

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

³ **Authors:** Kristina J. Anderson-Teixeira^{1,2*}

⁴ Valentine Herrmann¹

⁵ Becky Banbury Morgan

⁶ Ben Bond-Lamberty

⁷ Susan Cook-Patton

⁸ Abigail Ferson

⁹ Jennifer McGarvey

¹⁰ Helene C. Muller-Landau¹

¹¹ Maria Wang

¹² **Author Affiliations:**

¹³ 1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological Park,
¹⁴ Front Royal, VA 22630, USA

¹⁵ 2. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research
¹⁶ Institute; Panama, Republic of Panama

¹⁷ *corresponding author: teixeirak@si.edu; +1 540 635 6546

18 **Summary**

19 *Background.* The fate of Earth's climate closely linked to forests, which strongly influence atmospheric carbon
20 dioxide (CO_2) and climate through their influential role in the global carbon (C) cycle. Synthetic
21 understanding of global forest C cycles is needed to constrain model estimates of forest feedbacks to climate
22 change and to more accurately quantify the influence of land use decisions on climate.

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

29 *Review Results/ Synthesis.* The rate of C cycling generally increased from boreal to tropical regions, whereas
30 C stocks showed less directional variation. The majority of flux variables, together with most live biomass
31 pools, increased significantly with stand age, and the rate of increase again tended to increase from boreal to
32 tropical regions.

33 *Discussion.* [Discussion section will interpret results, highlighting new and significant findings, and discuss
34 implications. Tentative headings are "Stand level C cycling in forests globally", "Age trends in C cycling",
35 and "Implications for climate change mitigation".]

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

37 **Background**

38 Carbon (C) cycling in forests is central to sustaining life on Earth. Forest ecosystems globally influence
39 climate through their vital role in regulating atmospheric carbon dioxide (CO_2). Their annual gross CO_2
40 sequestration (gross primary productivity, GPP) is estimated at $>69 \text{ Gt C yr}^{-1}$ (Bagdley et al. 2019), or >7
41 times average annual fossil fuel emissions from 2007-2016 ($9.4 \pm 0.5 \text{ Gt C yr}^{-1}$; Le Quéré et al 2017)
42 (**update**). While most of this enormous C flux is counterbalanced by CO_2 releases to the atmosphere through
43 ecosystem respiration (R_{eco}) or fire, a small portion was retained in ecosystems over recent decades. The
44 resulting in C sink averaged $3.0 \pm 0.8 \text{ Gt C yr}^{-1}$ from 2007-2016, offsetting 32% of anthropogenic fossil fuel
45 emissions (Le Quéré et al 2017) (**update, give range**). Moreover, forests contain substantial C stocks: an
46 estimated 92% of terrestrial biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan
47 2008). Globally, net deforestation (*i.e.*, gross deforestation - regrowth) has been a source of CO_2 emissions,
48 estimated at $\sim 1.1 \text{ Gt C yr}^{-1}$ from YEAR-YEAR (Pan et al 2011), resulting in net C sink of $\sim 1.2\text{-}1.7 \text{ Gt C}$
49 yr^{-1} across Earth's forests (Le Quéré et al 2017, Schimel et al 2015) (**update, give range**). The future of
50 this sink is dependent both upon forest responses to a broad suite of global change drivers and to future land
51 use decisions, and will strongly influence the course of climate change. Understanding, modeling, and
52 managing forest-atmosphere CO_2 exchange is thereby central to efforts to mitigate climate change (Grassi *et*
53 *al* 2017) (Friedlingstein et al 2006, Cavalieri et al 2015, Griscom et al 2017; IPCC1.5).

54 On an ecosystem level, forest C cycling is central to the flow of energy and materials, and as the basis of food
55 webs...

56 Despite the centrality of forest C cycling in regulating both atmospheric CO_2 and ecosystem function and

57 diversity, we lack a comprehensive understanding of how C cycling varies with across biomes and with stand
58 age. While remote sensing measurements are increasingly useful for global- or regional-scale estimates of
59 forest *GPP* (Bagdley et al. 2019, (Li and Xiao 2019)), aboveground biomass (B_{ag}) (REFS), woody mortality
60 (*i.e.*, B_{ag} losses to mortality M_{woody}) (Clark et al 2004, Leitold et al 2018), and to some extent net
61 ecosystem exchange (*NEE*) (REFS), the remainder of C fluxes and stocks can only be quantified by
62 ground-based measurements. Moreover, data on stand characteristics—including species composition, age, and
63 disturbance history—are critical to interpreting and projecting into the future, but [usually rely on
64 ground-based measurements]. Thus, ground-based measurements are, and will continue to be, central to
65 characterizing forest C cycling.

66 Tens of thousands of ground-based forest C measurements have been published, but their distribution across
67 literally thousands of scientific articles— along with variation in data formats, units, measurement methods,
68 etc.—have made them effectively inaccessible for many global-scale analyses, including those attempting to
69 quantify the role of forests in the global C cycle (*e.g.*, Pan et al 2011), and model evaluation (Clark et al
70 2017, Luo et al 2012). Important progress has been made in synthesizing data to address how C cycling
71 varies across forest biomes (Luyssaert et al. 2007; REFS) and stand ages (REFS), yet generally consider only
72 a limited set of C variables (but see Anderson-Teixeira et al 2016 for the tropics) and do not consider
73 age-by-biome interactions. To address the need for global-scale analyses of forest C cycling, we have
74 developed an open-access Global Forest Carbon database, ForC (Anderson-Teixeira et al (2016),
75 Anderson-Teixeira et al (2018)). ForC contains data on forest ecosystem C stocks and annual fluxes (>50
76 variables) and associated data required for interpretation (*e.g.*, stand history, measurement methods)
77 amalgamated from numerous previous data compilations and directly from original publications. ForC
78 currently contains # records from # plots and # distinct geographic areas representing all forested
79 biogeographic and climate zones.

80 Here, we synthesize ForC data to provide a macroscopic overview of stand-level carbon cycling of the world's
81 major forest biomes and how it varies with stand age. We address two broad questions:

- 82 1. How do C cycling vary across the worlds major forest biomes (*i.e.*, tropical, temperate broadleaf and
83 deciduous, boreal)?
- 84 2. How does C cycling vary with stand age?

85 While components of these questions have been previously addressed (Luyssaert et al 2007,
86 Anderson-Teixeira et al 2016, pp @anderson-teixeira_forc:_2018, @banbury_morgan_global_nodate), our
87 analysis represents by far the most comprehensive analysis of C cycling in global forests, and thereby stands
88 to serve as a foundation for improved understanding of global forest C cycling.

89 Methods/ Design

90 This review synthesizes data from the ForC database (<https://github.com/forc-db/ForC>; Anderson-Teixeira
91 et al 2016, pp @anderson-teixeira_forc:_2018). ForC amalgamates numerous intermediary data sets (*e.g.*,
92 REFS) and original studies. Original publications were referenced to check values and obtain information not
93 contained in intermediary data sets, although this process has not been completed for all records. The
94 database was developed with goals of understanding how C cycling in forests varies across broad geographic
95 scales and as a function of stand age. As such, there has been a focus on incorporating data from regrowth
96 forests (*e.g.*, Anderson et al 2006, Martin et al 2013, Bonner et al 2013) and obtaining stand age data when

97 possible (83% of records in v.2.0; Anderson-Teixeira et al 2018). Particular attention was given to developing
98 the database for tropical forests (Anderson-Teixeira *et al* 2016), yet these represented only approximately
99 one-third of records in ForC v.2.0 (Anderson-Teixeira *et al* 2018). Since publication of ForC v.2.0, we added
100 the following data to ForC: the Global Database of Soil Respiration Database (SRDB v.##; Bond-Lamberty
101 and Thomson 2010), the Global Reforestation Opportunity Assessment (GROA) database (Cook-Patton et
102 al. in press), and GitHub list. We note that there remains a significant amount of relevant data that is not
103 yet included in ForC, particularly biomass data from national forest inventories (*e.g.*, REFS). The database
104 version used for this analysis has been tagged as a new release on Github (XX) and assigned a DOI through
105 Zenodo (DOI: XX).

106 For this analysis, we grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf,
107 temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones
108 were defined according to Köppen-Geiger zones, which were extracted based on site geographic coordinates
109 from the ESRI Köppen-Geiger map (downloaded June 2014 from

110 <http://maps3.arcgisonline.com/ArcGIS/rest/services/A-16/Köppen->
111 Geiger_Observed_and_Predicted_Climate_Shifts/MapServer; Rubel and Kottke 2010). Tropical climates
112 were defined to include all equatorial (A) zones, temperate climates were defined to include all warm
113 temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and boreal climates
114 were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B)
115 and polar (E) Köppen-Geiger zones were excluded from the analysis. Leaf type (broadleaf / needleleaf) was
116 defined based on descriptions in original publications (prioritized) or values extracted from a global map
117 based on satellite observations (SYNMAP; Jung et al 2006) and recorded in the dominant.veg field of the
118 ForC MEAUREMENTS table. Stand age was obtained from the stand.age field of MEASUREMENTS table,
119 and forests classified as “young” (< 100 years) or “mature” (\geq 100 years or classified as “mature”, “old
120 growth”, “intact”, or “undisturbed” in original publication). Records for which stand age was unknown were
121 excluded from the analysis. These groupings were defined based on ForC v.2.0(Anderson-Teixeira *et al* 2018),
122 for which they covered 91% of the primary variable records for forests of known age, or 86% of total records.
123 The most well-represented forest types excluded were boreal broadleaf and boreal and temperate mixed
124 broadleaf-needleleaf, each with <400 records total for stands of any age.

125 We drew upon records for # annual flux and # C stock variables (Table 1). For this analysis, we combined
126 some of ForC’s specific variables (*e.g.*, multiple variables for net primary productivity including various
127 components) into more broadly defined variables (Table 1, this table)). Although ForC contains information
128 that may be used to standardize or control for methodological differences (*e.g.*, area sampled, min stem
129 diameter sampled, allometric equations applied; Anderson-Teixeira et al 2018), for this analysis we included
130 all relevant data in ForC. Throughout ForC, for all measurements drawing from tree census data (*e.g.*,
131 biomass, productivity), the minimum stem diameter sampled was \leq 10cm. All records were measured
132 directly or derived from field measurements (as opposed to modeled).

133 Analyses drew from ForC-simplified (https://github.com/forc-db/ForC/blob/master/ForC_simplified),
134 which is a rearrangement of ForC intended to facilitate analyses. In generating ForC-simplified, all
135 measurements originally expressed in units of dry organic matter (*OM*) were converted to units of C using
136 the IPCC default of $C = 0.47 * OM$ (IPCC 2006). Duplicate or otherwise conflicting records were reconciled
137 as described in APPENDIX A. Records were filtered to remove plots that had undergone significant
138 anthropogenic management or major disturbance since the most recent stand establishment (*i.e.*, that

139 reflected by stand.age). Specifically, we removed all plots flagged as managed in ForC-simplified (managed
140 field). This included plots with any record of managements manipulating CO₂, temperature, hydrology,
141 nutrients, or biota, as well as any plots whose site or plot name contained the terms “plantation”, “planted”,
142 “managed”, “irrigated”, or “fertilized”. Plots flagged as disturbed in ForC-simplified included stands that had
143 undergone anthropogenic thinning or partial harvest (“Cut” or “Harvest” codes) unless this was very minor
144 (percent.mortality= “minor”). We retained sites that were grazed or had undergone low severity natural
145 disturbances (<10% mortality) including droughts, major storms, fires, and floods. We also removed all plots
146 for which no stand history information had been retrieved.

147 Data were analyzed to produce basic summaries of C cycle patterns across biomes and stand ages following
148 an approach similar to that of Anderson-Teixeira et al (2016). For mature forests, to obtain the values
149 reported in the C cycle schematics, we first averaged any repeated measurements within a plot, weighting
150 flux measurements according to the length of measurement periods (*i.e.*, end.date - start.date). Values were
151 then averaged across plots clustered within 25 km of one another (geographic.area field of SITES table, sensu
152 Anderson-Teixeira et al 2018), weighting by area.sampled (MEASUREMENTS table) or plot.area (PLOTS
153 table) if available for all records. This step was taken to avoid pseudo-replication and to combine any records
154 from sites with more than one name in ForC. Finally, we computed statistics with geographic.area as the unit
155 of replication. To compare across biomes, [Valentine, please describe]. There were enough data to run
156 this analysis for all focal variables but XX.

157 For young (<100yrs) forest types, we employed a mixed effects model (XX in R) with biome and
158 log10[stand.age] as fixed effects and plot nested within geographic.area as a random effect. When the effect
159 of stand.age was significant at p ≤ 0.05 and when each biome had records for stands of at least 10 different
160 ages, a biome - stand.age interaction was included in the model. In the C cycle schematics for young forests,
161 we report equations based on these models. In cases where there was no significant effect of stand.age,
162 records were averaged as for mature stands.

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

168 Review Results/ Synthesis

169 C cycling in mature forests

170 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests ≥ 100
171 years old and with no known major disturbance or significant anthropogenic management are presented in
172 Figures 2-5, and statistics for each biome type are also summarized at: [GitHub URL]. Of the # flux and #
173 stock variables mapped in these diagrams, ForC contained estimates from ≥ 7 distinct geographic areas for
174 # fluxes and # stocks in tropical broadleaf forests, # fluxes and # stocks in temperate broadleaf forests,
175 #fluxes and # stocks in temperate conifer forests, and fluxes and # stocks in boreal forests. For variables
176 with records from ≥ 7 distinct geographic areas, these ensemble C budgets were generally consistent. That is,
177 component fluxes and stocks summed to within 1 std of more inclusive fluxes in all but one instance (in
178 temperate conifer forests, *abovegroundwoodybiomass + foliagebiomass > abovegroundbiomass + 1std*; Fig.

¹⁷⁹ 4). update this: <https://github.com/forc-db/ERL-review/issues/16>

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>NEE</i>	net ecosystem exchange or net ecosystem production (- indicates C sink)	n	n	n	n.s.	-
<i>GPP</i>	gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEE$)	n	n	n	Tr > TeB = TeN > B	+
<i>NPP</i>	net primary production ($ANPP + BNPP$)	n	n	n	Tr > TeB = TeN > B	+
<i>ANPP</i>	aboveground <i>NPP</i>	n	n	n	Tr > TeB \geq TeN \geq B	+, xB
<i>ANPP_{woody}</i>	woody production ($ANPP_{stem} + ANPP_{branch}$)	n	n	n		
<i>ANPP_{stem}</i>	woody stem production	n	n	n		
<i>ANPP_{branch}</i>	branch turnover	n	n	n		
<i>ANPP_{foliage}</i>	foliage production, typically estimated as annual leaf litterfall	n	n	n		
<i>ANPP_{litterfall}</i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	n	n	n		
<i>ANPP_{repro}</i>	production of reproductive structures (flowers, fruits, seeds)	n	n	n		
<i>ANPP_{folivory}</i>	foliar biomass consumed by folivores	n	n	n		
<i>M_{woody}</i>	woody mortality—i.e., B_{ag} of trees that die	n	n	n		
<i>BNPP</i>	belowground NPP ($BNPP_{coarse} + BNPP_{fine}$)	n	n	n		
<i>BNPP_{coarse}</i>	coarse root production	n	n	n		
<i>BNPP_{fine}</i>	fine root production	n	n	n		
<i>R_{eco}</i>	ecosystem respiration ($R_{auto} + R_{het}$)	n	n	n		
<i>R_{auto}</i>	autotrophic respiration ($R_{auto-ag} + R_{root}$)	n	n	n		
<i>R_{auto-ag}</i>	aboveground autotrophic respiration (*i.e., leaves and stems)	n	n	n		
<i>R_{root}</i>	root respiration	n	n	n		
<i>R_{soil}</i>	soil respiration ($R_{het-soil} + R_{root}$)	n	n	n		
<i>R_{het-soil}</i>	soil heterotrophic respiration	n	n	n		
<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 ($B_{ag} + B_{root}$)	n	n	n		
<i>B_{ag}</i>	aboveground live biomass ($B_{ag-wood} + B_{foliage}$)	n	n	n		
<i>B_{ag-wood}</i>	woody component of aboveground biomass	n	n	n		
<i>B_{foliage}</i>	foliage biomass	n	n	n		
<i>B_{root}</i>	total root biomass ($B_{root-coarse} + B_{root-fine}$)	n	n	n		
<i>B_{root-coarse}</i>	coarse root biomass	n	n	n		
<i>B_{root-fine}</i>	fine root biomass	n	n	n		
<i>DW_{tot}</i>	deadwood ($DW_{standing} + DW_{down}$)	n	n	n		
<i>DW_{standing}</i>	standing dead wood	n	n	n		
<i>DW_{down}</i>	fallen dead wood, including coarse and sometimes fine woody debris	n	n	n		
<i>OL</i>	organic layer / litter/ forest floor	n	n	n		

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

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

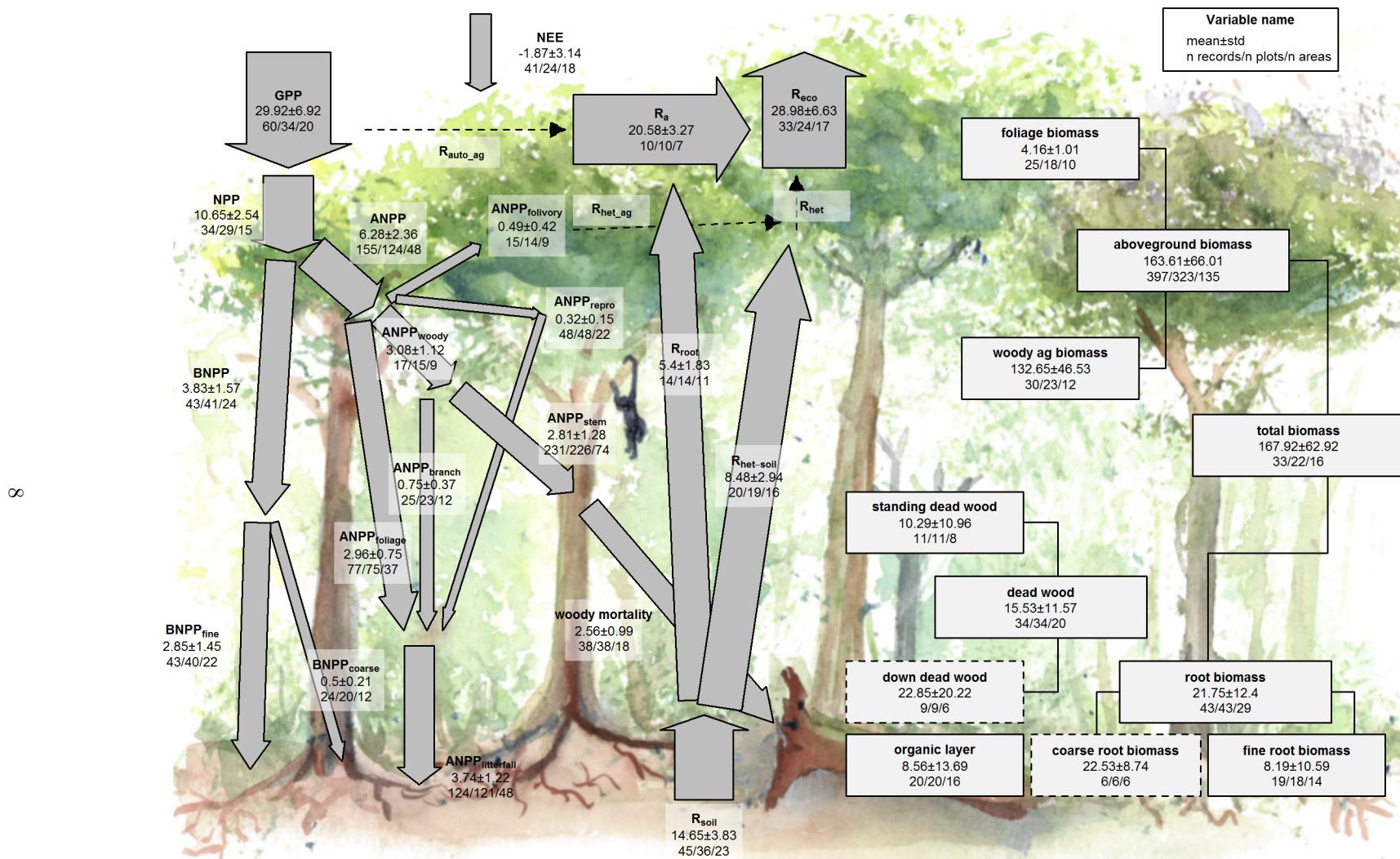


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are $Mg\text{ C ha}^{-1}\text{ yr}^{-1}$ (fluxes) or $Mg\text{ C ha}^{-1}$. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. Arrows are scaled as the **square root of flux divided by 5**.

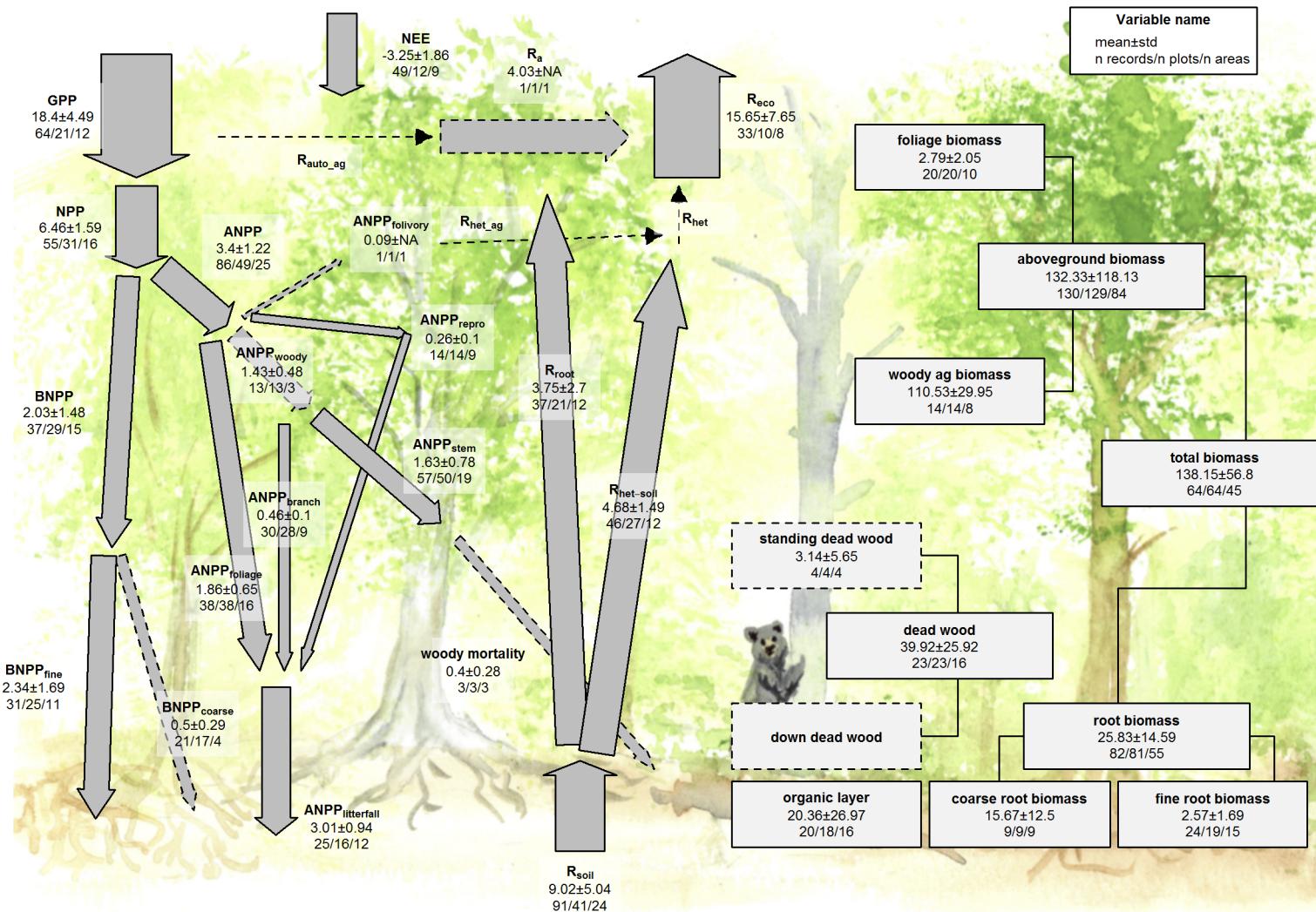


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables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

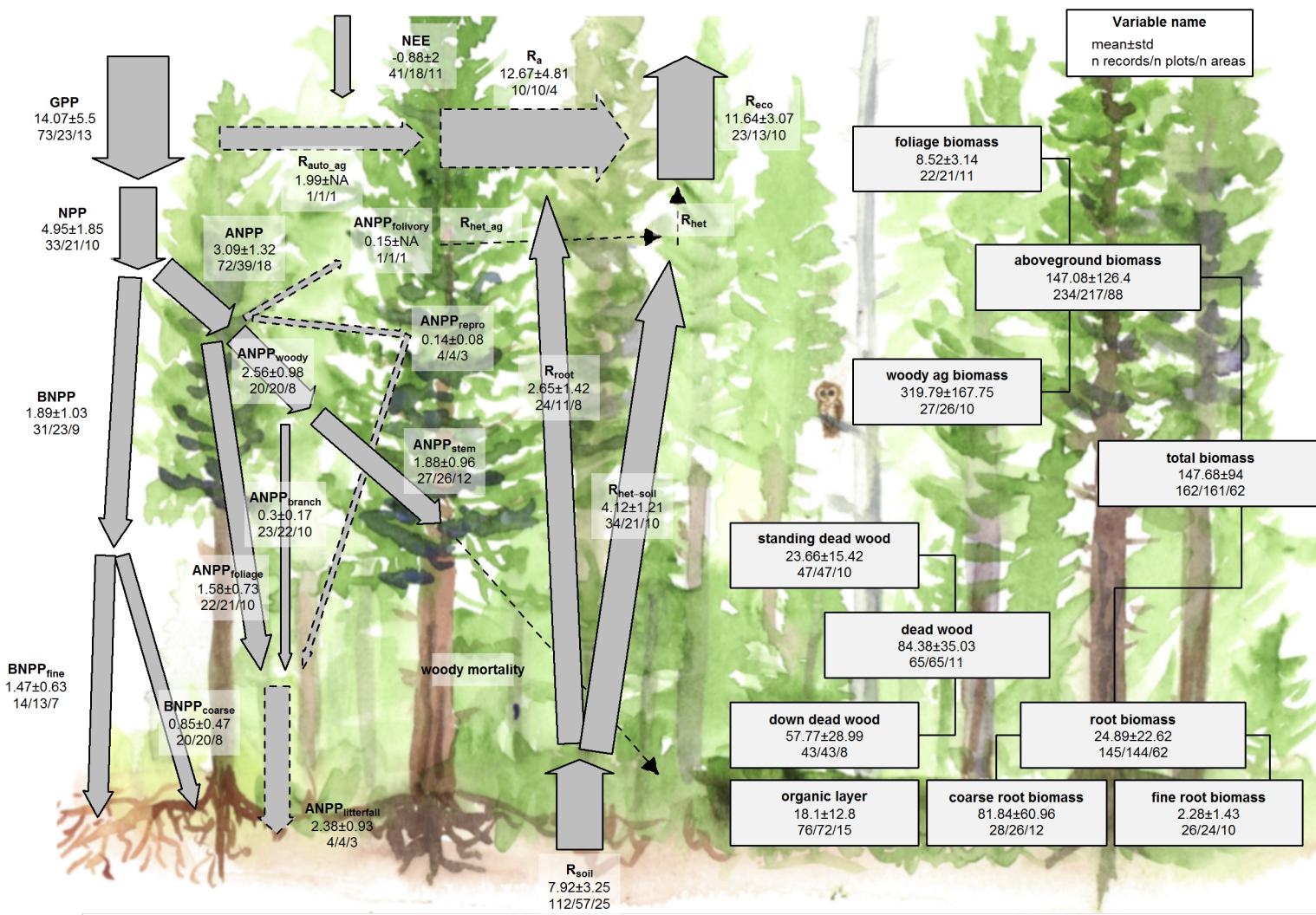


Figure 3 | C cycle diagram for mature temperate conifer forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

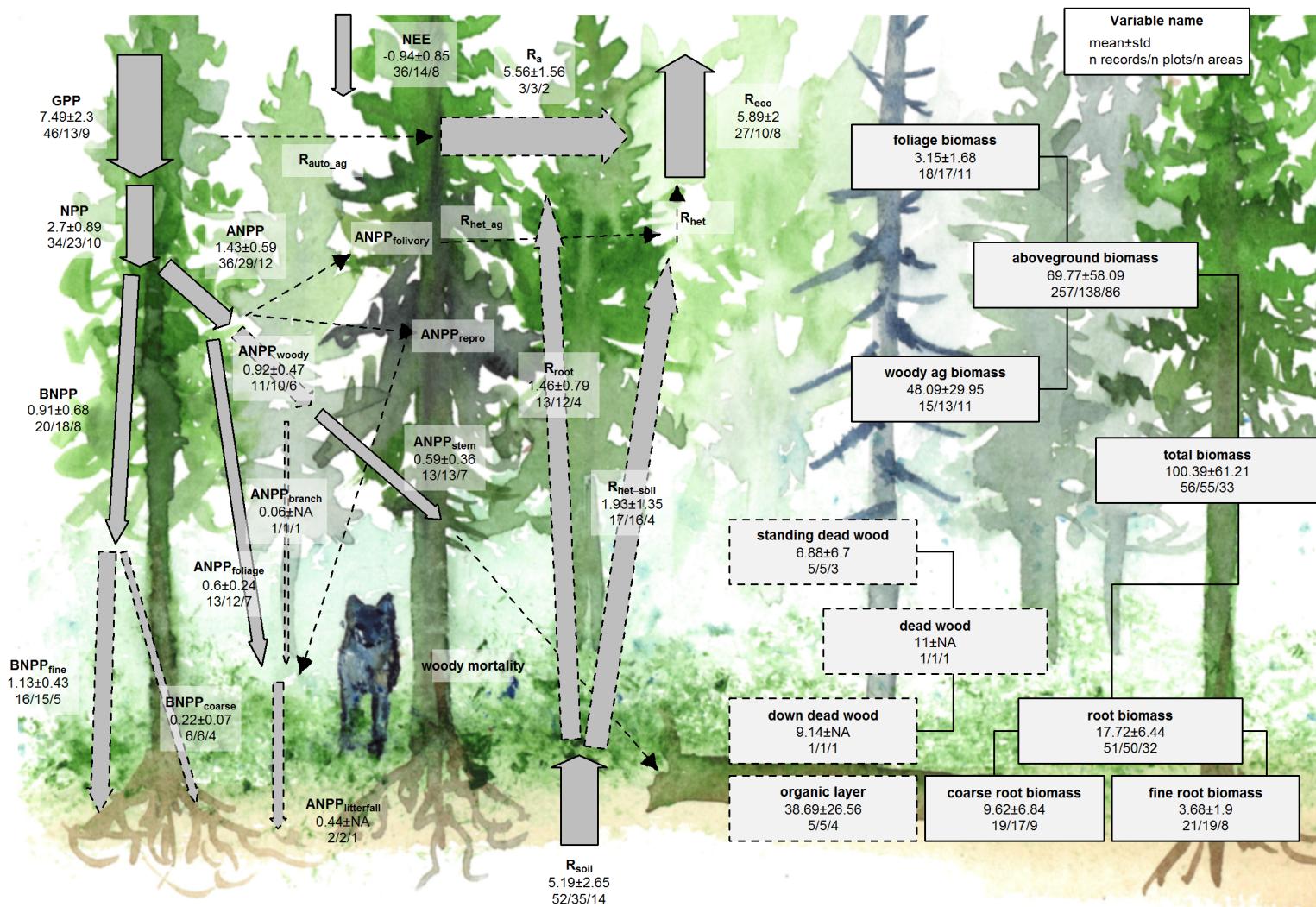


Figure 4 | C cycle diagram for mature boreal conifer forests. All units are $Mg\text{ C ha}^{-1}\text{ yr}^{-1}$ (fluxes) or $Mg\text{ C ha}^{-1}$. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

180 (check paragraph with latest data) The largest C fluxes—including *GPP*, *NPP*, *ANPP*, *BNPP*,
181 $R_{soil,et}$, R_{soil} , R_{eco} , — were highest in tropical forests, intermediate in temperate (broadleaf or conifer)
182 forests, and lowest in boreal forests (ForC_variable_averages_per_Biome) (Fig. 6). The same held true for
183 some of the subsidiary fluxes: *ANPP_foliage*, *ANPP_wood*, [OTHERS?]. Other subsidiary
184 fluxes—including *NPP_wood*, *ANPP_repro*, *ANPP_stem*, *ANPP_branch*, *woody.mortality*, *BNPP_coarse*,
185 *BNPP_fine*, [OTHERS?—deviated from this pattern and/or lacked data for some biomes. Net ecosystem
186 exchange (NEE) did not follow this pattern, with no significant differences across biomes but the largest
187 (negative) average in temperate broadleaf forests, followed by temperate conifer, boreal, and tropical forests.
188 Thus, C cycling rates generally decreased from tropical to temperate to boreal forests, but with less apparent
189 trends for some of the subsidiary fluxes and an important exception in the overall C balance (NEE).

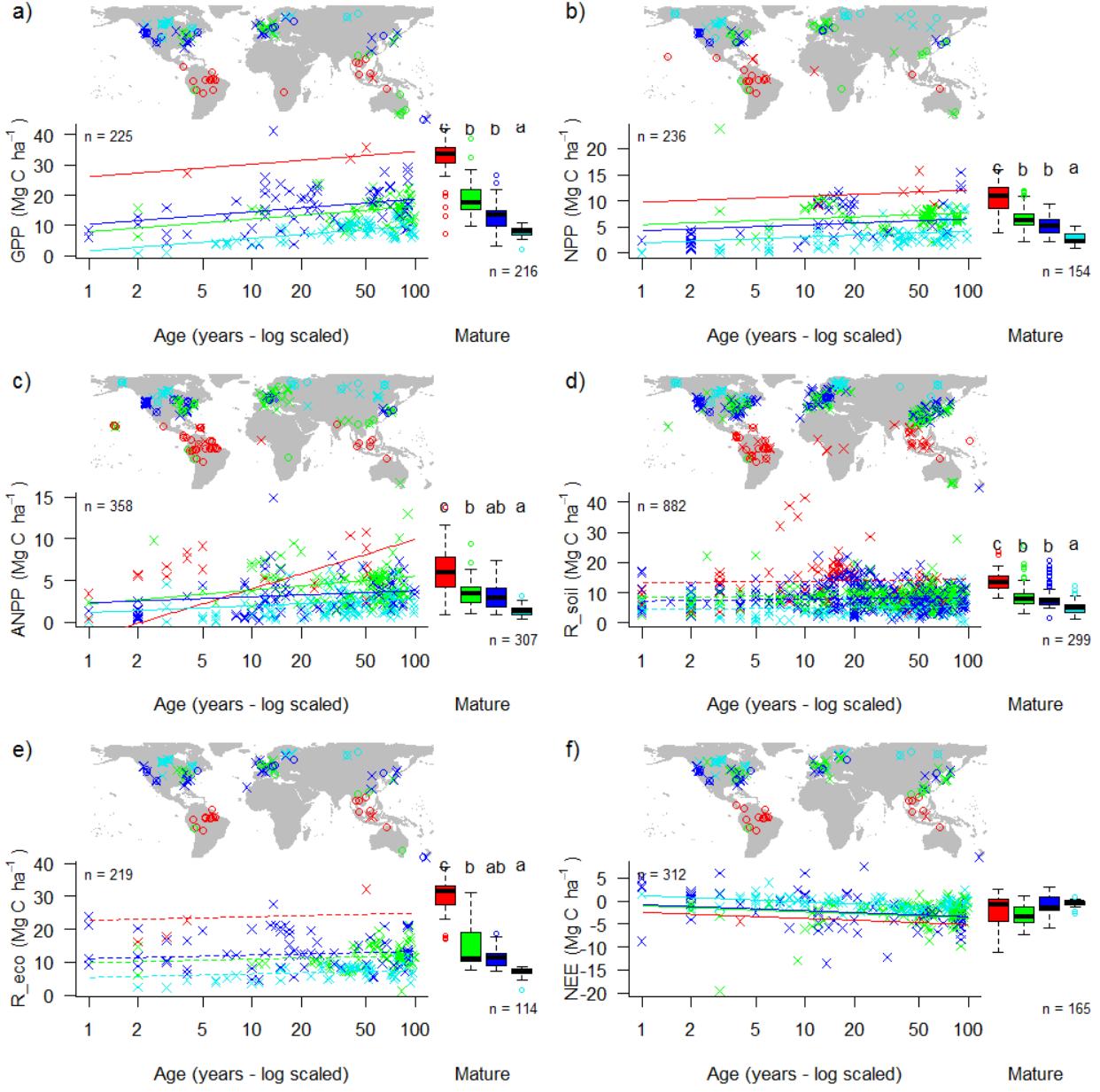


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEE . Map shows data sources (x and o indicate young and mature stands, respectively). Lines... .

190 There were less distinct trends in C stocks across biomes (Fig. 7). Biome means for live aboveground and
 191 total biomass followed the same general trend as the major fluxes, with biomass of tropical= temperate
 192 broadleaf \geq temperate conifer> boreal forests (Fig. 7a). However, the relative differences in these means
 193 were much smaller than for the major C fluxes, and there was significant variation within biomes. Maximum
 194 aboveground biomass values followed a very different trend than the means: temperate broadleaf> temperate
 195 conifer>boreal>tropical. There were some statistically significant biome differences in less frequently
 196 sampled C stocks (e.g., woody biomass, foliage biomass, deadwood), but given high within-biome variability
 197 in C stocks and relatively low sample sizes, these were likely attributable to sampling biases and
 198 methodological differences than to true differences across biomes.

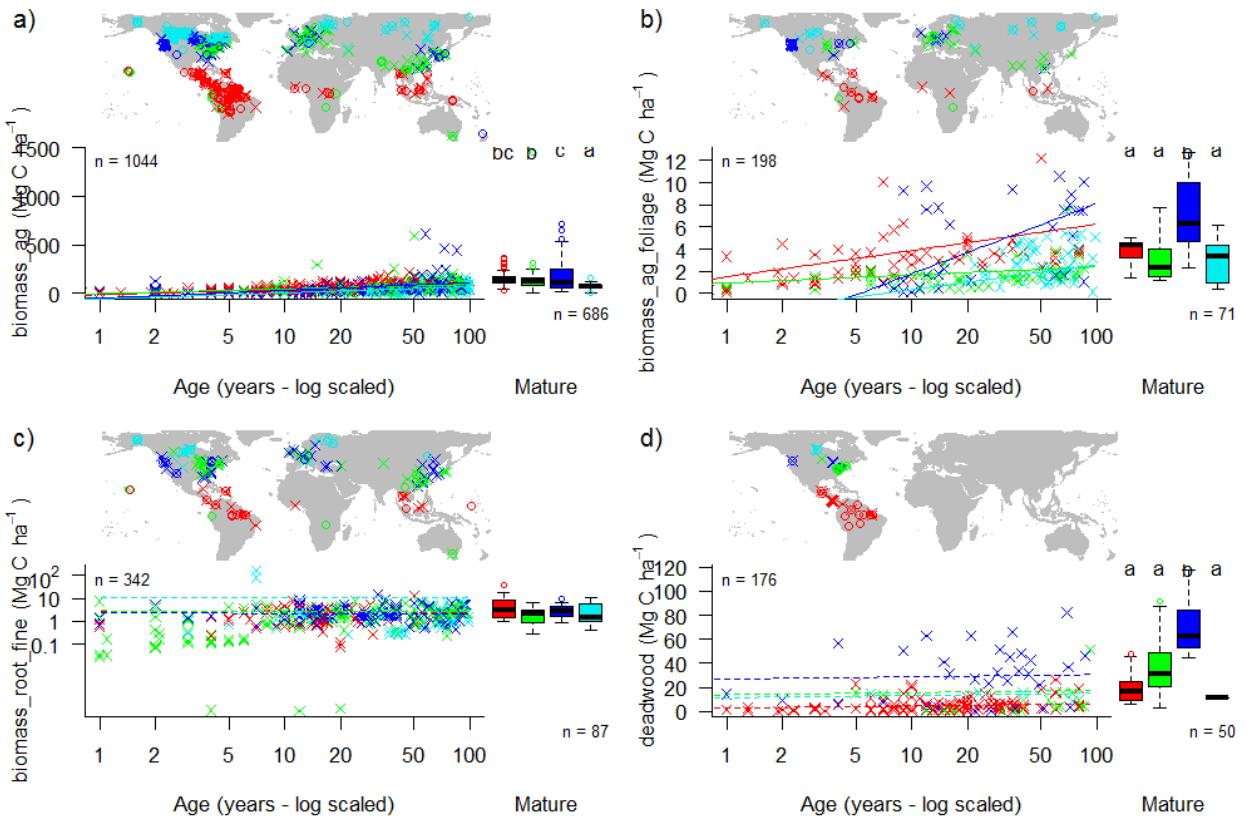


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood.

199 *C cycling in young forests*

200 **(check paragraph with latest data)** Average C cycles for forests <100 years old are presented in Figures
 201 8-11. In general, ForC contained roughly comparable information on C fluxes in regrowth vs mature forests,
 202 with the notable exception of tropical forests, for which there were no fluxes that had been measured in ≥ 7
 203 different geographic areas. C stocks were better documented for regrowth stands, with a total of # records
 204 from # distinct geographic areas. Both C stocks and fluxes commonly displayed significant trends with stand
 205 age for within-biome analyses (Fig. 6-11; detailed below). Differences across biomes typically paralleled those
 206 observed for mature forests, with C cycling generally most rapid in the tropics and slowest in boreal forests
 207 (Figs. 6-7).

208 **(check paragraph with latest data)** ForC contained 14 flux variables with sufficient data for cross-biome
 209 analyses of age trends in regrowth forests (see Methods) (Fig. 6-7 and S#- SI figures including plots for
 210 all variables). Of these, 9 increased significantly with $\log_{10}[\text{stand.age}]$: GPP , NPP , $ANPP$,
 211 $ANPP_{\text{foliage}}$, $ANPP_{\text{woody}}$, $ANPP_{\text{woody-stem}}$, $BNPP$, $BNPP_{\text{root-fine}}$, R_{Reco} , and net C sequestration
 212 ($-NEE$). The remaining five— $ANPP_{\text{woody-branch}}$, $BNPP_{\text{root-coarse}}$, $R_{\text{soil-het}}$, and $R_{\text{soil-het}}$ —displayed no
 213 significant relationship to stand age, although all displayed a positive trend. In terms of C stocks, 10
 214 variables had sufficient data to test for age trends. Six of these—total biomass, aboveground biomass,
 215 aboveground woody biomass, foliage biomass, root biomass, and coarse root biomass—increased significantly
 216 with $\log_{10}[\text{stand.age}]$. The remaining four displayed non-significant positive trends: fine root biomass, total

²¹⁷ dead wood, standing dead wood, and organic layer.

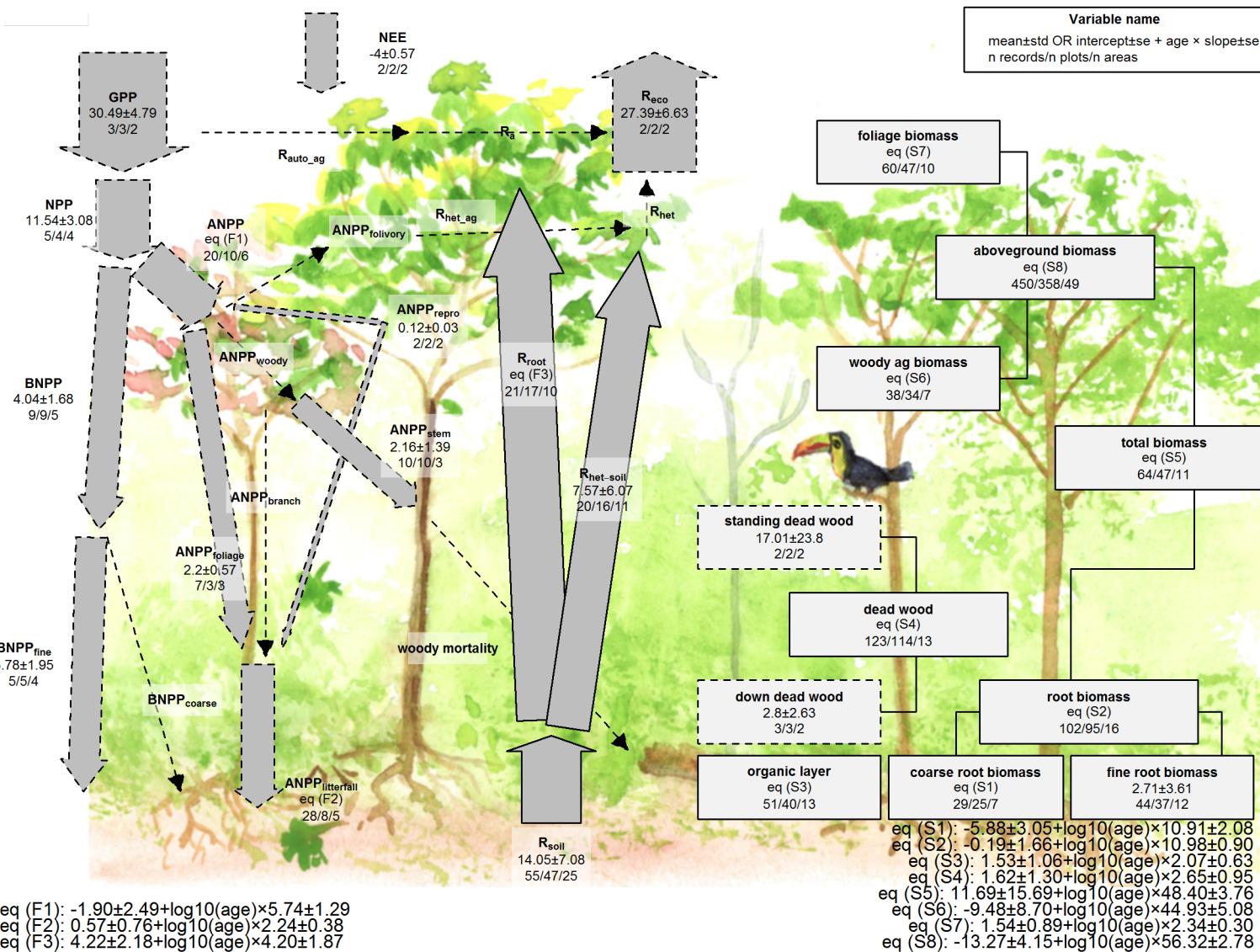


Figure 8 | C cycle diagram for young tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

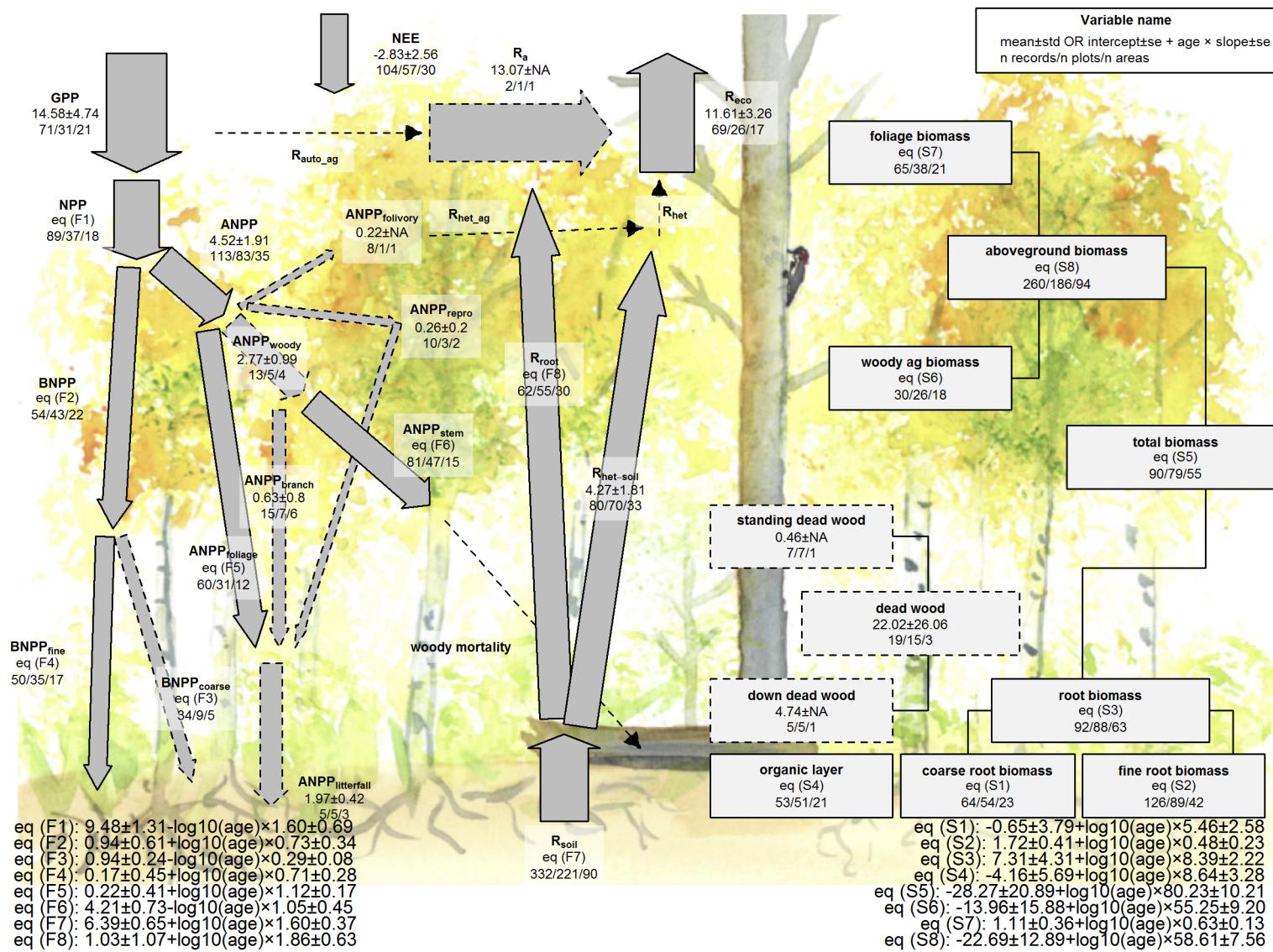


Figure 9 | C cycle diagram for young temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

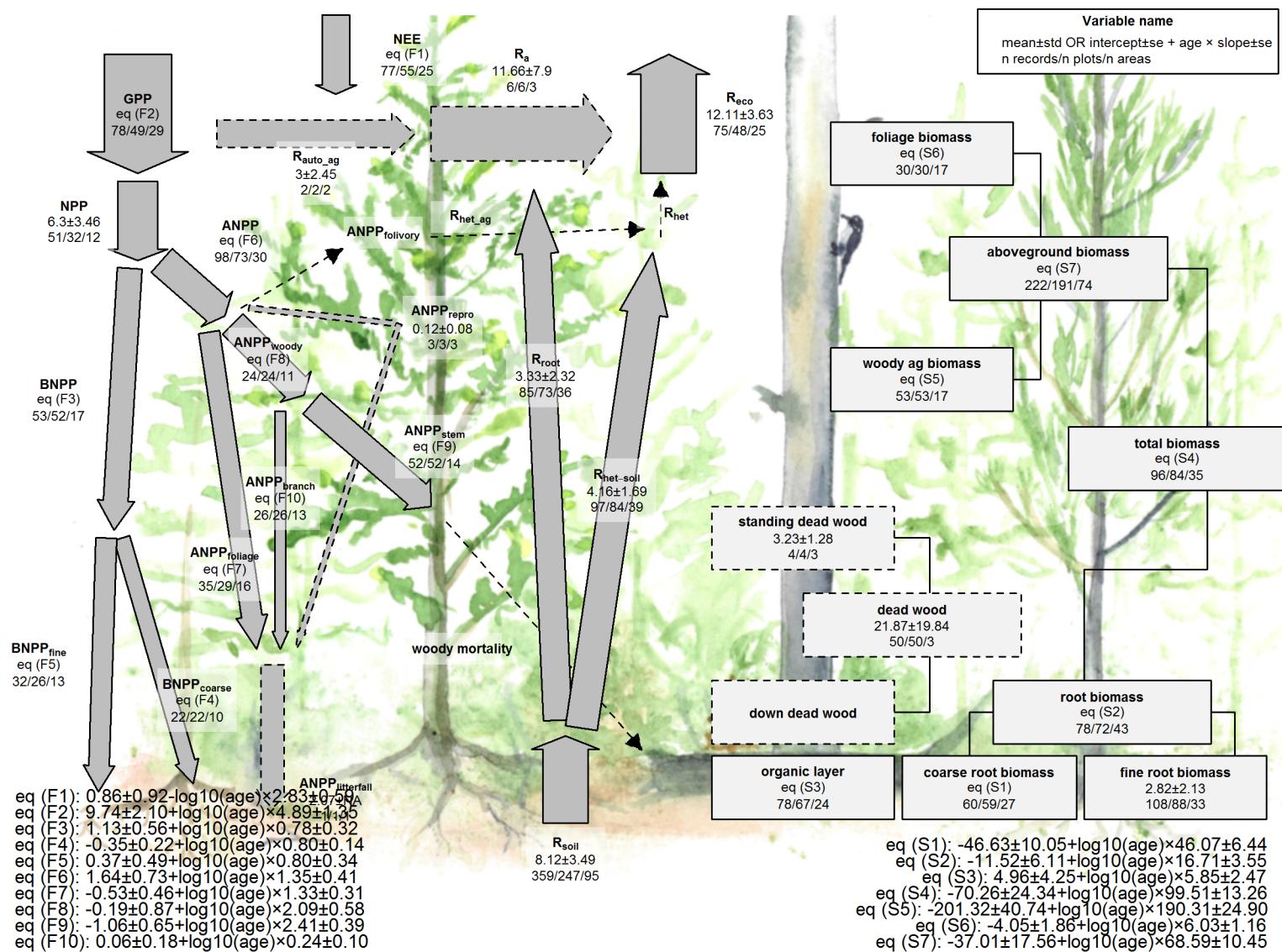


Figure 10 | C cycle diagram for young temperate conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

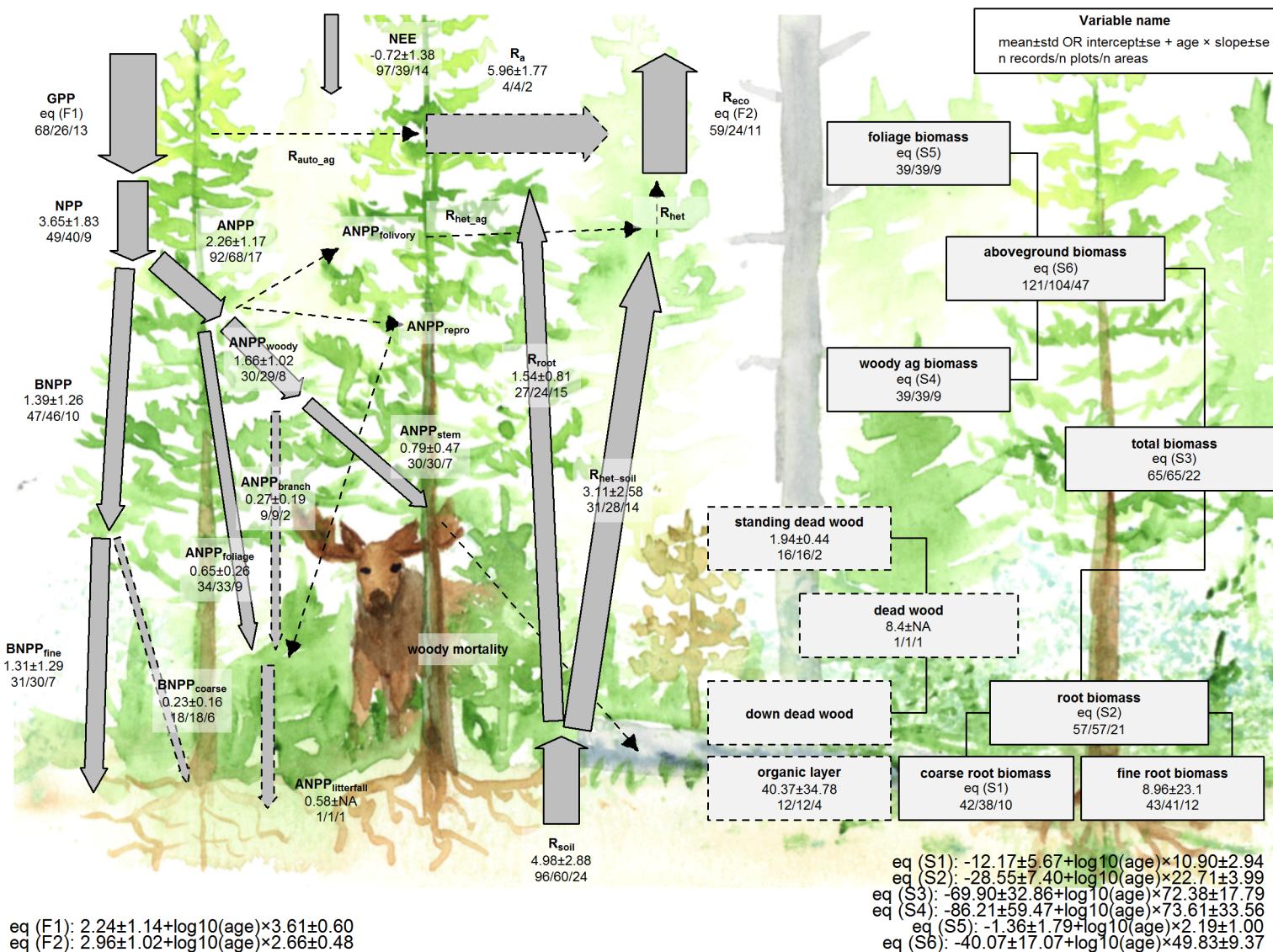


Figure 11 | C cycle diagram for young boreal conifer forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they are presented with numbered equations; otherwise, means are presented. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

218 **Discussion**

219 Carbon cycling rates generally increased from boreal to tropical regions and with stand age. Specifically, the
220 major C fluxes were highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and
221 lowest in boreal forests—a pattern that generally held for regrowth as well as mature forests (Figs. 6–7). In
222 contrast to C fluxes, there was little directional variation in mature forest C stocks across biomes (Figs. 2–5,
223 7). The majority of flux variables, together with most live biomass pools, increased significantly with stand
224 age (Figs. 6–7). Together, these results indicate that, moving from cold to tropical climates and from young
225 to old stands, there is a general acceleration of C cycling, whereas C stocks of mature forests are influenced
226 by a different set of drivers.

227 *C cycling across biomes*

228 *Age trends in C cycling*

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

232 **Acknowledgements**

233 All researchers whose data is included in ForC and this analysis. Thanks to Norbert Kunert for helpful
234 discussion. A Smithsonian Scholarly Studies grant to KAT and HML.

235 Anderson-Teixeira K J, Wang M M H, McGarvey J C, Herrmann V, Tepley A J, Bond-Lamberty B and
236 LeBauer D S 2018 ForC: A global database of forest carbon stocks and fluxes *Ecology* **99** 1507–7 Online:
237 <http://doi.wiley.com/10.1002/ecy.2229>

238 Anderson-Teixeira K J, Wang M M H, McGarvey J C and LeBauer D S 2016 Carbon dynamics of mature
239 and regrowth tropical forests derived from a pantropical database (TropForC-db) *Global Change Biology* **22**
240 1690–709 Online: <http://onlinelibrary.wiley.com/doi/10.1111/gcb.13226/abstract>

241 Banbury Morgan B, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau H C and Anderson-Teixeira
242 K J Global patterns of forest autotrophic carbon fluxes *Global Change Biology*

243 Bond-Lamberty B and Thomson A 2010 A global database of soil respiration data *Biogeosciences* **7** 1915–26
244 Online: <http://www.biogeosciences.net/7/1915/2010/>

245 Clark D B, Castro C S, Alvarado L D A and Read J M 2004 Quantifying mortality of tropical rain forest
246 trees using high-spatial-resolution satellite data *Ecology Letters* **7** 52–9 Online:
247 <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2003.00547.x>

248 Grassi G, House J, Dentener F, Federici S, Elzen M den and Penman J 2017 The key role of forests in
249 meeting climate targets requires science for credible mitigation *Nature Climate Change* **7** 220–6 Online:
250 <https://www.nature.com/articles/nclimate3227>

251 Leitold V, Morton D C, Longo M, dos-Santos M N, Keller M and Scaranello M 2018 El Niño drought
252 increased canopy turnover in Amazon forests *New Phytologist* **219** 959–71 Online:
253 <http://doi.wiley.com/10.1111/nph.15110>

- 254 Li X and Xiao J 2019 Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A
255 Global, Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2 *Remote Sensing* **11** 2563
256 Online: <https://www.mdpi.com/2072-4292/11/21/2563>
- 257 Luysaert S, Inglima I, Jung M, Richardson A D, Reichstein M, Papale D, Piao S L, Schulze E-D, Wingate L,
258 Matteucci G, Aragao L, Aubinet M, Beer C, Bernhofer C, Black K G, Bonal D, Bonnefond J-M, Chambers J,
259 Ciais P, Cook B, Davis K J, Dolman A J, Gielen B, Goulden M, Grace J, Granier A, Grelle A, Griffis T,
260 Grünwald T, Guidolotti G, Hanson P J, Harding R, Hollinger D Y, Hutyra L R, Kolari P, Kruijt B, Kutsch
261 W, Lagergren F, Laurila T, Law B E, Maire G L, Lindroth A, Loustau D, Malhi Y, Mateus J, Migliavacca M,
262 Misson L, Montagnani L, Moncrieff J, Moors E, Munger J W, Nikinmaa E, Ollinger S V, Pita G, Rebmann
263 C, Roupsard O, Saigusa N, Sanz M J, Seufert G, Sierra C, Smith M-L, Tang J, Valentini R, Vesala T and
264 Janssens I A 2007 CO₂ balance of boreal, temperate, and tropical forests derived from a global database
265 *Global Change Biology* **13** 2509–37 Online:
266 <http://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2007.01439.x>
- 267 Schimel D, Pavlick R, Fisher J B, Asner G P, Saatchi S, Townsend P, Miller C, Frankenberg C, Hibbard K
268 and Cox P 2015 Observing terrestrial ecosystems and the carbon cycle from space *Global Change Biology* **21**
269 1762–76 Online: <http://doi.wiley.com/10.1111/gcb.12822>