

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

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19 **Summary**

20 *Background.* The fate of Earth's climate is closely linked to forests, which strongly influence atmospheric  
21 carbon dioxide ( $\text{CO}_2$ ) and climate through their influential role in the global carbon (C) cycle. Synthetic  
22 understanding of global forest C cycles is needed to constrain model estimates of forest feedbacks to climate  
23 change and to more accurately quantify the influence of land use decisions on climate.

24 *Methods/Design.* Here, we draw from the Global Forest C Database, ForC, to provide a macroscopic  
25 overview of C cycling in the world's forests, giving special attention to stand age-related variation.  
26 Specifically, we draw upon ## records from ## geographic locations representing ## C cycle variables to  
27 characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate  
28 broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years)  
29 forests. For regrowth forests, we quantify age trends for all variables.

30 *Review Results/ Synthesis.* ForC v.XX yielded a fairly comprehensive picture of C cycling in the world's  
31 major forest biomes, with broad closure of C budgets. The rate of C cycling generally increased from boreal  
32 to tropical regions, whereas C stocks showed less directional variation. The majority of flux variables,  
33 together with most live biomass pools, increased significantly with stand age, *and the rate of increase again*  
34 *tended to increase from boreal to tropical regions.*

35 *Discussion.* This analysis yields a comprehensive and broadly consistent picture of C cycling across the  
36 world's forests. [Discussion section will interpret results, highlighting new and significant findings, and  
37 discuss implications. Tentative headings are "Stand level C cycling in forests globally", "Age trends in C  
38 cycling", and "Implications for climate change mitigation".]

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

40 **Background**

41 Forest ecosystems globally play a critical role in regulating atmospheric carbon dioxide ( $\text{CO}_2$ ), and thereby  
42 will shape the course of climate change (IPCC1.5). Their annual gross  $\text{CO}_2$  sequestration (gross primary  
43 productivity,  $GPP$ ) is estimated at  $>69 \text{ Gt C yr}^{-1}$  (???), or  $>7$  times average annual fossil fuel emissions  
44 from 2007-2016 ( $9.4 \pm 0.5 \text{ Gt C yr}^{-1}$ ; Le Quéré et al 2017) (**update**). While most of this enormous C flux is  
45 counterbalanced by  $\text{CO}_2$  releases to the atmosphere through ecosystem respiration ( $R_{eco}$ ) or fire, a small  
46 portion was retained in ecosystems over recent decades. The resulting  $\text{CO}_2$  sink averaged  $3.0 \pm 0.8 \text{ Gt C yr}^{-1}$   
47 from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update, give**  
48 **range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial biomass  
49 (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Globally, net deforestation (*i.e.*,  
50 gross deforestation - regrowth) has been a source of  $\text{CO}_2$  emissions, estimated at  $\sim 1.1 \text{ Gt C yr}^{-1}$  from  
51 YEAR-YEAR (Pan et al 2011), reducing the net forest sink to  $\sim 1.2\text{-}1.7 \text{ Gt C yr}^{-1}$  across Earth's forests (Le  
52 Quéré et al 2017, Schimel et al 2015) (**update, give range**). The future of this sink is dependent both  
53 upon forest responses to a broad suite of global change drivers and to future land use decisions, and will  
54 strongly influence the course of climate change. Regrowth forests in particular will play an important role  
55 (Pugh et al 2019), as these represent a large (~#%) and growing proportion of Earth's forests.  
56 Understanding, modeling, and managing forest-atmosphere  $\text{CO}_2$  exchange is thereby central to efforts to  
57 mitigate climate change [Grassi et al (2017); Griscom et al (2017); Cavaleri et al 2015].

Despite the centrality of forest C cycling in regulating atmospheric CO<sub>2</sub>, important uncertainties in climate models [(??); Krause *et al* (2018); REFS] and CO<sub>2</sub> accounting frameworks (Pan *et al* 2011) can be traced to lack of accessible, comprehensive data on how C cycling varies across forest types and in relation to stand history. These require large-scale databases with global coverage, which runs contrary to the nature in which forest C stocks and fluxes are measured and published. While remote sensing measurements are increasingly useful for global- or regional-scale estimates of a few critical variables [Li and Xiao (2019); **REFS for biomass, biomass change, net CO<sub>2</sub> flux**], measurement of most forest C stocks and fluxes require intensive on-the-ground data collection. Original studies typically cover only a small numbers of sites at a time, with rare exceptions spanning regions or continents [e.g., Lutz *et al* (2018); FLUXNET\_REF], typically coordinated through research networks such as ForestGEO (Anderson-Teixeira *et al* 2015) or FLUXNET (Baldocchi *et al* 2001). The result of decades of research on forest C cycling is that tens of thousands of records have been distributed across literally thousands of scientific articles –often behind paywalls– along with variation in data formats, units, measurement methods, *etc.*. In this format, the data are effectively inaccessible for many global-scale analyses, including those attempting to benchmark model performance with global data (Clark *et al* 2017, Luo *et al* 2012), quantify the role of forests in the global C cycle (e.g., Pan *et al* 2011), or use book-keeping methods to quantify actual or scenario-based exchanges of CO<sub>2</sub> between forests and the atmosphere (REFS).

To address the need for global-scale analyses of forest C cycling, we recently developed an open-access Global Forest Carbon database, ForC (Anderson-Teixeira *et al* (2016), Anderson-Teixeira *et al* (2018)). ForC contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables) based on ground-based measurements, along with associated data required for interpretation (e.g., stand history, measurement methods). These data have been amalgamated from original peer-reviewed publications, either directly or via intermediary data compilations. Since its most recent publication (Anderson-Teixeira *et al* 2018), ForC has been integrated with two large databases: the Global Soil Respiration Database (SRDB; Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020), both of which have also synthesized published forest C data. Following these additions, ForC currently contains # (~49,000!) records from # plots and # distinct geographic areas representing all forested biogeographic and climate zones.

Here, we synthesize ForC data (Fig. 1) to provide a macroscopic overview of stand-level carbon cycling of the world's major forest biomes and how it varies with stand age. Our primary goal is to provide a data-based summary of our current state of knowledge on broad trends in forest C cycling. We address three broad questions:

1. To what extent can we fully represent, and “close”, C budgets for each of the world's major forest biomes (*i.e.*, tropical, temperate broadleaf and deciduous, boreal) based on the current ForC data?
2. How do C cycling vary across the world's major forest biomes?
3. How does C cycling vary with stand age (in interaction with biome)?

While components of these questions have been previously addressed (Luyssaert *et al* 2007, Anderson-Teixeira *et al* 2016, Cook-Patton *et al* 2020, Banbury Morgan *et al* n.d.), our analysis represents by far the most comprehensive analysis of C cycling in global forests, and thereby stands to serve as a foundation for improved understanding of global forest C cycling.

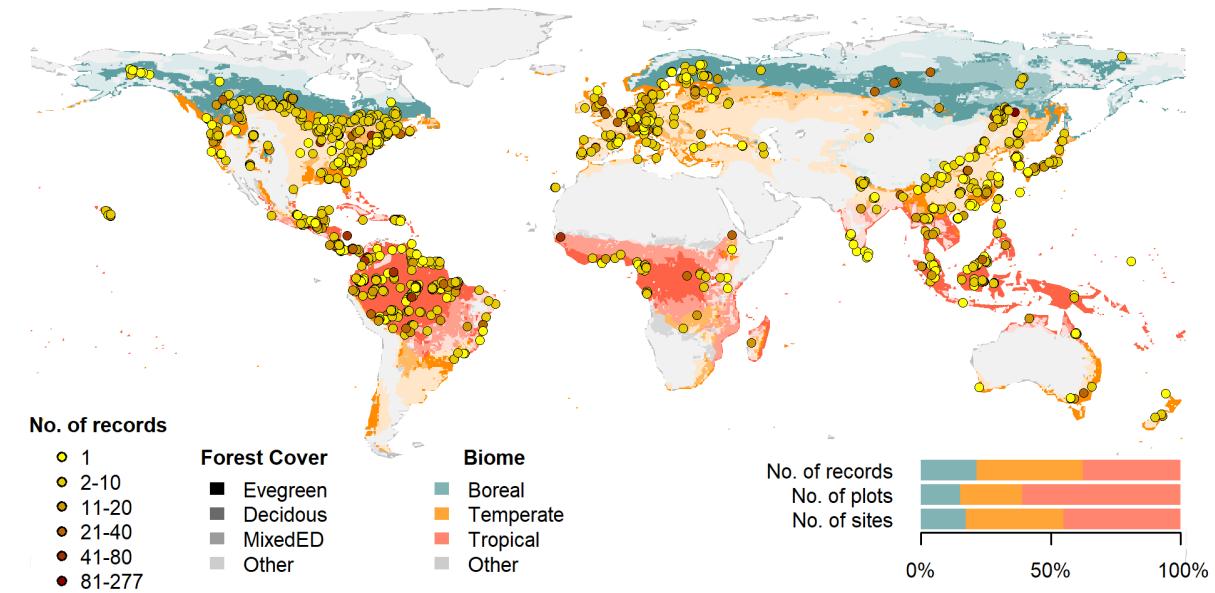


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

## 98 Methods/ Design

99 This review synthesizes data from the ForC database (Fig. 1; <https://github.com/forc-db/ForC>;

100 Anderson-Teixeira *et al* 2016, pp @anderson-teixeira\_forc\_2018). ForC amalgamates numerous intermediary

101 data sets (*e.g.*, REFS) and original studies. Original publications were referenced to check values and obtain

102 information not contained in intermediary data sets, although this process has not been completed for all

103 records. The database was developed with goals of understanding how C cycling in forests varies across broad

104 geographic scales and as a function of stand age. As such, there has been a focus on incorporating data from

105 regrowth forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age

106 data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention was given to

107 developing the database for tropical forests (Anderson-Teixeira *et al* 2016), yet these represented only

108 approximately one-third of records in ForC v.2.0 (Anderson-Teixeira *et al* 2018). Since publication of ForC

109 v.2.0, we added the following data to ForC: the Global Database of Soil Respiration Database (SRDB v.##;

110 Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment database (GROA

111 v1.0; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020), and data from several publications [*e.g.*, Taylor

112 *et al* (2017), Lutz *et al* (2018), Johnson *et al* (2018); detailed list at [https://github.com/forc-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)]. We note that there

114 remains a significant amount of relevant data that is not yet included in ForC, particularly biomass data

115 from national forest inventories (*e.g.*; REFS). The database version used for this analysis has been tagged as

116 a new release on Github (XX) and assigned a DOI through Zenodo (DOI: TBD).

117 For this analysis, we grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf,

temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones (Fig. 1) were defined based on site geographic coordinates according to Köppen-Geiger zones (Rubel and Kottek 2010). Tropical climates were defined to include all equatorial (A) zones, temperate climates were defined to include all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and boreal climates were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones were excluded from the analysis. Leaf type (broadleaf / needleleaf) was defined based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYNMAP; ???). Forests were classified as “young” (< 100 years) or “mature” ( $\geq$  100 years or classified as “mature”, “old growth”, “intact”, or “undisturbed” in original publication). Records for which stand age was unknown (#% of total database) were excluded from the analysis. *These groupings were defined based on ForC v.2.0 (Anderson-Teixeira et al 2018), for which they covered 91% of the primary variable records for forests of known age, or 86% of total records. The most well-represented forest types excluded were boreal broadleaf and boreal and temperate mixed broadleaf-needleleaf, each with <400 records total for stands of any age.*

We drew upon records for # annual flux and # C stock variables (Table 1). For this analysis, we combined some of ForC’s specific variables (*e.g.*, multiple variables for net primary productivity including various components) into more broadly defined variables (Table 1, this table)). Although ForC contains information that may be used to standardize or control for methodological differences (*e.g.*, area sampled, min stem diameter sampled, allometric equations applied; Anderson-Teixeira *et al* 2018), for this analysis we included all relevant data in ForC. Throughout ForC, for all measurements drawing from tree census data (*e.g.*, biomass, productivity), the minimum stem diameter sampled was  $\leq$  10cm. All records were measured directly or derived from field measurements (as opposed to modeled).

Analyses drew from ForC-simplified ([https://github.com/forc-db/ForC/blob/master/ForC\\_simplified](https://github.com/forc-db/ForC/blob/master/ForC_simplified)), which is a rearrangement of ForC intended to facilitate analyses. In generating ForC-simplified, all measurements originally expressed in units of dry organic matter (*OM*) were converted to units of C using the IPCC default of  $C = 0.47 * OM$  (IPCC 2006). Duplicate or otherwise conflicting records were reconciled as described in APPENDIX A. Records were filtered to remove plots that had undergone significant anthropogenic management or major disturbance since the most recent stand establishment (*i.e.*, that reflected by stand.age). Specifically, we removed all plots flagged as managed in ForC-simplified (managed field). This included plots with any record of managements manipulating CO<sub>2</sub>, temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”.

Plots flagged as disturbed in ForC-simplified included stands that had undergone anthropogenic thinning or partial harvest (“Cut” or “Harvest” codes) unless this was very minor (percent.mortality= “minor”). We retained sites that were grazed or had undergone low severity natural disturbances (<10% mortality) including droughts, major storms, fires, and floods. We also removed all plots for which no stand history information had been retrieved.

Data were analyzed to produce basic summaries of C cycle patterns across biomes and stand ages following an approach similar to that of Anderson-Teixeira *et al* (2016). For mature forests, to obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot, weighting flux measurements according to the length of measurement periods (*i.e.*, end.date - start.date). Values were then averaged across plots clustered within 25 km of one another (geographic.area field of SITES table, sensu

160 Anderson-Teixeira et al 2018), weighting by area.sampled (MEASUREMENTS table) or plot.area (PLOTS  
161 table) if available for all records. This step was taken to avoid pseudo-replication and to combine any records  
162 from sites with more than one name in ForC. Finally, for figures 6 and 7, the original values were analyzed  
163 via a linear mixed effects model ('lmer' function in 'lme4' R package) with biome as fixed effect and plot  
164 nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we  
165 looked at a Tukey's pairwise comparison to see which biomes were significantly different from one another.  
166 There were enough data to run this analysis for all focal variables but **biomass\_ag\_understory**,  
167 **BNPP\_root.turnover\_fine**, **deadwood\_down**, **total.ecosystem\_2**.  
168 For young (<100yrs) forest types, we employed a mixed effects model with biome and log10[stand.age] as  
169 fixed effects and plot nested within geographic.area as a random effect on the intercept. When the effect of  
170 stand.age was significant at  $p \leq 0.05$  and when each biome had records for stands of at least 10 different  
171 ages, a biome - stand.age interaction was included in the model. In the C cycle schematics for young forests,  
172 we report equations based on these models. In cases where there was no significant effect of stand.age,  
173 records were averaged as for mature stands.  
174 All database manipulation, analyses, and figure production were fully automated in R (version, citation).  
175 Materials required to fully reproduce these analyses, including data, R scripts, and image files, are archived  
176 in Zenodo (DOI: TBD]. Data, scripts, and results presented here are also available through the open-access  
177 ForC GitHub repository (<https://github.com/forc-db/ForC>), where many will be updated as the database  
178 develops.

## 179 Review Results/ Synthesis

### 180 Data Coverage

181 Of the # records in ForC v.#, # met the criteria for inclusion in this study (Fig. 1). (*Give some stats on*  
182 *coverage by age and biome*)

### 183 C cycling in mature forests

184 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq 100$   
185 years old and with no known major disturbance or significant anthropogenic management are presented in  
186 Figures 2-5, and statistics for each biome type are also summarized at: [GitHub URL]. Of the 23 flux and 11  
187 stock variables mapped in these diagrams, ForC contained estimates from  $\geq 7$  distinct geographic areas for  
188 # fluxes and # stocks in tropical broadleaf forests, # fluxes and # stocks in temperate broadleaf forests, #  
189 fluxes and # stocks in temperate conifer forests, and fluxes and # stocks in boreal forests. For variables with  
190 records from  $\geq 7$  distinct geographic areas, these ensemble C budgets were generally consistent. That is,  
191 component fluxes and stocks summed to within 1 std of more inclusive fluxes in all but one instance (in  
192 temperate conifer forests, *abovegroundwoodybiomass + foliagebiomass > abovegroundbiomass + 1std*; Fig.  
193 5). update this: <https://github.com/forc-db/ERL-review/issues/16>

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		
<b>Annual fluxes</b>						
<i>NEP</i>	net ecosystem production or net ecosystem exchange (+ indicates C sink)	n	n	n	n.s.	-
<i>GPP</i>	gross primary production ( $NPP + R_{auto}$ or $R_{eco} - NEP$ )	n	n	n	Tr > TeB = TeN > B	+
<i>NPP</i>	net primary production ( $ANPP + BNPP$ )	n	n	n	Tr > TeB = TeN > B	+
<i>ANPP</i>	aboveground <i>NPP</i>	n	n	n	Tr > TeB $\geq$ TeN $\geq$ B	+, xB
<i>ANPP<sub>woody</sub></i>	woody production ( $ANPP_{stem} + ANPP_{branch}$ )	n	n	n		
<i>ANPP<sub>stem</sub></i>	woody stem production	n	n	n		
<i>ANPP<sub>branch</sub></i>	branch turnover	n	n	n		
<i>ANPP<sub>foliage</sub></i>	foliage production, typically estimated as annual leaf litterfall	n	n	n		
<i>ANPP<sub>litterfall</sub></i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	n	n	n		
<i>ANPP<sub>repro</sub></i>	production of reproductive structures (flowers, fruits, seeds)	n	n	n		
<i>ANPP<sub>folivory</sub></i>	foliar biomass consumed by folivores	n	n	n		
<i>M<sub>woody</sub></i>	woody mortality—i.e., $B_{ag}$ of trees that die	n	n	n		
<i>BNPP</i>	belowground NPP ( $BNPP_{coarse} + BNPP_{fine}$ )	n	n	n		
<i>BNPP<sub>coarse</sub></i>	coarse root production	n	n	n		
<i>BNPP<sub>fine</sub></i>	fine root production	n	n	n		
<i>R<sub>eco</sub></i>	ecosystem respiration ( $R_{auto} + R_{het}$ )	n	n	n		
<i>R<sub>auto</sub></i>	autotrophic respiration ( $R_{auto-ag} + R_{root}$ )	n	n	n		
<i>R<sub>auto-ag</sub></i>	aboveground autotrophic respiration (i.e., leaves and stems)	n	n	n		
<i>R<sub>root</sub></i>	root respiration	n	n	n		
<i>R<sub>soil</sub></i>	soil respiration ( $R_{het-soil} + R_{root}$ )	n	n	n		
<i>R<sub>het-soil</sub></i>	soil heterotrophic respiration	n	n	n		
<i>R<sub>het-ag</sub></i>	aboveground heterotrophic respiration	0	0	0		
<i>R<sub>het</sub></i>	heterotrophic respiration ( $R_{het-ag} + R_{het-soil}$ )	0	0	0		
<b>Stocks</b>						
<i>B<sub>tot</sub></i>	total live biomass ( $B_{ag} + B_{root}$ )	n	n	n		
<i>B<sub>ag</sub></i>	aboveground live biomass ( $B_{ag-wood} + B_{foliage}$ )	n	n	n		
<i>B<sub>ag-wood</sub></i>	woody component of aboveground biomass	n	n	n		
<i>B<sub>foliage</sub></i>	foliage biomass	n	n	n		
<i>B<sub>root</sub></i>	total root biomass ( $B_{root-coarse} + B_{root-fine}$ )	n	n	n		
<i>B<sub>root-coarse</sub></i>	coarse root biomass	n	n	n		
<i>B<sub>root-fine</sub></i>	fine root biomass	n	n	n		
<i>DW<sub>tot</sub></i>	deadwood ( $DW_{standing} + DW_{down}$ )	n	n	n		
<i>DW<sub>standing</sub></i>	standing dead wood	n	n	n		
<i>DW<sub>down</sub></i>	fallen dead wood, including coarse and sometimes fine woody debris	n	n	n		
<i>OL</i>	organic layer / litter/ forest floor	n	n	n		

\* 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

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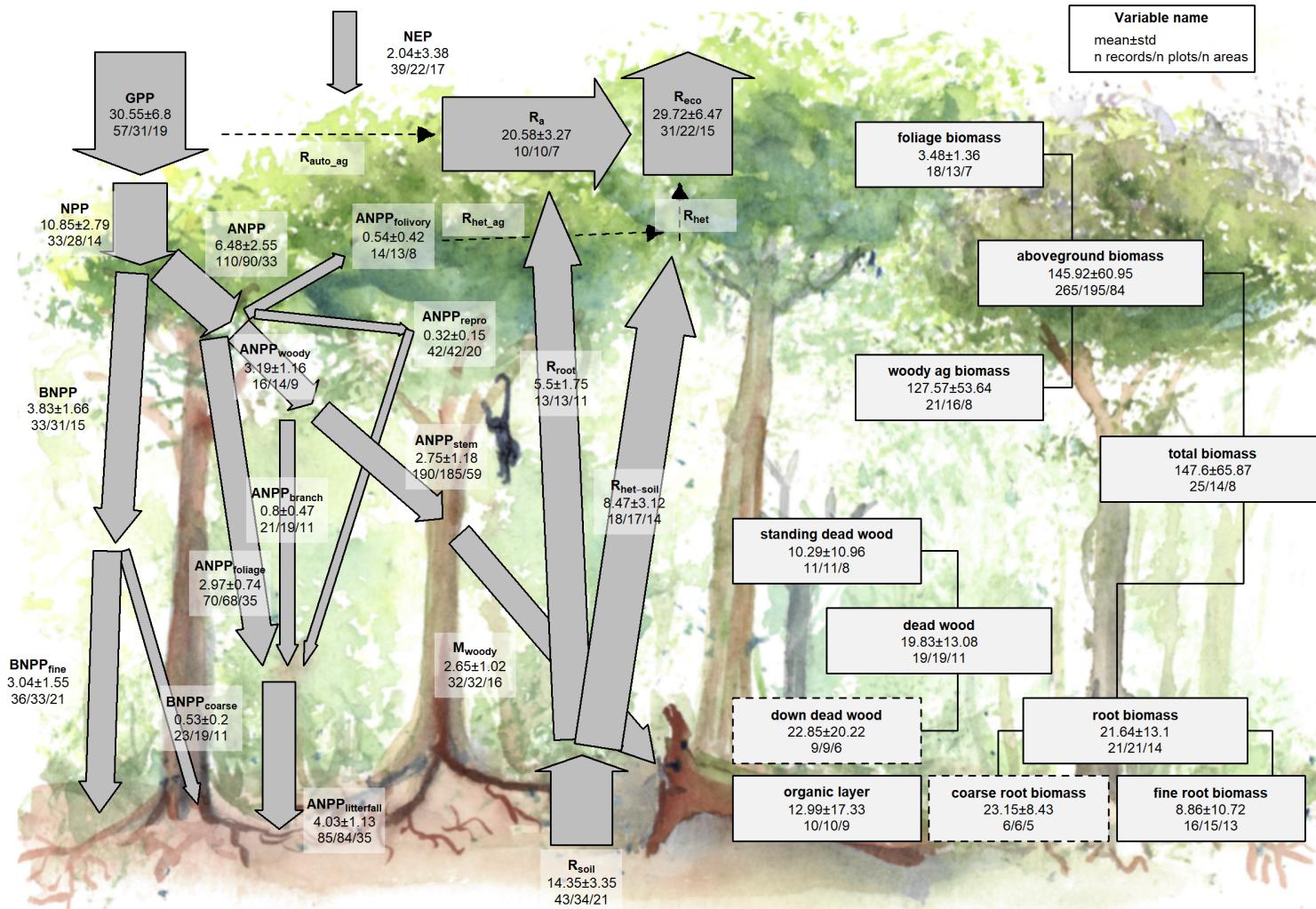


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. Arrows are scaled as the \*\*square root of flux divided by 5\*\*.

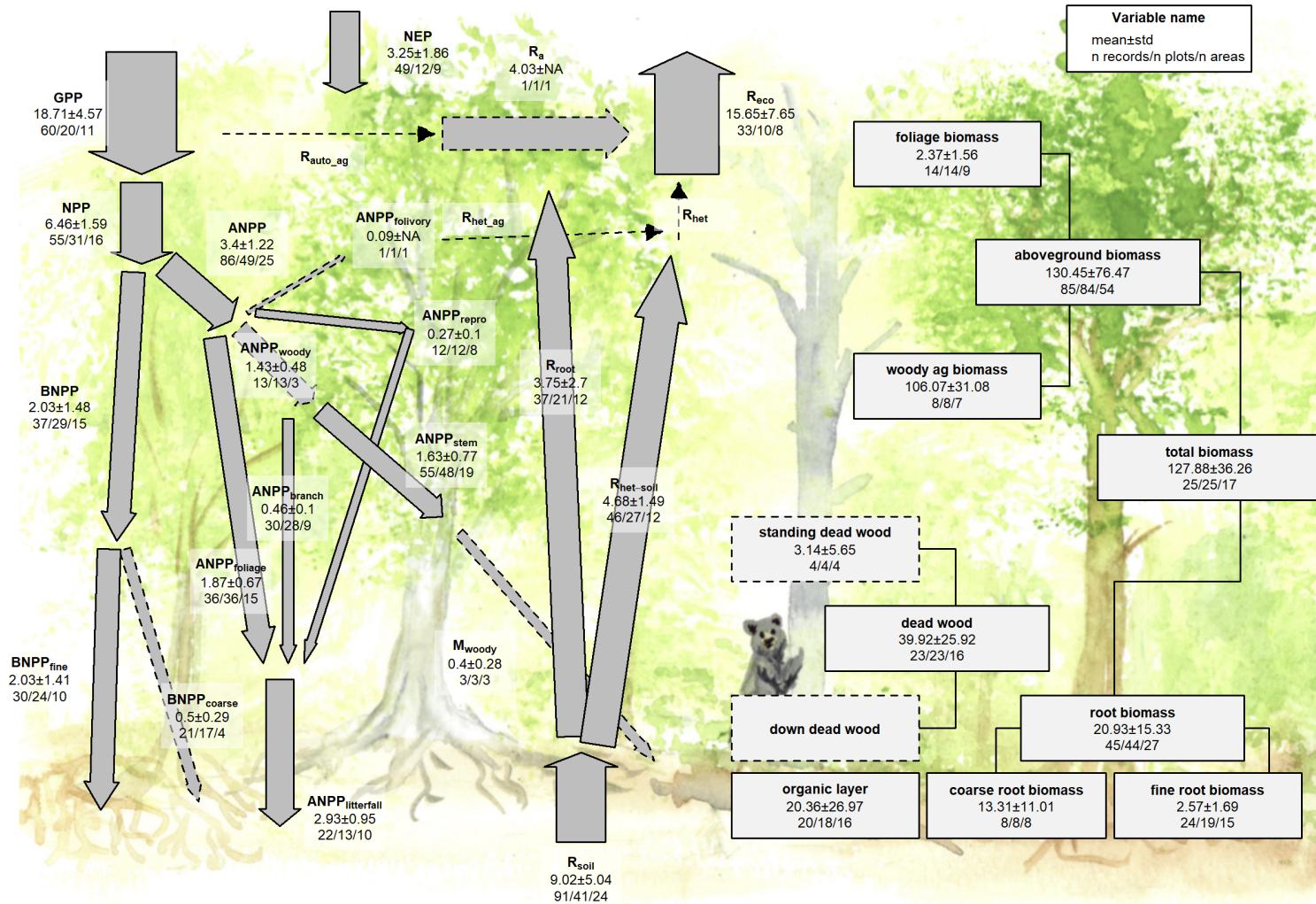


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

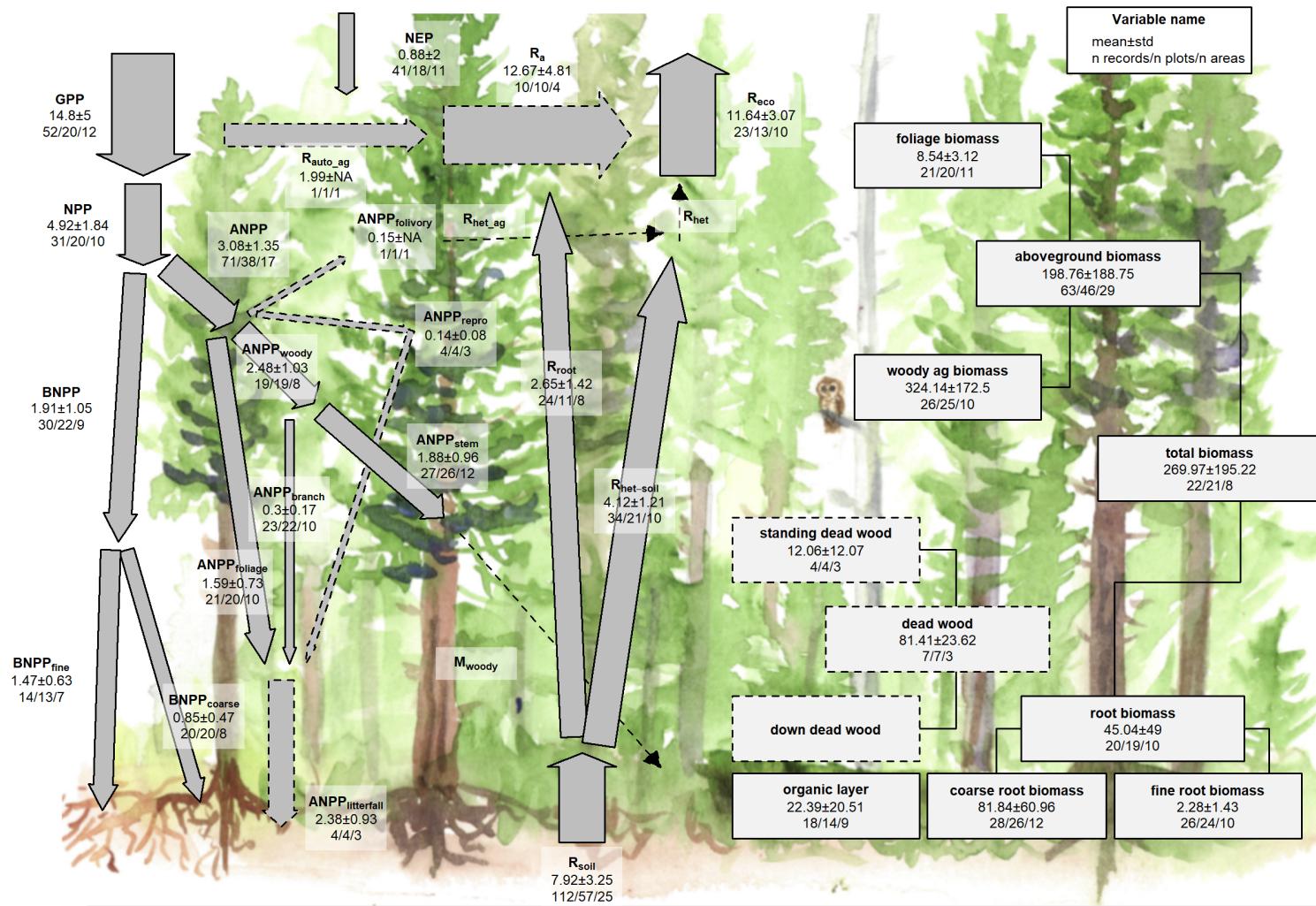


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

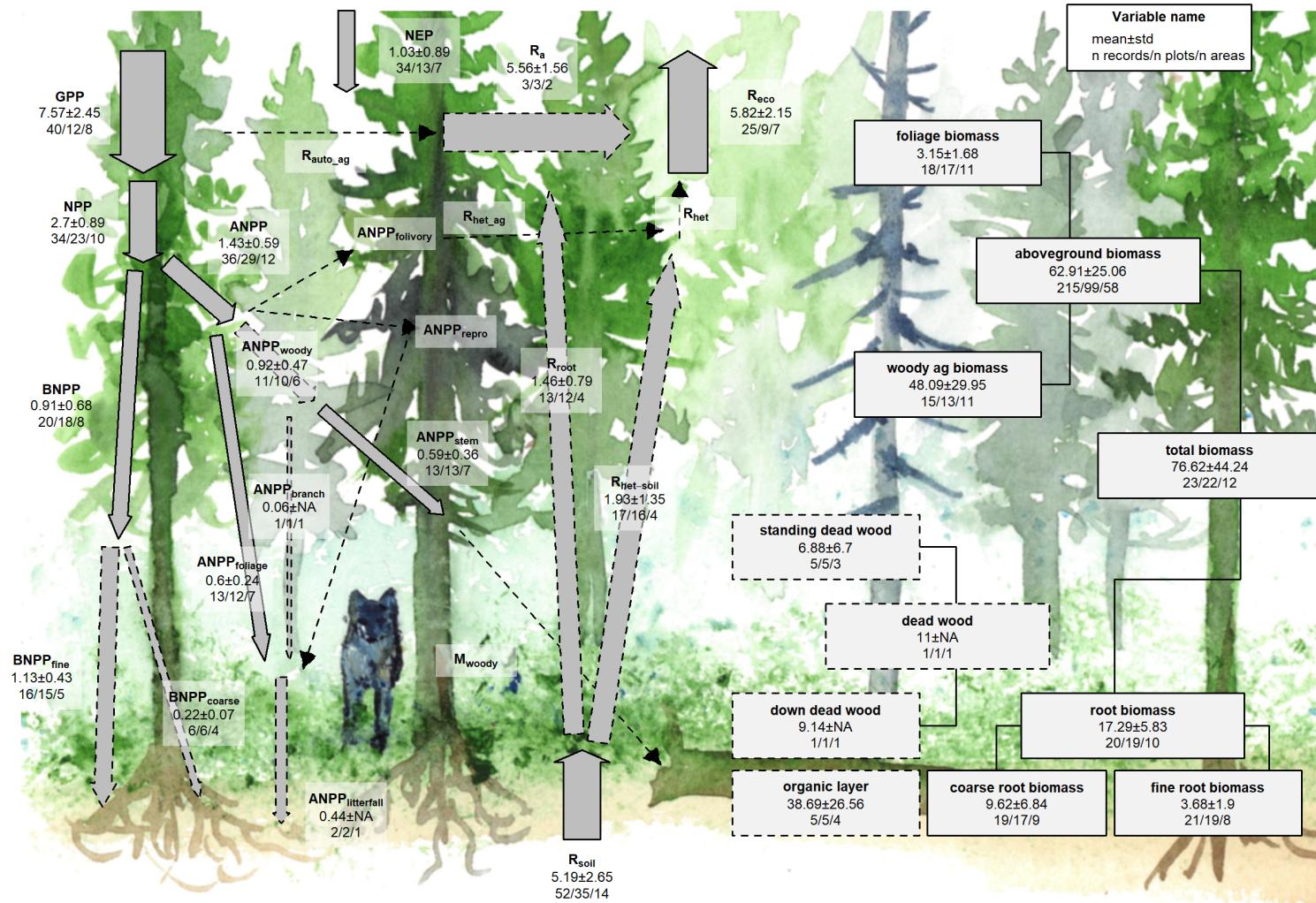


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

194 (check paragraph with latest data) The largest C fluxes—including *GPP*, *NPP*, *ANPP*, *BNPP*,  
195  $R_{soil,et}$ ,  $R_{soil}$ ,  $R_{eco}$ , — were highest in tropical forests, intermediate in temperate (broadleaf or conifer)  
196 forests, and lowest in boreal forests (ForC\_variable\_averages\_per\_Biome) (Fig. 6). The same held true for  
197 some of the subsidiary fluxes: *ANPP\_foliage*, *ANPP\_wood*, [OTHERS?]. Other subsidiary  
198 fluxes—including *NPP\_wood*, *ANPP\_repro*, *ANPP\_stem*, *ANPP\_branch*, *woody.mortality*, *BNPP\_coarse*,  
199 *BNPP\_fine*, [OTHERS?]-deviated from this pattern and/or lacked data for some biomes. Net ecosystem  
200 production (*NEP*) did not follow this pattern, with no significant differences across biomes but the largest  
201 average in temperate broadleaf forests, followed by temperate conifer, boreal, and tropical forests. Thus, C  
202 cycling rates generally decreased from tropical to temperate to boreal forests, but with less apparent trends  
203 for some of the subsidiary fluxes and an important exception in the overall C balance (*NEP*).

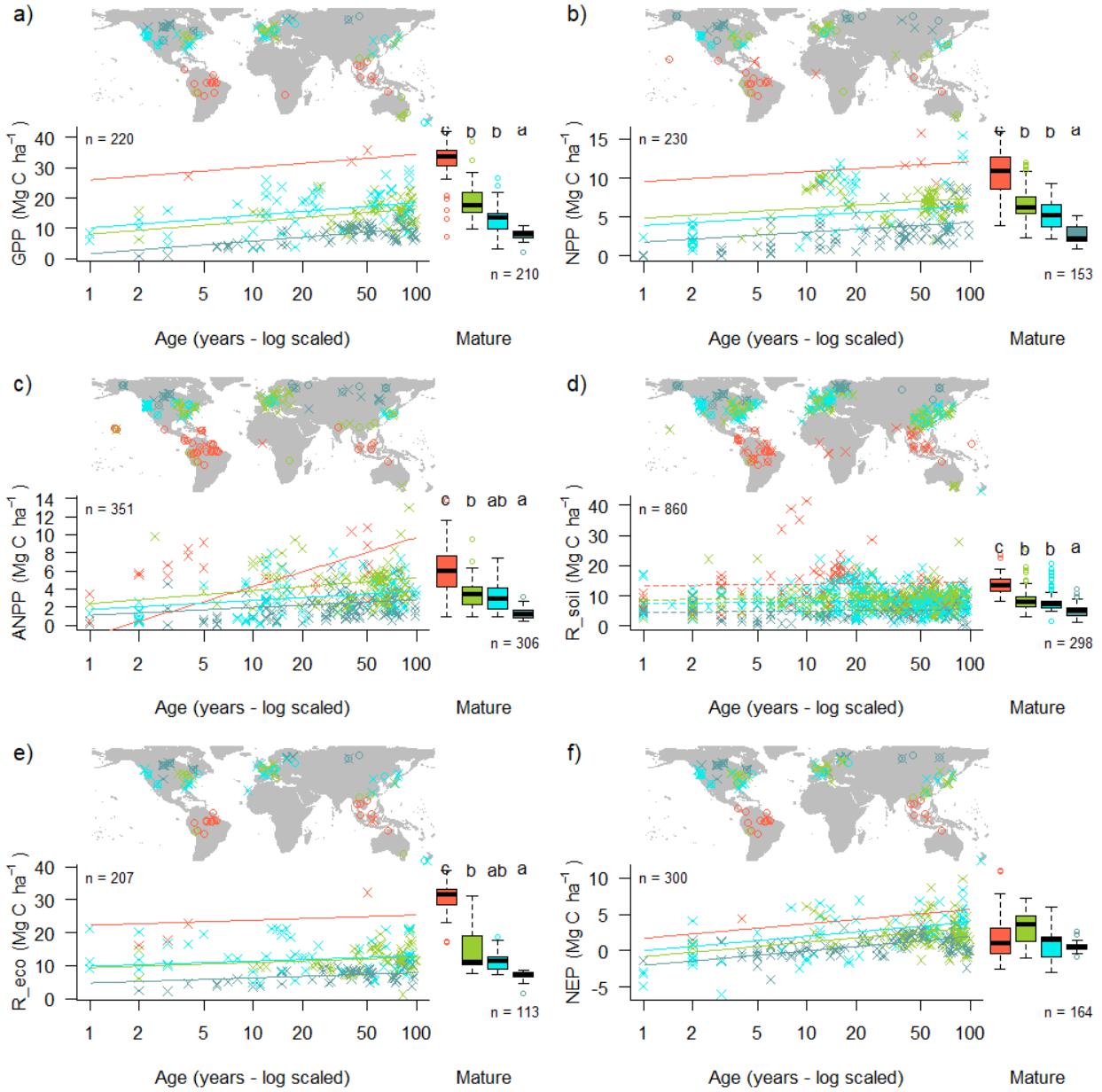


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP, (b) NPP, (c) ANPP, (d)  $R_{soil}$ , (e)  $R_{eco}$ , and (f) NEP. Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Lines... .

204 There were less distinct trends in C stocks across biomes (Fig. 7). Biome means for live aboveground and  
 205 total biomass followed the same general trend as the major fluxes, with biomass of tropical= temperate  
 206 broadleaf  $\geq$  temperate conifer> boreal forests (Fig. 7a). However, the relative differences in these means  
 207 were much smaller than for the major C fluxes, and there was significant variation within biomes. Maximum  
 208 aboveground biomass values followed a very different trend than the means: temperate broadleaf> temperate  
 209 conifer>boreal>tropical. There were some statistically significant biome differences in less frequently  
 210 sampled C stocks (e.g., woody biomass, foliage biomass, deadwood), but given high within-biome variability  
 211 in C stocks and relatively low sample sizes, these were likely attributable to sampling biases and  
 212 methodological differences than to true differences across biomes.

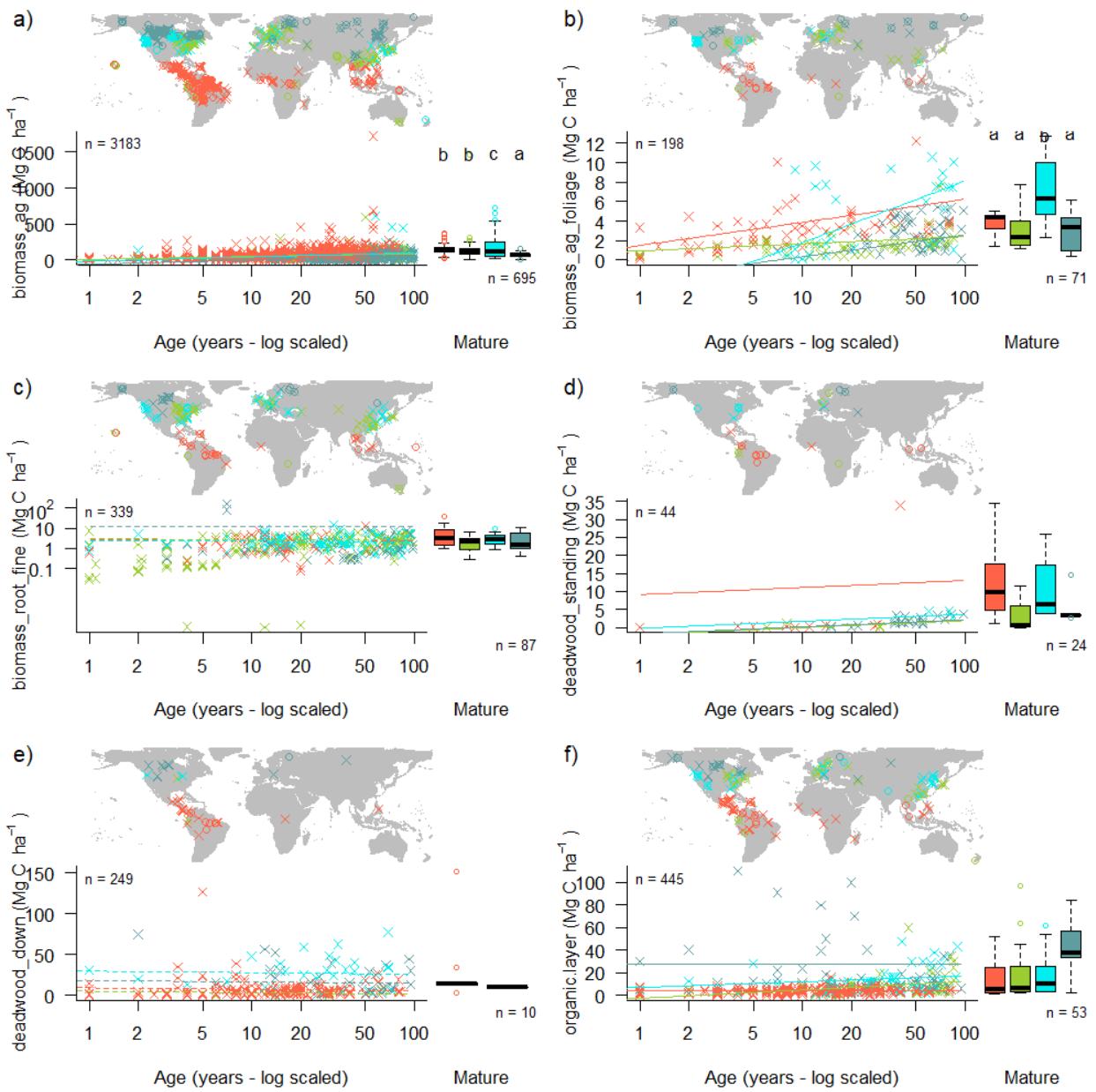


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood.

## 213 C cycling in young forests

214 **(check paragraph with latest data)** Average C cycles for forests <100 years old are presented in Figures  
 215 8-11. In general, ForC contained roughly comparable information on C fluxes in regrowth vs mature forests,  
 216 with the notable exception of tropical forests, for which there were no fluxes that had been measured in  $\geq 7$   
 217 different geographic areas. C stocks were better documented for regrowth stands, with a total of # records  
 218 from # distinct geographic areas. Both C stocks and fluxes commonly displayed significant trends with stand  
 219 age for within-biome analyses (Fig. 5-10; detailed below). Differences across biomes typically paralleled those  
 220 observed for mature forests, with C cycling generally most rapid in the tropics and slowest in boreal forests

221 (Figs. 6-7).

222 (**check paragraph with latest data**) ForC contained 14 flux variables with sufficient data for cross-biome  
223 analyses of age trends in regrowth forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for**  
224 **all variables**). Of these, 9 increased significantly with  $\log_{10}[\text{stand.age}]$ :  $GPP$ ,  $NPP$ ,  $ANPP$ ,  
225  $ANPP_{\text{foliage}}$ ,  $ANPP_{\text{woody}}$ ,  $ANPP_{\text{woody-stem}}$ ,  $BNPP$ ,  $BNPP_{\text{root-fine}}$ ,  $R_{\text{eco}}$ , and net C sequestration  
226 ( $NEP$ ). The remaining five— $ANPP_{\text{woody-branch}}$ ,  $BNPP_{\text{root-coarse}}$ ,  $R_{\text{soil-het}}$ , and  $R_{\text{soil-het}}$ —displayed no  
227 significant relationship to stand age, although all displayed a positive trend. In terms of C stocks, 10  
228 variables had sufficient data to test for age trends. Six of these—total biomass, aboveground biomass,  
229 aboveground woody biomass, foliage biomass, root biomass, and coarse root biomass—increased significantly  
230 with  $\log_{10}[\text{stand.age}]$ . The remaining four displayed non-significant positive trends: fine root biomass, total  
231 dead wood, standing dead wood, and organic layer.



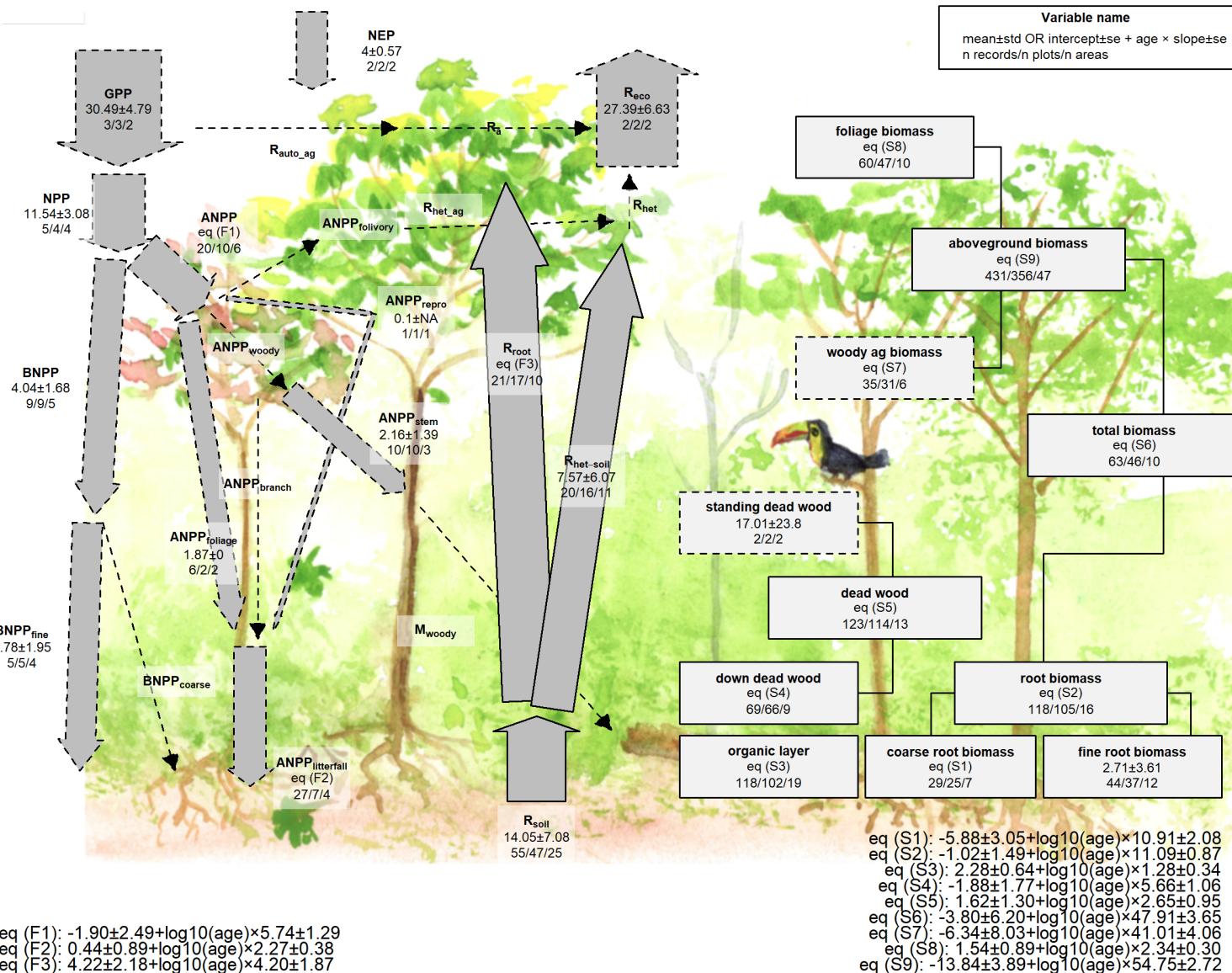


Figure 8 | C cycle diagram for young tropical broadleaf forests. All units are  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$  (fluxes) or  $\text{Mg C ha}^{-1}$ . Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

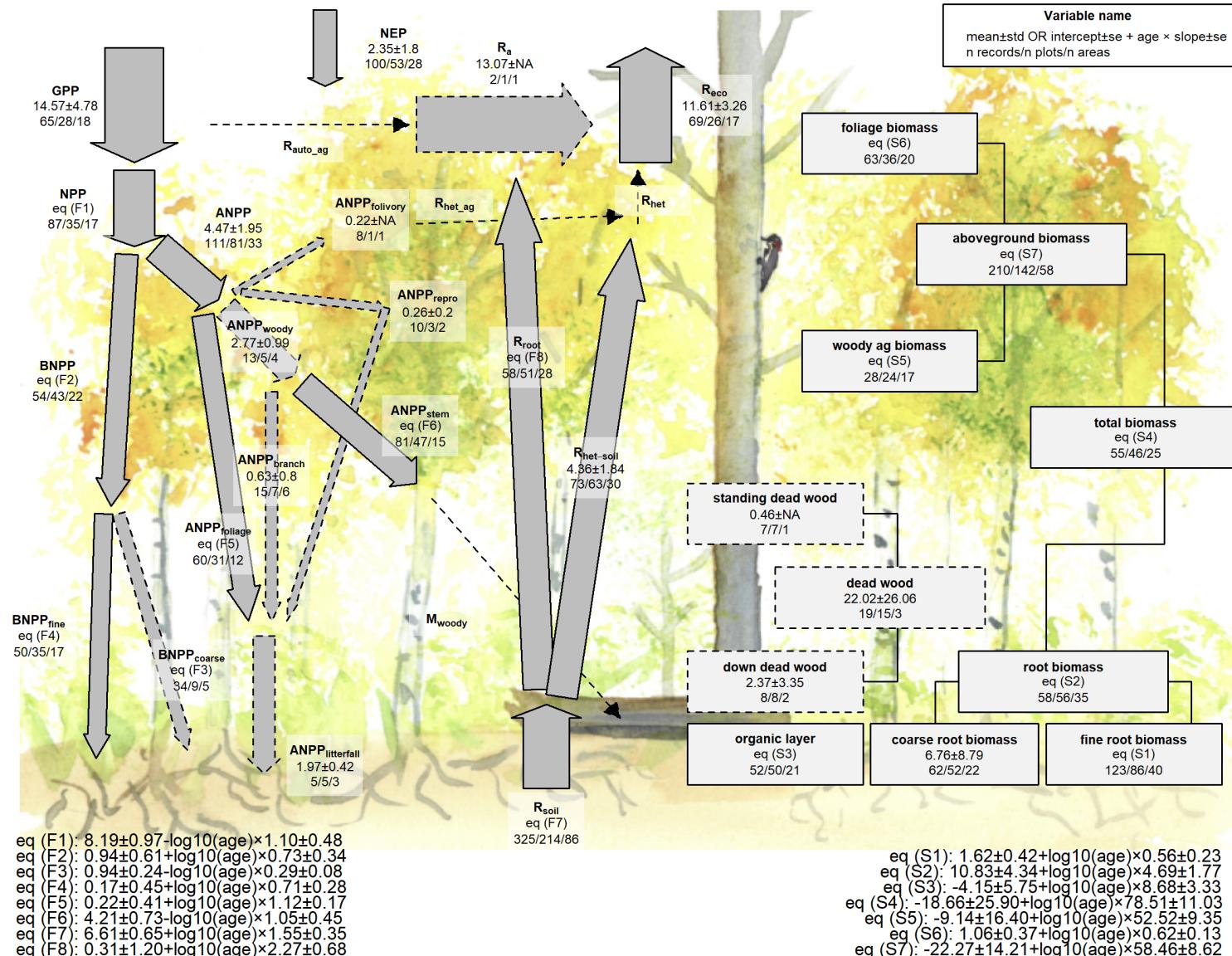


Figure 9 | C cycle diagram for young temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

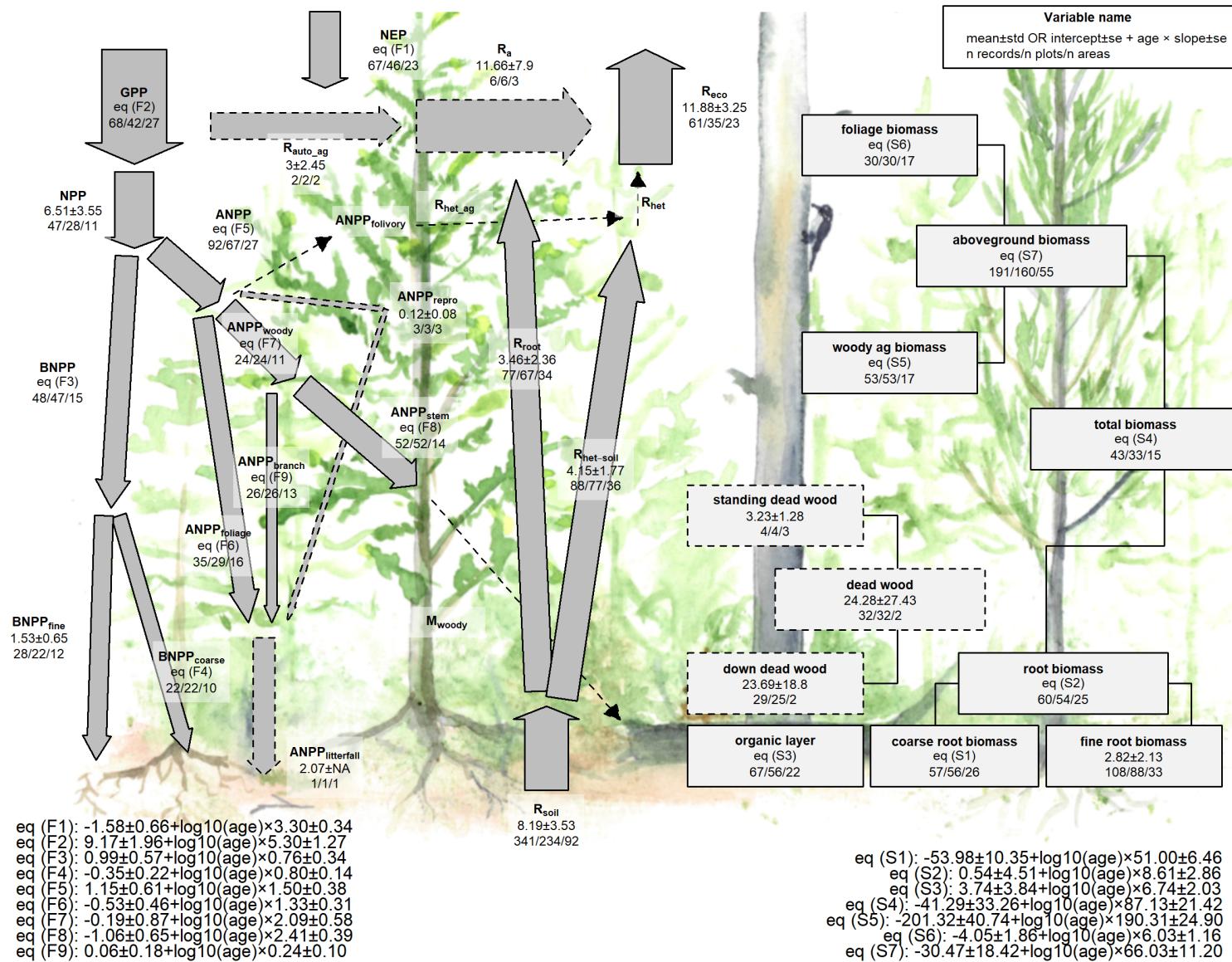


Figure 10 | C cycle diagram for young temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

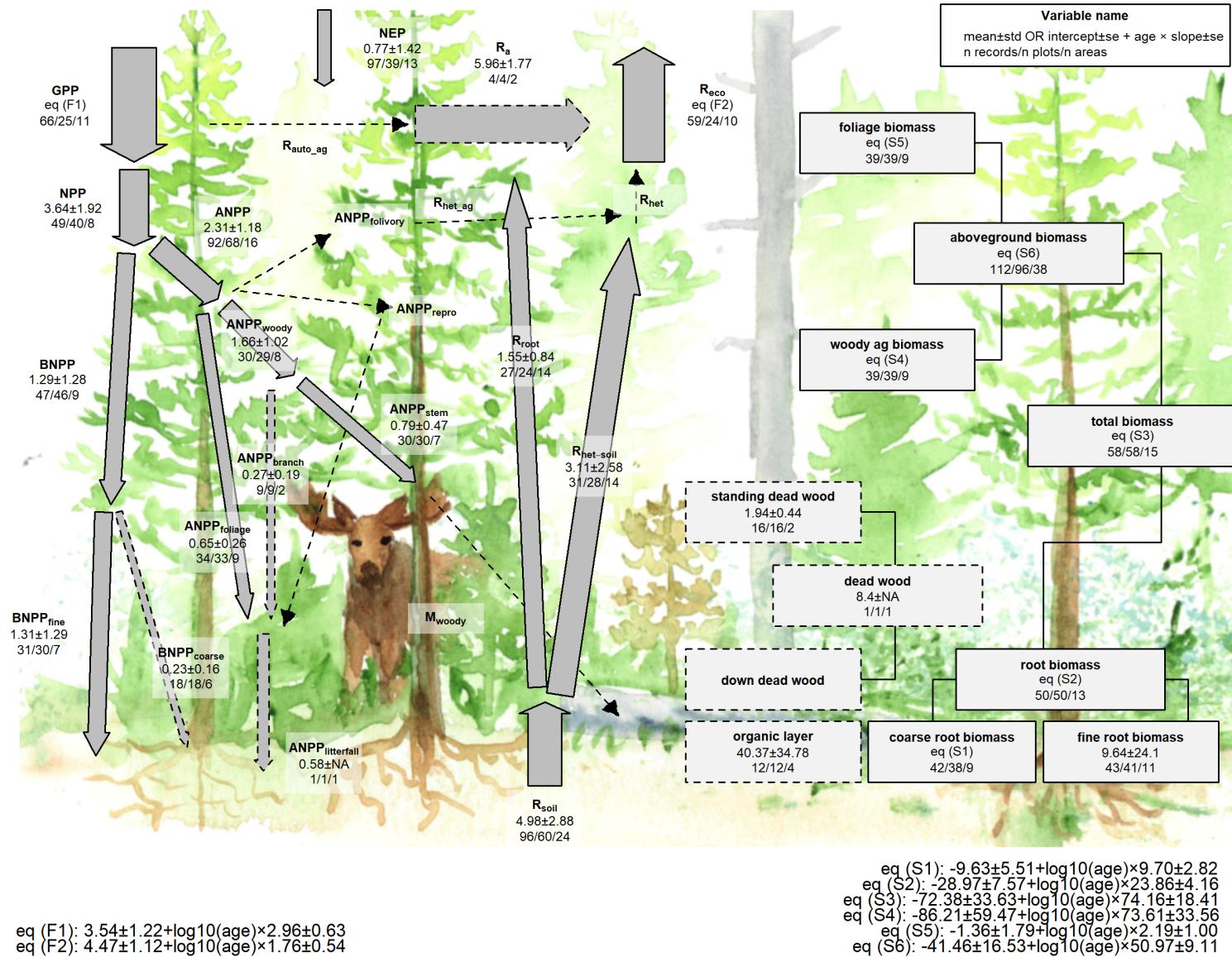


Figure 11 | C cycle diagram for young boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

232 **Discussion**

233 ForC v.XX yielded a fairly comprehensive and internally consistent picture of C cycling in the world's major  
234 forest biomes. Carbon cycling rates generally increased from boreal to tropical regions and with stand age.  
235 Specifically, the major C fluxes were highest in tropical forests, intermediate in temperate (broadleaf or  
236 conifer) forests, and lowest in boreal forests – a pattern that generally held for regrowth as well as mature  
237 forests (Figs. 6-7). In contrast to C fluxes, there was little directional variation in mature forest C stocks  
238 across biomes (Figs. 2-5, 7). The majority of flux variables, together with most live biomass pools, increased  
239 significantly with stand age (Figs. 6-11). Together, these results indicate that, moving from cold to tropical  
240 climates and from young to old stands, there is a general acceleration of C cycling, whereas C stocks of  
241 mature forests are influenced by a different set of drivers.

242 **C variable coverage and budget closure**

243 ForC provides fairly good coverage of most major variables. (*discuss how this improves upon previous data*  
244 *compilations/ for which variables does ForC make the greatest difference (e.g., not AGB or NEP/GPP/Reco,*  
245 *but by far the latest data compilation for dead wood, [variables])* (*Noteable holes include: fluxes: R\_auto\_ag,*  
246 *woody mortality, folivory/ herbivory and respiration of herbivores (and therefore total R\_het), ANPP\_repro;*  
247 *also fluxes in tropical regrowth forests) For the C stocks considered here, the most poorly covered is dead wood*  
248 *(none in E hemisphere!), despite a focused effort on this variable that has resulted in ForC being by far the*  
249 *largest collection of these data.* Thus, overall, we're lacking coverage of fluxes to herbivores and higher  
250 consumers, along with the woody mortality and dead wood. Geographically, all variables poorly covered in  
251 Africa and Siberia.

252 Closure of the C cycle budgets for mature forests (Figs. 2-5) is fairly good. However, SD's are often large,  
253 reflective of significant within-biome variation. This makes the standard for closure relatively loose. Lack of  
254 closure, in the few instances where it occurs, is probably more reflective of differences in the representation of  
255 forest types (e.g., disproportionate representation of US Pacific NW for aboveground woody biomass relative  
256 to AGB; Fig. 4) than of methodological accuracy. Thus, overall, a high degree of closure implies that ForC  
257 gives a consistent picture of C cycling within biomes. While these means are unlikely to be accurate  
258 representations of C cycling within any particular forest, they provide a useful baseline for comparison.

259 **C cycling across biomes**

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

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

273 **Age trends in C cycling**

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

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

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

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

282 NEP increases with log(age) to 100 -> strongest C sinks are established secondary forests.

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

284 The future of forest C cycling will shape trends in atmospheric CO<sub>2</sub> and the course of climate change. For a  
285 human society seeking to understand and mitigate climate change, the data contained in ForC and  
286 summarized here can help to meet two major challenges.

287 First, improved representation of forest C cycling in models is essential to improving predictions of the future  
288 course of climate change. To ensure that models are giving the right answers for the right reasons, it is  
289 important benchmark against multiple components of the C cycle. By making tens of thousands of records  
290 readily available in standardized format, ForC makes it feasible for the modeling community to draw upon  
291 these data to benchmark models. Integration of ForC with models is a goal (Fer *et al.*, in revision). On a  
292 more cursory level, the values summarized here can serve as a sanity check for modelers to determine whether  
293 model predictions for multiple C cycle variables are reasonable—i.e., within the range of previous observations.

294 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change  
295 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not  
296 feasible for the individuals and organizations designing such efforts to sort through literature, often behind  
297 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline  
298 through which information can flow efficiently from forest researchers to decision-makers working to  
299 implement forest conservation strategies at global, national, or landscape scales. This is already happening!  
300 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;  
301 Requena Suarez *et al* (2019); Rozendaal *et al* in prep], mapping C accumulation potential from natural forest  
302 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*  
303 2020).

304 There remain numerous data needs for improved accounting of forest carbon stocks and fluxes in GHG  
305 accounting. AGB is the largest stock, and most of the emphasis is on this variable. Remote sensing, with  
306 calibration based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019), is the  
307 best approach for mapping forest carbon (REFS). However, it is limited in that it is not associated with  
308 stand age and disturbance history, except in recent decades when satellite data can be used to detect forest

loss, gain, and some of their dominant drivers (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). ForC is therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020).

*remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP (Bagdley *et al.* 2019, (Li and Xiao 2019)), aboveground biomass ( $B_{ag}$ ) (REFS), woody mortality (i.e.,  $B_{ag}$  losses to mortality  $M_{woody}$ ) (Clark *et al* 2004, Leitold *et al* 2018), and to some extent net ecosystem exchange (NEP) (REFS),*

Other variables cannot be remotely sensed. In terms of C stocks, there is a paucity of data on dead wood and organic layer (Pan *et al.* ?). These can be significant. (*give some stats/ cite figures*). ForC does not include soil carbon, which is covered by other efforts (REFS). For fluxes, Fluxnet is the keeper of the best data on NEE, GPP, Reco (REFS), and SRDB remains the authority on soil respiration (REFS). ForC includes recent data from both, but is not continuously integrated. For C is the best source for most of the subsidiary fluxes: NPP, woody mortality...

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

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

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