

<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>25</sup> **Summary**

<sup>26</sup> *Background.* Earth's climate is closely linked to forests, which strongly influence atmospheric carbon dioxide  
<sup>27</sup> ( $\text{CO}_2$ ) and climate by their impact on the global carbon (C) cycle. However, efforts to incorporate forests  
<sup>28</sup> into climate models and  $\text{CO}_2$  accounting frameworks have been constrained by a lack of accessible,  
<sup>29</sup> global-scale data on how C cycling varies across forest types and stand ages.

<sup>30</sup> *Methods/Design.* Here, we draw from the Global Forest Carbon Database, ForC, to provide a macroscopic  
<sup>31</sup> overview of C cycling in the world's forests, giving special attention to stand age-related variation.

<sup>32</sup> Specifically, we use 11923 *ForC* records from 865 geographic locations representing 34 C cycle variables to  
<sup>33</sup> characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate  
<sup>34</sup> broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years)  
<sup>35</sup> forests. For regrowth forests, we quantify age trends for all variables with sufficient data.

<sup>36</sup> *Review Results/ Synthesis.* *ForC v3.0* yielded a comprehensive picture of C cycling in the world's major  
<sup>37</sup> forest biomes. The rate of C cycling generally increased from boreal to tropical regions in both mature and  
<sup>38</sup> regrowth forests, whereas C stocks showed less directional variation. The majority of flux variables, together  
<sup>39</sup> with most live biomass pools, increased significantly with stand age. Importantly, there was generally good  
<sup>40</sup> closure of C budgets, *i.e.*, internal consistency in the *ForC* data.

<sup>41</sup> *Discussion.* As climate change accelerates, understanding and managing the carbon dynamics of forests is  
<sup>42</sup> critical to forecasting, mitigation, and adaptation. This synthetic and internally consistent global overview of  
<sup>43</sup> C stocks and fluxes across biomes and stand ages will help to advance these efforts.

<sup>44</sup> *Key words:* forest ecosystems; carbon cycle; stand age; productivity; respiration; biomass; global

45 **Background**

46 Forest ecosystems are shaping the course of climate change through their influence on atmospheric carbon  
47 dioxide (CO<sub>2</sub>; Bonan 2008, Friedlingstein *et al* 2019, IPCC 2018). Despite the centrality of forest C cycling  
48 in regulating atmospheric CO<sub>2</sub>, important uncertainties in climate models (Friedlingstein *et al* 2006, Krause  
49 *et al* 2018, Bonan *et al* 2019, Di Vittorio *et al* 2020) and CO<sub>2</sub> accounting frameworks (Pan *et al* 2011) can be  
50 traced to lack of accessible, comprehensive data on how C cycling varies across forest types and in relation to  
51 stand history. These require large-scale databases with global coverage, which runs contrary to the nature in  
52 which forest C stocks and fluxes are measured and published. While remote sensing measurements are  
53 increasingly useful for global- or regional-scale estimates of a few critical variables (e.g., aboveground  
54 biomass: Hu *et al* 2016, Spawn *et al* 2020, gross primary productivity, *GPP*: Li and Xiao 2019, Saatchi *et al*  
55 2011), measurement and validation of most forest C stocks and fluxes require intensive on-the-ground data  
56 collection.

57 A robust understanding of forest impacts on global C cycling is essential. Annual gross CO<sub>2</sub> sequestration in  
58 forests (gross primary productivity, *GPP*) is estimated at >69 Gt C yr<sup>-1</sup> (Badgley *et al* 2019), or >7 times  
59 average annual fossil fuel emissions from 2009-2018 ( $9.5 \pm 0.5$  Gt C yr<sup>-1</sup>; Friedlingstein *et al* 2019). Most of  
60 this enormous C sequestration is counterbalanced by CO<sub>2</sub> releases to the atmosphere through ecosystem  
61 respiration ( $R_{eco}$ ) or fire, with forests globally dominant as sources of both soil respiration (Warner *et al*  
62 2019) and fire emissions (Werf *et al* 2017). In recent years, the remaining CO<sub>2</sub> sink averaged  $3.2 \pm 0.6$  GtC  
63 yr<sup>-1</sup> from 2009-2018, offsetting 29% of anthropogenic fossil fuel emissions (Friedlingstein *et al* 2019). Yet, this  
64 sink is reduced by deforestation, estimated at ~1 Gt C yr<sup>-1</sup> in recent decades (Pan *et al* 2011, Tubiello *et al*  
65 2020), reducing the net forest sink to ~1.1-2.2 Gt C yr<sup>-1</sup> across Earth's forests (Friedlingstein *et al* 2019).

66 The future of the current forest C sink is dependent both upon forest responses to climate change itself and  
67 human land use decisions, which will feedback and strongly influence the course of climate change.

68 Regrowing forests in particular will play an important role (Pugh *et al* 2019), as almost two-thirds of the  
69 world's forests were secondary as of 2010 (FAO 2010). As anthropogenic and climate-driven disturbances  
70 impact an growing proportion of Earth's forests (Andela *et al* 2017, McDowell *et al* 2020), understanding the  
71 carbon dynamics of regrowth forests is increasingly important (Anderson-Teixeira *et al* 2013). Although age  
72 trends in aboveground biomass have been relatively well-studied and synthesized globally (Cook-Patton *et al*  
73 2020), a relative dearth of data and synthesis on other C stocks and fluxes in secondary forests points to an  
74 under-filled need to characterize age-related trends in forest C cycling. Such understanding is particularly  
75 critical for reducing uncertainty regarding the potential for carbon uptake and climate change mitigation by  
76 regrowth forests (Krause *et al* 2018, Cook-Patton *et al* 2020). Understanding, modeling, and managing  
77 forest-atmosphere CO<sub>2</sub> exchange is thus central to efforts to mitigate climate change (Grassi *et al* 2017,  
78 Griscom *et al* 2017, Cavaleri *et al* 2015).

79 Despite the importance of forests, comprehensive global studies have historically been limited by the  
80 scattered and more local nature of research studies. Primary research articles typically cover only a small  
81 numbers of sites at a time. The rare exceptions that span regions or continents with rare exceptions spanning  
82 regions or continents are typically coordinated through research networks such as ForestGEO  
83 (Anderson-Teixeira *et al* 2015, e.g., Lutz *et al* 2018), NEON (Schimel *et al* 2007), or FLUXNET (Baldocchi  
84 *et al* 2001, e.g., Novick *et al* 2018). The result of decades of research on forest C cycling is that tens of  
85 thousands of records have been distributed across literally thousands of scientific articles –often behind  
86 paywalls– along with variation in data formats, units, measurement methods, *etc.* In this format, the data

87 are effectively inaccessible for many global-scale analyses, including those attempting to benchmark model  
88 performance with global data (Clark et al 2017, Luo et al 2012), quantify the role of forests in the global  
89 C cycle (e.g., Pan *et al* 2011), or use book-keeping methods to quantify actual or scenario-based exchanges of  
90 CO<sub>2</sub> between forests and the atmosphere (Griscom *et al* 2017, Houghton 2020).

91 To address the need for global-scale analyses of forest C cycling, we recently developed *ForC*  
92 (Anderson-Teixeira *et al* 2016, 2018). *ForC* contains published estimates of forest ecosystem C stocks and  
93 annual fluxes (>50 variables), with the different variables capturing the unique ecosystem pools (e.g., woody,  
94 foliage, and root biomass; dead wood) and flux types (e.g, gross and net primary productivity; soil, root, and  
95 ecosystem respiration). These data are ground-based measurements, and *ForC* contains associated data  
96 required for interpretation (e.g., stand history, measurement methods). Data have been amalgamated from  
97 original peer-reviewed publications, either directly or via intermediary data compilations. Since its most  
98 recent publication (Anderson-Teixeira *et al* 2018), *ForC* has grown to include two additional large databases:  
99 the Global Soil Respiration Database (SRDB; Bond-Lamberty and Thomson 2010) and the Global  
100 Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020) that also synthesized  
101 published forest C data. Following these additions, *ForC* currently contains 39762 records from 10608 plots  
102 and 1532 distinct geographic areas representing all forested biogeographic and climate zones. This represents  
103 an 129% increase in records from the prior publication (Anderson-Teixeira *et al* 2018).

104 Here, we provide a robust and comprehensive analysis of carbon cycling from a stand to global level, and by  
105 biome and stand age, using the largest global compilation of forest carbon data, which is available in our  
106 open source Global Carbon Forest database (*ForC*; Fig. 1). Our primary goal is to provide a data-driven  
107 summary of our current state of knowledge on broad trends in forest C cycling. Specifically, we address three  
108 broad questions:

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

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

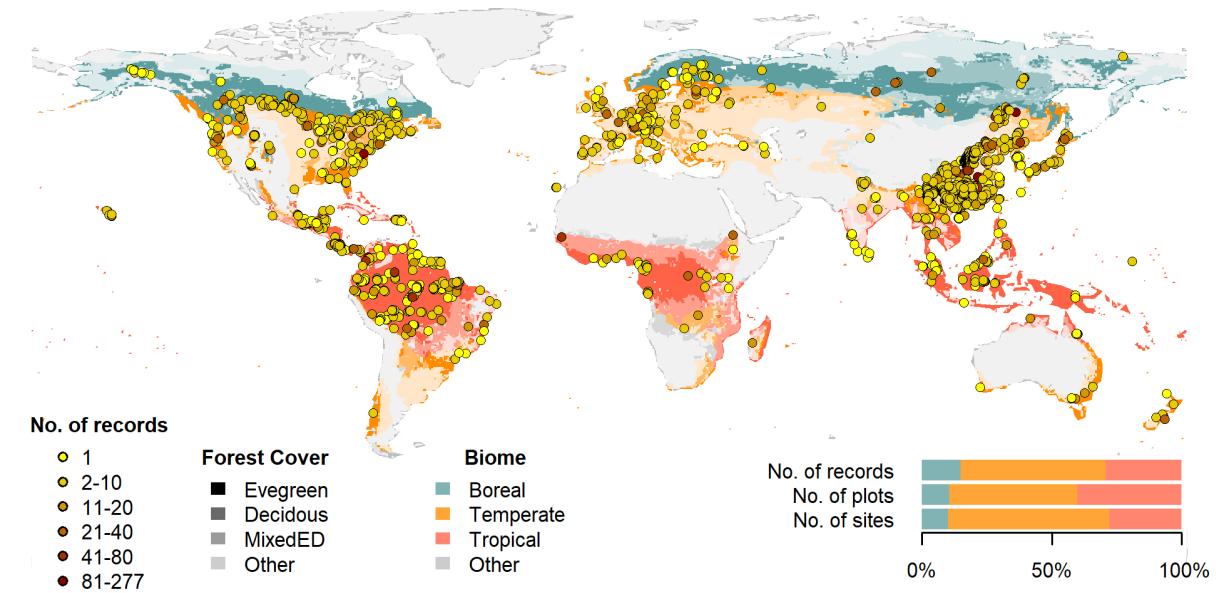


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

## 117 Methods/ Design

118 This review synthesizes data from the *ForC* database (Fig. 1; <https://github.com/forc-db/ForC>;  
 119 Anderson-Teixeira *et al* 2016, 2018). *ForC* amalgamates numerous intermediary data sets (*e.g.*, Luyssaert *et*  
 120 *al* 2007, Bond-Lamberty and Thomson 2010, Cook-Patton *et al* 2020) and original studies. Original  
 121 publications were referenced to check values and obtain information not contained in intermediary data sets,  
 122 although this process has not been completed for all records. The database was developed with goals of  
 123 understanding how C cycling in forests varies across broad geographic scales and as a function of stand age.  
 124 As such, there has been a focus on incorporating data from regrowth forests (*e.g.*, Anderson *et al* 2006,  
 125 Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age data when possible (83% of records in v.2.0;  
 126 Anderson-Teixeira *et al* 2018). Particular attention was given to developing the database for tropical forests  
 127 (Anderson-Teixeira *et al* 2016), which represented roughly one-third of records in *ForC* v2.0  
 128 (Anderson-Teixeira *et al* 2018). Since publication of *ForC* v2.0, we added the following data to *ForC*: the  
 129 Global Database of Soil Respiration Database (*SRDB* v4, 9488 records; Bond-Lamberty and Thomson 2010),  
 130 the Global Reforestation Opportunity Assessment database (*GROA* v1.0, 10116 records; Cook-Patton *et al*  
 131 2020, Anderson-Teixeira *et al* 2020). We have also added data from individual publications, with a particular  
 132 focus on productivity (*e.g.*, Taylor *et al* 2017), dead wood, and ForestGEO sites (*e.g.*, Lutz *et al* 2018, p  
 133 @johnson\_climate\_2018). The database version used for this analysis has been tagged as a new release on  
 134 Github (v3.0) and assigned a DOI through Zenodo (DOI: TBD).  
 135 To facilitate analyses, we created a simplified version of *ForC*, *ForC-simplified*  
 136 ([https://github.com/forc-db/ForC/blob/master/ForC\\_simplified](https://github.com/forc-db/ForC/blob/master/ForC_simplified)), which we analyzed here. In generating

137 *ForC-simplified*, all measurements originally expressed in units of dry organic matter ( $OM$ ) were converted  
138 to units of C using the IPCC default of  $C = 0.47 * OM$  (IPCC 2018). Duplicate or otherwise conflicting  
139 records were reconciled as described in Appendix S1, resulting in a total of 22265 records (56% size of total  
140 database). Records were filtered to remove plots that had undergone significant anthropogenic management  
141 or major disturbance since the most recent stand initiation event. Specifically, we removed all plots flagged  
142 as managed in ForC-simplified (13.9%). This included plots with any record of managements manipulating  
143  $CO_2$ , temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the  
144 terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”. Plots flagged as disturbed in  
145 ForC-simplified (5.6%) included stands that had undergone any notable anthropogenic thinning or partial  
146 harvest. We retained sites that were grazed or had undergone low severity natural disturbances (<10%  
147 mortality) including droughts, major storms, fires, and floods. We removed all plots for which no stand  
148 history information had been retrieved (5.7%). In total, this resulted in 17349 records (43.6% of the records  
149 in the database) being eligible for inclusion in the analysis.

150 We selected 23 annual flux and 11 C stock variables for inclusion in the analysis (Table 1). These different  
151 flux and stock variables represent different pools (e.g., aboveground biomass, root biomass, dead wood) and  
152 levels of combination (e.g., total net primary productivity,  $NPP$ , versus the individual elements of  $NPP$   
153 such as foliage, roots, and branches). Note that two flux variables, aboveground heterotrophic ( $R_{het-ag}$ ) and  
154 total ( $R_{het}$ ) respiration, were included for conceptual completeness but had no records in *ForC* (Table 1).  
155 Records for our focal variables represented 90.3% of the total records eligible for inclusion. For this analysis,  
156 we combined some of ForC’s specific variables into more broadly defined variables. Specifically, net ecosystem  
157 exchange (measured by eddy-covariance; Baldocchi *et al* 2001) and biometric estimates of  $NEP$  were  
158 combined into the single variable  $NEP$  (Table 1). Furthermore, for  $NPP$ , aboveground  $NPP$  ( $ANPP$ ),  
159 and the litterfall component of  $ANPP$  ( $ANPP_{litterfall}$ ), *ForC* variables specifying inclusion of different  
160 components were combined (e.g., measurements including or excluding fruit and flower production and  
161 herbivory). Throughout ForC, for all measurements drawing from tree census data (e.g., biomass,  
162 productivity), the minimum diameter breast height (DBH) threshold for tree census was  $\leq 10\text{cm}$ . All records  
163 were measured directly or derived from field measurements (as opposed to modeled).

164 We grouped forests into four broad biome types based on climate zones and dominant vegetation type  
165 (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age  
166 classifications (young and mature). Climate zones (Fig. 1) were defined based on site geographic coordinates  
167 according to Köppen-Geiger zones (Rubel and Kottek 2010). We defined the tropical biome as including all  
168 equatorial (A) zones, temperate biomes as including all warm temperate (C) zones and warmer snow  
169 climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and the boreal biome as including the colder snow climates  
170 (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones were  
171 excluded from the analysis. We defined leaf type (broadleaf / needleleaf) was based on descriptions in  
172 original publications (prioritized) or values extracted from a global map based on satellite observations  
173 (SYNMAP; Jung *et al* 2006). For young tropical forests imported from *GROA* but not yet classified by leaf  
174 type, we assumed that all were broadleaf, consistent with the rarity of naturally regenerating needleleaf  
175 forests in the tropics. We also classified forests as “young” ( $< 100$  years) or “mature” ( $\geq 100$  years or  
176 classified as “mature”, “old growth”, “intact”, or “undisturbed” in original publication). Assigning stands to  
177 these groupings required the exclusion of records for which *ForC* lacked geographic coordinates (0.4% of sites  
178 in full database) or records of stand age (5.7% of records in full database). We also excluded records of stand

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)	329	146	88	n.s.	+; xB
<i>GPP</i>	gross primary production ( $NPP + R_{auto}$ or $R_{eco} - NEE$ )	303	115	84	TrB > TeB $\geq$ TeN $\geq$ BoN	+; xB
<i>NPP</i>	net primary production ( $ANPP + BNPP$ )	214	112	74	TrB > TeB $\geq$ TeN $>$ BoN	n.s.
<i>ANPP</i>	aboveground <i>NPP</i>	343	236	131	TrB > TeB $\geq$ TeN $>$ BoN	+; xB
<i>ANPP<sub>woody</sub></i>	woody production ( $ANPP_{stem} + ANPP_{branch}$ )	64	53	37	n.s.	+
<i>ANPP<sub>stem</sub></i>	woody stem production	217	190	117	TrB > TeN $\geq$ TeB $\geq$ BoN	n.s.
<i>ANPP<sub>branch</sub></i>	branch turnover	69	59	42	TrB > TeB $\geq$ TeN	n.s.
<i>ANPP<sub>foliage</sub></i>	foliage production, typically estimated as annual leaf litterfall	162	132	88	TrB > TeB $\geq$ TeN $>$ BoN	+
<i>ANPP<sub>litterfall</sub></i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	82	70	55	n.s.	+
<i>ANPP<sub>repro</sub></i>	production of reproductive structures (flowers, fruits, seeds)	51	44	34	n.t.	n.t.
<i>ANPP<sub>folivory</sub></i>	foliar biomass consumed by folivores	20	12	11	n.t.	n.t.
<i>M<sub>woody</sub></i>	woody mortality—i.e., $B_{ag}$ of trees that die	18	18	18	n.t.	n.t.
<i>BNPP</i>	belowground NPP ( $BNPP_{coarse} + BNPP_{fine}$ )	148	116	79	TrB > TeN $\geq$ TeB $\geq$ BoN	+
<i>BNPP<sub>coarse</sub></i>	coarse root production	77	56	36	TeN $\geq$ TrB	n.s.
<i>BNPP<sub>fine</sub></i>	fine root production	123	99	66	n.s.	+
<i>R<sub>eco</sub></i>	ecosystem respiration ( $R_{auto} + R_{het}$ )	213	98	70	TrB > TeB $\geq$ TeN	+
<i>R<sub>auto</sub></i>	autotrophic respiration ( $(R_{auto-ag} + R_{root})$ )	24	23	15	n.t.	n.t.
<i>R<sub>auto-ag</sub></i>	aboveground autotrophic respiration (i.e., leaves and stems)	2	2	1	n.t.	n.t.
<i>R<sub>root</sub></i>	root respiration	181	139	95	TrB $\geq$ TeB	+
<i>R<sub>soil</sub></i>	soil respiration ( $(R_{het-soil} + R_{root})$ )	627	411	229	TrB > TeB $>$ TeN $\geq$ BoN	n.s.
<i>R<sub>het-soil</sub></i>	soil heterotrophic respiration	197	156	100	TrB > TeB $\geq$ TeN	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 ( $B_{ag} + B_{root}$ )	188	157	87	TrB $\geq$ TeB $>$ BoN	+; xB
<i>B<sub>ag</sub></i>	aboveground live biomass ( $B_{ag-wood} + B_{foliage}$ )	4466	4072	621	TrB $\geq$ TeN $\geq$ TeB $>$ BoN	+; xB
<i>B<sub>ag-wood</sub></i>	woody component of aboveground biomass	115	102	64	TeN $>$ TrB $\geq$ BoN	+; xB
<i>B<sub>foliage</sub></i>	foliage biomass	134	115	72	TeN $>$ TrB $\geq$ BoN $\geq$ TeB	+; xB
<i>B<sub>root</sub></i>	total root biomass ( $(B_{root-coarse} + B_{root-fine})$ )	2329	2298	360	n.s.	+; xB
<i>B<sub>root-coarse</sub></i>	coarse root biomass	134	120	73	TeN $>$ TeB $\geq$ BoN	+; xB
<i>B<sub>root-fine</sub></i>	fine root biomass	226	180	109	n.s.	+; xB
<i>DW<sub>tot</sub></i>	deadwood ( $DW_{standing} + DW_{down}$ )	79	73	42	n.t.	+; xB
<i>DW<sub>standing</sub></i>	standing dead wood	36	35	22	n.t.	n.t.
<i>DW<sub>down</sub></i>	fallen dead wood, including coarse and sometimes fine woody debris	278	265	37	n.t.	+; xB
<i>OL</i>	organic layer / litter/ forest floor	474	413	115	n.s.	+; xB

\* Tr: Tropical, TeB: Temperate Broadleaf, TeN: Temperate Needleleaf, B: Boreal, n.s.: no significant differences, n.t.: not tested

† + or -: significant positive or negative trend, xB: significant age x biome interaction, n.s.: no significant age trend, n.t.: not tested

179 age = 0 year (0.8% of records in full database). In total, our analysis retained 76.1 of the focal variable

180 records for forests of known age. Numbers of records by biome and age class are given in Table S1.

181 Data were summarized to produce schematics of C cycling across the eight biome by age group combinations  
182 identified above. To obtain the values reported in the C cycle schematics, we first averaged any repeated  
183 measurements within a plot. Values were then averaged across geographically distinct areas, defined as plots  
184 clustered within 25 km of one another (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if  
185 available for all records. This step was taken to avoid pseudo-replication.

186 We tested whether the C budgets described above “closed”—*i.e.*, whether they were internally consistent.  
187 Specifically, we first defined relationships among variables: for example,  $NEP = GPP - R_{eco}$ ,  
188  $BNPP = BNPP_{coarse} + BNPP_{fine}$ ,  $DW_{tot} = DW_{standing} + DW_{down}$ ). Henceforth, we refer to the  
189 variables on the left side of the equation as “aggregate” fluxes or stocks, and those that are summed as  
190 “component” fluxes or stocks, noting that the same variable can take both aggregate and component positions  
191 in different relationships. We considered the C budget for a given relationship “closed” when component  
192 variables summed to within one standard deviation of the aggregate variable.

193 To test for differences across mature forest biomes, we also examined how stand age impacted fluxes and  
194 stocks, employing a mixed effects model (“lmer” function in “lme4” R package; Bates *et al* 2015) with biome  
195 as fixed effect and plot nested within geographic.area as random effects on the intercept. When Biome had a  
196 significant effect, we looked at a Tukey’s pairwise comparison to see which biomes were significantly different  
197 from one another. This analysis was run for variables with records for at least seven distinct geographic areas  
198 in more than one biome, excluding any biomes that failed this criteria (Table 1).

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

205 To facilitate the accessibility of our results and data, and to allow for rapid updates as additional data  
206 become available, we have automated all database manipulation, analyses, and figure production in R (R  
207 Core Team 2020).

## 208 Review Results/ Synthesis

### 209 Data Coverage

210 Of the 39762 records in *ForC* v3.0, 11923 met our strict criteria for inclusion in this study (Fig. 1). These  
211 records were distributed across 5062 plots in 865 distinct geographic areas. Of the 23 flux and 11 stock  
212 variables mapped in these diagrams, *ForC* contained sufficient mature forest data for inclusion in our  
213 statistical analyses (*i.e.*, records from  $\geq 7$  distinct geographic areas) for 20 fluxes and 9 stocks in tropical  
214 broadleaf forests, 15 fluxes and 8 stocks in temperate broadleaf forests, 14 fluxes and 7 stocks in temperate  
215 conifer forests, and 8 fluxes and 7 stocks in boreal forests. For regrowth forests (<100 yrs), *ForC* contained  
216 sufficient data for inclusion in our statistical analyses (*i.e.*, records from  $\geq 3$  distinct geographic areas) for 11  
217 fluxes and 10 stocks in tropical broadleaf forests, 16 fluxes and 10 stocks in temperate broadleaf forests, 16  
218 fluxes and 10 stocks in temperate conifer forests, and 14 fluxes and 9 stocks in boreal forests.

219 **C cycling in mature forests**

220 Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq$   
221 100 years old and with no known major natural or anthropogenic disturbance are presented in Figures 2-5  
222 (and available in tabular format in the *ForC* release accompanying this publication:  
223 [ForC/numbers\\_and\\_facts/ForC\\_variable\\_averages\\_per\\_Biome.csv](#)).

224 For variables with records from  $\geq 7$  distinct geographic areas, these ensemble C budgets were generally  
225 consistent. That is, component variables summed to within one standard deviation of their respective  
226 aggregate variables in all but one instance. In the temperate conifer biome, the average composite measure of  
227 root biomass ( $B_{root}$ ) was less than the combined average value of coarse and fine root biomass ( $B_{root-coarse}$   
228 and  $B_{root-fine}$ , respectively). This lack of closure was driven by very high estimates of  $B_{root-coarse}$  from  
229 high-biomass forests of the US Pacific Northwest.

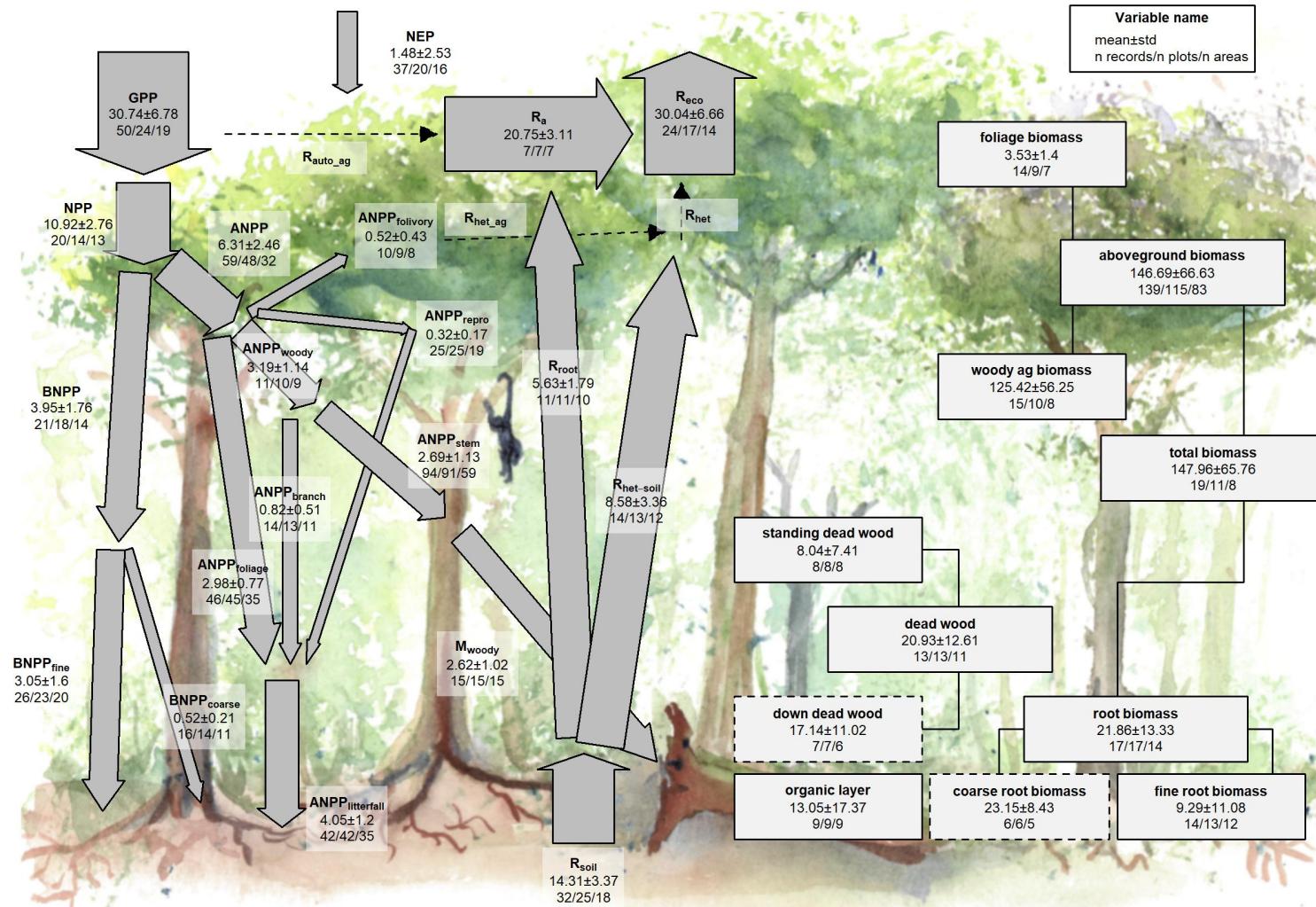


Figure 2 | C cycle diagram for mature tropical broadleaf forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as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

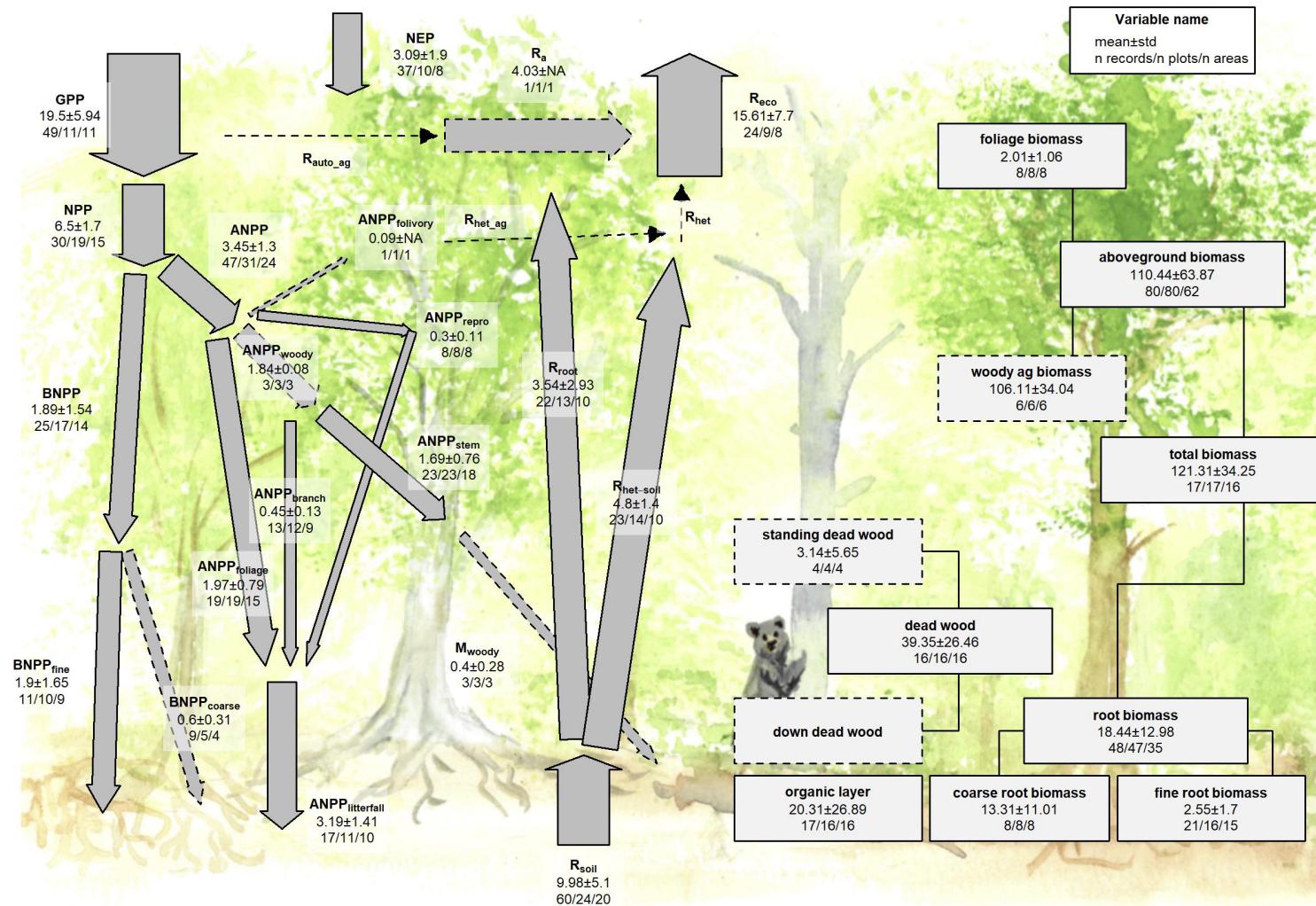


Figure 3 | C cycle diagram for mature temperate broadleaf forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication.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

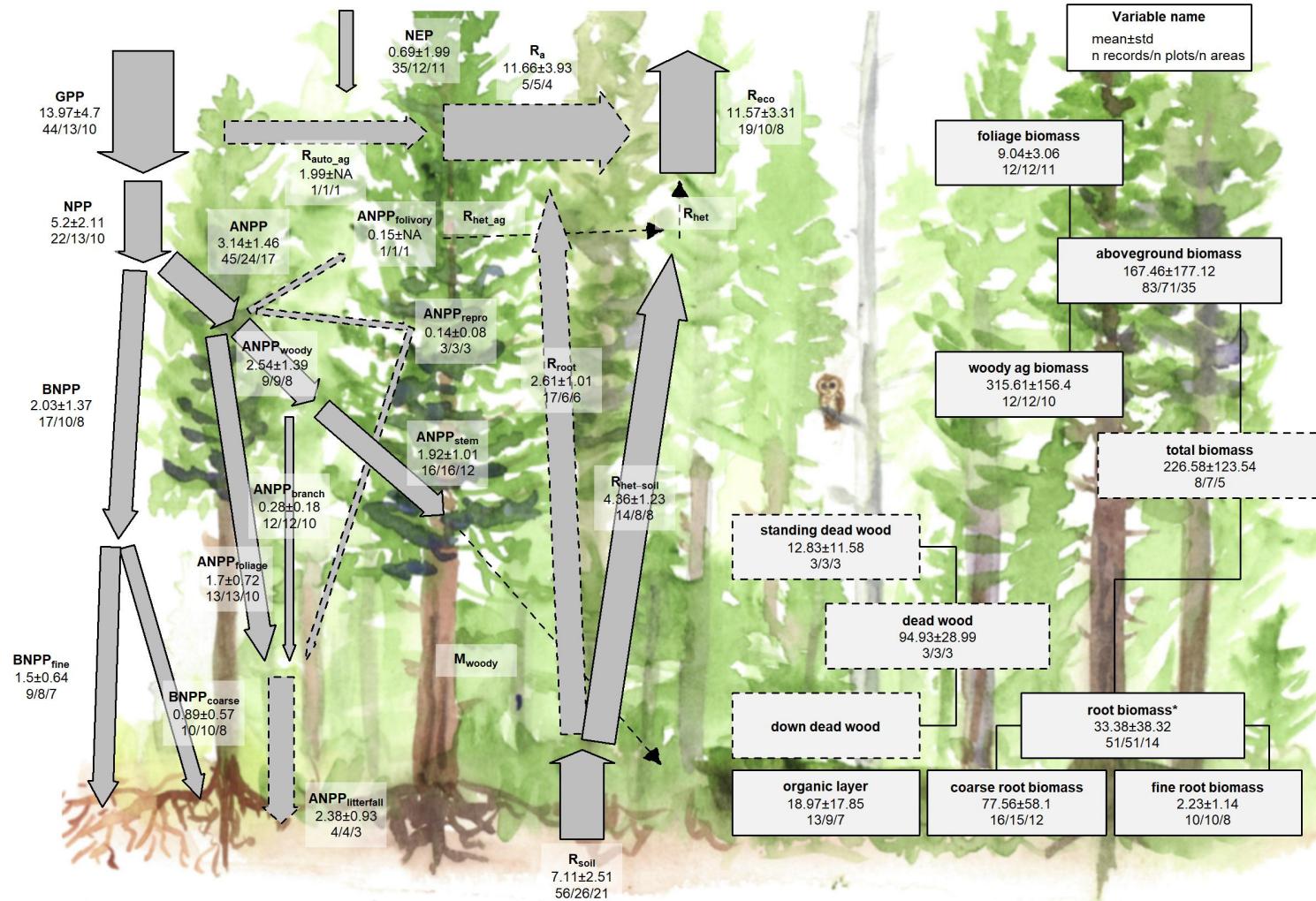


Figure 4 | C cycle diagram for mature temperate conifer forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as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

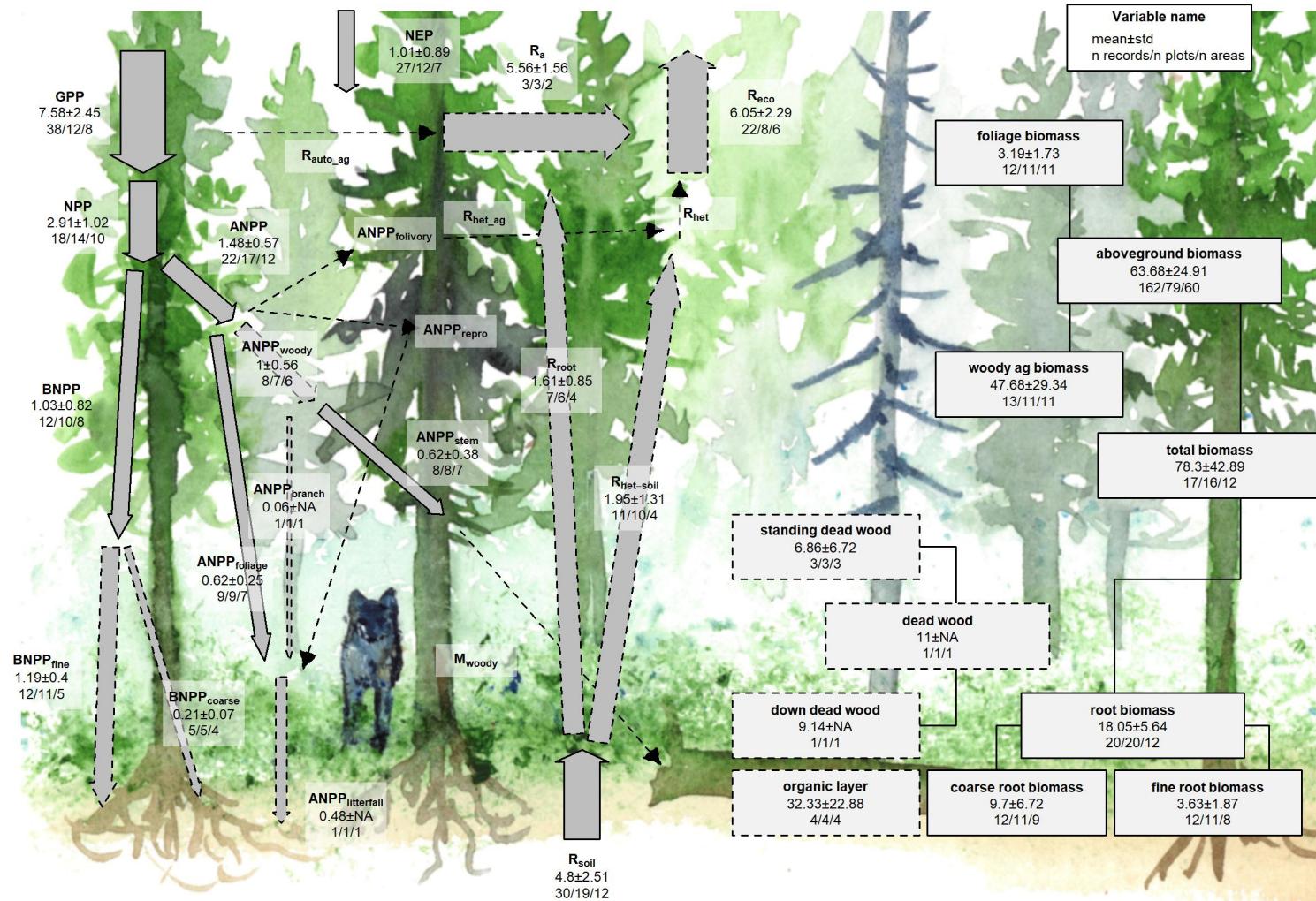


Figure 5 | C cycle diagram for mature boreal conifer forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the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

230 There were sufficient data to assess mature forest biome differences for 15 flux variables, and significant  
231 differences among biomes were detected for 12 variables (Table 1). In all of these cases—including C fluxes  
232 into, within, and out of the ecosystem—C fluxes were highest in tropical forests, intermediate in temperate  
233 (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 6, S1-S15). Differences between  
234 tropical and boreal forests were always significant, with temperate forests intermediate and significantly  
235 different from one or both. Fluxes tended to be numerically greater in temperate broadleaf than conifer  
236 forests, but the difference was never statistically significant. This pattern held for the following variables:  
237  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{stem}$ ,  $ANPP_{branch}$ ,  $ANPP_{foliage}$ ,  $BNPP$ ,  $R_{eco}$ ,  $R_{root}$ ,  $R_{soil}$ , and  $R_{het-soil}$ .  
238 For two of the variables without significant differences among biomes ( $ANPP_{litterfall}$  and  $BNPP_{fine}$ ; Figs.  
239 S8 and S11, respectively), the same general trends applied but were not statistically significant. Another  
240 exception was for  $BNPP_{root-coarse}$ , where all records came from high-biomass forests in the US Pacific  
241 Northwest, resulting in marginally higher values for the temperate conifer biome (Table 1, Fig. S10;  
242 differences significant in mixed effects model but not in post-hoc pairwise comparison).

243 The most notable exception to the pattern of decreasing flux from tropical to boreal biomes was  $NEP$ , with  
244 no significant differences across biomes but with the largest average in temperate broadleaf forests, followed  
245 by tropical, boreal, and temperate conifer forests (Figs. 5,S1).

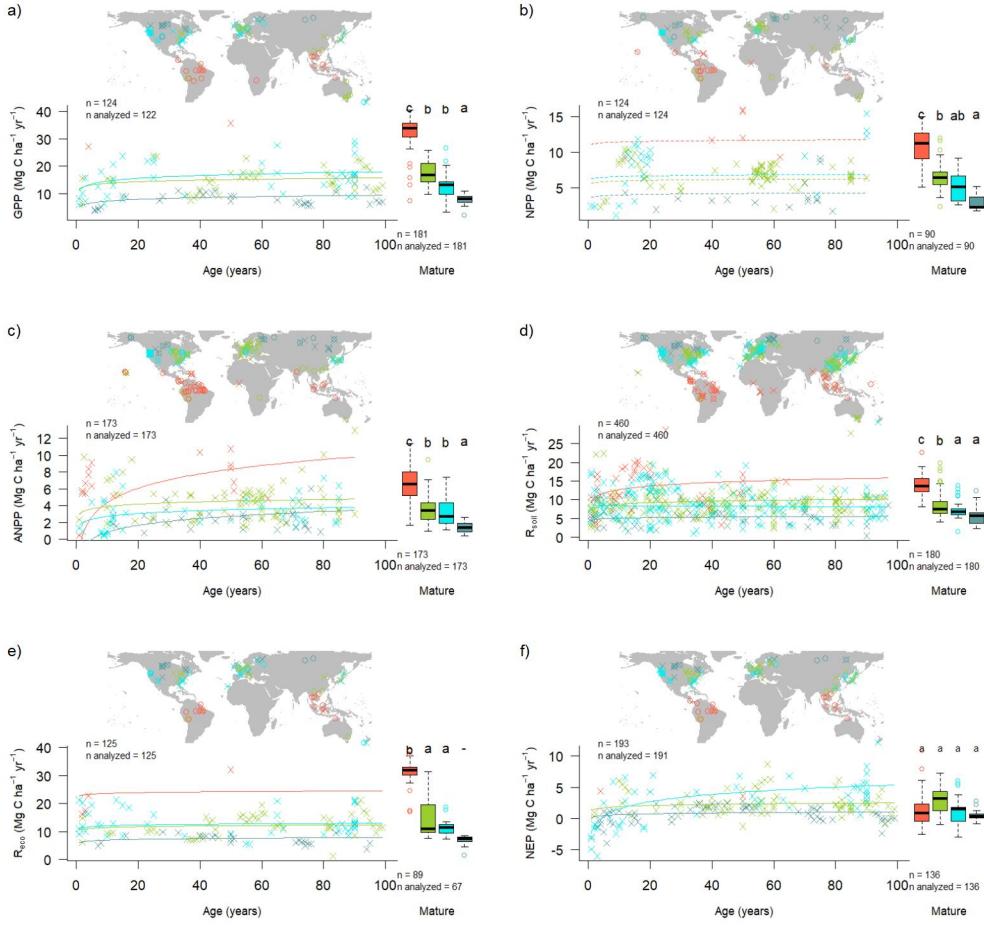


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a)  $GPP$ , (b)  $NPP$ , (c)  $ANPP$ , (d)  $R_{soil}$ , (e)  $R_{eco}$ , and (f)  $NEP$ . Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). In each panel, the left scatterplot shows age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

246 There were sufficient data to assess mature forest biome differences for nine stock variables, and significant  
 247 differences among biomes were detected for five variables ( $B_{tot}$ ,  $B_{ag}$ ,  $B_{ag-wood}$ ,  $B_{foliage}$ ,  $B_{root-coarse}$ ; Table  
 248 1). C stocks had less consistent patterns across biomes (Figs. 7, S16-S26). For  $B_{tot}$  and  $B_{ag}$ , tropical  
 249 broadleaf forests had the highest biomass and boreal forests the lowest, with temperate broadleaf and  
 250 needleleaf ( $B_{ag}$  only) intermediate. For three variables that had been disproportionately sampled in the  
 251 high-biomass forests of the US Pacific Northwest ( $B_{ag-wood}$ ,  $B_{foliage}$ , and  $B_{root-coarse}$ ), temperate conifer  
 252 forests had significantly higher stocks than the other biomes, which were not significantly different from one  
 253 another.

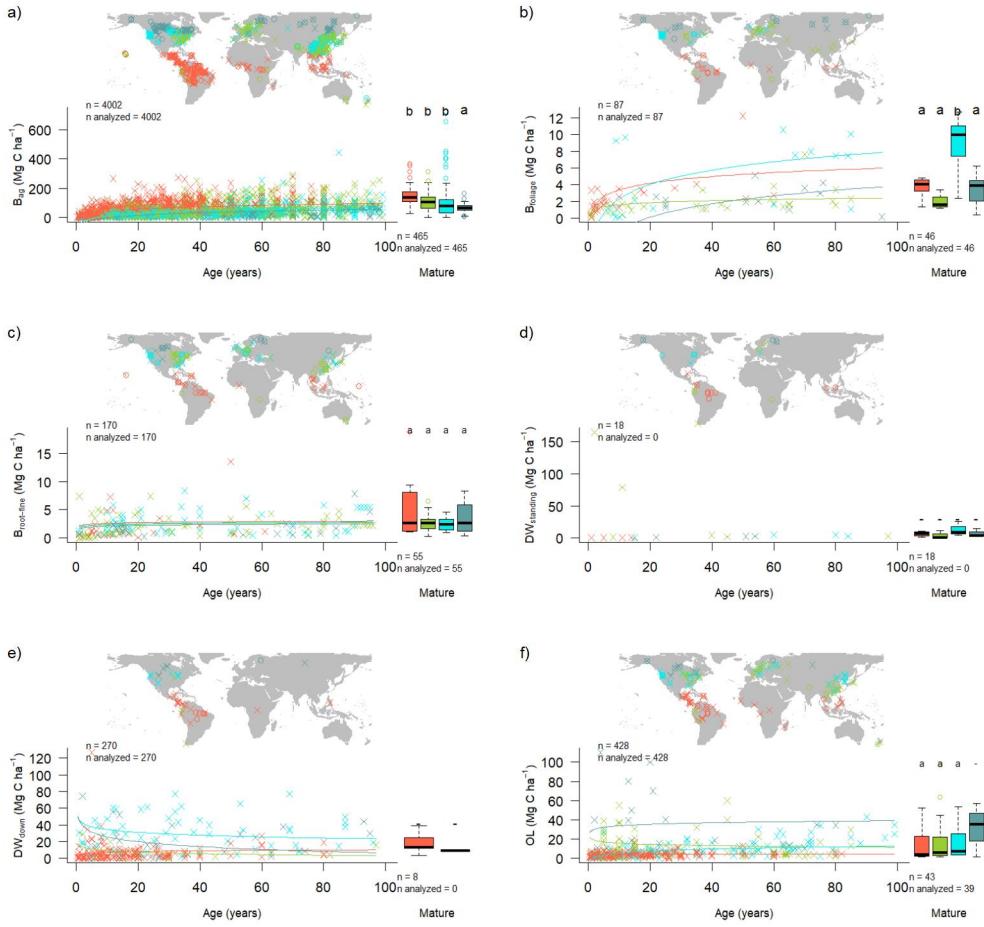


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources ( $x$  and  $o$  indicate young and mature stands, respectively). In each panel, the left scatterplot shows age trends in forests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

## 254 C cycling in young forests

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

257 *ForC* contained 16 C flux variables with sufficient data for analyses of age trends in young forests (see  
 258 Methods) (Figs. 6, S1-S15). Of these, ten increased significantly with age: *NEP*, *GPP*, *ANPP*,  
 259 *ANPP<sub>woody</sub>*, *ANPP<sub>foliage</sub>*, *ANPP<sub>litterfall</sub>*, *BNPP*, *BNPP<sub>fine</sub>*, *R<sub>eco</sub>*, and *R<sub>root</sub>*. The remaining six—*NPP*,  
 260 *ANPP<sub>stem</sub>*, *ANPP<sub>branch</sub>*, *BNPP<sub>coarse</sub>*, *R<sub>soil-het</sub>*, and *R<sub>soil-het</sub>*—displayed no significant relationship to  
 261 stand age.

262 Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling  
 263 generally most rapid in the tropics and slowest in boreal forests. The single exception was *ANPP<sub>stem</sub>*, for  
 264 which temperate broadleaf and conifer forests had similar flux rates than tropical forests. Notably, and in

265 contrast to the lack of biome differences in *NEP* for mature forests (Fig. 6), the tendency for temperate  
266 forests to have greater fluxes than boreal forests held for *NEP* in regrowth forests (tropical forests excluded  
267 because of insufficient data).

268 In terms of C stocks, ten variables (all but standing deadwood,  $DW_{standing}$ ) had sufficient data to test for age trends (Table 1, Figs. 7, S16-26). All of these displayed a significant overall increase with  $\log_{10}[stand.age]$ . There were sufficient data to model age  $\times$  biome interactions were also significant for all 269 ten of these C stock variables (Table S2), with living C stocks tending to accumulate more rapidly during the 270 early stages of forest regrowth in tropical forests (Figs. 7, S16-S22). In the case of two non-living C stocks 271 ( $DW_{down}$  and  $OL$ ), age  $\times$  biome interactions were such that Specifically,  $DW_{down}$  declined with age in 272 temperate and boreal forests, compared to an increase with age in tropical forests (Figs. 7, S25). Similarly, 273  $OL$  declined slightly with age in temperate broadleaf forests, contrasting an increase in the other three 274 biomes (Figs. 7, S26).  
275

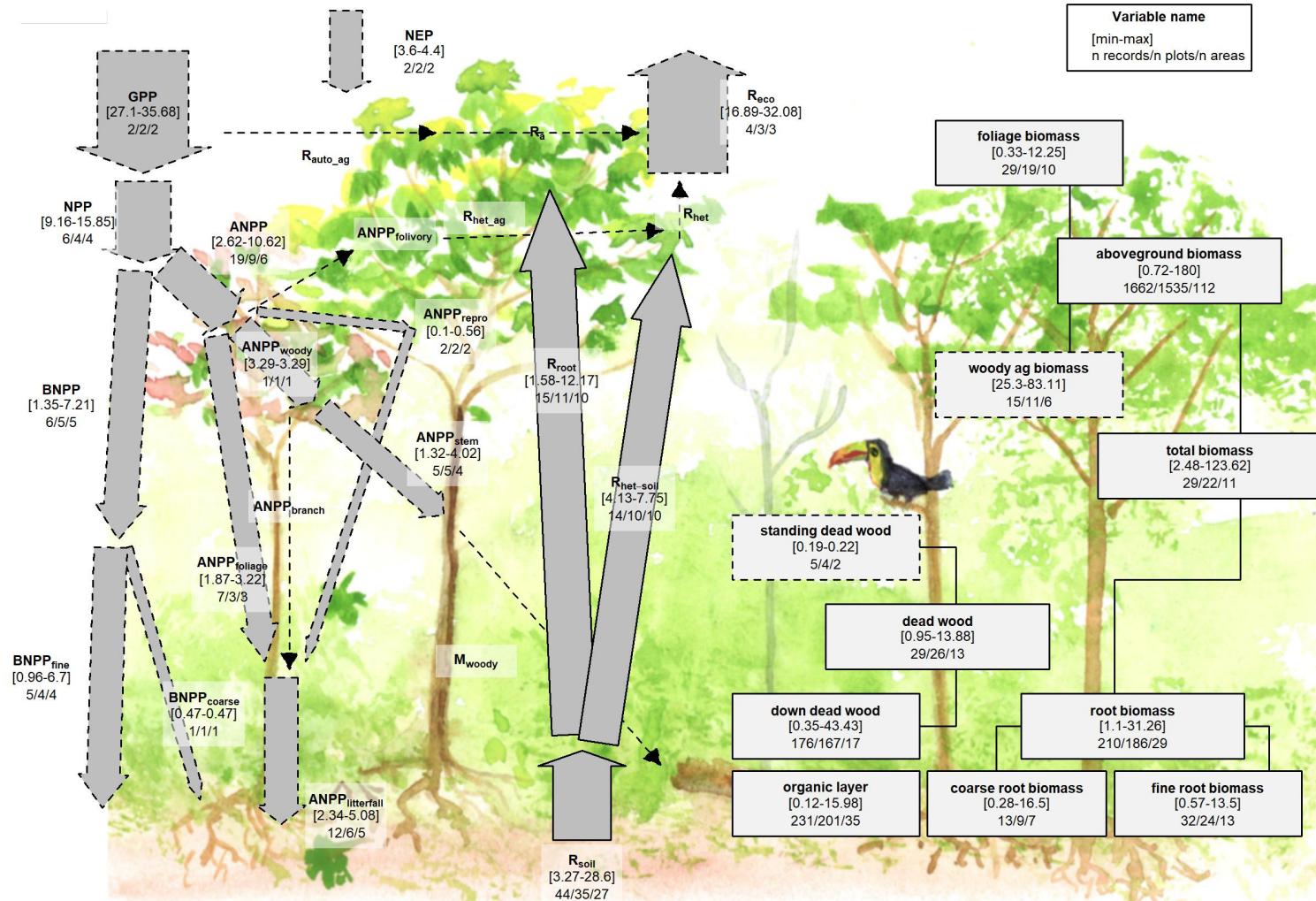


Figure 8 | C cycle diagram for young tropical broadleaf forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the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

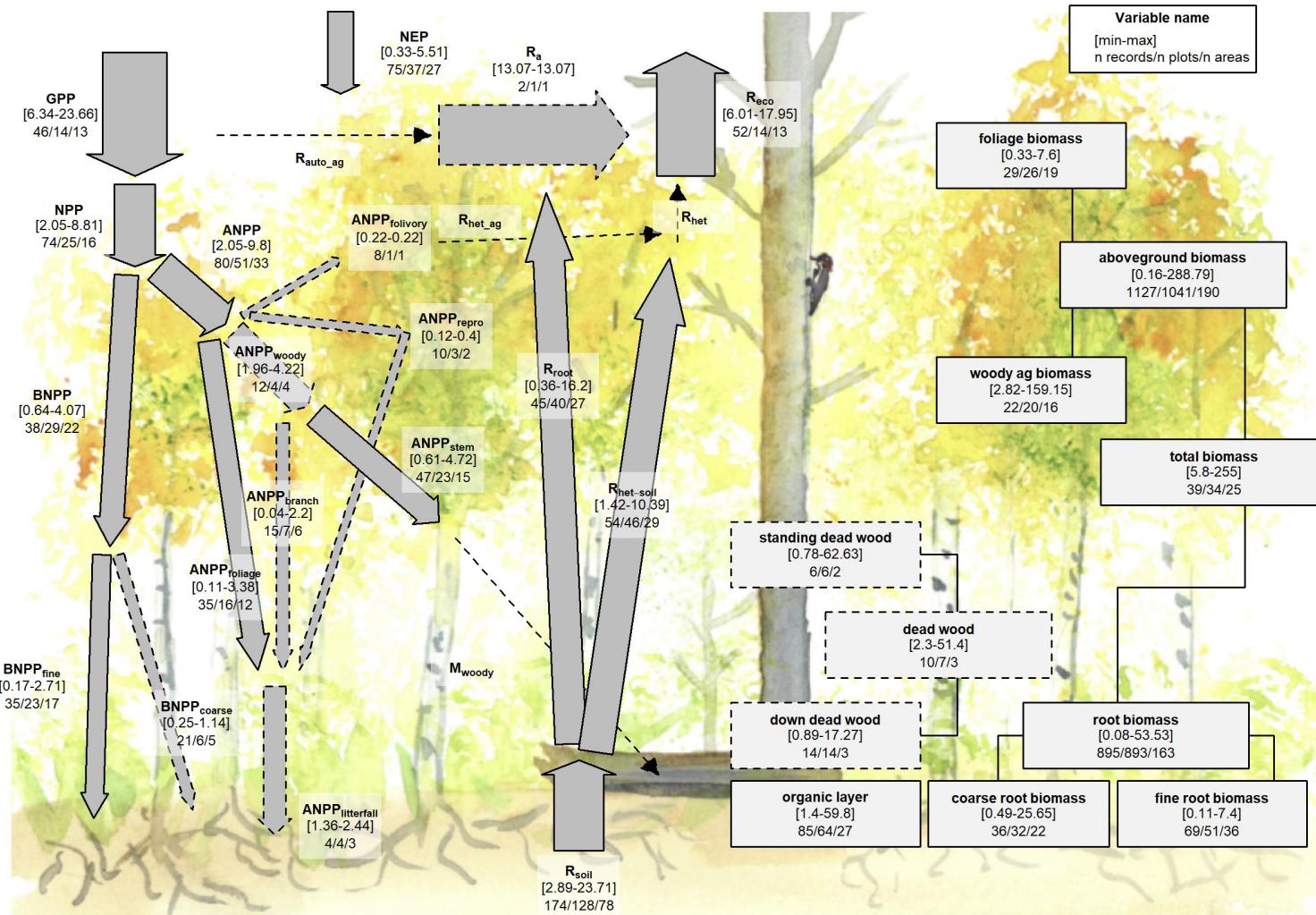


Figure 9 | C cycle diagram for young temperate broadleaf forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication.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

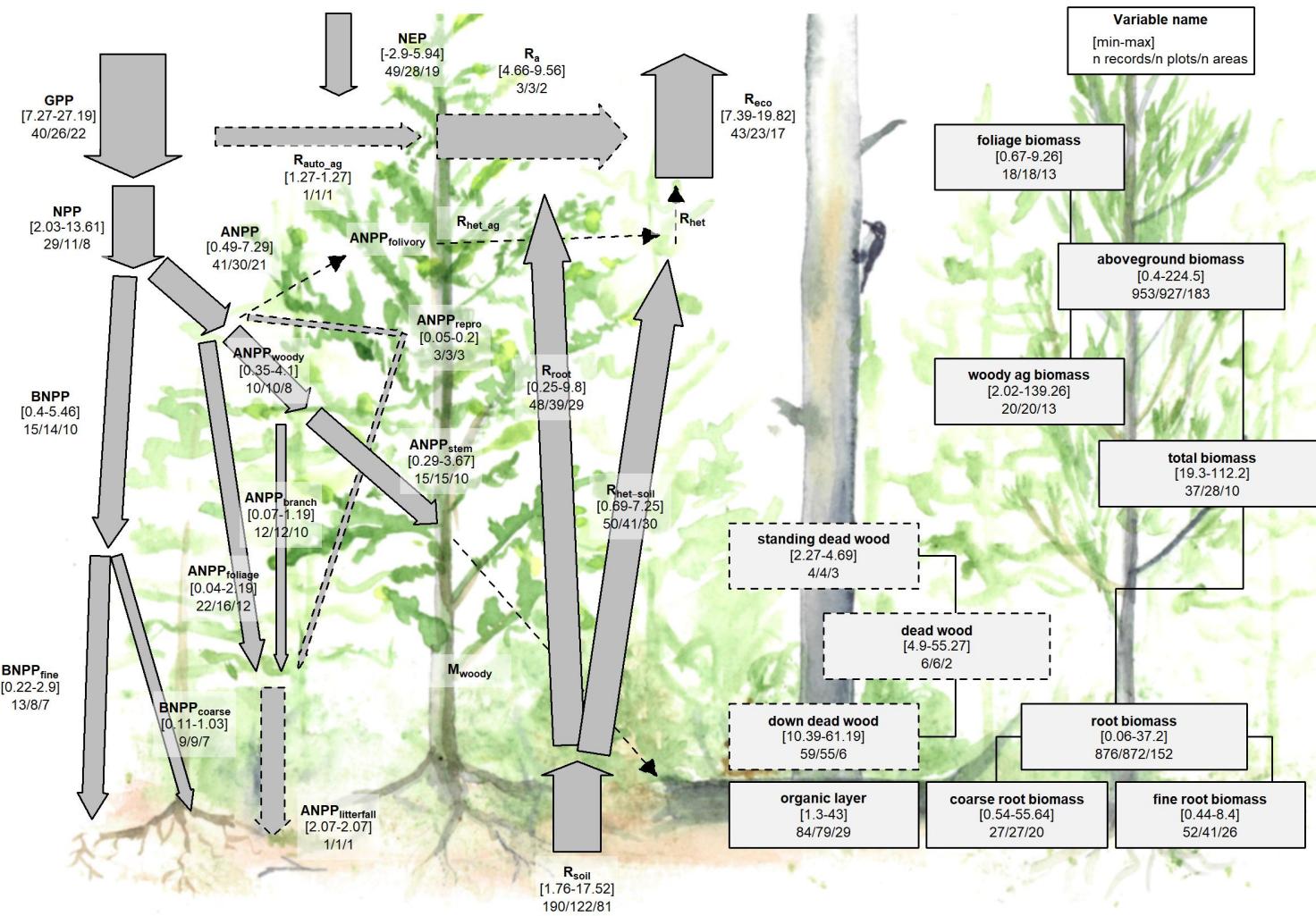


Figure 10 | C cycle diagram for young temperate conifer forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the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

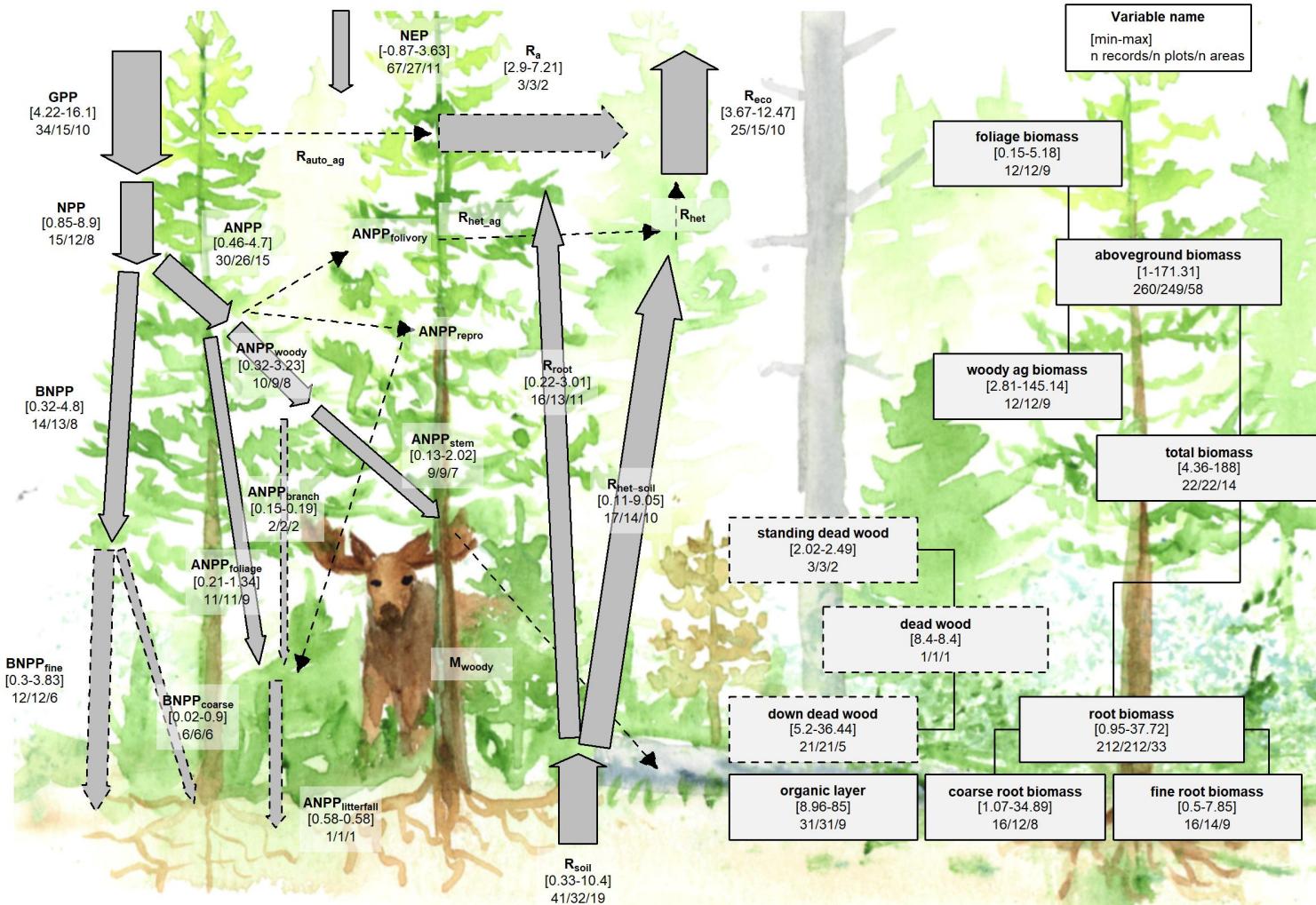


Figure 11 | C cycle diagram for young boreal conifer forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the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

277 **Discussion**

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

287 **C variable coverage and budget closure**

288 The large number of C cycle variables covered by *ForC*, and the general consistency between them, provide  
289 confidence that our overall reported means provide accurate and useful baselines for analysis – with the  
290 caveats that they are unlikely to be accurate representations of C cycling for any particular forest, and that  
291 these sample means almost certainly do not represent true biome means (particularly for temperate conifer  
292 forests where high-biomass stands are over-represented in *ForC*).

293 There are of course notable holes in the *ForC* variable coverage (Fig. 1) that limit the scope of our inferences  
294 here. Notably, *ForC* currently has sparse—if any—coverage of fluxes to herbivores and higher consumers, along  
295 with the woody mortality ( $M_{woody}$ ) and dead wood stocks (Tables 1, Figs. S23-S25). Geographically, all  
296 variables are poorly covered in Africa and Siberia, a common problem in the carbon-cycle community (Xu  
297 and Shang 2016, Schimel *et al* 2015). *ForC* does not include soil carbon, which is covered by other efforts  
298 (e.g., Köchy *et al* 2015). *ForC* is not intended to replace databases that are specialized for particular parts of  
299 the C cycle analyses, e.g., aboveground biomass (Spawn *et al* 2020), land-atmosphere fluxes (Baldocchi *et al*  
300 2001), soil respiration (Jian *et al* 2020), or the human footprint in global forests (Magnani *et al* 2007).

301 In this analysis, the C cycle budgets for mature forests (Figs. 2-5) generally “close”—that is, the sums of  
302 component variables do not differ from the larger fluxes by more than one standard deviation. On the one  
303 hand, this reflects the general fact that ecosystem-scale measurements tend to close the C budget more easily  
304 and consistently than, for example, for energy balance (Stoy *et al* 2013). On the other, however, *ForC*  
305 derives data from multiple heterogeneous sources, and standard deviations within each biome are high; as a  
306 result, the standard for C closure is relatively loose (*c.f.* Houghton 2020). Nonetheless, the lack of closure, in  
307 the one instance where it occurs, is probably more reflective of differences in the representation of forest  
308 types (*i.e.*, disproportionate representation of US Pacific NW for  $B_{root-coarse}$  relative to  $B_{root}$ ; Fig. 4) than  
309 of methodological accuracy. The overall high degree of closure implies that *ForC* gives a consistent picture of  
310 C cycling within biomes. This is an important and useful test, because it allows for consistency checks within  
311 the C cycle, for example leveraging separate and independently-measured fluxes to constrain errors in  
312 another (Phillips *et al* 2017, Williams *et al* 2014, Harmon *et al* 2011), or producing internally consistent  
313 global data products (Wang *et al* 2018).

314 **C cycling across biomes**

315 Our analysis reveals that carbon cycling is most rapid in the tropics and slowest in boreal regions, including  
316 C fluxes into ( $GPP$ ), within (e.g.,  $NPP$  and its components), and out of (e.g.,  $R_{soil}$ ,  $R_{eco}$ ) the ecosystem.

317 For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes  
318 generally decline with latitude (or increase with temperature) on a global scale (e.g., Luyssaert *et al* 2007,  
319 Gillman *et al* 2015, Li and Xiao 2019, Banbury Morgan *et al* n.d.). The consistency with which this occurs  
320 across numerous fluxes is not surprising, but has never been simultaneously assessed across such a large  
321 number of variables (but see Banbury Morgan *et al* n.d. for nine autotrophic fluxes).

322 The notable exception to the pattern of fluxes decreasing from tropical to boreal regions is  $NEP$  (Fig. 6f),  
323 which showed no significant differences across biomes. Unlike the other C flux variables,  $NEP$  does not  
324 characterize the rate at which C cycles through the ecosystem, but is the balance between C sequestration  
325 ( $GPP$ ) and respiratory losses ( $R_{eco}$ ) and represents net CO<sub>2</sub> sequestration (or release) by the ecosystem.  
326  $NEP$  tends to be relatively small in mature forest stands (discussed further below), which accumulate  
327 carbon slowly relative to younger stands, if at all (Luyssaert *et al* 2008, Amiro *et al* 2010, Besnard *et al*  
328 2018). It is therefore unsurprising that there are no pronounced differences across biomes, suggesting that  
329 variation in  $NEP$  of mature forests is controlled less by climate and more by other factors including  
330 moderate disturbances (Curtis and Gough 2018) or disequilibrium of  $R_{soil}$  relative to C inputs (e.g., in  
331 peatlands where anoxic conditions inhibit decomposition; Wilson *et al* 2016).

332 In contrast to the patterns observed for  $NEP$  in mature stands,  $NEP$  of stands between 20 and 100 years of  
333 age varied across biomes, being lowest in boreal forests, intermediate in temperate broadleaf forests, and  
334 highest in temperate conifer forests (with insufficient data to assess tropical forests; Figs. 6f, S1). This is  
335 consistent with findings that live biomass accumulation rates (e.g.,  $\Delta B_{ag}$  or  $\Delta B_{tot}$ ) during early secondary  
336 succession decrease with latitude (Figs. 7a, S16-S22; Anderson *et al* 2006, Cook-Patton *et al* 2020). Note,  
337 though, that  $NEP$  includes not only  $\Delta B_{tot}$ , but also changes in  $DW_{tot}$ ,  $OL$ , and soil carbon, and biome  
338 differences in the accumulation rates of these variables have not been detected, in part because these  
339 variables do not consistently increase with stand age (Figs. 7, S23-S26, and see discussion below;  
340 Cook-Patton *et al* 2020).

341 For regrowth forests, little is known about cross-biome differences in carbon fluxes, and we are not aware of  
342 any previous large-scale comparisons of C fluxes that have been limited to regrowth forests. Thus, this  
343 analysis was the first to examine flux trends in regrowth forests across biomes. The observed tendency for  
344 young forest fluxes to decrease from tropical to boreal regions paralleled patterns in mature forests (Figs. 6,  
345 S1-S15), suggesting that regrowth forests follow latitudinal trends in carbon cycling similar to those of  
346 mature forests (e.g., Banbury Morgan *et al* n.d.).

347 In contrast to C fluxes and biomass accumulation rates in regrowth forests, stocks showed less systematic  
348 variation across biomes. For aboveground biomass, which is the variable in *ForC* with broadest geographical  
349 representation, the modest trend of declining biomass from tropical to boreal regions mirrors observations  
350 from spaceborne lidar that reveal a decline in aboveground biomass (for all forests, including secondary) with  
351 latitude across the N hemisphere (Hu *et al* 2016). The highest- biomass forests on Earth are, however, found  
352 in coastal temperate climates of both the southern and northern hemisphere (Keith *et al* 2009, Smithwick *et*  
353 *al* 2002, Hu *et al* 2016). Disproportionate representation of forests in one such region—the US Pacific  
354 Northwest—inflated estimates of temperate conifer fluxes and stocks for some variables and was responsible

355 for all of the anomalous results described here (e.g., lack of complete C budget closure, anomalous trend  
356 across biomes for  $BNPP_{coarse}$ ). Thus, biome differences should always be interpreted relative to the  
357 geographic distribution of sampling, which only rarely covers the majority of forested area within a biome.  
358 Whereas biomass can be remotely sensed and receives significant research attention, far less is known about  
359 geographical variation in deadwood and organic layer ( $OL$ ) across biomes, which has proved a limitation for  
360 C accounting efforts (Pan *et al* 2011). Although these stocks can be important—exceeding 100 Mg C ha<sup>-1</sup> in  
361 some stands (Figs. 7d-e, S23-S25), this study is the first to synthesize deadwood data on a global scale (but  
362 see Cook-Patton *et al* 2020 for young forests). Unfortunately, data remain too sparse for statistical  
363 comparison across biomes (Figs. 7, S23-S25; but see below for age trends), pointing to a need for more  
364 widespread quantification of both standing and downed deadwood. *ForC* coverage of  $OL$  stocks is more  
365 comprehensive, revealing no significant differences across temperate and tropical biomes, but a tendency  
366 towards higher  $OL$  in boreal forests, consistent with the idea that slower decomposition in colder climates  
367 results in more buildup of organic matter (Allen *et al* 2002). Further research on non-living C stocks in the  
368 world's forests will be essential to completing the picture.

### 369 Age trends in C cycling

370 Our study reveals that most C fluxes quickly increase to a plateau as stands age (Fig. 6), consistent with  
371 current understanding of age trends in forest C cycling (e.g., Anderson-Teixeira *et al* 2013, Amiro *et al* 2010,  
372 Magnani *et al* 2007). While limited records in very young (*i.e.*, <5 year old) stands resulted in poor  
373 resolution of the earliest phases of this increase for many variables (sometimes detecting no age trend; Table  
374 1), any autotrophic C flux (e.g.,  $GPP$ ,  $NPP$  and its components,  $R_{auto}$ ) would be minimal immediately  
375 following a stand-clearing disturbance. These would be expected to increase rapidly with the most  
376 metabolically active components of biomass, foliage and fine roots, which also increase rapidly with stand age  
377 (Fig. 7). In contrast, soil heterotrophic respiration ( $R_{het-soil}$ ) and total soil respiration ( $R_{soil}$ ) are expected  
378 to be non-zero following stand-clearing disturbance, although these may decrease with a reduction of root  
379 respiration ( $R_{soil}$  only) and C exudates or increase in response to an influx of dead roots and litter  
380 (Ribeiro-Kumara *et al* 2020, Maurer *et al* 2016, Bond-Lamberty *et al* 2004). In this study, we detect no  
381 significant age trends in either variable.

382 Notably, net carbon sequestration ( $NEP$ ) increases with age up to the 100-yr threshold examined here, with  
383 more pronounced patterns in temperate than boreal forests (Fig. 6f). This finding is largely consistent with,  
384 but built from a far larger dataset than, previous studies showing an increase in  $NEP$  across relatively  
385 young stand ages (Pregitzer and Euskirchen 2004, Baldocchi *et al* 2001, Luyssaert *et al* 2008). However,  
386  $NEP$  has been observed to decline from intermediate to old stands (Luyssaert *et al* 2008), and the  $NEP$   
387 estimated by our model for 100-year-old temperate conifer stands (~5 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) exceeds the mean of  
388 mature forests in the same biome (0.7 Mg C ha<sup>-1</sup> yr<sup>-1</sup>; Fig. 4). A decrease in  $NEP$  is consistent with the  
389 observed deceleration of biomass accumulation as stands age, although both biomass and non-living C stocks  
390 will often continue to increase well beyond the 100-yr threshold used here to delimit young and mature  
391 stands (Luyssaert *et al* 2008, McGarvey *et al* 2014, Lichstein *et al* 2009).

392 In terms of stocks, our study reveals consistent increases in live biomass stocks with stand age—a pattern that  
393 is well-known and expected (e.g., Lichstein *et al* 2009, Yang *et al* 2011)—and more variable age trends in  
394 deadwood and  $OL$ . The latter are particularly sensitive to the type of disturbance, where disturbances that  
395 remove most organic material (e.g., logging, agriculture) result in negligible deadwood in young stands,

followed by a buildup over time (tropical stands in Fig. 7e; e.g., Vargas *et al* 2008). In contrast, natural disturbances (e.g., fire, drought) can produce large amounts of deadwood (mostly  $DW_{standing}$ ) that slowly decomposes as the stand recovers, resulting in declines across young stand ages (e.g., temperate and boreal stands in Fig. 7e; e.g., Carmona *et al* 2002). Again, further study and synthesis of non-living C stocks across biomes and stand ages will be valuable to giving a more comprehensive picture.

#### Relevance for climate change prediction and mitigation

The future of forest C cycling (Song *et al* 2019) will shape trends in atmospheric CO<sub>2</sub> and the course of climate change (Schimel *et al* 2015). Our findings, and more generally the data contained in *ForC* and summarized here, can help to meet two major challenges.

First, improved representation of forest C cycling in models is essential to improving predictions of the future course of climate change, for the simple reason that by definition future projections extend our existing observations and understanding to conditions that do not currently exist on Earth (McDowell *et al* 2018, Bonan and Doney 2018, Gustafson *et al* 2018). To ensure that models are giving the right answers for the right reasons (Sulman *et al* 2018), it is important to benchmark against multiple components of the C cycle that are internally consistent with each other (Collier *et al* 2018, Wang *et al* 2018). *ForC*'s tens of thousands of records are readily available in a standardized format, and our analyses here indicate that their internal consistency is reasonably high. Integration of *ForC* with models will be valuable to improving the accuracy and reliability of models.

Second, *ForC* can serve as a pipeline through which information can flow efficiently from forest researchers to decision-makers working to implement forest conservation strategies at global, national, or landscape scales. This is already happening: *ForC* has contributed to updating the IPCC guidelines for carbon accounting in forests (IPCC 2019, Requena Suarez *et al* 2019), mapping C accumulation potential from natural forest regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al* 2020).

It is also interesting to consider the complementary utility of global-scale but spatially discontinuous databases such as *ForC* and remote wall-to-wall remote sensing products. The latter provide unparalleled insight into aboveground carbon stocks, but less constraint on belowground stocks or carbon fluxes in general (Bond-Lamberty *et al* 2016, Anav *et al* 2015). Combining observational data and remote observations may provide a much more comprehensive and accurate picture of global forest C cycling, particularly when used in formal data assimilation systems (Konings *et al* 2019, Liu *et al* 2018). Biomass is the largest C stock in most forests, and most of the emphasis has traditionally been on this variable. Remote-sensing driven biomass estimates (e.g., Saatchi *et al* 2011), calibrated based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019), are well suited for this task. Note, however, that factors such as stand age and disturbance history are difficult, if possible, to detect remotely, and can only be characterized for very recent decades (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). Ground-based data such as *ForC* are therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020), and thus constraining variables such as carbon sink potential (Luyssaert *et al* 2008).

In contrast, carbon allocation within forest ecosystems and respiration fluxes cannot be remotely sensed. Efforts such as the Global Carbon Project (Friedlingstein *et al* 2019) and NASA's Carbon Monitoring System (Liu *et al* 2018) typically compute respiration as residuals of all other terms (Bond-Lamberty *et al*

436 2016, Harmon *et al* 2011). This means that the errors on respiration outputs are likely to be large and  
437 certainly poorly constrained, offering a unique opportunity for databases such as ForC and SRDB (Jian *et al*  
438 2020) to provide observational benchmarks. For example, Konings *et al* (2019) produced a unique top-down  
439 estimate of global heterotrophic respiration that can both be compared with extant bottom-up estimates  
440 (Bond-Lamberty 2018) and used as an internal consistency check on other parts of the carbon cycle (Phillips  
441 *et al* 2017).

## 442 Conclusions

443 As climate change accelerates, understanding and managing the carbon dynamics of forests—notably  
444 including dynamics and fluxes that cannot be observed by satellites—is critical to forecasting, mitigation, and  
445 adaptation. The C data in *ForC*, as summarized here, will be valuable to these efforts. Notably, the fact that  
446 tropical forests tend to have both the highest rates of C sequestration in young stands (Fig. 7; Cook-Patton  
447 *et al* 2020), fueled by their generally high C flux rates (Table 1; Fig. 6), and the highest mean biomass (Fig.  
448 7; Table 1; Hu *et al* 2016, Jian *et al* 2020) reinforces the concept that conservation and restoration of these  
449 forests is a priority for climate change mitigation, along with high-biomass old-growth temperate stands  
450 (Grassi *et al* 2017, Goldstein *et al* 2020). It is also important to note the trade-off in climate mitigation  
451 potential of restoration of young forests, with high rates of CO<sub>2</sub> sequestration (*NEP*; Cook-Patton *et al*  
452 2020), versus conservation and management of mature forests, with low *NEP* but high C stocks that could  
453 not be recovered on a time scale relevant to climate change mitigation (Goldstein *et al* 2020). Generally  
454 speaking, the conservation of mature forests will yield greater climate benefits (Anderson-Teixeira and  
455 DeLucia 2011), but both approaches are critical to avoiding catastrophic climate change (IPCC 2018).

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## 461 Data availability statement

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

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