

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

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²⁶ ## [1] 0

²⁷ **NOTES TO COAUTHORS:**

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

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

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

³⁴ **Summary**

³⁵ *Background.* The fate of Earth's climate is closely linked to forests, which strongly influence atmospheric
³⁶ carbon dioxide (CO₂) and climate through their influential role in the global carbon (C) cycle. Synthetic
³⁷ understanding of global forest C cycles is needed to constrain model estimates of forest feedbacks to climate
³⁸ change and to more accurately quantify the influence of land use decisions on climate.

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

⁴⁵ *Review Results/ Synthesis.* ForC v3.0 yielded a fairly comprehensive picture of C cycling in the world's major
⁴⁶ forest biomes, with broad closure of C budgets. The rate of C cycling generally increased from boreal to
⁴⁷ tropical regions in both mature and regrowth forests, whereas C stocks showed less directional variation. The
⁴⁸ majority of flux variables, together with most live biomass pools, increased significantly with stand age, *and*
⁴⁹ *the rate of increase again tended to increase from boreal to tropical regions.*

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

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

52 **Background**

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

54 Forest ecosystems will play a critical role in shaping the course of climate change (IPCC1.5) through their
55 influence on atmospheric carbon dioxide (CO₂). Their annual gross CO₂ sequestration (gross primary
56 productivity, *GPP*) is estimated at >69 Gt C yr⁻¹ (???), or >7 times average annual fossil fuel emissions
57 from 2007-2016 (9.4 ± 0.5 Gt C yr⁻¹; Le Quéré et al 2017) (**update**). While most of this enormous C flux is
58 counterbalanced by CO₂ releases to the atmosphere through ecosystem respiration (*R_{eco}*) or fire, a small
59 portion has been retained in ecosystems over recent decades. The resulting CO₂ sink averaged 3.0 ± 0.8 Gt C
60 yr⁻¹ from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update**,
61 **give range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial
62 biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Forests are also globally
63 dominant as a source of soil respiration (???). Globally, net deforestation (*i.e.*, gross deforestation -
64 regrowth) has been a source of CO₂ emissions, estimated at ~1.1 Gt C yr⁻¹ from YEAR-YEAR (Pan et al
65 2011), reducing the net forest sink to ~1.2-1.7 Gt C yr⁻¹ across Earth's forests (Le Quéré et al 2017, Schimel
66 et al 2015) (**update, give range**). The future of the current forest C is dependent both upon forest
67 responses to a broad suite of global change drivers and to future land use decisions, and will strongly
68 influence the course of climate change. Regrowing forests in particular will play an important role (Pugh et
69 al 2019), as these represent a large (~#%) and growing proportion of Earth's forests (McDowell et al 2020).
70 Understanding, modeling, and managing forest-atmosphere CO₂ exchange is thus central to efforts to
71 mitigate climate change [Grassi et al (2017); Griscom et al (2017); **Cavaleri et al 2015**].

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

89 To address the need for global-scale analyses of forest C cycling, we recently developed an open-access Global
90 Forest Carbon database, ForC (Anderson-Teixeira et al (2016), Anderson-Teixeira et al (2018)). ForC
91 contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables) based on
92 ground-based measurements, along with associated data required for interpretation (*e.g.*, stand history,
93 measurement methods). These data have been amalgamated from original peer-reviewed publications, either

94 directly or via intermediary data compilations. Since its most recent publication (Anderson-Teixeira *et al*
95 2018), ForC has been integrated with two large databases: the Global Soil Respiration Database (SRDB;
96 Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database
97 (GROA; Cook-Patton *et al* 2020), both of which have also synthesized published forest C data. Following
98 these additions, ForC currently contains 47846 records from 10609 plots and 1532 distinct geographic areas
99 representing all forested biogeographic and climate zones.

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

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

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

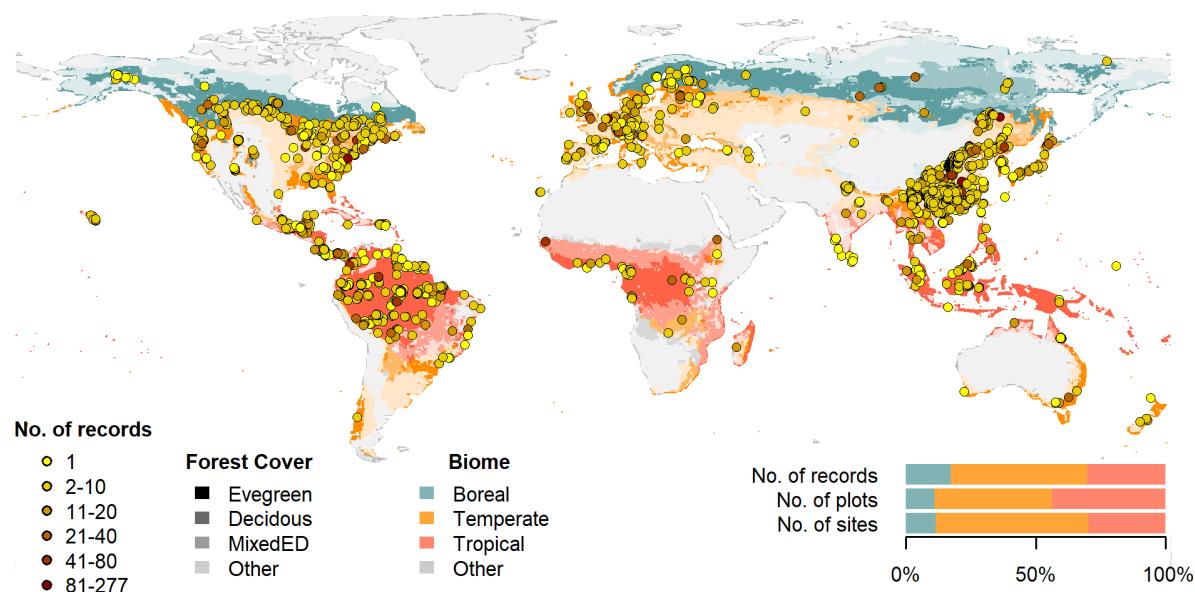


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung *et al.* 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

112 **Methods/ Design**

113 This review synthesizes data from the ForC database (Fig. 1; <https://github.com/forc-db/ForC>;
114 Anderson-Teixeira *et al* 2016, pp @anderson-teixeira_forc_2018). ForC amalgamates numerous intermediary
115 data sets (*e.g.*, **REFS**) and original studies. Original publications were referenced to check values and obtain
116 information not contained in intermediary data sets, although this process has not been completed for all
117 records. The database was developed with goals of understanding how C cycling in forests varies across
118 broad geographic scales and as a function of stand age. As such, there has been a focus on incorporating
119 data from regrowth forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining
120 stand age data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention
121 was given to developing the database for tropical forests (Anderson-Teixeira *et al* 2016). Since publication of
122 ForC v.2.0, we added the following data to ForC: the Global Database of Soil Respiration Database (SRDB
123 v.##, 9497 records; Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment
124 database (GROA v1.0, 18143 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020). We've also
125 added data from individual publications (detailed list at https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv), with a particular
126 focus on productivity (Banbury Morgan *et al* n.d., *e.g.*, Taylor *et al* 2017), dead wood, and ForestGEO sites
127 (*e.g.*, Lutz *et al* 2018, p @johnson_climate_2018). We note that there remains a significant amount of
128 relevant data that is not yet included in ForC, particularly biomass data from national forest inventories
129 (*e.g.*; **REFS**). The database version used for this analysis has been tagged as a new release on Github (**XX**)
130 and assigned a DOI through Zenodo (DOI: TBD).

132 Analyses drew from ForC-simplified (https://github.com/forc-db/ForC/blob/master/ForC_simplified),
133 which is a rearrangement of ForC intended to facilitate analyses. In generating ForC-simplified, all
134 measurements originally expressed in units of dry organic matter (*OM*) were converted to units of C using
135 the IPCC default of $C = 0.47 * OM$ (IPCC 2006). Duplicate or otherwise conflicting records were reconciled
136 as described in APPENDIX S1, resulting in a total of 32862 records (68.7% size of total database). Records
137 were filtered to remove plots that had undergone significant anthropogenic management or major disturbance
138 since the most recent stand initiation event. Specifically, we removed all plots flagged as managed in
139 ForC-simplified (18.8%). This included plots with any record of managements manipulating CO₂,
140 temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the terms
141 “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”. Plots flagged as disturbed in ForC-simplified
142 (5.7%) included stands that had undergone anthropogenic thinning or partial harvest unless this was very
143 minor. We retained sites that were grazed or had undergone low severity natural disturbances (<10%
144 mortality) including droughts, major storms, fires, and floods. We removed all plots for which no stand
145 history information had been retrieved (7.2%). In total, this resulted in 23528 records (49.2% of the records
146 in the database) being eligible for inclusion in the analysis.

147 We selected 23 annual flux and 11 C stock variables for inclusion in the analysis, although two flux variables
148 (R_{het-ag} and R_{het}) were included for conceptual completeness but had no records in ForC (Table 1).
149 Records for these variables represented 89.6% of the total records eligible for inclusion. For this analysis, we
150 combined some of ForC's specific variables (*e.g.*, multiple variables for net primary productivity including
151 various components) into more broadly defined variables. Specifically, net ecosystem exchange (measured by
152 eddy-covariance; **FLUXNET REF**) and biometric estimates of *NEP* were combined into the single
153 variable *NEP* (Table 1). Furthermore, for *NPP*, *ANPP*, and *ANPP_{litterfall}*, ForC variables specifying

154 inclusion of different components were combined. Throughout ForC, for all measurements drawing from tree
155 census data (*e.g.*, biomass, productivity), the minimum threshold for tree census was \leq 10cm. All records
156 were measured directly or derived from field measurements (as opposed to modeled).

157 For this analysis, we grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf,
158 temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones
159 (Fig. 1) were defined based on site geographic coordinates according to Köppen-Geiger zones (Rubel and
160 Kottek 2010). Tropical climates were defined to include all equatorial (A) zones, temperate climates were
161 defined to include all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and
162 Dfb), and boreal climates were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and
163 Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones were excluded from the analysis. Leaf type
164 (broadleaf / needleleaf) was defined based on descriptions in original publications (prioritized) or values
165 extracted from a global map based on satellite observations (SYNMAP; ???). Forests were classified as
166 “young” (< 100 years) or “mature” (≥ 100 years or classified as “mature”, “old growth”, “intact”, or
167 “undisturbed” in original publication). Assigning stands to these groupings required the exclusion of records
168 for which ForC lacked records of stand age (4.8% of records in full database), or geographic coordinates
169 (0.4% of sites in full database). We also excluded records of stand age = 0 year (0.8% of records in full
170 database). In total, our analysis retained 66.9 of the focal variable records for forests of known age. Numbers
171 of records by biome and age class are given in Table S1.

172 Data were summarized to produce schematics of C cycling across the eight biome - age group combinations
173 identified above. To obtain the values reported in the C cycle schematics, we first averaged any repeated
174 measurements within a plot. Values were then averaged across plots clustered within 25 km of one another
175 (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if available for all records. This step was
176 taken to avoid pseudo-replication and to combine any records from sites with more than one name in ForC.

177 To test for differences across mature forest biomes, the original values were analyzed via a linear mixed
178 effects model [‘lmer’ function in ‘lme4’ R package version **x.xx; REF**] with biome as fixed effect and plot
179 nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we
180 looked at a Tukey’s pairwise comparison to see which biomes were significantly different from one another.
181 *This analysis was run for variables with records for ≥ 7 distinct geographic areas in each biome, excluding*
182 *any biomes that failed this criteria and dropping variable where less than two biomes met the criteria (Table*
183 *1). (issue 40)]*

184 To test for age trends in young (<100yrs) forests, we employed a mixed effects model with biome and
185 log10[stand.age] as fixed effects and plot nested within geographic.area as a random effect on the intercept.
186 When the effect of stand.age was significant at $p \leq 0.05$ and when each biome had records for stands of at
187 least 10 different ages, a biome * stand.age interaction was included in the model.

188 All database manipulation, analyses, and figure production were fully automated in R (**version, citation**).

189 Review Results/ Synthesis

190 Data Coverage

191 Of the 47846 records in ForC v3.0, 14105 met the criteria for inclusion in this study (Fig. 1). These records
192 were distributed across 4358 plots in 821 distinct geographic areas. Of the 23 flux and 11 stock variables

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

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

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

193 mapped in these diagrams, ForC contained mature forest estimates from ≥ 7 distinct geographic areas for 20
194 fluxes and 9 stocks in tropical broadleaf forests, 15 fluxes and 9 stocks in temperate broadleaf forests, 15
195 fluxes and 8 stocks in temperate conifer forests, and 9 fluxes and 7 stocks in boreal forests. For regrowth
196 forests (<100 yrs), ForC contained estimates from ≥ 7 distinct geographic areas for 3 fluxes and 9 stocks in
197 tropical broadleaf forests, 12 fluxes and 8 stocks in temperate broadleaf forests, 15 fluxes and 8 stocks in
198 temperate conifer forests, and 12 fluxes and 12 stocks in boreal forests. (**issue 29**)

199 **C cycling in mature forests**

200 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests ≥ 100
201 years old and with no known major disturbance or significant anthropogenic management are presented in
202 Figures 2-5 (and available in tabular format in the ForC release accompanying this publication:
203 [ForC/numbers_and_facts/ForC_variable_averages_per_Biome.csv](#)).

204 For variables with records from ≥ 7 distinct geographic areas, these ensemble C budgets were generally
205 consistent. *That is, component fluxes and stocks summed to within one standard deviation of more inclusive*
206 *fluxes in all but two instances, both in temperate conifer forests (Fig. 5). (check this with final results:*
207 https://github.com/forc-db/ForC/blob/master/numbers_and_facts/C_cycle_closure.csv)

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

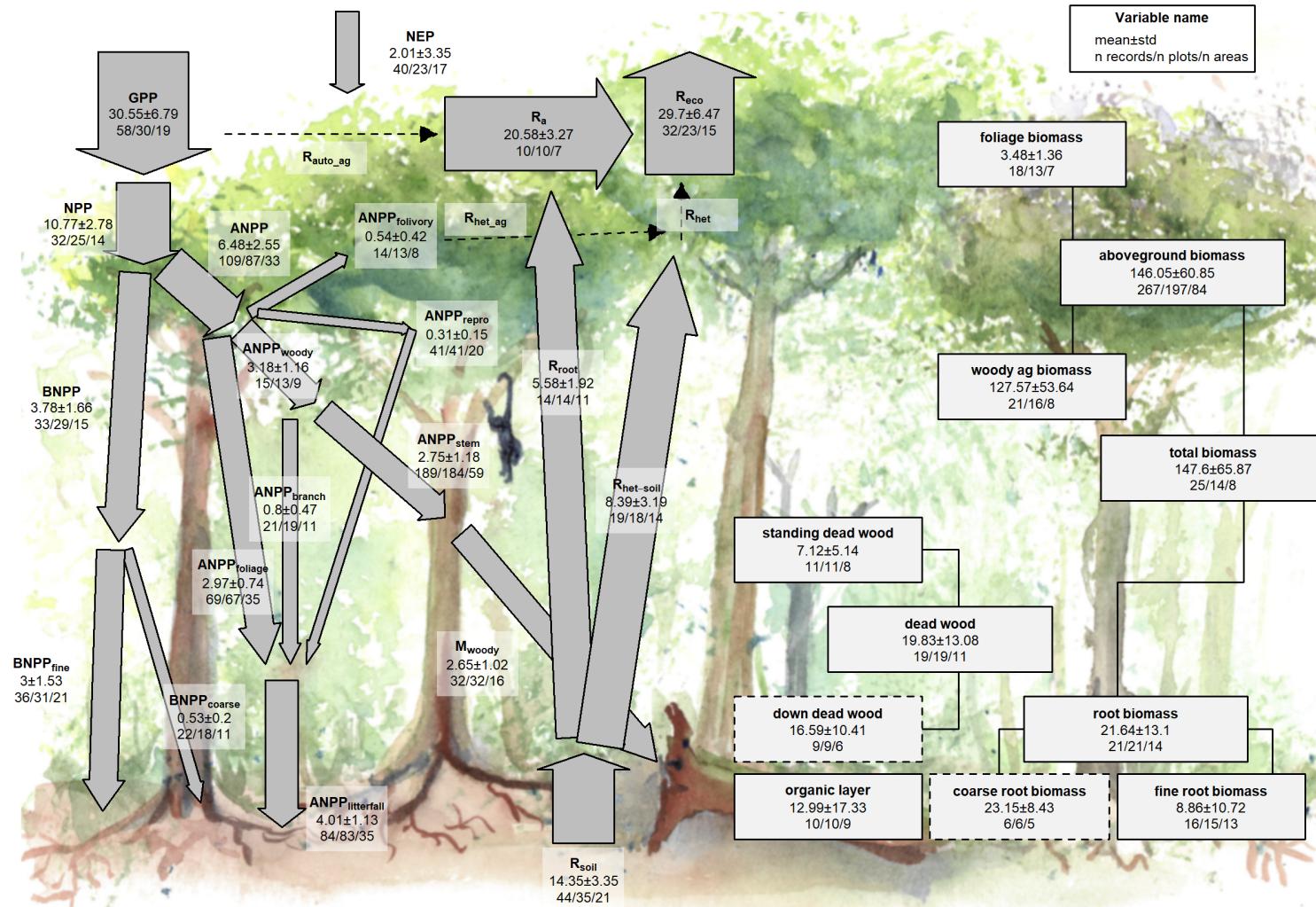


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

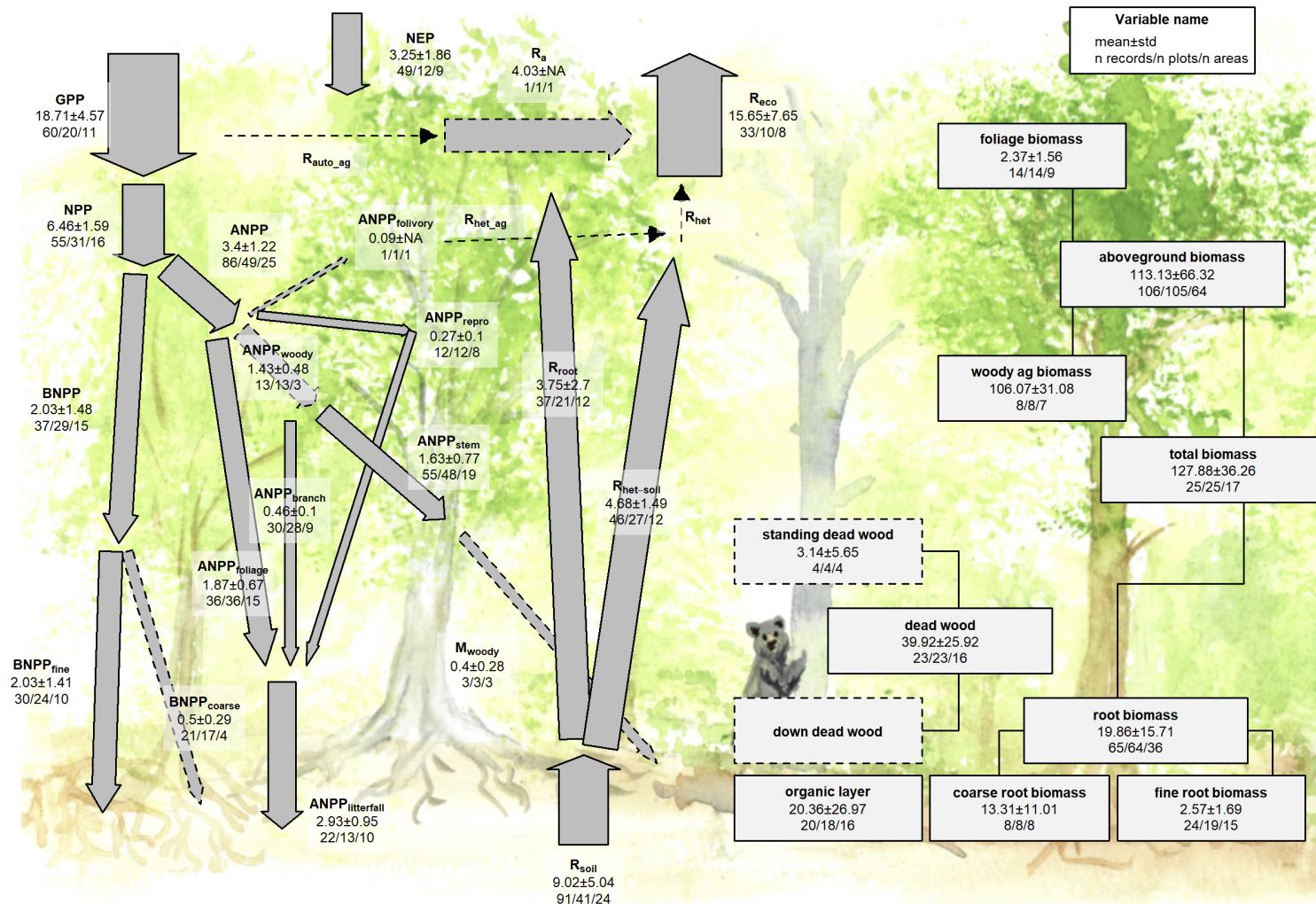


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

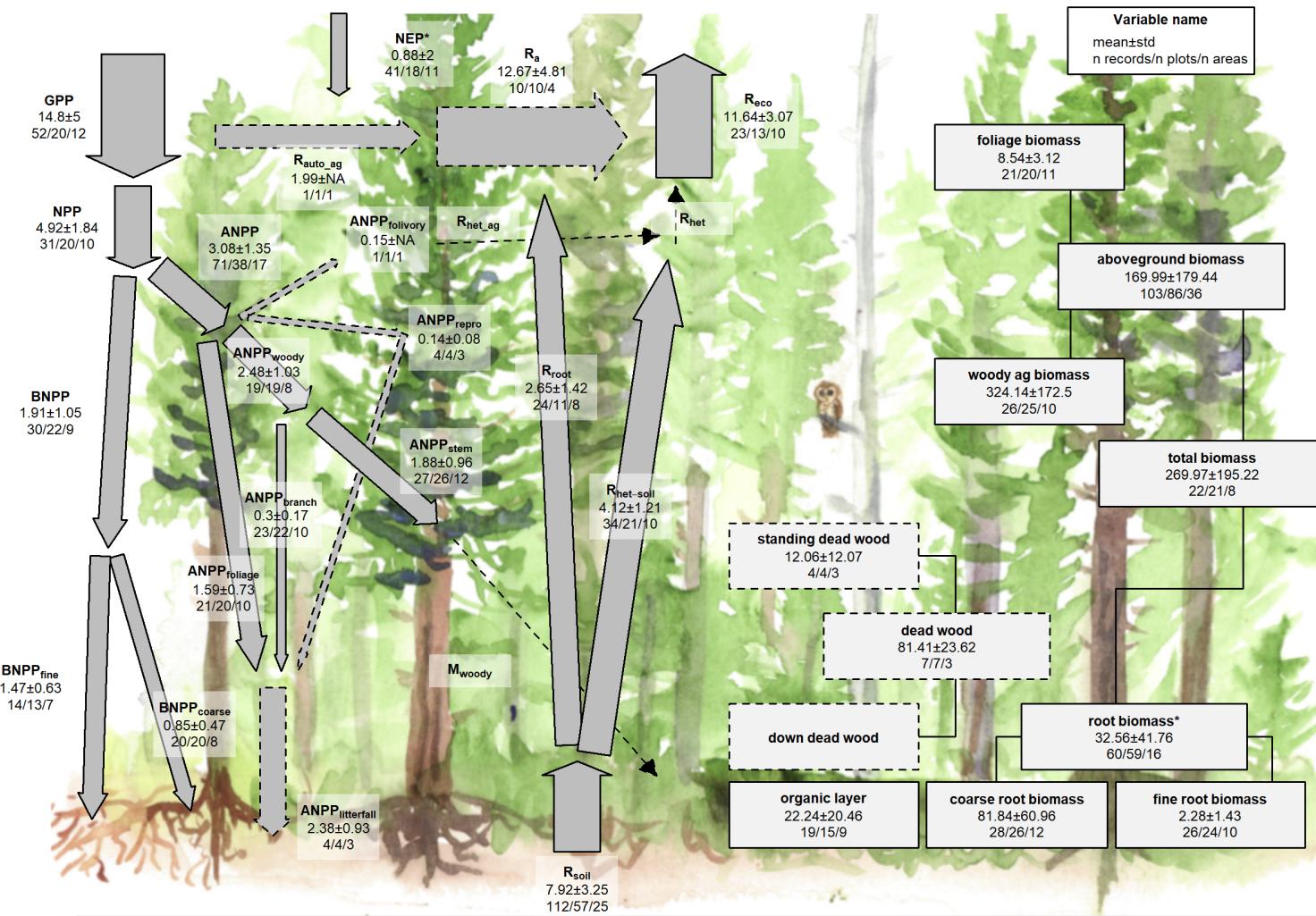


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

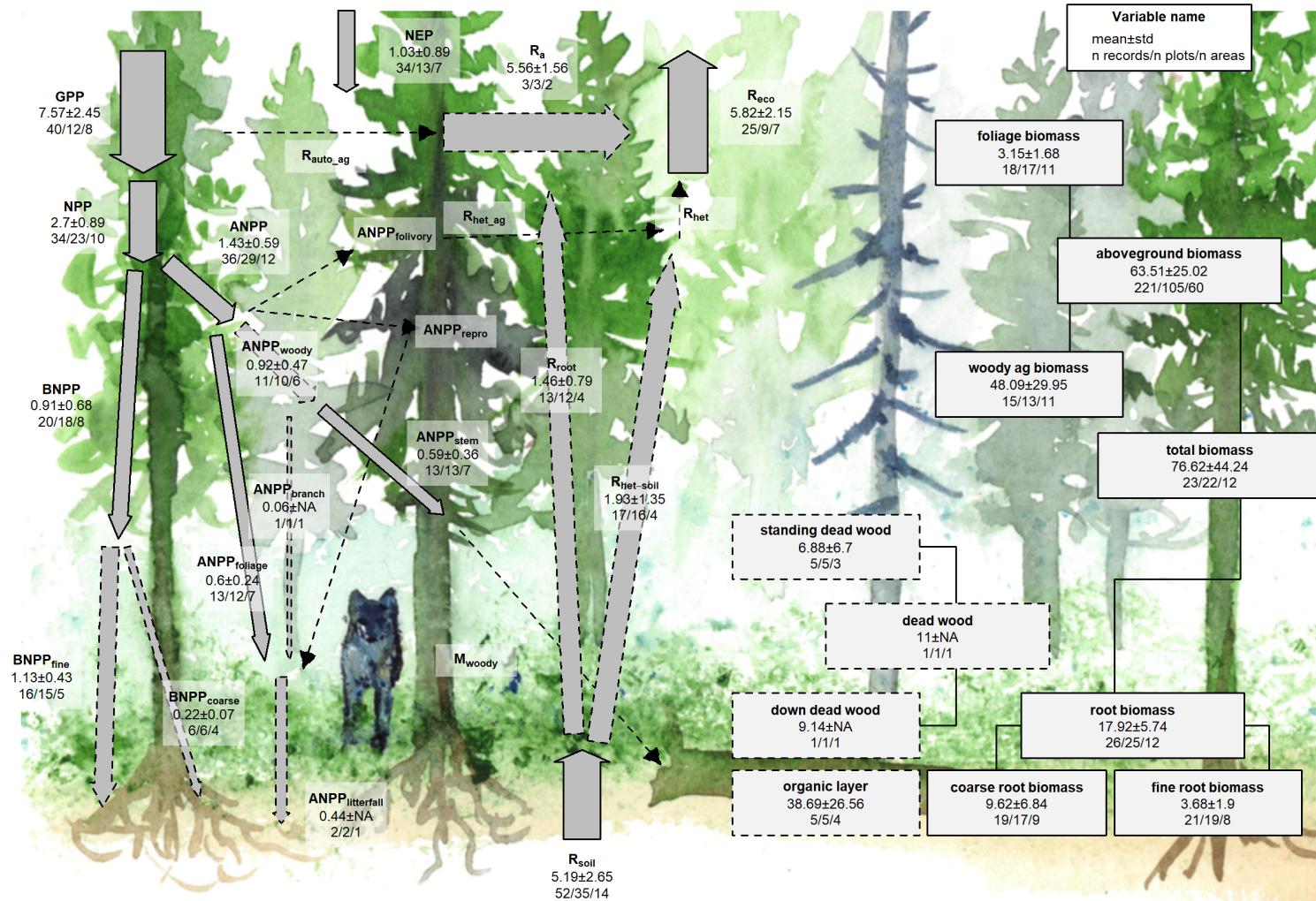


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

211 **check this with final data (based on Table 1):** There were sufficient data to assess mature forest
212 biome differences for **20** flux variables, and significant differences among biomes were detected for **14**
213 variables (Table 1). With only **one** exception (R_{auto} , which had low sample size; **issue 40**), C fluxes were
214 highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and lowest in boreal
215 forests (Table 1, Figs. 6, S1-S15). Differences between tropical and boreal forests were always significant,
216 with temperate forests intermediate and significantly different from one or both. Fluxes tended to be
217 numerically greater in temperate broadleaf than conifer forests, but the difference was never statistically
218 significant. This pattern held for the following variables: **** GPP , NPP , $ANPP$, $ANPP_{woody}$,**
219 **$ANPP_{stem}$, $ANPP_{branch}$, $ANPP_{foliage}$, $ANPP_{litterfall}$, M_{woody} , $BNPP$, R_{eco} , R_{soil} , and $R_{het-soil}$ **.** For
220 variables without significant differences among biomes, the same general trends applied.

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

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

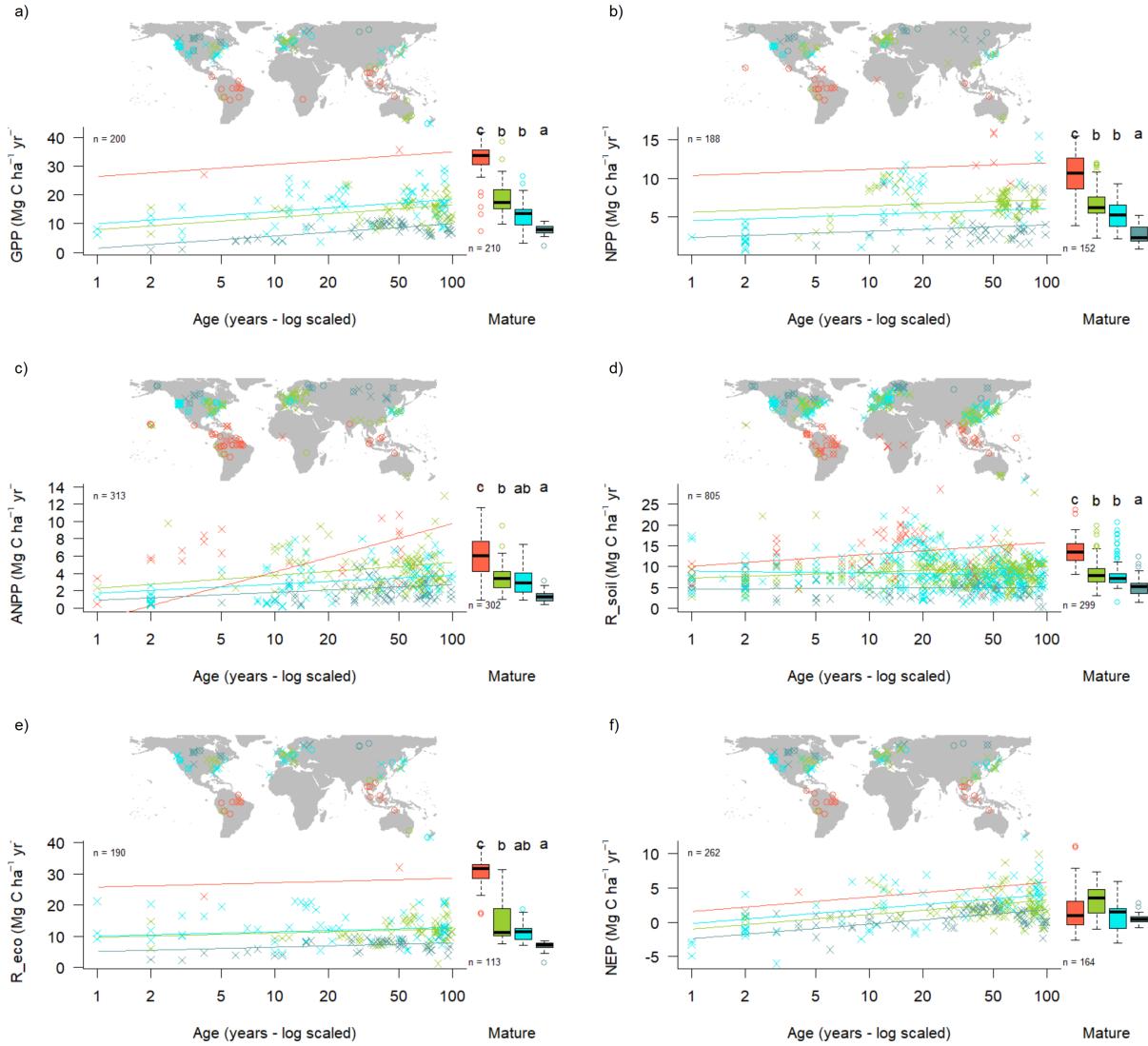


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized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

228 **check this with final data (based on Table 1):** There were sufficient data to assess mature forest
 229 biome differences for **9** stock variables, and significant differences among biomes were detected for **6** variables
 230 (B_{tot} , B_{ag} , $B_{\text{ag-wood}}$, B_{foliage} , $B_{\text{root-coarse}}$, DW_{tot} ; Table 1). C stocks had less consistent patterns across
 231 biomes (Figs. 7, S16-S26). In **four of the six** cases (B_{tot} , $B_{\text{ag-wood}}$, $B_{\text{root-coarse}}$, DW_{tot}), temperate
 232 conifer forests were in the highest significance grouping, and boreal forests in the lowest, with tropical and
 233 temperate broadleaf forests in between—most commonly being significantly different from temperate conifer
 234 but not boreal forests. For B_{ag} , which had by far the highest sample size, tropical forests exceeded temperate
 235 conifer forests (but not significantly). For B_{foliage} , temperate broadleaf forests were lowest (again, not
 236 significantly). Once again, the high values for the temperate conifer biome were driven by the very

237 high-biomass forests of the US Pacific Northwest, which are disproportionately represented in the current
 238 version of ForC. Thus, biome differences should be interpreted more as driven more by geographic
 239 distribution of sampling than by true differences.

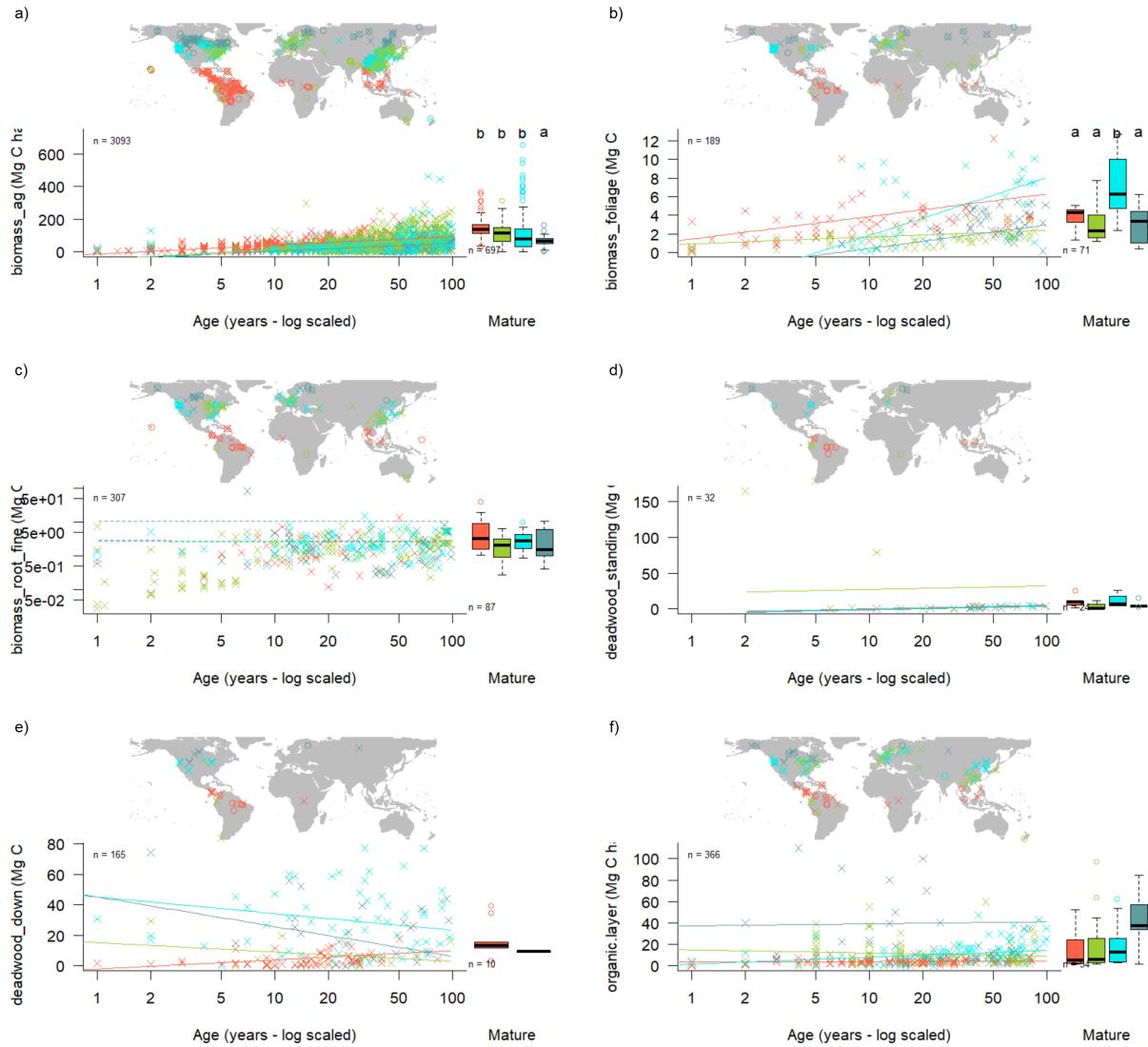


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) dead roots, (d) dead wood. Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized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

240 C cycling in young forests

- 241 Average C cycles for forests <100 years old are presented in Figures 8-11.
 242 Both C stocks and fluxes commonly displayed significant trends with stand age for within-biome analyses
 243 (Tables 1, S2, Figs. 6-11, S1-S26; detailed below).
 244 ForC contained 14 flux variables with sufficient data for cross-biome analyses of age trends in regrowth

245 forests (see Methods) (Fig. 6-7 and S#- SI figures including plots for all variables). Of these, 9
246 increased significantly with $\log_{10}[\text{stand.age}]$: GPP , NPP , $ANPP$, $ANPP_{\text{foliage}}$, $ANPP_{\text{woody}}$,
247 $ANPP_{\text{woody-stem}}$, $BNPP$, $BNPP_{\text{root-fine}}$, R_{eco} , and net C sequestration (NEP). The remaining
248 five— $ANPP_{\text{woody-branch}}$, $BNPP_{\text{root-coarse}}$, $R_{\text{soil-het}}$, and $R_{\text{soil-het}}$ —displayed no significant relationship to
249 stand age, although all displayed a positive trend.

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

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

254 Notably, the trend of tropical > temperate > boreal held for NEP in regrowth forests, in contrast to the
255 lack of biome differences in NEP for mature forests (Fig. 6).

256 There were only ## flux variables with sufficient data to test for biome x age interactions: $ANPP$,
257 $ANPP_{\text{woody}}$, $ANPP_{\text{stem}}$, $ANPP_{\text{litterfall}}$, and $BNPP$ (Table S2). (**more could be added if age trends
258 become significant after outliers are resolved**) For three of these ($ANPP$, $ANPP_{\text{litterfall}}$, $BNPP$),
259 the increase in C flux with age was steepest increase in tropical forests, followed by temperate and then
260 boreal forests (Figs S#). Similarly, $ANPP_{\text{woody}}$ displayed a steeper increase with age in temperate than
261 boreal boreal forests (no tropical data for this variable). In contrast, for $ANPP_{\text{stem}}$, tropical and temperate
262 broadleaf forests had the highest flux rates at young ages, but were surpassed by temperate conifer forests
263 between ages 20 and 50 (Fig. S6).

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

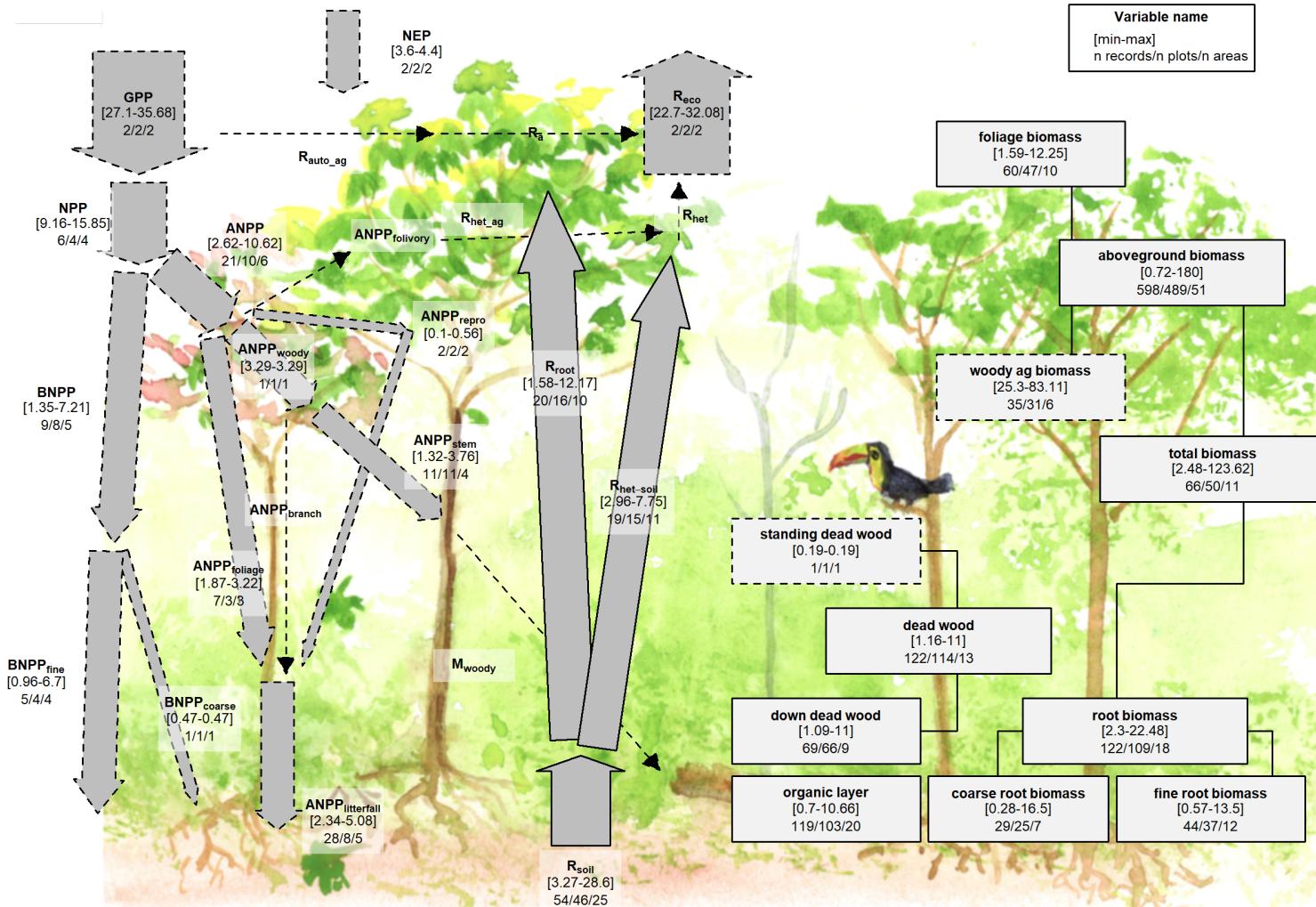


Figure 8 | C cycle diagram for young tropical broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $Mg\ C\ ha^{-1}\ yr^{-1}$ (fluxes) or $Mg\ C\ ha^{-1}$ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed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

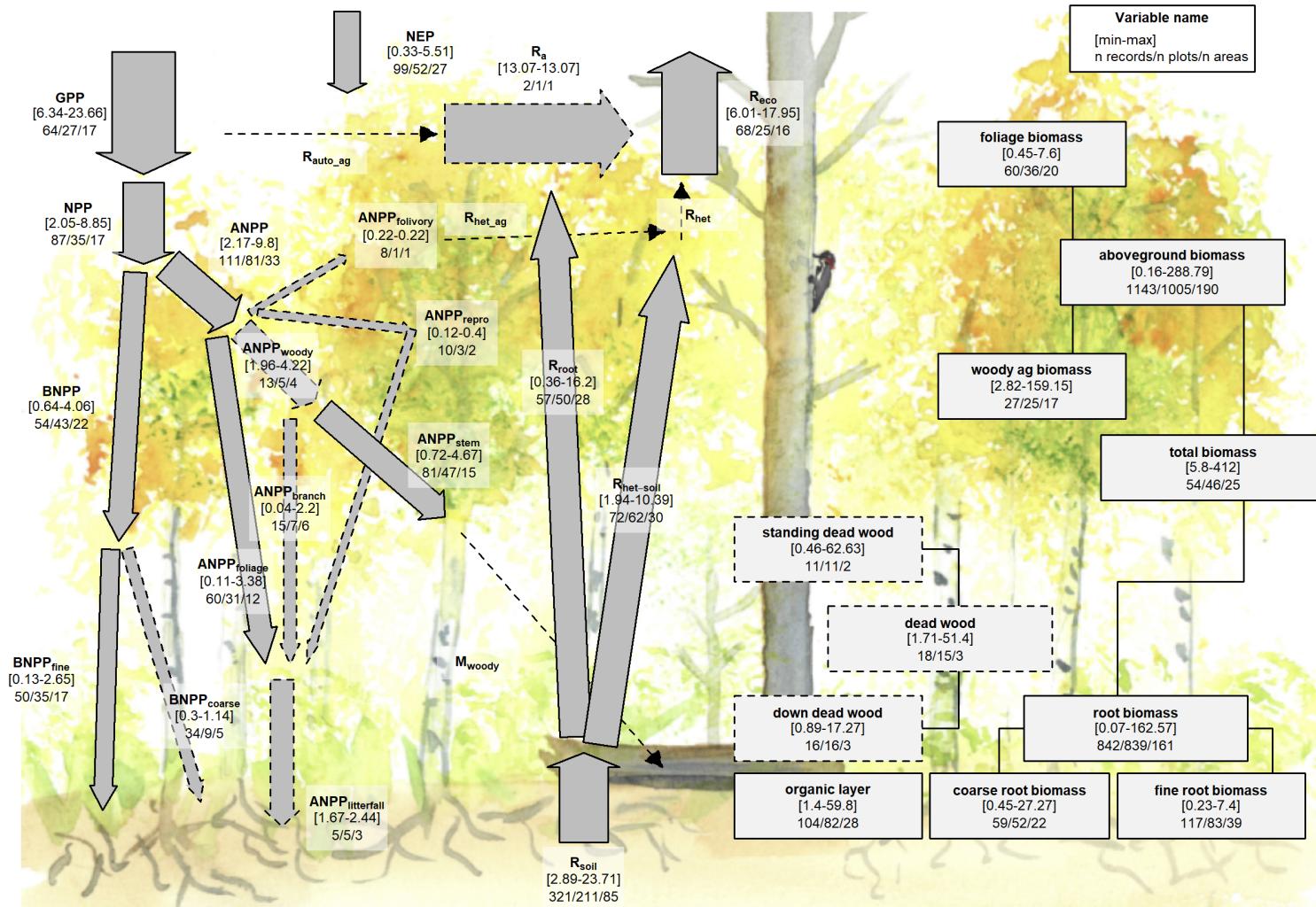


Figure 9 | C cycle diagram for young temperate broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines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

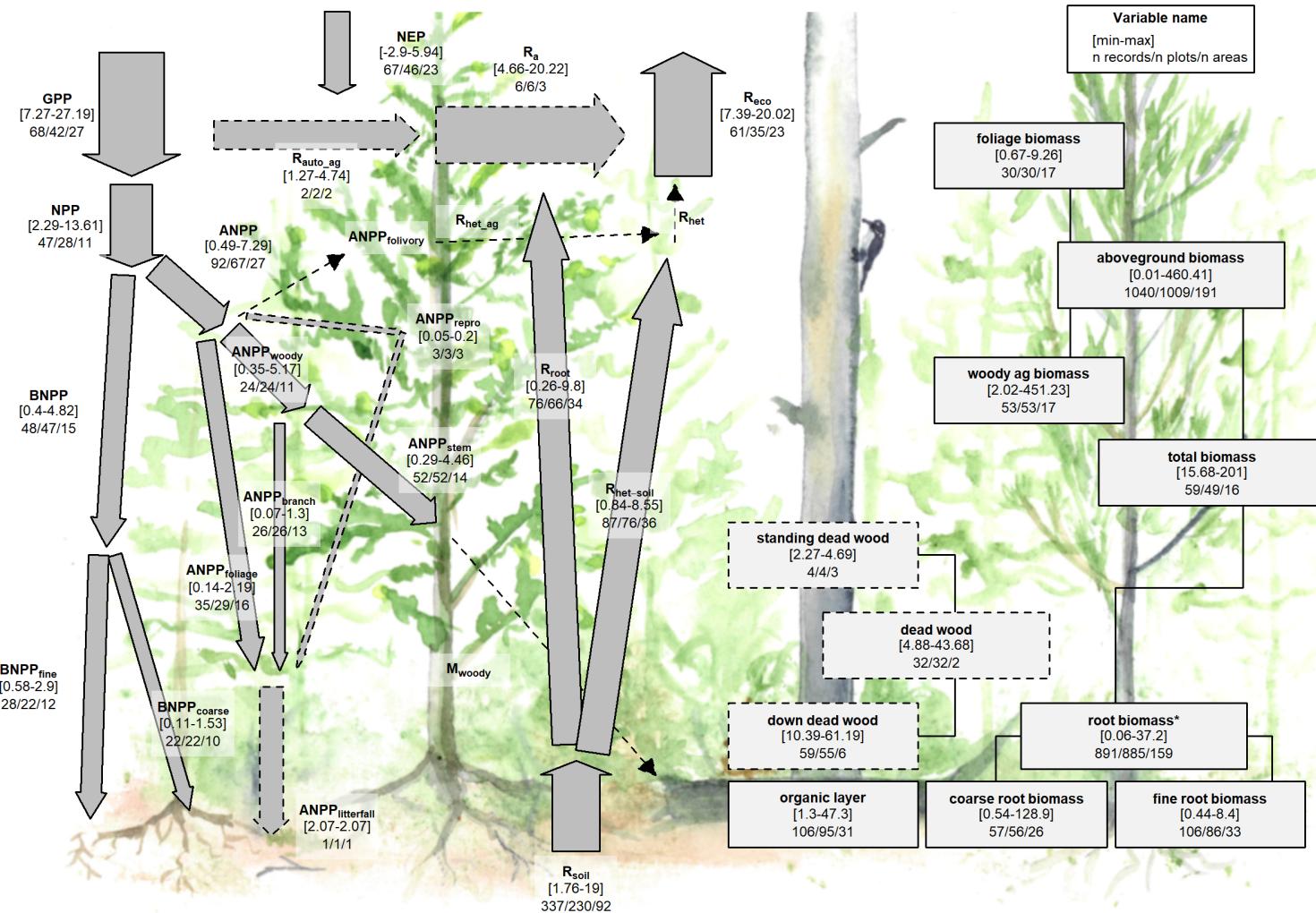


Figure 10 | C cycle diagram for young temperate conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $Mg\ C\ ha^{-1}\ yr^{-1}$ (fluxes) or $Mg\ C\ ha^{-1}$ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed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

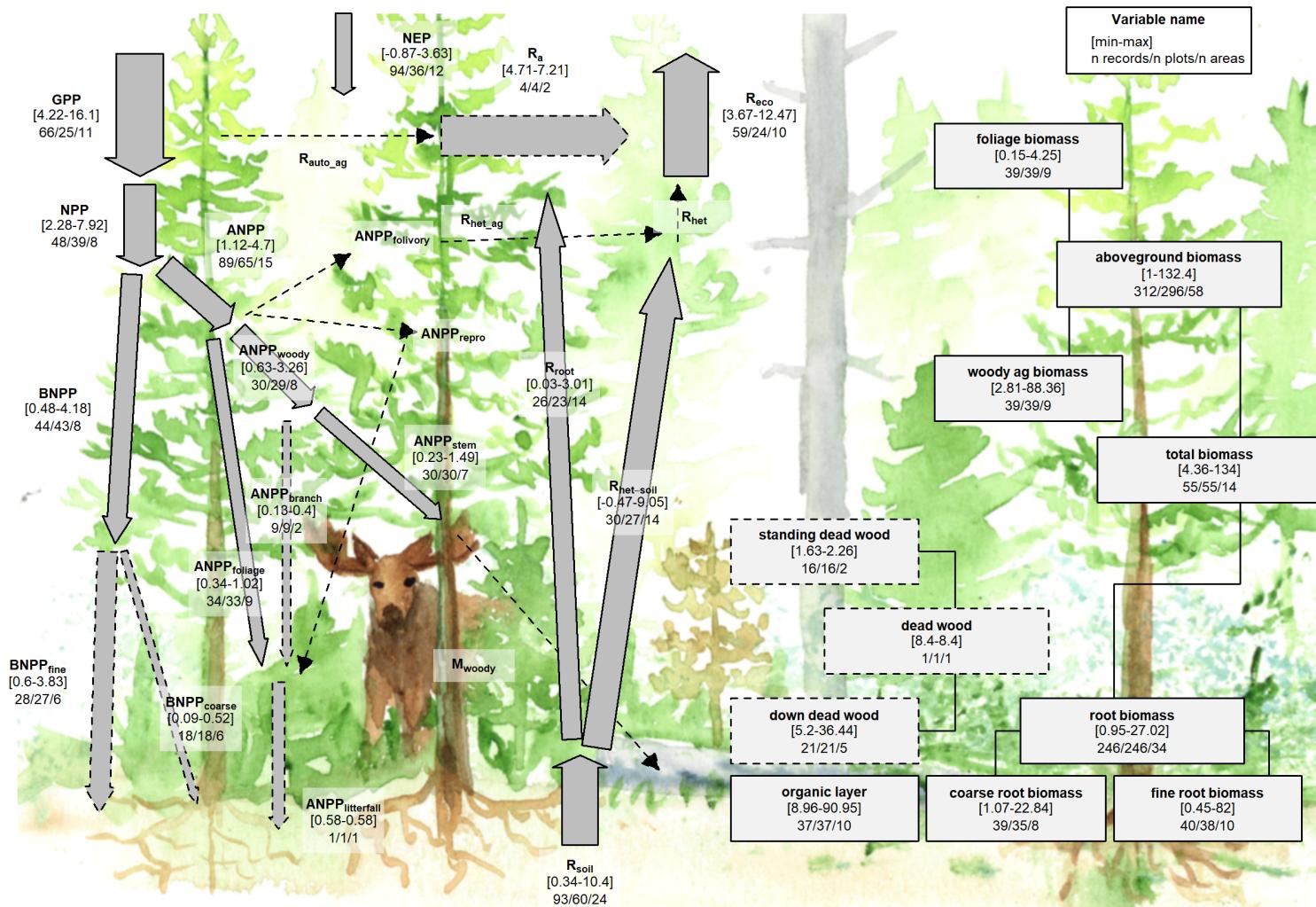


Figure 11 | C cycle diagram for young boreal conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

269 **Discussion**

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

279 **C variable coverage and budget closure**

280 ForC provides unprecedented coverage of most major variables. (*discuss how this improves upon*
281 *previous data compilations/ for which variables does ForC make the greatest difference (e.g., not AGB or*
282 *NEP/GPP/Reco, but by far the latest data compilation for dead wood, [variables]) (Noteable holes include:*
283 *fluxes: R_auto_ag, woody mortality, folivory/ herbivory and respiration of herbivores (and therefore total*
284 *R_het), ANPP_repro; also fluxes in tropical regrowth forests) For the C stocks considered here, the most*
285 *poorly covered is dead wood (none in E hemisphere!), despite a focused effort on this variable that has*
286 *resulted in ForC being by far the largest collection of these data.* Thus, overall, we're lacking coverage of
287 fluxes to herbivores and higher consumers, along with the woody mortality and dead wood. Geographically,
288 all variables poorly covered in Africa and Siberia.

289 **notes from Ben on the above par:** Pregitzer and Euskirchen 2004

290 <http://dx.doi.org/10.1111/j.1365-2486.2004.00866.x> “Aggregated biome-level estimates of NPP and NEP
291 were higher in intermediate-aged forests (e.g., 30–120 years), while older forests (e.g., 4120 years) were
292 generally less productive. The mean NEP in the youngest forests (0–10 years) was negative (source to the
293 atmosphere) in both boreal and temperate biomes... Forest age is a highly significant source of variability in
294 NEP at the biome scale”

295 Amiro et al. 2010 <http://dx.doi.org/10.1029/2010JG001390> Houghton et al. 2020

296 <https://doi.org/10.1111/gcb.15050>

297 Turnover: Pugh et al. 2020 <http://dx.doi.org/10.5194/bg-2019-491> Yu et al. 2019

298 <http://dx.doi.org/10.1073/pnas.1821387116>

299 Human footprint in global forests <http://dx.doi.org/10.1038/nature05847>

300 <http://dx.doi.org/10.1038/nature02619>

301 Mention consistency (or lack of) with e.g. GOLUM-CNP? <http://dx.doi.org/10.5194/gmd-11-3903-2018>

302 In terms of C stocks, there is a paucity of data on dead wood and organic layer (Pan et al. ?). These can be
303 significant. (**Note that we've given a lot of emphasis to dead wood (work by Abby, and also**
304 **Jenny), and as a result this work really advances knowledge of dead wood. We'll want to**
305 **highlight that here.) (give some stats/ cite figures).** ForC does not include soil carbon, which is covered
306 by other efforts (REFS). For fluxes, Fluxnet is the keeper of the best data on NEE, GPP, Reco (REFS), and
307 SRDB remains the authority on soil respiration (REFS). ForC includes recent data from both, but is not

308 continuously integrated. For C is the best source for most of the subsidiary fluxes: NPP, woody mortality...
309 The C cycle budgets for mature forests (Figs. 2-5) generally “close”—that is, the sums of component variables
310 do not differ from the larger fluxes by more than one standard deviation. However, standard deviations are
311 often large, reflective of significant within-biome variation. This makes the standard for closure relatively
312 loose. *Lack of closure, in the few instances where it occurs, is probably more reflective of differences in the*
313 *representation of forest types (e.g., disproportionate representation of US Pacific NW for aboveground woody*
314 *biomass relative to AGB; Fig. 4) than of methodological accuracy.* Thus, overall, a high degree of closure
315 implies that ForC gives a consistent picture of C cycling within biomes. While these means are unlikely to be
316 accurate representations of C cycling within any particular forest, they provide a useful baseline for
317 comparison, always keeping in mind that sample means do not necessarily represent the true mean of the
318 entire biome.

319 **C cycling across biomes**

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

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

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

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

338 **Age trends in C cycling**

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

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

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

345 It's also important to understand secondary forest C sequestration to reduce uncertainty regarding the
346 potential for carbon uptake by regrowth forests (???, Cook-Patton *et al* 2020).
347 NEP increases with log(age) to 100 -> strongest C sinks are established secondary forests. (But presumably
348 this exact number is an artifact; don't over-emphasize.)

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

350 The future of forest C cycling (???) will shape trends in atmospheric CO₂ and the course of climate change.
351 For a human society seeking to understand and mitigate climate change, the data contained in ForC and
352 summarized here can help to meet two major challenges.
353 First, improved representation of forest C cycling in models is essential to improving predictions of the future
354 course of climate change. To ensure that models are giving the right answers for the right reasons, it is
355 important to benchmark against multiple components of the C cycle that are internally consistent with each
356 other. By making tens of thousands of records readily available in standardized format, ForC makes it
357 feasible for the modeling community to draw upon these data to benchmark models. Integration of ForC
358 with models is a goal (Fer *et al.*, in revision).
359 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change
360 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not
361 feasible for the individuals and organizations designing such efforts to sort through literature, often behind
362 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline
363 through which information can flow efficiently from forest researchers to decision-makers working to
364 implement forest conservation strategies at global, national, or landscape scales. This is already happening!
365 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;
366 Requena Suarez *et al* (2019); Rozendaal *et al* in prep], mapping C accumulation potential from natural forest
367 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*
368 2020).

369 **ForC can complement remote sensing to provide a comprehensive picture of global forest C
370 cycling.** (*here, discuss what is well-covered by remote sensing, where ForC is useful for calibrating remote
371 sensing, and what ForC can get that remote sensing can't.*) AGB is the largest stock, and most of the
372 emphasis is on this variable. Remote sensing, with calibration based on high-quality ground-based data
373 (Schepaschenko *et al* 2019, Chave *et al* 2019), is the best approach for mapping forest carbon (REFS).
374 However, it is limited in that it is not associated with stand age and disturbance history, except in recent
375 decades when satellite data can be used to detect forest loss, gain, and some of their dominant drivers
376 (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). ForC is therefore valuable in defining age-based
377 trajectories in biomass, as in Cook-Patton *et al* (2020).

378 *Remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP
379 (Bagdley *et al.* 2019, (Li and Xiao 2019)), aboveground biomass (B_{ag}) (REFS), woody mortality (i.e., B_{ag}
380 losses to mortality M_{woody}) (Clark *et al* 2004, Leitold *et al* 2018), and to some extent net ecosystem
381 exchange (NEP) (REFS). Other variables, in particular respiration fluxes, cannot be remotely sensed
382 ((????)), and efforts such as the Global Carbon Project (le quere REF) and NASA CMS (citation:
383 https://carbon.nasa.gov/pdfs/CMS_Phase-1_Report_Final_optimized.pdf but maybe
384 better to cite open literature, one of the papers listed at*

385 <https://cmsflux.jpl.nasa.gov/get-data/publication-data-sets>) typically compute them as residuals
386 only. (Ben, it would be particularly helpful if you could flesh this out some more.)

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

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

394 Acknowledgements

395 All researchers whose data is included in ForC and this analysis. Ian McGregor for help with the database.
396 Thanks to Norbert Kunert and [Helene’s intern] for helpful input at an earlier phase. A Smithsonian
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398 Data availability statement

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

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