

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

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

40 **Background**

41 Carbon (C) cycling in forests is central to sustaining life on Earth. Forest ecosystems globally influence  
42 climate through their vital role in regulating atmospheric carbon dioxide ( $\text{CO}_2$ ). Their annual gross  $\text{CO}_2$   
43 sequestration (gross primary productivity,  $GPP$ ) is estimated at >69 Gt C  $\text{yr}^{-1}$  (Bagdley et al. 2019), or >7  
44 times average annual fossil fuel emissions from 2007-2016 ( $9.4 \pm 0.5 \text{ Gt C yr}^{-1}$ ; Le Quéré et al 2017)  
45 (update). While most of this enormous C flux is counterbalanced by  $\text{CO}_2$  releases to the atmosphere through  
46 ecosystem respiration ( $R_{\text{eco}}$ ) or fire, a small portion was retained in ecosystems over recent decades. The  
47 resulting in C sink averaged  $3.0 \pm 0.8 \text{ Gt C yr}^{-1}$  from 2007-2016, offsetting 32% of anthropogenic fossil fuel  
48 emissions (Le Quéré et al 2017) (update, give range). Moreover, forests contain substantial C stocks: an  
49 estimated 92% of terrestrial biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan  
50 2008). Globally, net deforestation (i.e., gross deforestation - regrowth) has been a source of  $\text{CO}_2$  emissions,  
51 estimated at  $\sim 1.1 \text{ Gt C yr}^{-1}$  from YEAR-YEAR (Pan et al 2011), resulting in net C sink of  $\sim 1.2\text{-}1.7 \text{ Gt C}$   
52  $\text{yr}^{-1}$  across Earth's forests (Le Quéré et al 2017, Schimel et al 2015) (update, give range). The future of  
53 this sink is dependent both upon forest responses to a broad suite of global change drivers and to future land  
54 use decisions, and will strongly influence the course of climate change. Understanding, modeling, and  
55 managing forest-atmosphere  $\text{CO}_2$  exchange is thereby central to efforts to mitigate climate change (Grassi et  
56 al 2017) (Friedlingstein et al 2006, Cavalieri et al 2015, Griscom et al 2017; IPCC1.5).

57 Despite the centrality of forest C cycling in regulating both atmospheric  $\text{CO}_2$  and ecosystem function and

58 diversity, we lack a comprehensive understanding of how C cycling varies with across biomes and with stand  
59 age. While remote sensing measurements are increasingly useful for global- or regional-scale estimates of  
60 forest *GPP* (Bagdley et al. 2019, (Li and Xiao 2019)), aboveground biomass ( $B_{ag}$ ) (REFS), woody mortality  
61 (*i.e.*,  $B_{ag}$  losses to mortality  $M_{woody}$ ) (Clark et al 2004, Leitold et al 2018), and to some extent net  
62 ecosystem exchange (*NEP*) (REFS), the remainder of C fluxes and stocks can only be quantified by  
63 ground-based measurements. Moreover, data on stand characteristics—including species composition, age, and  
64 disturbance history—are critical to interpreting and projecting into the future, but [usually rely on  
65 ground-based measurements]. Thus, ground-based measurements are, and will continue to be, central to  
66 characterizing forest C cycling.

67 Tens of thousands of ground-based forest C measurements have been published, but their distribution across  
68 literally thousands of scientific articles— along with variation in data formats, units, measurement methods,  
69 etc.—have made them effectively inaccessible for many global-scale analyses, including those attempting to  
70 quantify the role of forests in the global C cycle (*e.g.*, Pan et al 2011), and model evaluation (Clark et al  
71 2017, Luo et al 2012). Important progress has been made in synthesizing data to address how C cycling  
72 varies across forest biomes (Luyssaert et al. 2007; REFS) and stand ages (REFS), yet generally consider only  
73 a limited set of C variables (but see Anderson-Teixeira et al 2016 for the tropics) and do not consider  
74 age-by-biome interactions. To address the need for global-scale analyses of forest C cycling, we have  
75 developed an open-access Global Forest Carbon database, ForC (Anderson-Teixeira et al (2016),  
76 Anderson-Teixeira et al (2018)). ForC contains data on forest ecosystem C stocks and annual fluxes (>50  
77 variables) and associated data required for interpretation (*e.g.*, stand history, measurement methods)  
78 amalgamated from numerous previous data compilations and directly from original publications. ForC  
79 currently contains # (~49,000!) records from # plots and # distinct geographic areas representing all  
80 forested biogeographic and climate zones.

81 Here, we synthesize ForC data (Fig. 1) to provide a macroscopic overview of stand-level carbon cycling of the  
82 world’s major forest biomes and how it varies with stand age. We address three broad questions:

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

87 While components of these questions have been previously addressed (Luyssaert et al 2007,  
88 Anderson-Teixeira et al 2016, pp @anderson-teixeira\_forc\_2018, @banbury\_morgan\_global\_nodate), our  
89 analysis represents by far the most comprehensive analysis of C cycling in global forests, and thereby stands  
90 to serve as a foundation for improved understanding of global forest C cycling.

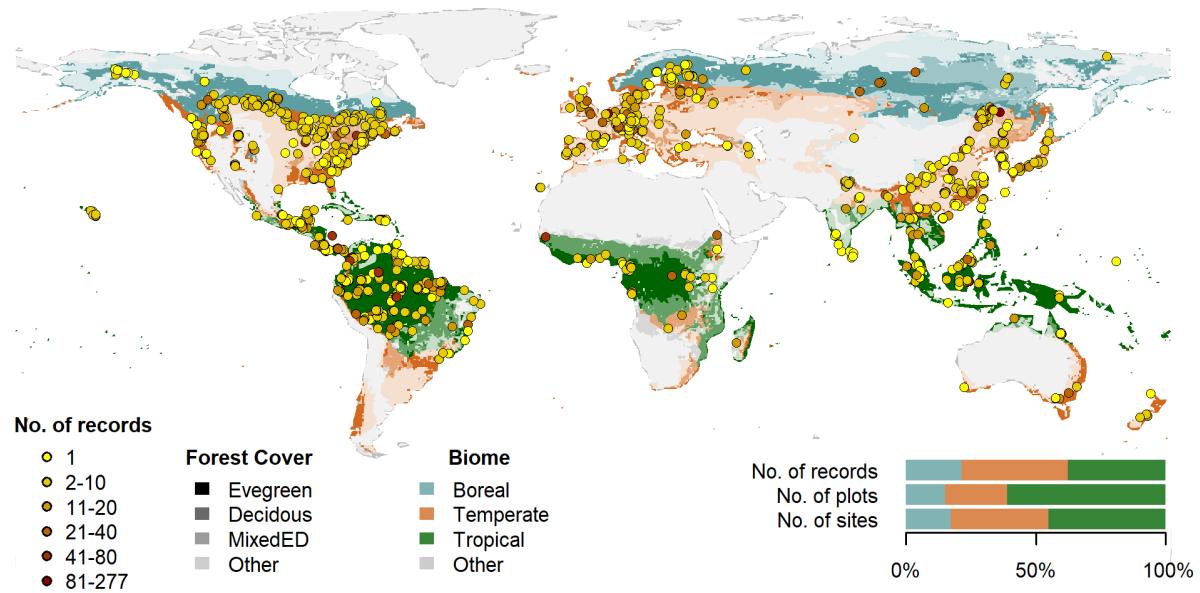


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

## 91 Methods/ Design

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

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

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

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

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

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

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

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

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

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

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

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

104 v1.0; Cook-Patton *et al*. in press; ZenodoDOI), and data from several publications (Taylor *et al*. 2017, Lutz

105 *et al*. 2018, Johnson\_2018\_csss; see GitHub repo for complete list) (GitHub list). We note that there

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

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

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

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

110 temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones

were defined according to Köppen-Geiger zones, which were extracted based on site geographic coordinates from the ESRI Köppen-Geiger map (downloaded June 2014 from [http://maps3.arcgis.com/ArcGIS/rest/services/A-16/Köppen-Geiger\\_Observed\\_and\\_Predicted\\_Climate\\_Shifts/MapServer](http://maps3.arcgis.com/ArcGIS/rest/services/A-16/Köppen-Geiger_Observed_and_Predicted_Climate_Shifts/MapServer); Rubel and Kottke 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; Jung et al 2006) and recorded in the dominant.veg field of the ForC MEAUREMENTS table. Stand age was obtained from the stand.age field of MEAUREMENTS table, and forests 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 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  $\leq 10$ cm. 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

153 reported in the C cycle schematics, we first averaged any repeated measurements within a plot, weighting  
154 flux measurements according to the length of measurement periods (*i.e.*, end.date - start.date). Values were  
155 then averaged across plots clustered within 25 km of one another (geographic.area field of SITES table, sensu  
156 Anderson-Teixeira et al 2018), weighting by area.sampled (MEASUREMENTS table) or plot.area (PLOTS  
157 table) if available for all records. This step was taken to avoid pseudo-replication and to combine any records  
158 from sites with more than one name in ForC. Finally, for figures 6 and 7, the original values were analyzed  
159 via a linear mixed effects model ('lmer' function in 'lme4' R package) with biome as fixed effect and plot  
160 nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we  
161 looked at a Tukey's pairwise comparison to see which biomes were significantly different from one another.  
162 There were enough data to run this analysis for all focal variables but **biomass\_ag\_understory**,  
163 **BNPP\_root.turnover\_fine, deadwood\_down, total.ecosystem\_2**.

164 For young (<100yrs) forest types, we employed a mixed effects model with biome and log10[stand.age] as  
165 fixed effects and plot nested within geographic.area as a random effect on the intercept. When the effect of  
166 stand.age was significant at  $p \leq 0.05$  and when each biome had records for stands of at least 10 different  
167 ages, a biome - stand.age interaction was included in the model. In the C cycle schematics for young forests,  
168 we report equations based on these models. In cases where there was no significant effect of stand.age,  
169 records were averaged as for mature stands.

170 All database manipulation, analyses, and figure production were fully automated in R (version, citation).  
171 Materials required to fully reproduce these analyses, including data, R scripts, and image files, are archived  
172 in Zenodo (DOI: TBD]. Data, scripts, and results presented here are also available through the open-access  
173 ForC GitHub repository (<https://github.com/forc-db/ForC>), where many will be updated as the database  
174 develops.

## 175 Review Results/ Synthesis

### 176 C cycling in mature forests

177 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq 100$   
178 years old and with no known major disturbance or significant anthropogenic management are presented in  
179 Figures 2-5, and statistics for each biome type are also summarized at: [GitHub URL]. Of the 23 flux and 11  
180 stock variables mapped in these diagrams, ForC contained estimates from  $\geq 7$  distinct geographic areas for  
181 # fluxes and # stocks in tropical broadleaf forests, # fluxes and # stocks in temperate broadleaf forests, #  
182 fluxes and # stocks in temperate conifer forests, and fluxes and # stocks in boreal forests. For variables with  
183 records from  $\geq 7$  distinct geographic areas, these ensemble C budgets were generally consistent. That is,  
184 component fluxes and stocks summed to within 1 std of more inclusive fluxes in all but one instance (in  
185 temperate conifer forests, *abovegroundwoodybiomass + foliagebiomass > abovegroundbiomass + 1std*; Fig.  
186 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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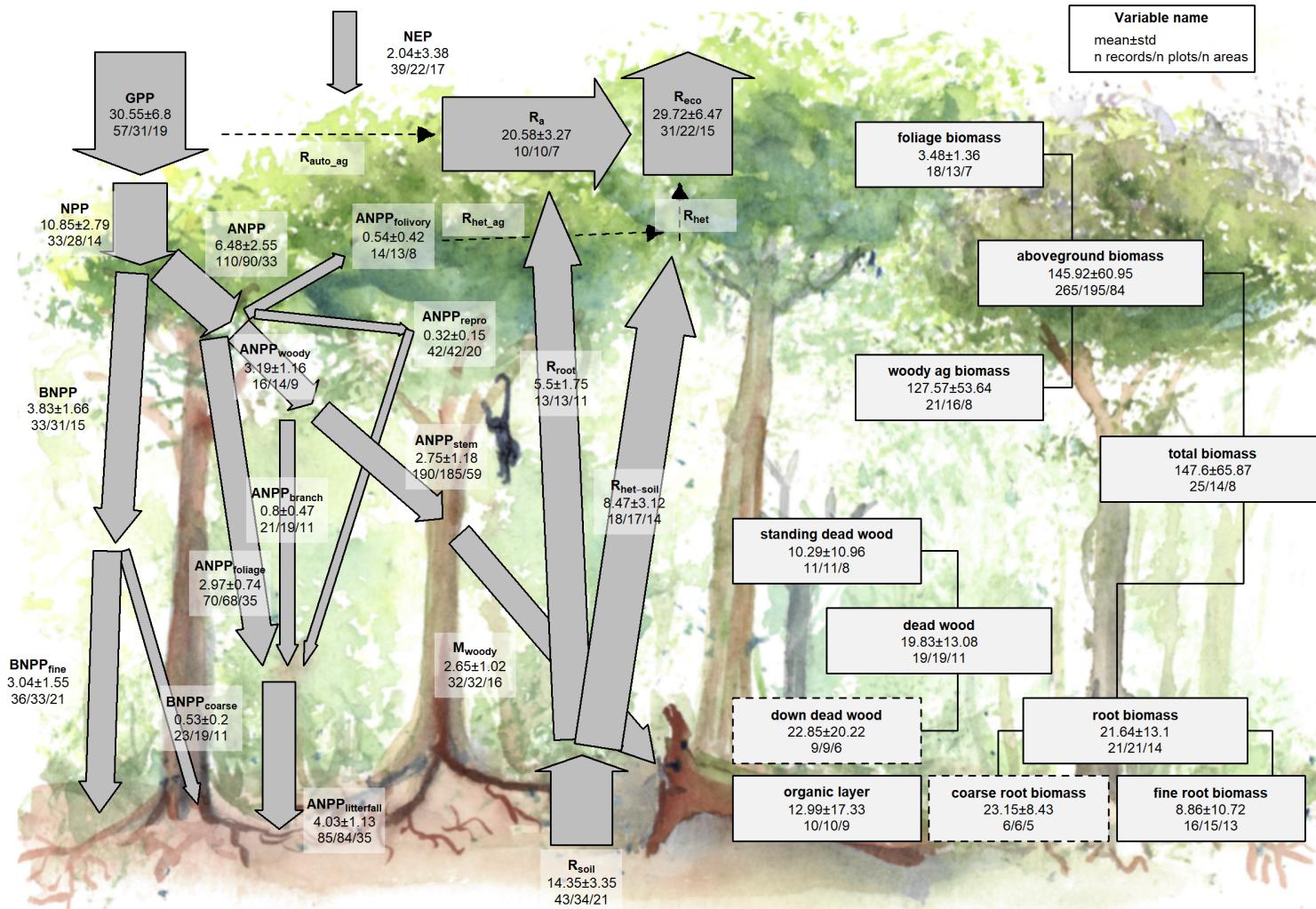


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed 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\*\*.

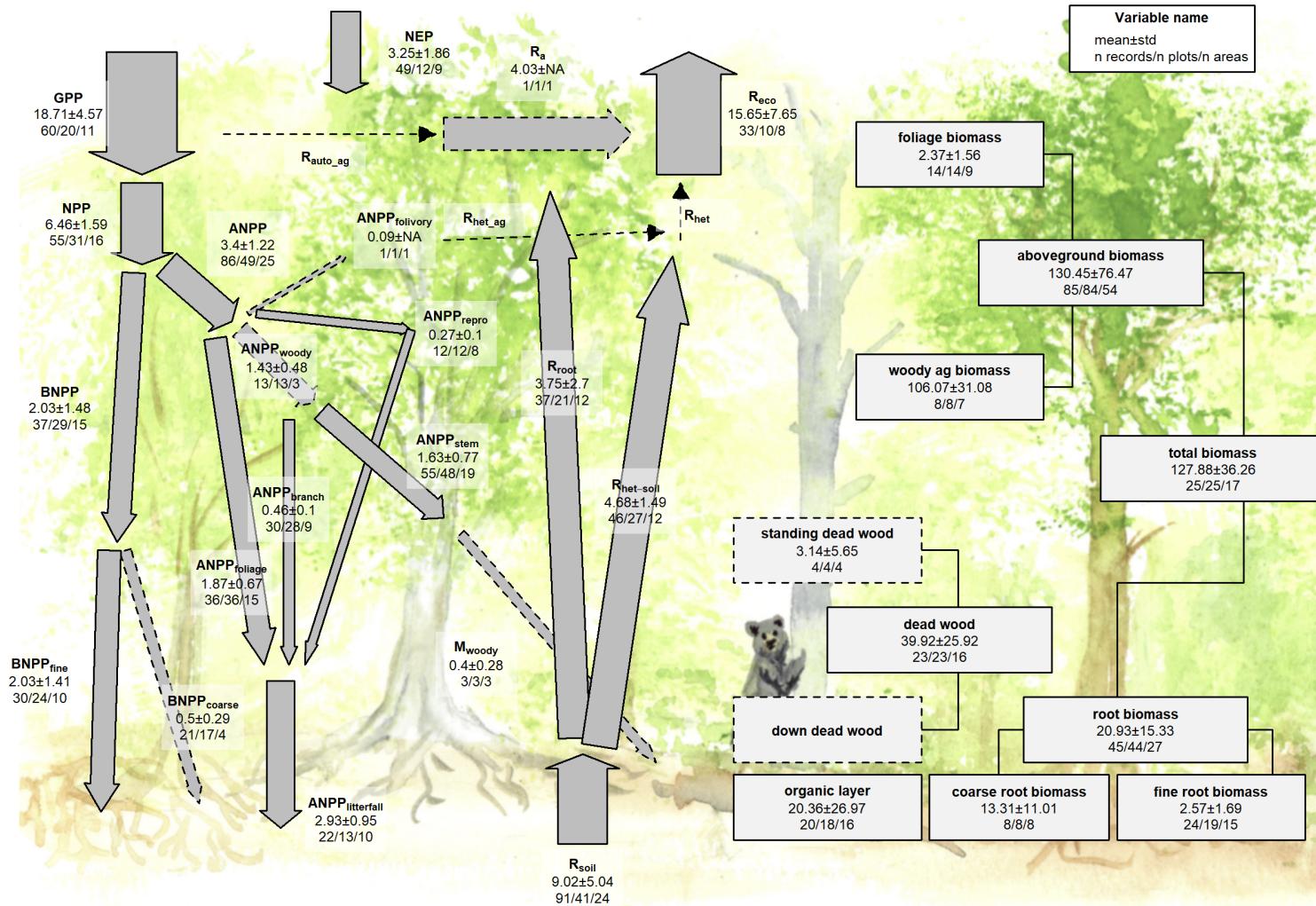


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are  $Mg C ha^{-1} yr^{-1}$  (fluxes) or  $Mg C ha^{-1}$ . Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape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

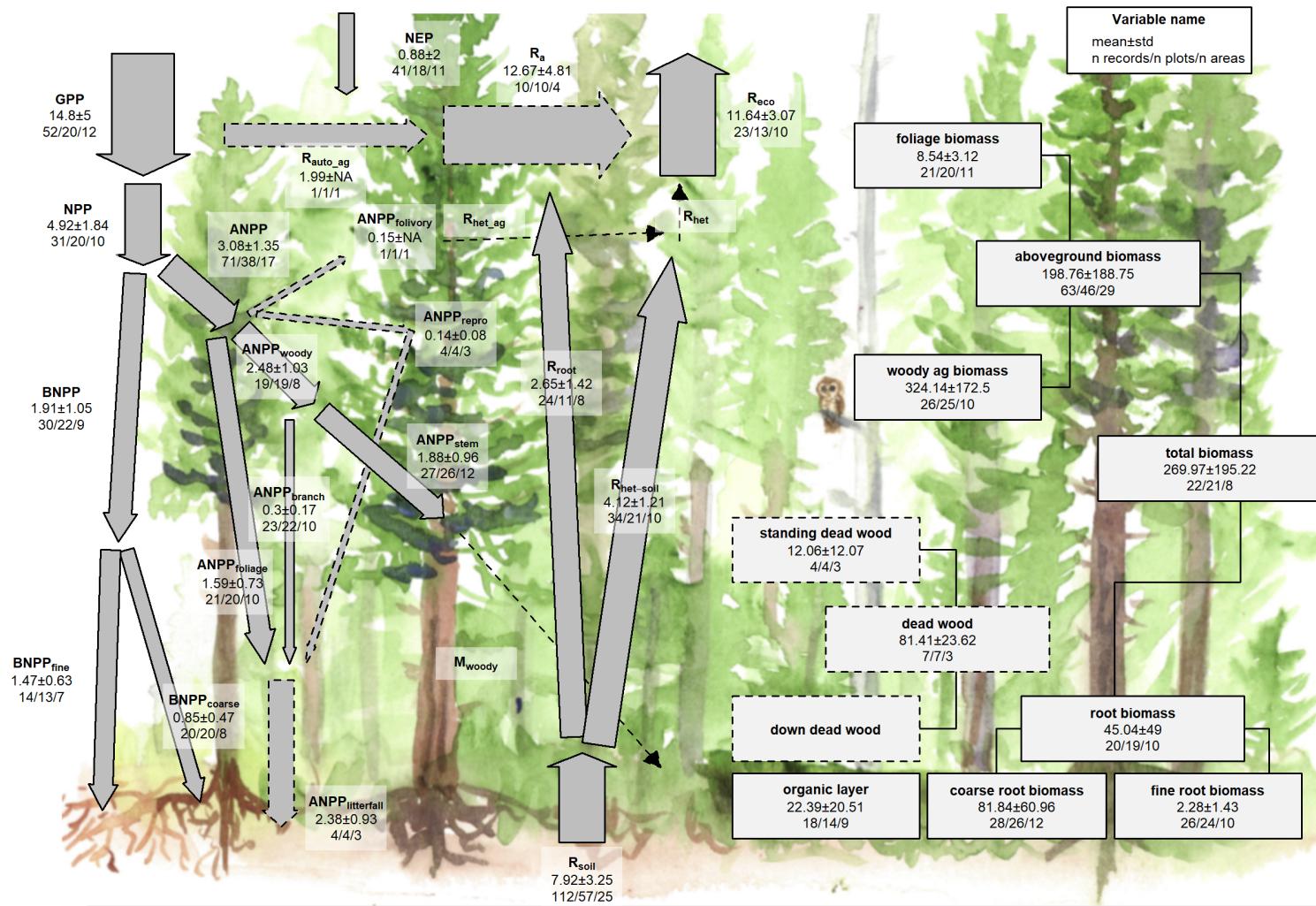


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

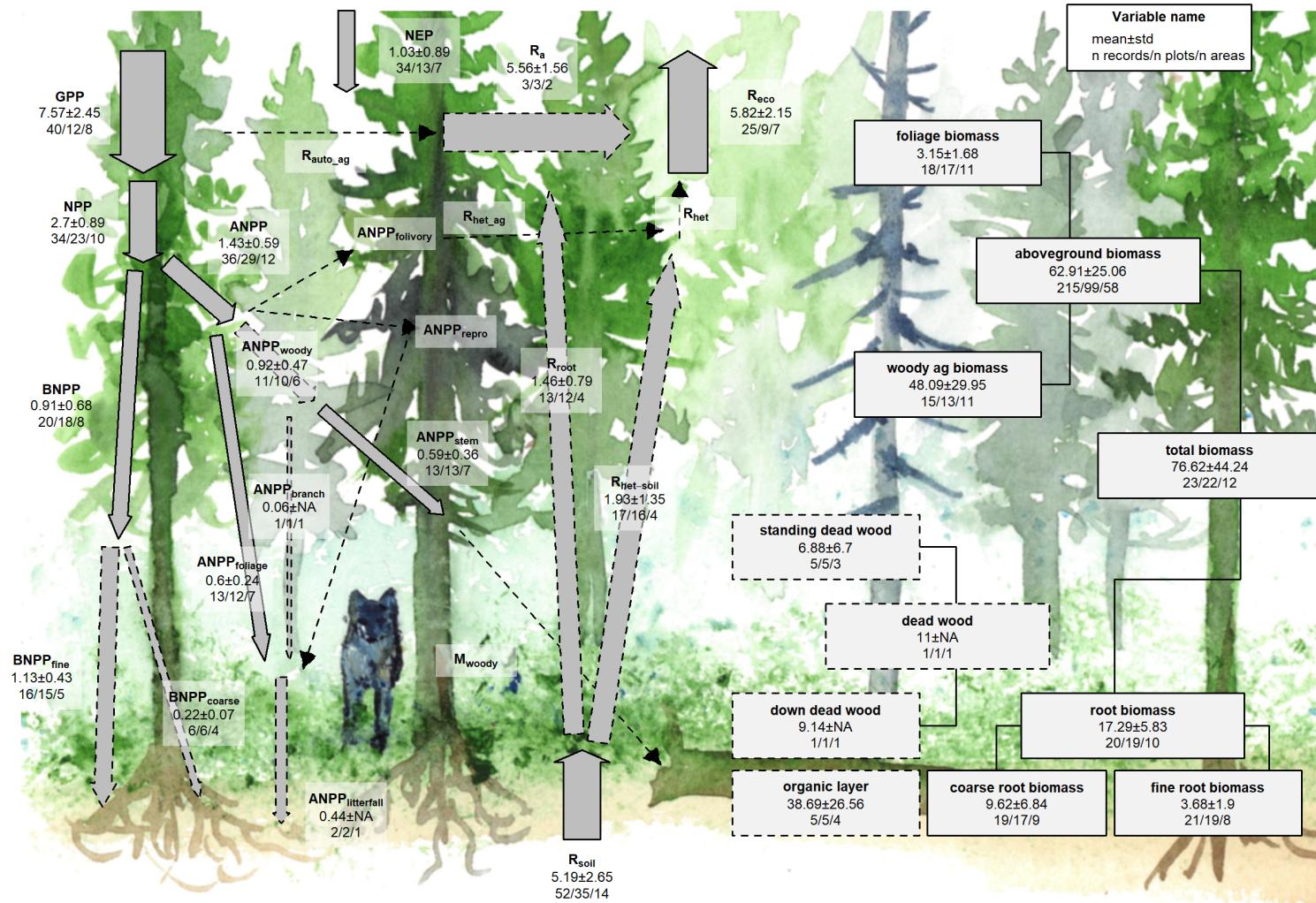


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

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

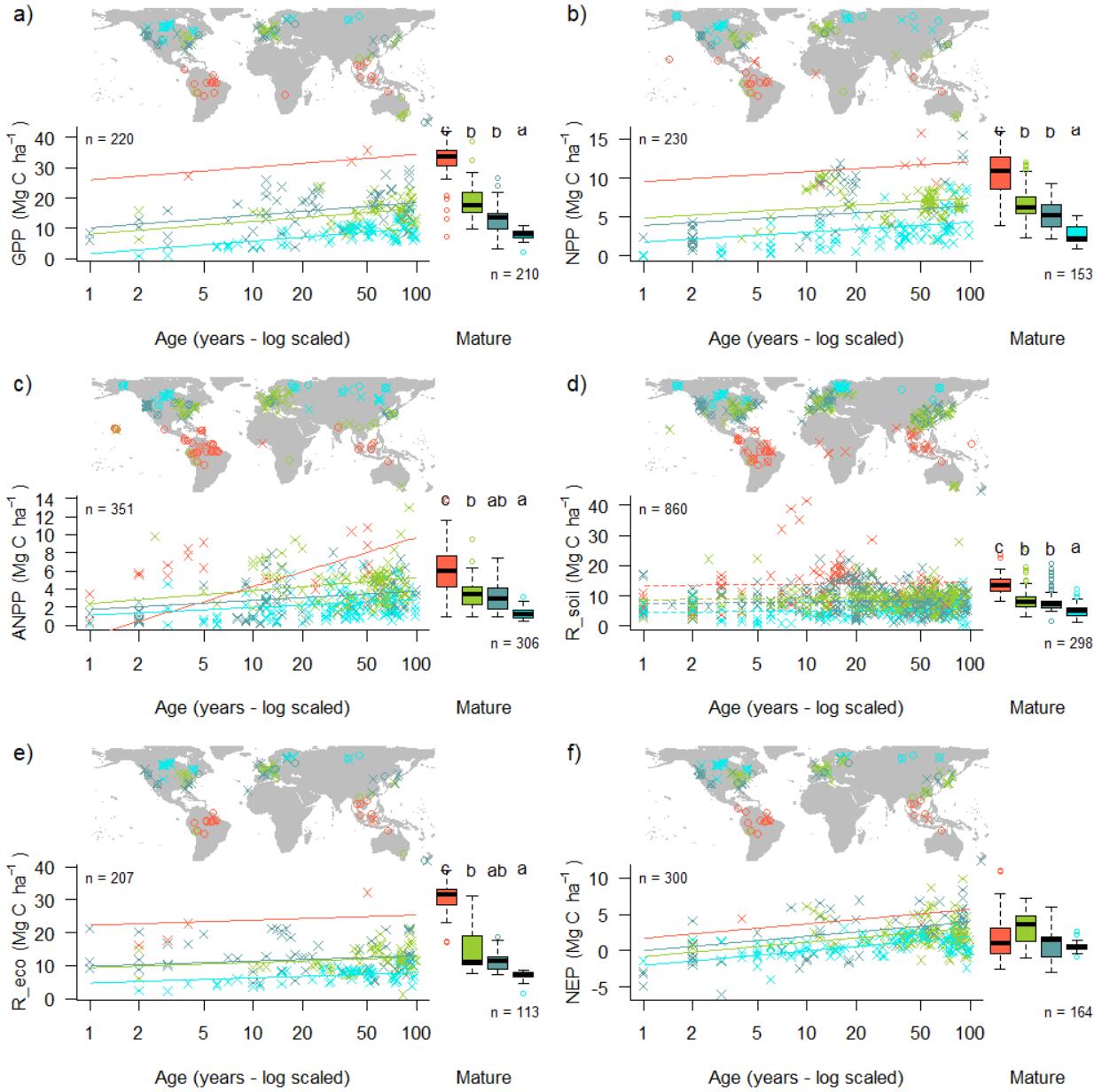


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP, (b) NPP, (c) ANPP, (d)  $R_{soil}$ , (e)  $R_{eco}$ , and (f) NEP. Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Lines... .

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

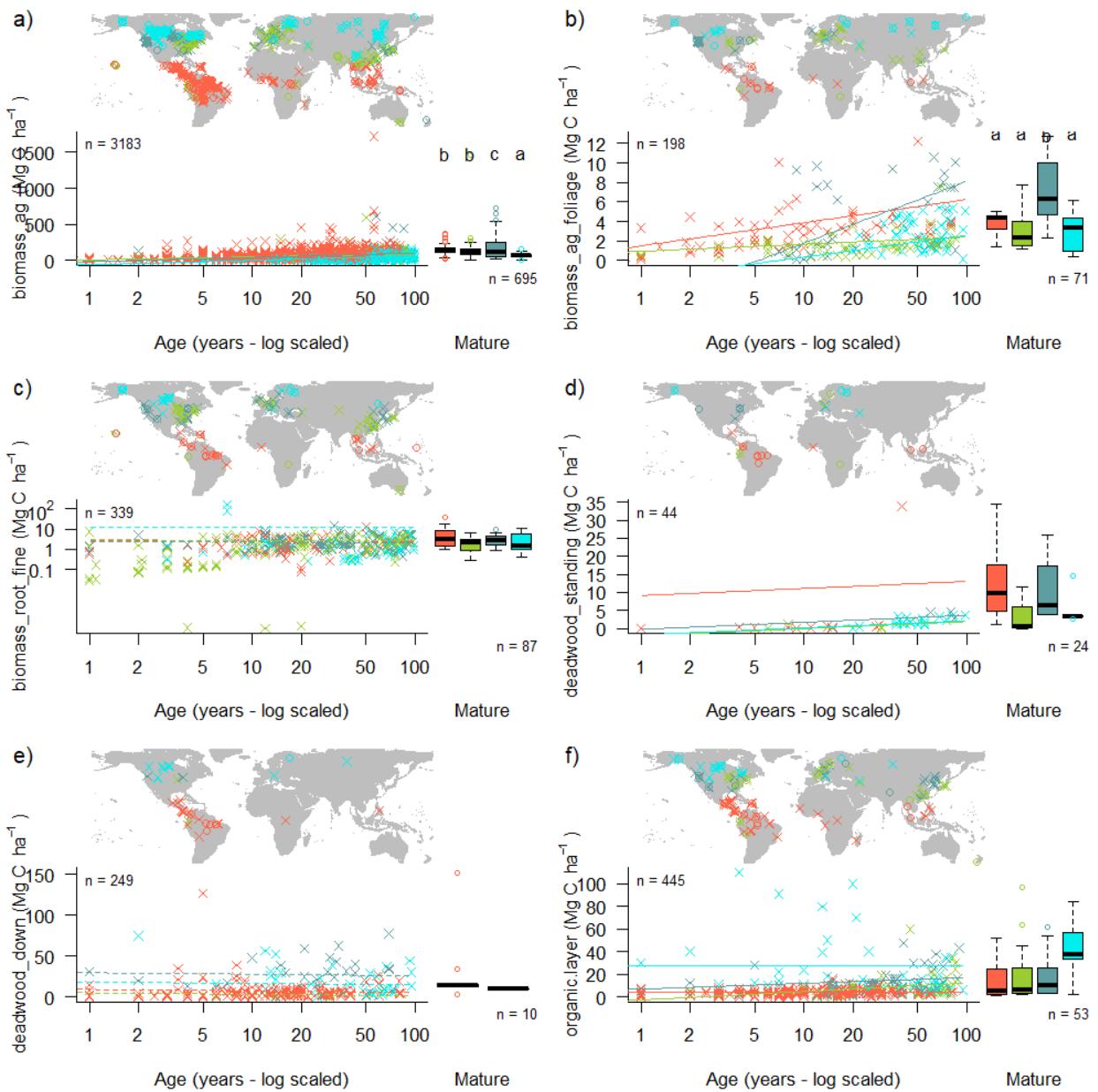


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood.

## 206 C cycling in young forests

207 **(check paragraph with latest data)** Average C cycles for forests <100 years old are presented in Figures  
 208 8-11. In general, ForC contained roughly comparable information on C fluxes in regrowth vs mature forests,  
 209 with the notable exception of tropical forests, for which there were no fluxes that had been measured in  $\geq 7$   
 210 different geographic areas. C stocks were better documented for regrowth stands, with a total of # records  
 211 from # distinct geographic areas. Both C stocks and fluxes commonly displayed significant trends with stand  
 212 age for within-biome analyses (Fig. 5-10; detailed below). Differences across biomes typically paralleled those  
 213 observed for mature forests, with C cycling generally most rapid in the tropics and slowest in boreal forests

<sup>214</sup> (Figs. 6-7).

<sup>215</sup> **(check paragraph with latest data)** ForC contained 14 flux variables with sufficient data for cross-biome  
<sup>216</sup> analyses of age trends in regrowth forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for**  
<sup>217</sup> **all variables**). Of these, 9 increased significantly with  $\log_{10}[\text{stand.age}]$ :  $GPP$ ,  $NPP$ ,  $ANPP$ ,  
<sup>218</sup>  $ANPP_{\text{foliage}}$ ,  $ANPP_{\text{woody}}$ ,  $ANPP_{\text{woody-stem}}$ ,  $BNPP$ ,  $BNPP_{\text{root-fine}}$ ,  $R_{\text{eco}}$ , and net C sequestration  
<sup>219</sup> ( $NEP$ ). The remaining five— $ANPP_{\text{woody-branch}}$ ,  $BNPP_{\text{root-coarse}}$ ,  $R_{\text{soil-het}}$ , and  $R_{\text{soil-het}}$ —displayed no  
<sup>220</sup> significant relationship to stand age, although all displayed a positive trend. In terms of C stocks, 10  
<sup>221</sup> variables had sufficient data to test for age trends. Six of these—total biomass, aboveground biomass,  
<sup>222</sup> aboveground woody biomass, foliage biomass, root biomass, and coarse root biomass—increased significantly  
<sup>223</sup> with  $\log_{10}[\text{stand.age}]$ . The remaining four displayed non-significant positive trends: fine root biomass, total  
<sup>224</sup> dead wood, standing dead wood, and organic layer.



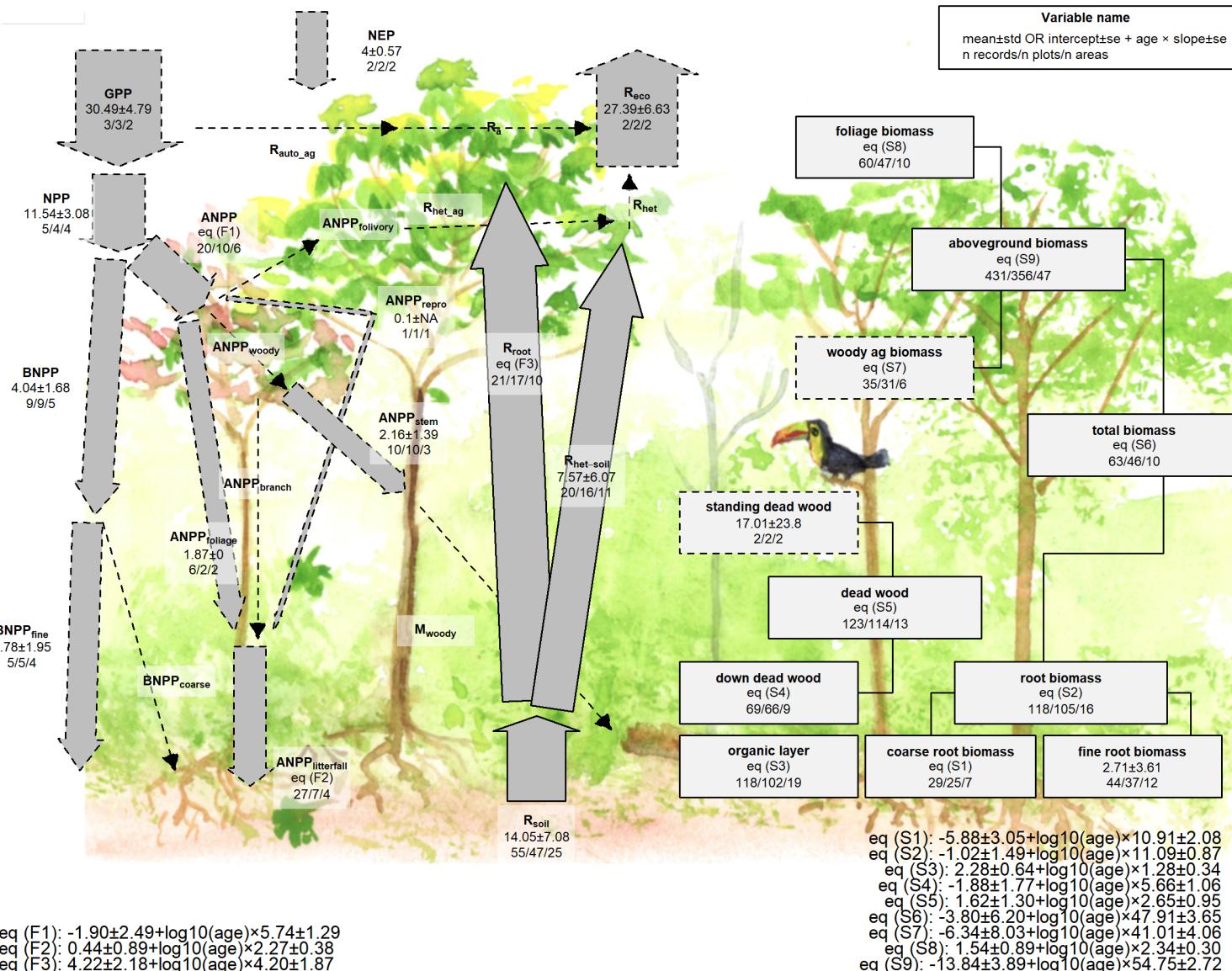


Figure 8 | C cycle diagram for young tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When 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.

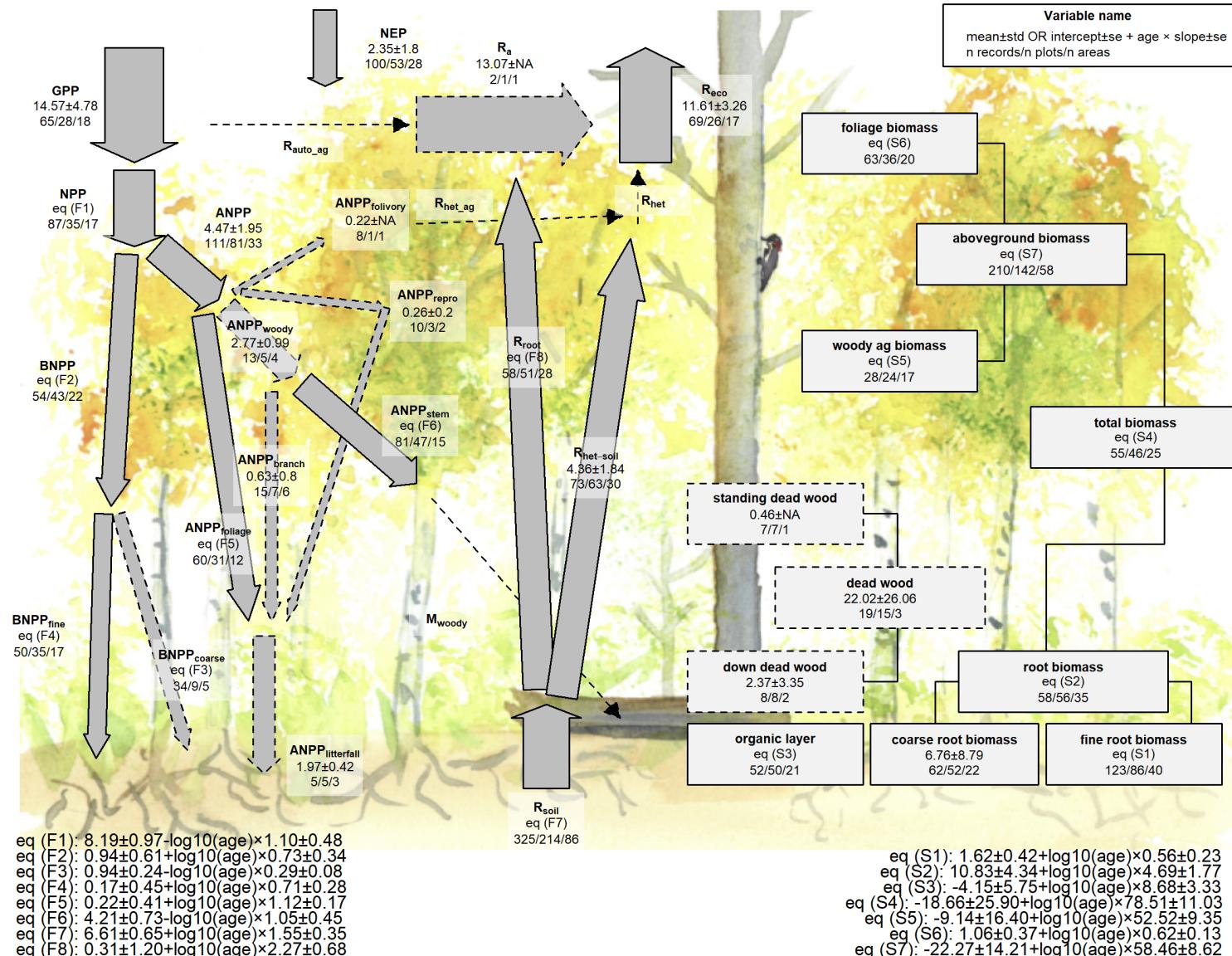


Figure 9 | C cycle diagram for young temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When 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.

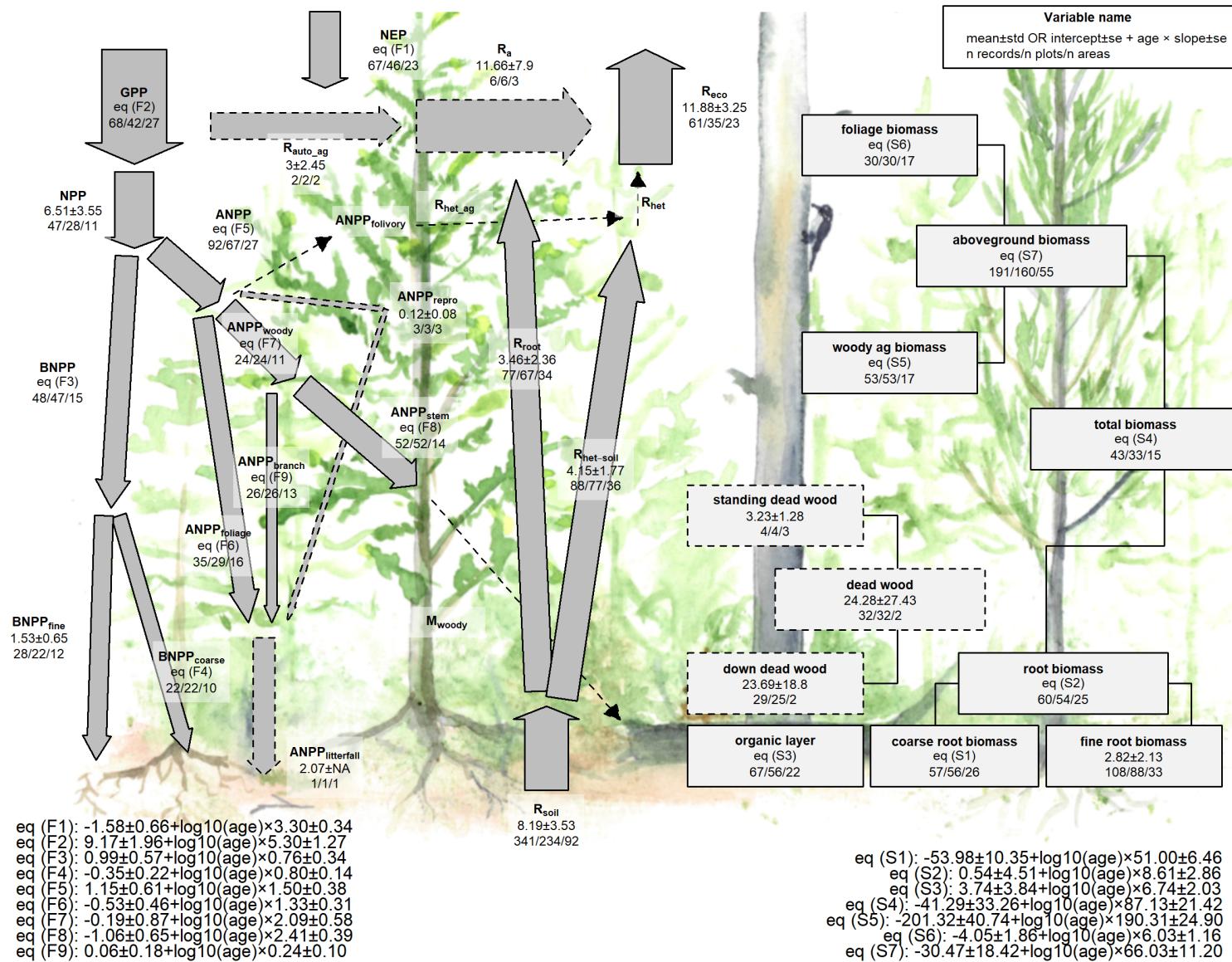


Figure 10 | C cycle diagram for young temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When 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.

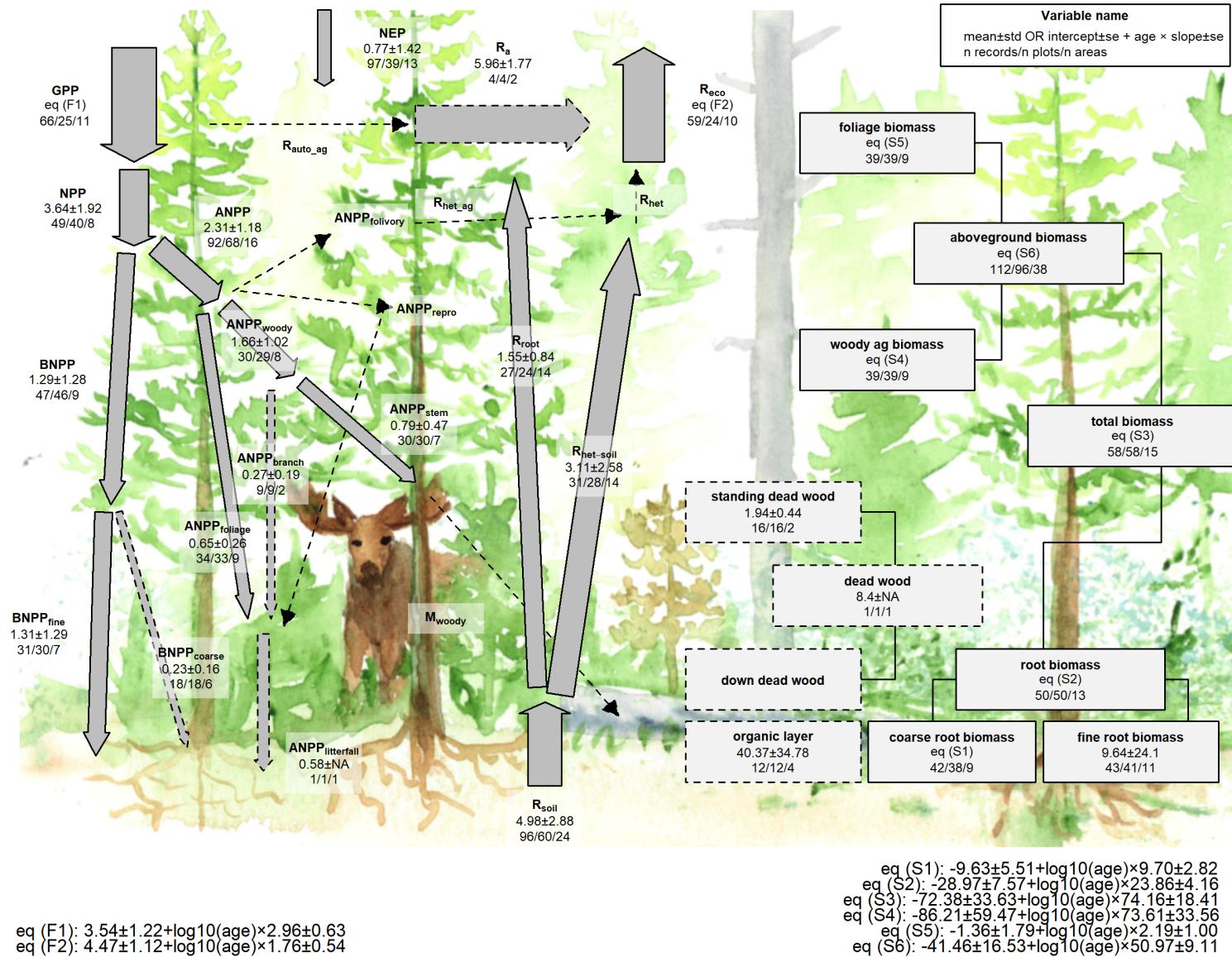


Figure 11 | C cycle diagram for young boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When 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.

225 **Discussion**

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

235 *C variable coverage and budget closure*

236 Coverage:

- 237 • We have fairly good coverage of most major variables
- 238 • (note how this improves upon previous data compilations/ for which variables does ForC make the  
239 greatest difference (e.g., not AGB or NEP/GPP/Reco, but by far the latest data compilation for dead  
240 wood, [variables])
- 241 • Noteable holes include: fluxes: R\_auto\_ag, woody mortality, folivory/ herbivory and respiration of  
242 herbivores (and therefore total R\_het), ANPP\_repro; also fluxes in tropical regrowth forests
- 243 • for the C stocks considered here, the most poorly covered is dead wood (none in E hemisphere!),  
244 despite a focused effort on this variable that has resulted in ForC being by far the largest collection of  
245 these data.
- 246 • all variables poorly covered in Africa

247 Thus, overall, we're lacking coverage of fluxes to herbivores and higher consumers, along with the woody  
248 mortality and dead wood.

249 Closure:

- 250 • C cycle closure is fairly good.
- 251 • However, SD's are often large, reflective of significant within-biome variation. This makes the standard  
252 for closure relatively loose.
- 253 • Lack of closure, in the few instances where it occurs, is probably more reflective of differences in the  
254 representation of forest types (e.g., disproportionate representation of US Pacific NW for aboveground  
255 woody biomass relative to AGB; Fig. 4) than of methodological accuracy.

256 Thus, overall, a high degree of closure implies that ForC gives a consistent picture of C cycling within biomes.  
257 While these means are unlikely to be accurate representations of C cycling within any particular forest, they  
258 provide a useful baseline for comparison.

- 259 • note that our equations are unlikely to be the best possible for any given flux

260 *C cycling across biomes*

261 Banbury Morgan *et al* (n.d.)

262 *Age trends in C cycling*

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

266 *Relevance for climate change modeling and mitigation*

267 Importance of forest C in climate change modeling and mitigation...

268 For C can help models by serving as benchmark data.

- 269 • (cite Dietze paper that we reviewed)

270 For some variables, such as AGB of mature forests, we sources other than ForC can provide the best  
271 available data. However, for others, ForC provides by far the most comprehensive source:

- 272 • agb age trends (GROA; Cook-Patton et al. 2020)

- 273 • dead wood (cite need for this)

- 274 • fluxes

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

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