

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

³ **Authors:**

⁴ Kristina J. Anderson-Teixeira^{1,2*}

⁵ Valentine Herrmann¹

⁶ Becky Banbury Morgan³

⁷ Ben Bond-Lamberty⁴

⁸ Susan C. Cook-Patton⁵

⁹ Abigail E. Ferson^{1,6}

¹⁰ Jennifer C. McGarvey¹

¹¹ Helene C. Muller-Landau¹

¹² Maria M. H. Wang^{1,7}

¹³ **Author Affiliations:**

¹⁴ 1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological Park,
¹⁵ Front Royal, VA 22630, USA

¹⁶ 2. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research
¹⁷ Institute; Panama, Republic of Panama

¹⁸ 3. School of Geography, University of Leeds, Leeds, UK

¹⁹ 4. Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park
²⁰ Maryland 20740, USA

²¹ 5. The Nature Conservancy; Arlington VA 22203, USA

²² 6. College of Natural Resources, University of Idaho; Moscow, Idaho 83843, USA

²³ 7. Grantham Centre for Sustainable Futures and Department of Animal and Plant Sciences, University of
²⁴ Sheffield, Western Bank, Sheffield, South Yorkshire S10 2TN, UK

²⁵ *corresponding author: teixeirak@si.edu; +1 540 635 6546

²⁶ ## [1] 0

²⁷ **NOTES TO COAUTHORS:**

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

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

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

34 Summary

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

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

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

50 Discussion. NEED TO WRITE THIS!!!

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

52 Background

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

54 Forest ecosystems will play a critical role in shaping the course of climate change (IPCC1.5) through their
55 influence on atmospheric carbon dioxide (CO_2). Their annual gross CO_2 sequestration (gross primary
56 productivity, GPP) is estimated at $>69 \text{ Gt C yr}^{-1}$ (???, or >7 times average annual fossil fuel emissions
57 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
58 counterbalanced by CO_2 releases to the atmosphere through ecosystem respiration (R_{eco}) or fire, a small
59 portion has been retained in ecosystems over recent decades. The resulting CO_2 sink averaged $3.0 \pm 0.8 \text{ Gt C}$
60 yr^{-1} from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017) (**update**,
61 **give range**). Moreover, forests contain substantial carbon (C) stocks: an estimated 92% of terrestrial
62 biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Forests are also globally
63 dominant as a source of soil respiration (???). Globally, net deforestation (*i.e.*, gross deforestation -
64 regrowth) has been a source of CO_2 emissions, estimated at $\sim 1.1 \text{ Gt C yr}^{-1}$ from YEAR-YEAR (Pan et al
65 2011), reducing the net forest sink to $\sim 1.2\text{--}1.7 \text{ Gt C yr}^{-1}$ across Earth's forests (Le Quéré et al 2017, Schimel
66 *et al* 2015) (**update, give range**). The future of the current forest C is dependent both upon forest
67 responses to a broad suite of global change drivers and to future land use decisions, and will strongly
68 influence the course of climate change. Regrowing forests in particular will play an important role (Pugh *et*
69 *al* 2019), as these represent a large (~#%) and growing proportion of Earth's forests (McDowell *et al* 2020).
70 Understanding, modeling, and managing forest-atmosphere CO_2 exchange is thus central to efforts to
71 mitigate climate change [Grassi *et al* (2017); Griscom *et al* (2017); **Cavaleri et al 2015**].

72 Despite the centrality of forest C cycling in regulating atmospheric CO_2 , important uncertainties in climate

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

89 To address the need for global-scale analyses of forest C cycling, we recently developed an open-access Global
90 Forest Carbon database, ForC (Anderson-Teixeira *et al* (2016), Anderson-Teixeira *et al* (2018)). ForC
91 contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables) based on
92 ground-based measurements, along with associated data required for interpretation (*e.g.*, stand history,
93 measurement methods). These data have been amalgamated from original peer-reviewed publications, either
94 directly or via intermediary data compilations. Since the its most recent publication (Anderson-Teixeira *et al*
95 2018), ForC has been integrated with two large databases: the Global Soil Respiration Database (SRDB;
96 Bond-Lamberty and Thomson 2010) and the Global Reforestation Opportunity Assessment database
97 (GROA; Cook-Patton *et al* 2020), both of which have also synthesized published forest C data. Following
98 these additions, ForC currently contains 47846 records from 10609 plots and 1532 distinct geographic areas
99 representing all forested biogeographic and climate zones.

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

- 104 1. To what extent can we fully represent, and “close”, C budgets for each of the world’s major forest
105 biomes (*i.e.*, tropical, temperate broadleaf and deciduous, boreal) based on the current ForC data?
 - 106 2. How do C cycling vary across the world’s major forest biomes?
 - 107 3. How does C cycling vary with stand age (in interaction with biome)?
- 108 While components of these questions have been previously addressed (Luyssaert *et al* 2007,
109 Anderson-Teixeira *et al* 2016, Cook-Patton *et al* 2020, Banbury Morgan *et al* n.d.), our analysis represents
110 by far the most comprehensive analysis of C cycling in global forests, and will serve as a foundation for
111 improved understanding of global forest C cycling.

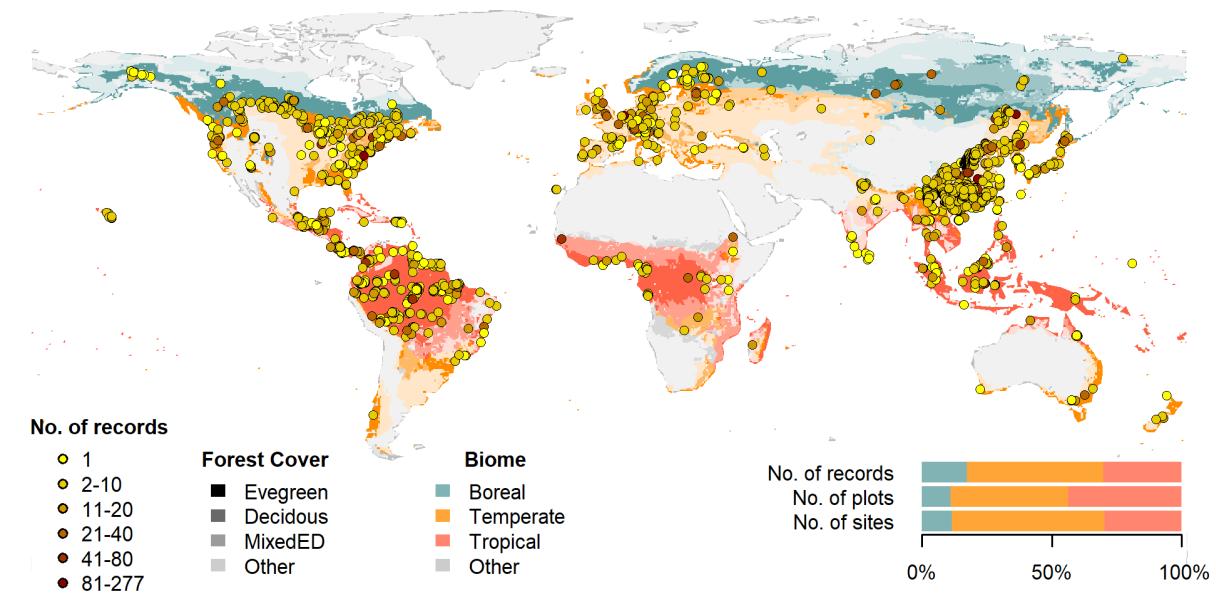


Figure 1 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying map shows coverage of evergreen, deciduous, and mixed forests (from SYNMAP; Jung et al. 2006) and biomes. Distribution of sites, plots, and records among biomes is shown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

112 Methods/ Design

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

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 32862 records (68.7% 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 (18.8%). 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 (5.7%) 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 23528 records (49.2% 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 89.6% 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 threshold for tree census 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 Köttek 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 (4.8% of records in full database), or geographic coordinates (0.4% of sites in full database). We also excluded records of stand age = 0 year (0.8% of records in full database). In total, our analysis retained 66.9 of the focal variable records for forests of known age.

Data were summarized to produce schematics of C cycling across the eight biome - age group combinations identified above. 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 any records from sites with more than one name in ForC.

Table 1. Carbon cycle variables included in this analysis, their sample sizes, and summary of biome differences and age trends.

Variable	Description	N records			biome differences*	age trend†
		records	plots	geographic areas		
Annual fluxes						
<i>NEP</i>	net ecosystem production or net ecosystem exchange (+ indicates C sink)	426	200	91	n.s.	+
<i>GPP</i>	gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEE$)	410	175	92	$TrB > TeB \geq TeN > BoN$	+
<i>NPP</i>	net primary production ($ANPP + BNPP$)	340	205	76	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP</i>	aboveground <i>NPP</i>	615	426	136	$TrB > TeB \geq TeN \geq BoN$	++; xB
<i>ANPP_{woody}</i>	woody production ($ANPP_{stem} + ANPP_{branch}$)	126	114	37	$TrB \geq TeN \geq TeB \geq BoN$	+
<i>ANPP_{stem}</i>	woody stem production	458	411	118	$TrB > TeN \geq TeB > BoN$	-; xB
<i>ANPP_{branch}</i>	branch turnover	125	112	42	$TrB > TeB \geq TeN \geq BoN$	n.s.
<i>ANPP_{foliage}</i>	foliage production, typically estimated as annual leaf litterfall	275	231	89	$TrB > TeB \geq TeN > BoN$	+
<i>ANPP_{litterfall}</i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	147	117	55	$TrB \geq TeB \geq TeN \geq BoN$	+
<i>ANPP_{repro}</i>	production of reproductive structures (flowers, fruits, seeds)	72	65	35	n.s.	n.s.
<i>ANPP_{folivory}</i>	foliar biomass consumed by folivores	24	16	11	n.s.	n.s.
<i>M_{woody}</i>	woody mortality—i.e., B_{ag} of trees that die	35	35	19	$TrB > TeB$	n.s.
<i>BNPP</i>	belowground NPP ($BNPP_{coarse} + BNPP_{fine}$)	275	239	82	$TrB > TeN \geq TeB \geq BoN$	+
<i>BNPP_{coarse}</i>	coarse root production	144	111	36	n.s.	n.s.
<i>BNPP_{fine}</i>	fine root production	207	171	69	n.s.	+
<i>R_{eco}</i>	ecosystem respiration ($R_{auto} + R_{het}$)	303	140	80	$TrB > TeB \geq TeN \geq BoN$	+
<i>R_{auto}</i>	autotrophic respiration ($(R_{auto-ag} + R_{root})$)	36	35	15	$TrB > TeN \geq BoN \geq TeB$	n.s.
<i>R_{auto-ag}</i>	aboveground autotrophic respiration (i.e., leaves and stems)	3	3	2	$TrB > TeN \geq BoN \geq TeB$	n.s.
<i>R_{root}</i>	root respiration	267	213	102	n.s.	++; xB
<i>R_{soil}</i>	soil respiration ($R_{het-soil} + R_{root}$)	1104	715	241	$TrB > TeB \geq TeN > BoN$	++; xB
<i>R_{het-soil}</i>	soil heterotrophic respiration	324	262	110	$TrB > TeB \geq TeN \geq BoN$	n.s.
<i>R_{het-ag}</i>	aboveground heterotrophic respiration	0	0	0	-	-
<i>R_{het}</i>	heterotrophic respiration ($(R_{het-ag} + R_{het-soil})$)	0	0	0	-	-
Stocks						
<i>B_{tot}</i>	total live biomass ($B_{ag} + B_{root}$)	329	282	88	$TeN \geq TrB \geq TeB \geq BoN$	++; xB
<i>B_{ag}</i>	aboveground live biomass ($B_{ag-wood} + B_{foliage}$)	3790	3264	569	$TrB \geq TeN \geq TeB > BoN$	++; xB
<i>B_{ag-wood}</i>	woody component of aboveground biomass	224	210	66	$TeN > TrB \geq TeB \geq BoN$	++; xB
<i>B_{foliage}</i>	foliage biomass	260	216	74	$TeN > TrB \geq BoN \geq TeB$	++; xB
<i>B_{root}</i>	total root biomass ($B_{root-coarse} + B_{root-fine}$)	2273	2248	352	n.s.	++; xB
<i>B_{root-coarse}</i>	coarse root biomass	245	225	74	$TeN > TrB \geq TeB \geq BoN$	++; xB
<i>B_{root-fine}</i>	fine root biomass	394	321	113	n.s.	n.s.
<i>DW_{tot}</i>	deadwood ($DW_{standing} + DW_{down}$)	223	212	42	$TeN > TeB \geq TrB \geq BoN$	+
<i>DW_{standing}</i>	standing dead wood	56	56	21	n.s.	+
<i>DW_{down}</i>	fallen dead wood, including coarse and sometimes fine woody debris	175	168	29	n.s.	++; xB
<i>OL</i>	organic layer / litter/ forest floor	420	365	99	n.s.	++; xB

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

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

174 To test for differences across mature forest biomes, the original values were analyzed via a linear mixed
175 effects model ['lmer' function in 'lme4' R package version **x.xx; REF**] with biome as fixed effect and plot
176 nested within geographic.area as random effects on the intercept. When Biome had a significant effect, we
177 looked at a Tukey's pairwise comparison to see which biomes were significantly different from one another.
178 There were enough data to run this analysis for all focal variables but DW_{down} .

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

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

184 Review Results/ Synthesis

185 Data Coverage

186 Of the 47846 records in ForC v.#, 14105 met the criteria for inclusion in this study (Fig. 1). These records
187 were distributed across 4358 plots in 821 distinct geographic areas. Of the 23 flux and 11 stock variables
188 mapped in these diagrams, ForC contained mature forest estimates from ≥ 7 distinct geographic areas for 20
189 fluxes and 9 stocks in tropical broadleaf forests, 15 fluxes and 9 stocks in temperate broadleaf forests, 15
190 fluxes and 8 stocks in temperate conifer forests, and 9 fluxes and 7 stocks in boreal forests. For regrowth
191 forests (<100 yrs), ForC contained estimates from ≥ 7 distinct geographic areas for 3 fluxes and 9 stocks in
192 tropical broadleaf forests, 12 fluxes and 8 stocks in temperate broadleaf forests, 15 fluxes and 8 stocks in
193 temperate conifer forests, and 12 fluxes and 12 stocks in boreal forests.

194 C cycling in mature forests

195 Average C cycles for tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests ≥ 100
196 years old and with no known major disturbance or significant anthropogenic management are presented in
197 Figures 2-5 (and available in tabular format in the ForC release accompanying this publication).

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

202 https://github.com/forc-db/ForC/blob/master/numbers_and_facts/C_cycle_closure.csv)
203 Within this biome, $B_{ag} < B_{ag-wood} + B_{foliage}$ and $B_{root} < B_{root-coarse} + B_{root-fine}$ because $B_{ag-wood}$ and
204 $B_{root-coarse}$ were very high, with strongly disproportionate numbers of records from the high-biomass forests
205 of the US Pacific Northwest (Figs. S18, S21).

∞

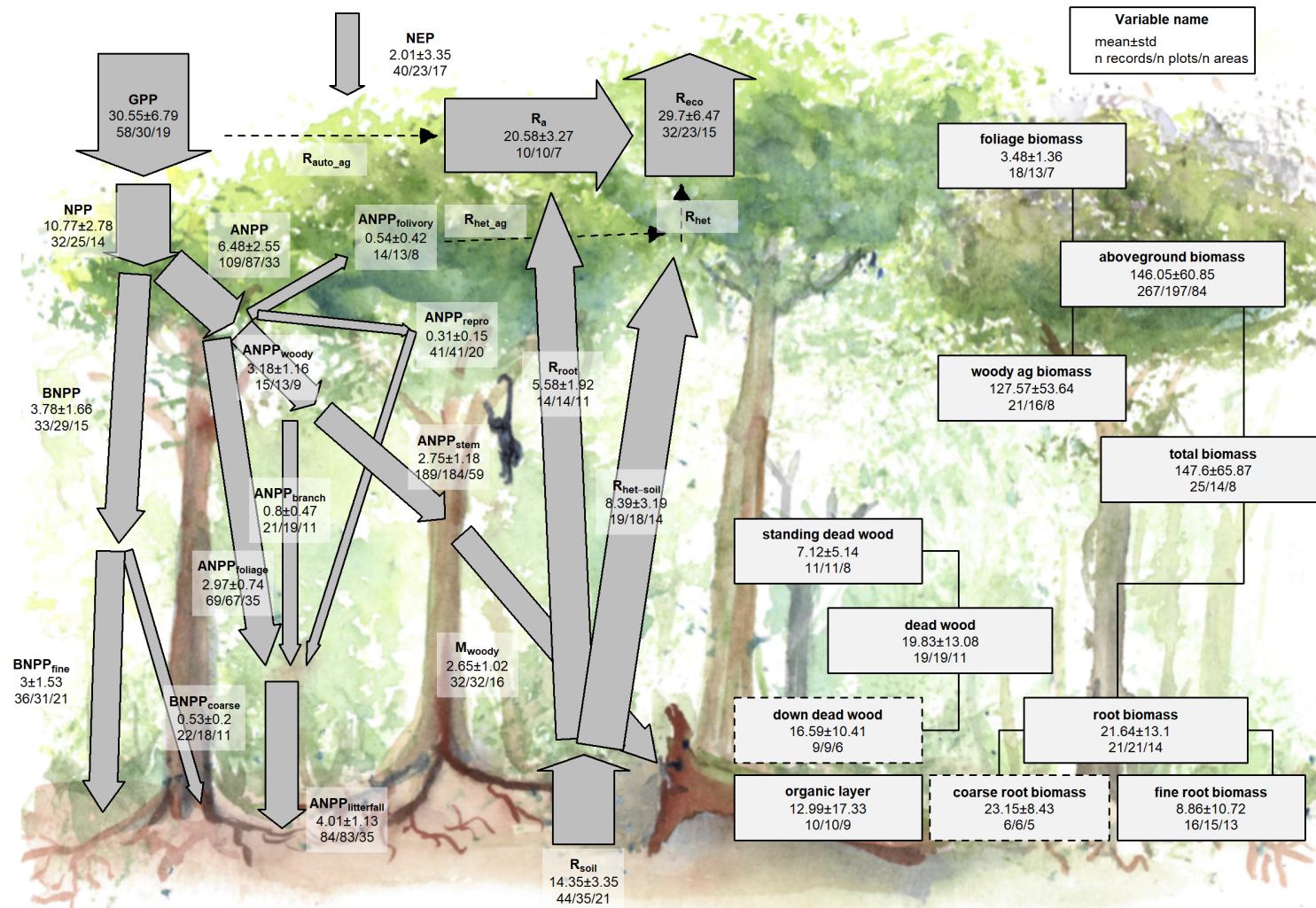


Figure 2 | C cycle diagram for mature tropical broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

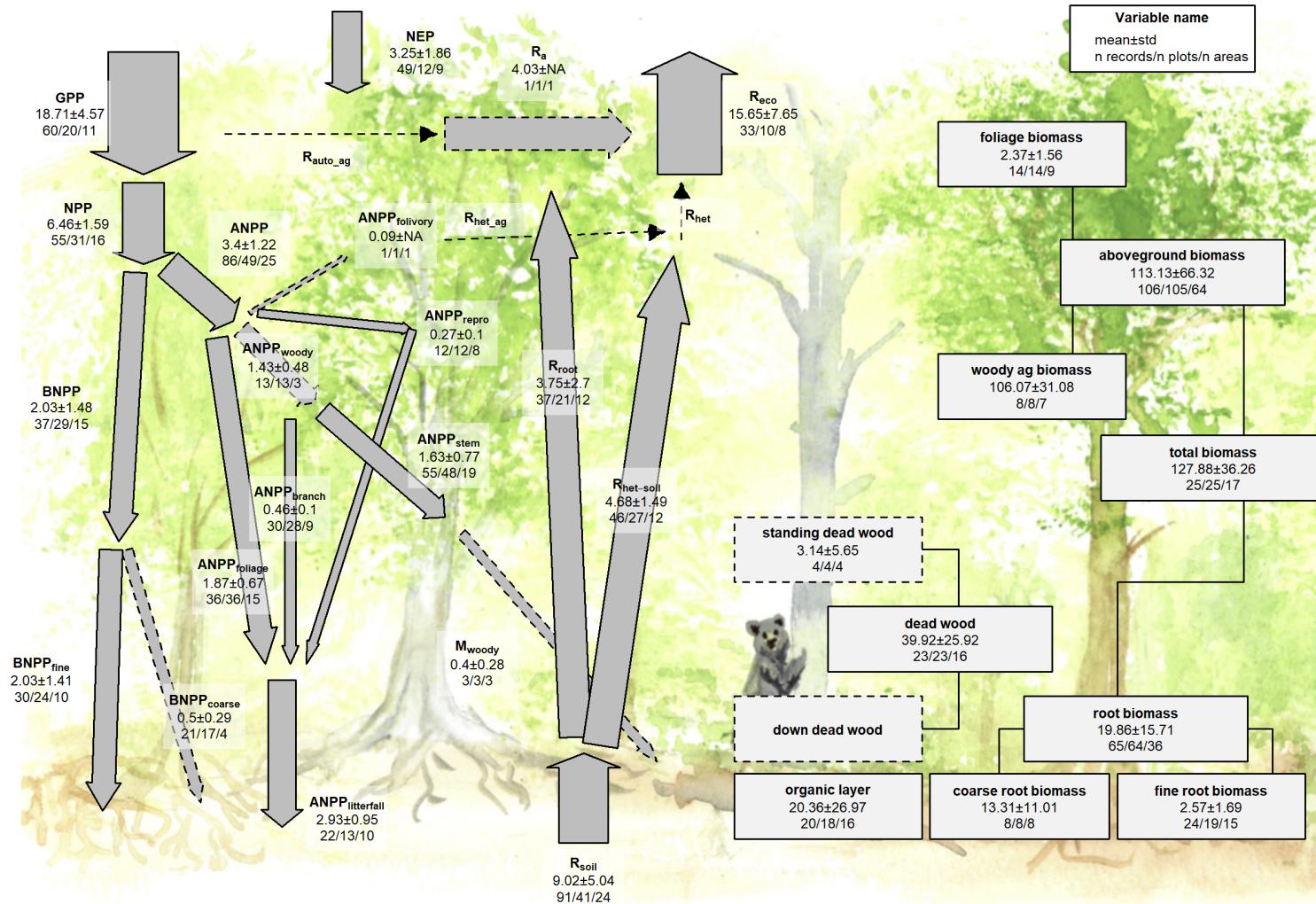


Figure 3 | C cycle diagram for mature temperate broadleaf forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

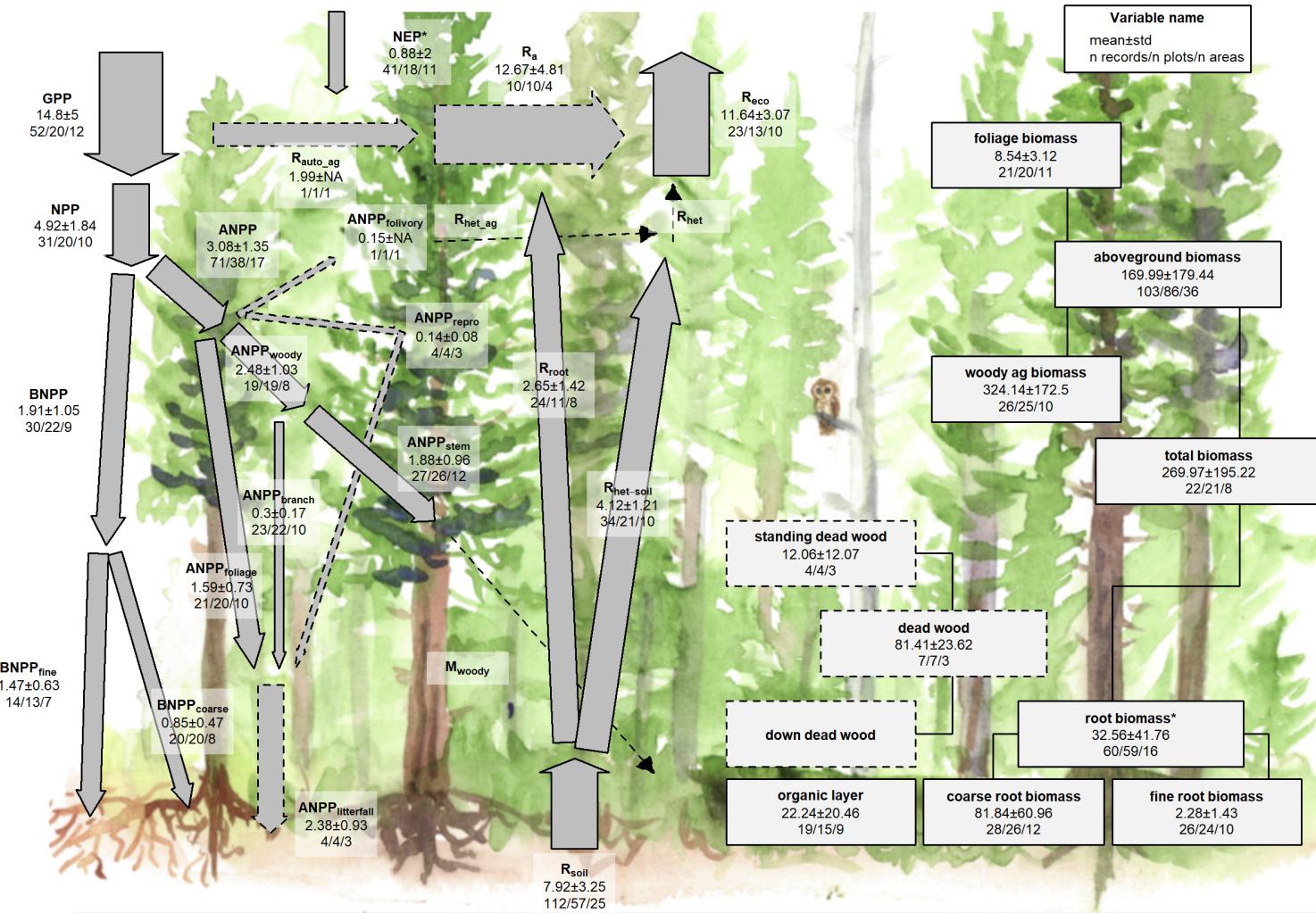


Figure 4 | C cycle diagram for mature temperate conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

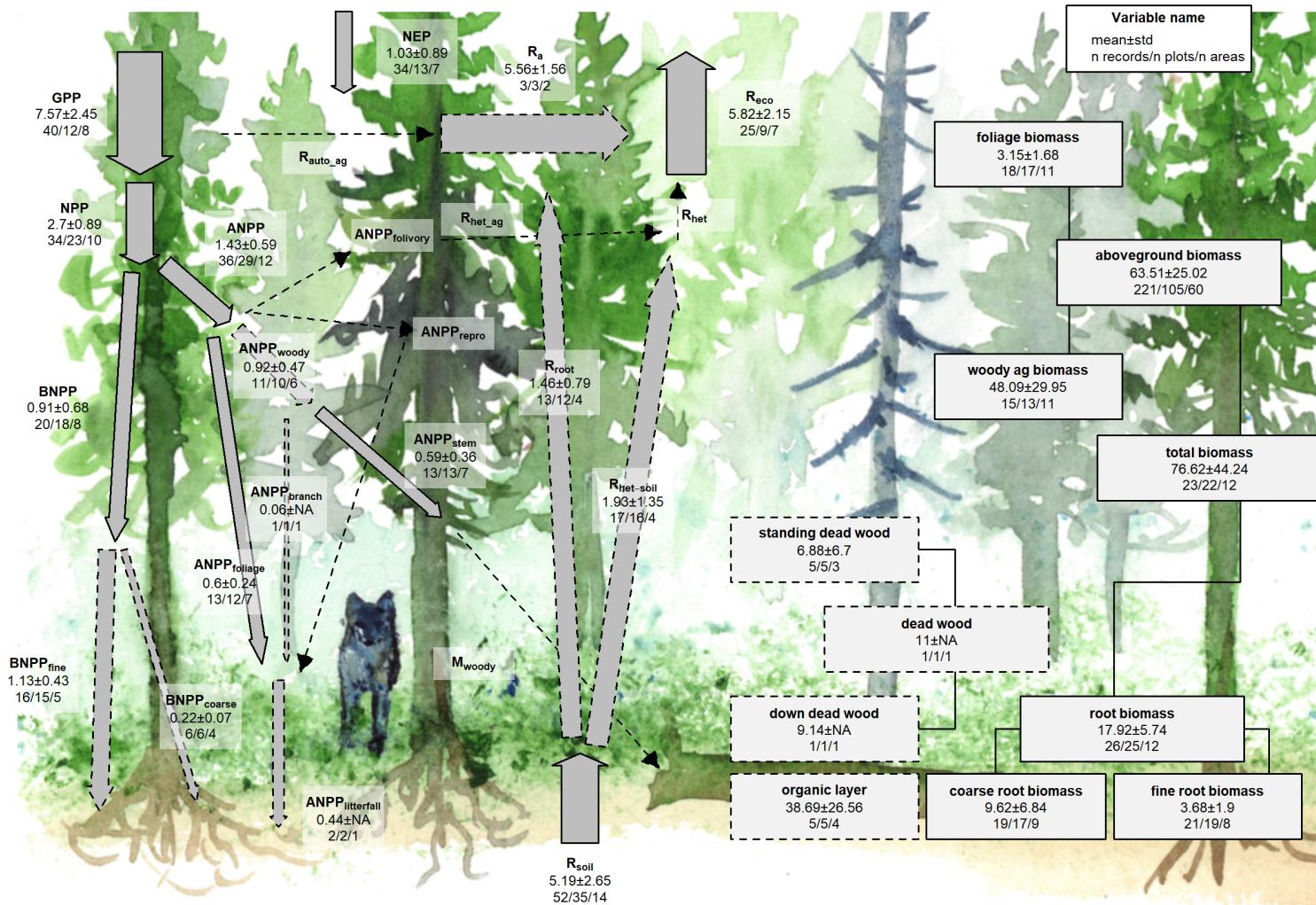


Figure 5 | C cycle diagram for mature boreal conifer forests. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks), presented as mean ± std, where geographically distinct areas are treated as the unit of replication. Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

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

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

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

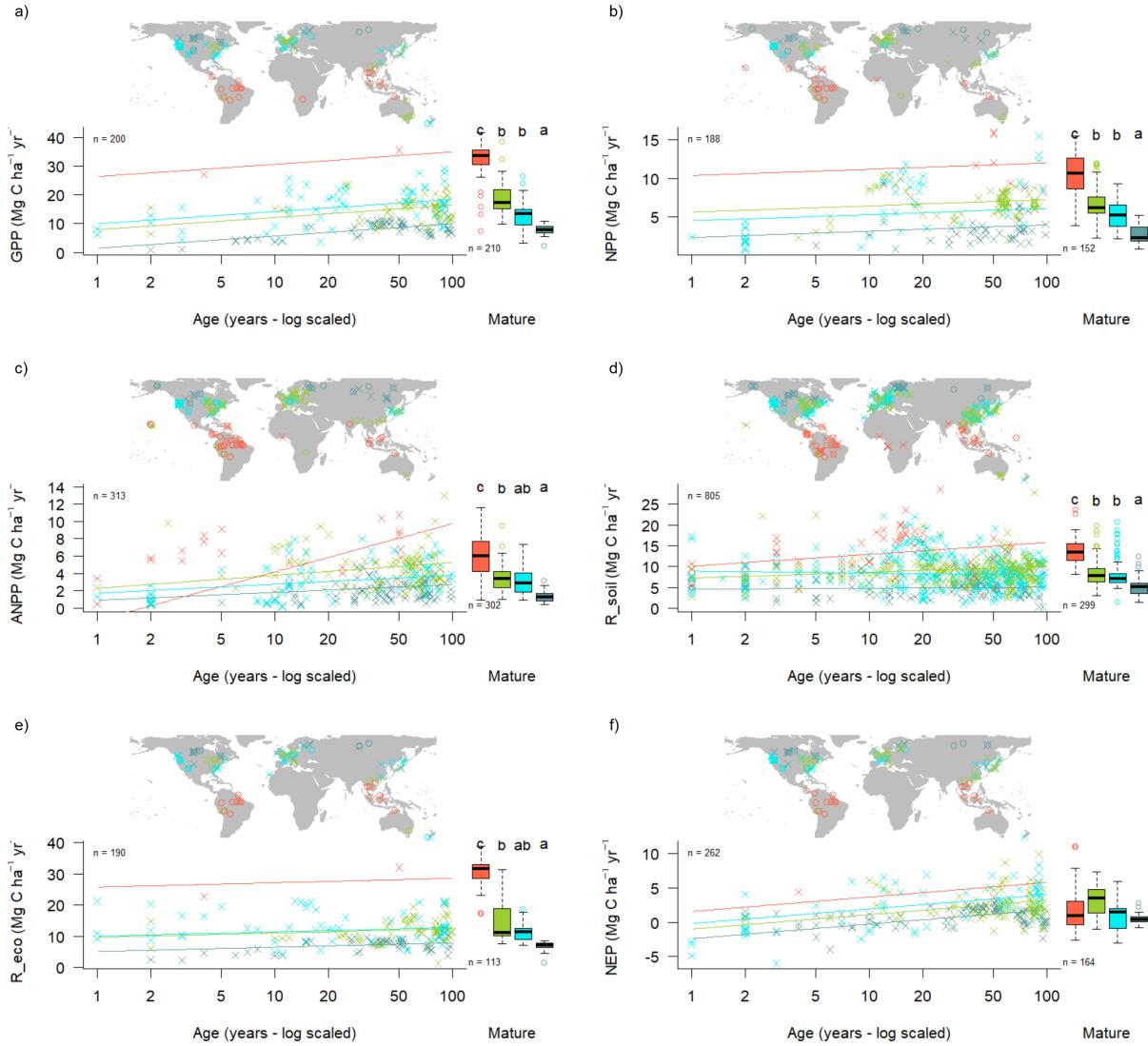


Figure 6 | Age trends and biome differences in some of the major C fluxes: (a) GPP , (b) NPP , (c) $ANPP$, (d) R_{soil} , (e) R_{eco} , and (f) NEP . Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized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

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

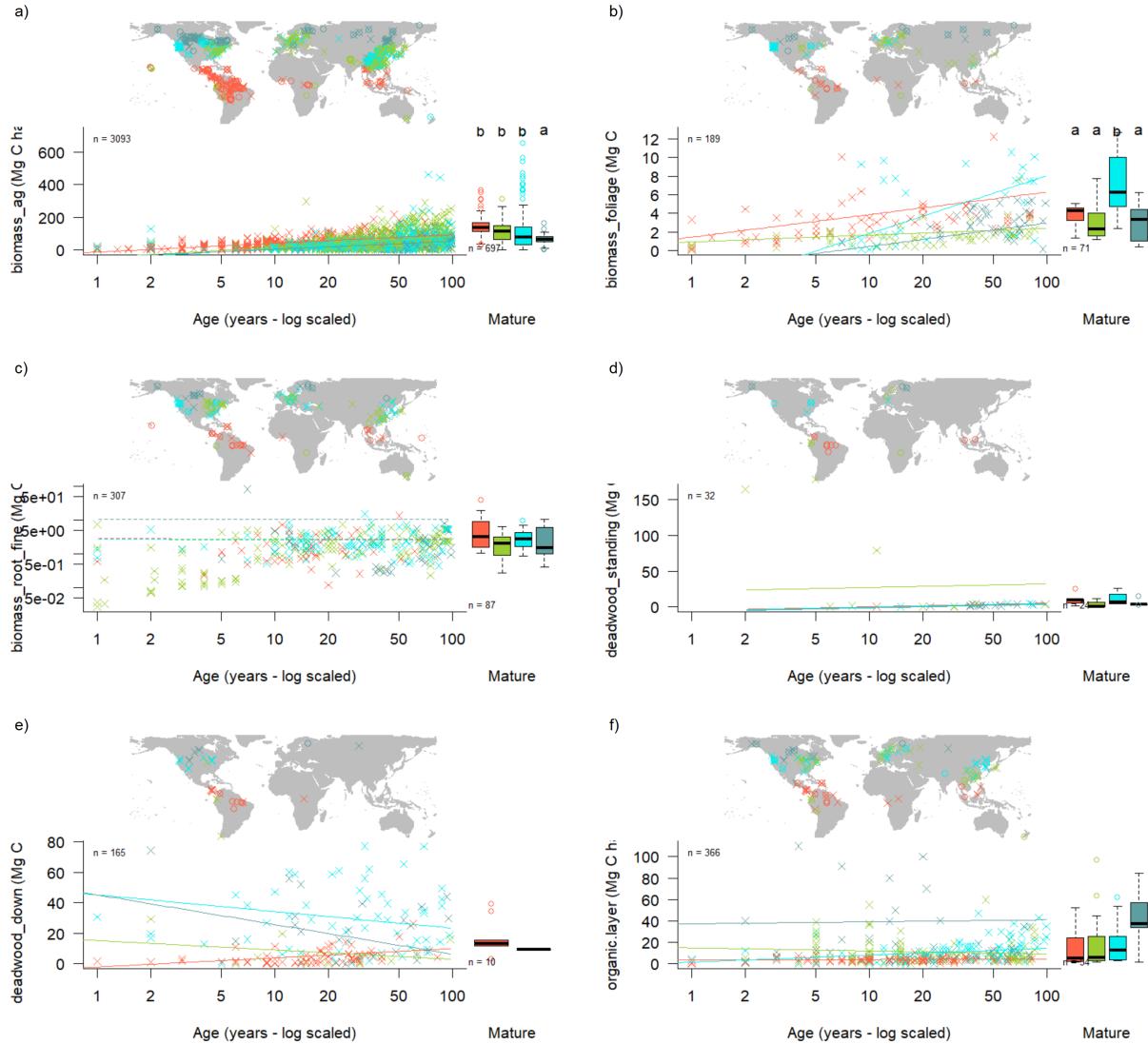


Figure 7 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. Map shows data sources (x and o indicate young and mature stands, respectively). Left plot shows age trends in forests up to 100 years old, as characterized 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).

229 C cycling in young forests

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

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

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

241 The single exception was $ANPP_{stem}$, for which temperate broadleaf forests and temperate conifer forests of
242 age $>\sim 30$ had slightly higher flux rates than tropical forests (*represented by a single chronosequence*).
243 Notably, the trend of tropical > temperate > boreal held for NEP in regrowth forests, in contrast to the
244 lack of biome differences in NEP for mature forests (Fig. 6).

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

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

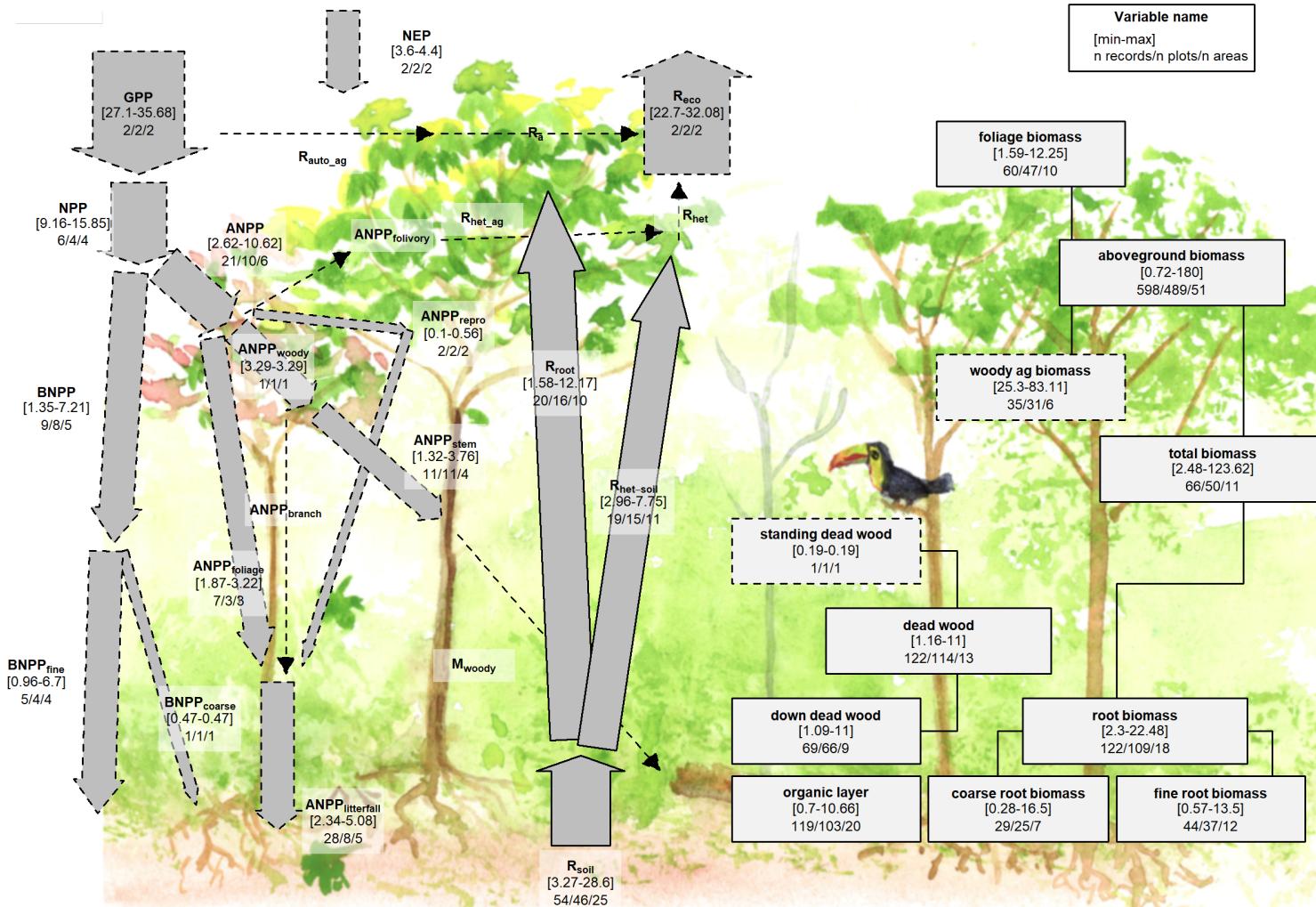


Figure 8 | C cycle diagram for young tropical broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $Mg\ C\ ha^{-1}\ yr^{-1}$ (fluxes) or $Mg\ C\ ha^{-1}$ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed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

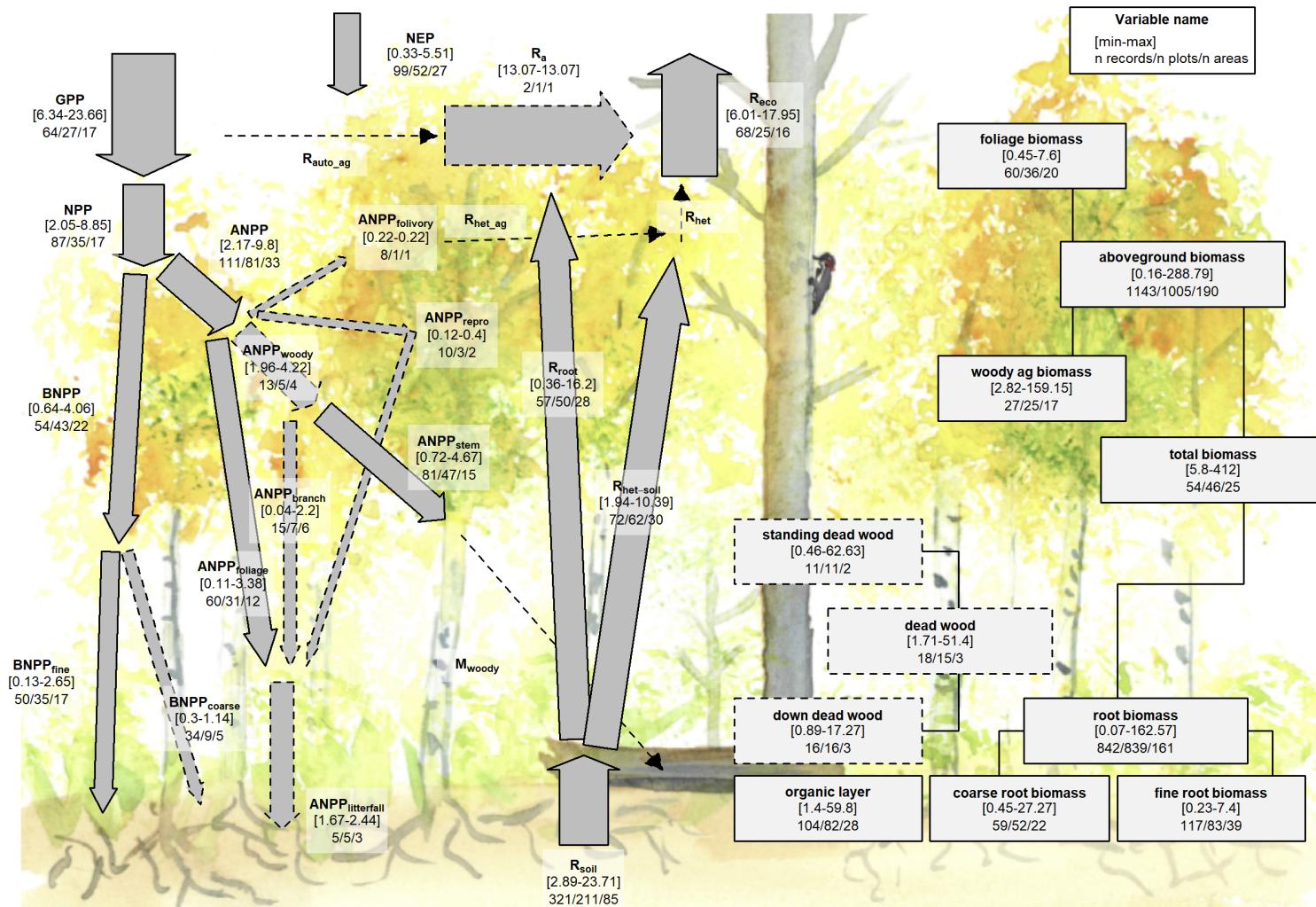


Figure 9 | C cycle diagram for young temperate broadleaf forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines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

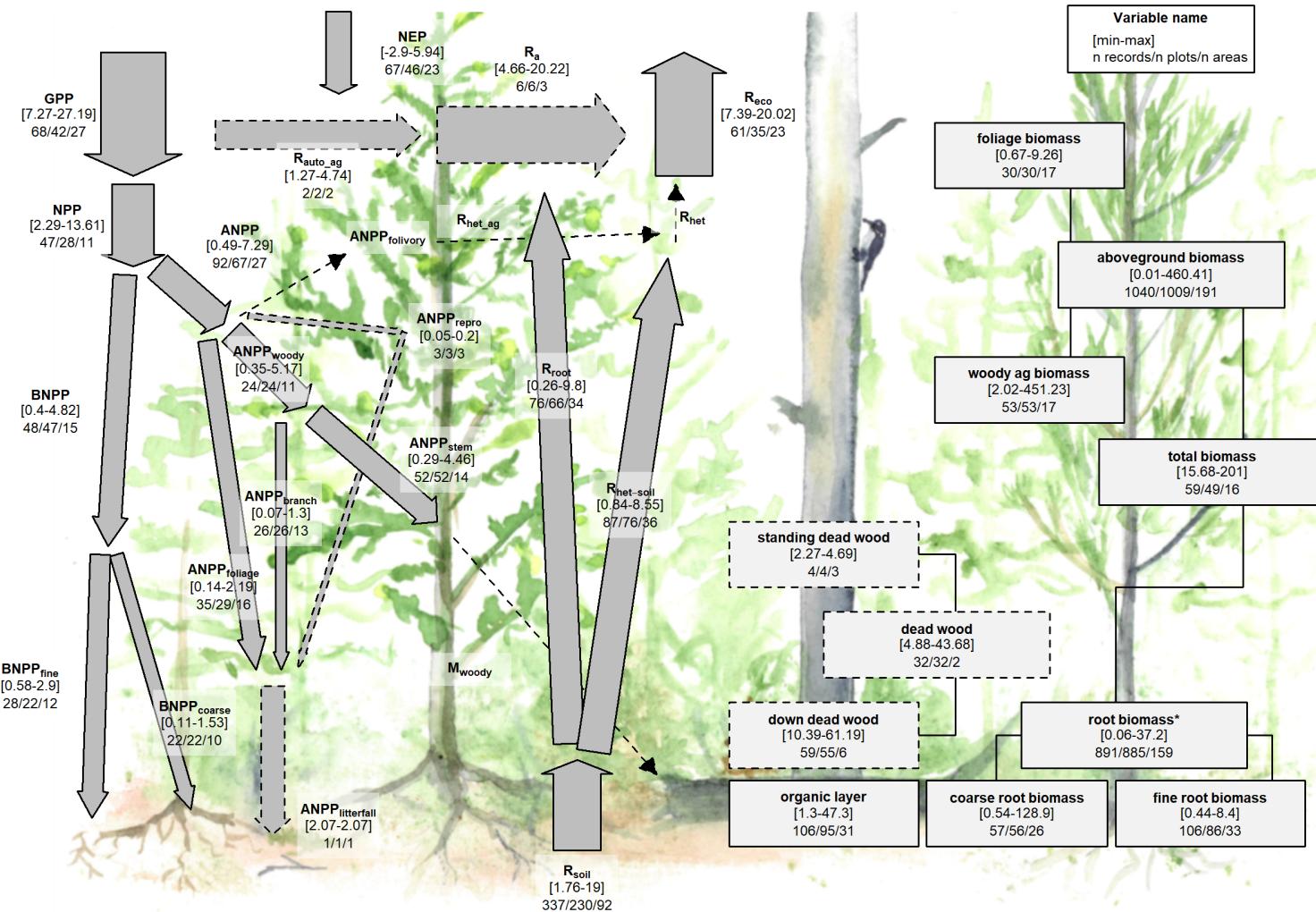


Figure 10 | C cycle diagram for young temperate conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are $Mg\ C\ ha^{-1}\ yr^{-1}$ (fluxes) or $Mg\ C\ ha^{-1}$ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed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

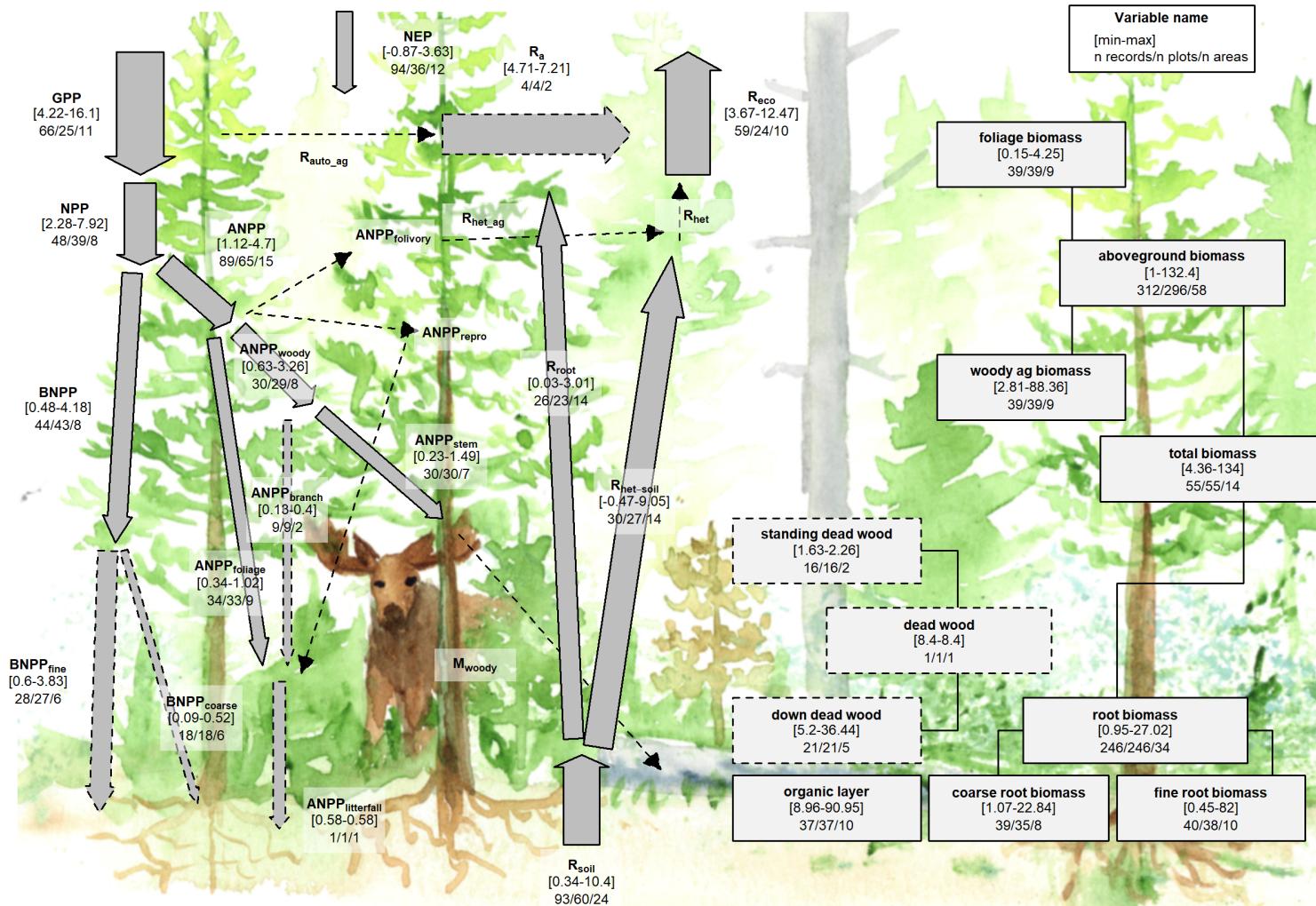


Figure 11 | C cycle diagram for young boreal conifer forests. Presented are observed ranges, where geographically distinct areas are treated as the unit of replication. All units are Mg C ha⁻¹ yr⁻¹ (fluxes) or Mg C ha⁻¹ (stocks). Arrows indicate fluxes, boxes indicate stocks. Dashed shape outlines indicate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

258 **Discussion**

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

268 **C variable coverage and budget closure**

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

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

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

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

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

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

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

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

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

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

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

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

307 **C cycling across biomes**

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

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

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

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

326 **Age trends in C cycling**

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

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

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

333 It’s also important to understand secondary forest C sequestration to reduce uncertainty regarding the
334 potential for carbon uptake by regrowth forests (???, Cook-Patton *et al* 2020).

335 NEP increases with log(age) to 100 -> strongest C sinks are established secondary forests. (But presumably
336 this exact number is an artifact; don't over-emphasize.)

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

338 The future of forest C cycling (???) will shape trends in atmospheric CO₂ and the course of climate change.

339 For a human society seeking to understand and mitigate climate change, the data contained in ForC and
340 summarized here can help to meet two major challenges.

341 First, improved representation of forest C cycling in models is essential to improving predictions of the future
342 course of climate change. To ensure that models are giving the right answers for the right reasons, it is
343 important to benchmark against multiple components of the C cycle that are internally consistent with each
344 other. By making tens of thousands of records readily available in standardized format, ForC makes it
345 feasible for the modeling community to draw upon these data to benchmark models. Integration of ForC
346 with models is a goal (Fer et al., in revision).

347 Second, ForC can serve as a pipeline through which forest science can inform forest-based climate change
348 mitigation efforts. Such efforts will be most effective when informed by the best available data, yet it is not
349 feasible for the individuals and organizations designing such efforts to sort through literature, often behind
350 paywalls, with data reported in varying units, terminology, etc. One goal for ForC is to serve as a pipeline
351 through which information can flow efficiently from forest researchers to decision-makers working to
352 implement forest conservation strategies at global, national, or landscape scales. This is already happening!
353 ForC has already contributed to updating the IPCC guidelines for carbon accounting in forests [IPCC 2019;
354 Requena Suarez et al (2019); Rozendaal et al in prep], mapping C accumulation potential from natural forest
355 regrowth globally (Cook-Patton et al 2020), and informing ecosystem conservation priorities (Goldstein et al
356 2020).

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

366 *Remote sensing measurements are increasingly useful for global- or regional-scale estimates of forest GPP*
367 *(Bagdley et al. 2019, (Li and Xiao 2019)), aboveground biomass (B_{ag}) (REFS), woody mortality (i.e., B_{ag}*
368 *losses to mortality M_{woody}) (Clark et al 2004, Leitold et al 2018), and to some extent net ecosystem*
369 *exchange (NEP) (REFS). Other variables, in particular respiration fluxes, cannot be remotely sensed*
370 *((??)), and efforts such as the Global Carbon Project (le quere REF) and NASA CMS (citation:*
371 *https://carbon.nasa.gov/pdfs/CMS_Phase-1_Report_Final_optimized.pdf but maybe*
372 *better to cite open literature, one of the papers listed at*
373 *<https://cmsflux.jpl.nasa.gov/get-data/publication-data-sets>* typically compute them as residuals
374 *only. (Ben, it woudl be particularly helpful if you could flesh this out some more.)*

375 **Move to data availability statement, or methods?:** We recommend that use of ForC data go to the
376 original database, as opposed to using “off-the-shelf” values from this publication. This is because (1) ForC is
377 constantly being updated, (2) analyses should be designed to match the application, (3) age equations
378 presented here all fit a single functional form that is not necessarily the best possible for all the variables.
379 As climate change accelerates, understanding and managing the carbon dynamics of forests will be critical to
380 forecasting, mitigation, and adaptation. The C data in ForC, as summarized here, will be valuable to these
381 efforts.

382 Acknowledgements

383 All researchers whose data is included in ForC and this analysis. Ian McGregor for help with the database.
384 Thanks to Norbert Kunert and [Helene’s intern] for helpful input at an earlier phase. A Smithsonian
385 Scholarly Studies grant to KAT and HML. WLS grant to KAT.

386 Data availability statement

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

391 ORCID iD

392 References

- 393 Anderson K J, Allen A P, Gillooly J F and Brown J H 2006 Temperature-dependence of biomass
394 accumulation rates during secondary succession *Ecology Letters* **9** 673–82 Online:
395 <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1461-0248.2006.00914.x>
- 396 Anderson-Teixeira K, Herrmann V, CookPatton, Ferson A and Lister K 2020 Forc-db/GROA: Release with
397 Cook-Patton et al. 2020, Nature. Online: <https://zenodo.org/record/3983644>
- 398 Anderson-Teixeira K J, Davies S J, Bennett A C, Gonzalez-Akre E B, Muller-Landau H C, Joseph Wright S,
399 Abu Salim K, Almeyda Zambrano A M, Alonso A, Baltzer J L, Basset Y, Bourg N A, Broadbent E N,
400 Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Butt N, Cao M, Cardenas D, Chuyong G B, Clay K,
401 Cordell S, Dattaraja H S, Deng X, Detto M, Du X, Duque A, Erikson D L, Ewango C E N, Fischer G A,
402 Fletcher C, Foster R B, Giardina C P, Gilbert G S, Gunatilleke N, Gunatilleke S, Hao Z, Hargrove W W,
403 Hart T B, Hau B C H, He F, Hoffman F M, Howe R W, Hubbell S P, Inman-Narahari F M, Jansen P A,
404 Jiang M, Johnson D J, Kanzaki M, Kassim A R, Kenfack D, Kibet S, Kinnaird M F, Korte L, Kral K,
405 Kumar J, Larson A J, Li Y, Li X, Liu S, Lum S K Y, Lutz J A, Ma K, Maddalena D M, Makana J-R, Malhi
406 Y, Marthews T, Mat Serudin R, McMahon S M, McShea W J, Memiaghe H R, Mi X, Mizuno T, Morecroft
407 M, Myers J A, Novotny V, Oliveira A A de, Ong P S, Orwig D A, Ostertag R, Ouden J den, Parker G G,
408 Phillips R P, Sack L, Sainge M N, Sang W, Sri-ngernyuang K, Sukumar R, Sun I-F, Sungpalee W, Suresh H
409 S, Tan S, Thomas S C, Thomas D W, Thompson J, Turner B L, Uriarte M, Valencia R, et al 2015
410 CTFS-ForestGEO: A worldwide network monitoring forests in an era of global change *Global Change Biology*
411 **21** 528–49 Online: <http://onlinelibrary.wiley.com/doi/10.1111/gcb.12712/abstract>

- 412 Anderson-Teixeira K J, Wang M M H, McGarvey J C, Herrmann V, Tepley A J, Bond-Lamberty B and
413 LeBauer D S 2018 ForC: A global database of forest carbon stocks and fluxes *Ecology* **99** 1507–7 Online:
414 <http://doi.wiley.com/10.1002/ecy.2229>
- 415 Anderson-Teixeira K J, Wang M M H, McGarvey J C and LeBauer D S 2016 Carbon dynamics of mature
416 and regrowth tropical forests derived from a pantropical database (TropForC-db) *Global Change Biology* **22**
417 1690–709 Online: <http://onlinelibrary.wiley.com/doi/10.1111/gcb.13226/abstract>
- 418 Baldocchi D, Falge E, Gu L, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R,
419 Fuentes J, Goldstein A, Katul G, Law B, Lee X, Malhi Y, Meyers T, Munger W, Oechel W, Paw K T,
420 Pilegaard K, Schmid H P, Valentini R, Verma S, Vesala T, Wilson K and Wofsy S 2001 FLUXNET: A New
421 Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon Dioxide, Water Vapor, and
422 Energy Flux Densities *Bulletin of the American Meteorological Society* **82** 2415–34 Online:
423 [http://journals.ametsoc.org/doi/abs/10.1175/1520-0477\(2001\)082%3C2415:FANTTS%3E2.3.CO;2](http://journals.ametsoc.org/doi/abs/10.1175/1520-0477(2001)082%3C2415:FANTTS%3E2.3.CO;2)
- 424 Banbury Morgan B, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau H C and Anderson-Teixeira
425 K J Global patterns of forest autotrophic carbon fluxes *Global Change Biology*
- 426 Bonan G B 2008 Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests
427 *Science* **320** 1444–9 Online: <http://www.sciencemag.org/cgi/content/abstract/320/5882/1444>
- 428 Bond-Lamberty B and Thomson A 2010 A global database of soil respiration data *Biogeosciences* **7** 1915–26
429 Online: <http://www.biogeosciences.net/7/1915/2010/>
- 430 Chave J, Davies S J, Phillips O L, Lewis S L, Sist P, Schepaschenko D, Armston J, Baker T R, Coomes D,
431 Disney M, Duncanson L, Héault B, Labrière N, Meyer V, Réjou-Méchain M, Scipal K and Saatchi S 2019
432 Ground Data are Essential for Biomass Remote Sensing Missions *Surveys in Geophysics* **40** 863–80 Online:
433 <https://doi.org/10.1007/s10712-019-09528-w>
- 434 Clark D B, Castro C S, Alvarado L D A and Read J M 2004 Quantifying mortality of tropical rain forest
435 trees using high-spatial-resolution satellite data *Ecology Letters* **7** 52–9 Online:
436 <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2003.00547.x>
- 437 Cook-Patton S C, Leavitt S M, Gibbs D, Harris N L, Lister K, Anderson-Teixeira K J, Briggs R D, Chazdon
438 R L, Crowther T W, Ellis P W, Griscom H P, Herrmann V, Holl K D, Houghton R A, Larrosa C, Lomax G,
439 Lucas R, Madsen P, Malhi Y, Paquette A, Parker J D, Paul K, Routh D, Roxburgh S, Saatchi S, Hoogen J
440 van den, Walker W S, Wheeler C E, Wood S A, Xu L and Griscom B W 2020 Mapping carbon accumulation
441 potential from global natural forest regrowth *Nature* **585** 545–50 Online:
442 <http://www.nature.com/articles/s41586-020-2686-x>
- 443 Curtis P G, Slay C M, Harris N L, Tyukavina A and Hansen M C 2018 Classifying drivers of global forest
444 loss *Science* **361** 1108–11 Online: <http://science.sciencemag.org/content/361/6407/1108>
- 445 Goldstein A, Turner W R, Spawn S A, Anderson-Teixeira K J, Cook-Patton S, Fargione J, Gibbs H K,
446 Griscom B, Hewson J H, Howard J F, Ledezma J C, Page S, Koh L P, Rockström J, Sanderman J and Hole
447 D G 2020 Protecting irrecoverable carbon in Earth's ecosystems *Nature Climate Change* 1–9 Online:
448 <http://www.nature.com/articles/s41558-020-0738-8>
- 449 Grassi G, House J, Dentener F, Federici S, Elzen M den and Penman J 2017 The key role of forests in
450 meeting climate targets requires science for credible mitigation *Nature Climate Change* **7** 220–6 Online:

- 451 https://www.nature.com/articles/nclimate3227
- 452 Griscom B W, Adams J, Ellis P W, Houghton R A, Lomax G, Miteva D A, Schlesinger W H, Shoch D,
453 Siikamäki J V, Smith P, Woodbury P, Zganjar C, Blackman A, Campari J, Conant R T, Delgado C, Elias P,
454 Gopalakrishna T, Hamsik M R, Herrero M, Kiesecker J, Landis E, Laestadius L, Leavitt S M, Minnemeyer S,
455 Polasky S, Potapov P, Putz F E, Sanderman J, Silvius M, Wollenberg E and Fargione J 2017 Natural climate
456 solutions *Proceedings of the National Academy of Sciences* **114** 11645–50 Online:
457 http://www.pnas.org/lookup/doi/10.1073/pnas.1710465114
- 458 Hansen M C, Potapov P V, Moore R, Hancher M, Turubanova S A, Tyukavina A, Thau D, Stehman S V,
459 Goetz S J, Loveland T R, Kommareddy A, Egorov A, Chini L, Justice C O and Townshend J R G 2013
460 High-Resolution Global Maps of 21st-Century Forest Cover Change *Science* **342** 850–3 Online:
461 http://www.sciencemag.org/cgi/doi/10.1126/science.1244693
- 462 Johnson D J, Needham J, Xu C, Massoud E C, Davies S J, Anderson-Teixeira K J, Bunyavejchewin S,
463 Chambers J Q, Chang-Yang C-H, Chiang J-M, Chuyong G B, Condit R, Cordell S, Fletcher C, Giardina C P,
464 Giambelluca T W, Gunatilleke N, Gunatilleke S, Hsieh C-F, Hubbell S, Inman-Narahari F, Kassim A R,
465 Katabuchi M, Kenfack D, Litton C M, Lum S, Mohamad M, Nasardin M, Ong P S, Ostertag R, Sack L,
466 Swenson N G, Sun I F, Tan S, Thomas D W, Thompson J, Umaña M N, Uriarte M, Valencia R, Yap S,
467 Zimmerman J, McDowell N G and McMahon S M 2018 Climate sensitive size-dependent survival in tropical
468 trees *Nature Ecology & Evolution* **2** 1436–42 Online: http://www.nature.com/articles/s41559-018-0626-z
- 469 Krause A, Pugh T A M, Bayer A D, Li W, Leung F, Bondeau A, Doelman J C, Humpenöder F, Anthoni P,
470 Bodirsky B L, Ciais P, Müller C, Murray-Tortarolo G, Olin S, Popp A, Sitch S, Stehfest E and Arneth A
471 2018 Large uncertainty in carbon uptake potential of land-based climate-change mitigation efforts *Global
472 Change Biology* **24** 3025–38 Online: https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14144
- 473 Leitold V, Morton D C, Longo M, dos-Santos M N, Keller M and Scaranello M 2018 El Niño drought
474 increased canopy turnover in Amazon forests *New Phytologist* **219** 959–71 Online:
475 http://doi.wiley.com/10.1111/nph.15110
- 476 Li X and Xiao J 2019 Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A
477 Global, Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2 *Remote Sensing* **11** 2563
478 Online: https://www.mdpi.com/2072-4292/11/21/2563
- 479 Lutz J A, Furniss T J, Johnson D J, Davies S J, Allen D, Alonso A, Anderson-Teixeira K J, Andrade A,
480 Baltzer J, Becker K M L, Blomdahl E M, Bourg N A, Bunyavejchewin S, Burslem D F R P, Cansler C A,
481 Cao K, Cao M, Cárdenas D, Chang L-W, Chao K-J, Chao W-C, Chiang J-M, Chu C, Chuyong G B, Clay K,
482 Condit R, Cordell S, Dattaraja H S, Duque A, Ewango C E N, Fischer G A, Fletcher C, Freund J A,
483 Giardina C, Germain S J, Gilbert G S, Hao Z, Hart T, Hau B C H, He F, Hector A, Howe R W, Hsieh C-F,
484 Hu Y-H, Hubbell S P, Inman-Narahari F M, Itoh A, Janík D, Kassim A R, Kenfack D, Korte L, Král K,
485 Larson A J, Li Y, Lin Y, Liu S, Lum S, Ma K, Makana J-R, Malhi Y, McMahon S M, McShea W J,
486 Memighe H R, Mi X, Morecroft M, Musili P M, Myers J A, Novotny V, Oliveira A de, Ong P, Orwig D A,
487 Ostertag R, Parker G G, Patankar R, Phillips R P, Reynolds G, Sack L, Song G-Z M, Su S-H, Sukumar R,
488 Sun I-F, Suresh H S, Swanson M E, Tan S, Thomas D W, Thompson J, Uriarte M, Valencia R, Vicentini A,
489 Vrška T, Wang X, Weiblen G D, Wolf A, Wu S-H, Xu H, Yamakura T, Yap S and Zimmerman J K 2018
490 Global importance of large-diameter trees *Global Ecology and Biogeography* **27** 849–64 Online:

- 491 https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12747
- 492 Luyssaert S, Inglima I, Jung M, Richardson A D, Reichstein M, Papale D, Piao S L, Schulze E-D, Wingate L,
 493 Matteucci G, Aragao L, Aubinet M, Beer C, Bernhofer C, Black K G, Bonal D, Bonnefond J-M, Chambers J,
 494 Ciais P, Cook B, Davis K J, Dolman A J, Gielen B, Goulden M, Grace J, Granier A, Grelle A, Griffis T,
 495 Grünwald T, Guidolotti G, Hanson P J, Harding R, Hollinger D Y, Hutyra L R, Kolari P, Kruijt B, Kutsch
 496 W, Lagergren F, Laurila T, Law B E, Maire G L, Lindroth A, Loustau D, Malhi Y, Mateus J, Migliavacca M,
 497 Misson L, Montagnani L, Moncrieff J, Moors E, Munger J W, Nikinmaa E, Ollinger S V, Pita G, Rebmann
 498 C, Roupsard O, Saigusa N, Sanz M J, Seufert G, Sierra C, Smith M-L, Tang J, Valentini R, Vesala T and
 499 Janssens I A 2007 CO₂ balance of boreal, temperate, and tropical forests derived from a global database
 500 *Global Change Biology* **13** 2509–37 Online:
 501 http://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2007.01439.x
- 502 McDowell N G, Allen C D, Anderson-Teixeira K, Aukema B H, Bond-Lamberty B, Chini L, Clark J S,
 503 Dietze M, Grossiord C, Hanbury-Brown A, Hurtt G C, Jackson R B, Johnson D J, Kueppers L, Lichstein J
 504 W, Ogle K, Poulter B, Pugh T A M, Seidl R, Turner M G, Uriarte M, Walker A P and Xu C 2020 Pervasive
 505 shifts in forest dynamics in a changing world *Science* **368** Online:
 506 https://science.sciencemag.org/content/368/6494/eaaz9463
- 507 Pan Y, Birdsey R A, Fang J, Houghton R, Kauppi P E, Kurz W A, Phillips O L, Shvidenko A, Lewis S L,
 508 Canadell J G, Ciais P, Jackson R B, Pacala S, McGuire A D, Piao S, Rautiainen A, Sitch S and Hayes D
 509 2011 A Large and Persistent Carbon Sink in the World's Forests *Science* **333** 988–93 Online:
 510 http://www.sciencemag.org/content/early/2011/07/27/science.1201609.abstract
- 511 Pugh T A M, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V and Calle L 2019 Role of forest
 512 regrowth in global carbon sink dynamics *Proceedings of the National Academy of Sciences* **116** 4382–7
 513 Online: http://www.pnas.org/lookup/doi/10.1073/pnas.1810512116
- 514 Requena Suarez D, Rozendaal D M A, Sy V D, Phillips O L, Alvarez-Dávila E, Anderson-Teixeira K,
 515 Araujo-Murakami A, Arroyo L, Baker T R, Bongers F, Brienen R J W, Carter S, Cook-Patton S C,
 516 Feldpausch T R, Griscom B W, Harris N, Héault B, Coronado E N H, Leavitt S M, Lewis S L, Marimon B
 517 S, Mendoza A M, N'dja J K, N'Guessan A E, Poorter L, Qie L, Rutishauser E, Sist P, Sonké B, Sullivan M J
 518 P, Vilanova E, Wang M M H, Martius C and Herold M 2019 Estimating aboveground net biomass change for
 519 tropical and subtropical forests: Refinement of IPCC default rates using forest plot data *Global Change
 520 Biology* **25** 3609–24 Online: http://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14767
- 521 Schepaschenko D, Chave J, Phillips O L, Lewis S L, Davies S J, Réjou-Méchain M, Sist P, Scipal K, Perger
 522 C, Herault B, Labrière N, Hofhansl F, Affum-Baffoe K, Aleinikov A, Alonso A, Amani C, Araujo-Murakami
 523 A, Armston J, Arroyo L, Ascarrunz N, Azevedo C, Baker T, Balazy R, Bedeau C, Berry N, Bilous A M,
 524 Bilous S Y, Bissiengou P, Blanc L, Bobkova K S, Braslavskaya T, Brienen R, Burslem D F R P, Condit R,
 525 Cuni-Sánchez A, Danilina D, Torres D del C, Derroire G, Descroix L, Sotta E D, d'Oliveira M V N, Dresel C,
 526 Erwin T, Evdokimenko M D, Falck J, Feldpausch T R, Foli E G, Foster R, Fritz S, Garcia-Abril A D,
 527 Gornov A, Gornova M, Gothard-Bassébé E, Gourlet-Fleury S, Guedes M, Hamer K C, Susanty F H, Higuchi
 528 N, Coronado E N H, Hubau W, Hubbell S, Ilstedt U, Ivanov V V, Kanashiro M, Karlsson A, Karminov V N,
 529 Killeen T, Koffi J-C K, Konovalova M, Kraxner F, Krejza J, Krisnawati H, Krivobokov L V, Kuznetsov M A,
 530 Lakyda I, Lakyda P I, Licona J C, Lucas R M, Lukina N, Lussetti D, Malhi Y, Manzanera J A, Marimon B,
 531 Junior B H M, Martinez R V, Martynenko O V, Matsala M, Matyashuk R K, Mazzei L, Memiaghe H,

- 532 Mendoza C, Mendoza A M, Moroziuk O V, Mukhortova L, Musa S, Nazimova D I, Okuda T, Oliveira L C,
533 et al 2019 The Forest Observation System, building a global reference dataset for remote sensing of forest
534 biomass *Scientific Data* **6** 1–11 Online: <http://www.nature.com/articles/s41597-019-0196-1>
- 535 Schimel D, Pavlick R, Fisher J B, Asner G P, Saatchi S, Townsend P, Miller C, Frankenberg C, Hibbard K
536 and Cox P 2015 Observing terrestrial ecosystems and the carbon cycle from space *Global Change Biology* **21**
537 1762–76 Online: <http://doi.wiley.com/10.1111/gcb.12822>
- 538 Song X-P, Hansen M C, Stehman S V, Potapov P V, Tyukavina A, Vermote E F and Townshend J R 2018
539 Global land change from 1982 to 2016 *Nature* **560** 639–43 Online:
540 <http://www.nature.com/articles/s41586-018-0411-9/>
- 541 Taylor P G, Cleveland C C, Wieder W R, Sullivan B W, Doughty C E, Dobrowski S Z and Townsend A R
542 2017 Temperature and rainfall interact to control carbon cycling in tropical forests ed L Liu *Ecology Letters*
543 **20** 779–88 Online: <http://doi.wiley.com/10.1111/ele.12765>