleaf / needleleaf) was based on descriptions in
¹⁸² original publications (prioritized) or values extracted from a global map based on satellite observations
¹⁸³ (SYNMAP; ???). For young tropical forests imported from *GROA* but not yet classified by leaf type, we
¹⁸⁴ assumed that all were broadleaf, consistent with the rarity of naturally regenerating needleleaf forests in the

Table 1. Carbon cycle variables included in this analysis, their sample sizes, and summary of biome differences and age trends.

Variable	Description	N records			biome differences*	age trend†
		records	plots	geographic areas		
Annual fluxes						
<i>NEP</i>	net ecosystem production or net ecosystem exchange (+ indicates C sink)	377	163	89	n.s.	+; xB
<i>GPP</i>	gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEE$)	309	117	72	$TrB > TeB \geq TeN \geq BoN$	+; xB
<i>NPP</i>	net primary production ($ANPP + BNPP$)	292	165	74	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP</i>	aboveground <i>NPP</i>	566	384	135	$TrB > TeB \geq TeN \geq BoN$	+; xB
<i>ANPP_{woody}</i>	woody production ($ANPP_{stem} + ANPP_{branch}$)	126	114	37	n.s.	+; xB
<i>ANPP_{stem}</i>	woody stem production	458	411	118	$TrB > TeN \geq TeB > BoN$	-; xB
<i>ANPP_{branch}</i>	branch turnover	125	112	42	$TrB > TeB \geq TeN$	n.s.
<i>ANPP_{foliage}</i>	foliage production, typically estimated as annual leaf litterfall	275	231	89	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP_{litterfall}</i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	147	117	55	$TrB > TeB$	+
<i>ANPP_{repro}</i>	production of reproductive structures (flowers, fruits, seeds)	72	65	35	n.s.	-
<i>ANPP_{folivory}</i>	foliar biomass consumed by folivores	24	16	11	-	-
<i>M_{woody}</i>	woody mortality—i.e., B_{ag} of trees that die	35	35	19	-	-
<i>BNPP</i>	belowground NPP ($BNPP_{coarse} + BNPP_{fine}$)	210	178	76	$TrB > TeB \geq TeN \geq BoN$	+
<i>BNPP_{coarse}</i>	coarse root production	144	111	36	n.s.	n.s.
<i>BNPP_{fine}</i>	fine root production	167	136	62	n.s.	+
<i>R_{eco}</i>	ecosystem respiration ($R_{auto} + R_{het}$)	197	81	59	$TrB > TeN$	+; xB
<i>R_{auto}</i>	autotrophic respiration ($(R_{auto-ag} + R_{root})$)	36	35	15	-	-
<i>R_{auto-ag}</i>	aboveground autotrophic respiration (i.e., leaves and stems)	3	3	2	-	-
<i>R_{root}</i>	root respiration	227	183	98	n.s.	+
<i>R_{soil}</i>	soil respiration ($R_{het-soil} + R_{root}$)	644	468	219	$TrB > TeB \geq TeN > BoN$	n.s.
<i>R_{het-soil}</i>	soil heterotrophic respiration	213	178	93	$TrB > TeB \geq TeN$	-; xB
<i>R_{het-ag}</i>	aboveground heterotrophic respiration	0	0	0	-	-
<i>R_{het}</i>	heterotrophic respiration ($(R_{het-ag} + R_{het-soil})$)	0	0	0	-	-
Stocks						
<i>B_{tot}</i>	total live biomass ($B_{ag} + B_{root}$)	299	252	85	$TeN > TeB \geq TrB \geq BoN$	+; xB
<i>B_{ag}</i>	aboveground live biomass ($B_{ag-wood} + B_{foliage}$)	5371	4761	621	$TrB \geq TeN \geq TeB > BoN$	+; xB
<i>B_{ag-wood}</i>	woody component of aboveground biomass	224	210	66	$TeN > TrB \geq TeB \geq BoN$	+; xB
<i>B_{foliage}</i>	foliage biomass	260	216	74	$TeN > TrB \geq BoN \geq TeB$	+; xB
<i>B_{root}</i>	total root biomass ($B_{root-coarse} + B_{root-fine}$)	2380	2337	359	n.s.	+; xB
<i>B_{root-coarse}</i>	coarse root biomass	204	190	68	$TeN > TeB \geq BoN$	+; xB
<i>B_{root-fine}</i>	fine root biomass	335	266	107	n.s.	n.s.
<i>DW_{tot}</i>	deadwood ($DW_{standing} + DW_{down}$)	223	212	42	$TeB > TrB$	+; xB
<i>DW_{standing}</i>	standing dead wood	65	61	22	-	-
<i>DW_{down}</i>	fallen dead wood, including coarse and sometimes fine woody debris	284	271	37	-	+; xB
<i>OL</i>	organic layer / litter/ forest floor	555	482	113	n.s.	+; xB

* Tr: Tropical, TeB: Temperate Broadleaf, TeN: Temperate Needleleaf, B: Boreal, n.s.: no significant differences

† + or -: significant positive or negative trend, xB: significant age x biome interaction, n.s.: no significant age trend

185 tropics (**REF**). We also classified forests as “young” (< 100 years) or “mature” (≥ 100 years or classified as
186 “mature”, “old growth”, “intact”, or “undisturbed” in original publication). Assigning stands to these
187 groupings required the exclusion of records for which *ForC* lacked geographic coordinates (0.4% of sites in
188 full database) or records of stand age (4.8% of records in full database). We also excluded records of stand
189 age = 0 year (0.8% of records in full database). In total, our analysis retained 76.2 of the focal variable
190 records for forests of known age. Numbers of records by biome and age class are given in Table S1.

191 Data were summarized to produce schematics of C cycling across the eight biome by age group combinations
192 identified above. To obtain the values reported in the C cycle schematics, we first averaged any repeated
193 measurements within a plot. Values were then averaged across geographically distinct areas, defined as plots
194 clustered within 25 km of one another (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if
195 available for all records. This step was taken to avoid pseudo-replication and to combine any records from
196 sites with more than one name in ForC.

197 We tested whether the C budgets described above “closed”—*i.e.*, whether they were internally consistent.
198 Specifically, we first defined relationships among variables: for example, $NEP = GPP - R_{eco}$,
199 $BNPP = BNPP_{coarse} + BNPP_{fine}$, $DW_{tot} = DW_{standing} + DW_{down}$. (**issue #44—but just delete**
200 **this chunk if not resolved before submission**) Henceforth, we refer to the variables on the left side of
201 the equation as “aggregate” fluxes or stocks, and those that are summed as “component” fluxes or stocks,
202 noting that the same variable can take both aggregate and component positions in different relationships.
203 We considered the C budget for a given relationship “closed” when component variables summed to within
204 one standard deviation of the aggregate variable.

205 To test for differences across mature forest biomes, we also examined how stand age impacted fluxes and
206 stocks, employing a mixed effects model [‘lmer’ function in ‘lme4’ R package version **x.xx**; **REF**] with biome
207 as fixed effect and plot nested within geographic.area as random effects on the intercept. When Biome had a
208 significant effect, we looked at a Tukey’s pairwise comparison to see which biomes were significantly different
209 from one another. This analysis was run for variables with records for at least seven distinct geographic areas
210 in more than one biome, excluding any biomes that failed this criteria (Table 1).

211 To test for age trends in young (<100yrs) forests, we employed a mixed effects model with biome and
212 $\log_{10}[\text{stand.age}]$ as fixed effects and plot nested within geographic.area as a random effect on the intercept.
213 This analysis was run for variables with records for at least three distinct geographic areas in more than one
214 biome, excluding any biomes that failed this criteria (Table 1). When the effect of stand age was significant
215 at $p \leq 0.05$ and when each biome had records for stands of at least 10 different ages, a biome \times stand.age
216 interaction was included in the model.

217 To facilitate the accessibility of our results and data, and to allow for rapid updates as additional data
218 become available, we have automated all database manipulation, analyses, and figure production in R
219 (**version, citation**).

220 Review Results/ Synthesis

221 Data Coverage

222 Of the 47846 records in *ForC* v3.0, 14847 met our strict criteria for inclusion in this study (Fig. 1). These
223 records were distributed across 5889 plots in 874 distinct geographic areas. Of the 23 flux and 11 stock

variables mapped in these diagrams, *ForC* contained sufficient mature forest data for inclusion in our statistical analyses (*i.e.*, records from ≥ 7 distinct geographic areas) for 20 fluxes and 9 stocks in tropical broadleaf forests, 14 fluxes and 9 stocks in temperate broadleaf forests, 15 fluxes and 8 stocks in temperate conifer forests, and 8 fluxes and 7 stocks in boreal forests. For regrowth forests (<100 yrs), *ForC* contained sufficient data for inclusion in our statistical analyses (*i.e.*, records from ≥ 3 distinct geographic areas) for 10 fluxes and 10 stocks in tropical broadleaf forests, 16 fluxes and 10 stocks in temperate broadleaf forests, 17 fluxes and 10 stocks in temperate conifer forests, and 14 fluxes and 9 stocks in boreal forests.

231 C cycling in mature forests

Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests ≥ 100 years old and with no known major natural or anthropogenic disturbance are presented in Figures 2-5 (and available in tabular format in the *ForC* release accompanying this publication: [ForC/numbers_and_facts/ForC_variable_averages_per_Biome.csv](#)).

For variables with records from ≥ 7 distinct geographic areas, these ensemble C budgets were generally consistent. *That is, component variables summed to within one standard deviation of their respective aggregate variables in all but two instances, both in temperate conifer forests (Fig. 5). (check all this with final results:*

https://github.com/forc-db/ForC/blob/master/numbers_and_facts/C_cycle_closure.csv, and be sure to write out variable names at first occurrence, and provide a bit more detail) For the temperate conifer biome, the average composite measure of aboveground biomass (B_{ag}) was less than the combined average value of woody biomass ($B_{ag-wood}$) and foliage biomass ($B_{foliage}$), partly due to the very high estimates of $B_{ag-wood}$. Within this biome, $B_{ag} < B_{ag-wood} + B_{foliage}$ and $B_{root} < B_{root-coarse} + B_{root-fine}$ because $B_{ag-wood}$ and $B_{root-coarse}$ were very high, with strongly disproportionate numbers of records from the high-biomass forests of the US Pacific Northwest (Figs. S18, S21).

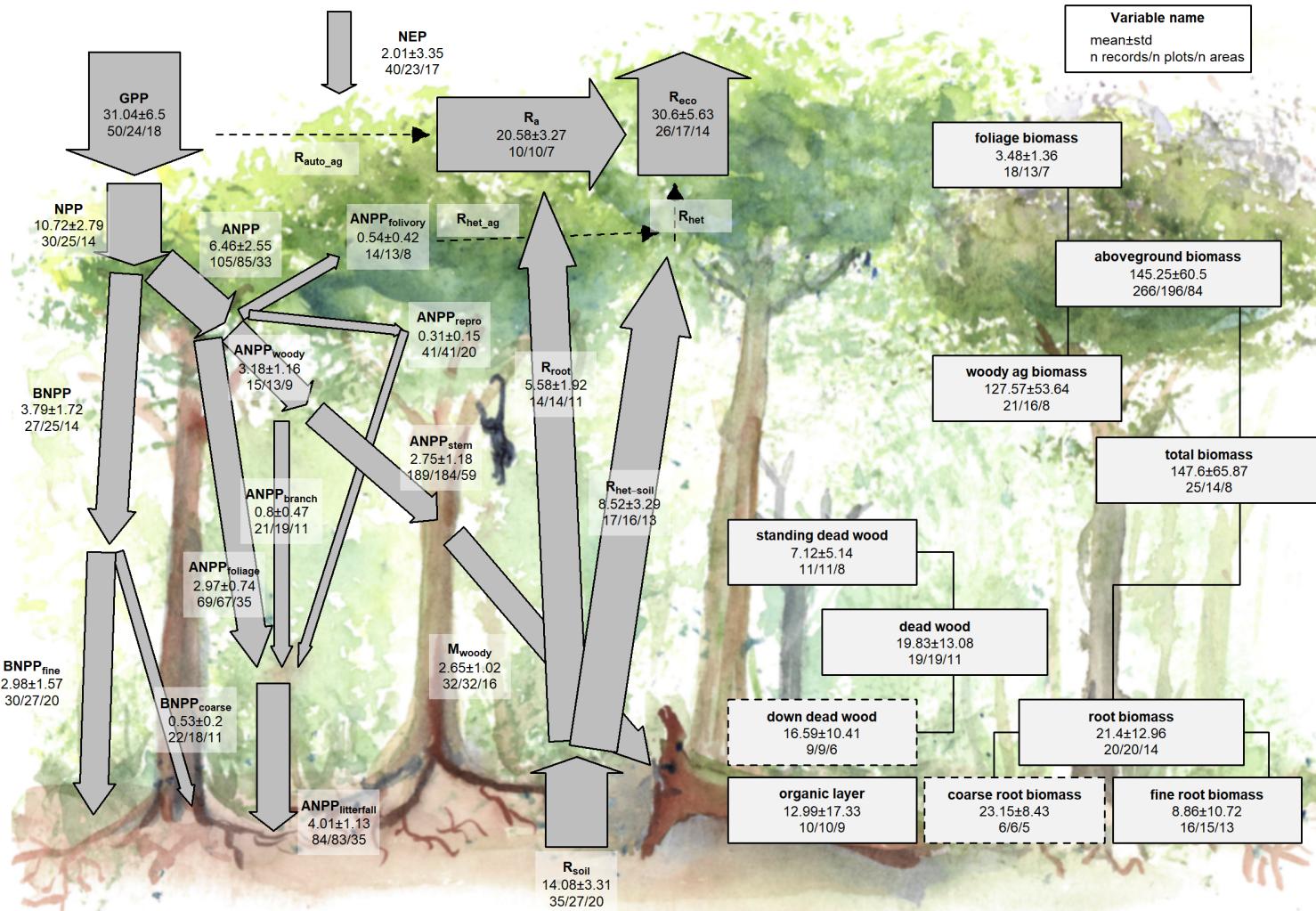


Figure 2 | C cycle diagram for mature tropical broadleaf forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux. Asterisk after variable name indicates lack of C cycle closure.

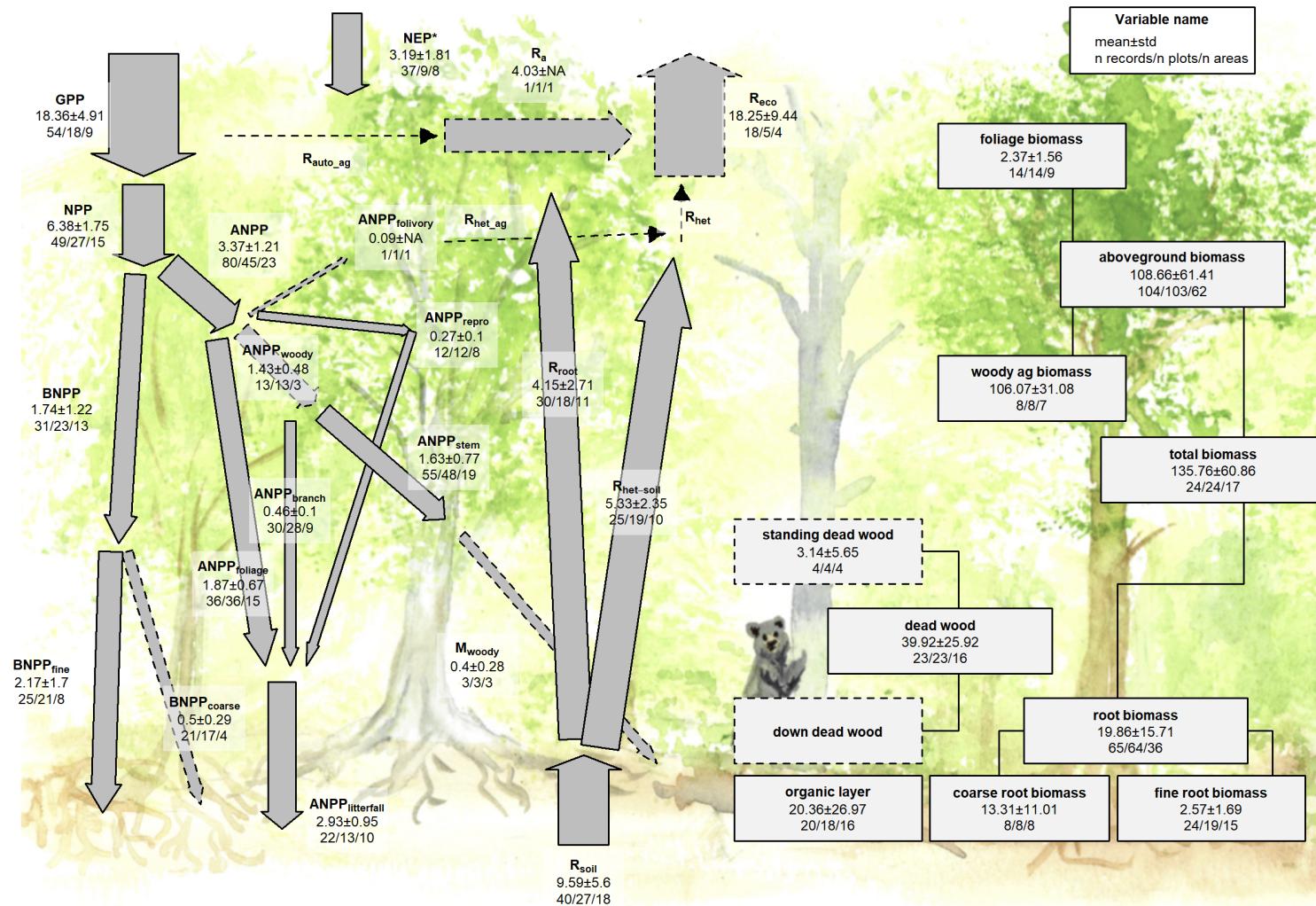


Figure 3 | C cycle diagram for mature temperate broadleaf forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux. Asterisk after variable name indicates lack of C cycle closure.

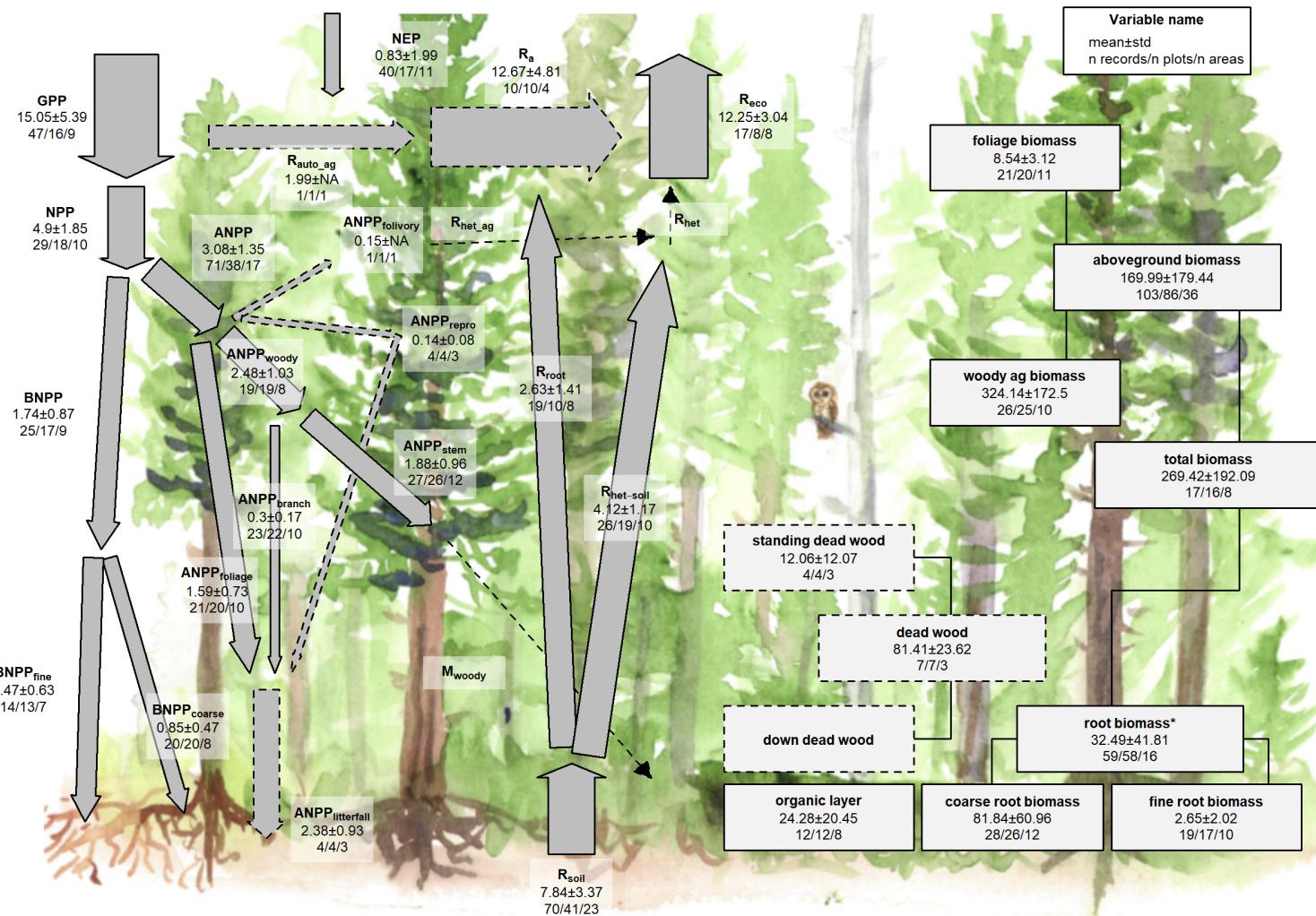


Figure 4 | C cycle diagram for mature temperate conifer forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux. Asterisk after variable name indicates lack of C cycle closure.

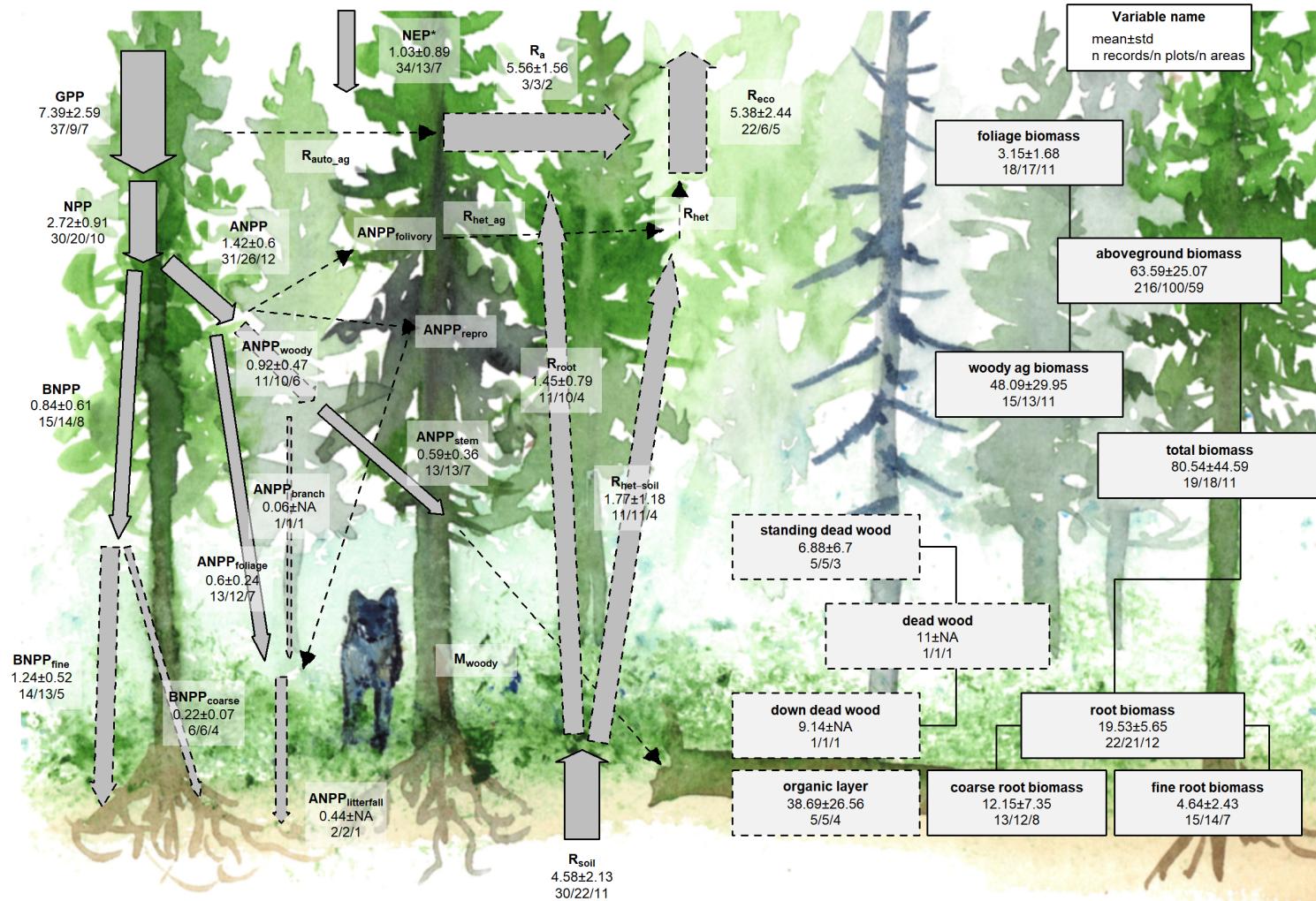


Figure 5 | C cycle diagram for mature boreal conifer forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux. Asterisk after variable name indicates lack of C cycle closure.

248 **check this with final data (based on Table 1):** There were sufficient data to assess mature forest
249 biome differences for **20** flux variables, and significant differences among biomes were detected for **14**
250 variables (Table 1). In all cases—including C fluxes into, within, and out of the ecosystem—C fluxes were
251 highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and lowest in boreal
252 forests (Table 1, Figs. 6, S1-S15). Differences between tropical and boreal forests were always significant,
253 with temperate forests intermediate and significantly different from one or both. Fluxes tended to be
254 numerically greater in temperate broadleaf than conifer forests, but the difference was never statistically
255 significant. This pattern held for the following variables: **** GPP , NPP , $ANPP$, $ANPP_{woody}$,**
256 **$ANPP_{stem}$, $ANPP_{branch}$, $ANPP_{foliage}$, $ANPP_{litterfall}$, M_{woody} , $BNPP$, R_{eco} , R_{soil} , and $R_{het-soil}$ **.** For
257 variables without significant differences among biomes, the same general trends applied.

258 The most notable exception to this pattern was NEP , with no significant differences across biomes but with
259 the largest average in temperate broadleaf forests, followed by temperate conifer, boreal, and tropical forests
260 (Figs. 5,S1). Another exception was for $BNPP_{root-coarse}$, where all records came from high-biomass forests
261 in the US Pacific Northwest, resulting in high values for the temperate conifer biome and no significant
262 differences across biomes (Fig. S10).

263 Thus, C cycling rates generally decreased from tropical to temperate to boreal forests, with the important
264 exception in the overall C balance (NEP).

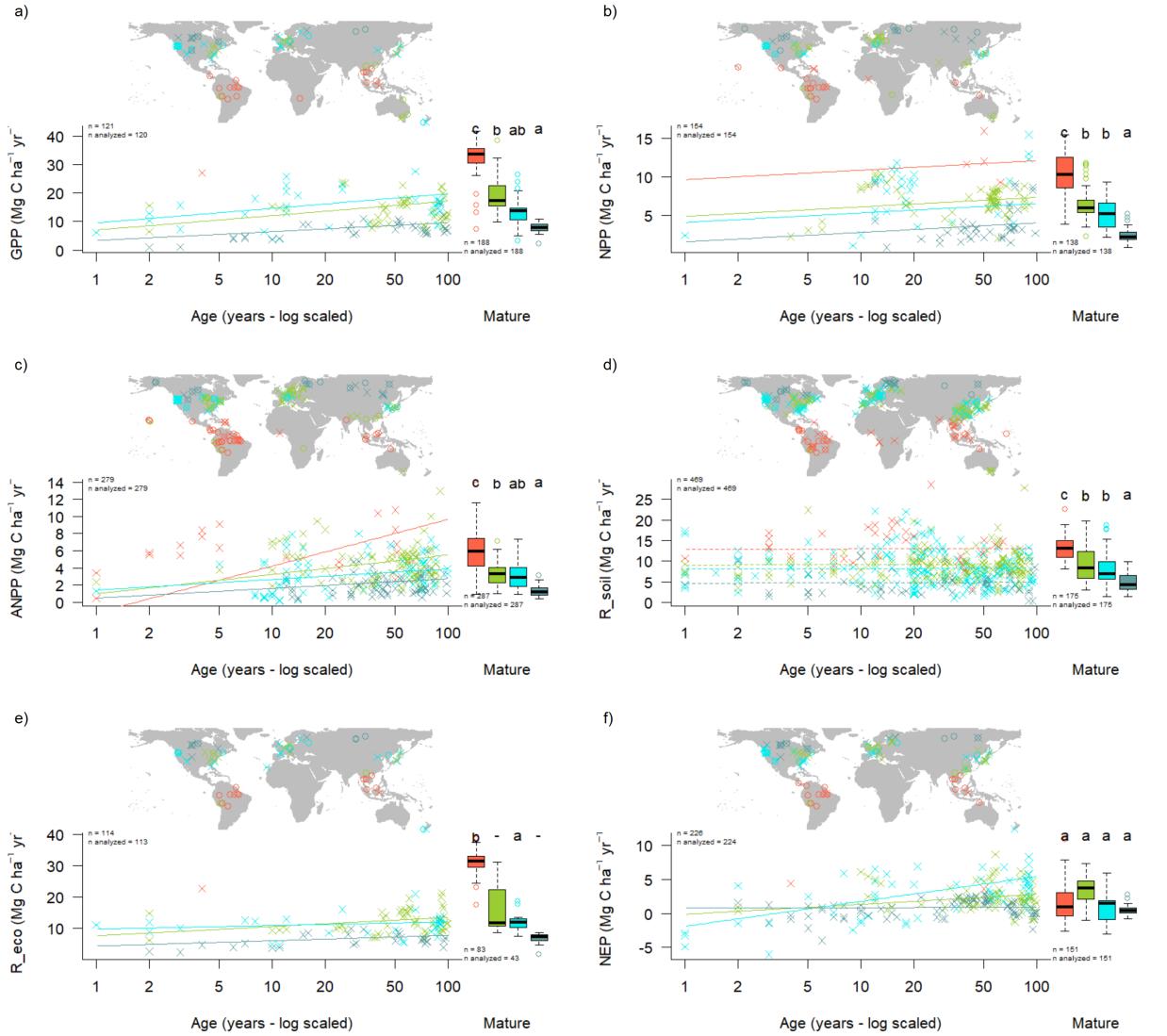


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of age and biome. The fitted line indicates the effect of age on flux (solid lines: significant at $p < 0.05$, dashed lines: non-significant), and non-parallel lines indicate a significant age \times biome interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each flux with sufficient data are given in the Supplement (Figs. S1-S15).

265 **check this with final data (based on Table 1):** There were sufficient data to assess mature forest
 266 biome differences for **9** stock variables, and significant differences among biomes were detected for **6** variables
 267 (B_{tot} , B_{ag} , $B_{ag-wood}$, $B_{foliage}$, $B_{root-coarse}$, DW_{tot} ; Table 1). C stocks had less consistent patterns across
 268 biomes (Figs. 7, S16-S26). In **four of the six** cases (B_{tot} , $B_{ag-wood}$, $B_{root-coarse}$, DW_{tot}), temperate
 269 conifer forests had significantly higher stocks than the other biomes, and boreal forests in the lowest, with
 270 tropical and temperate broadleaf forests in between. For B_{ag} , which had by far the highest sample size,
 271 tropical forests exceeded temperate conifer forests (but not significantly). For $B_{foliage}$, temperate broadleaf
 272 forests were lowest (again, not significantly). The high values for the temperate conifer biome were driven by

273 the very high-biomass forests of the US Pacific Northwest, which are disproportionately represented in the
 274 current version of ForC. Thus, biome differences should be interpreted more as driven more by geographic
 275 distribution of sampling than by true differences.

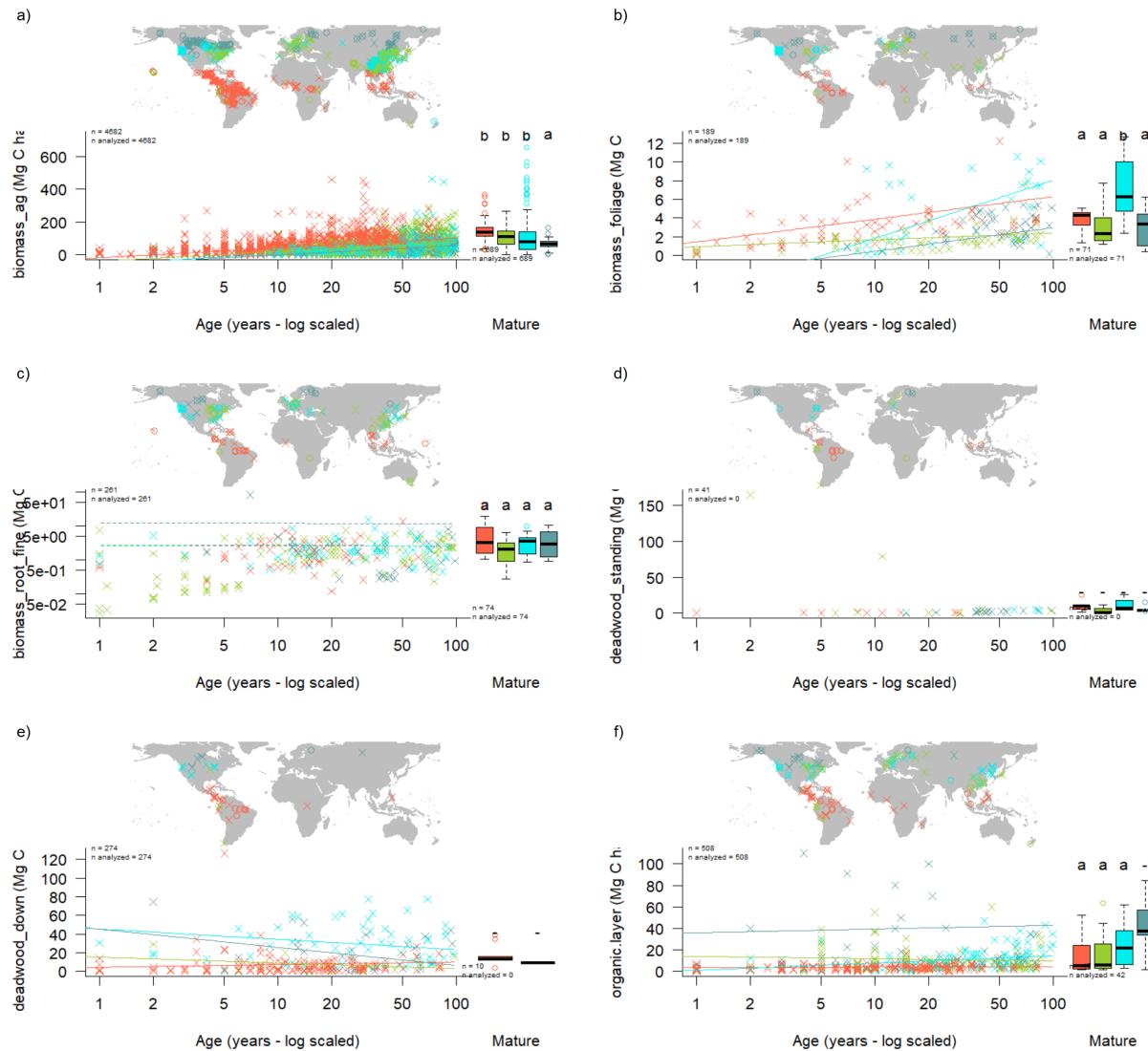


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources (x and o indicate young and mature stands, respectively). In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of age and biome. The fitted line indicates the effect of age on flux (solid lines: significant at $p < 0.05$, dashed lines: non-significant), and non-parallel lines indicate a significant age x biome interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each stock with sufficient data are given in the Supplement (Figs. S16-S26).

276 C cycling in young forests

277 Average C cycles for forests <100 years old are presented in Figures 8-11.
 278 Both C stocks and fluxes commonly increased significantly with stand age (Tables 1, S2, Figs. 6-11, S1-S26;
 279 detailed below).

280 *ForC* contained 14 flux variables with sufficient data for cross-biome analyses of age trends in regrowth
281 forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for all variables**). Of these, 9
282 increased significantly with age: *GPP*, *NPP*, *ANPP*, *ANPP_{foliage}*, *ANPP_{woody}*, *ANPP_{woody-stem}*,
283 *BNPP*, *BNPP_{root-fine}*, *R_{eco}*, and net C sequestration (*NEP*). The remaining five—*ANPP_{woody-branch}*,
284 *BNPP_{root-coarse}*, *R_{soil-het}*, and *R_{soil-het}*—displayed no significant relationship to stand age, although all
285 displayed a positive trend.

286 Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling
287 generally most rapid in the tropics and slowest in boreal forests.

288 The single exception was *ANPP_{stem}*, for which temperate broadleaf forests and temperate conifer forests of
289 age >~30 had slightly higher flux rates than tropical forests (*represented by a single chronosequence*).

290 Notably, the trend of tropical > temperate > boreal held for *NEP* in regrowth forests, in contrast to the
291 lack of biome differences in *NEP* for mature forests (Fig. 6).

292 There were only ## flux variables with sufficient data to test for biome x age interactions: *ANPP*,
293 *ANPP_{woody}*, *ANPP_{stem}*, *ANPP_{litterfall}*, and *BNPP* (Table S2). (**more could be added if age trends
294 become significant after outliers are resolved**) For three of these (*ANPP*, *ANPP_{litterfall}*, *BNPP*),
295 the increase in C flux with age was steepest increase in tropical forests, followed by temperate and then
296 boreal forests (Figs S#). Similarly, *ANPP_{woody}* displayed a steeper increase with age in temperate than
297 boreal forests (no tropical data for this variable). In contrast, for *ANPP_{stem}*, tropical and temperate
298 broadleaf forests had the highest flux rates at young ages, but were surpassed by temperate conifer forests
299 between ages 20 and 50 (Fig. S6).

300 (**this needs to be updated with latest data**) In terms of C stocks, 10 variables had sufficient data to
301 test for age trends. Six of these—*total biomass*, *aboveground biomass*, *aboveground woody biomass*, *foliage
302 biomass*, *root biomass*, and *coarse root biomass*—increased significantly with $\log_{10}[\text{stand.age}]$. The
303 remaining four displayed non-significant positive trends: *fine root biomass*, *total dead wood*, *standing dead
304 wood*, and *organic layer*. (*discuss rates of increase*)

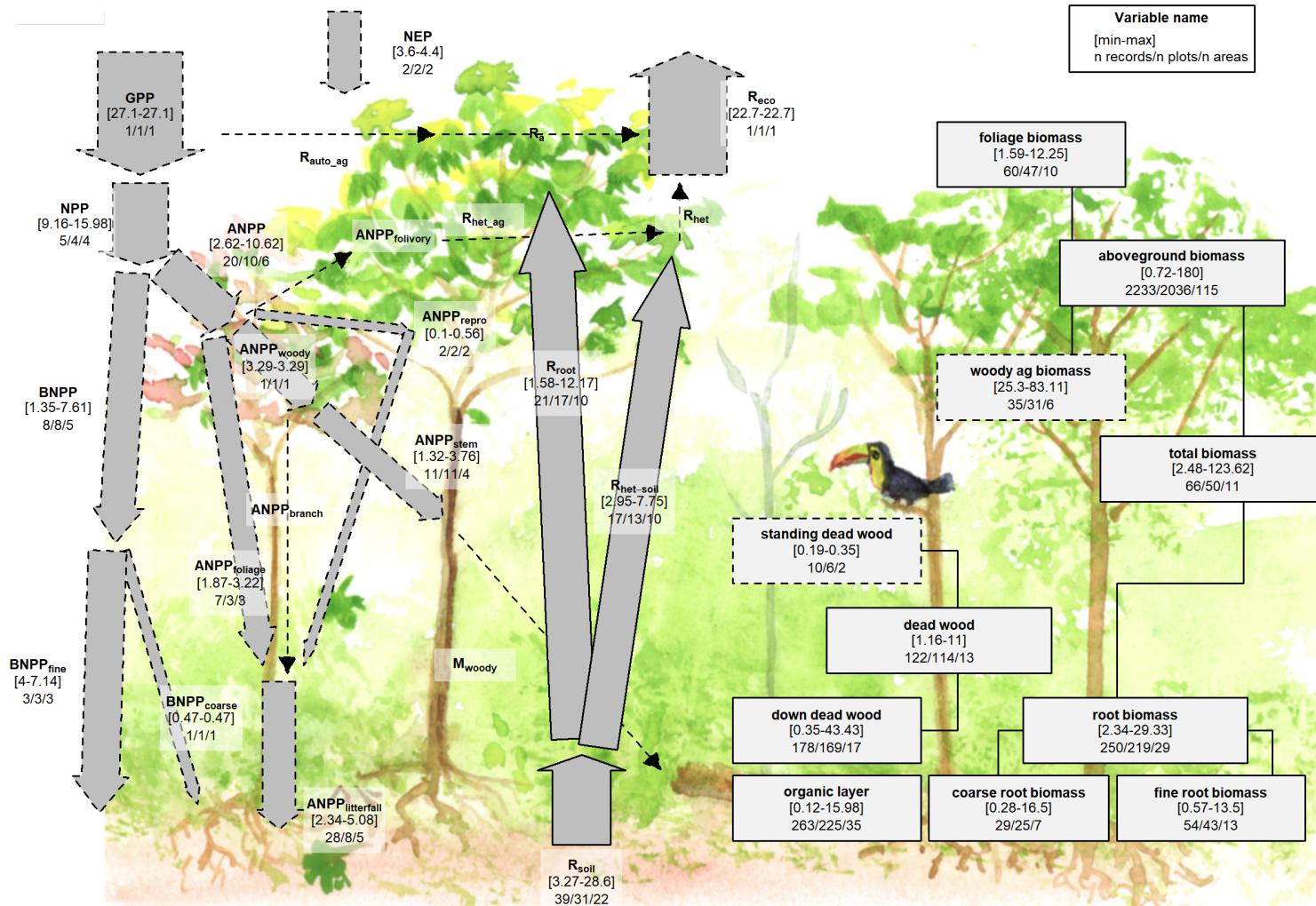


Figure 8 | C cycle diagram for young tropical broadleaf forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} (stocks). Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux.

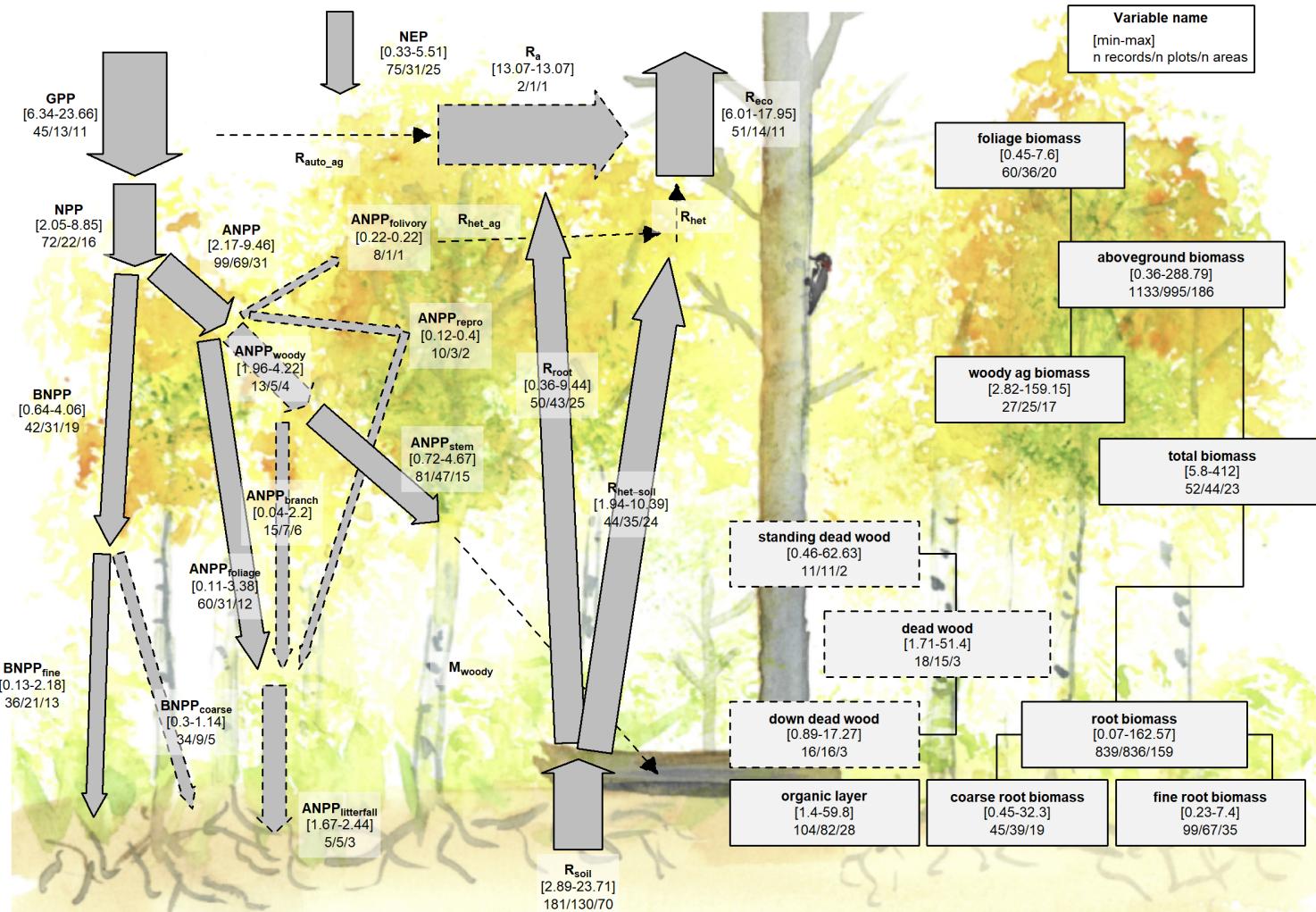


Figure 9 | C cycle diagram for young temperate broadleaf forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} (stocks). Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux.

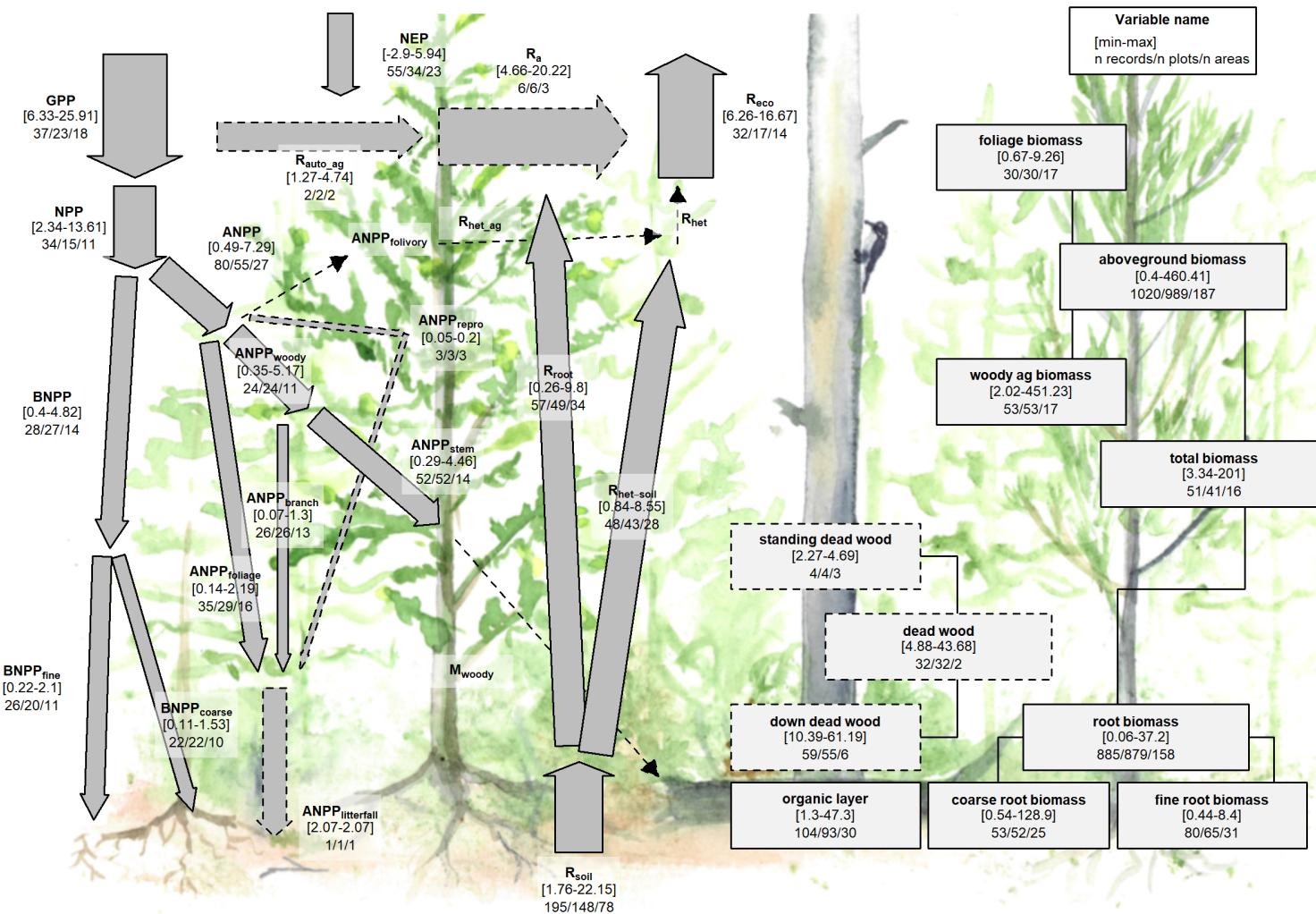


Figure 10 | C cycle diagram for young temperate conifer forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} (stocks). Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux.

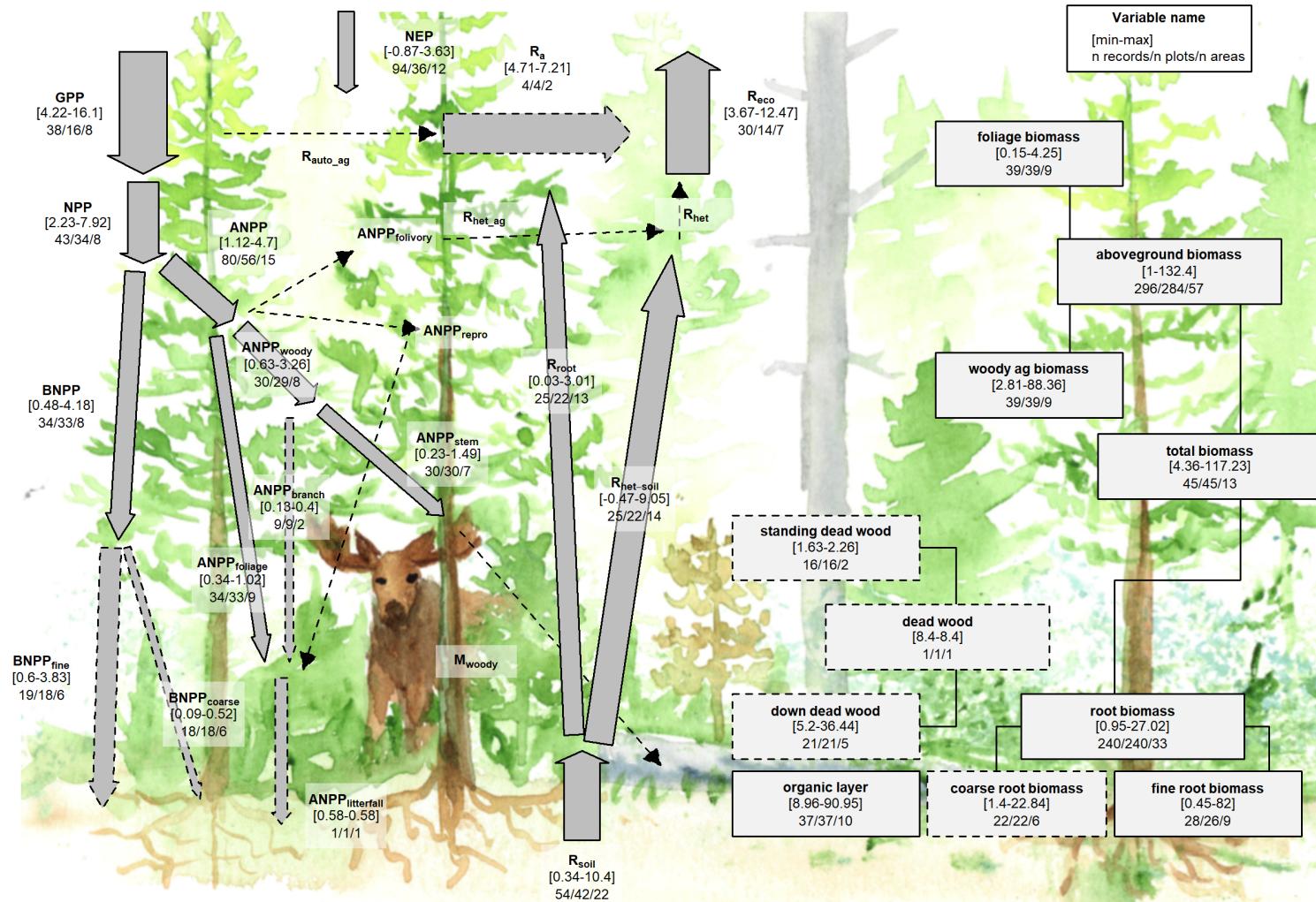


Figure 11 | C cycle diagram for young boreal conifer forests. Arrows indicate fluxes ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$); boxes indicate stocks (Mg C ha^{-1}), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} (stocks). Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow size is proportional to the square root of corresponding flux.

305 **Discussion**

306 *ForC* v3.0 brought together an unprecedented amount of data to yield an internally consistent picture of C
307 cycling in the world's major forest biomes. Carbon cycling rates generally increased from boreal to tropical
308 regions and with stand age. Specifically, the major C fluxes were highest in tropical forests, intermediate in
309 temperate (broadleaf or conifer) forests, and lowest in boreal forests – a pattern that generally held for
310 regrowth as well as mature forests (Figs. 6-7). In contrast to C fluxes, there was little directional variation in
311 mature forest C stocks across biomes (Figs. 2-5, 7). The majority of flux variables, together with most live
312 biomass pools, increased significantly with stand age (Figs. 6-11). Together, these results indicate that,
313 moving from cold to tropical climates and from young to old stands, there is a general acceleration of C
314 cycling, whereas C stocks and *NEP* of mature forests are correlated with a different set of factors.

315 **C variable coverage and budget closure**

316 *ForC* provides provides unprecedented coverage of most major variables. (*discuss how this improves upon*
317 *previous data compilations/ for which variables does ForC make the greatest difference (e.g., not AGB or*
318 *NEP/GPP/Reco, but by far the latest data compilation for dead wood, [variables]) (Noteable holes include:*
319 *fluxes: R_auto_ag, woody mortality, folivory/ herbivory and respiration of herbivores (and therefore total*
320 *R_het), ANPP_repro; also fluxes in tropical regrowth forests) For the C stocks considered here, the most*
321 *poorly covered is dead wood (none in E hemisphere!), despite a focused effort on this variable that has*
322 *resulted in ForC being by far the largest collection of these data.* Thus, overall, we're lacking coverage of
323 fluxes to herbivores and higher consumers, along with the woody mortality and dead wood. Geographically,
324 all variables poorly covered in Africa and Siberia.

325 **notes from Ben on the above par:** Pregitzer and Euskirchen 2004

326 <http://dx.doi.org/10.1111/j.1365-2486.2004.00866.x> “Aggregated biome-level estimates of NPP and NEP
327 were higher in intermediate-aged forests (e.g., 30–120 years), while older forests (e.g., 4120 years) were
328 generally less productive. The mean NEP in the youngest forests (0–10 years) was negative (source to the
329 atmosphere) in both boreal and temperate biomes... Forest age is a highly significant source of variability in
330 NEP at the biome scale”

331 Amiro et al. 2010 <http://dx.doi.org/10.1029/2010JG001390> Houghton et al. 2020

332 <https://doi.org/10.1111/gcb.15050>

333 Turnover: Pugh et al. 2020 <http://dx.doi.org/10.5194/bg-2019-491> Yu et al. 2019

334 <http://dx.doi.org/10.1073/pnas.1821387116>

335 Human footprint in global forests <http://dx.doi.org/10.1038/nature05847>

336 <http://dx.doi.org/10.1038/nature02619>

337 Mention consistency (or lack of) with e.g. GOLUM-CNP? <http://dx.doi.org/10.5194/gmd-11-3903-2018>

338 In terms of C stocks, there is a paucity of data on dead wood and organic layer (Pan et al. ?). These can be
339 significant. (**Note that we've given a lot of emphasis to dead wood (work by Abby, and also**
340 **Jenny), and as a result this work really advances knowledge of dead wood. We'll want to**
341 **highlight that here.) (give some stats/ cite figures).** *ForC* does not include soil carbon, which is covered
342 by other efforts (REFS). For fluxes, Fluxnet is the keeper of the best data on NEE, GPP, Reco (REFS), and
343 SRDB remains the authority on soil respiration (REFS). *ForC* includes recent data from both, but is not

344 continuously integrated. For C is the best source for most of the subsidiary fluxes: NPP, woody mortality... .
345 The C cycle budgets for mature forests (Figs. 2-5) generally “close”—that is, the sums of component variables
346 do not differ from the larger fluxes by more than one standard deviation. However, standard deviations are
347 often large, reflective of significant within-biome variation. This makes the standard for closure relatively
348 loose. *Lack of closure, in the few instances where it occurs, is probably more reflective of differences in the*
349 *representation of forest types (e.g., disproportionate representation of US Pacific NW for aboveground woody*
350 *biomass relative to AGB; Fig. 4) than of methodological accuracy.* Thus, overall, a high degree of closure
351 implies that *ForC* gives a consistent picture of C cycling within biomes. While these means are unlikely to
352 be accurate representations of C cycling within any particular forest, they provide a useful baseline for
353 comparison, always keeping in mind that sample means do not necessarily represent the true mean of the
354 entire biome.

355 **C cycling across biomes**

356 Our analysis reveals a general acceleration of carbon cycling from the tropics to the high latitudes. For
357 mature forests, this is consistent with a large body of previous work demonstrating that C fluxes generally
358 decline with latitude (e.g., Banbury Morgan *et al* n.d.). For regrowth forests, more rapid accumulation of
359 biomass at lower latitudes has been well-established (Anderson *et al* 2006, Cook-Patton *et al* 2020), whereas
360 this is the first study to compare age trends in deadwood and organic layer across biomes (but see
361 Cook-Patton *et al* 2020). For most C flux variables, this analysis is the first to examine flux trends in
362 regrowth forests across biomes (i.e., age x biome interaction). Data remain sparse, but for better-represented
363 variables, we often see faster acceleration of C cycling in the warmer climates. Further work will be required
364 to explore age x climate interactions, but our broad-brush overview indicates that C cycling of regrowth
365 forests is not only higher in the tropics, parallel to fluxes in mature forests (Banbury Morgan *et al* n.d.), but
366 also that it accelerates more rapidly with stand age in the tropics, consistent with more rapid biomass
367 accumulation.

368 In contrast to C fluxes and accumulation rates in regrowth forests, stocks... .

369 Thus, biome differences should be interpreted more as driven more by geographic distribution of sampling
370 than by true differences.

371 Higher NEP in temperate forests – implications? Invariant NEP in older forests? This could be built out a
372 bit; thinking of Luyssaert 2008 <http://dx.doi.org/10.1038/nature07276> and following papers arguing about
373 this.

374 (discuss NEP well- intuition for some would be that NEP is higher in tropics. Note biome differences for
375 young mut not mature forests, link to latitudinal differences in C sequestration potential (Anderson 2006,
376 Cook-Patton *et al* (2020))

377 **Age trends in C cycling**

378 (*Just some rough notes at this point*)

379 A relative dearth of data on C cycling in secondary forests, particularly in the tropics (Anderson-Teixeira et
380 al 2016), is problematic in that almost 2/3 of the world’s forests were secondary as of 2010 (FAO 2010),
381 implying an under-filled need to characterize age-related trends in forest C cycling.

382 Moreover, as disturbances increase (???, McDowell *et al* 2020), understanding the carbon dynamics of
383 regrowth forests will be increasingly important.

384 It's also important to understand secondary forest C sequestration to reduce uncertainty regarding the
385 potential for carbon uptake by regrowth forests (???, Cook-Patton *et al* 2020).

386 (discuss NEP well, including) NEP increases with log(age) to 100 -> strongest C sinks are established
387 secondary forests. (But presumably this exact number is an artifact; don't over-emphasize.)

388 **Relevance for climate change prediction and mitigation**

389 The future of forest C cycling (???) will shape trends in atmospheric CO₂ and the course of climate change.
390 For a human society seeking to understand and mitigate climate change, the data contained in *ForC* and
391 summarized here can help to meet two major challenges.

392 First, improved representation of forest C cycling in models is essential to improving predictions of the future
393 course of climate change. To ensure that models are giving the right answers for the right reasons, it is
394 important to benchmark against multiple components of the C cycle that are internally consistent with each
395 other. By making tens of thousands of records readily available in standardized format, *ForC* makes it
396 feasible for the modeling community to draw upon these data to benchmark models. Integration of *ForC*
397 with models is a goal (Fer *et al.*, in revision).

398 Second, *ForC* can serve as a pipeline through which forest science can inform forest-based climate change
399 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not
400 feasible for the individuals and organizations designing such efforts to sort through literature, often behind
401 paywalls, with data reported in varying units, terminology, etc. One goal for *ForC* is to serve as a pipeline
402 through which information can flow efficiently from forest researchers to decision-makers working to
403 implement forest conservation strategies at global, national, or landscape scales. This is already happening!
404 *ForC* has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;
405 Requena Suarez *et al* (2019); Rozendaal et al in prep], mapping C accumulation potential from natural forest
406 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*
407 2020).

408 ***ForC* can complement remote sensing to provide a comprehensive picture of global forest C
409 cycling.** (*here, discuss what is well-covered by remote sensing, where ForC is useful for calibrating remote
410 sensing, and what ForC can get that remote sensing can't.*) AGB is the largest stock, and most of the
411 emphasis is on this variable. Remote sensing, with calibration based on high-quality ground-based data
412 (Schepaschenko *et al* 2019, Chave *et al* 2019), is the best approach for mapping forest carbon (REFS).
413 However, it is limited in that it is not associated with stand age and disturbance history, except in recent
414 decades when satellite data can be used to detect forest loss, gain, and some of their dominant drivers
415 (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). *ForC* is therefore valuable in defining age-based
416 trajectories in biomass, as in Cook-Patton *et al* (2020).

417 *Remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP
418 (Bagdley *et al.* 2019, (Li and Xiao 2019)), aboveground biomass (B_{ag}) (REFS), woody mortality (i.e., B_{ag}
419 losses to mortality M_{woody}) (Clark *et al* 2004, Leitold *et al* 2018), and to some extent net ecosystem
420 exchange (NEP) (REFS).* Other variables, in particular respiration fluxes, cannot be remotely sensed

421 ((????)), and efforts such as the Global Carbon Project (**le quere REF**) and NASA CMS (**citation:**
422 https://carbon.nasa.gov/pdfs/CMS_Phase-1_Report_Final_optimized.pdf **but maybe**
423 **better to cite open literature, one of the papers listed at**
424 <https://cmsflux.jpl.nasa.gov/get-data/publication-data-sets>) typically compute them as residuals
425 only. (**Ben, it woudl be particularly helpful if you could flesh this out some more.**)

426 **Move to data availability statement, or methods?:** We recommend that use of *ForC* data go to the
427 original database, as opposed to using “off-the-shelf” values from this publication. This is because (1) *ForC*
428 is constantly being updated, (2) analyses should be designed to match the application, (3) age equations
429 presented here all fit a single functional form that is not necessarily the best possible for all the variables.

430 As climate change accelerates, understanding and managing the carbon dynamics of forests will be critical to
431 forecasting, mitigation, and adaptation. The C data in *ForC*, as summarized here, will be valuable to these
432 efforts.

433 Acknowledgements

434 All researchers whose data is included in *ForC* and this analysis. Ian McGregor for help with the database.
435 Thanks to Norbert Kunert and [Helene’s intern] for helpful input at an earlier phase. A Smithsonian
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437 Data availability statement

438 Materials required to fully reproduce these analyses, including data, R scripts, and image files, are archived
439 in Zenodo (DOI: TBD]. Data, scripts, and results presented here are also available through the open-access
440 *ForC* GitHub repository (<https://github.com/forc-db/ForC>), where many will be updated as the database
441 develops.

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