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3 ¹ **Title:** Carbon cycling in mature and regrowth forests globally: a macroecological synthesis based on the
4 ² Global Forest Carbon (ForC) database
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1 2 25 Summary

3
4 26 *Background.* Earth's climate is closely linked to forests, which strongly influence atmospheric carbon dioxide
5 27 (CO_2) and climate by their impact on the global carbon (C) cycle. However, efforts to incorporate forests
6 28 into climate models and CO_2 accounting frameworks have been constrained by a lack of accessible,
7 29 global-scale data on how C cycling varies across forest types and stand ages.

8
9 30 *Methods/Design.* Here, we draw from the Global Forest Carbon Database, *ForC*, to provide a macroscopic
10 31 overview of C cycling in the world's forests, giving special attention to stand age-related variation.

11 32 Specifically, we use 11923 *ForC* records from 865 geographic locations representing 34 C cycle variables to
12 33 characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate
13 34 broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years)
14 35 forests. For regrowth forests, we quantify age trends for all variables with sufficient data.

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16 36 *Review Results/ Synthesis.* *ForC v3.0* yielded a comprehensive picture of C cycling in the world's major
17 37 forest biomes. The rate of C cycling generally increased from boreal to tropical regions in both mature and
18 38 regrowth forests, whereas C stocks showed less directional variation. The majority of flux variables, together
19 39 with most live biomass pools, increased significantly with stand age. Importantly, there was generally good
20 40 closure of C budgets, *i.e.*, internal consistency in the *ForC* data.

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22 41 *Discussion.* As climate change accelerates, understanding and managing the carbon dynamics of forests is
23 42 critical to forecasting, mitigation, and adaptation. This synthetic and internally consistent global overview of
24 43 C stocks and fluxes across biomes and stand ages will help to advance these efforts.

25
26 44 *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 (CO₂; Bonan 2008, Friedlingstein *et al* 2019, IPCC 2018). Despite the centrality of forest C cycling
48 in regulating atmospheric CO₂, important uncertainties in climate models (Friedlingstein *et al* 2006, Krause
49 *et al* 2018, Bonan *et al* 2019, Di Vittorio *et al* 2020) and CO₂ 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 CO₂ sequestration in
58 forests (gross primary productivity, *GPP*) is estimated at >69 Gt C yr⁻¹ (Badgley *et al* 2019), or >7 times
59 average annual fossil fuel emissions from 2009-2018 (9.5 ± 0.5 Gt C yr⁻¹; Friedlingstein *et al* 2019). Most of
60 this enormous C sequestration is counterbalanced by CO₂ 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 CO₂ sink averaged 3.2 ± 0.6 GtC
63 yr⁻¹ 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⁻¹ 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⁻¹ 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 CO₂ 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

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3 87 are effectively inaccessible for many global-scale analyses, including those attempting to benchmark model
4 88 performance with global data (Clark et al 2017, Luo et al 2012), quantify the the role of forests in the global
5 89 C cycle (*e.g.*, Pan *et al* 2011), or use book-keeping methods to quantify actual or scenario-based exchanges of
6 90 CO₂ between forests and the atmosphere (Griscom *et al* 2017, Houghton 2020).

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8 91 To address the need for global-scale analyses of forest C cycling, we recently developed *ForC*
9 92 (Anderson-Teixeira *et al* 2016, 2018). *ForC* contains published estimates of forest ecosystem C stocks and
10 93 annual fluxes (>50 variables), with the different variables capturing the unique ecosystem pools (*e.g.*, woody,
11 94 foliage, and root biomass; dead wood) and flux types (*e.g.*, gross and net primary productivity; soil, root, and
12 95 ecosystem respiration). These data are ground-based measurements, and *ForC* contains associated data
13 96 required for interpretation (*e.g.*, stand history, measurement methods). Data have been amalgamated from
14 97 original peer-reviewed publications, either directly or via intermediary data compilations. Since its most
15 98 recent publication (Anderson-Teixeira *et al* 2018), *ForC* has grown to include two additional large databases:
16 99 the Global Soil Respiration Database (SRDB; Bond-Lamberty and Thomson 2010) and the Global
17 100 Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020) that also synthesized
18 101 published forest C data. Following these additions, *ForC* currently contains 39762 records from 10608 plots
19 102 and 1532 distinct geographic areas representing all forested biogeographic and climate zones. This represents
20 103 an 129% increase in records from the prior publication (Anderson-Teixeira *et al* 2018).

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22 104 Here, we provide a robust and comprehensive analysis of carbon cycling from a stand to global level, and by
23 105 biome and stand age, using the largest global compilation of forest carbon data, which is available in our
24 106 open source Global Carbon Forest database (*ForC*; Fig. 1). Our primary goal is to provide a data-driven
25 107 summary of our current state of knowledge on broad trends in forest C cycling. Specifically, we address three
26 108 broad questions:

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28 109 1. How thoroughly can we represent C budgets for each of the world's major forest biomes (*i.e.*, tropical,
29 110 temperate broadleaf and deciduous, boreal) based on the current *ForC* data?
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31 111 2. How do C cycling vary across the world's major forest biomes?
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33 112 3. How does C cycling vary with stand age (in interaction with biome)?

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35 113 While components of these questions have been previously addressed (Luyssaert *et al* 2007,
36 114 Anderson-Teixeira *et al* 2016, Cook-Patton *et al* 2020, Banbury Morgan *et al* n.d.), our analysis represents
37 115 by far the most comprehensive analysis of C cycling in global forests, and will serve as a foundation for
38 116 improved understanding of global forest C cycling and highlight where key sources of uncertainty still reside.

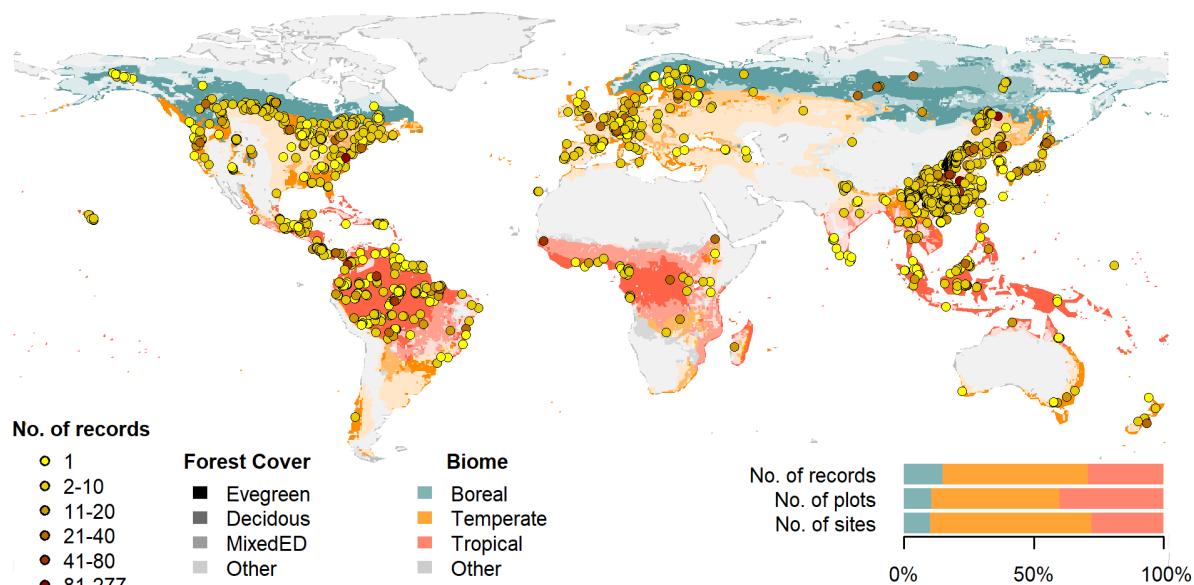


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

Methods/ Design

This review synthesizes data from the *ForC* database (Fig. 1; <https://github.com/forc-db/ForC>; Anderson-Teixeira *et al* 2016, 2018). *ForC* amalgamates numerous intermediary data sets (*e.g.*, Luyssaert *et al* 2007, Bond-Lamberty and Thomson 2010, Cook-Patton *et al* 2020) and original studies. Original publications were referenced to check values and obtain information not contained in intermediary data sets, although this process has not been completed for all records. The database was developed with goals of understanding how C cycling in forests varies across broad geographic scales and as a function of stand age. As such, there has been a focus on incorporating data from regrowth forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention was given to developing the database for tropical forests (Anderson-Teixeira *et al* 2016), which represented roughly one-third of records in *ForC* v2.0 (Anderson-Teixeira *et al* 2018). Since publication of *ForC* v2.0, we added the following data to *ForC*: the Global Database of Soil Respiration Database (*SRDB* v4, 9488 records; Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment database (*GROA* v1.0, 10116 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020). We have also added data from individual publications, with a particular focus on productivity (*e.g.*, Taylor *et al* 2017), dead wood, and ForestGEO sites (*e.g.*, Lutz *et al* 2018, p @johnson_climate_2018). The database version used for this analysis has been tagged as a new release on Github (v3.0) and assigned a DOI through Zenodo (DOI: TBD).

To facilitate analyses, we created a simplified version of *ForC*, *ForC-simplified* (https://github.com/forc-db/ForC/blob/master/ForC_simplified), which we analyzed here. In generating

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3 137 *ForC-simplified*, all measurements originally expressed in units of dry organic matter (OM) were converted
4 138 to units of C using the IPCC default of $C = 0.47 * OM$ (IPCC 2018). Duplicate or otherwise conflicting
5 139 records were reconciled as described in Appendix S1, resulting in a total of 22265 records (56% size of total
6 140 database). Records were filtered to remove plots that had undergone significant anthropogenic management
7 141 or major disturbance since the most recent stand initiation event. Specifically, we removed all plots flagged
8 142 as managed in *ForC-simplified* (13.9%). This included plots with any record of managements manipulating
9 143 CO_2 , temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the
10 144 terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”. Plots flagged as disturbed in
11 145 *ForC-simplified* (5.6%) included stands that had undergone any notable anthropogenic thinning or partial
12 146 harvest. We retained sites that were grazed or had undergone low severity natural disturbances (<10%
13 147 mortality) including droughts, major storms, fires, and floods. We removed all plots for which no stand
14 148 history information had been retrieved (5.7%). In total, this resulted in 17349 records (43.6% of the records
15 149 in the database) being eligible for inclusion in the analysis.
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18 150 We selected 23 annual flux and 11 C stock variables for inclusion in the analysis (Table 1). These different
19 151 flux and stock variables represent different pools (e.g., aboveground biomass, root biomass, dead wood) and
20 152 levels of combination (e.g., total net primary productivity, NPP , versus the individual elements of NPP
21 153 such as foliage, roots, and branches). Note that two flux variables, aboveground heterotrophic (R_{het-ag}) and
22 154 total (R_{het}) respiration, were included for conceptual completeness but had no records in *ForC* (Table 1).
23 155 Records for our focal variables represented 90.3% of the total records eligible for inclusion. For this analysis,
24 156 we combined some of *ForC*'s specific variables into more broadly defined variables. Specifically, net ecosystem
25 157 exchange (measured by eddy-covariance; Baldocchi *et al* 2001) and biometric estimates of NEP were
26 158 combined into the single variable NEP (Table 1). Furthermore, for NPP , aboveground NPP ($ANPP$),
27 159 and the litterfall component of $ANPP$ ($ANPP_{litterfall}$), *ForC* variables specifying inclusion of different
28 160 components were combined (e.g., measurements including or excluding fruit and flower production and
29 161 herbivory). Throughout *ForC*, for all measurements drawing from tree census data (e.g., biomass,
30 162 productivity), the minimum diameter breast height (DBH) threshold for tree census was $\leq 10cm$. All records
31 163 were measured directly or derived from field measurements (as opposed to modeled).
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34 164 We grouped forests into four broad biome types based on climate zones and dominant vegetation type
35 165 (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age
36 166 classifications (young and mature). Climate zones (Fig. 1) were defined based on site geographic coordinates
37 167 according to Köppen-Geiger zones (Rubel and Kottek 2010). We defined the tropical biome as including all
38 168 equatorial (A) zones, temperate biomes as including all warm temperate (C) zones and warmer snow
39 169 climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and the boreal biome as including the colder snow climates
40 170 (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones were
41 171 excluded from the analysis. We defined leaf type (broadleaf / needleleaf) was based on descriptions in
42 172 original publications (prioritized) or values extracted from a global map based on satellite observations
43 173 (SYNMAP; Jung *et al* 2006). For young tropical forests imported from *GROA* but not yet classified by leaf
44 174 type, we assumed that all were broadleaf, consistent with the rarity of naturally regenerating needleleaf
45 175 forests in the tropics. We also classified forests as “young” (< 100 years) or “mature” (≥ 100 years or
46 176 classified as “mature”, “old growth”, “intact”, or “undisturbed” in original publication). Assigning stands to
47 177 these groupings required the exclusion of records for which *ForC* lacked geographic coordinates (0.4% of sites
48 178 in full database) or records of stand age (5.7% of records in full database). We also excluded records of stand
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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		
Annual fluxes						
<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_{woody}</i>	woody production ($ANPP_{stem} + ANPP_{branch}$)	64	53	37	n.s.	+
<i>ANPP_{stem}</i>	woody stem production	217	190	117	TrB > TeN \geq TeB \geq BoN	n.s.
<i>ANPP_{branch}</i>	branch turnover	69	59	42	TrB > TeB \geq TeN	n.s.
<i>ANPP_{foliage}</i>	foliage production, typically estimated as annual leaf litterfall	162	132	88	TrB > TeB \geq TeN $>$ BoN	+
<i>ANPP_{litterfall}</i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	82	70	55	n.s.	+
<i>ANPP_{repro}</i>	production of reproductive structures (flowers, fruits, seeds)	51	44	34	n.t.	n.t.
<i>ANPP_{folivory}</i>	foliar biomass consumed by folivores	20	12	11	n.t.	n.t.
<i>M_{woody}</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_{coarse}</i>	coarse root production	77	56	36	TeN \geq TrB	n.s.
<i>BNPP_{fine}</i>	fine root production	123	99	66	n.s.	+
<i>R_{eco}</i>	ecosystem respiration ($R_{auto} + R_{het}$)	213	98	70	TrB > TeB \geq TeN	+
<i>R_{auto}</i>	autotrophic respiration ($(R_{auto-ag} + R_{root})$)	24	23	15	n.t.	n.t.
<i>R_{auto-ag}</i>	aboveground autotrophic respiration (i.e., leaves and stems)	2	2	1	n.t.	n.t.
<i>R_{root}</i>	root respiration	181	139	95	TrB \geq TeB	+
<i>R_{soil}</i>	soil respiration ($R_{het-soil} + R_{root}$)	627	411	229	TrB > TeB $>$ TeN \geq BoN	n.s.
<i>R_{het-soil}</i>	soil heterotrophic respiration	197	156	100	TrB > TeB \geq TeN	n.s.
<i>R_{het-ag}</i>	aboveground heterotrophic respiration	0	0	0	-	-
<i>R_{het}</i>	heterotrophic respiration ($(R_{het-ag} + R_{het-soil})$)	0	0	0	-	-
Stocks						
<i>B_{tot}</i>	total live biomass ($B_{ag} + B_{root}$)	188	157	87	TrB \geq TeB $>$ BoN	+; xB
<i>B_{ag}</i>	aboveground live biomass ($B_{ag-wood} + B_{foliage}$)	4466	4072	621	TrB \geq TeN \geq TeB $>$ BoN	+; xB
<i>B_{ag-wood}</i>	woody component of aboveground biomass	115	102	64	TeN $>$ TrB \geq BoN	+; xB
<i>B_{foliage}</i>	foliage biomass	134	115	72	TeN $>$ TrB \geq BoN \geq TeB	+; xB
<i>B_{root}</i>	total root biomass ($B_{root-coarse} + B_{root-fine}$)	2329	2298	360	n.s.	+; xB
<i>B_{root-coarse}</i>	coarse root biomass	134	120	73	TeN $>$ TeB \geq BoN	+; xB
<i>B_{root-fine}</i>	fine root biomass	226	180	109	n.s.	+; xB
<i>DW_{tot}</i>	deadwood ($DW_{standing} + DW_{down}$)	79	73	42	n.t.	+; xB
<i>DW_{standing}</i>	standing dead wood	36	35	22	n.t.	n.t.
<i>DW_{down}</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.

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3 181 Data were summarized to produce schematics of C cycling across the eight biome by age group combinations
4 182 identified above. To obtain the values reported in the C cycle schematics, we first averaged any repeated
5 183 measurements within a plot. Values were then averaged across geographically distinct areas, defined as plots
6 184 clustered within 25 km of one another (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if
7 185 available for all records. This step was taken to avoid pseudo-replication.
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10 186 We tested whether the C budgets described above “closed”—*i.e.*, whether they were internally consistent.
11 187 Specifically, we first defined relationships among variables: for example, $NEP = GPP - R_{eco}$,
12 188 $BNPP = BNPP_{coarse} + BNPP_{fine}$, $DW_{tot} = DW_{standing} + DW_{down}$). Henceforth, we refer to the
13 189 variables on the left side of the equation as “aggregate” fluxes or stocks, and those that are summed as
14 190 “component” fluxes or stocks, noting that the same variable can take both aggregate and component positions
15 191 in different relationships. We considered the C budget for a given relationship “closed” when component
16 192 variables summed to within one standard deviation of the aggregate variable.
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19 193 To test for differences across mature forest biomes, we also examined how stand age impacted fluxes and
20 194 stocks, employing a mixed effects model (“lmer” function in “lme4” R package; Bates *et al* 2015) with biome
21 195 as fixed effect and plot nested within geographic.area as random effects on the intercept. When Biome had a
22 196 significant effect, we looked at a Tukey’s pairwise comparison to see which biomes were significantly different
23 197 from one another. This analysis was run for variables with records for at least seven distinct geographic areas
24 198 in more than one biome, excluding any biomes that failed this criteria (Table 1).
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27 199 To test for age trends in young (<100yrs) forests, we employed a mixed effects model with biome and
28 200 $\log_{10}[\text{stand.age}]$ as fixed effects and plot nested within geographic.area as a random effect on the intercept.
29 201 This analysis was run for variables with records for at least three distinct geographic areas in more than one
30 202 biome, excluding any biomes that failed this criteria (Table 1). When the effect of stand age was significant
31 203 at $p \leq 0.05$ and when each biome had records for stands of at least 10 different ages, a biome \times stand.age
32 204 interaction was included in the model.
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35 205 To facilitate the accessibility of our results and data, and to allow for rapid updates as additional data
36 206 become available, we have automated all database manipulation, analyses, and figure production in R (R
37 207 Core Team 2020).
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40 208 Review Results/ Synthesis

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42 209 Data Coverage

43 210 Of the 39762 records in *ForC* v3.0, 11923 met our strict criteria for inclusion in this study (Fig. 1). These
44 211 records were distributed across 5062 plots in 865 distinct geographic areas. Of the 23 flux and 11 stock
45 212 variables mapped in these diagrams, *ForC* contained sufficient mature forest data for inclusion in our
46 213 statistical analyses (*i.e.*, records from ≥ 7 distinct geographic areas) for 20 fluxes and 9 stocks in tropical
47 214 broadleaf forests, 15 fluxes and 8 stocks in temperate broadleaf forests, 14 fluxes and 7 stocks in temperate
48 215 conifer forests, and 8 fluxes and 7 stocks in boreal forests. For regrowth forests (<100 yrs), *ForC* contained
49 216 sufficient data for inclusion in our statistical analyses (*i.e.*, records from ≥ 3 distinct geographic areas) for 11
50 217 fluxes and 10 stocks in tropical broadleaf forests, 16 fluxes and 10 stocks in temperate broadleaf forests, 16
51 218 fluxes and 10 stocks in temperate conifer forests, and 14 fluxes and 9 stocks in boreal forests.
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3 **C cycling in mature forests**
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5 Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests \geq
6 100 years old and with no known major natural or anthropogenic disturbance are presented in Figures 2-5
7 (and available in tabular format in the *ForC* release accompanying this publication:
8 *ForC/numbers_and_facts/ForC_variable_averages_per_Biome.csv*).

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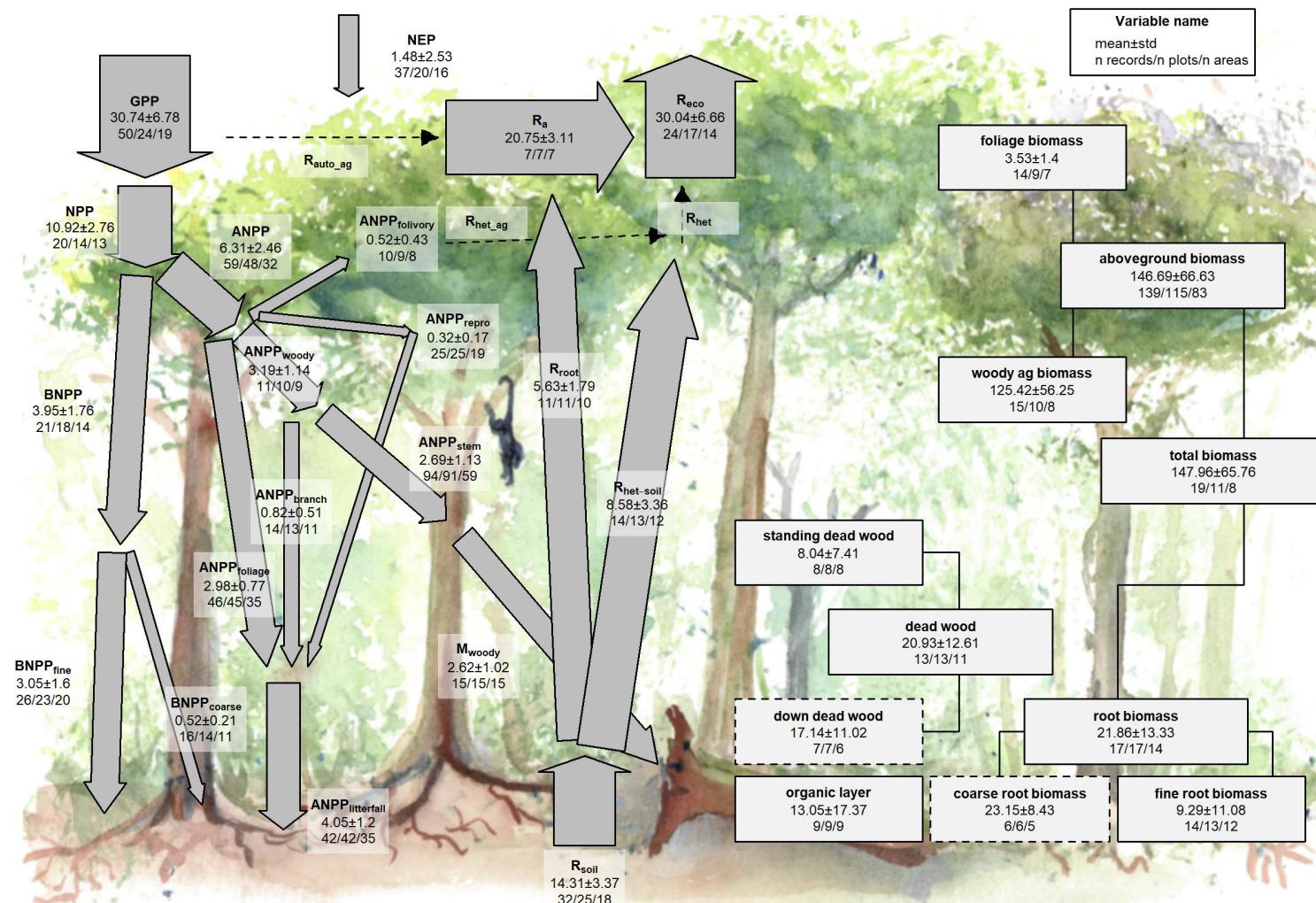


Figure 2 | C cycle diagram for mature tropical broadleaf forests. Arrows indicate fluxes ($Mg C ha^{-1} yr^{-1}$); boxes indicate stocks ($Mg C ha^{-1}$), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed 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.

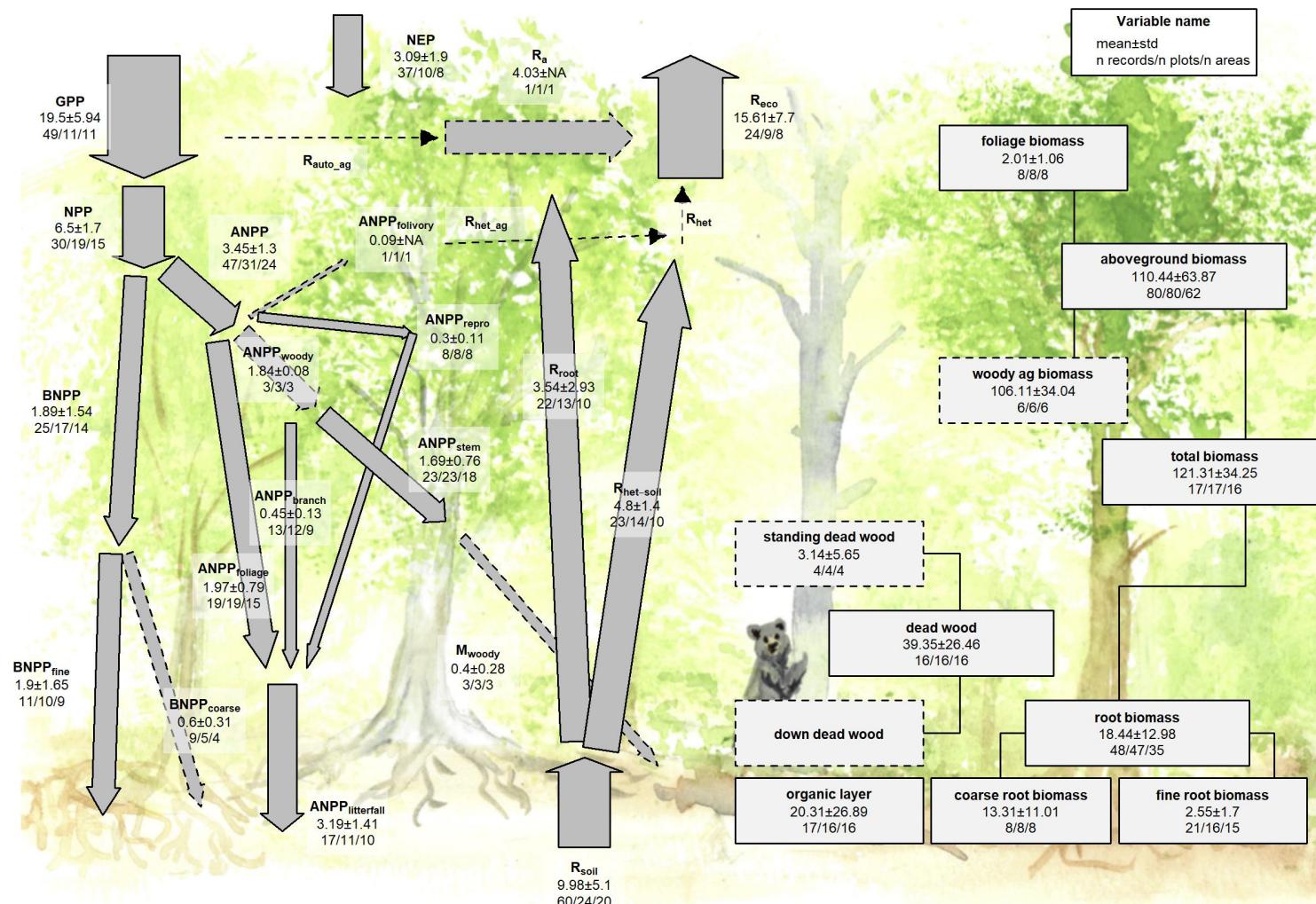


Figure 3 | C cycle diagram for mature temperate broadleaf forests. Arrows indicate fluxes ($Mg C ha^{-1} yr^{-1}$); boxes indicate stocks ($Mg C ha^{-1}$), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed 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.

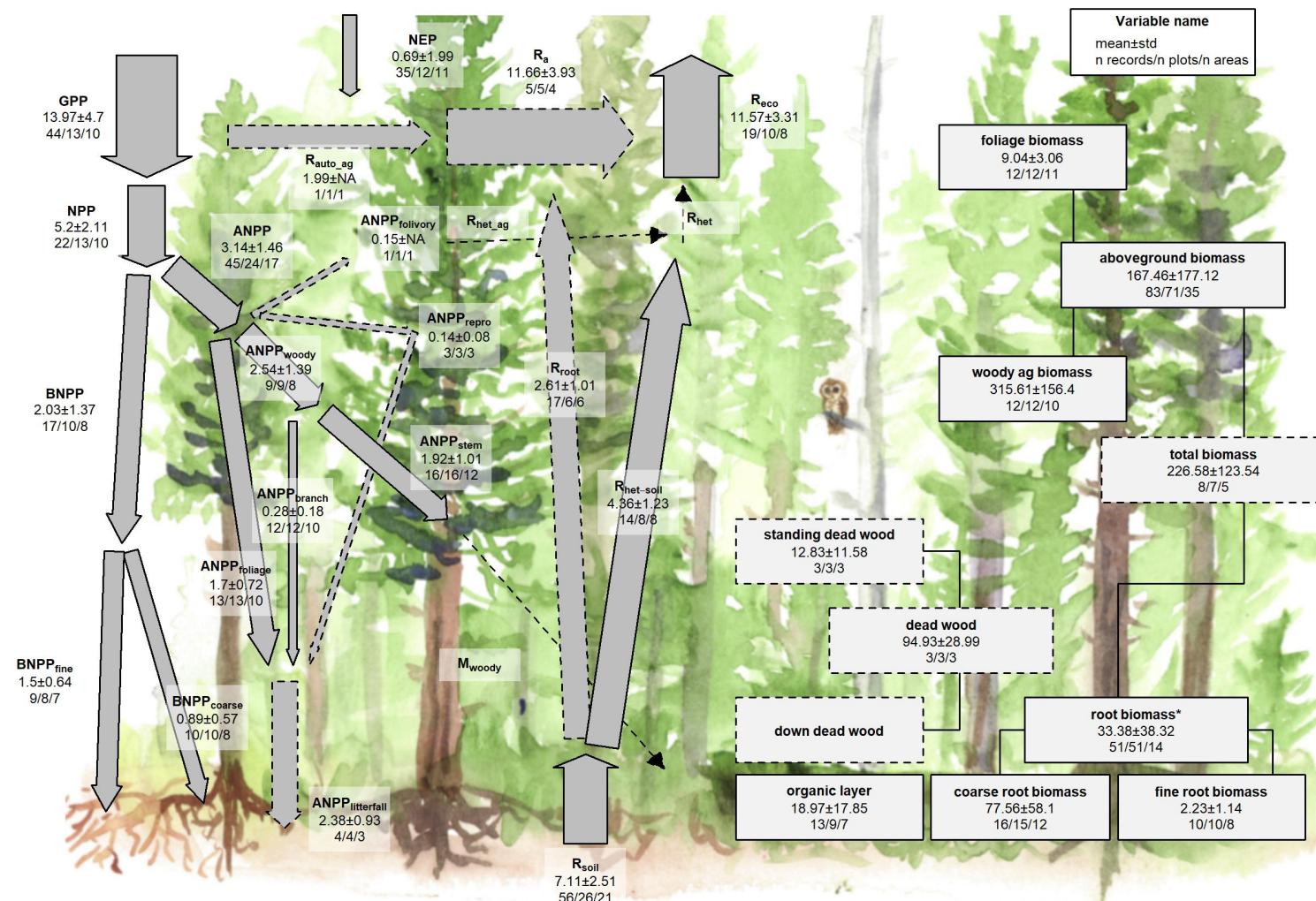


Figure 4 | C cycle diagram for mature temperate conifer forests. Arrows indicate fluxes ($Mg\ C\ ha^{-1}\ yr^{-1}$); boxes indicate stocks ($Mg\ C\ ha^{-1}$), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. 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.

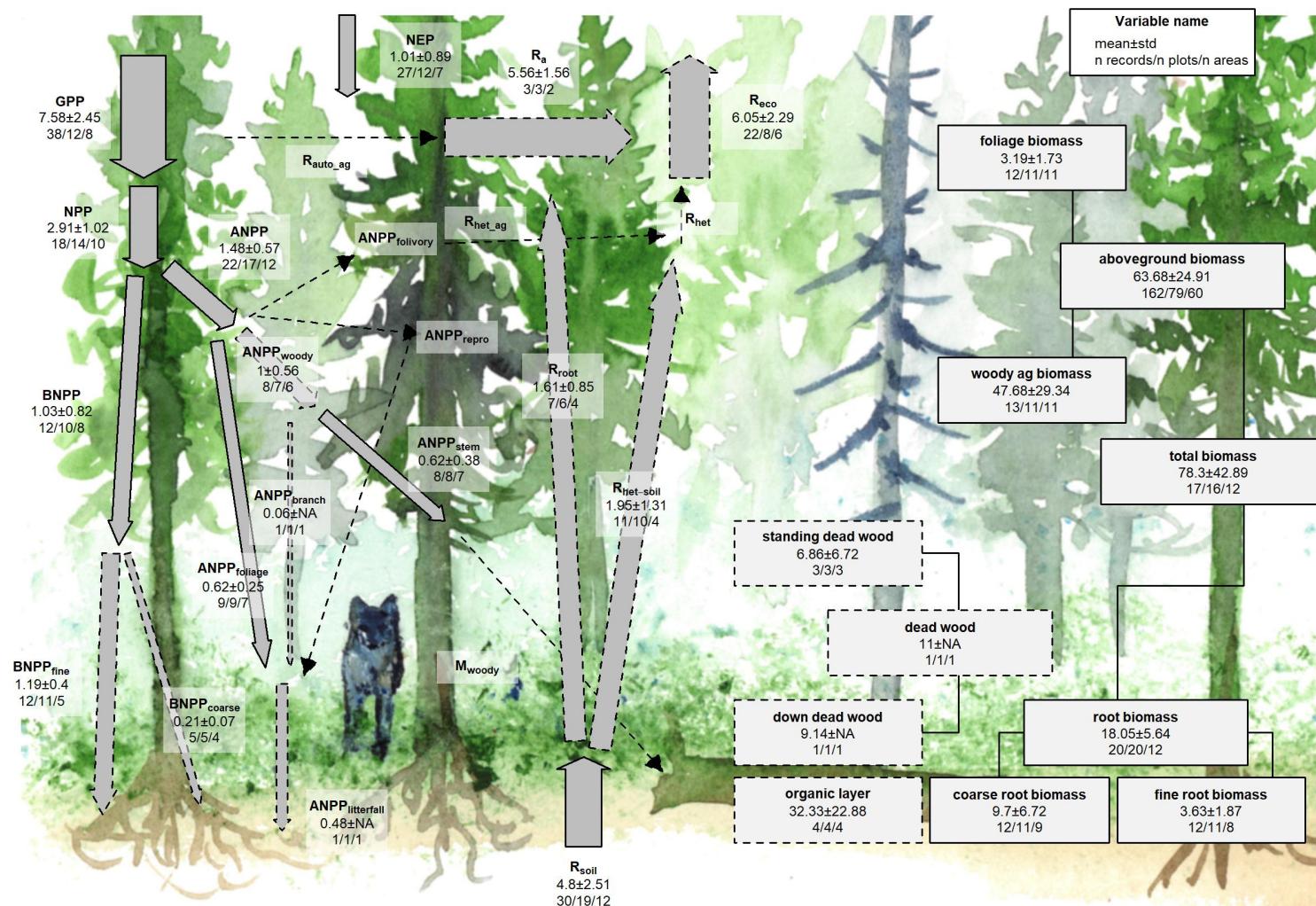


Figure 5 | C cycle diagram for mature boreal conifer forests. Arrows indicate fluxes ($Mg\ C\ ha^{-1}\ yr^{-1}$); boxes indicate stocks ($Mg\ C\ ha^{-1}$), with variables as defined in Table 1. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Dashed 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.

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3 There were sufficient data to assess mature forest biome differences for 15 flux variables, and significant
4 differences among biomes were detected for 12 variables (Table 1). In all of these cases—including C fluxes
5 into, within, and out of the ecosystem—C fluxes were highest in tropical forests, intermediate in temperate
6 (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 6, S1-S15). Differences between
7 tropical and boreal forests were always significant, with temperate forests intermediate and significantly
8 different from one or both. Fluxes tended to be numerically greater in temperate broadleaf than conifer
9 forests, but the difference was never statistically significant. This pattern held for the following variables:
10 GPP , NPP , $ANPP$, $ANPP_{stem}$, $ANPP_{branch}$, $ANPP_{foliage}$, $BNPP$, R_{eco} , R_{root} , R_{soil} , and $R_{het-soil}$.
11 For two of the variables without significant differences among biomes ($ANPP_{litterfall}$ and $BNPP_{fine}$; Figs.
12 S8 and S11, respectively), the same general trends applied but were not statistically significant. Another
13 exception was for $BNPP_{root-coarse}$, where all records came from high-biomass forests in the US Pacific
14 Northwest, resulting in marginally higher values for the temperate conifer biome (Table 1, Fig. S10;
15 differences significant in mixed effects model but not in post-hoc pairwise comparison).
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17 The most notable exception to the pattern of decreasing flux from tropical to boreal biomes was NEP , with
18 no significant differences across biomes but with the largest average in temperate broadleaf forests, followed
19 by tropical, boreal, and temperate conifer forests (Figs. 5,S1).
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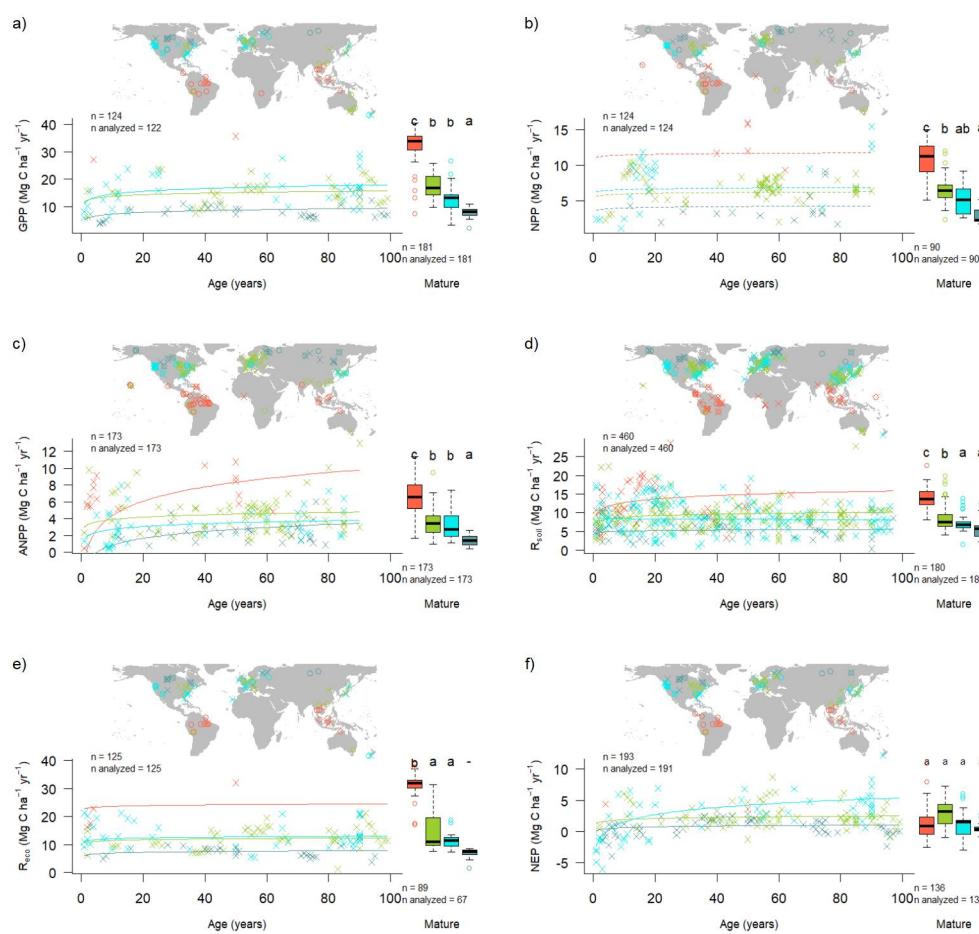


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). In each panel, the left scatterplot shows age trends in forests up to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

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

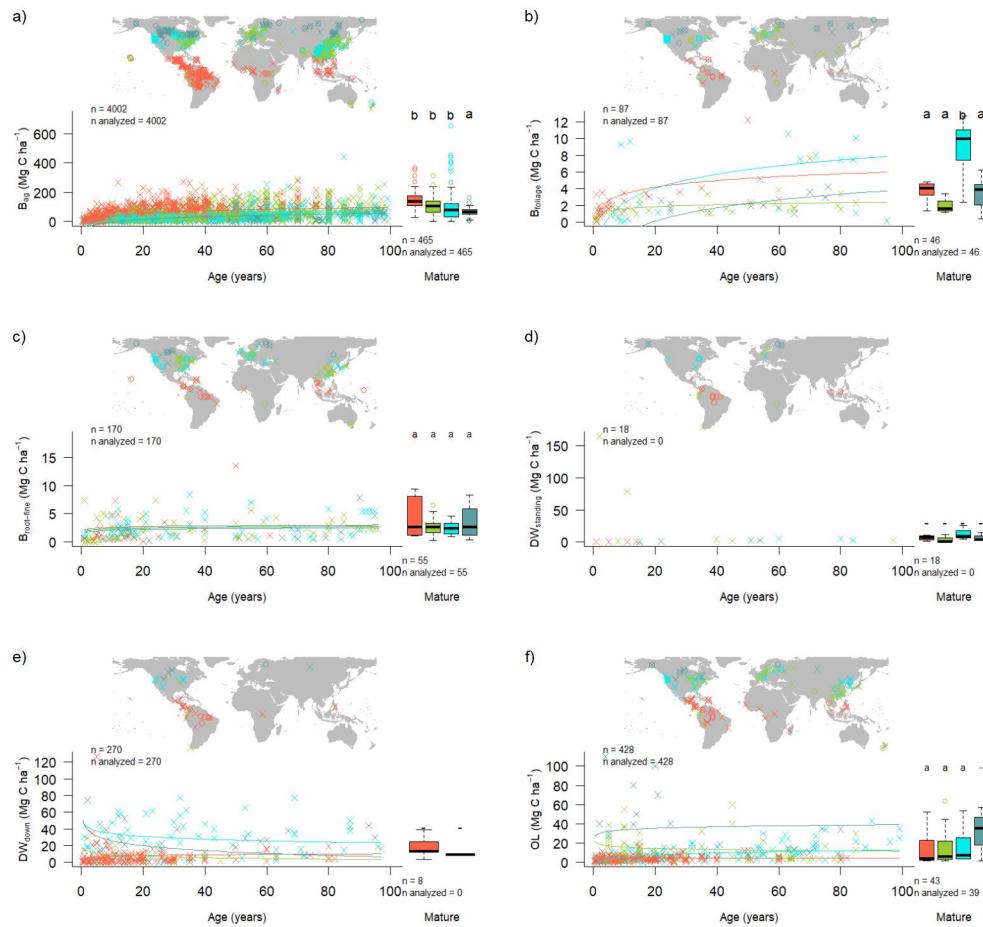


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources (x and o indicate young and mature stands, respectively). In each panel, the left scatterplot shows age trends in forests up to 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 x 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).

42 C cycling in young forests

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

47 For C contained 16 C flux variables with sufficient data for analyses of age trends in young forests (see
 48 Methods) (Figs. 6, S1-S15). Of these, ten increased significantly with age: NEP , GPP , $ANPP$,
 49 $ANPP_{woody}$, $ANPP_{foliage}$, $ANPP_{litterfall}$, $BNPP$, $BNPP_{fine}$, R_{eco} , and R_{root} . The remaining six— NPP ,
 50 $ANPP_{stem}$, $ANPP_{branch}$, $BNPP_{coarse}$, $R_{soil-het}$, and $R_{soil-het}$ —displayed no significant relationship to
 51 stand age.

53 Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling
 54 generally most rapid in the tropics and slowest in boreal forests. The single exception was $ANPP_{stem}$, for
 55 which temperate broadleaf and conifer forests had similar flux rates than tropical forests. Notably, and in
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3 265 contrast to the lack of biome differences in *NEP* for mature forests (Fig. 6), the tendency for temperate
4 266 forests to have greater fluxes than boreal forests held for *NEP* in regrowth forests (tropical forests excluded
5 267 because of insufficient data).

6
7 268 In terms of C stocks, ten variables (all but standing deadwood, $DW_{standing}$) had sufficient data to test for
8 269 age trends (Table 1, Figs. 7, S16-26). All of these displayed a significant overall increase with with
9 270 $\log_{10}[stand.age]$. There were sufficient data to model age \times biome interactions were also significant for all
10 271 ten of these C stock variables (Table S2), with living C stocks tending to accumulate more rapidly during the
11 272 early stages of forest regrowth in tropical forests (Figs. 7, S16-S22). In the case of two non-living C stocks
12 273 (DW_{down} and OL), age \times biome interactions were such that Specifically, DW_{down} declined with age in
13 274 temperate and boreal forests, compared to an increase with age in tropical forests (Figs. 7, S25). Similarly,
14 275 OL declined slightly with age in temperate broadleaf forests, contrasting an increase in the other three
15 276 biomes (Figs. 7, S26).

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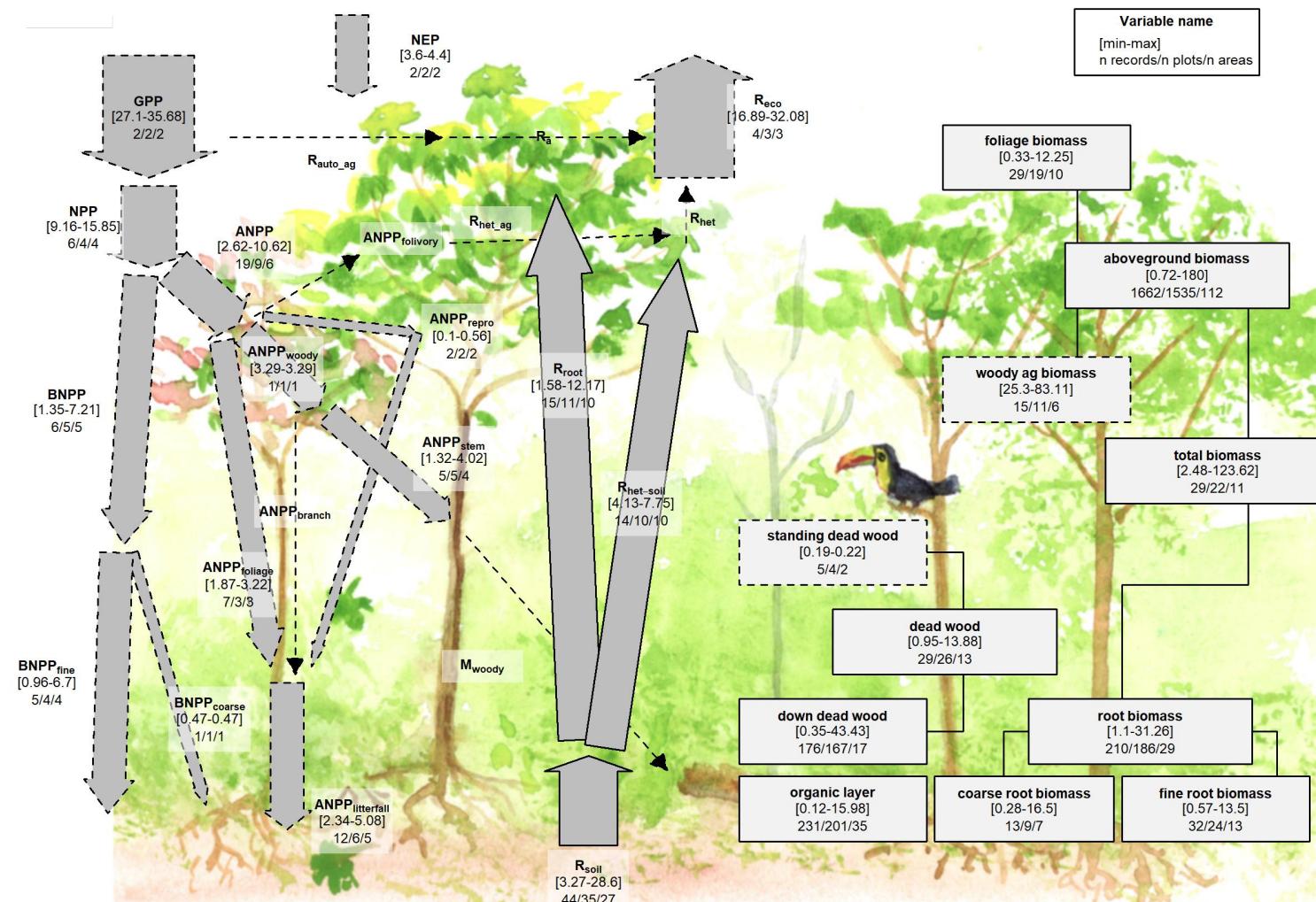


Figure 8 | C cycle diagram for young tropical broadleaf forests. Arrows indicate fluxes ($Mg C ha^{-1} yr^{-1}$); boxes indicate stocks ($Mg C ha^{-1}$), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All 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.

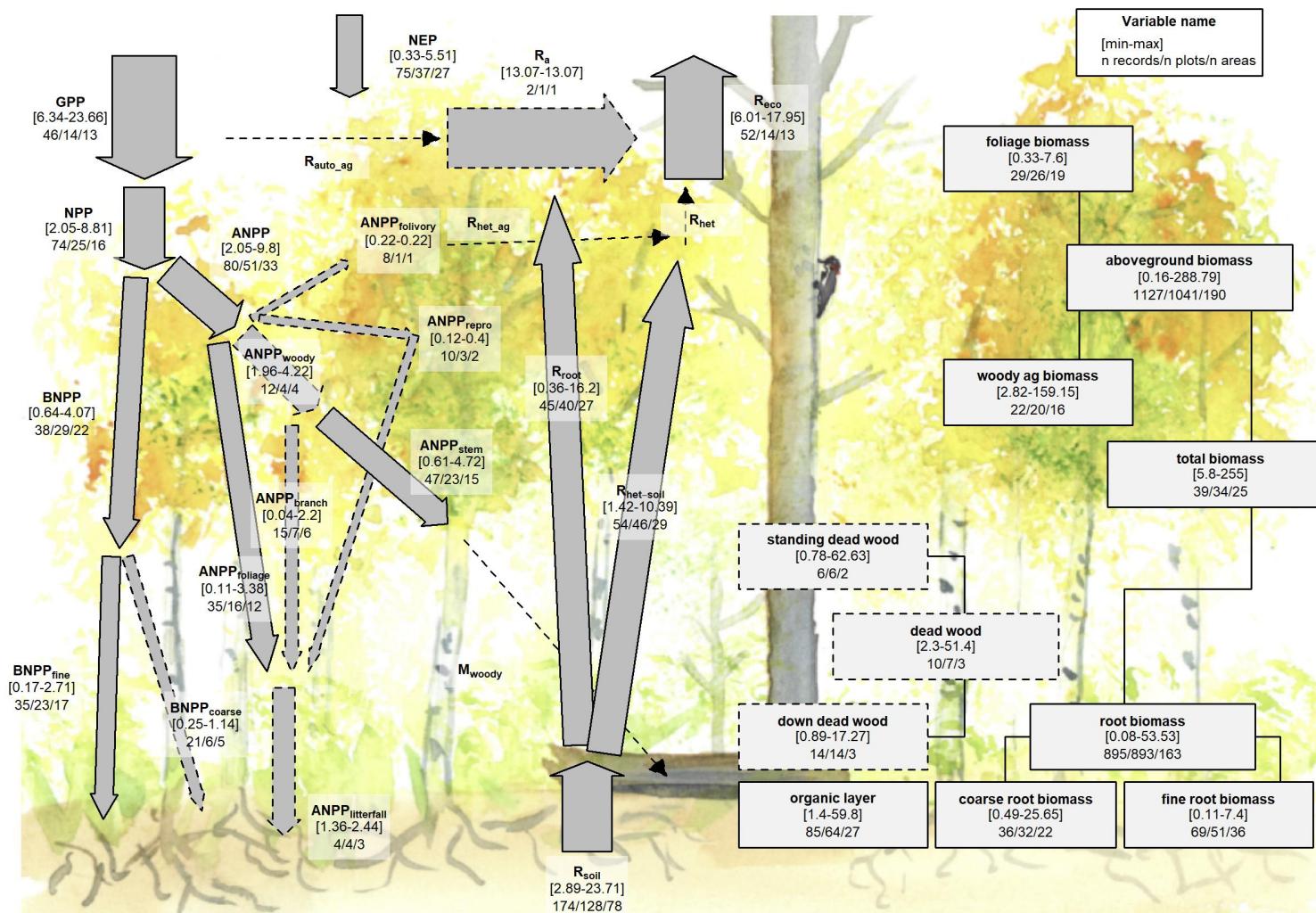


Figure 9 | C cycle diagram for young temperate broadleaf forests. Arrows indicate fluxes ($Mg\ C\ ha^{-1}\ yr^{-1}$); boxes indicate stocks ($Mg\ C\ ha^{-1}$), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. 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.

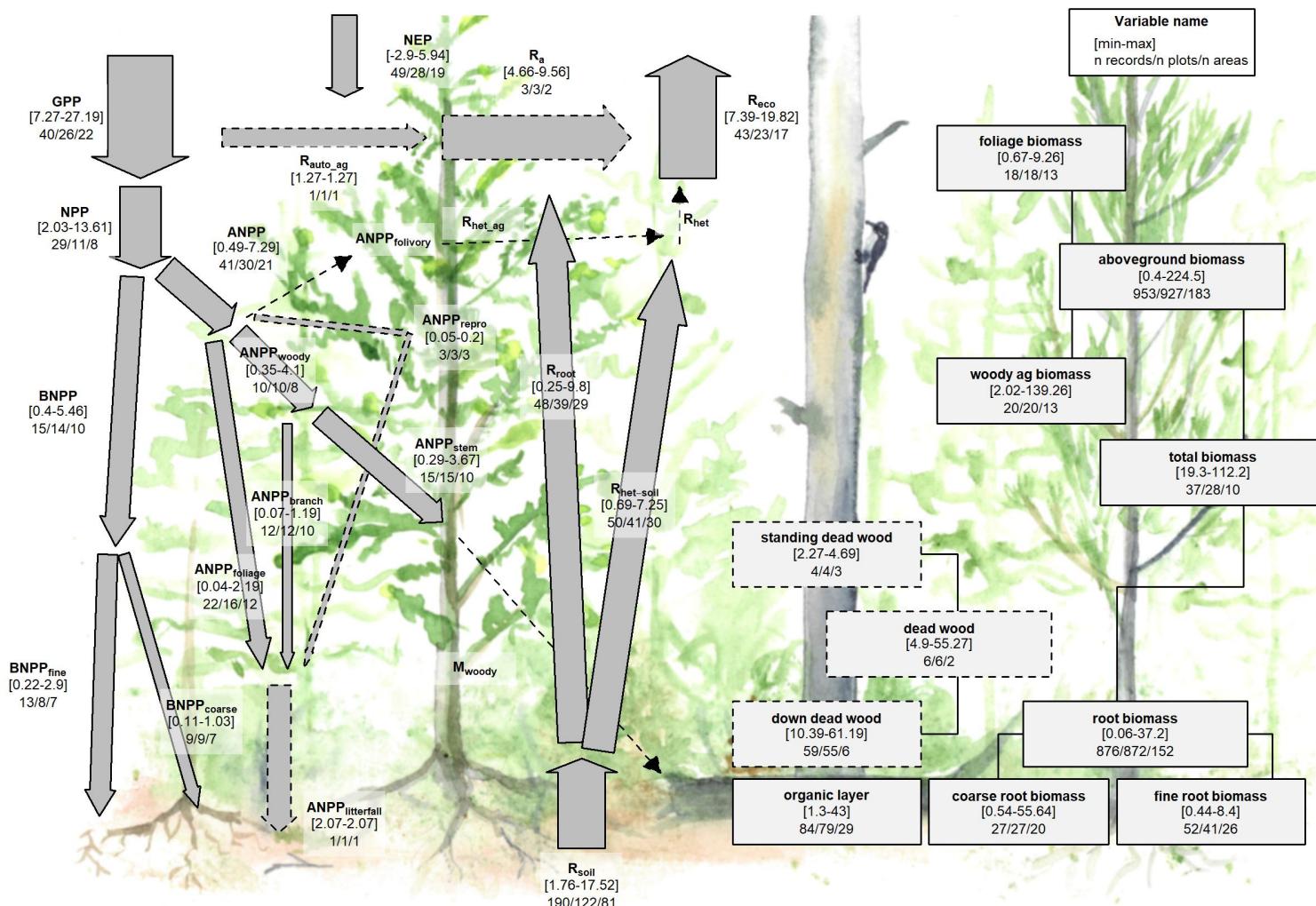


Figure 10 | C cycle diagram for young temperate conifer forests. Arrows indicate fluxes ($Mg C ha^{-1} yr^{-1}$); boxes indicate stocks ($Mg C ha^{-1}$), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All 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.

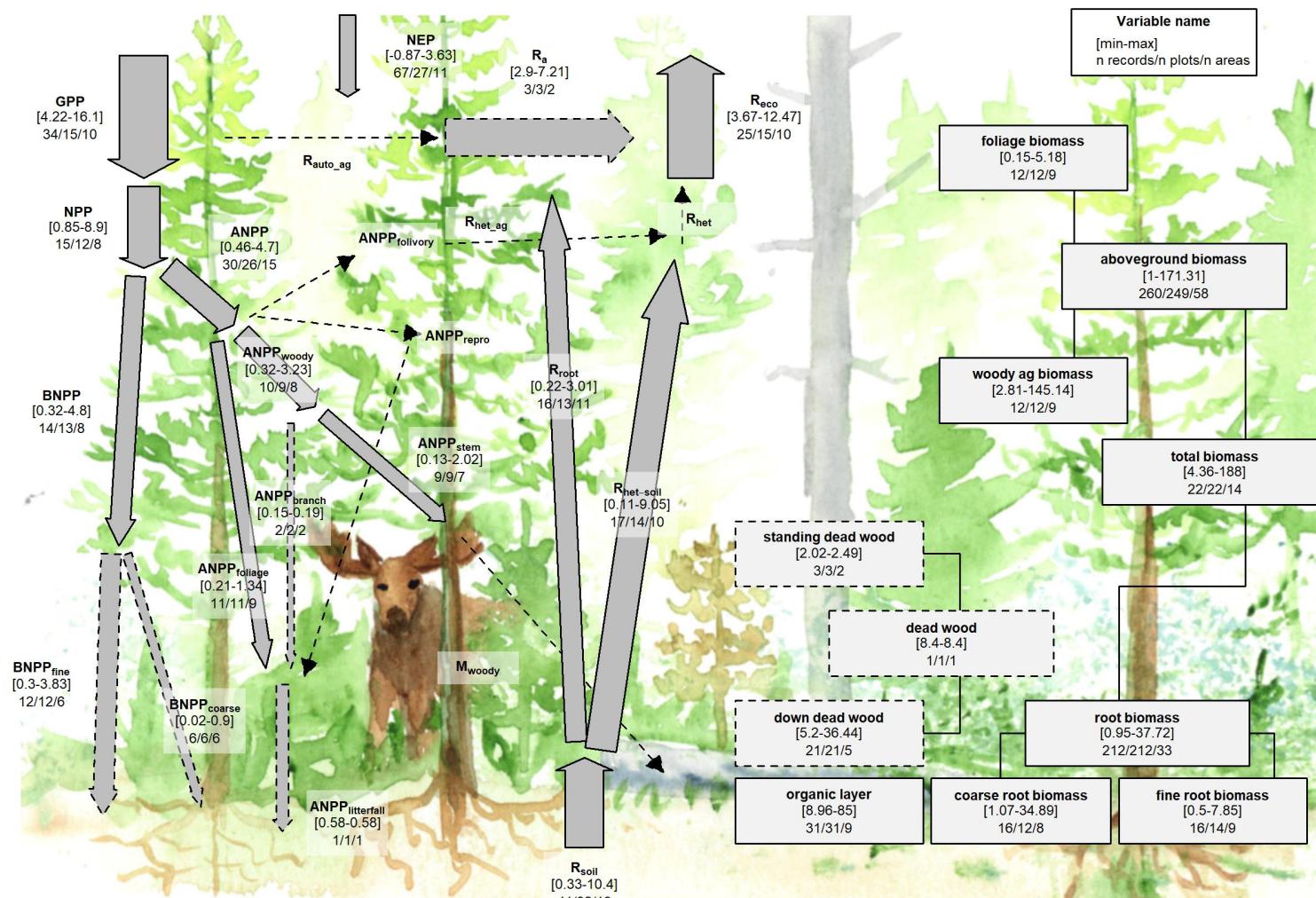


Figure 11 | C cycle diagram for young boreal conifer forests. Arrows indicate fluxes ($Mg\ C\ ha^{-1}\ yr^{-1}$); boxes indicate stocks ($Mg\ C\ ha^{-1}$), with variables as defined in Table 1. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. 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.

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).

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3 **314 C cycling across biomes**
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6 Our analysis reveals that carbon cycling is most rapid in the tropics and slowest in boreal regions, including
7 C fluxes into (GPP), within (e.g., NPP and its components), and out of (e.g., R_{soil} , R_{eco}) the ecosystem.
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9 For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes
10 generally decline with latitude (or increase with temperature) on a global scale (e.g., Luyssaert *et al* 2007,
11 Gillman *et al* 2015, Li and Xiao 2019, Banbury Morgan *et al* n.d.). The consistency with which this occurs
12 across numerous fluxes is not surprising, but has never been simultaneously assessed across such a large
13 number of variables (but see Banbury Morgan *et al* n.d. for nine autotrophic fluxes).

14 The notable exception to the pattern of fluxes decreasing from tropical to boreal regions is NEP (Fig. 6f),
15 which showed no significant differences across biomes. Unlike the other C flux variables, NEP does not
16 characterize the rate at which C cycles through the ecosystem, but is the balance between C sequestration
17 (GPP) and respiratory losses (R_{eco}) and represents net CO₂ sequestration (or release) by the ecosystem.
18
19 NEP tends to be relatively small in mature forest stands (discussed further below), which accumulate
20 carbon slowly relative to younger stands, if at all (Luyssaert *et al* 2008, Amiro *et al* 2010, Besnard *et al*
21 2018). It is therefore unsurprising that there are no pronounced differences across biomes, suggesting that
22 variation in NEP of mature forests is controlled less by climate and more by other factors including
23 moderate disturbances (Curtis and Gough 2018) or disequilibrium of R_{soil} relative to C inputs (e.g., in
24 peatlands where anoxic conditions inhibit decomposition; Wilson *et al* 2016).
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27 In contrast to the patterns observed for NEP in mature stands, NEP of stands between 20 and 100 years of
28 age varied across biomes, being lowest in boreal forests, intermediate in temperate broadleaf forests, and
29 highest in temperate conifer forests (with insufficient data to assess tropical forests; Figs. 6f, S1). This is
30 consistent with findings that live biomass accumulation rates (e.g., ΔB_{ag} or ΔB_{tot}) during early secondary
31 succession decrease with latitude (Figs. 7a, S16-S22; Anderson *et al* 2006, Cook-Patton *et al* 2020). Note,
32 though, that NEP includes not only ΔB_{tot} , but also changes in DW_{tot} , OL , and soil carbon, and biome
33 differences in the accumulation rates of these variables have not been detected, in part because these
34 variables do not consistently increase with stand age (Figs. 7, S23-S26, and see discussion below;
35 Cook-Patton *et al* 2020).
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38 For regrowth forests, little is known about cross-biome differences in carbon fluxes, and we are not aware of
39 any previous large-scale comparisons of C fluxes that have been limited to regrowth forests. Thus, this
40 analysis was the first to examine flux trends in regrowth forests across biomes. The observed tendency for
41 young forest fluxes to decrease from tropical to boreal regions paralleled patterns in mature forests (Figs. 6,
42 S1-S15), suggesting that regrowth forests follow latitudinal trends in carbon cycling similar to those of
43 mature forests (e.g., Banbury Morgan *et al* n.d.).
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46 In contrast to C fluxes and biomass accumulation rates in regrowth forests, stocks showed less systematic
47 variation across biomes. For aboveground biomass, which is the variable in *ForC* with broadest geographical
48 representation, the modest trend of declining biomass from tropical to boreal regions mirrors observations
49 from spaceborne lidar that reveal a decline in aboveground biomass (for all forests, including secondary) with
50 latitude across the N hemisphere (Hu *et al* 2016). The highest- biomass forests on Earth are, however, found
51 in coastal temperate climates of both the southern and northern hemisphere (Keith *et al* 2009, Smithwick *et*
52 al 2002, Hu *et al* 2016). Disproportionate representation of forests in one such region—the US Pacific
53 Northwest—inflated estimates of temperate conifer fluxes and stocks for some variables and was responsible
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3 for all of the anomalous results described here (e.g., lack of complete C budget closure, anomalous trend
4 across biomes for $BNPP_{coarse}$). Thus, biome differences should always be interpreted relative to the
5 geographic distribution of sampling, which only rarely covers the majority of forested area within a biome.
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7 Whereas biomass can be remotely sensed and receives significant research attention, far less is known about
8 geographical variation in deadwood and organic layer (OL) across biomes, which has proved a limitation for
9 C accounting efforts (Pan *et al* 2011). Although these stocks can be important—exceeding 100 Mg C ha^{-1} in
10 some stands (Figs. 7d-e, S23-S25), this study is the first to synthesize deadwood data on a global scale (but
11 see Cook-Patton *et al* 2020 for young forests). Unfortunately, data remain too sparse for statistical
12 comparison across biomes (Figs. 7, S23-S25; but see below for age trends), pointing to a need for more
13 widespread quantification of both standing and downed deadwood. *ForC* coverage of OL stocks is more
14 comprehensive, revealing no significant differences across temperate and tropical biomes, but a tendency
15 towards higher OL in boreal forests, consistent with the idea that slower decomposition in colder climates
16 results in more buildup of organic matter (Allen *et al* 2002). Further research on non-living C stocks in the
17 world's forests will be essential to completing the picture.
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22 **369 Age trends in C cycling**
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24 Our study reveals that most C fluxes quickly increase to a plateau as stands age (Fig. 6), consistent with
25 current understanding of age trends in forest C cycling (e.g., Anderson-Teixeira *et al* 2013, Amiro *et al* 2010,
26 Magnani *et al* 2007). While limited records in very young (*i.e.*, <5 year old) stands resulted in poor
27 resolution of the earliest phases of this increase for many variables (sometimes detecting no age trend; Table
28 1), any autotrophic C flux (e.g., GPP , NPP and its components, R_{auto}) would be minimal immediately
29 following a stand-clearing disturbance. These would be expected to increase rapidly with the most
30 metabolically active components of biomass, foliage and fine roots, which also increase rapidly with stand age
31 (Fig. 7). In contrast, soil heterotrophic respiration ($R_{het-soil}$) and total soil respiration (R_{soil}) are expected
32 to be non-zero following stand-clearing disturbance, although these may decrease with a reduction of root
33 respiration (R_{soil} only) and C exudates or increase in response to an influx of dead roots and litter
34 (Ribeiro-Kumara *et al* 2020, Maurer *et al* 2016, Bond-Lamberty *et al* 2004). In this study, we detect no
35 significant age trends in either variable.
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38 Notably, net carbon sequestration (NEP) increases with age up to the 100-yr threshold examined here, with
39 more pronounced patterns in temperate than boreal forests (Fig. 6f). This finding is largely consistent with,
40 but built from a far larger dataset than, previous studies showing an increase in NEP across relatively
41 young stand ages (Pregitzer and Euskirchen 2004, Baldocchi *et al* 2001, Luyssaert *et al* 2008). However,
42 NEP has been observed to decline from intermediate to old stands (Luyssaert *et al* 2008), and the NEP
43 estimated by our model for 100-year-old temperate conifer stands (~ 5 Mg C $ha^{-1} yr^{-1}$) exceeds the mean of
44 mature forests in the same biome (0.7 Mg C $ha^{-1} yr^{-1}$; Fig. 4). A decrease in NEP is consistent with the
45 observed deceleration of biomass accumulation as stands age, although both biomass and non-living C stocks
46 will often continue to increase well beyond the 100-yr threshold used here to delimit young and mature
47 stands (Luyssaert *et al* 2008, McGarvey *et al* 2014, Lichstein *et al* 2009).
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50 In terms of stocks, our study reveals consistent increases in live biomass stocks with stand age—a pattern that
51 is well-known and expected (e.g., Lichstein *et al* 2009, Yang *et al* 2011)—and more variable age trends in
52 deadwood and OL . The latter are particularly sensitive to the type of disturbance, where disturbances that
53 remove most organic material (e.g., logging, agriculture) result in negligible deadwood in young stands,
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3 followed by a buildup over time (tropical stands in Fig. 7e; e.g., Vargas *et al* 2008). In contrast, natural
4 disturbances (e.g., fire, drought) can produce large amounts of deadwood (mostly $DW_{standing}$) that slowly
5 decomposes as the stand recovers, resulting in declines across young stand ages (e.g., temperate and boreal
6 stands in Fig. 7e; e.g., Carmona *et al* 2002). Again, further study and synthesis of non-living C stocks across
7 biomes and stand ages will be valuable to giving a more comprehensive picture.
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10 **401 Relevance for climate change prediction and mitigation**

11 **402** The future of forest C cycling (Song *et al* 2019) will shape trends in atmospheric CO₂ and the course of
12 climate change (Schimel *et al* 2015). Our findings, and more generally the data contained in *ForC* and
13 summarized here, can help to meet two major challenges.

14 **405** First, improved representation of forest C cycling in models is essential to improving predictions of the future
15 course of climate change, for the simple reason that by definition future projections extend our existing
16 observations and understanding to conditions that do not currently exist on Earth (McDowell *et al* 2018,
17 Bonan and Doney 2018, Gustafson *et al* 2018). To ensure that models are giving the right answers for the
18 right reasons (Sulman *et al* 2018), it is important to benchmark against multiple components of the C cycle
19 that are internally consistent with each other (Collier *et al* 2018, Wang *et al* 2018). *ForC*'s tens of thousands
20 of records are readily available in a standardized format, and our analyses here indicate that their internal
21 consistency is reasonably high. Integration of *ForC* with models will be valuable to improving the accuracy
22 and reliability of models.

23 **414** Second, *ForC* can serve as a pipeline through which information can flow efficiently from forest researchers to
24 decision-makers working to implement forest conservation strategies at global, national, or landscape scales.
25 This is already happening: *ForC* has contributed to updating the IPCC guidelines for carbon accounting in
26 forests (IPCC 2019, Requena Suarez *et al* 2019), mapping C accumulation potential from natural forest
27 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*
28 2020).

29 **420** It is also interesting to consider the complementary utility of global-scale but spatially discontinuous
30 databases such as *ForC* and remote wall-to-wall remote sensing products. The latter provide unparalleled
31 insight into aboveground carbon stocks, but less constraint on belowground stocks or carbon fluxes in general
32 (Bond-Lamberty *et al* 2016, Anav *et al* 2015). Combining observational data and remote observations may
33 provide a much more comprehensive and accurate picture of global forest C cycling, particularly when used
34 in formal data assimilation systems (Konings *et al* 2019, Liu *et al* 2018). Biomass is the largest C stock in
35 most forests, and most of the emphasis has traditionally been on this variable. Remote-sensing driven
36 biomass estimates (e.g., Saatchi *et al* 2011), calibrated based on high-quality ground-based data
37 (Schepaschenko *et al* 2019, Chave *et al* 2019), are well suited for this task. Note, however, that factors such
38 as stand age and disturbance history are difficult, if possible, to detect remotely, and can only be
39 characterized for very recent decades (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). Ground-based
40 data such as *ForC* are therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al*
41 (2020), and thus constraining variables such as carbon sink potential (Luyssaert *et al* 2008).

42 **433** In contrast, carbon allocation within forest ecosystems and respiration fluxes cannot be remotely sensed.
43 Efforts such as the Global Carbon Project (Friedlingstein *et al* 2019) and NASA's Carbon Monitoring
44 System (Liu *et al* 2018) typically compute respiration as residuals of all other terms (Bond-Lamberty *et al*
45 2016).

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3 436 2016, Harmon *et al* 2011). This means that the errors on respiration outputs are likely to be large and
4 437 certainly poorly constrained, offering a unique opportunity for databases such as ForC and SRDB (Jian *et al*
5 438 2020) to provide observational benchmarks. For example, Konings *et al* (2019) produced a unique top-down
6 439 estimate of global heterotrophic respiration that can both be compared with extant bottom-up estimates
7 440 (Bond-Lamberty 2018) and used as an internal consistency check on other parts of the carbon cycle (Phillips
8 441 *et al* 2017).

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11 442 **Conclusions**

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13 443 As climate change accelerates, understanding and managing the carbon dynamics of forests—notably
14 444 including dynamics and fluxes that cannot be observed by satellites—is critical to forecasting, mitigation, and
15 445 adaptation. The C data in *ForC*, as summarized here, will be valuable to these efforts. Notably, the fact that
16 446 tropical forests tend to have both the highest rates of C sequestration in young stands (Fig. 7; Cook-Patton
17 447 *et al* 2020), fueled by their generally high C flux rates (Table 1; Fig. 6), and the highest mean biomass (Fig.
18 448 7; Table 1; Hu *et al* 2016, Jian *et al* 2020) reinforces the concept that conservation and restoration of these
19 449 forests is a priority for climate change mitigation, along with high-biomass old-growth temperate stands
20 450 (Grassi *et al* 2017, Goldstein *et al* 2020). It is also important to note the trade-off in climate mitigation
21 451 potential of restoration of young forests, with high rates of CO₂ sequestration (*NEP*; Cook-Patton *et al*
22 452 2020), versus conservation and management of mature forests, with low *NEP* but high C stocks that could
23 453 not be recovered on a time scale relevant to climate change mitigation (Goldstein *et al* 2020). Generally
24 454 speaking, the conservation of mature forests will yield greater climate benefits (Anderson-Teixeira and
25 455 DeLucia 2011), but both approaches are critical to avoiding catastrophic climate change (IPCC 2018).

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36 461 **Data availability statement**

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38 462 Materials required to fully reproduce these analyses, including data, R scripts, and image files, are archived
39 463 in Zenodo [DOI: TBD]. Data, scripts, and results presented here are also available through the open-access
40 464 *ForC* GitHub repository (<https://github.com/forc-db/ForC>), where many will be updated as the database
41 465 develops.

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