

<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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<sup>27</sup> **NOTES TO COAUTHORS:**

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

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

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

**34    Summary**

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

**39    Methods/Design.** Here, we draw from the Global Forest C Database, ForC, to provide a macroscopic  
40    overview of C cycling in the world's forests, giving special attention to stand age-related variation.  
41    Specifically, we use 14105 ForC records from 821 geographic locations representing 34 C cycle variables to  
42    characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate  
43    broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age  $<100$  years)  
44    forests. For regrowth forests, we quantify age trends for all variables.

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

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

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

**52    Background**

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

**54    Forest ecosystems** will play a critical role in shaping the course of climate change (IPCC1.5) through their  
55    influence on atmospheric carbon dioxide ( $\text{CO}_2$ ). Their annual gross  $\text{CO}_2$  sequestration (gross primary  
56    productivity,  $GPP$ ) is estimated at  $>69 \text{ Gt C yr}^{-1}$  (???, or  $>7$  times average annual fossil fuel emissions  
57    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  
58    counterbalanced by  $\text{CO}_2$  releases to the atmosphere through ecosystem respiration ( $R_{\text{eco}}$ ) or fire, a small  
59    portion has been retained in ecosystems over recent decades. The resulting  $\text{CO}_2$  sink averaged  $3.0 \pm 0.8 \text{ Gt C}$   
60     $\text{yr}^{-1}$  from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update**,  
61    **give range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial  
62    biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Forests are also globally  
63    dominant as a source of soil respiration (???). Globally, net deforestation (*i.e.*, gross deforestation -  
64    regrowth) has been a source of  $\text{CO}_2$  emissions, estimated at  $\sim 1.1 \text{ Gt C yr}^{-1}$  from YEAR-YEAR (Pan et al  
65    2011), reducing the net forest sink to  $\sim 1.2\text{-}1.7 \text{ Gt C yr}^{-1}$  across Earth's forests (Le Quéré et al 2017, Schimel  
66    *et al* 2015) (**update, give range**). The future of the current forest C is dependent both upon forest  
67    responses to a broad suite of global change drivers and to future land use decisions, and will strongly  
68    influence the course of climate change. Regrowing forests in particular will play an important role (Pugh *et*  
69    *al* 2019), as these represent a large (~#%) and growing proportion of Earth's forests (McDowell *et al* 2020).  
70    Understanding, modeling, and managing forest-atmosphere  $\text{CO}_2$  exchange is thus central to efforts to  
71    mitigate climate change [Grassi *et al* (2017); Griscom *et al* (2017); **Cavaleri et al 2015**].

**72    Despite** the centrality of forest C cycling in regulating atmospheric  $\text{CO}_2$ , important uncertainties in climate

73 models (???, ???, ???, Krause *et al* 2018) and CO<sub>2</sub> accounting frameworks (Pan *et al* 2011) can be traced  
74 to lack of accessible, comprehensive data on how C cycling varies across forest types and in relation to stand  
75 history. These require large-scale databases with global coverage, which runs contrary to the nature in which  
76 forest C stocks and fluxes are measured and published. While remote sensing measurements are increasingly  
77 useful for global- or regional-scale estimates of a few critical variables [Li and Xiao (2019); **REFS for**  
78 **biomass, biomass change, net CO2 flux**], measurement of most forest C stocks and fluxes require  
79 intensive on-the-ground data collection. Original studies typically cover only a small numbers of sites at a  
80 time, with rare exceptions spanning regions or continents [e.g., Lutz *et al* (2018); **FLUXNET\_REF**],  
81 typically coordinated through research networks such as ForestGEO (Anderson-Teixeira *et al* 2015) or  
82 FLUXNET (Baldocchi *et al* 2001). The result of decades of research on forest C cycling is that tens of  
83 thousands of records have been distributed across literally thousands of scientific articles –often behind  
84 paywalls– along with variation in data formats, units, measurement methods, *etc..* In this format, the data  
85 are effectively inaccessible for many global-scale analyses, including those attempting to benchmark model  
86 performance with global data (Clark *et al* 2017, Luo *et al* 2012), quantify the the role of forests in the global  
87 C cycle (*e.g.*, Pan *et al* 2011), or use book-keeping methods to quantify actual or scenario-based exchanges of  
88 CO<sub>2</sub> between forests and the atmosphere (**REFS**).

89 To address the need for global-scale analyses of forest C cycling, we recently developed an open-access Global  
90 Forest Carbon database, ForC (Anderson-Teixeira *et al* (2016), Anderson-Teixeira *et al* (2018)). ForC  
91 contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables) based on  
92 ground-based measurements, along with associated data required for interpretation (*e.g.*, stand history,  
93 measurement methods). These data have been amalgamated from original peer-reviewed publications, either  
94 directly or via intermediary data compilations. Since the its most recent publication (Anderson-Teixeira *et al*  
95 2018), ForC has been integrated with two large databases: the Global Soil Respiration Database (SRDB;  
96 Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database  
97 (GROA; Cook-Patton *et al* 2020), both of which have also synthesized published forest C data. Following  
98 these additions, ForC currently contains 47846 records from 10609 plots and 1532 distinct geographic areas  
99 representing all forested biogeographic and climate zones.

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

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

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

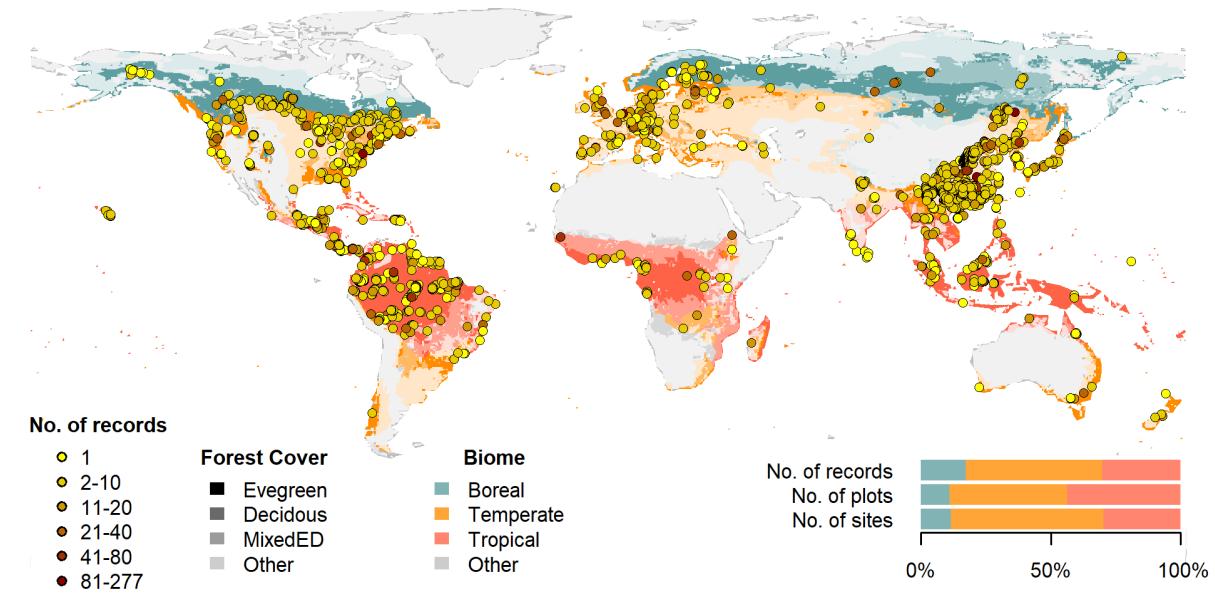


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

## 112 Methods/ Design

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

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

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

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

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

118 broad geographic scales and as a function of stand age. As such, there has been a focus on incorporating

119 data from regrowth forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining

120 stand age data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention

121 was given to developing the database for tropical forests (Anderson-Teixeira *et al* 2016). Since publication of

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

123 v.##, 9497 records; Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment

124 database (GROA v1.0, 18143 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020), and data from

125 several publications [*e.g.*, Taylor *et al* (2017), Lutz *et al* (2018), Johnson *et al* (2018); detailed list at

126 [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

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

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

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

130 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*, resulting in a total of 32862 records (68.7% size of total database). Records were filtered to remove plots that had undergone significant anthropogenic management or major disturbance since the most recent stand initiation event. Specifically, we removed all plots flagged as managed in ForC-simplified (18.8%). 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 (5.7%) included stands that had undergone anthropogenic thinning or partial harvest unless this was very minor. We retained sites that were grazed or had undergone low severity natural disturbances (<10% mortality) including droughts, major storms, fires, and floods. We removed all plots for which no stand history information had been retrieved (7.2%). In total, this resulted in 23528 records (49.2% of the records in the database) being eligible for inclusion in the analysis.

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). Records for these variables represented 89.6% of the total records eligible for inclusion. 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 threshold for tree census was  $\leq 10\text{cm}$ . All records were measured directly or derived from field measurements (as opposed to modeled).

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). Assigning stands to these groupings required the exclusion of records for which ForC lacked records of stand age (4.8% of records in full database), or geographic coordinates (0.4% of sites in full database). We also excluded records of stand age = 0 year (0.8% of records in full database). In total, our analysis retained 66.9 of the focal variable records for forests of known age.

Data were summarized to produce schematics of C cycling across the eight biome - age group combinations identified above. 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.

To test for differences across mature forest biomes, the original values were analyzed via a linear mixed

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)	426	200	91	n.s.	+
<i>GPP</i>	gross primary production ( $NPP + R_{auto}$ or $R_{eco} - NEE$ )	410	175	92	$TrB > TeB \geq TeN > BoN$	+
<i>NPP</i>	net primary production ( $ANPP + BNPP$ )	340	205	76	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP</i>	aboveground <i>NPP</i>	615	426	136	$TrB > TeB \geq TeN \geq BoN$	++; xB
<i>ANPP<sub>woody</sub></i>	woody production ( $ANPP_{stem} + ANPP_{branch}$ )	126	114	37	$TrB \geq TeN \geq TeB \geq BoN$	+
<i>ANPP<sub>stem</sub></i>	woody stem production	458	411	118	$TrB > TeN \geq TeB > BoN$	-; xB
<i>ANPP<sub>branch</sub></i>	branch turnover	125	112	42	$TrB > TeB \geq TeN \geq BoN$	n.s.
<i>ANPP<sub>foliage</sub></i>	foliage production, typically estimated as annual leaf litterfall	275	231	89	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP<sub>litterfall</sub></i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	147	117	55	$TrB \geq TeB \geq TeN \geq BoN$	+
<i>ANPP<sub>repro</sub></i>	production of reproductive structures (flowers, fruits, seeds)	72	65	35	n.s.	n.s.
<i>ANPP<sub>folivory</sub></i>	foliar biomass consumed by folivores	24	16	11	n.s.	n.s.
<i>M<sub>woody</sub></i>	woody mortality—i.e., $B_{ag}$ of trees that die	35	35	19	$TrB > TeB$	n.s.
<i>BNPP</i>	belowground NPP ( $BNPP_{coarse} + BNPP_{fine}$ )	275	239	82	$TrB > TeN \geq TeB \geq BoN$	+
<i>BNPP<sub>coarse</sub></i>	coarse root production	144	111	36	n.s.	n.s.
<i>BNPP<sub>fine</sub></i>	fine root production	207	171	69	n.s.	+
<i>R<sub>eco</sub></i>	ecosystem respiration ( $R_{auto} + R_{het}$ )	303	140	80	$TrB > TeB \geq TeN \geq BoN$	+
<i>R<sub>auto</sub></i>	autotrophic respiration ( $(R_{auto-ag} + R_{root})$ )	36	35	15	$TrB > TeN \geq BoN \geq TeB$	n.s.
<i>R<sub>auto-ag</sub></i>	aboveground autotrophic respiration (i.e., leaves and stems)	3	3	2	$TrB > TeN \geq BoN \geq TeB$	n.s.
<i>R<sub>root</sub></i>	root respiration	267	213	102	n.s.	++; xB
<i>R<sub>soil</sub></i>	soil respiration ( $R_{het-soil} + R_{root}$ )	1104	715	241	$TrB > TeB \geq TeN > BoN$	++; xB
<i>R<sub>het-soil</sub></i>	soil heterotrophic respiration	324	262	110	$TrB > TeB \geq TeN \geq BoN$	n.s.
<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 ( $B_{ag} + B_{root}$ )	329	282	88	$TeN \geq TrB \geq TeB \geq BoN$	++; xB
<i>B<sub>ag</sub></i>	aboveground live biomass ( $B_{ag-wood} + B_{foliage}$ )	3790	3264	569	$TrB \geq TeN \geq TeB > BoN$	++; xB
<i>B<sub>ag-wood</sub></i>	woody component of aboveground biomass	224	210	66	$TeN > TrB \geq TeB \geq BoN$	++; xB
<i>B<sub>foliage</sub></i>	foliage biomass	260	216	74	$TeN > TrB \geq BoN \geq TeB$	++; xB
<i>B<sub>root</sub></i>	total root biomass ( $B_{root-coarse} + B_{root-fine}$ )	2273	2248	352	n.s.	++; xB
<i>B<sub>root-coarse</sub></i>	coarse root biomass	245	225	74	$TeN > TrB \geq TeB \geq BoN$	++; xB
<i>B<sub>root-fine</sub></i>	fine root biomass	394	321	113	n.s.	n.s.
<i>DW<sub>tot</sub></i>	deadwood ( $DW_{standing} + DW_{down}$ )	223	212	42	$TeN > TeB \geq TrB \geq BoN$	+
<i>DW<sub>standing</sub></i>	standing dead wood	56	56	21	n.s.	+
<i>DW<sub>down</sub></i>	fallen dead wood, including coarse and sometimes fine woody debris	175	168	29	n.s.	++; xB
<i>OL</i>	organic layer / litter/ forest floor	420	365	99	n.s.	++; xB

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

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

174 effects model ['lmer' function in 'lme4' R package version **x.xx; REF**] with biome as fixed effect and plot  
175 nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we  
176 looked at a Tukey's pairwise comparison to see which biomes were significantly different from one another.  
177 There were enough data to run this analysis for all focal variables but  $DW_{down}$ .  
  
178 To test for age trends in young (<100yrs) forests, we employed a mixed effects model with biome and  
179  $\log_{10}[\text{stand.age}]$  as fixed effects and plot nested within geographic.area as a random effect on the intercept.  
180 When the effect of stand.age was significant at  $p \leq 0.05$  and when each biome had records for stands of at  
181 least 10 different ages, a biome \* stand.age interaction was included in the model.  
  
182 All database manipulation, analyses, and figure production were fully automated in R (**version, citation**).  
183 Materials required to fully reproduce these analyses, including data, R scripts, and image files, are archived  
184 in Zenodo (DOI: TBD). Data, scripts, and results presented here are also available through the open-access  
185 ForC GitHub repository (<https://github.com/forc-db/ForC>), where many will be updated as the database  
186 develops.

## 187 Review Results/ Synthesis

### 188 Data Coverage

189 Of the 47846 records in ForC v.#, 14105 met the criteria for inclusion in this study (Fig. 1). These records  
190 were distributed across 4358 plots in 821 distinct geographic areas. Of the 23 flux and 11 stock variables  
191 mapped in these diagrams, ForC contained mature forest estimates from  $\geq 7$  distinct geographic areas for 20  
192 fluxes and 9 stocks in tropical broadleaf forests, 15 fluxes and 9 stocks in temperate broadleaf forests, 15  
193 fluxes and 8 stocks in temperate conifer forests, and 9 fluxes and 7 stocks in boreal forests. For regrowth  
194 forests (<100 yrs), ForC contained estimates from  $\geq 7$  distinct geographic areas for 3 fluxes and 9 stocks in  
195 tropical broadleaf forests, 12 fluxes and 8 stocks in temperate broadleaf forests, 15 fluxes and 8 stocks in  
196 temperate conifer forests, and 12 fluxes and 12 stocks in boreal forests.

### 197 C cycling in mature forests

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

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

205 [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))  
206 Within this biome,  $B_{ag} < B_{ag-wood} + B_{foliage}$  and  $B_{root} < B_{root-coarse} + B_{root-fine}$  because  $B_{ag-wood}$  and  
207  $B_{root-coarse}$  were very high, with strongly disproportionate numbers of records from the high-biomass forests  
208 of the US Pacific Northwest (Figs. S18, S21).

$\infty$

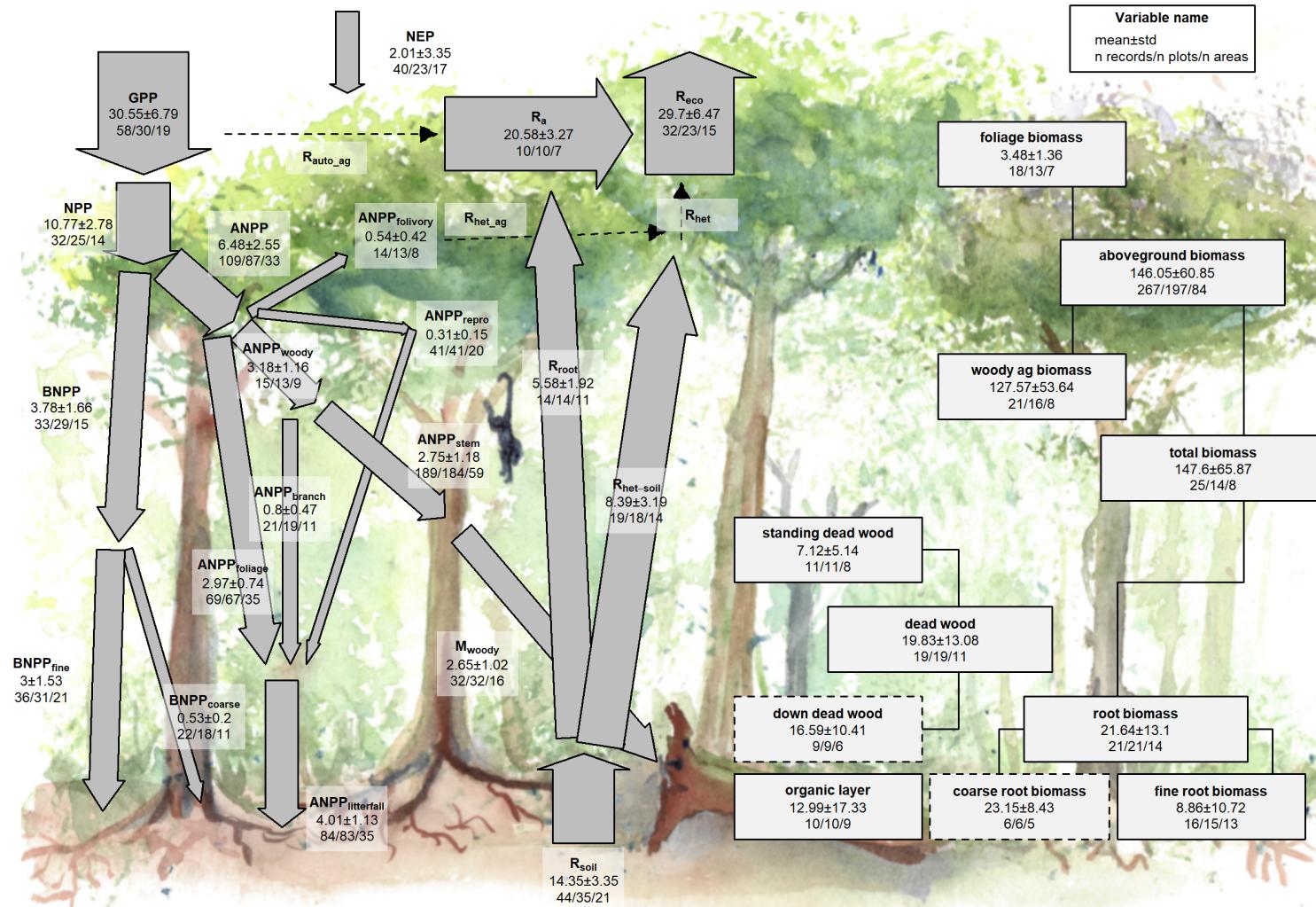


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks.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

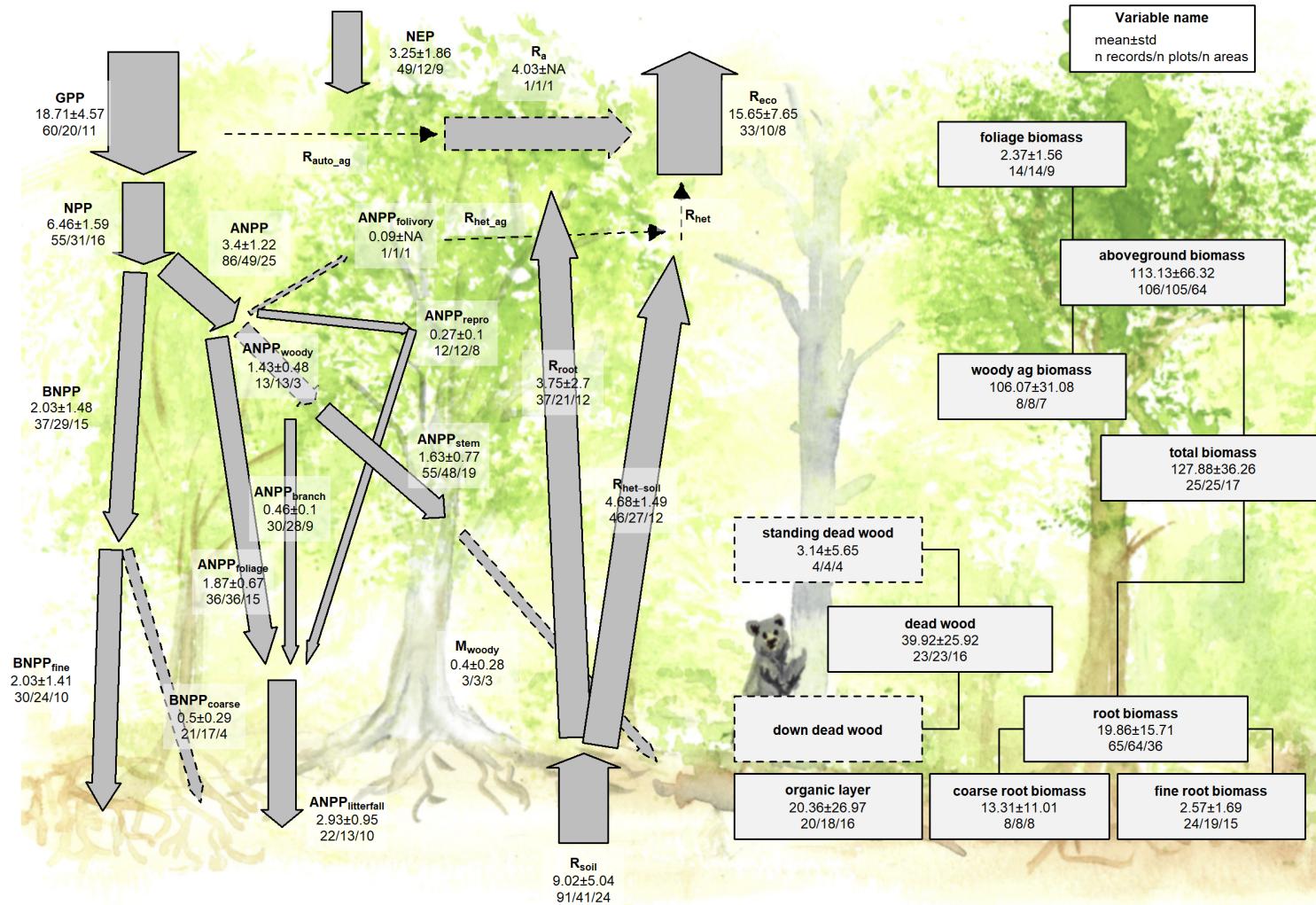


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate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

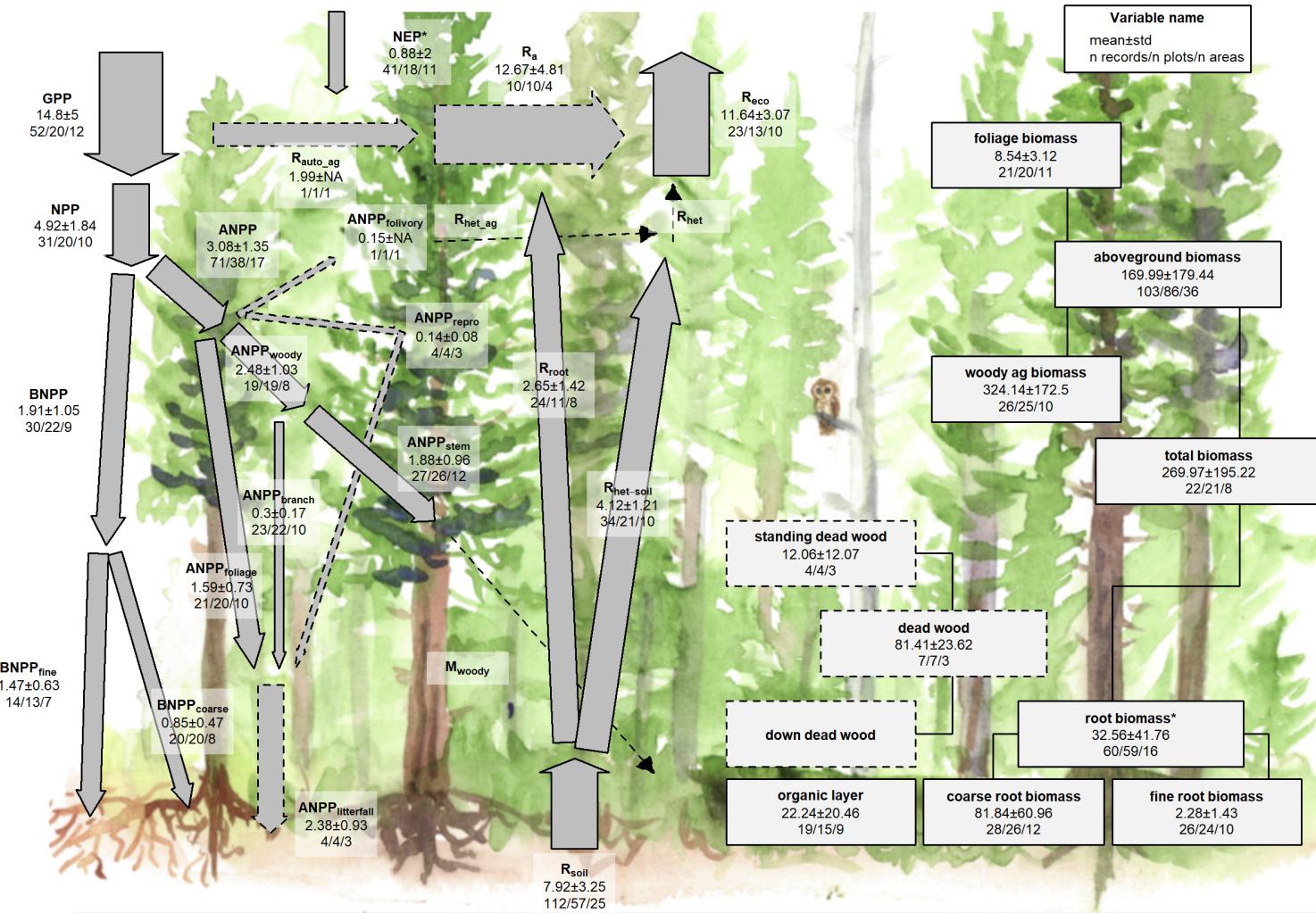


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks.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

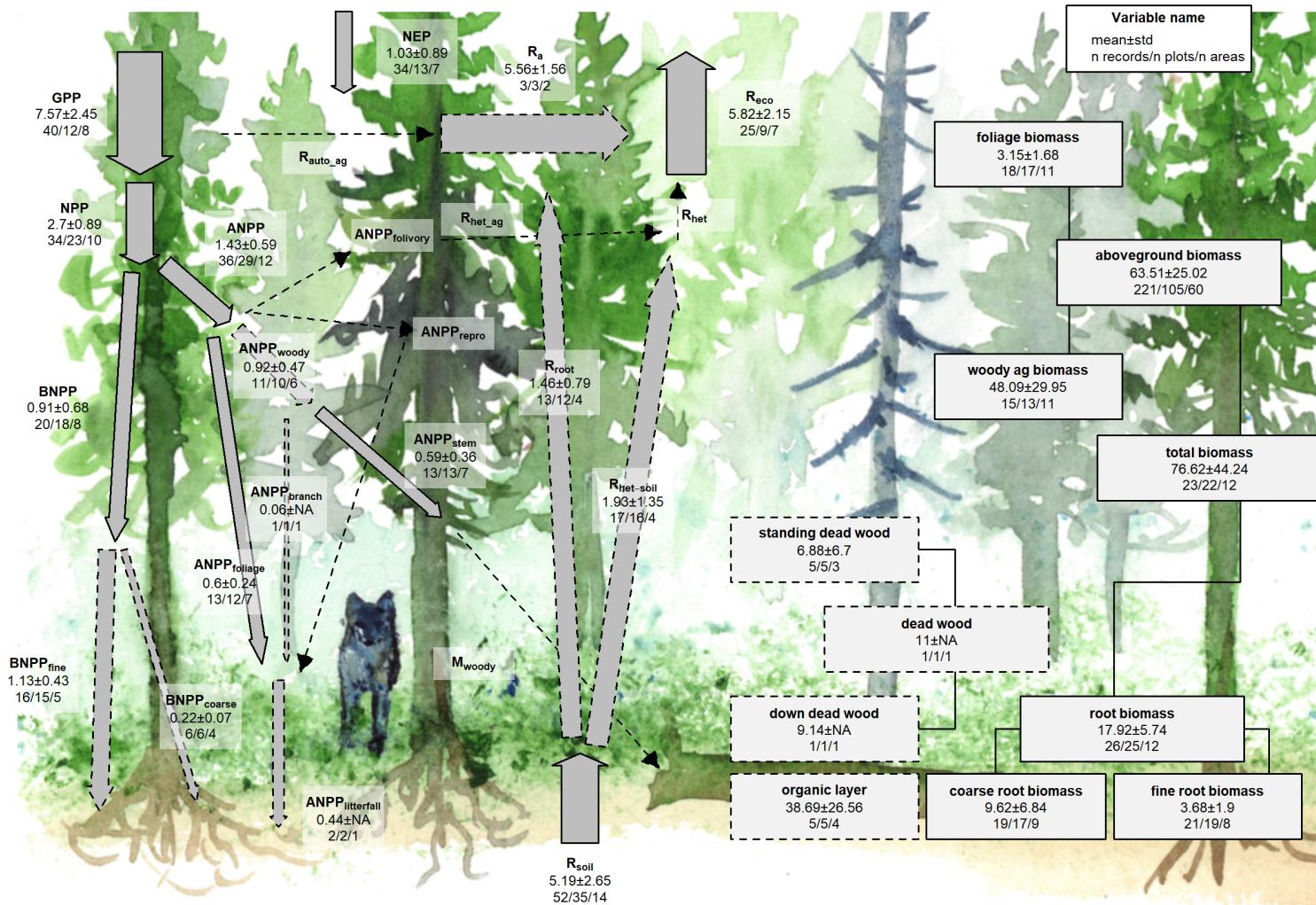


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks.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

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

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

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

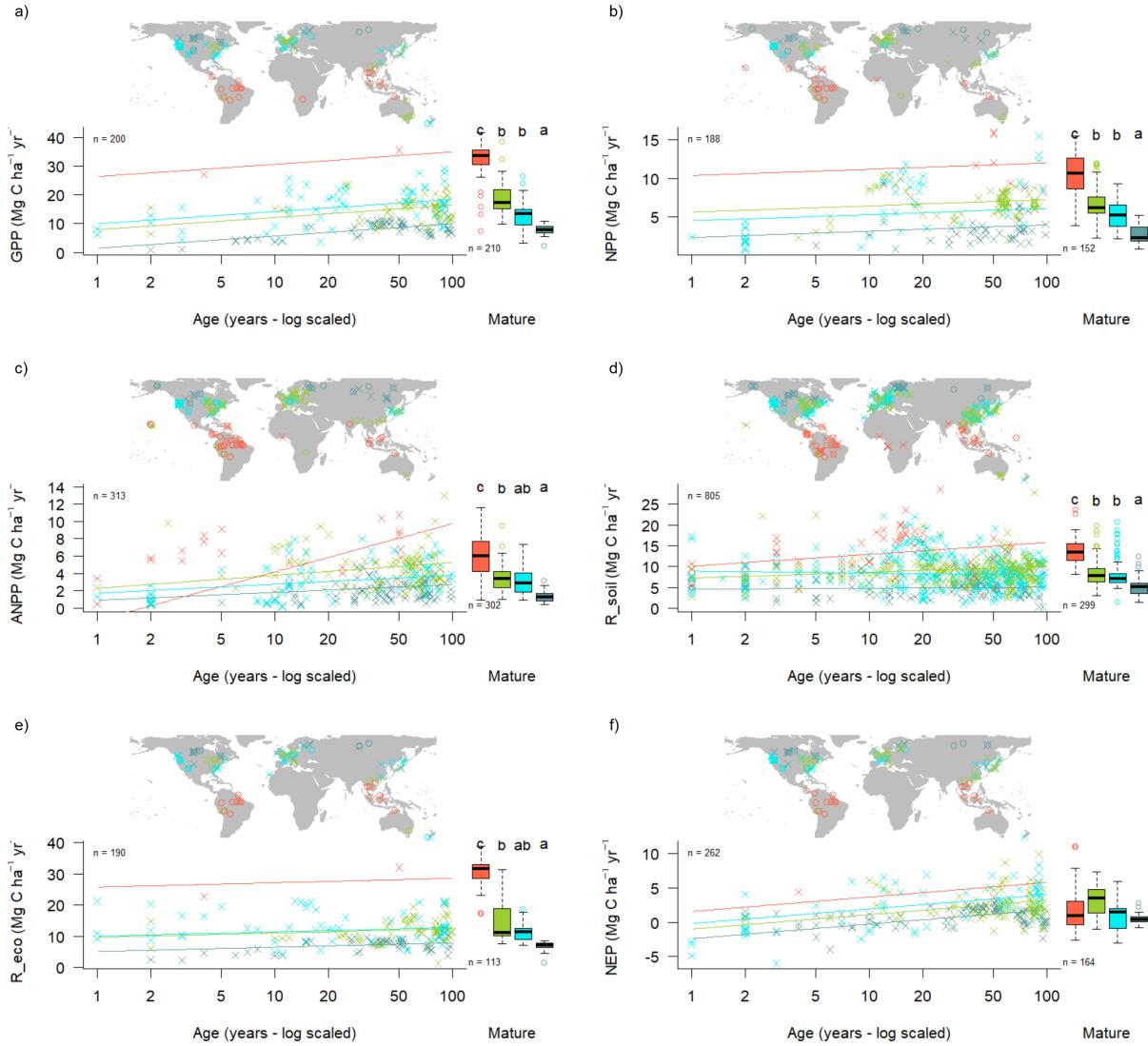


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a)  $GPP$ , (b)  $NPP$ , (c)  $ANPP$ , (d)  $R_{soil}$ , (e)  $R_{eco}$ , and (f)  $NEP$ . Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 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).

224 There were fewer distinct trends in C stocks across biomes (Figs. 7, S16-S26). Specifically, there were  
 225 significant differences for only ## of ## variables: **LIST**. In all of these cases, temperate conifer forests  
 226 were in the highest significance grouping, and boreal forests in the lowest. Tropical and temperate broadleaf  
 227 forests fell in between—most commonly being significantly different from temperate conifer but not boreal  
 228 forests. Once again, the high values for the temperate conifer biome were driven by the very high-biomass  
 229 forests of the US Pacific Northwest, which are disproportionately represented in the current version of ForC.  
 230 Thus, biome differences should be interpreted more as driven more by geographic distribution of sampling  
 231 than by true differences.

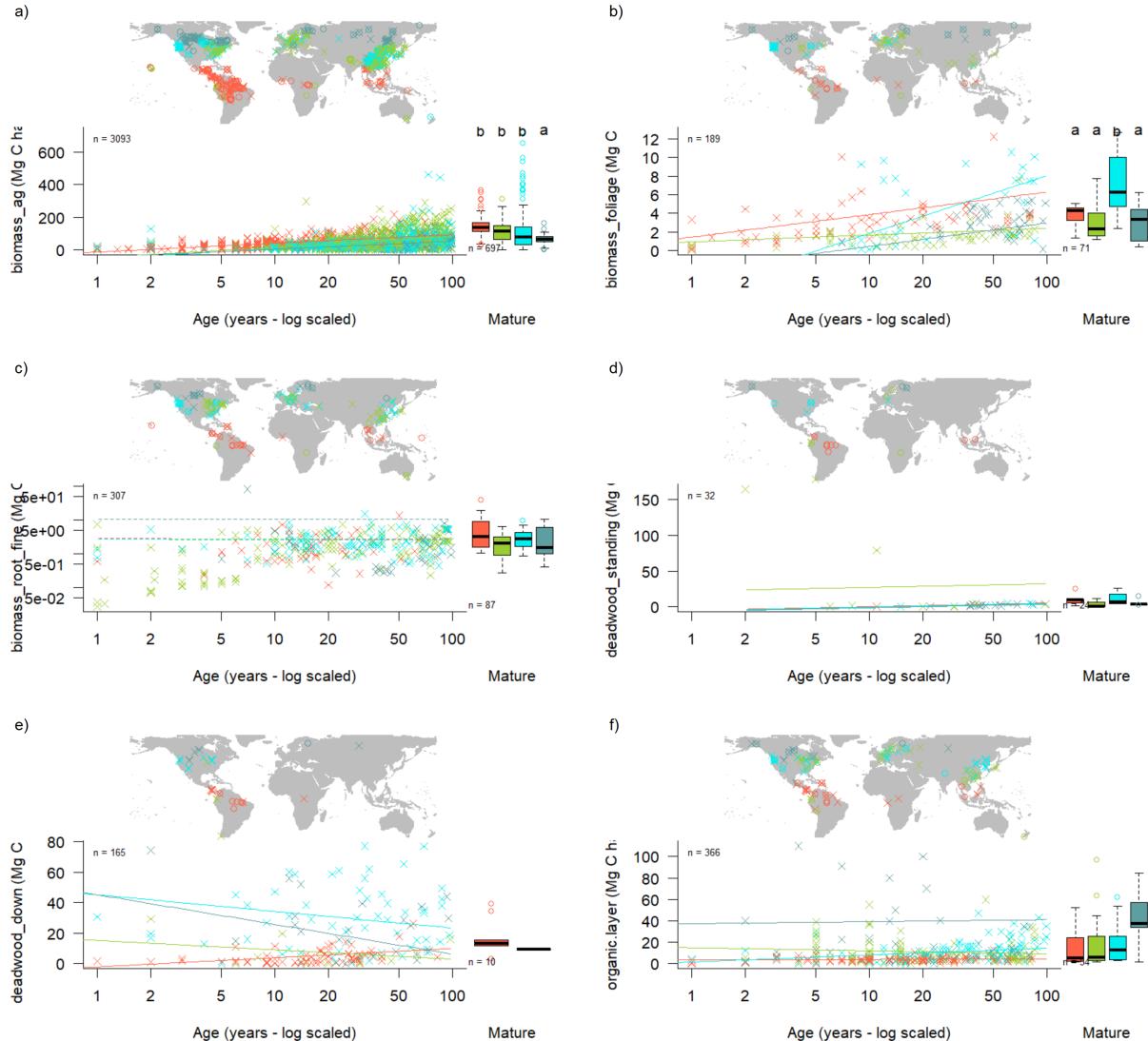


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as 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  $\times$  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).

## 232 C cycling in young forests

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

234 Both C stocks and fluxes commonly displayed significant trends with stand age for within-biome analyses  
 235 (Table 1, Figs. 6-11, S1-S26; detailed below).

236 ForC contained 14 flux variables with sufficient data for cross-biome analyses of age trends in regrowth  
 237 forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for all variables**). Of these, 9  
 238 increased significantly with  $\log_{10}[\text{stand.age}]$ :  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{\text{foliage}}$ ,  $ANPP_{\text{woody}}$ ,  
 239  $ANPP_{\text{woody-stem}}$ ,  $BNPP$ ,  $BNPP_{\text{root-fine}}$ ,  $R_{\text{eco}}$ , and net C sequestration ( $NEP$ ). The remaining

240 five— $ANPP_{woody-branch}$ ,  $BNPP_{root-coarse}$ ,  $R_{soil-het}$ , and  $R_{soil-het}$ —displayed no significant relationship to  
241 stand age, although all displayed a positive trend.

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

244 The single exception was  $ANPP_{stem}$ , for which temperate broadleaf forests and temperate conifer forests of  
245 age  $>\sim 30$  had slightly higher flux rates than tropical forests (*represented by a single chronosequence*).  
246 Notably, the trend of tropical > temperate > boreal held for  $NEP$  in regrowth forests, in contrast to the  
247 lack of biome differences in  $NEP$  for mature forests (Fig. 6).

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

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



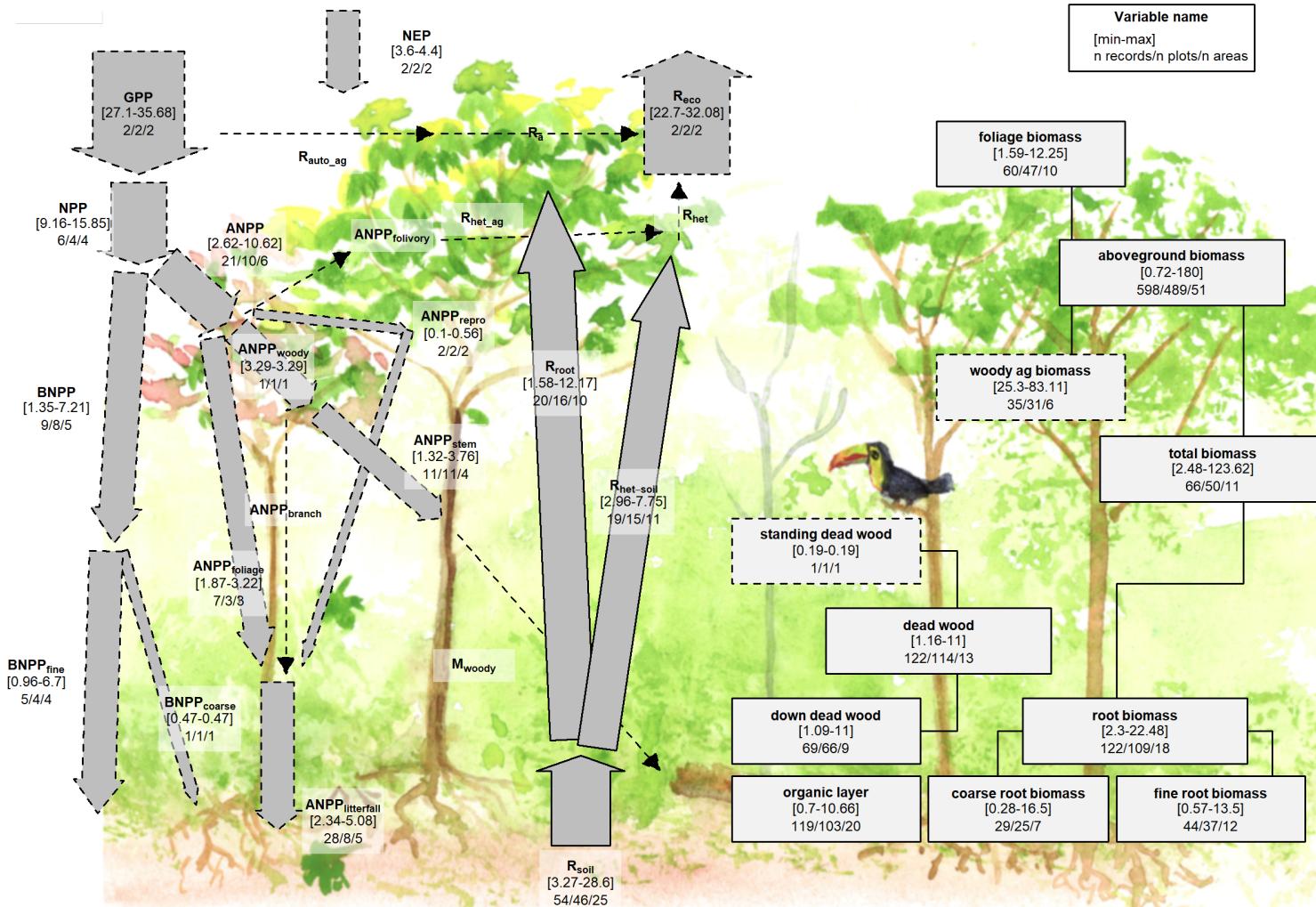


Figure 8 | C cycle diagram for young tropical broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are  $Mg\ C\ ha^{-1}\ yr^{-1}$  (fluxes) or  $Mg\ C\ ha^{-1}$  (stocks). Arrows indicate fluxes, boxes indicate stocks.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

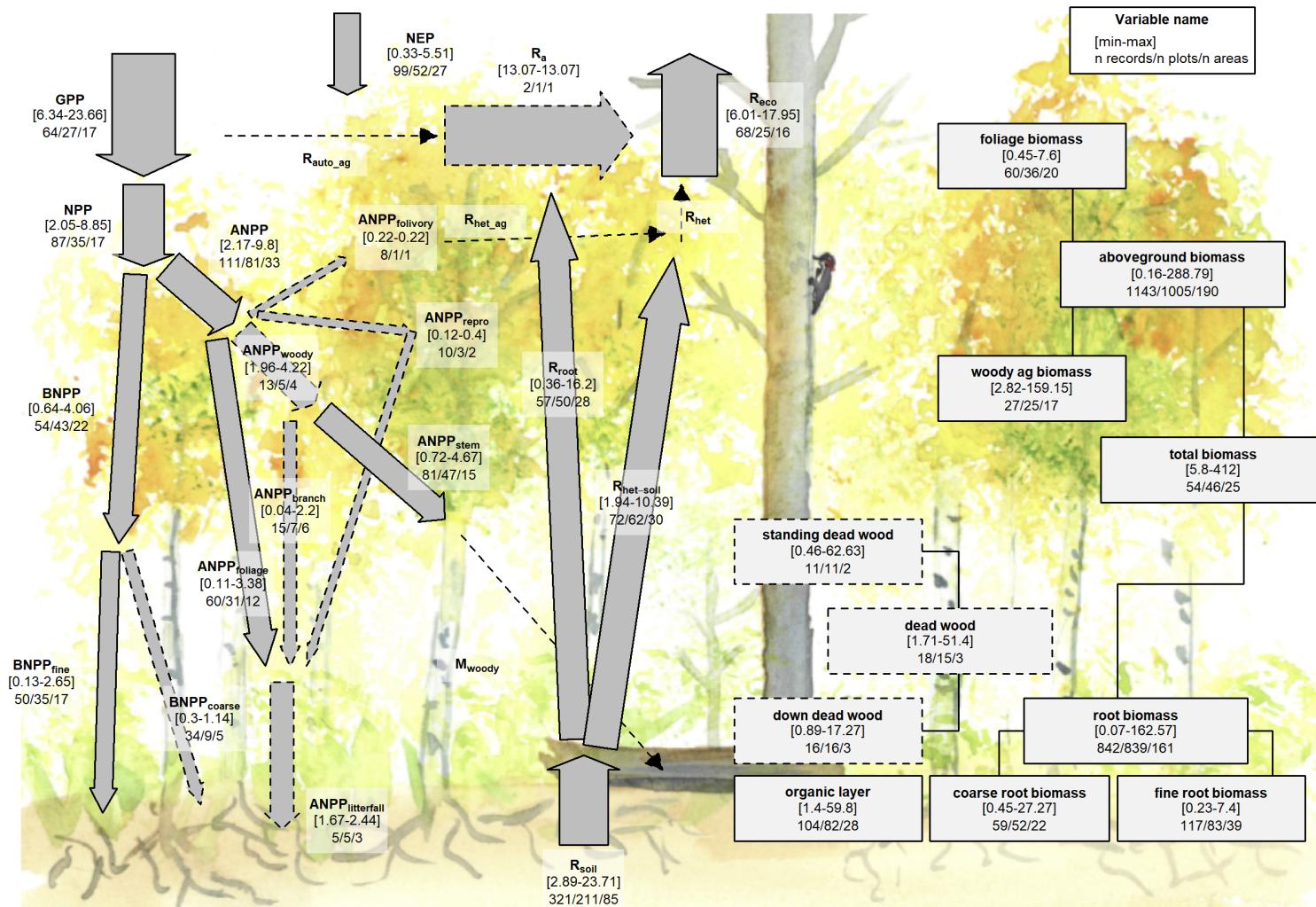


Figure 9 | C cycle diagram for young temperate broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. Arrow size is proportional to the square root of corresponding flux.

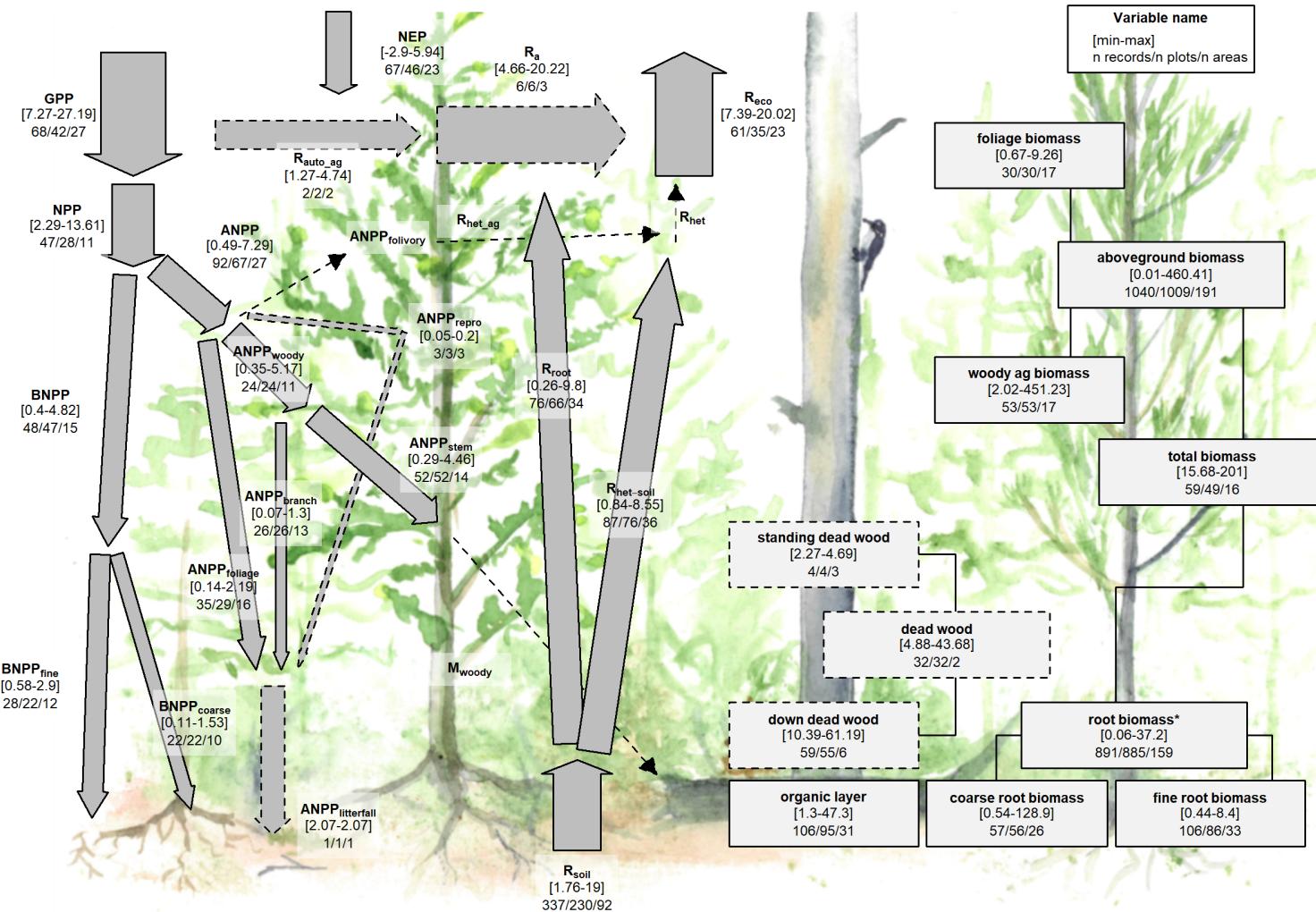


Figure 10 | C cycle diagram for young temperate conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are  $Mg\ C\ ha^{-1}\ yr^{-1}$  (fluxes) or  $Mg\ C\ ha^{-1}$  (stocks). Arrows indicate fluxes, boxes indicate stocks.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

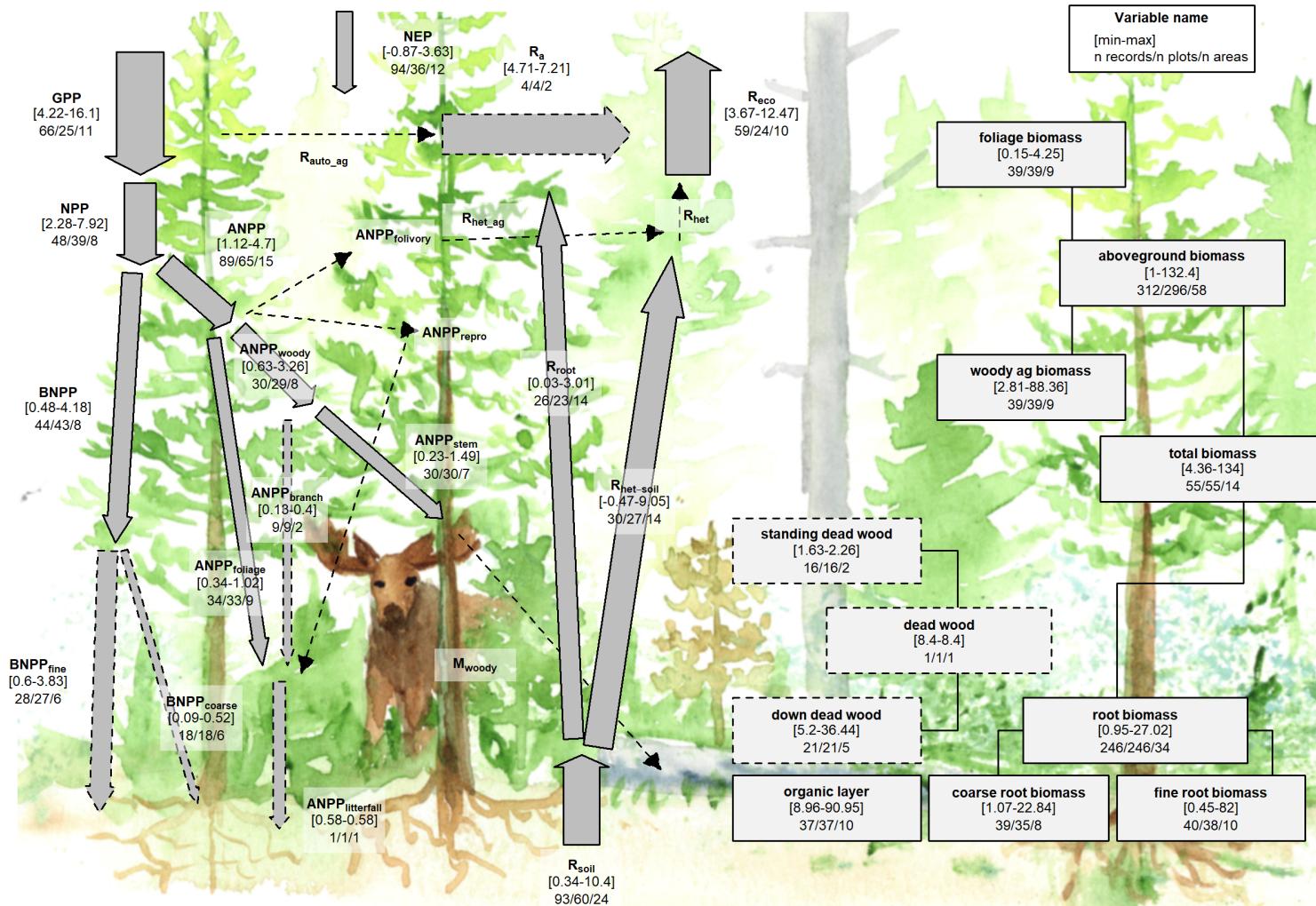


Figure 11 | C cycle diagram for young boreal conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha<sup>-1</sup> yr<sup>-1</sup> (fluxes) or Mg C ha<sup>-1</sup> (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. Arrow size is proportional to the square root of corresponding flux.

261 **Discussion**

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

271 **C variable coverage and budget closure**

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

281 The C cycle budgets for mature forests (Figs. 2-5) generally “close”—that is, the sums of component variables  
282 do not differ significantly from the larger fluxes. However, standard deviations are often large, reflective of  
283 significant within-biome variation. This makes the standard for closure relatively loose. Lack of closure, in  
284 the few instances where it occurs, is probably more reflective of differences in the representation of forest  
285 types (e.g., disproportionate representation of US Pacific NW for aboveground woody biomass relative to  
286 AGB; Fig. 4) than of methodological accuracy. Thus, overall, a high degree of closure implies that ForC  
287 gives a consistent picture of C cycling within biomes. While these means are unlikely to be accurate  
288 representations of C cycling within any particular forest, they provide a useful baseline for comparison,  
289 always keeping in mind that sample means do not necessarily represent the true mean of the entire biome.

290 **C cycling across biomes**

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

301 also that it accelerates more rapidly with stand age in the tropics, consistent with more rapid biomass  
302 accumulation.

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

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

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

### 309 **Age trends in C cycling**

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

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

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

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

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

### 320 **Relevance for climate change prediction and mitigation**

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

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

330 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change  
331 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not  
332 feasible for the individuals and organizations designing such efforts to sort through literature, often behind  
333 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline  
334 through which information can flow efficiently from forest researchers to decision-makers working to  
335 implement forest conservation strategies at global, national, or landscape scales. This is already happening!  
336 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;  
337 Requena Suarez *et al* (2019); Rozendaal et al in prep], mapping C accumulation potential from natural forest

338 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*  
339 2020).

340 There remain numerous data needs for improved accounting of forest carbon stocks and fluxes in GHG  
341 accounting. AGB is the largest stock, and most of the emphasis is on this variable. Remote sensing, with  
342 calibration based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019), is the  
343 best approach for mapping forest carbon (REFS). However, it is limited in that it is not associated with  
344 stand age and disturbance history, except in recent decades when satellite data can be used to detect forest  
345 loss, gain, and some of their dominant drivers (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). ForC  
346 is therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020).

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

351 Other variables, in particular respiration fluxes, cannot be remotely sensed ((??)), and efforts such as the  
352 Global Carbon Project (**le quere REF**) and NASA CMS (**citation:**  
353 [https://carbon.nasa.gov/pdfs/CMS\\_Phase-1\\_Report\\_Final\\_optimized.pdf](https://carbon.nasa.gov/pdfs/CMS_Phase-1_Report_Final_optimized.pdf) but maybe  
354 better to cite open literature, one of the papers listed at  
355 <https://cmsflux.jpl.nasa.gov/get-data/publication-data-sets>) typically compute them as residuals  
356 only.

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

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

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

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