

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 **Summary**

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

31 *Methods/Design.* Here, we draw from the Global Forest C Database, ForC, to provide a macroscopic
32 overview of C cycling in the world's forests, giving special attention to stand age-related variation.
33 Specifically, we draw upon 9793 records from NA geographic locations representing 34 C cycle variables to
34 characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate
35 broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years)
36 forests. For regrowth forests, we quantify age trends for all variables.

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

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

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

47 **Background**

48 Forest ecosystems will play a critical role in shaping the course of climate change (IPCC1.5) through their
49 influence on atmospheric carbon dioxide (CO_2). Their annual gross CO_2 sequestration (gross primary
50 productivity, GPP) is estimated at $>69 \text{ Gt C yr}^{-1}$ (???), or >7 times average annual fossil fuel emissions
51 from 2007-2016 ($9.4 \pm 0.5 \text{ Gt C yr}^{-1}$; Le Quéré et al 2017) (**update**). While most of this enormous C flux is
52 counterbalanced by CO_2 releases to the atmosphere through ecosystem respiration (R_{eco}) or fire, a small
53 portion was retained in ecosystems over recent decades. The resulting CO_2 sink averaged $3.0 \pm 0.8 \text{ Gt C}$
54 yr^{-1} from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update**,
55 **give range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial
56 biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Globally, net
57 deforestation (*i.e.*, gross deforestation - regrowth) has been a source of CO_2 emissions, estimated at $\sim 1.1 \text{ Gt}$
58 C yr^{-1} from YEAR-YEAR (Pan et al 2011), reducing the net forest sink to $\sim 1.2\text{--}1.7 \text{ Gt C yr}^{-1}$ across Earth's
59 forests (Le Quéré et al 2017, Schimel et al 2015) (**update, give range**). The future of this sink is
60 dependent both upon forest responses to a broad suite of global change drivers and to future land use
61 decisions, and will strongly influence the course of climate change. Regrowth forests in particular will play an
62 important role (Pugh et al 2019), as these represent a large (~#%) and growing proportion of Earth's forests.
63 Understanding, modeling, and managing forest-atmosphere CO_2 exchange is thereby central to efforts to
64 mitigate climate change [Grassi et al (2017); Griscom et al (2017); Cavaleri et al 2015].

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

To address the need for global-scale analyses of forest C cycling, we recently developed an open-access Global Forest Carbon database, ForC (Anderson-Teixeira *et al* (2016), Anderson-Teixeira *et al* (2018)). ForC contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables) based on ground-based measurements, along with associated data required for interpretation (e.g., stand history, measurement methods). These data have been amalgamated from original peer-reviewed publications, either directly or via intermediary data compilations. Since its most recent publication (Anderson-Teixeira *et al* 2018), ForC has been integrated with two large databases: the Global Soil Respiration Database (SRDB; Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020), both of which have also synthesized published forest C data. Following these additions, ForC currently contains 47846 records from 10671 plots and 1533 distinct geographic areas representing all forested biogeographic and climate zones.

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

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

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

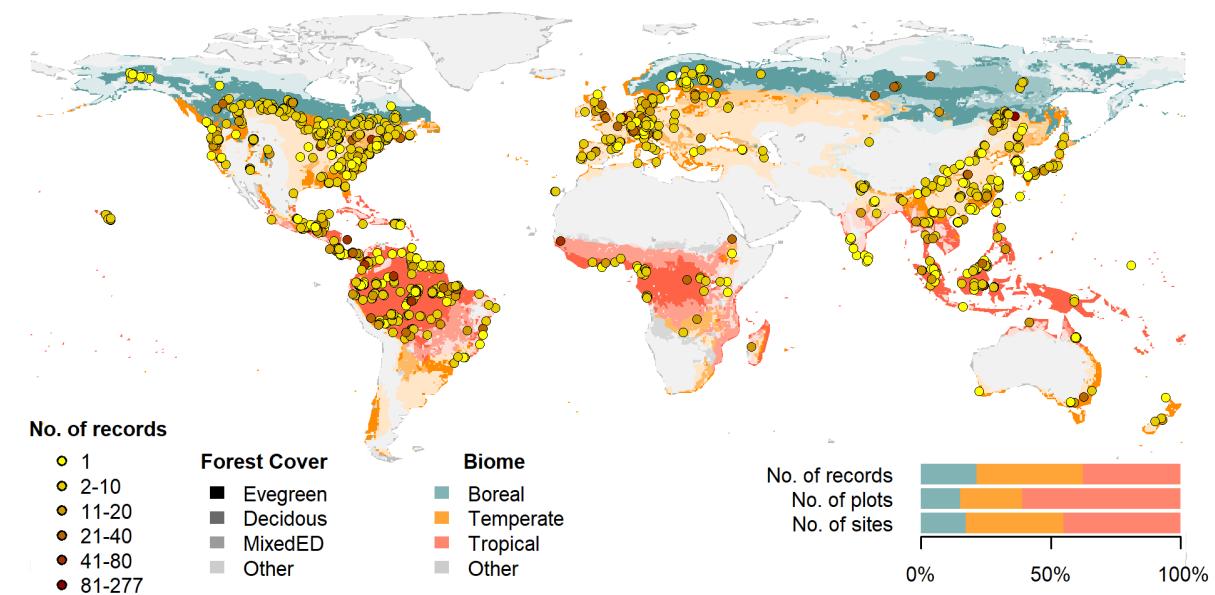


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

105 Methods/ Design

106 This review synthesizes data from the ForC database (Fig. 1; <https://github.com/forc-db/ForC>;

107 Anderson-Teixeira *et al* 2016, pp @anderson-teixeira_forc_2018). ForC amalgamates numerous intermediary

108 data sets (*e.g.*, REFS) and original studies. Original publications were referenced to check values and obtain

109 information not contained in intermediary data sets, although this process has not been completed for all

110 records. The database was developed with goals of understanding how C cycling in forests varies across broad

111 geographic scales and as a function of stand age. As such, there has been a focus on incorporating data from

112 regrowth forests (*e.g.*, Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age

113 data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention was given to

114 developing the database for tropical forests (Anderson-Teixeira *et al* 2016), yet these represented only

115 approximately one-third of records in ForC v.2.0 (Anderson-Teixeira *et al* 2018). Since publication of ForC

116 v.2.0, we added the following data to ForC: the Global Database of Soil Respiration Database (SRDB v.##;

117 Bond-Lamberty and Thomson 2010), the Global Reforestation Opportunity Assessment database (GROA

118 v1.0; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020), and data from several publications [*e.g.*, Taylor

119 *et al* (2017), Lutz *et al* (2018), Johnson *et al* (2018); detailed list at https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv]. We note that there

120 remains a significant amount of relevant data that is not yet included in ForC, particularly biomass data

121 from national forest inventories (*e.g.*; REFS). The database version used for this analysis has been tagged as

122 a new release on Github (XX) and assigned a DOI through Zenodo (DOI: TBD).

123 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 S1*, resulting in a total of 32921 records (68.8% size of total database). Records were filtered to remove plots that had undergone significant anthropogenic management or major disturbance since the most recent stand initiation event. Specifically, we removed all plots flagged as managed in ForC-simplified (18.7%). 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 (5.6%) included stands that had undergone anthropogenic thinning or partial harvest unless this was very minor. We retained sites that were grazed or had undergone low severity natural disturbances (<10% mortality) including droughts, major storms, fires, and floods. We removed all plots for which no stand history information had been retrieved (7.2%). In total, this resulted in NA records (NA% of the records in the database) being eligible for inclusion in the analysis.

We selected 23 annual flux and 11 C stock variables for inclusion in the analysis, although two flux variables (R_{het-ag} and R_{het}) were included for conceptual completeness but had no records in ForC (Table 1). Records for these variables represented NA% of the total records eligible for inclusion. For this analysis, we combined some of ForC’s specific variables (*e.g.*, multiple variables for net primary productivity including various components) into more broadly defined variables (Tables 1, S#(variable mapping)). Throughout ForC, for all measurements drawing from tree census data (*e.g.*, biomass, productivity), the minimum stem diameter sampled was $\leq 10\text{cm}$. All records were measured directly or derived from field measurements (as opposed to modeled).

For this analysis, we grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones (Fig. 1) were defined based on site geographic coordinates according to Köppen-Geiger zones (Rubel and Kottek 2010). Tropical climates were defined to include all equatorial (A) zones, temperate climates were defined to include all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and boreal climates were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Any forests in dry (B) and polar (E) Köppen-Geiger zones were excluded from the analysis. Leaf type (broadleaf / needleleaf) was defined based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYNMAP; ???). Forests were classified as “young” (< 100 years) or “mature” (≥ 100 years or classified as “mature”, “old growth”, “intact”, or “undisturbed” in original publication). Assigning stands to these groupings required the exclusion of records for which ForC lacked records of stand age (n=NA% of total database), or geographic coordinates (n=NA% of total database). In total, our analysis retained NA of the focal variable records for forests of known age. The most well-represented forest types excluded were boreal broadleaf (NA records) and boreal and temperate mixed broadleaf-needleleaf (NA and NA records, respectively).

Data were analyzed to produce basic summaries of C cycle patterns across biomes and stand ages. **(this part & following are confusing/ incomplete–needs work)** For mature forests, to obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot. Values were then averaged across plots clustered within 25 km of one another (*sensu* Anderson-Teixeira *et al* 2018), weighting by area sampled if available for all records. This step was taken to avoid pseudo-replication and to combine

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)	425	199	91	n.s.	+
<i>GPP</i>	gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEE$)	410	177	92	$TrB > TeB \geq TeN > BoN$	+
<i>NPP</i>	net primary production ($ANPP + BNPP$)	340	208	76	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP</i>	aboveground <i>NPP</i>	615	429	136	$TrB > TeB \geq TeN \geq BoN$	++; xB
<i>ANPP_{woody}</i>	woody production ($ANPP_{stem} + ANPP_{branch}$)	126	114	37	$TrB \geq TeN \geq TeB \geq BoN$	++; xB
<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	242	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	174	69	$TrB \geq TeB \geq TeN \geq BoN$	+
<i>R_{eco}</i>	ecosystem respiration ($R_{auto} + R_{het}$)	302	139	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	$TrB > TeN \geq BoN \geq TeB$	n.s.
<i>R_{root}</i>	root respiration	266	212	102	$TrB > TeB \geq TeN \geq BoN$	++; xB
<i>R_{soil}</i>	soil respiration ($R_{het-soil} + R_{root}$)	1106	717	242	$TrB > TeB \geq TeN > BoN$	++; xB
<i>R_{het-soil}</i>	soil heterotrophic respiration	323	261	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 ($B_{ag} + B_{root}$)	309	262	87	$TeN \geq TrB \geq TeB \geq BoN$	++; xB
<i>B_{ag}</i>	aboveground live biomass ($B_{ag-wood} + B_{foliage}$)	1563	1145	335	$TeN \geq TrB \geq TeB > BoN$	++; xB
<i>B_{ag-wood}</i>	woody component of aboveground biomass	222	209	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 ($B_{root-coarse} + B_{root-fine}$)	390	366	121	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	397	324	114	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	53	53	21	n.s.	n.s.
<i>DW_{down}</i>	fallen dead wood, including coarse and sometimes fine woody debris	116	109	19	n.s.	+
<i>OL</i>	organic layer / litter/ forest floor	301	266	80	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

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. There were enough data to run this analysis for all focal variables but DW_{down} .

For young (<100yrs) forest types, we employed a mixed effects model with biome and $\log_{10}[\text{stand.age}]$ 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

NOTE TO COAUTHORS: THIS SECTION HAS A TON OF FIGURES, BUT VERY LITTLE TEXT. IS THERE ANYTHING THAT SHOULD BE ADDED?

Data Coverage

Of the 47846 in ForC v.#, 9793 met the criteria for inclusion in this study (Fig. 1). These records were distributed across NA plots in NA distinct geographic areas. Of the 23 flux and 11 stock variables mapped in these diagrams, ForC contained mature forest estimates from ≥ 7 distinct geographic areas for NA fluxes and NA stocks in tropical broadleaf forests, NA fluxes and NA stocks in temperate broadleaf forests, NA fluxes and NA stocks in temperate conifer forests, and NA fluxes and NA stocks in boreal forests. For regrowth forests (<100 yrs), ForC contained estimates from ≥ 7 distinct geographic areas for NA fluxes and NA stocks in tropical broadleaf forests, NA fluxes and NA stocks in temperate broadleaf forests, NA fluxes and NA stocks in temperate conifer forests, and NA fluxes and NA stocks in boreal forests.

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 Figures 2-5 (and available in tabular format in the ForC release accompanying this publication).

For variables with records from ≥ 7 distinct geographic areas, these ensemble C budgets were generally consistent. That is, component fluxes and stocks summed to within one standard deviation of more inclusive fluxes in all but two instances, both for living C stocks in temperate conifer forests (Fig. 5). **(check this with final results:)**

https://github.com/forc-db/ForC/blob/master/numbers_and_facts/C_cycle_closure.csv

Within this biome, $B_{ag} < B_{ag-wood} + B_{foliage}$ and $B_{root} < B_{root-coarse} + B_{root-fine}$ because $B_{ag-wood}$ and

²⁰⁵ $B_{root-coarse}$ were very high, with strongly disproportionate numbers of records from the high-biomass forests
²⁰⁶ of the US Pacific Northwest (Figs. S18, S21).

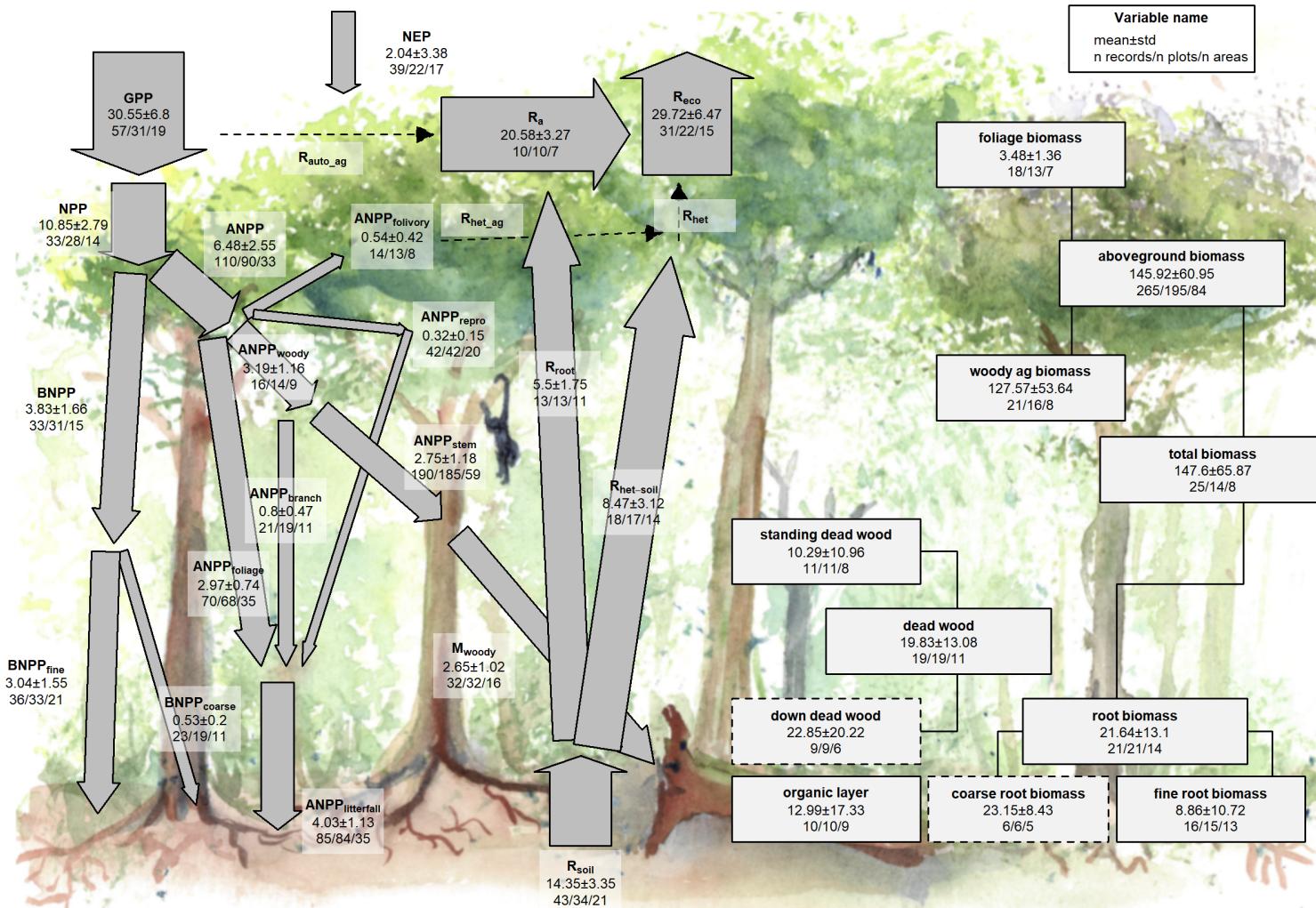


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables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

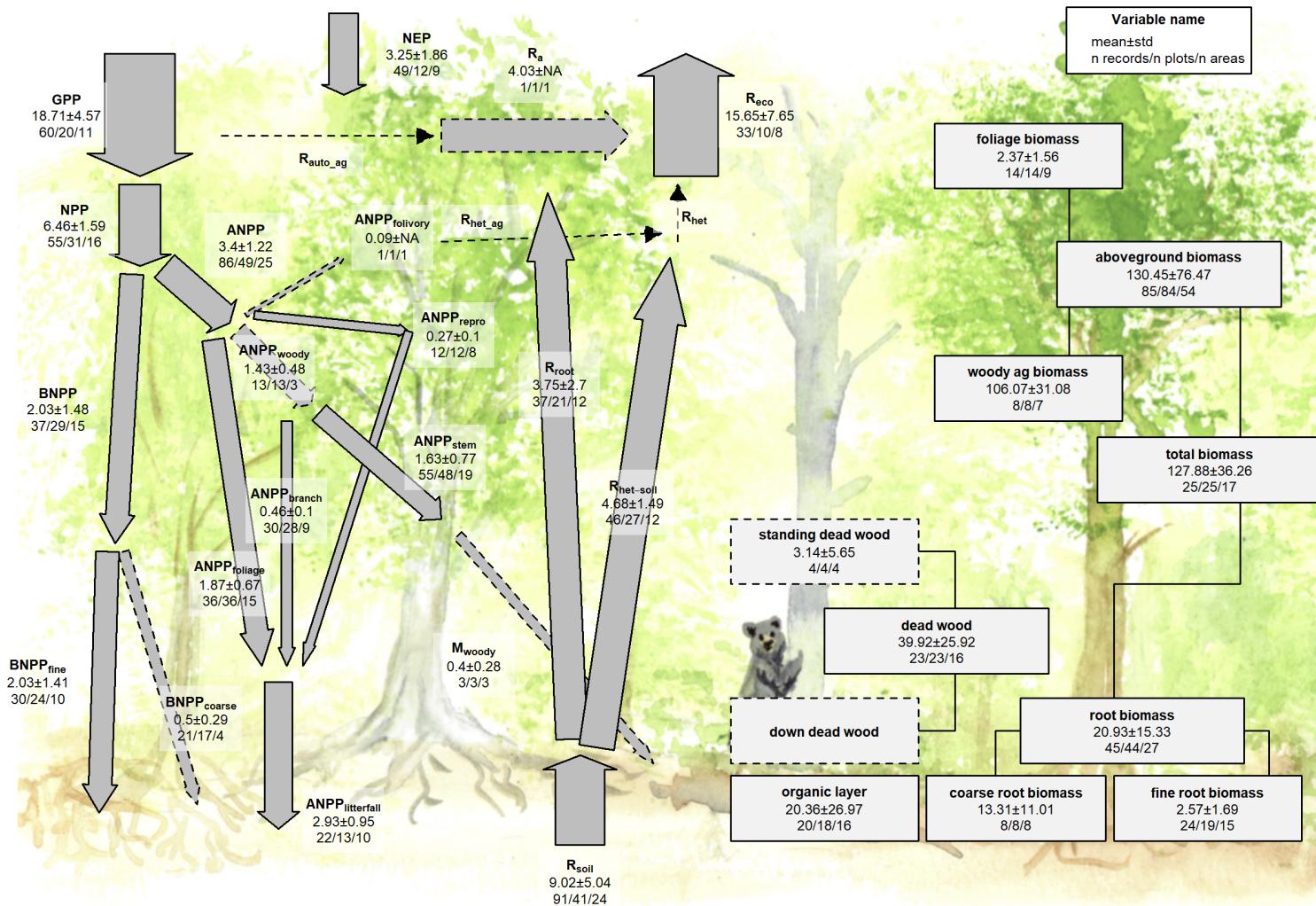


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed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

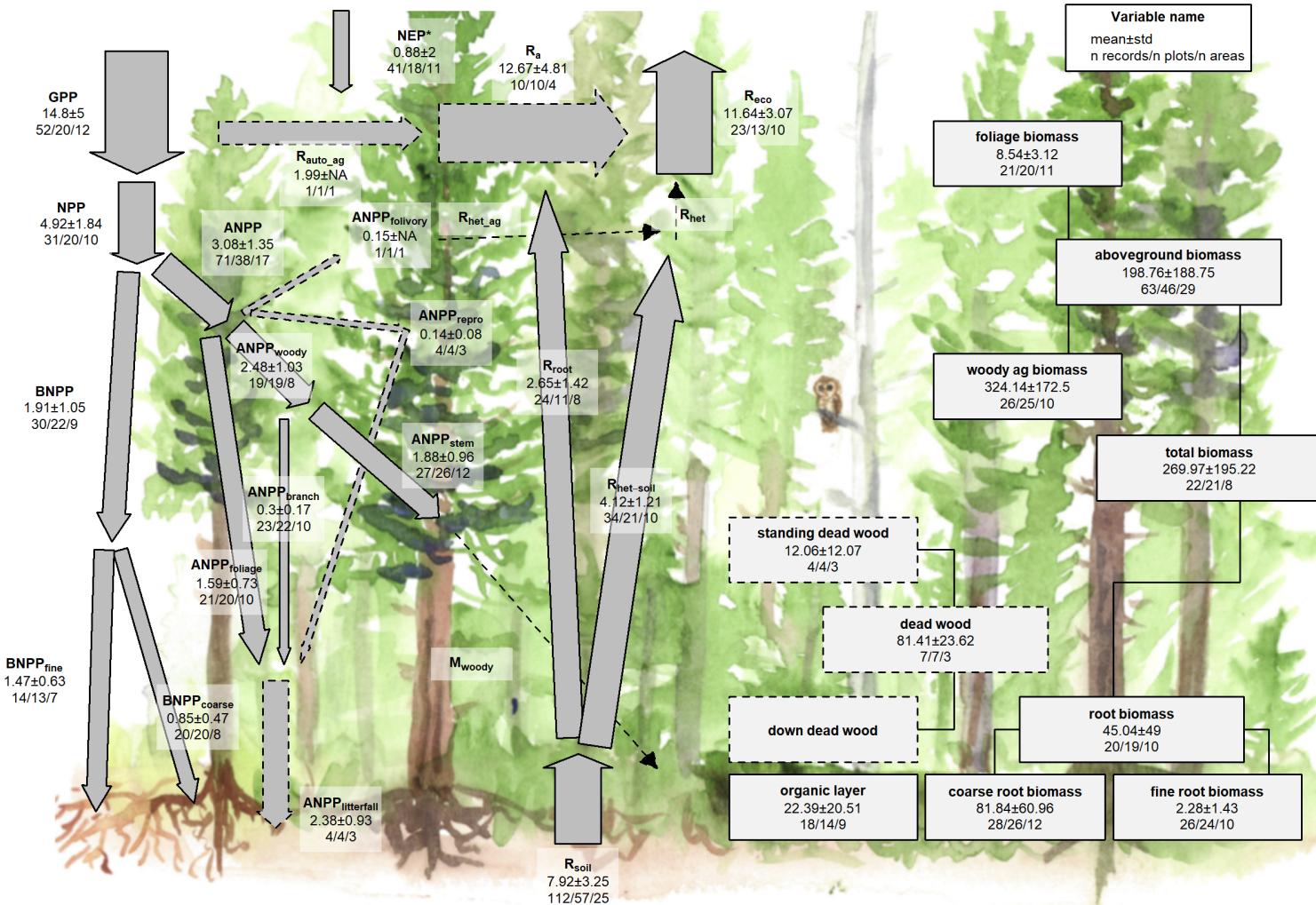


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables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

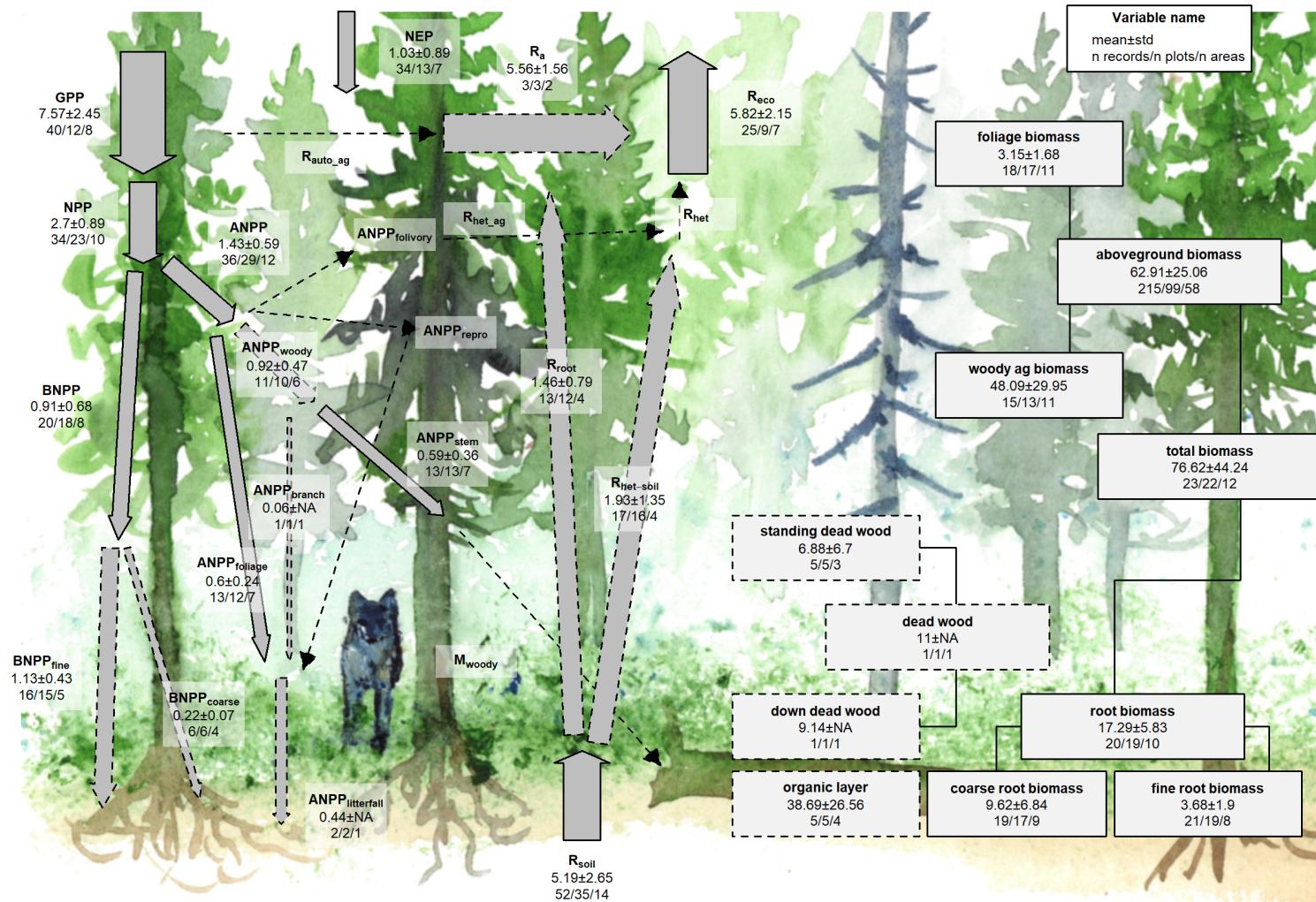


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are mean \pm std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape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

207 (The following covers only the variables with age trends figures; there maybe a few more
208 without much age data) With only ## exceptions, C fluxes were highest in tropical forests, intermediate
209 in temperate (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 6, S1-S15). In this
210 majority of cases, differences between tropical and boreal forests were always significant, with temperate
211 forests intermediate and significantly different from one or both. Fluxes tended to be greater in temperate
212 broadleaf than conifer forests, but the difference was never significant. This pattern held for the following
213 variables: *GPP*, *NPP*, *ANPP*, *ANPP_{woody}*, *ANPP_{stem}*, *ANPP_{foliage}*, *ANPP_{litterfall}*, *BNPP*,
214 *BNPP_{fine}*, *R_{eco}*, *R_{root}*, *R_{soil}*, and *R_{het-soil}*.

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

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

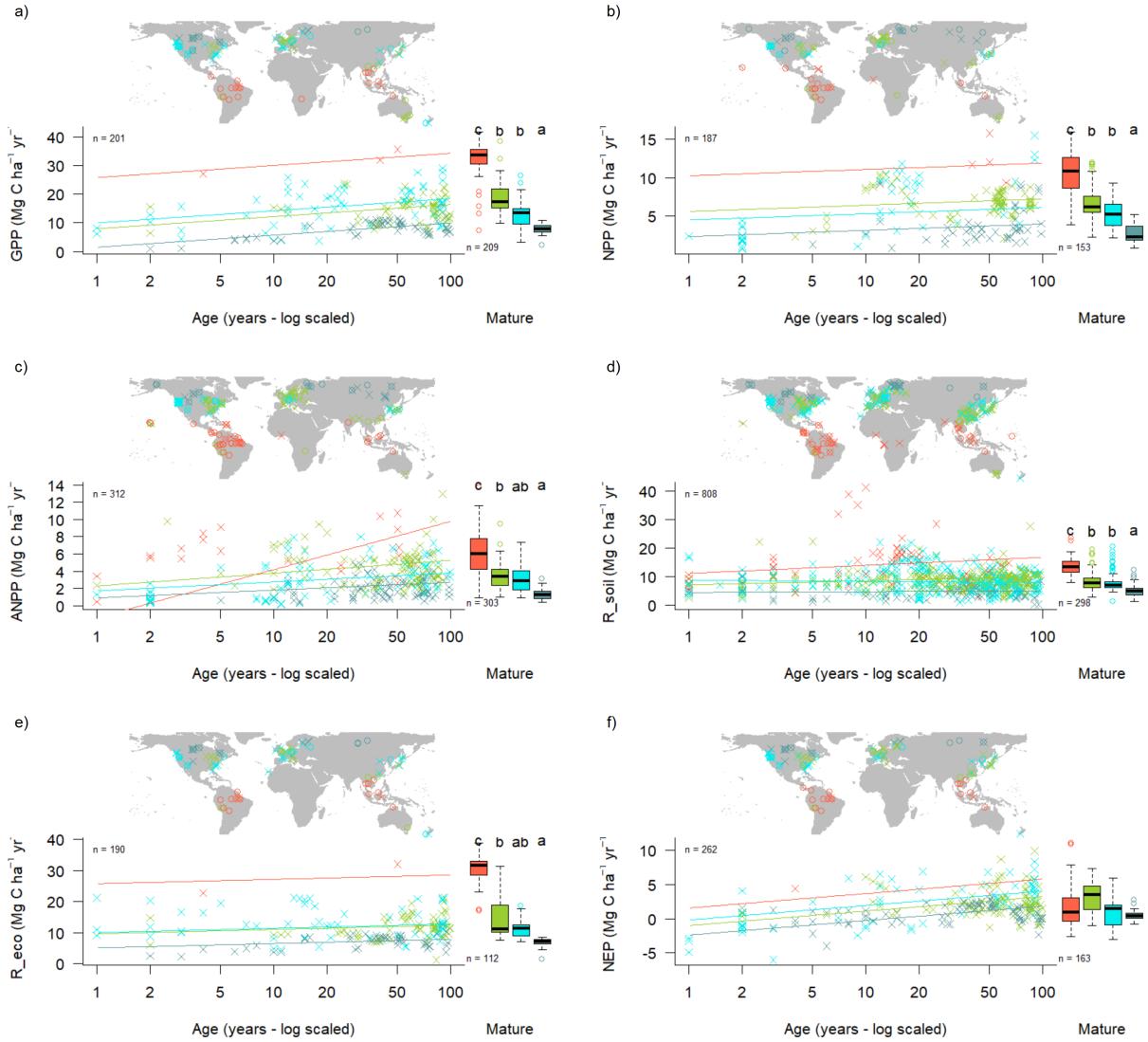


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized 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).

222 There were fewer distinct trends in C stocks across biomes (Figs. 7, S16-S26). Specifically, there were
 223 significant differences for only ## of ## variables: *LIST*. In all of these cases, temperate conifer forests
 224 were in the highest significance grouping, and boreal forests in the lowest. Tropical and temperate broadleaf
 225 forests fell in between—most commonly being significantly different from temperate conifer but not boreal
 226 forests. Once again, the high values for the temperate conifer biome were driven by the very high-biomass
 227 forests of the US Pacific Northwest, which are disproportionately represented in the current version of ForC.
 228 Thus, biome differences should be interpreted more as driven more by geographic distribution of sampling
 229 than by true differences.)*

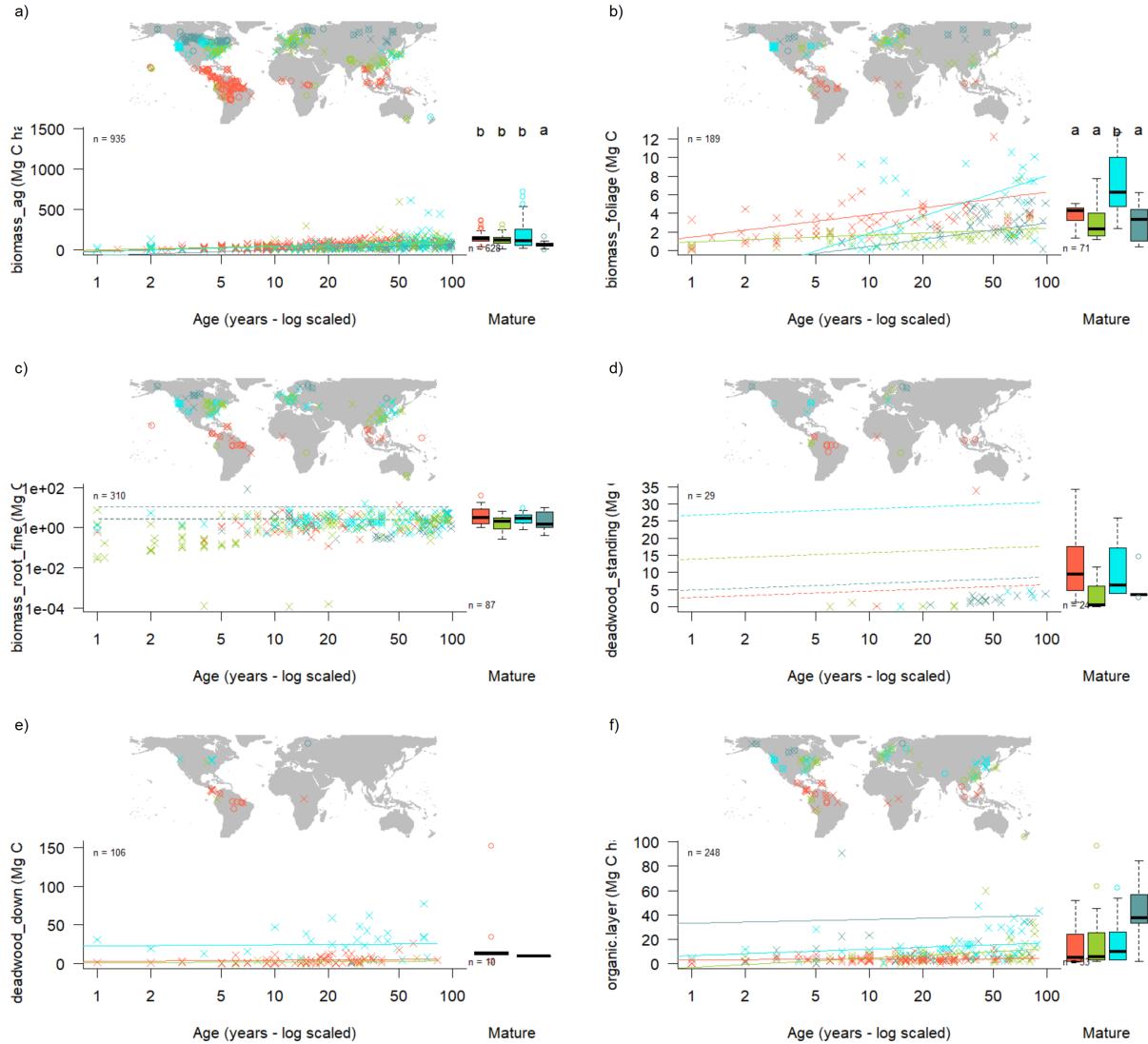


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of age and biome. Solid lines indicate significant effect of age, non-parallel lines indicate a significant age \times 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).

230 C cycling in young forests

- 231 Average C cycles for forests <100 years old are presented in Figures 8-11.
 232 Both C stocks and fluxes commonly displayed significant trends with stand age for within-biome analyses
 233 (Table 1, Figs. 6-11, S1-S26; detailed below).
 234 ForC contained 14 flux variables with sufficient data for cross-biome analyses of age trends in regrowth
 235 forests (see Methods) (Fig. 6-7 and **S#- SI figures including plots for all variables**). Of these, 9
 236 increased significantly with $\log_{10}[\text{stand.age}]$: GPP , NPP , $ANPP$, $ANPP_{\text{foliage}}$, $ANPP_{\text{woody}}$,
 237 $ANPP_{\text{woody-stem}}$, $BNPP$, $BNPP_{\text{root-fine}}$, R_{eco} , and net C sequestration (NEP). The remaining

238 five— $ANPP_{woody-branch}$, $BNPP_{root-coarse}$, $R_{soil-het}$, and $R_{soil-het}$ —displayed no significant relationship to
239 stand age, although all displayed a positive trend.

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

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

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

246 There were only ## flux variables with sufficient data to test for biome x age interactions: $ANPP$,
247 $ANPP_{woody}$, $ANPP_{stem}$, $ANPP_{litterfall}$, and $BNPP$. (**more could be added if age trends become**
248 **significant after outliers are resolved**) For three of these ($ANPP$, $ANPP_{litterfall}$, $BNPP$), the
249 increase in C flux with age was steepest increase in tropical forests, followed by temperate and then boreal
250 forests (Figs S#). Similarly, $ANPP_{woody}$ displayed a steeper increase with age in temperate than boreal
251 boreal forests (no tropical data for this variable). In contrast, for $ANPP_{stem}$, tropical and temperate
252 broadleaf forests had the highest flux rates at young ages, but were surpassed by temperate conifer forests
253 between ages 20 and 50 (Fig. S6).

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

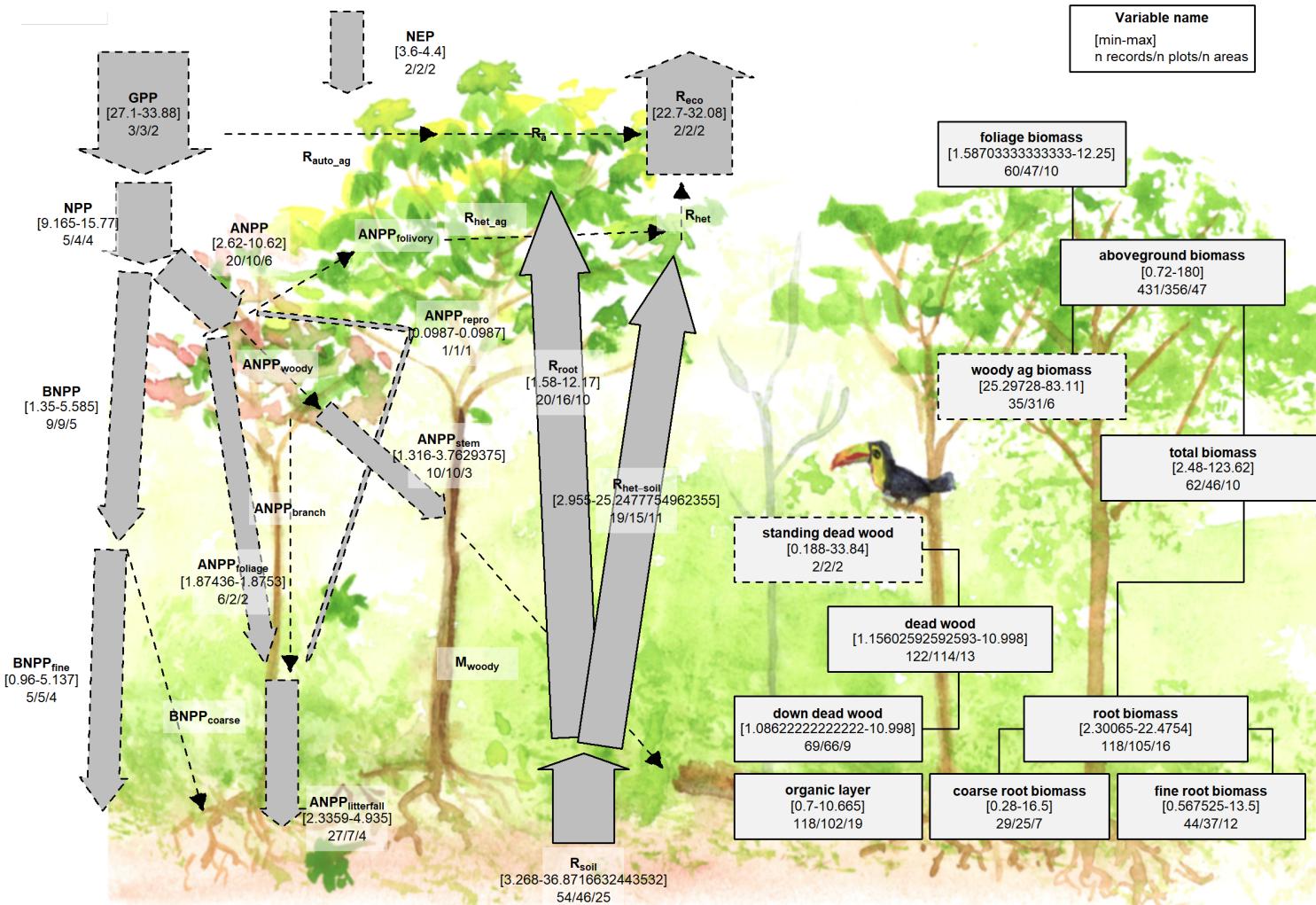


Figure 8 | C cycle diagram for young tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

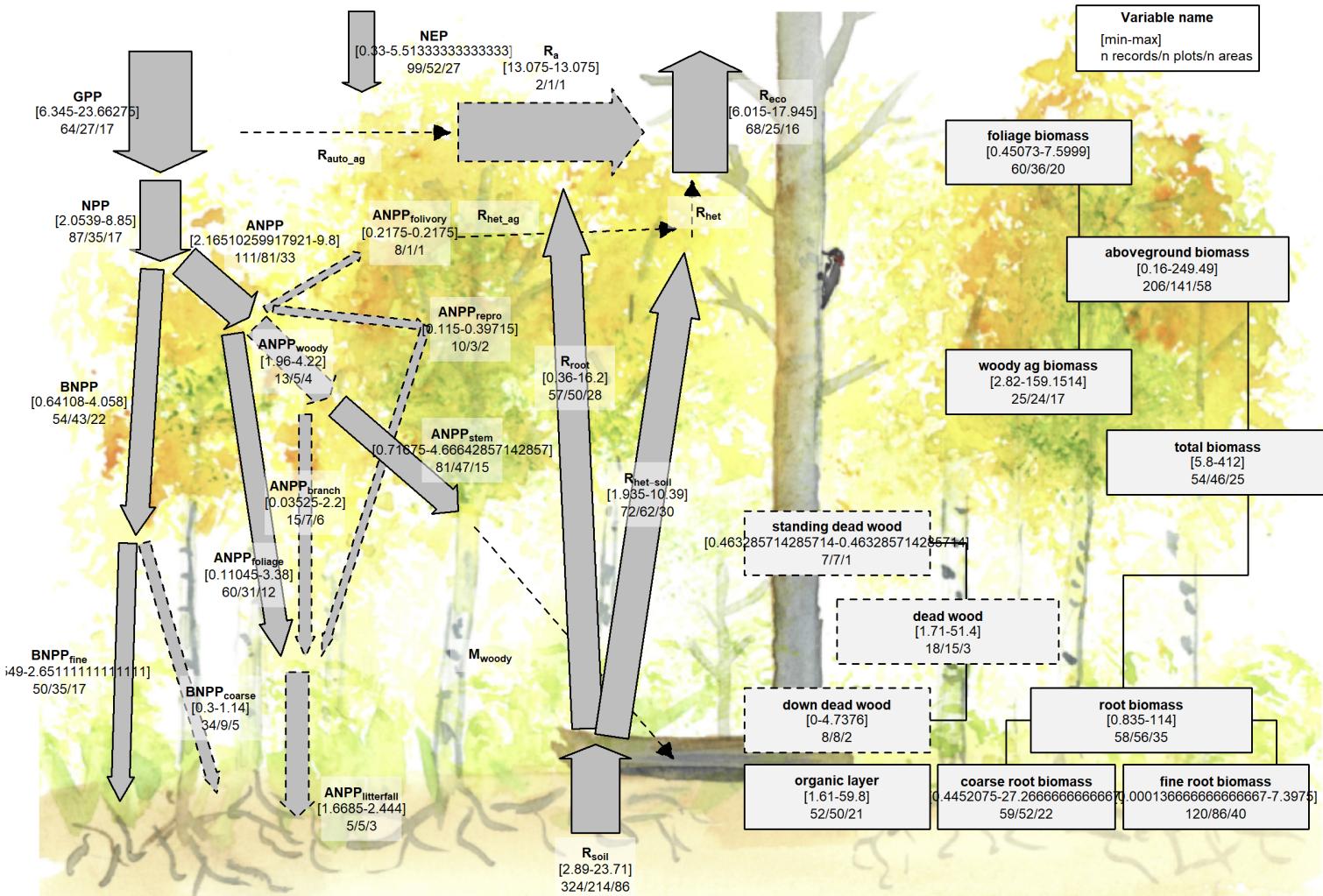


Figure 9 | C cycle diagram for young temperate broadleaf forests. All units are $Mg\ C\ ha^{-1}\ yr^{-1}$ (fluxes) or $Mg\ C\ ha^{-1}$. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

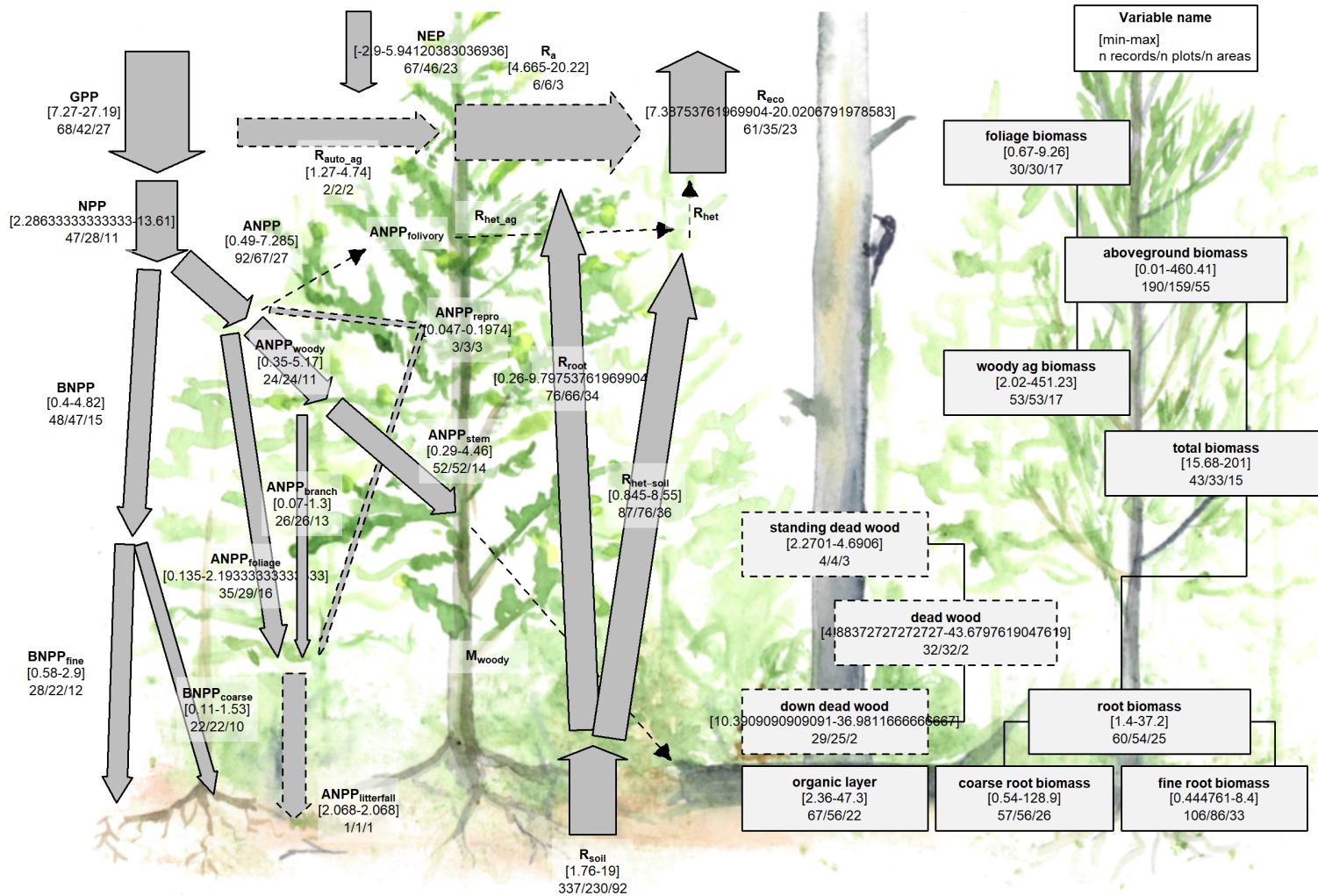


Figure 10 | C cycle diagram for young temperate conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

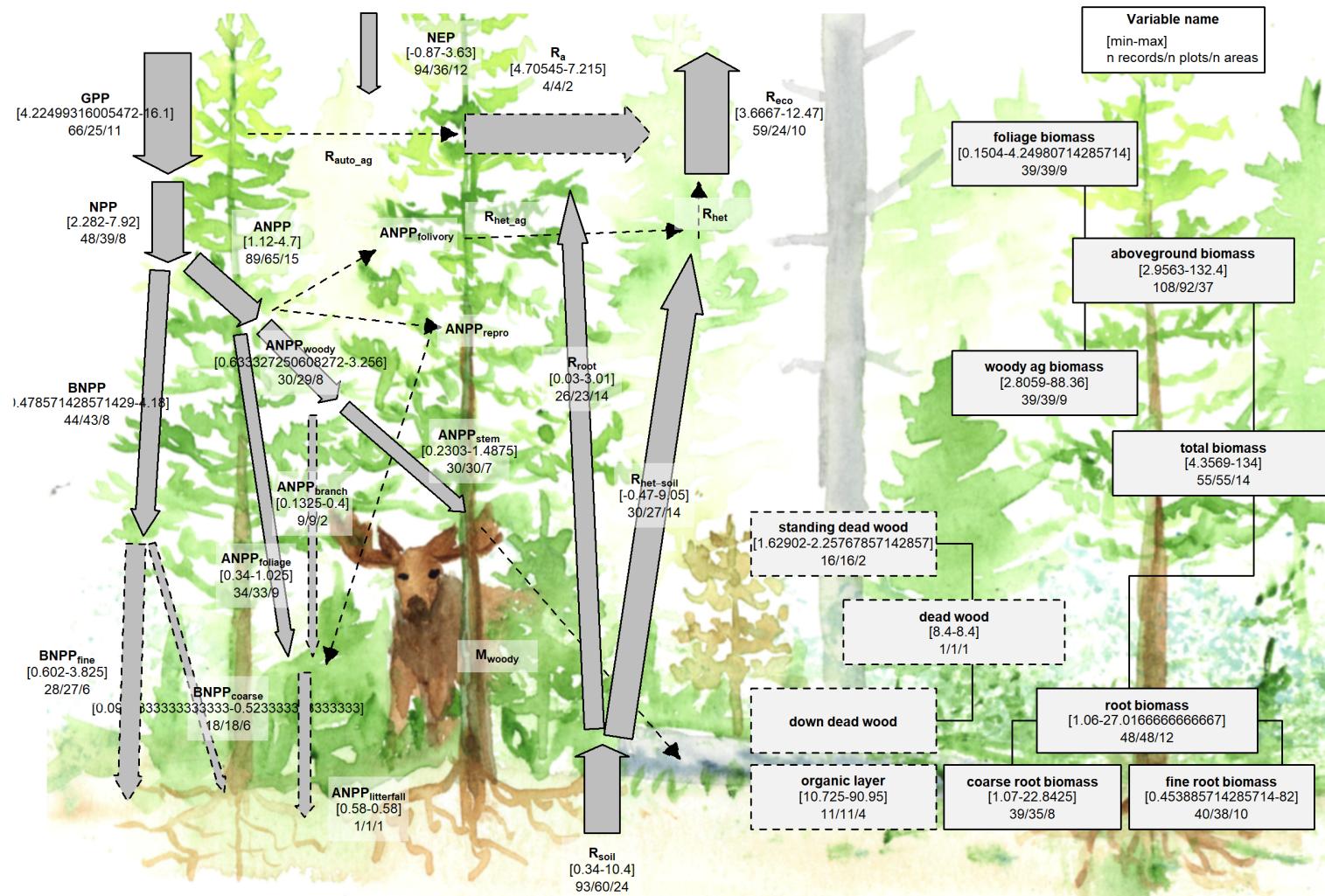


Figure 11 | C cycle diagram for young boreal conifer forests. All units are $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (fluxes) or Mg C ha^{-1} . Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data.

259 **Discussion**

260 ForC v.XX yielded a fairly comprehensive and internally consistent picture of C cycling in the world's major
261 forest biomes. Carbon cycling rates generally increased from boreal to tropical regions and with stand age.
262 Specifically, the major C fluxes were highest in tropical forests, intermediate in temperate (broadleaf or
263 conifer) forests, and lowest in boreal forests – a pattern that generally held for regrowth as well as mature
264 forests (Figs. 6-7). In contrast to C fluxes, there was little directional variation in mature forest C stocks
265 across biomes (Figs. 2-5, 7). The majority of flux variables, together with most live biomass pools, increased
266 significantly with stand age (Figs. 6-11). Together, these results indicate that, moving from cold to tropical
267 climates and from young to old stands, there is a general acceleration of C cycling, whereas C stocks and
268 *NEP* of mature forests are influenced by a different set of drivers.

269 **C variable coverage and budget closure**

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

279 Closure of the C cycle budgets for mature forests (Figs. 2-5) is fairly good. However, SD's are often large,
280 reflective of significant within-biome variation. This makes the standard for closure relatively loose. Lack of
281 closure, in the few instances where it occurs, is probably more reflective of differences in the representation of
282 forest types (e.g., disproportionate representation of US Pacific NW for aboveground woody biomass relative
283 to AGB; Fig. 4) than of methodological accuracy. Thus, overall, a high degree of closure implies that ForC
284 gives a consistent picture of C cycling within biomes. While these means are unlikely to be accurate
285 representations of C cycling within any particular forest, they provide a useful baseline for comparison,
286 always keeping in mind that sample means do not necessarily represent the true mean of the entire biome.

287 **C cycling across biomes**

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

299 accumulation.
300 In contrast to C fluxes and accumulation rates in regrowth forests, stocks...
301 Thus, biome differences should be interpreted more as driven more by geographic distribution of sampling
302 than by true differences.

303 **Age trends in C cycling**

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

305 A relative dearth of data on C cycling in secondary forests, particularly in the tropics (Anderson-Teixeira et
306 al 2016), is problematic in that almost 2/3 of the world's forests were secondary as of 2010 (FAO 2010),
307 implying an under-filled need to characterize age-related trends in forest C cycling.
308 Moreover, as disturbances increase (???, McDowell *et al* 2020), understanding the carbon dynamics of
309 regrowth forests will be increasingly important.
310 It's also important to understand secondary forest C sequestration to reduce uncertainty regarding the
311 potential for carbon uptake by regrowth forests (???, Cook-Patton *et al* 2020).
312 NEP increases with log(age) to 100 -> strongest C sinks are established secondary forests.

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

314 The future of forest C cycling will shape trends in atmospheric CO₂ and the course of climate change. For a
315 human society seeking to understand and mitigate climate change, the data contained in ForC and
316 summarized here can help to meet two major challenges.
317 First, improved representation of forest C cycling in models is essential to improving predictions of the future
318 course of climate change. To ensure that models are giving the right answers for the right reasons, it is
319 important benchmark against multiple components of the C cycle. By making tens of thousands of records
320 readily available in standardized format, ForC makes it feasible for the modeling community to draw upon
321 these data to benchmark models. Integration of ForC with models is a goal (Fer *et al.*, in revision). On a
322 more cursory level, the values summarized here can serve as a sanity check for modelers to determine whether
323 model predictions for multiple C cycle variables are reasonable—i.e., within the range of previous observations.
324 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change
325 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not
326 feasible for the individuals and organizations designing such efforts to sort through literature, often behind
327 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline
328 through which information can flow efficiently from forest researchers to decision-makers working to
329 implement forest conservation strategies at global, national, or landscape scales. This is already happening!
330 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;
331 Requena Suarez *et al* (2019); Rozendaal et al in prep], mapping C accumulation potential from natural forest
332 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*
333 2020).
334 There remain numerous data needs for improved accounting of forest carbon stocks and fluxes in GHG
335 accounting. AGB is the largest stock, and most of the emphasis is on this variable. Remote sensing, with

336 calibration based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019), is the
337 best approach for mapping forest carbon (REFS). However, it is limited in that it is not associated with
338 stand age and disturbance history, except in recent decades when satellite data can be used to detect forest
339 loss, gain, and some of their dominant drivers (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). ForC
340 is therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020).

341 *remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP*
342 (*Bagdley et al. 2019, (Li and Xiao 2019)*), *aboveground biomass (B_{ag}) (REFS)*, *woody mortality (i.e., B_{ag}*
343 *losses to mortality M_{woody}) (Clark et al 2004, Leitold et al 2018)*, and to some extent net ecosystem
344 *exchange (NEP) (REFS)*,

345 Other variables cannot be remotely sensed. In terms of C stocks, there is a paucity of data on dead wood
346 and organic layer (Pan *et al.* ?). These can be significant. (*give some stats/ cite figures*). ForC does not
347 include soil carbon, which is covered by other efforts (REFS). For fluxes, Fluxnet is the keeper of the best
348 data on NEE, GPP, Reco (REFS), and SRDB remains the authority on soil respiration (REFS). ForC
349 includes recent data from both, but is not continuously integrated. For C is the best source for most of the
350 subsidiary fluxes: NPP, woody mortality...

351 We recommend that use of ForC data go to the original database, as opposed to using “off-the-shelf” values
352 from this publication. This is because (1) ForC is constantly being updated, (2) analyses should be designed
353 to match the application, (3) age equations presented here all fit a single functional form that is not
354 necessarily the best possible for all the variables.

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

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