

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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19 **Summary**

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

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

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

35 *Discussion.* This analysis yields a comprehensive, largely consistent picture of C cycling across the world's
36 forests. [Discussion section will interpret results, highlighting new and significant findings, and discuss
37 implications. Tentative headings are "Stand level C cycling in forests globally", "Age trends in C cycling",
38 and "Implications for climate change mitigation".]

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

40 **Background**

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

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

58 webs... (support of biodiversity) (human reliance as source of food, fuel, fiber)

59 Despite the centrality of forest C cycling in regulating both atmospheric CO₂ and ecosystem function and
60 diversity, we lack a comprehensive understanding of how C cycling varies with across biomes and with stand
61 age. While remote sensing measurements are increasingly useful for global- or regional-scale estimates of
62 forest *GPP* (Bagdley et al. 2019, (Li and Xiao 2019)), aboveground biomass (B_{ag}) (REFS), woody mortality
63 (*i.e.*, B_{ag} losses to mortality M_{woody}) (Clark et al 2004, Leitold et al 2018), and to some extent net
64 ecosystem exchange (*NEP*) (REFS), the remainder of C fluxes and stocks can only be quantified by
65 ground-based measurements. Moreover, data on stand characteristics—including species composition, age, and
66 disturbance history—are critical to interpreting and projecting into the future, but [usually rely on
67 ground-based measurements]. Thus, ground-based measurements are, and will continue to be, central to
68 characterizing forest C cycling.

69 Tens of thousands of ground-based forest C measurements have been published, but their distribution across
70 literally thousands of scientific articles—along with variation in data formats, units, measurement methods,
71 etc.—have made them effectively inaccessible for many global-scale analyses, including those attempting to
72 quantify the role of forests in the global C cycle (*e.g.*, Pan et al 2011), and model evaluation (Clark et al
73 2017, Luo et al 2012). Important progress has been made in synthesizing data to address how C cycling
74 varies across forest biomes (Luyssaert et al. 2007; REFS) and stand ages (REFS), yet generally consider only
75 a limited set of C variables (but see Anderson-Teixeira et al 2016 for the tropics) and do not consider
76 age-by-biome interactions. To address the need for global-scale analyses of forest C cycling, we have
77 developed an open-access Global Forest Carbon database, ForC (Anderson-Teixeira et al (2016),
78 Anderson-Teixeira et al (2018)). ForC contains data on forest ecosystem C stocks and annual fluxes (>50
79 variables) and associated data required for interpretation (*e.g.*, stand history, measurement methods)
80 amalgamated from numerous previous data compilations and directly from original publications. ForC
81 currently contains # (~49,000!) records from # plots and # distinct geographic areas representing all
82 forested biogeographic and climate zones.

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

85 1. To what extent can we fully represent, and “close”, C budgets for each of the world's major forest
86 biomes (*i.e.*, tropical, temperate broadleaf and deciduous, boreal) based on the current ForC data?

87 2. How do C cycling vary across the worlds major forest biomes?

88 3. How does C cycling vary with stand age?

89 While components of these questions have been previously addressed (Luyssaert et al 2007,
90 Anderson-Teixeira et al 2016, pp @anderson-teixeira_forc_2018, @banbury_morgan_global_nodate), our
91 analysis represents by far the most comprehensive analysis of C cycling in global forests, and thereby stands
92 to serve as a foundation for improved understanding of global forest C cycling.

93 Methods/ Design

94 This review synthesizes data from the ForC database (<https://github.com/forc-db/ForC>; Anderson-Teixeira
95 et al 2016, pp @anderson-teixeira_forc_2018). ForC amalgamates numerous intermediary data sets (*e.g.*,
96 REFS) and original studies. Original publications were referenced to check values and obtain information not

97 contained in intermediary data sets, although this process has not been completed for all records. The
98 database was developed with goals of understanding how C cycling in forests varies across broad geographic
99 scales and as a function of stand age. As such, there has been a focus on incorporating data from regrowth
100 forests (*e.g.*, Anderson et al 2006, Martin et al 2013, Bonner et al 2013) and obtaining stand age data when
101 possible (83% of records in v.2.0; Anderson-Teixeira et al 2018). Particular attention was given to developing
102 the database for tropical forests (Anderson-Teixeira *et al* 2016), yet these represented only approximately
103 one-third of records in ForC v.2.0 (Anderson-Teixeira *et al* 2018). Since publication of ForC v.2.0, we added
104 the following data to ForC: the Global Database of Soil Respiration Database (SRDB v.##; Bond-Lamberty
105 and Thomson 2010), the Global Reforestation Opportunity Assessment database (GROA v1.0; Cook-Patton
106 et al. in press; ZenodoDOI), and data from several publications (Taylor et al. 2017, Lutz et al. 2018,
107 Johnson_2018_csss; see GitHub repo for complete list) (GitHub list). We note that there remains a
108 significant amount of relevant data that is not yet included in ForC, particularly biomass data from national
109 forest inventories (*e.g.*: REFS). The database version used for this analysis has been tagged as a new release
110 on Github (XX) and assigned a DOI through Zenodo (DOI: TBD).

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

115 <http://maps3.arcgisonline.com/ArcGIS/rest/services/A-16/Köppen->
116 Geiger_Observed_and_Predicted_Climate_Shifts/MapServer; Rubel and Kottek 2010). Tropical climates
117 were defined to include all equatorial (A) zones, temperate climates were defined to include all warm
118 temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and boreal climates
119 were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B)
120 and polar (E) Köppen-Geiger zones were excluded from the analysis. Leaf type (broadleaf / needleleaf) was
121 defined based on descriptions in original publications (prioritized) or values extracted from a global map
122 based on satellite observations (SYNMAP; Jung et al 2006) and recorded in the dominant.veg field of the
123 ForC MEAUREMENTS table. Stand age was obtained from the stand.age field of MEASUREMENTS table,
124 and forests classified as “young” (< 100 years) or “mature” (\geq 100 years or classified as “mature”, “old
125 growth”, “intact”, or “undisturbed” in original publication). Records for which stand age was unknown were
126 excluded from the analysis. These groupings were defined based on ForC v.2.0 (Anderson-Teixeira *et al*
127 2018), for which they covered 91% of the primary variable records for forests of known age, or 86% of total
128 records. The most well-represented forest types excluded were boreal broadleaf and boreal and temperate
129 mixed broadleaf-needleleaf, each with <400 records total for stands of any age.

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

138 Analyses drew from ForC-simplified (https://github.com/forc-db/ForC/blob/master/ForC_simplified),

which is a rearrangement of ForC intended to facilitate analyses. In generating ForC-simplified, all measurements originally expressed in units of dry organic matter (*OM*) were converted to units of C using the IPCC default of $C = 0.47 * OM$ (IPCC 2006). Duplicate or otherwise conflicting records were reconciled as described in APPENDIX A. Records were filtered to remove plots that had undergone significant anthropogenic management or major disturbance since the most recent stand establishment (*i.e.*, that reflected by stand.age). Specifically, we removed all plots flagged as managed in ForC-simplified (managed field). This included plots with any record of managements manipulating CO₂, temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized”.

Plots flagged as disturbed in ForC-simplified included stands that had undergone anthropogenic thinning or partial harvest (“Cut” or “Harvest” codes) unless this was very minor (percent.mortality= “minor”). We retained sites that were grazed or had undergone low severity natural disturbances (<10% mortality) including droughts, major storms, fires, and floods. We also removed all plots for which no stand history information had been retrieved.

Data were analyzed to produce basic summaries of C cycle patterns across biomes and stand ages following an approach similar to that of Anderson-Teixeira et al (2016). For mature forests, to obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot, weighting flux measurements according to the length of measurement periods (*i.e.*, end.date - start.date). Values were then averaged across plots clustered within 25 km of one another (geographic.area field of SITES table, sensu Anderson-Teixeira et al 2018), weighting by area.sampled (MEASUREMENTS table) or plot.area (PLOTS table) if available for all records. This step was taken to avoid pseudo-replication and to combine any records from sites with more than one name in ForC. Finally, for figures 6 and 7, the original values were analyzed via a linear mixed effects model ('lmer' function in 'lme4' R package) with biome as fixed effect and plot nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we looked at a Tukey's pairwise comparison to see which biomes were significantly different from one another.

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

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

Review Results/ Synthesis

C cycling in mature forests

Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests ≥ 100 years old and with no known major disturbance or significant anthropogenic management are presented in

179 Figures 1-4, and statistics for each biome type are also summarized at: [GitHub URL]. Of the 23 flux and 11
180 stock variables mapped in these diagrams, ForC contained estimates from ≥ 7 distinct geographic areas for
181 # fluxes and # stocks in tropical broadleaf forests, # fluxes and # stocks in temperate broadleaf forests,
182 #fluxes and # stocks in temperate conifer forests, and fluxes and # stocks in boreal forests. For variables
183 with records from ≥ 7 distinct geographic areas, these ensemble C budgets were generally consistent. That is,
184 component fluxes and stocks summed to within 1 std of more inclusive fluxes in all but one instance (in
185 temperate conifer forests, *abovegroundwoodybiomass + foliagebiomass > abovegroundbiomass + 1std*; Fig.
186 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>NEP</i> | net ecosystem production or net ecosystem exchange (+ indicates C sink) | n | n | n | n.s. | - |
| <i>GPP</i> | gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEP$) | 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

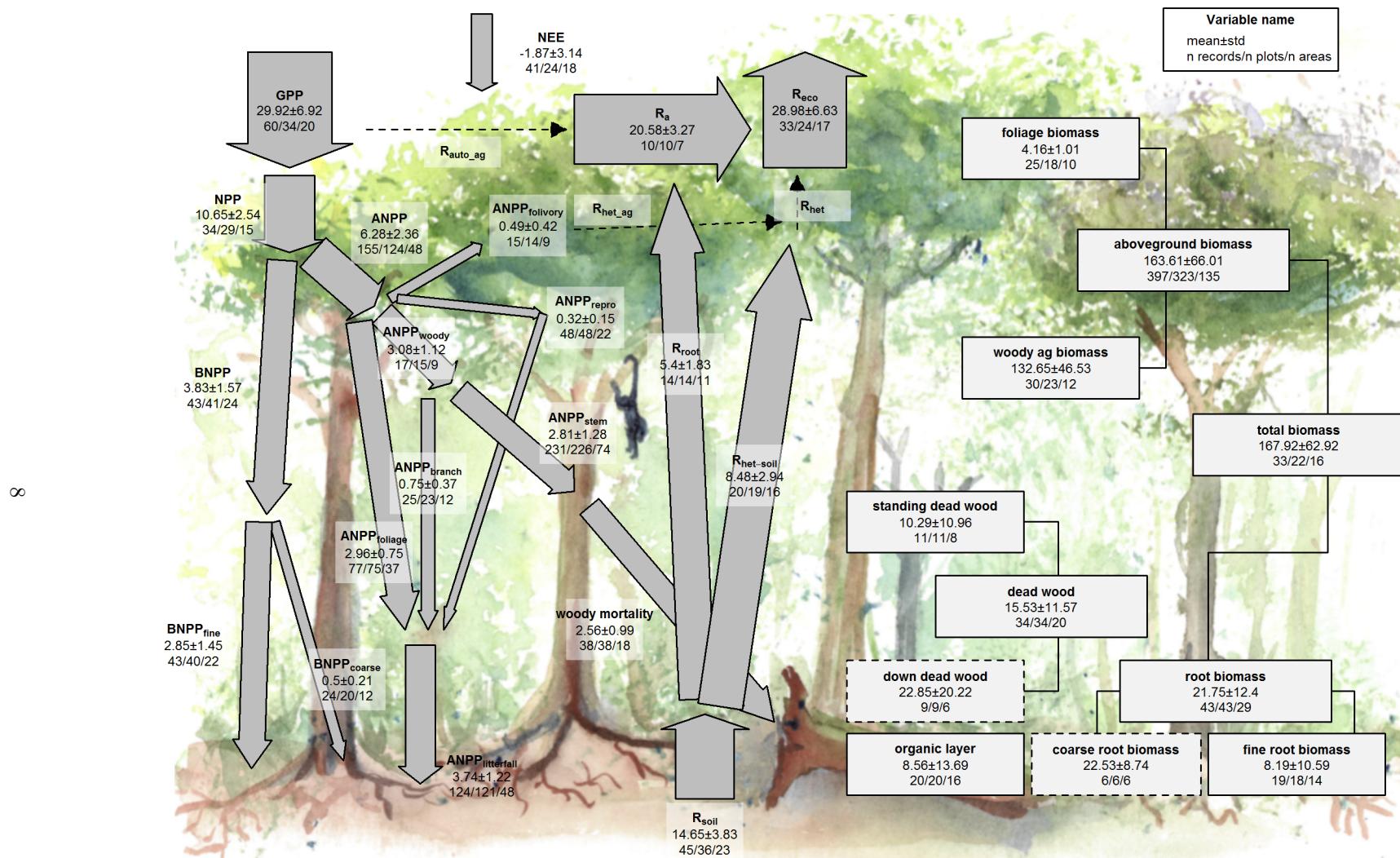


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

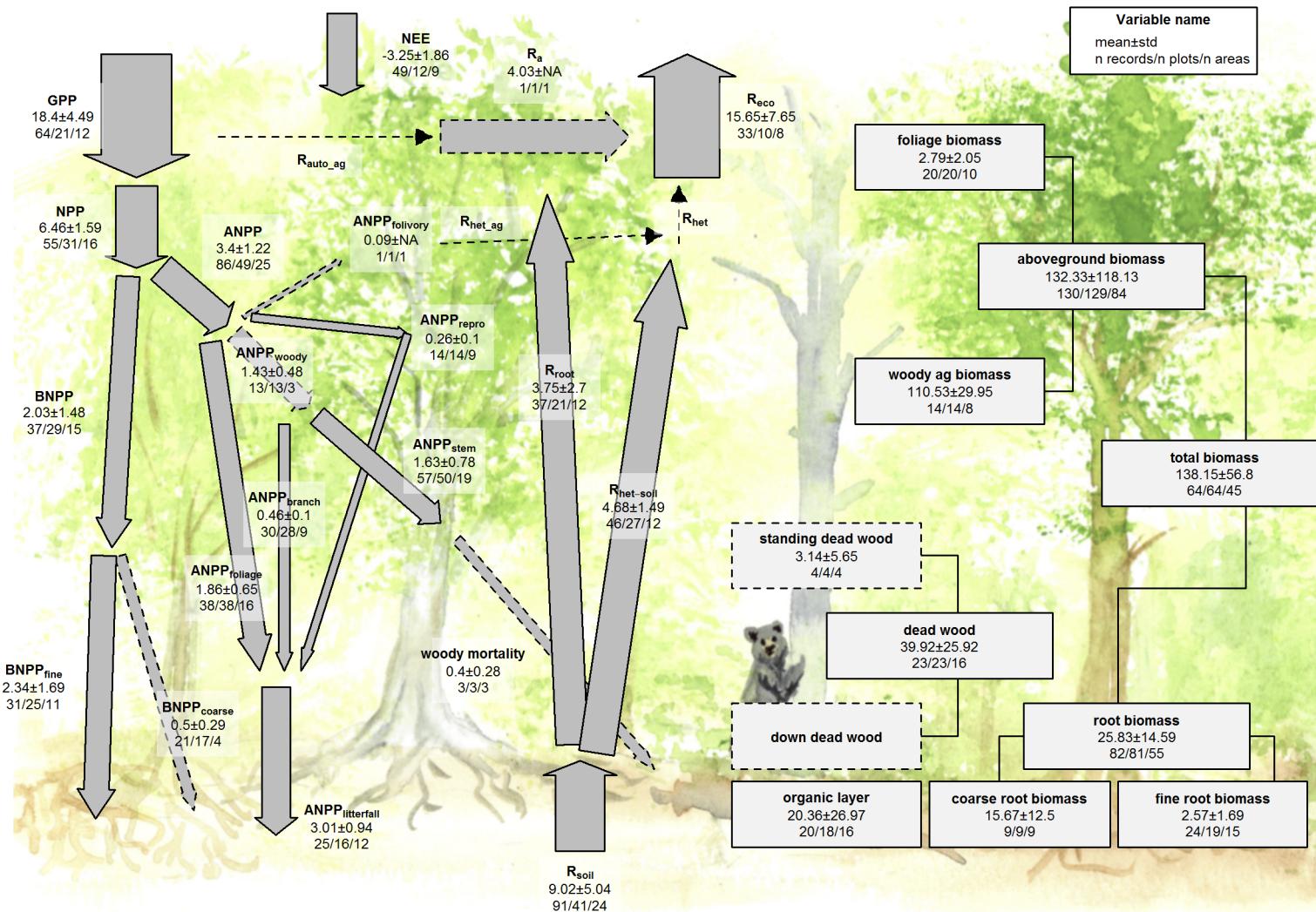


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables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

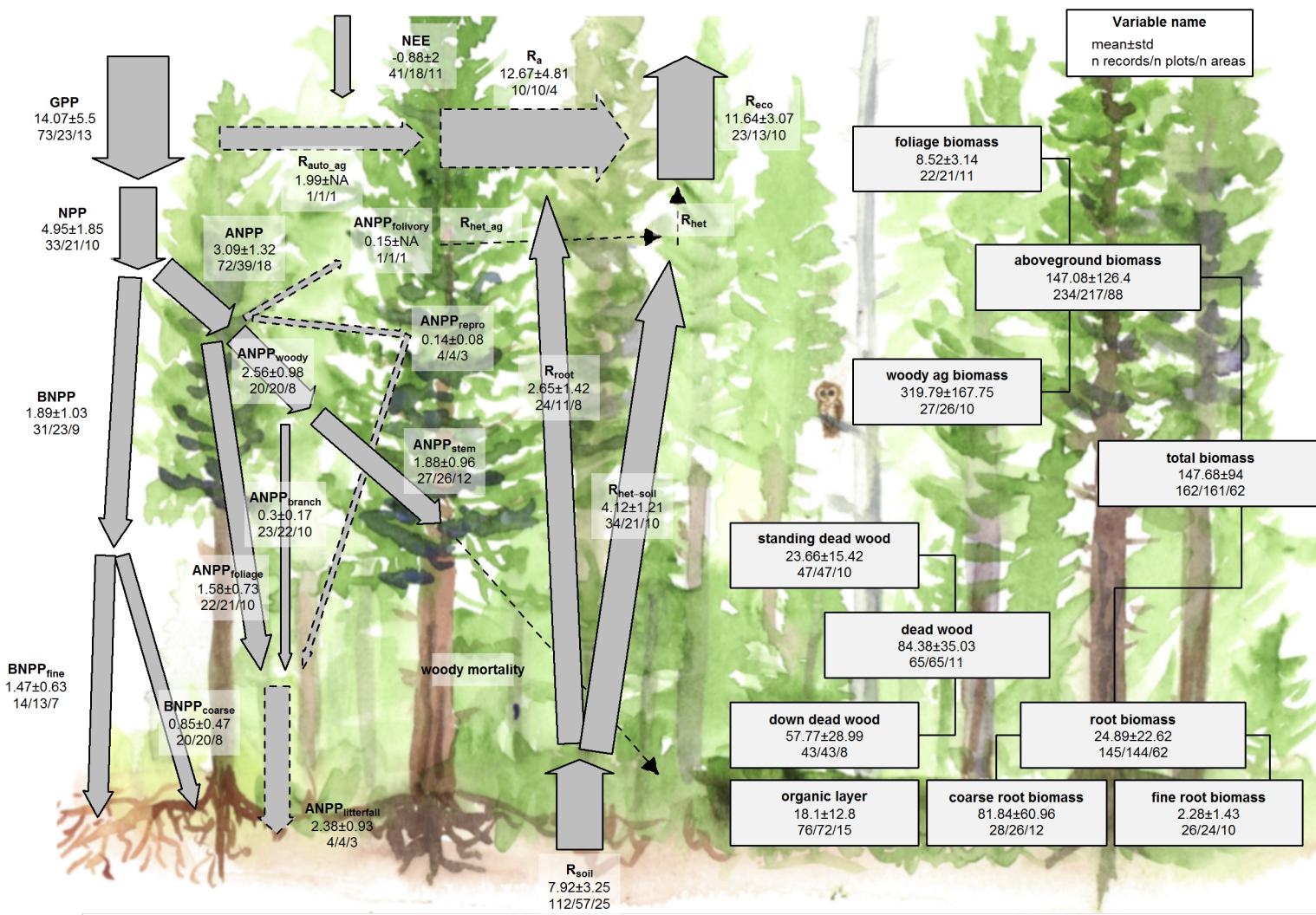


Figure 3 | C cycle diagram for mature temperate conifer forests. All units are $Mg\text{ C ha}^{-1}\text{ yr}^{-1}$ (fluxes) or $Mg\text{ C ha}^{-1}$. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks.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

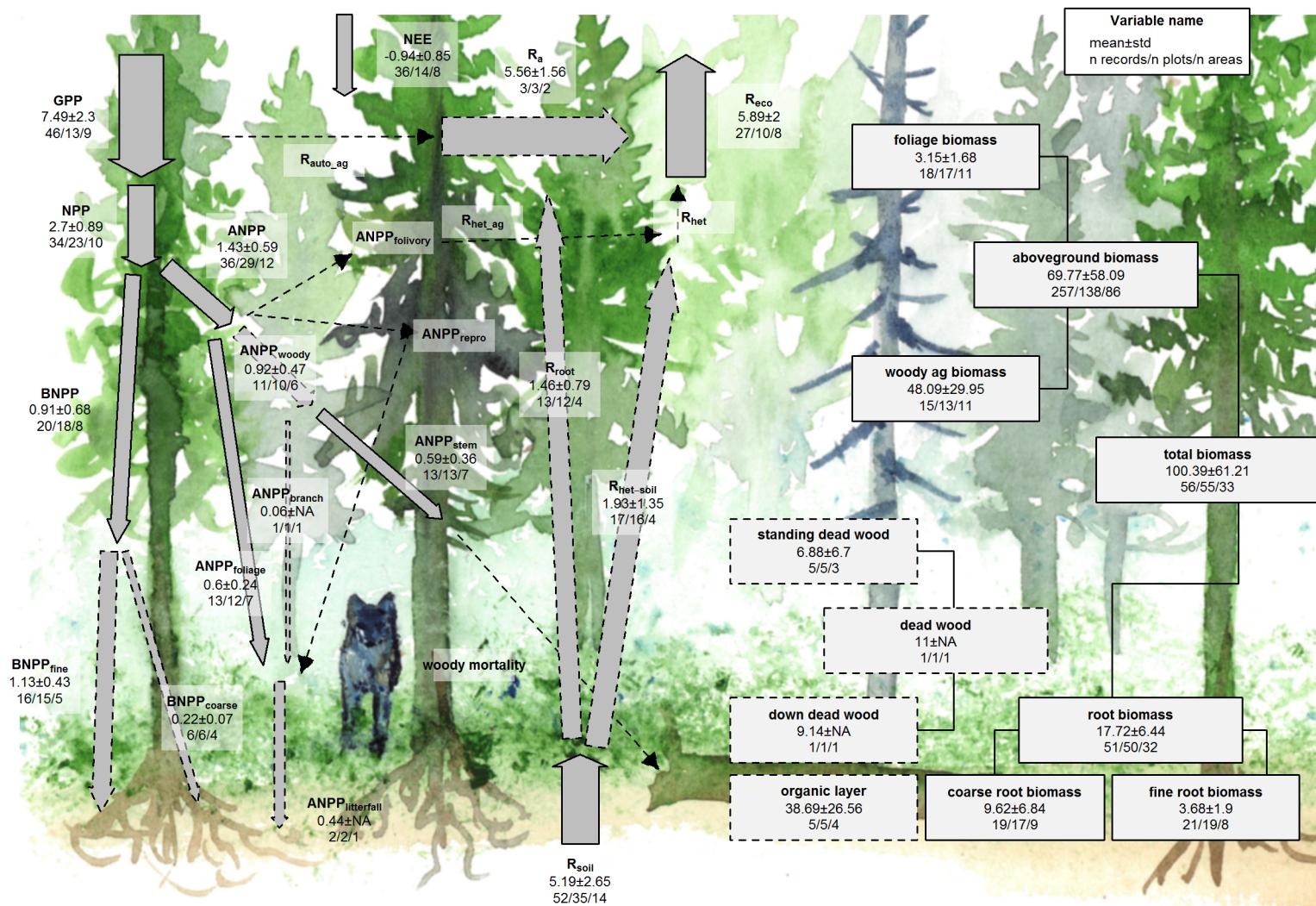


Figure 4 | C cycle diagram for mature boreal conifer forests. All units are $Mg C ha^{-1} yr^{-1}$ (fluxes) or $Mg C ha^{-1}$. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

187 (check paragraph with latest data) The largest C fluxes—including *GPP*, *NPP*, *ANPP*, *BNPP*,
188 $R_{soil,et}$, R_{soil} , R_{eco} , — were highest in tropical forests, intermediate in temperate (broadleaf or conifer)
189 forests, and lowest in boreal forests (ForC_variable_averages_per_Biome) (Fig. 5). The same held true for
190 some of the subsidiary fluxes: *ANPP_foliage*, *ANPP_wood*, [OTHERS?]. Other subsidiary
191 fluxes—including *NPP_wood*, *ANPP_repro*, *ANPP_stem*, *ANPP_branch*, *woody.mortality*, *BNPP_coarse*,
192 *BNPP_fine*, [OTHERS?—deviated from this pattern and/or lacked data for some biomes. Net ecosystem
193 production (*NEP*) did not follow this pattern, with no significant differences across biomes but the largest
194 (negative) average in temperate broadleaf forests, followed by temperate conifer, boreal, and tropical forests.
195 Thus, C cycling rates generally decreased from tropical to temperate to boreal forests, but with less apparent
196 trends for some of the subsidiary fluxes and an important exception in the overall C balance (*NEP*).

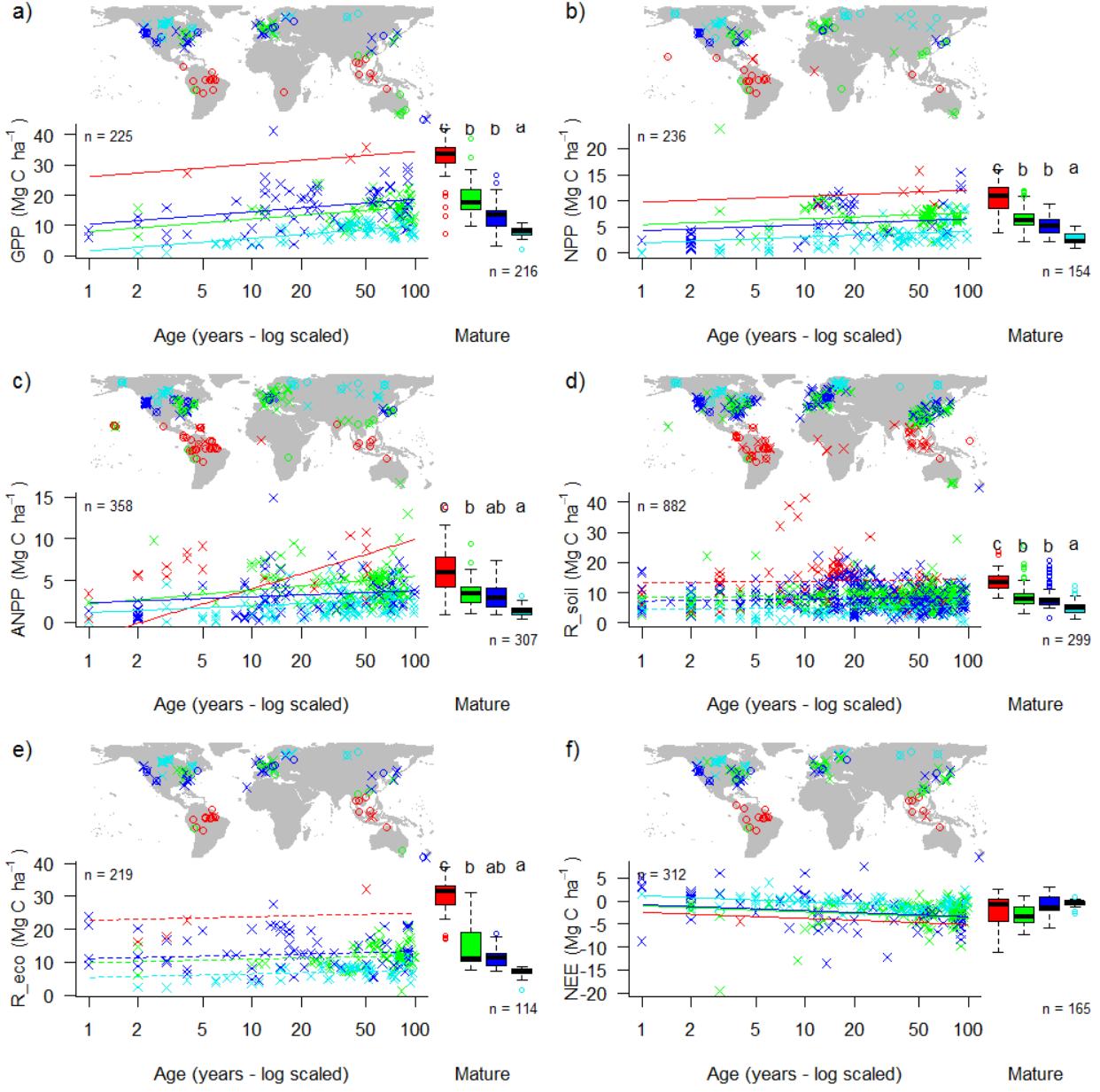


Figure 5 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). Lines... .

197 There were less distinct trends in C stocks across biomes (Fig. 6). Biome means for live aboveground and
 198 total biomass followed the same general trend as the major fluxes, with biomass of tropical= temperate
 199 broadleaf \geq temperate conifer> boreal forests (Fig. 6a). However, the relative differences in these means
 200 were much smaller than for the major C fluxes, and there was significant variation within biomes. Maximum
 201 aboveground biomass values followed a very different trend than the means: temperate broadleaf> temperate
 202 conifer>boreal>tropical. There were some statistically significant biome differences in less frequently
 203 sampled C stocks (e.g., woody biomass, foliage biomass, deadwood), but given high within-biome variability
 204 in C stocks and relatively low sample sizes, these were likely attributable to sampling biases and
 205 methodological differences than to true differences across biomes.

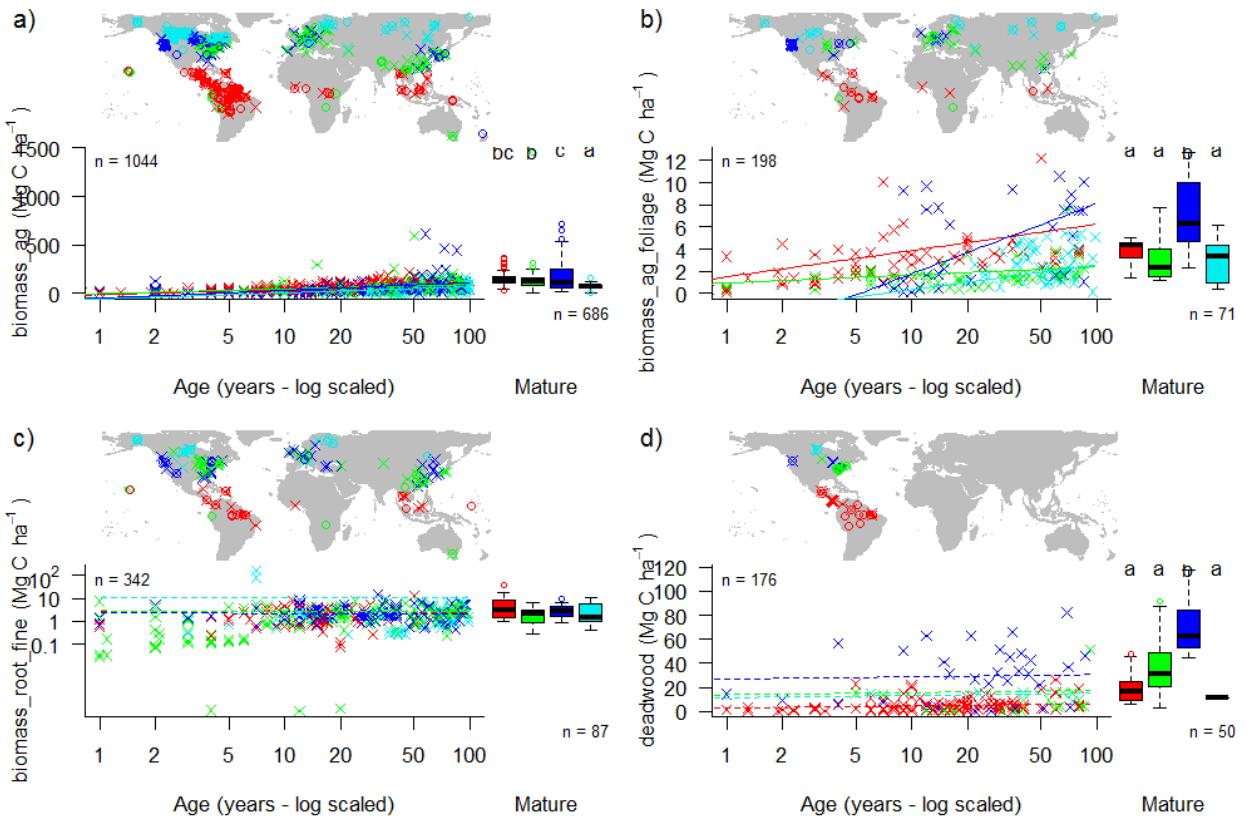


Figure 6 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood.

206 C cycling in young forests

207 **(check paragraph with latest data)** Average C cycles for forests <100 years old are presented in Figures
 208 7-10. In general, ForC contained roughly comparable information on C fluxes in regrowth vs mature forests,
 209 with the notable exception of tropical forests, for which there were no fluxes that had been measured in ≥ 7
 210 different geographic areas. C stocks were better documented for regrowth stands, with a total of # records
 211 from # distinct geographic areas. Both C stocks and fluxes commonly displayed significant trends with stand
 212 age for within-biome analyses (Fig. 5-10; detailed below). Differences across biomes typically paralleled those
 213 observed for mature forests, with C cycling generally most rapid in the tropics and slowest in boreal forests
 214 (Figs. 5-6).

215 **(check paragraph with latest data)** ForC contained 14 flux variables with sufficient data for cross-biome
 216 analyses of age trends in regrowth forests (see Methods) (Fig. 5-6 and S#- SI figures including plots for
 217 all variables). Of these, 9 increased significantly with $\text{log10}[\text{stand.age}]$: GPP , NPP , $ANPP$,
 218 $ANPP_{\text{foliage}}$, $ANPP_{\text{woody}}$, $ANPP_{\text{woody-stem}}$, $BNPP$, $BNPP_{\text{root-fine}}$, R_{eco} , and net C sequestration
 219 (NEP). The remaining five— $ANPP_{\text{woody-branch}}$, $BNPP_{\text{root-coarse}}$, $R_{\text{soil-het}}$, and $R_{\text{soil-het}}$ —displayed no
 220 significant relationship to stand age, although all displayed a positive trend. In terms of C stocks, 10
 221 variables had sufficient data to test for age trends. Six of these—total biomass, aboveground biomass,
 222 aboveground woody biomass, foliage biomass, root biomass, and coarse root biomass—increased significantly
 223 with $\text{log10}[\text{stand.age}]$. The remaining four displayed non-significant positive trends: fine root biomass, total

²²⁴ dead wood, standing dead wood, and organic layer.

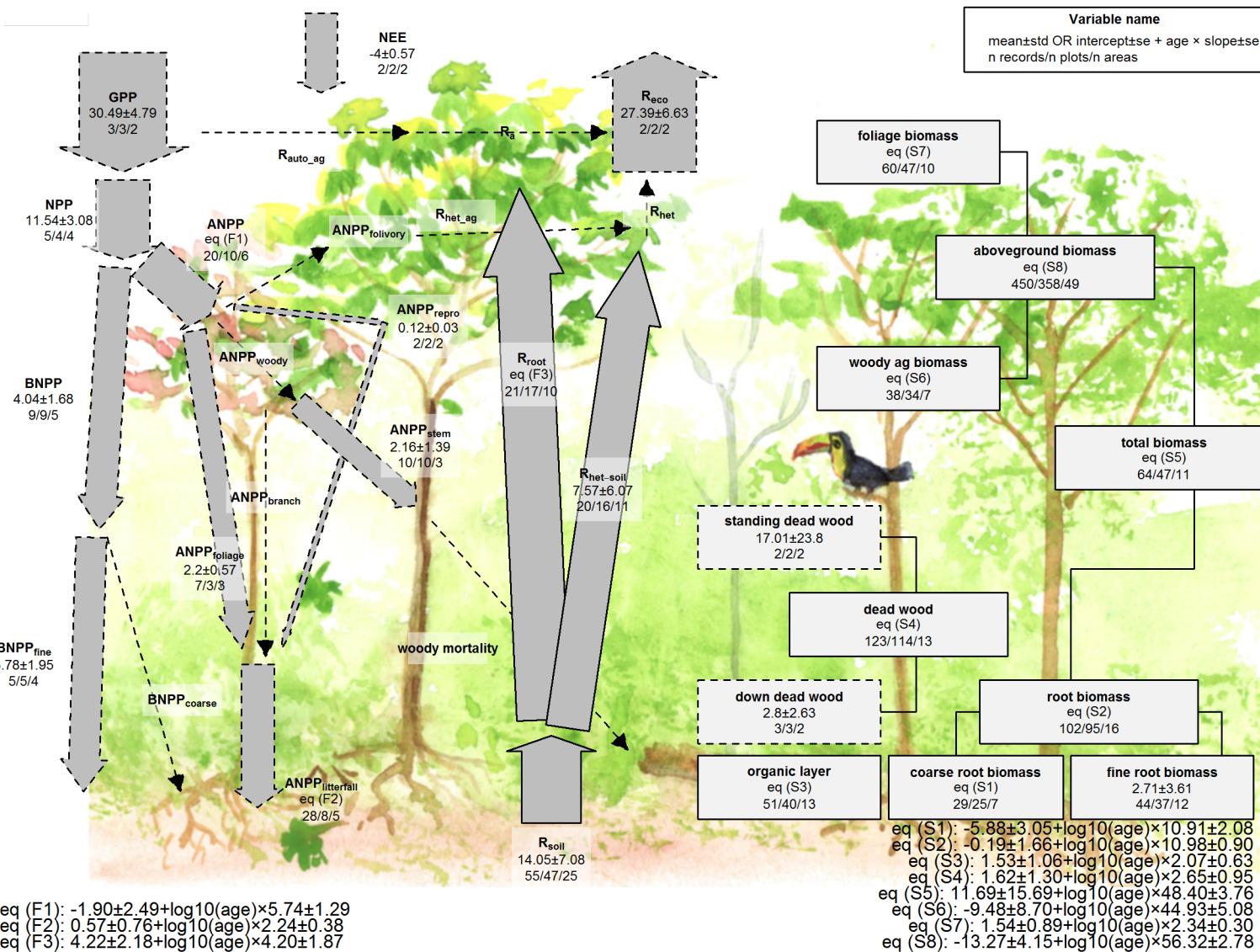


Figure 7 | C cycle diagram for young tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they 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.

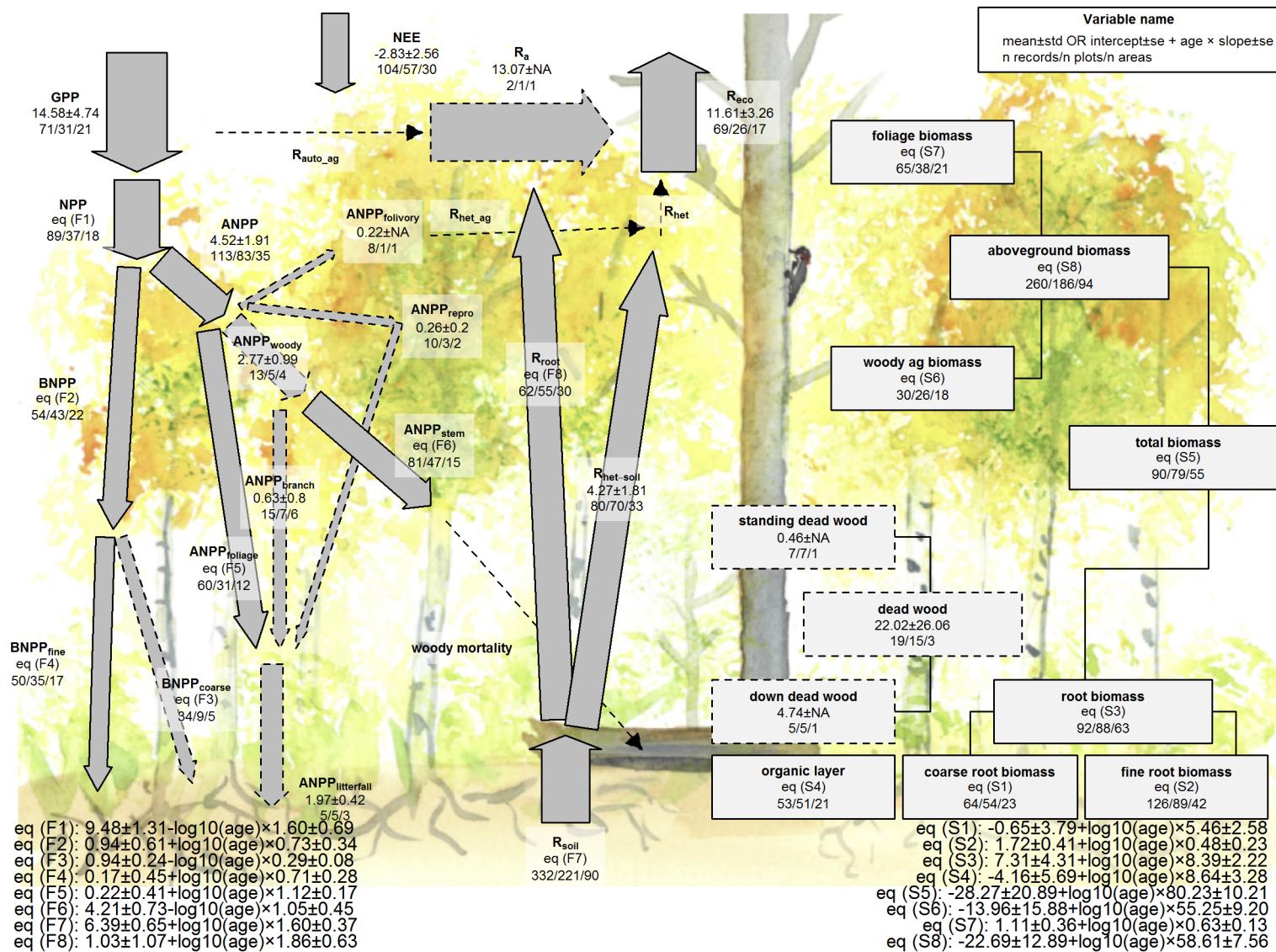


Figure 8 | C cycle diagram for young temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age trends are significant, they 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.

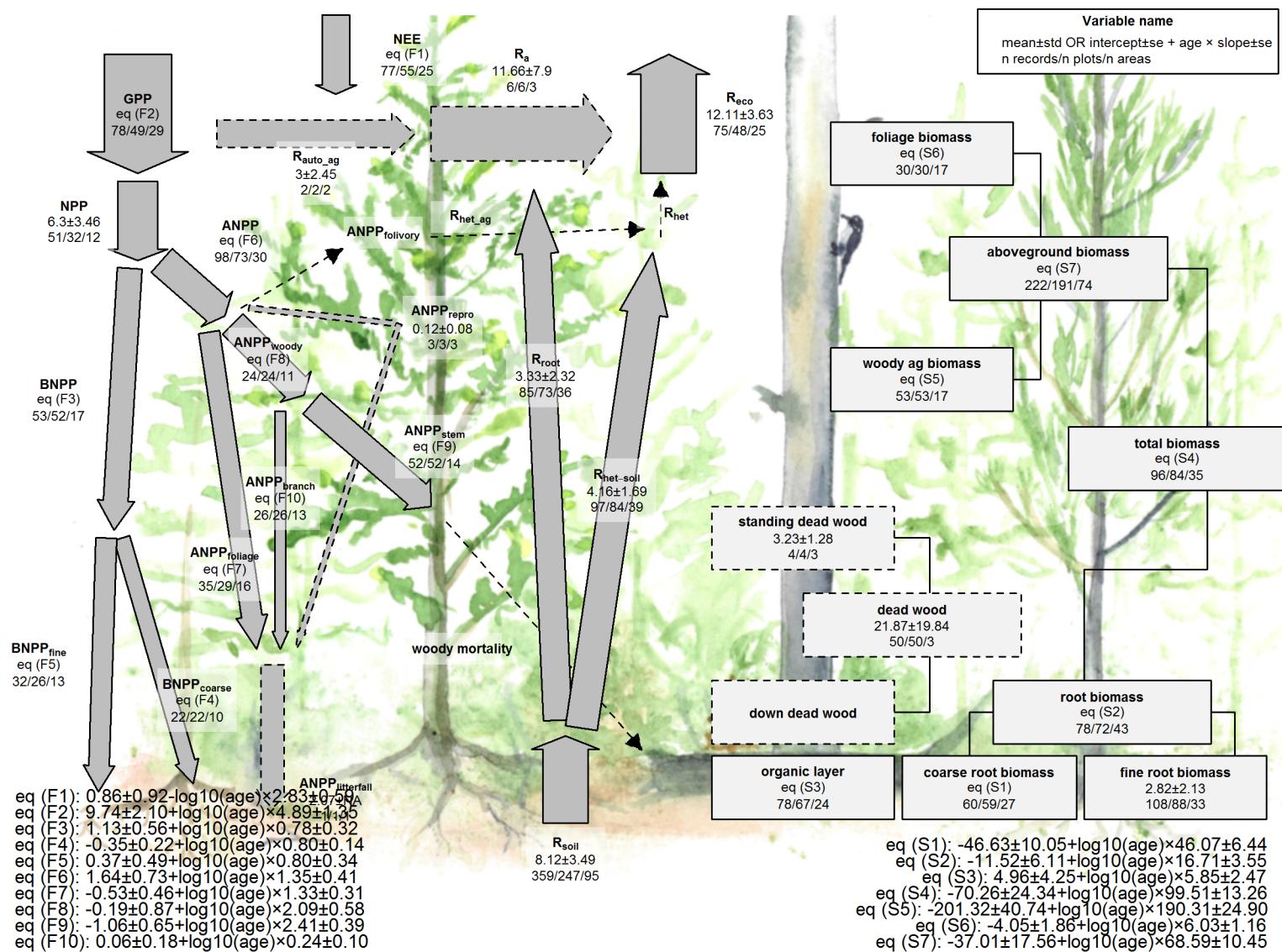


Figure 9 | C cycle diagram for young temperate conifer forests. All units are $Mg\text{ C ha}^{-1}\text{ yr}^{-1}$ (fluxes) or $Mg\text{ C ha}^{-1}$. Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. 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.

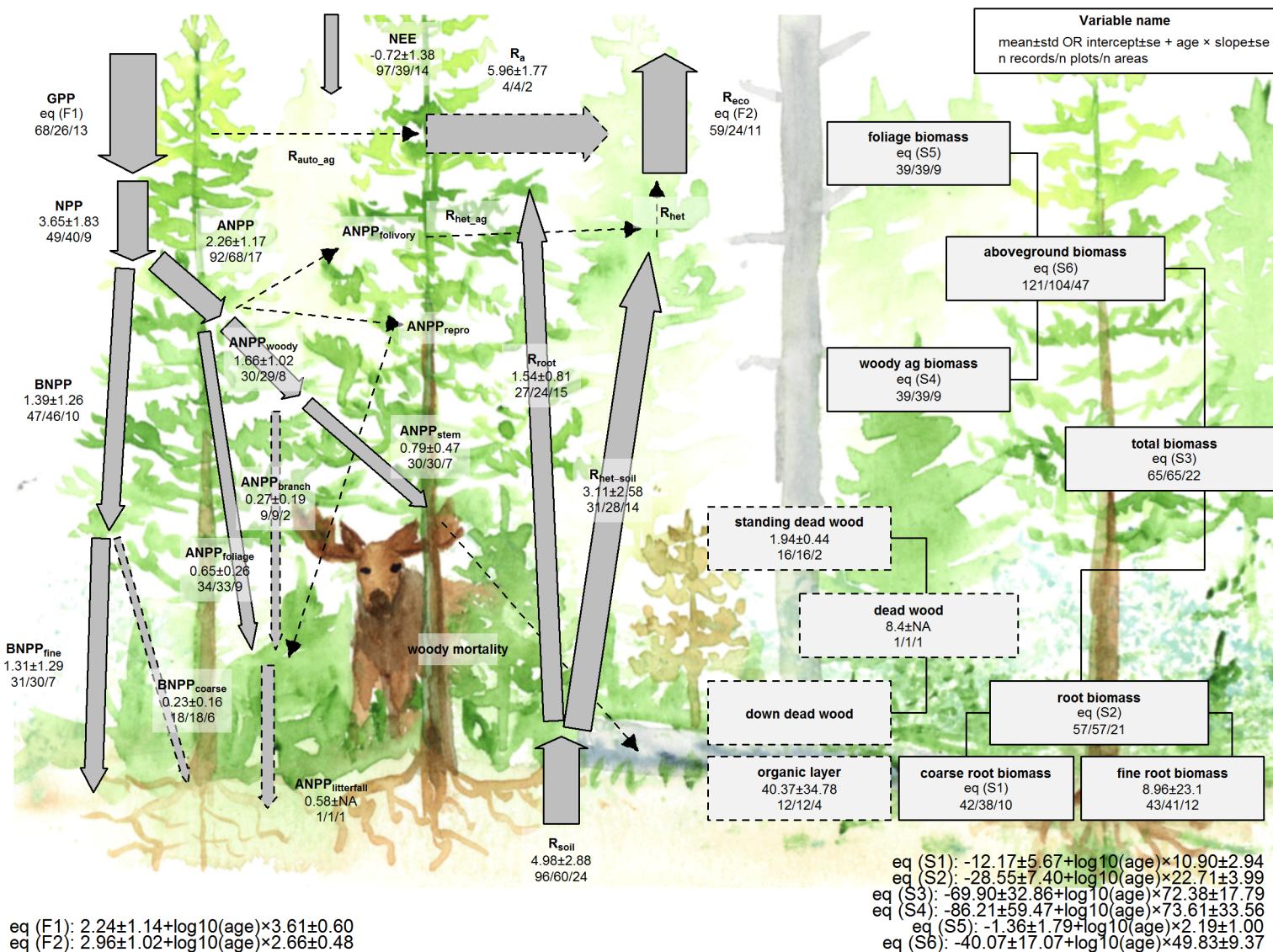


Figure 10 | C cycle diagram for young boreal conifer forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. When age 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.

225 **Discussion**

226 ForC v.XX yielded a fairly comprehensive picture of C cycling in the world's major forest biomes. Carbon
227 cycling rates generally increased from boreal to tropical regions and with stand age. Specifically, the major C
228 fluxes were highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and lowest in
229 boreal forests – a pattern that generally held for regrowth as well as mature forests (Figs. 5-6). In contrast
230 to C fluxes, there was little directional variation in mature forest C stocks across biomes (Figs. 1-4, 6). The
231 majority of flux variables, together with most live biomass pools, increased significantly with stand age (Figs.
232 5-10). Together, these results indicate that, moving from cold to tropical climates and from young to old
233 stands, there is a general acceleration of C cycling, whereas C stocks of mature forests are influenced by a
234 different set of drivers.

235 *C variable coverage and budget closure*

236 Coverage:

- 237 • We have fairly good coverage of most major variables
- 238 • (note how this improves upon previous data compilations/ for which variables does ForC make the
239 greatest difference (e.g., not AGB or NEP/GPP/Reco, but by far the latest data compilation for dead
240 wood, [variables])
- 241 • Noteable holes include: fluxes: R_auto_ag, woody mortality, folivory/ herbivory and respiration of
242 herbivores (and therefore total R_het), ANPP_repro; also fluxes in tropical regrowth forests
- 243 • for the C stocks considered here, the most poorly covered is dead wood (none in E hemisphere!),
244 despite a focused effort on this variable that has resulted in ForC being by far the largest collection of
245 these data.
- 246 • all variables poorly covered in Africa

247 Thus, overall, we're lacking coverage of fluxes to herbivores and higher consumers, along with the woody
248 mortality and dead wood.

249 Closure:

- 250 • C cycle closure is fairly good.
- 251 • However, SD's are often large, reflective of significant within-biome variation. This makes the standard
252 for closure relatively loose.
- 253 • Lack of closure, in the few instances where it occurs, is probably more reflective of differences in the
254 representation of forest types (e.g., disproportionate representation of US Pacific NW for aboveground
255 woody biomass relative to AGB; Fig. 3) than of methodological accuracy.

256 Thus, overall, a high degree of closure implies that ForC gives a consistent picture of C cycling within biomes.
257 While these means are unlikely to be accurate representations of C cycling within any particular forest, they
258 provide a useful baseline for comparison.

259 *C cycling across biomes*

260 Banbury Morgan *et al* (n.d.)

261 *Age trends in C cycling*

262 A relative dearth of data on C cycling in secondary forests, particularly in the tropics (Anderson-Teixeira et

263 al 2016), is problematic in that almost 2/3 of the world's forests were secondary as of 2010 (FAO 2010),
264 implying an under-filled need to characterize age-related trends in forest C cycling.

265 *Relevance for climate change modeling and mitigation*

266 Importance of forest C in climate change modeling and mitigation...

267 For C can help models by serving as benchmark data.

- 268 • (cite Dietze paper that we reviewed)

269 For some variables, such as AGB of mature forests, we sources other than ForC can provide the best
270 available data. However, for others, ForC provides by far the most comprehensive source:

- 271 • agb age trends (GROA; Cook-Patton et al. 2020)
272 • dead wood (cite need for this)
273 • fluxes

274 **Acknowledgements**

275 All researchers whose data is included in ForC and this analysis. Thanks to Norbert Kunert and [Helene's
276 intern] for helpful input at an earlier phase. A Smithsonian Scholarly Studies grant to KAT and HML.

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