

<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 in both mature and regrowth forests, whereas C stocks showed less directional variation.  
33 The majority of flux variables, together with most live biomass pools, increased significantly with stand age,  
34 and the rate of increase again 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 will play a critical role in shaping the course of climate change (IPCC1.5) through their  
42 influence on atmospheric carbon dioxide ( $\text{CO}_2$ ). 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  $3.0 \pm 0.8 \text{ Gt C}$   
47  $\text{yr}^{-1}$  from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update**,  
48 **give range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial  
49 biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Globally, net  
50 deforestation (*i.e.*, gross deforestation - regrowth) has been a source of  $\text{CO}_2$  emissions, estimated at  $\sim 1.1 \text{ Gt}$   
51  $\text{C yr}^{-1}$  from 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  
52 forests (Le Quéré et al 2017, Schimel et al 2015) (**update, give range**). The future of this sink is  
53 dependent both upon forest responses to a broad suite of global change drivers and to future land use  
54 decisions, and will strongly influence the course of climate change. Regrowth forests in particular will play an  
55 important role (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.

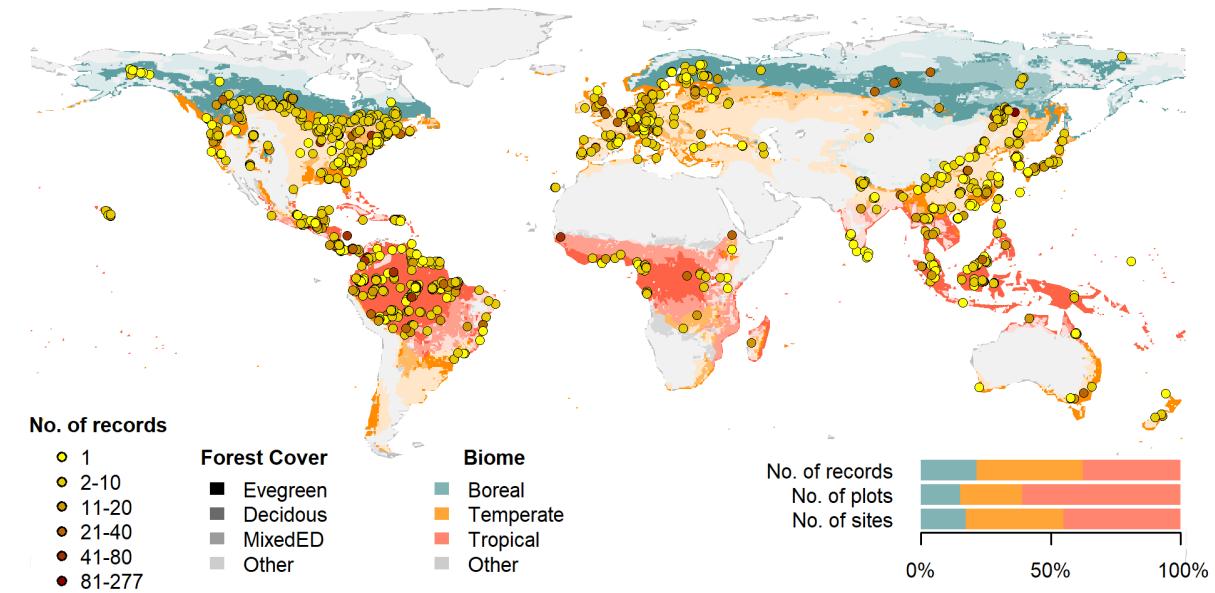


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown 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 covered #% of the primary variable records for forests of known age, or #% of total records. The most well-represented forest types excluded were boreal broadleaf and boreal and temperate mixed broadleaf-needleleaf, each with # records total.

We selected 23 annual flux and 11 C stock variables for inclusion in the analysis, although two flux variables ( $R_{het-ag}$  and  $R_{het}$ ) were included for conceptual completeness but had no records in ForC (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 (Tables 1, S#(variable mapping)). 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 S1. 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. **(this part & following are confusing/ incomplete-needs work)** For mature forests, to obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot. Values were then averaged across plots clustered within 25 km of one another (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if available for all records. This step was taken to avoid pseudo-replication and to combine any records from sites with more than one name in ForC. Finally, for figures 6 and 7, the original values were analyzed via a linear mixed effects model (‘lmer’ function in ‘lme4’ R package) with biome as fixed effect and

160 plot nested within geographic.area as random effects on the intercept. When Biome had a significant effect,  
161 we 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  $DW_{down}$ .

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

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

## 174 Review Results/ Synthesis

175 *NOTE TO COAUTHORS: THIS SECTION HAS A TON OF FIGURES, BUT VERY LITTLE TEXT. IS  
176 THERE ANYTHING THAT SHOULD BE ADDED?*

### 177 Data Coverage

178 Of the # records in ForC v.#, # met the criteria for inclusion in this study (Fig. 1). These records were  
179 distributed across # plots in # distinct geographic areas. Of the 23 flux and 11 stock variables mapped in  
180 these diagrams, ForC contained estimates from  $\geq 7$  distinct geographic areas for # fluxes and # stocks in  
181 tropical broadleaf forests, # fluxes and # stocks in temperate broadleaf forests, # fluxes and # stocks in  
182 temperate conifer forests, and fluxes and # stocks in boreal forests. For regrowth forests (<100 yrs), ForC  
183 contained estimates from  $\geq 7$  distinct geographic areas for # fluxes and # stocks in tropical broadleaf  
184 forests, # fluxes and # stocks in temperate broadleaf forests, # fluxes and # stocks in temperate conifer  
185 forests, and fluxes and # stocks in boreal forests.

### 186 C cycling in mature forests

187 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq 100$   
188 years old and with no known major disturbance or significant anthropogenic management are presented in  
189 Figures 2-5 (and available in tabular format in the ForC release accompanying this publication).

190 For variables with records from  $\geq 7$  distinct geographic areas, these ensemble C budgets were generally  
191 consistent. That is, component fluxes and stocks summed to within one standard deviation of more inclusive  
192 fluxes in all but two instances, both for living C stocks in temperate conifer forests (Fig. 5). **(check this  
193 with final results:)**

194 [https://github.com/forc-db/ForC/blob/master/numbers\\_and\\_facts/C\\_cycle\\_closure.csv](https://github.com/forc-db/ForC/blob/master/numbers_and_facts/C_cycle_closure.csv))

195 Within this biome,  $B_{ag} < B_{ag-wood} + B_{foliage}$  and  $B_{root} < B_{root-coarse} + B_{root-fine}$  because  $B_{ag-wood}$  and  
196  $B_{root-coarse}$  were very high, with strongly disproportionate numbers of records from the high-biomass forests  
197 of the US Pacific Northwest (Figs. S18, S21).

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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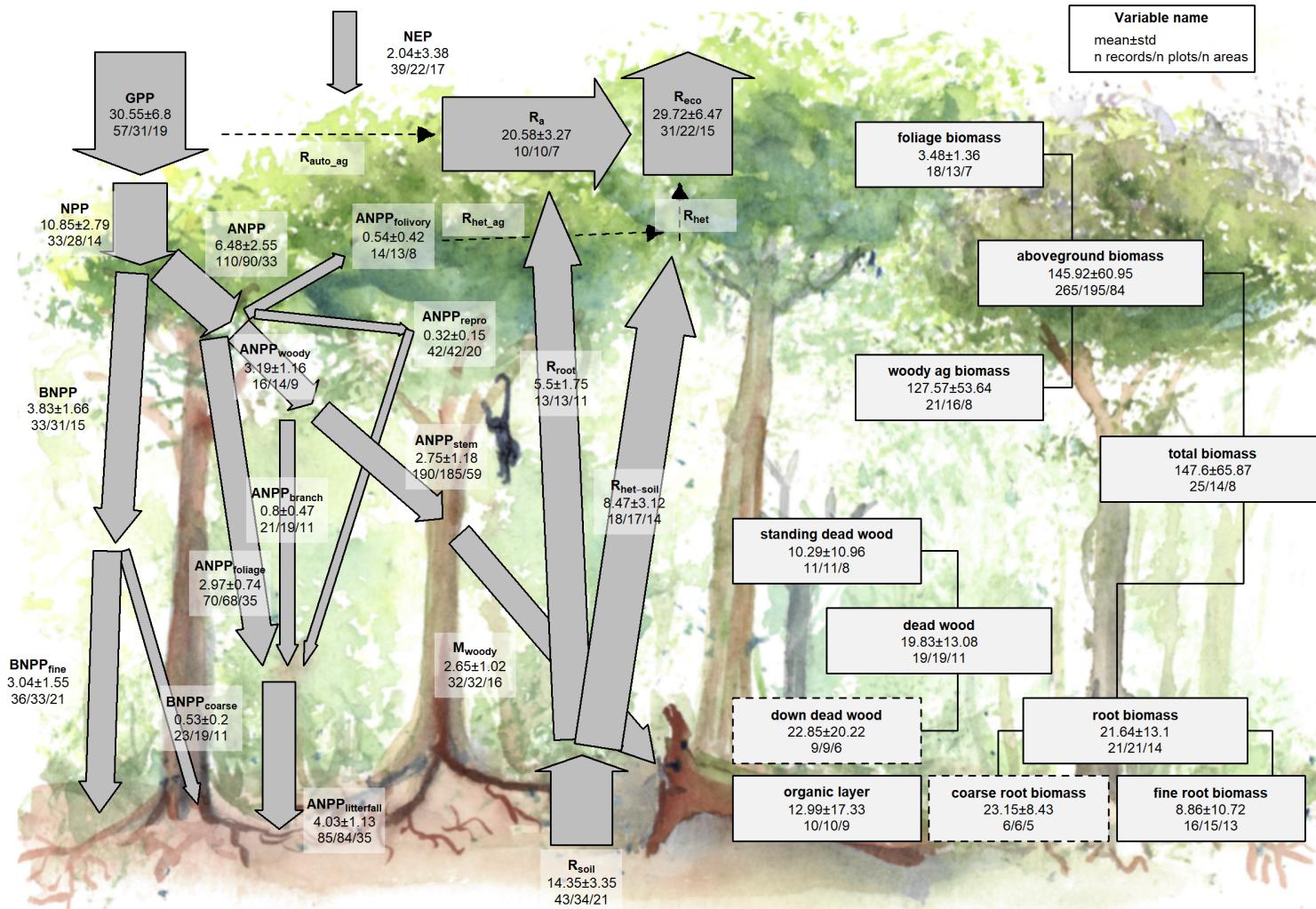


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

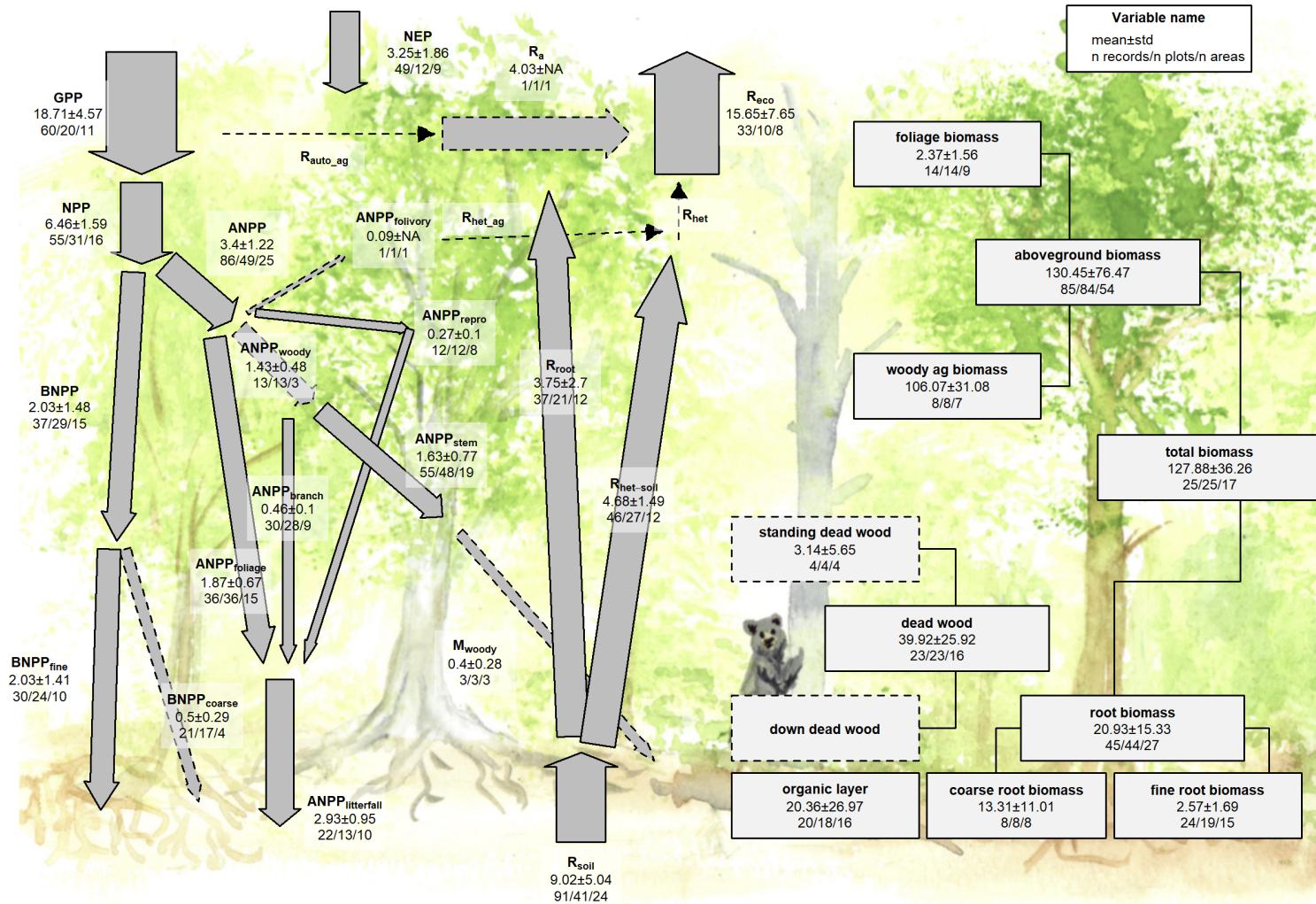


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks.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

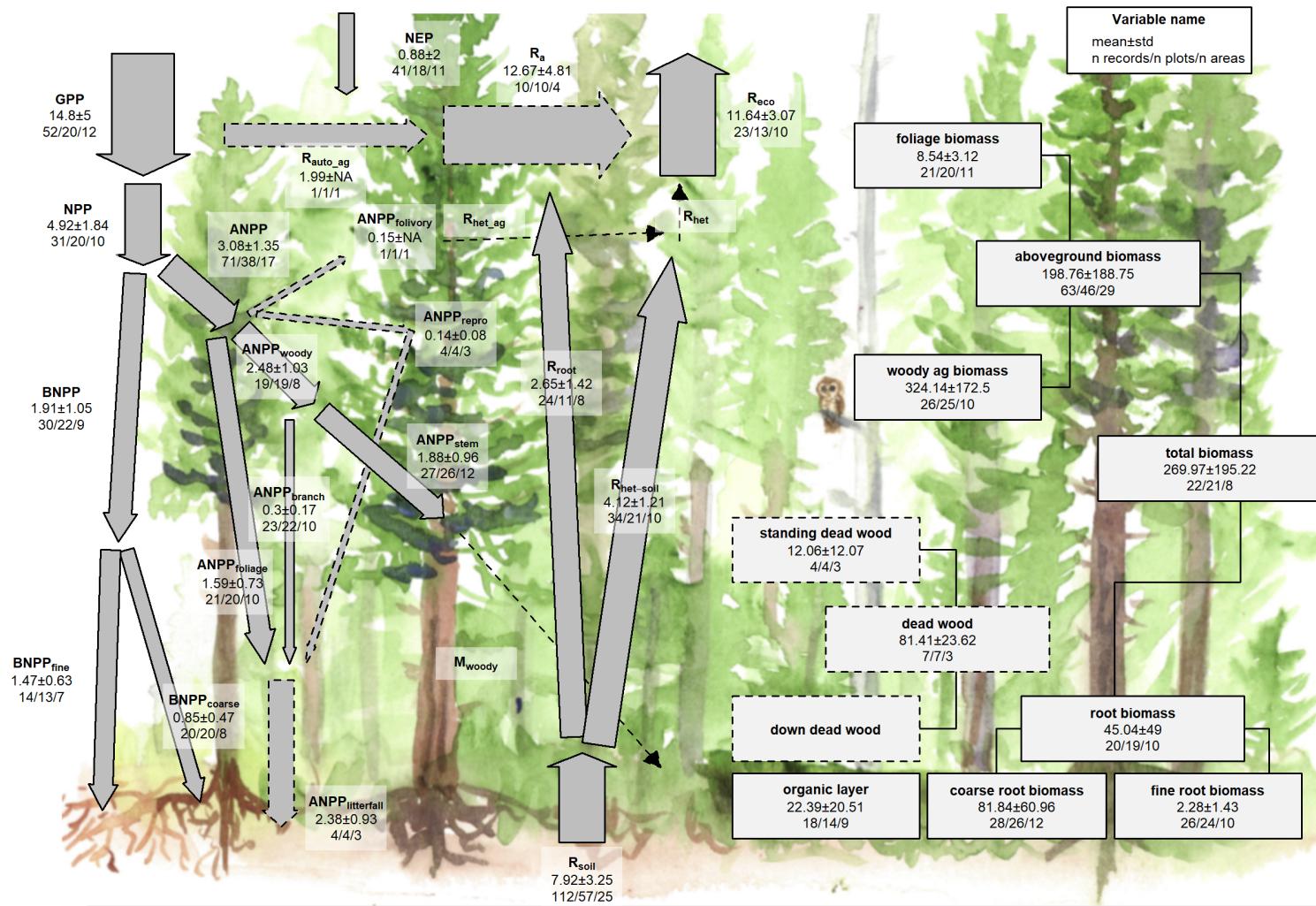


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

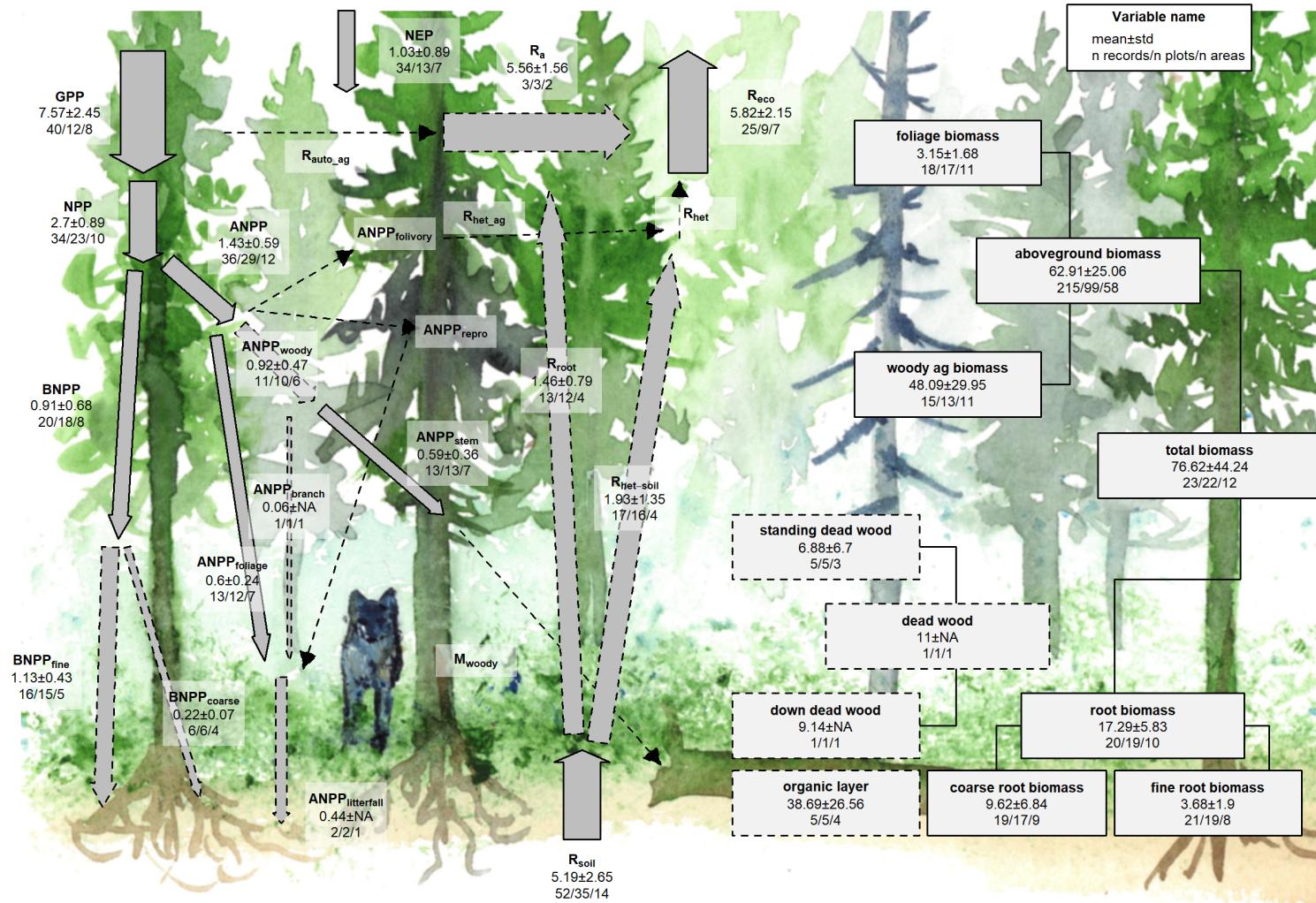


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

198 (The following covers only the variables with age trends figures; there maybe a few more  
199 without much age data) With only # exceptions, C fluxes were highest in tropical forests, intermediate  
200 in temperate (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 6, S1-S15). In this  
201 majority of cases, differences between tropical and boreal forests were always significant, with temperate  
202 forests intermediate and significantly different from one or both. Fluxes tended to be greater in temperate  
203 broadleaf than conifer forests, but the difference was never significant. This pattern held for the following  
204 variables:  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{woody}$ ,  $ANPP_{stem}$ ,  $ANPP_{foliage}$ ,  $ANPP_{litterfall}$ ,  $BNPP$ ,  
205  $BNPP_{fine}$ ,  $R_{eco}$ ,  $R_{root}$ ,  $R_{soil}$ , and  $R_{het-soil}$ .

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

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

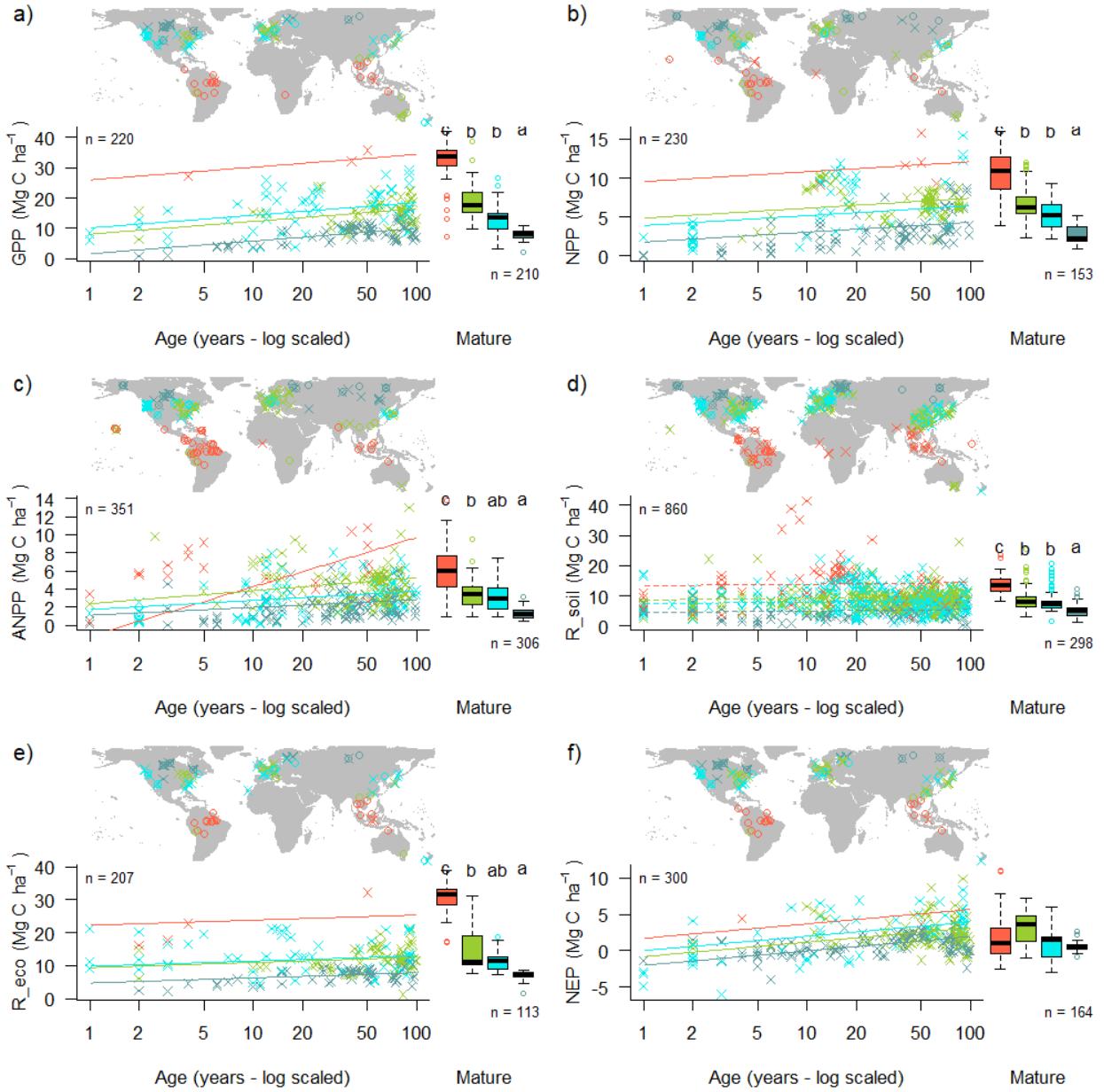


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a)  $GPP$ , (b)  $NPP$ , (c)  $ANPP$ , (d)  $R_{soil}$ , (e)  $R_{eco}$ , and (f)  $NEP$ . Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of age and biome. Solid lines indicate significant effect of age, non-parallel lines indicate a significant age x biome interaction. Boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Individual figures for each flux with sufficient data given in the Supplement (Figs. S1-S15).

213 There were fewer distinct trends in C stocks across biomes (Figs. 7, S16-S26). Specifically, there were  
 214 significant differences for only # of # variables: *LIST*. In all of these cases, temperate conifer forests were in  
 215 the highest significance grouping, and boreal forests in the lowest. Tropical and temperate broadleaf forests  
 216 fell in between—most commonly being significantly different from temperate conifer but not boreal forests.  
 217 Once again, the high values for the temperate conifer biome were driven by the very high-biomass forests of  
 218 the US Pacific Northwest, which are disproportionately represented in the current version of ForC. Thus,

219 biome differences should be interpreted more as driven more by geographic distribution of sampling than by  
 220 true differences.)\*

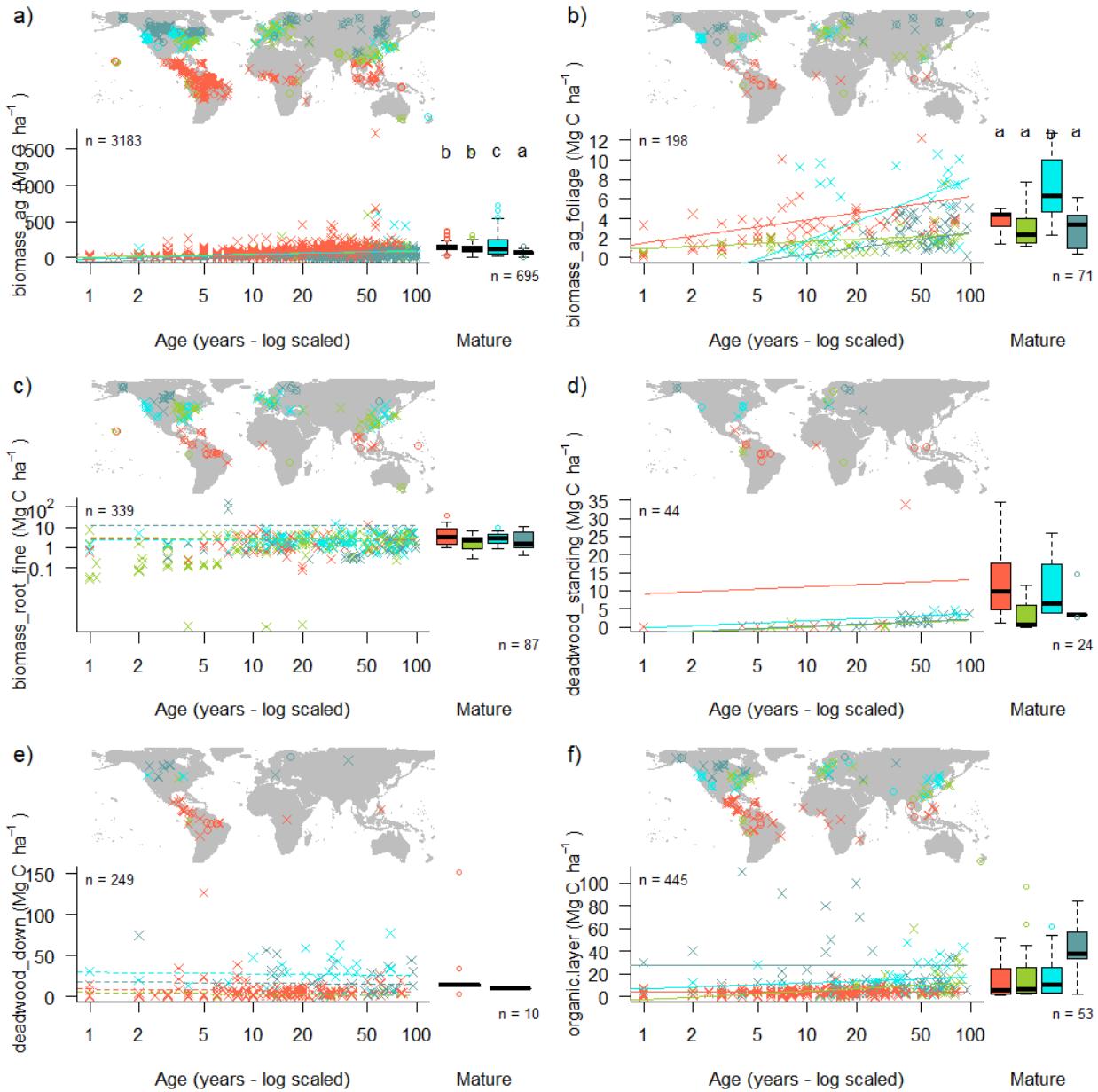


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of age and biome. Solid lines indicate significant effect of age, non-parallel lines indicate a significant age x biome interaction. Boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Individual figures for each stock with sufficient data given in the Supplement (Figs. S16-S26).

## 221 C cycling in young forests

222 Average C cycles for forests <100 years old are presented in Figures 8-11.

223 Both C stocks and fluxes commonly displayed significant trends with stand age for within-biome analyses

<sup>224</sup> (Table 1, Figs. 6-11, S1-S26; detailed below).

<sup>225</sup> ForC contained 14 flux variables with sufficient data for cross-biome analyses of age trends in regrowth  
<sup>226</sup> forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for all variables**). Of these, 9  
<sup>227</sup> increased significantly with  $\log_{10}[\text{stand.age}]$ :  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{foliage}$ ,  $ANPP_{woody}$ ,  
<sup>228</sup>  $ANPP_{woody-stem}$ ,  $BNPP$ ,  $BNPP_{root-fine}$ ,  $R_{eco}$ , and net C sequestration ( $NEP$ ). The remaining  
<sup>229</sup> five— $ANPP_{woody-branch}$ ,  $BNPP_{root-coarse}$ ,  $R_{soil-het}$ , and  $R_{soil-het-}$ —displayed no significant relationship to  
<sup>230</sup> stand age, although all displayed a positive trend.

<sup>231</sup> Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling  
<sup>232</sup> generally most rapid in the tropics and slowest in boreal forests.

<sup>233</sup> The single exception was  $ANPP_{stem}$ , for which temperate broadleaf forests and temperate conifer forests of  
<sup>234</sup> age  $>\sim 30$  had slightly higher flux rates than tropical forests (*represented by a single chronosequence*).

<sup>235</sup> Notably, the trend of tropical > temperate > boreal held for  $NEP$  in regrowth forests, in contrast to the  
<sup>236</sup> lack of biome differences in  $NEP$  for mature forests (Fig. 6).

<sup>237</sup> There were only # flux variables with sufficient data to test for biome x age interactions:  $ANPP$ ,  
<sup>238</sup>  $ANPP_{woody}$ ,  $ANPP_{stem}$ ,  $ANPP_{litterfall}$ , and  $BNPP$ . (**more could be added if age trends become**  
<sup>239</sup> **significant after outliers are resolved**) For three of these ( $ANPP$ ,  $ANPP_{litterfall}$ ,  $BNPP$ ), the  
<sup>240</sup> increase in C flux with age was steepest increase in tropical forests, followed by temperate and then boreal  
<sup>241</sup> forests (Figs S#). Similarly,  $ANPP_{woody}$  displayed a steeper increase with age in temperate than boreal  
<sup>242</sup> boreal forests (no tropical data for this variable). In contrast, for  $ANPP_{stem}$ , tropical and temperate  
<sup>243</sup> broadleaf forests had the highest flux rates at young ages, but were surpassed by temperate conifer forests  
<sup>244</sup> between ages 20 and 50 (Fig. S6).

<sup>245</sup> (**this needs to be updated with latest data**) In terms of C stocks, 10 variables had sufficient data to  
<sup>246</sup> test for age trends. Six of these—*total biomass, aboveground biomass, aboveground woody biomass, foliage*  
<sup>247</sup> *biomass, root biomass, and coarse root biomass*—increased significantly with  $\log_{10}[\text{stand.age}]$ . The  
<sup>248</sup> remaining four displayed non-significant positive trends: *fine root biomass, total dead wood, standing dead*  
<sup>249</sup> *wood, and organic layer. (discuss rates of increase)*



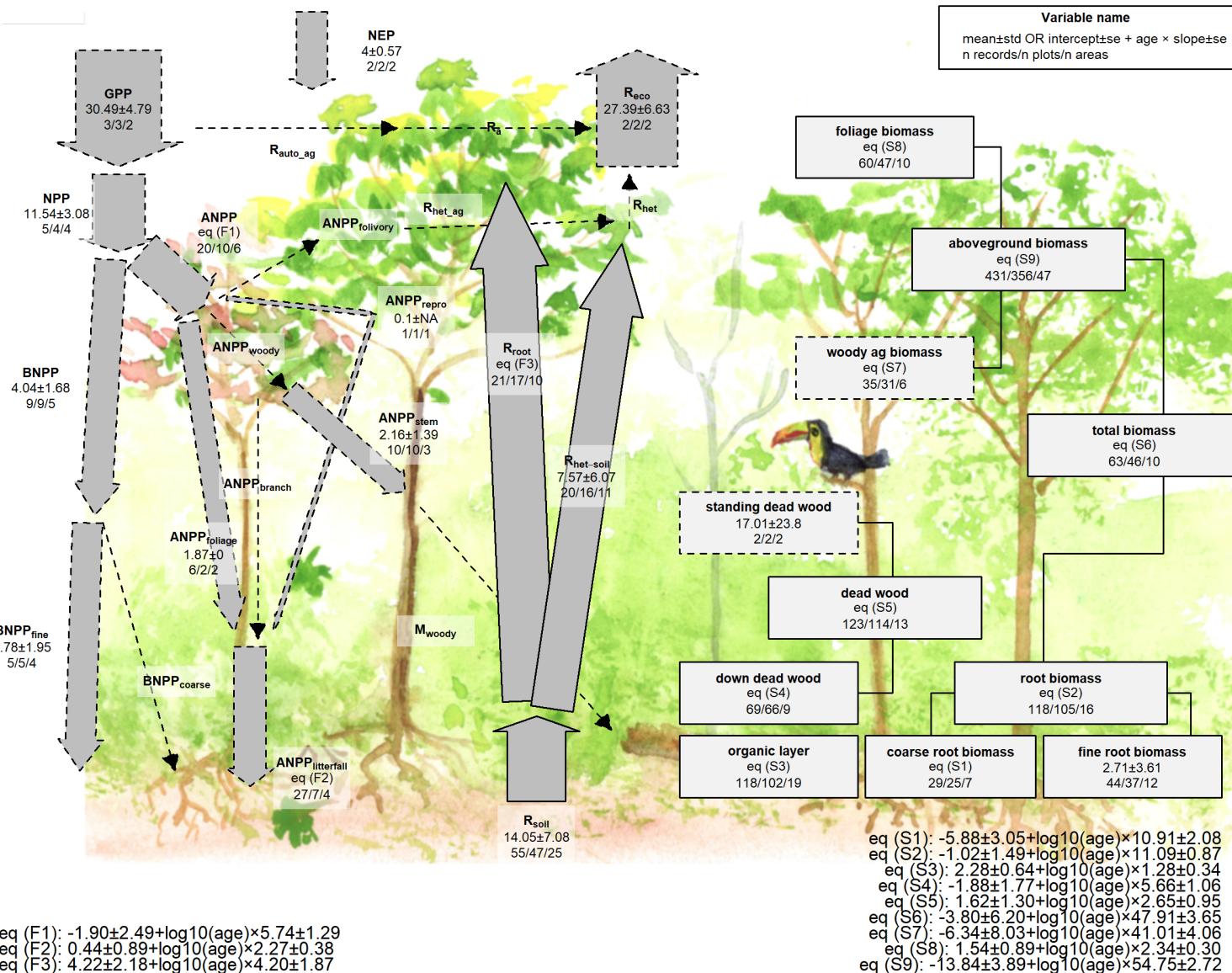


Figure 8 | C cycle diagram for young tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When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

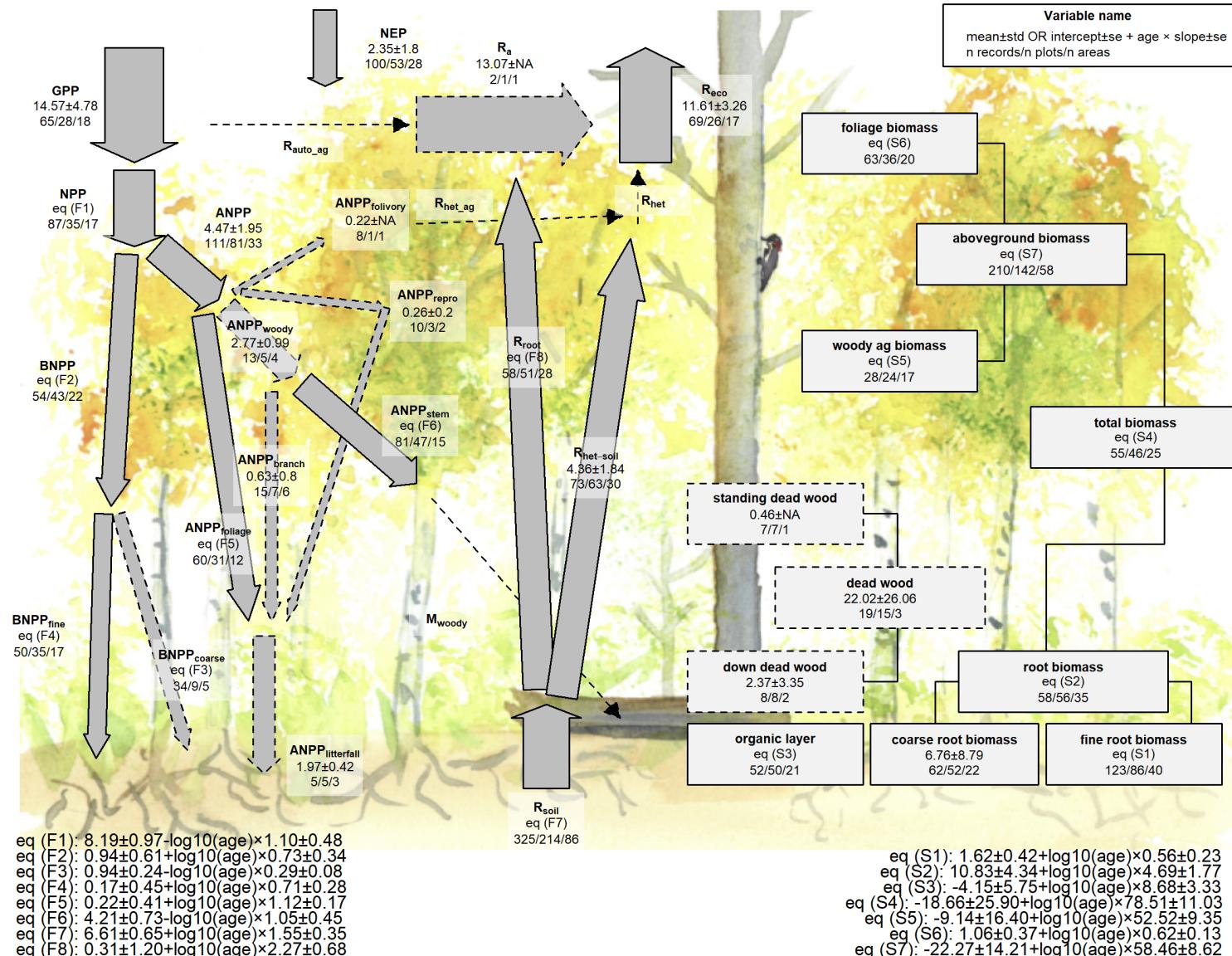


Figure 9 | C cycle diagram for young temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When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

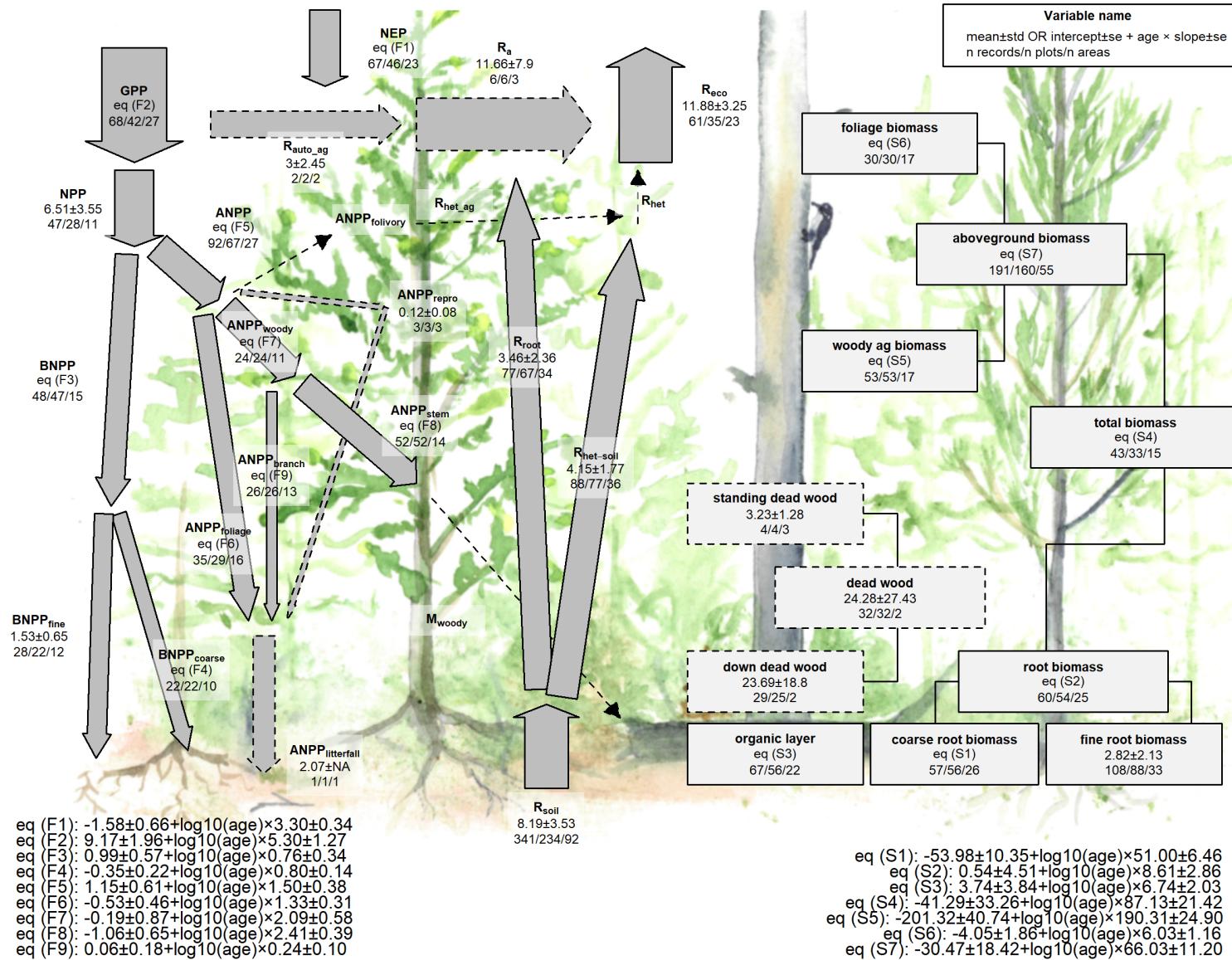


Figure 10 | C cycle diagram for young temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When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

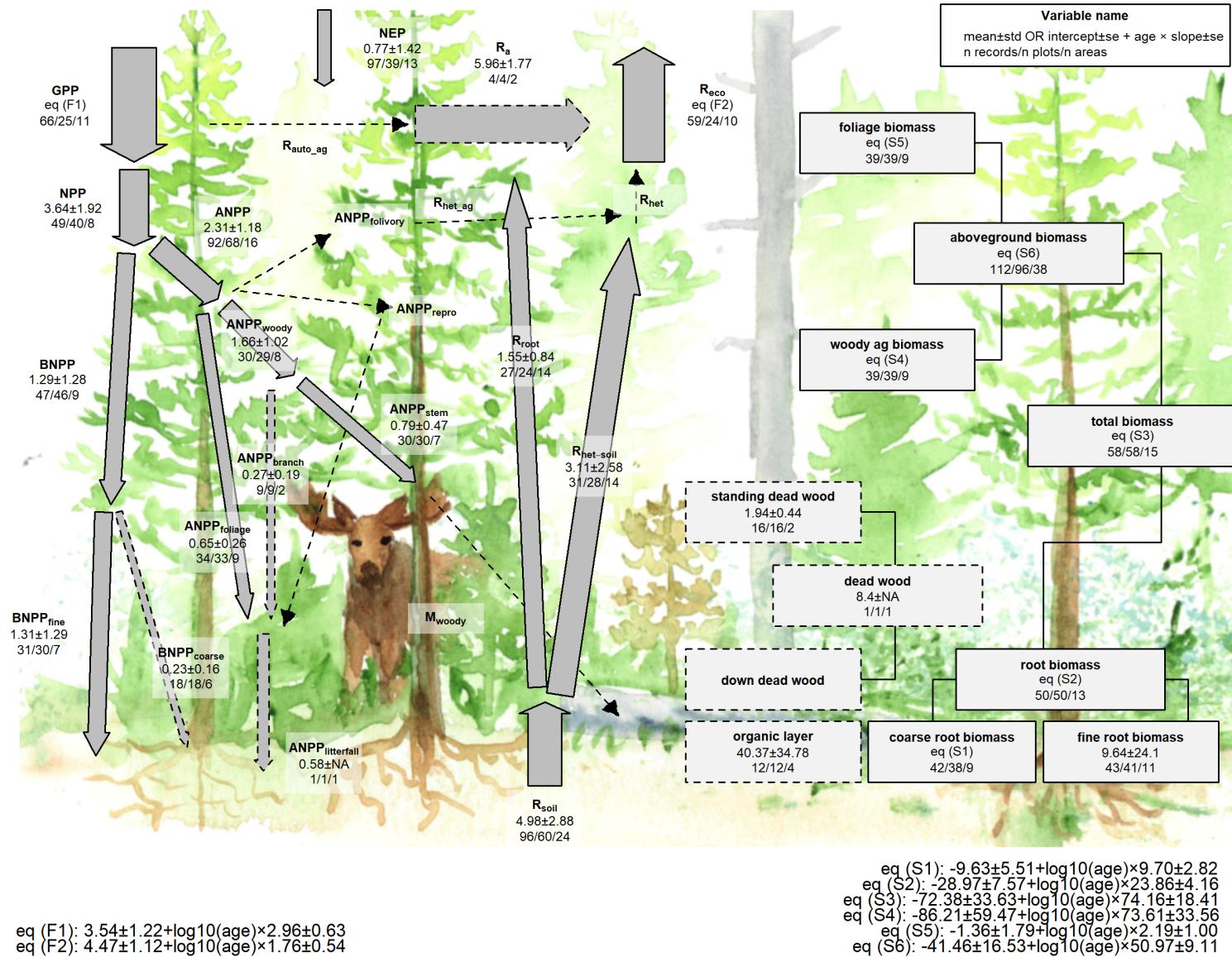


Figure 11 | C cycle diagram for young boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup>. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When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

250 **Discussion**

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

260 **C variable coverage and budget closure**

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

270 Closure of the C cycle budgets for mature forests (Figs. 2-5) is fairly good. However, SD's are often large,  
271 reflective of significant within-biome variation. This makes the standard for closure relatively loose. Lack of  
272 closure, in the few instances where it occurs, is probably more reflective of differences in the representation of  
273 forest types (e.g., disproportionate representation of US Pacific NW for aboveground woody biomass relative  
274 to AGB; Fig. 4) than of methodological accuracy. Thus, overall, a high degree of closure implies that ForC  
275 gives a consistent picture of C cycling within biomes. While these means are unlikely to be accurate  
276 representations of C cycling within any particular forest, they provide a useful baseline for comparison,  
277 always keeping in mind that sample means do not necessarily represent the true mean of the entire biome.

278 **C cycling across biomes**

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

290 accumulation.  
291 In contrast to C fluxes and accumulation rates in regrowth forests, stocks...  
292 Thus, biome differences should be interpreted more as driven more by geographic distribution of sampling  
293 than by true differences.

294 **Age trends in C cycling**

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

296 A relative dearth of data on C cycling in secondary forests, particularly in the tropics (Anderson-Teixeira et  
297 al 2016), is problematic in that almost 2/3 of the world's forests were secondary as of 2010 (FAO 2010),  
298 implying an under-filled need to characterize age-related trends in forest C cycling.  
299 Moreover, as disturbances increase (???, McDowell *et al* 2020), understanding the carbon dynamics of  
300 regrowth forests will be increasingly important.  
301 It's also important to understand secondary forest C sequestration to reduce uncertainty regarding the  
302 potential for carbon uptake by regrowth forests (???, Cook-Patton *et al* 2020).  
303 NEP increases with log(age) to 100 -> strongest C sinks are established secondary forests.

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

305 The future of forest C cycling will shape trends in atmospheric CO<sub>2</sub> and the course of climate change. For a  
306 human society seeking to understand and mitigate climate change, the data contained in ForC and  
307 summarized here can help to meet two major challenges.  
308 First, improved representation of forest C cycling in models is essential to improving predictions of the future  
309 course of climate change. To ensure that models are giving the right answers for the right reasons, it is  
310 important benchmark against multiple components of the C cycle. By making tens of thousands of records  
311 readily available in standardized format, ForC makes it feasible for the modeling community to draw upon  
312 these data to benchmark models. Integration of ForC with models is a goal (Fer *et al.*, in revision). On a  
313 more cursory level, the values summarized here can serve as a sanity check for modelers to determine whether  
314 model predictions for multiple C cycle variables are reasonable—i.e., within the range of previous observations.  
315 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change  
316 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not  
317 feasible for the individuals and organizations designing such efforts to sort through literature, often behind  
318 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline  
319 through which information can flow efficiently from forest researchers to decision-makers working to  
320 implement forest conservation strategies at global, national, or landscape scales. This is already happening!  
321 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;  
322 Requena Suarez *et al* (2019); Rozendaal et al in prep], mapping C accumulation potential from natural forest  
323 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*  
324 2020).  
325 There remain numerous data needs for improved accounting of forest carbon stocks and fluxes in GHG  
326 accounting. AGB is the largest stock, and most of the emphasis is on this variable. Remote sensing, with

327 calibration based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019), is the  
328 best approach for mapping forest carbon (REFS). However, it is limited in that it is not associated with  
329 stand age and disturbance history, except in recent decades when satellite data can be used to detect forest  
330 loss, gain, and some of their dominant drivers (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). ForC  
331 is therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020).

332 *remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP*  
333 (*Bagdley et al.* 2019, (*Li and Xiao 2019*)), *aboveground biomass (B<sub>ag</sub>) (REFS)*, *woody mortality (i.e., B<sub>ag</sub>*  
334 *losses to mortality M<sub>woody</sub>) (Clark et al 2004, Leitold et al 2018)*, and to some extent net ecosystem  
335 *exchange (NEP) (REFS)*,

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

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

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

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