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3   **1** **Title:** Carbon cycling in mature and regrowth forests globally  
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## 2    Summary

3    *Background.* Forests are major components of the global carbon (C) cycle and thereby strongly influence  
4    atmospheric carbon dioxide (CO<sub>2</sub>) and climate. However, efforts to incorporate forests into climate models  
5    and CO<sub>2</sub> accounting frameworks have been constrained by a lack of accessible, global-scale synthesis on how  
6    C cycling varies across forest types and stand ages.

7    *Methods/Design.* Here, we draw from the Global Forest Carbon Database, ForC, to provide a macroscopic  
8    overview of C cycling in the world's forests, giving special attention to stand age-related variation.

9    Specifically, we use 11923 *ForC* records for 34 C cycle variables from 865 geographic locations to characterize  
10   ensemble C budgets for four broad forest types – tropical broadleaf evergreen, temperate broadleaf,  
11   temperate conifer, and boreal. We calculate statistics for both mature and regrowth (age <100 years) forests,  
12   and quantify trends with stand age in regrowth forests for all variables with sufficient data.

13   *Review Results/ Synthesis.* The rate of C cycling generally decreased from tropical to boreal regions in both  
14   mature and regrowth forests, whereas C stocks showed less directional variation. Net ecosystem production  
15   of mature forests was indistinguishable across biomes. The majority of flux variables, together with most live  
16   biomass pools, increased significantly with stand age when fit with logarithmic functions.

17   *Discussion.* As climate change accelerates, understanding and managing the carbon dynamics of forests is  
18   critical to forecasting, mitigation, and adaptation. This comprehensive and synthetic global overview of C  
19   stocks and fluxes across biomes and stand ages will help to advance these efforts.

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

## Background

Forest ecosystems are shaping the course of climate change through their influence on atmospheric carbon dioxide (CO<sub>2</sub>; Bonan 2008, Friedlingstein *et al* 2019, IPCC 2018). Despite the centrality of forest C cycling in regulating atmospheric CO<sub>2</sub>, important uncertainties in climate models (Friedlingstein *et al* 2006, Krause *et al* 2018, Bonan *et al* 2019, Di Vittorio *et al* 2020) and CO<sub>2</sub> accounting frameworks (Pan *et al* 2011, IPCC 2019) can be traced to lack of understanding on how C cycling varies across forest types and in relation to stand history. This requires accessible, comprehensive, and large-scale databases with global coverage, which runs contrary to the traditional way forest C stocks and fluxes have been measured and published.

Large-scale synthesis is critical to benchmarking model performance with global data (Clark *et al* 2017, Luo *et al* 2012), quantifying the role of forests in the global C cycle (e.g., Pan *et al* 2011), and using book-keeping methods to quantify actual or potential exchanges of CO<sub>2</sub> between forests and the atmosphere (Griscom *et al* 2017, Houghton 2020).

## Forests in the global C cycle: current and future

A robust understanding of forest impacts on global C cycling is essential. Total annual photosynthesis in forests (gross primary productivity, GPP) is estimated at approximately 69 Gt C yr<sup>-1</sup> (Badgley *et al* 2019), more than seven times the average annual fossil fuel emissions during 2009-2018 (9.5 ± 0.5 Gt C yr<sup>-1</sup>; Friedlingstein *et al* 2019). Most of this enormous C uptake is counterbalanced by releases to the atmosphere through ecosystem respiration ( $R_{eco}$ ) and fire, with forests globally dominant as sources of both soil respiration (Warner *et al* 2019) and fire (van der Werf *et al* 2017). In recent years, total forest C uptake has exceeded releases, such that globally forests have been a C sink (Harris *et al* 2021). Considering only areas remaining in forest, this C sink has averaged 3.2 ± 0.6 Gt C yr<sup>-1</sup> for 2009-2018, offsetting 29% of anthropogenic fossil fuel emissions (Friedlingstein *et al* 2019). However, deforestation, estimated at ~1 Gt C yr<sup>-1</sup> in recent decades (Pan *et al* 2011, Tubiello *et al* 2020), reduces the net forest sink to ~1.1-2.2 Gt C yr<sup>-1</sup> (Friedlingstein *et al* 2019, Harris *et al* 2021).

The future of the current forest C sink is dependent both upon forest responses to climate change itself and human land use decisions, which will feedback and strongly influence the course of climate change (Friedlingstein *et al* 2006). Regrowing forests in particular will play an important role (Pugh *et al* 2019), as almost two-thirds of the world's forests were secondary as of 2010 (FAO 2010). As anthropogenic and climate-driven disturbances impact an growing proportion of Earth's forests (Andela *et al* 2017, McDowell *et al* 2020), understanding the carbon dynamics of regrowth forests is increasingly important (Anderson-Teixeira *et al* 2013). Although age trends in aboveground biomass have been well-studied and synthesized globally (Cook-Patton *et al* 2020), a relative dearth of data and synthesis on other C stocks and fluxes in secondary forests points to an under-filled need to characterize age-related trends in forest C cycling. Such understanding is particularly critical for reducing uncertainty regarding the potential for carbon uptake and climate change mitigation by regrowth forests (Krause *et al* 2018, Cook-Patton *et al* 2020). Understanding, modeling, and managing forest-atmosphere CO<sub>2</sub> exchange is thus central to efforts to mitigate climate change (Grassi *et al* 2017, Griscom *et al* 2017, Cavalieri *et al* 2015).

## Evolution of forest C cycle research

For more than half a century, researchers have sought to understand how forest carbon cycling varies across stands, including those of different biomes (e.g., Lieth 1973, Luyssaert *et al* 2007) and stand ages (e.g.,

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3 Odum 1969, Luyssaert *et al* 2008). Over this time, an increasingly refined conceptual understanding of the  
4 elements of ecosystem C cycles has developed, as a growing number of variables have been defined (e.g.,  
5 Chapin *et al* 2006), along with appropriate measurement methods (e.g., Clark *et al* 2001). New technology  
6 has also enabled researchers to directly measure an expanding set of variables, notably including the  
7 development of continuous measurements of soil CO<sub>2</sub> efflux (Kuzyakov 2006) and ecosystem-atmosphere CO<sub>2</sub>  
8 exchange (Baldocchi *et al* 2001). Measurement techniques have been increasingly standardized; for example,  
9 of the biomass allometries that strongly influence estimates of most C cycle variables (e.g., Chave *et al* 2014).  
10 Further standardization has been made possible through research networks such as ForestGEO  
11 (Anderson-Teixeira *et al* 2015, Davies *et al* 2021), NEON (Schimel *et al* 2007), and FLUXNET (Baldocchi *et*  
12 *al* 2001, Novick *et al* 2018). Remote sensing technology has become increasingly useful for global- or  
13 regional-scale estimates of a few critical variables (e.g., aboveground biomass,  $B_{ag}$ : Saatchi *et al* 2011, Hu *et*  
14 *al* 2016, Spawn *et al* 2020, gross primary productivity,  $GPP$ : Li and Xiao 2019), yet measurement and  
15 validation of most forest C stocks and fluxes necessarily requires intensive on-the-ground data collection.  
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17 Alongside these conceptual and methodological developments, there has been a proliferation of measurements  
18 across the world's forests. The result of decades of research on forest C cycling is tens of thousands of records  
19 distributed across thousands of scientific articles, varying in data formats, units, measurement methods, *etc.*  
20 To address global-scale questions, researchers began synthesizing data into increasingly large databases (e.g.,  
21 Lieth 1973, Luyssaert *et al* 2007, Bond-Lamberty and Thomson 2010, Anderson-Teixeira *et al* 2016, 2018,  
22 Cook-Patton *et al* 2020). The current largest, most comprehensive database on forest C cycling is *ForC*  
23 (Anderson-Teixeira *et al* 2016, 2018), which contains published estimates of forest ecosystem C stocks and  
24 annual fluxes (>50 variables), with different variables capturing distinct ecosystem pools (e.g., woody, foliage,  
25 and root biomass; dead wood) and flux types (e.g., gross and net primary productivity; soil, root, and  
26 ecosystem respiration). These data represent ground-based measurements, and *ForC* contains associated  
27 data required for interpretation (e.g., stand history, measurement methods). Since its most recent  
28 publication (*ForC v2.0-Ecology*; Anderson-Teixeira *et al* 2018), *ForC* has grown 129%, primarily through the  
29 incorporation of two additional large databases that also synthesized published forest C data: the Global Soil  
30 Respiration Database (SRDB; Bond-Lamberty and Thomson 2010, Jian *et al* 2020) and the Global  
31 Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020). Following these additions,  
32 *ForC* currently contains 39762 records from 10608 plots and 1532 distinct geographic areas representing all  
33 forested biogeographic and climate zones, making it ideal for assessing how forest C cycling varies across  
34 biomes and with respect to stand age.  
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## 92 Biome differences

45 Forest C cycling varies enormously across biomes, which categorize the world's forests according to major  
46 differences in climate, vegetation, *etc.* Since the early 19th century, it has been recognized that climate plays  
47 a dominant role in shaping differences among forests on a global scale (Humboldt and Bonpland 1807,  
48 Holdridge 1947). Global scale data syntheses have shown that C fluxes including  $GPP$ , net primary  
49 productivity ( $NPP$ ), and soil respiration ( $R_{soil}$ ) decrease with latitude or, correspondingly, increase with  
50 mean annual temperature (Fig. 1; e.g., Lieth 1973, Luyssaert *et al* 2007, Hursh *et al* 2017, Banbury Morgan  
51 *et al* n.d.). C stocks of mature forests show less directional variation (Fig. 1). On average, aboveground  
52 biomass ( $B_{ag}$ ) tends to decrease with latitude, but not as dramatically as fluxes, and with the highest  $B_{ag}$   
53 forests in relatively cool, moist temperate regions (Keith *et al* 2009, Smithwick *et al* 2002, Hu *et al* 2016). In  
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3 contrast, standing and downed dead wood ( $DW_{standing}$  and  $DW_{down}$ , respectively, summing to  $DW_{tot}$ ) and  
4 the organic layer ( $OL$ ) tend to accumulate more in colder climates where decomposition is slow relative to  
5  $NPP$  (Harmon *et al* 1986, Allen *et al* 2002).

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7 Correlative analyses relating C cycle variables to climate and other environmental variables have recently  
8 been taken to a new level through use of machine-learning algorithms that relate ground-based C cycle data  
9 to global maps of environmental covariates, making it possible to create fine-scale global maps of C cycling  
10 (e.g., Warner *et al* 2019, Cook-Patton *et al* 2020). This approach can be particularly effective when paired  
11 with satellite measurements that correlate to C cycle variables of interest; for example, solar-induced  
12 chlorophyll fluorescence is useful for fine-scale mapping of gross primary productivity ( $GPP$ ; Li and Xiao  
13 2019), while LiDAR, radar, and optical imagery are being used to estimate  $B_{ag}$  at regional to global scales  
14 (e.g., Saatchi *et al* 2011, Hu *et al* 2016). Any such analysis is however constrained by the quality and  
15 coverage of ground-based estimates of forest C fluxes or stocks (e.g., Schepaschenko *et al* 2019). While  
16 estimates of some variables (e.g.,  $B_{ag}$ ,  $GPP$ ,  $NPP$ ,  $R_{soil}$ ) are widely available, many remain poorly  
17 characterized (e.g.,  $DW_{tot}$ ;  $OL$ ; autotrophic respiration,  $R_{auto}$ ) –even at the coarse resolution of biomes.  
18 This is a critical limitation not only for understanding forest C cycling, but also for quantifying forest-based  
19 climate change mitigation across forest biomes or ecozones (e.g., IPCC 2019).

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24 **118 Age trends and their variation across biomes**

25 Stand age is another important axis of variation in forest C cycling (Fig. 1). In 1969, E.P. Odum's "The  
26 Strategy of Ecosystem Development" laid out predictions as to how forest energy flows and organic matter  
27 stocks vary with stand age (Odum 1969). Although the conceptualization of the C cycle in this paper was  
28 simplistic by current standards, the paper was foundational in framing the theory around which research on  
29 the subject still revolves (Corman *et al* 2019), and the basic framework still holds, albeit with modest  
30 modifications (Fig. 1; Anderson-Teixeira *et al* 2013). Following stand-clearing disturbance,  $GPP$ ,  $NPP$ , and  
31 biomass of leaves ( $B_{foliage}$ ) and fine roots ( $B_{root-fine}$ ) increase rapidly and thereafter remain relatively  
32 stable ( $B_{foliage}$ ,  $B_{root-fine}$ , sometimes  $GPP$ ) or decline slightly ( $NPP$ , sometimes  $GPP$ ; e.g., Law *et al*  
33 2003, Pregitzer and Euskirchen 2004, Amiro *et al* 2010, Goulden *et al* 2011). The decline in  $NPP$  occurs  
34 because  $R_{auto}$  increases relative to  $GPP$  as forests age, corresponding to declining carbon use efficiency with  
35 stand age (DeLucia *et al* 2007, Collalti *et al* 2020). Heterotrophic respiration, most of which originates from  
36 the soil ( $R_{het-soil}$ ) remains relatively constant with stand age (Law *et al* 2003, Pregitzer and Euskirchen  
37 2004, Goulden *et al* 2011), with the result that net ecosystem production ( $NEP = GPP - R_{eco}$ , where  $R_{eco}$   
38 is total ecosystem respiration) is initially negative, increases to a maximum at intermediate ages, and  
39 declines—typically to a small positive value—thereafter (Law *et al* 2003, Pregitzer and Euskirchen 2004, Amiro  
40 *et al* 2010, Goulden *et al* 2011, Luyssaert *et al* 2008). The result is that biomass accumulates rapidly in young  
41 forests, followed by a slow decline to near zero in old forests (e.g., Lichstein *et al* 2009, Yang *et al* 2011).  
42 While these trends have been subject of fairly recent qualitative review (Anderson-Teixeira *et al* 2013), there  
43 is need for a synthetic, quantitative review taking advantage of the greatly expanded data now available.

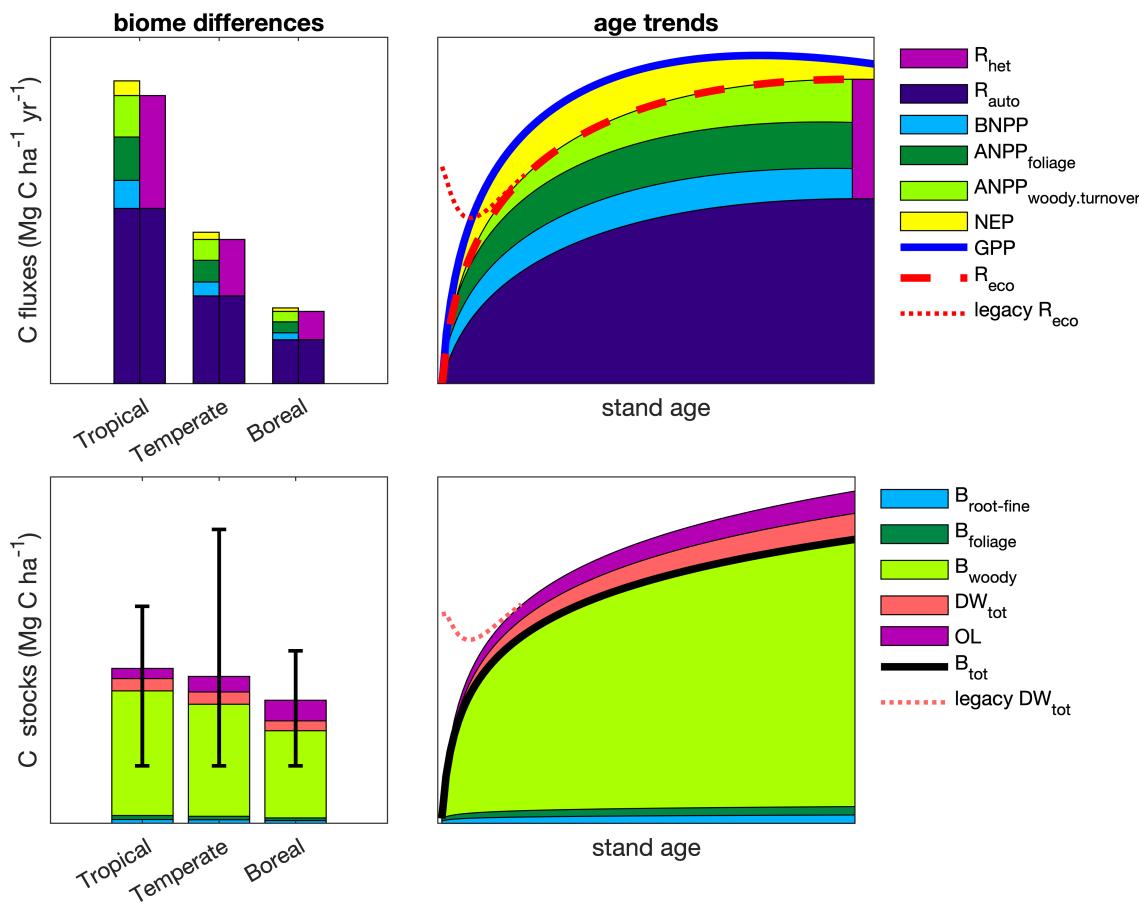
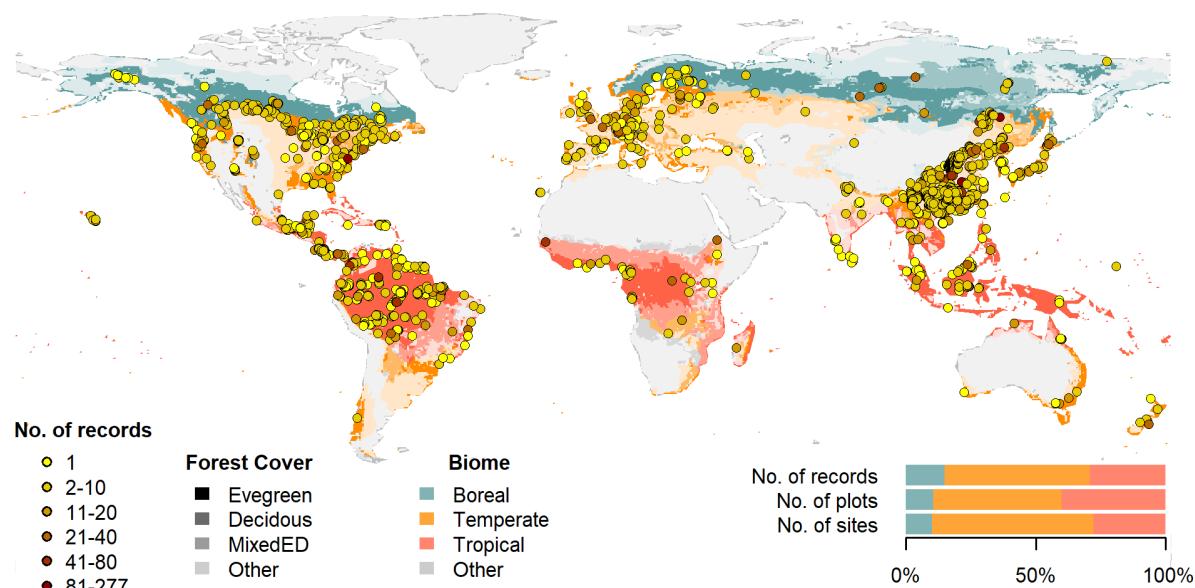


Figure 1 | Schematic diagram summarizing current understanding of biome differences and age trends in forest C cycling. Variables are defined in Table 1. Age trends, which represent idealized dynamics following a disturbance that removes all living vegetation, are an updated version of the classic figure from Odum (1969), with heavy lines corresponding to those in Odum's figure and  $NEP$  corresponding to Odum's 'net production'. Here,  $NEP$  consists primarily of woody aboveground net primary production ( $ANPP_{\text{woody}}$ ), while  $ANPP_{\text{woody.turnover}}$  is the sum of woody mortality and branch turnover. Dotted lines refer to decomposition of potential 'legacy' organic material produced prior to the disturbance and remaining at the site (e.g., standing and fallen dead wood,  $DW_{\text{tot}}$ ; soil organic matter). Error bars on C stocks plot represent within-biome variability, wherein mean biomass is highest in the tropics, but maximum biomass is highest in temperate regions.

In the past few decades, researchers have started asking how age trends—mostly in  $B_{\text{ag}}$  or total biomass ( $B_{\text{tot}}$ ) accumulation—vary across biomes. Early research on this theme showed that biomass accumulation rates during secondary succession increase with temperature on a global scale (Johnson *et al* 2000, Anderson *et al* 2006) and with water availability in the neotropics (Poorter *et al* 2016). Most recently, Cook-Patton *et al* (2020) reinforced these earlier findings with a much larger dataset and created a high-resolution global map of estimated potential C accumulation rates. However, there has been little synthesis of cross-biome differences in variables other than biomass and its accumulation rate (but see Cook-Patton *et al* (2020) for  $DW$ ,  $OL$ , and soil C accumulation in young stands). Given the important role of secondary forests in the current and future global C cycle, concrete understanding of age trends in C fluxes and stocks and how these vary across biomes is critical to better understanding of the global C cycle. Accurate estimates of C sequestration rates by regrowth forests are also critical for national greenhouse gas accounting under the IPCC framework (IPCC 2019, Requena Suarez *et al* 2019) and to quantifying the value of regrowth forests for climate change mitigation (Anderson-Teixeira and DeLucia 2011, Goldstein *et al* 2020).

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3     151 Here, we conduct a data-based review of carbon cycling from a stand to global level, and by biome and stand  
4     152 age, using the largest global compilation of forest carbon data, which is available in our open source Global  
5     153 Carbon Forest database (*ForC*; Fig. 2). Our goal is to provide a comprehensive synthesis on broad trends in  
6     154 forest C cycling that can serve as a foundation for improved understanding of global forest C cycling and  
7     155 highlight where key sources of uncertainty still reside.  
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34     Figure 2 | Map of sites included in this analysis. Symbols are colored according to the number of records at each site. Underlying  
35     map shows coverage of evergreen, deciduous, and mixed forests (shading differences; data from Jung et al. 2006) and biomes  
36     (color differences). Distribution of sites, plots, and records among biomes is shown in the inset.  
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## 38     156 Methods/ Design

40     157 This review synthesizes data from the *ForC* database (Fig. 2; <https://github.com/forc-db/ForC>;  
41     158 Anderson-Teixeira *et al* 2016, 2018). *ForC* amalgamates numerous intermediary data sets (*e.g.*, Luyssaert *et*  
42     159 *al* 2007, Bond-Lamberty and Thomson 2010, Cook-Patton *et al* 2020) and original studies. Original  
43     160 publications were referenced to check values and obtain information not contained in intermediary data sets,  
44     161 although this process has not been completed for all records. The database was developed with goals of  
45     162 understanding how C cycling in forests varies across broad geographic scales and as a function of stand age.  
46     163 As such, there has been a focus on incorporating data from regrowth forests (*e.g.*, Anderson *et al* 2006,  
47     164 Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age data when possible (83% of records in v.2.0;  
48     165 Anderson-Teixeira *et al* 2018). Particular attention was given to developing the database for tropical forests  
49     166 (Anderson-Teixeira *et al* 2016), which represented roughly one-third of records in *ForC* v2.0  
50     167 (Anderson-Teixeira *et al* 2018). Since publication of *ForC* v2.0, we imported three large additional databases  
51     168 into *ForC* via a combination of R scripts and manual edits. First, we imported (via R script) the Global  
52     169 Database of Soil Respiration Database (*SRDB* v4, 9488 records; Bond-Lamberty and Thomson 2010), and  
53     170 corrections and improvements to *SRDB* arising from this process were incorporated in *SRDB* v5 (Jian *et al*  
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3 171 2020). Second, we imported (via R script) the Global Reforestation Opportunity Assessment database  
4 172 (*GROA* v1.0, 10116 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020), which itself had drawn  
5 173 on an earlier version of *ForC*. Because all records in *GROA* were checked against original publications, these  
6 174 records were given priority over duplicates in *ForC* (Appendix S1). Third, we incorporated records of annual  
7 175 *NEP*, *GPP*, and *R<sub>eco</sub>* from the FLUXNET2015 dataset (Pastorello *et al* 2020), treating these records as  
8 176 authoritative when they duplicated earlier records (Appendix S1). We have also added data from individual  
9 177 publications, with a particular focus on productivity (e.g., Taylor *et al* 2017), dead wood, and ForestGEO  
10 178 sites (e.g., Lutz *et al* 2018, Johnson *et al* 2018). A record of data sets added to *ForC* over the course of its  
11 179 development is available at [https://github.com/forc-  
12 db/ForC/blob/master/database\\_management\\_records/ForC\\_data\\_additions\\_log.csv](https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv). The database  
13 180 version used for this analysis has been tagged as a new release on Github (v3.0) and assigned a DOI through  
14 181 Zenodo (DOI: TBD).

18 182 All measurements originally expressed in units of dry organic matter (*OM*) were converted to units of C  
19 183 using the IPCC default of  $C = 0.47 * OM$  (IPCC 2018). Duplicate or otherwise conflicting records were  
20 184 purged as described in Appendix S1, resulting in a total of 22265 records (56% size of total database).  
21 185 Records were filtered to remove plots that had undergone significant anthropogenic management or major  
22 186 disturbance since the most recent stand initiation event. Specifically, we removed plots with any record of  
23 187 managements manipulating CO<sub>2</sub>, temperature, hydrology, nutrients, or biota, as well as any plots whose site  
24 188 or plot name contained the terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized” (13.9% of  
25 189 duplicate-purged records). We also removed stands that had undergone any notable anthropogenic thinning  
26 190 or partial harvest (5.6% of duplicate-purged records). We retained sites that were grazed or had undergone  
27 191 low severity natural disturbances (<10% mortality) including droughts, major storms, fires, and floods. We  
28 192 removed all plots for which no stand history information had been retrieved (5.7% of duplicate-purged  
29 193 records). In total, this resulted in 17349 records (43.6% of the records in the database) being eligible for  
30 194 inclusion in the analysis.

31 195 We selected 23 annual flux and 11 C stock variables for inclusion in the analysis (Table 1). These different  
32 196 flux and stock variables represent different pools (e.g., aboveground biomass, root biomass, dead wood) and  
33 197 levels of combination (e.g., total net primary productivity, *NPP*, versus the individual elements of *NPP*  
34 198 such as foliage, roots, and branches). We did not analyze soil carbon, which is not a focus of the *ForC*  
35 199 database. Note that two flux variables, aboveground heterotrophic respiration (*R<sub>het-ag</sub>*) and total respiration  
36 200 (*R<sub>het</sub>*), were included for conceptual completeness but had no records in *ForC* (Table 1). Records for our  
37 201 focal variables represented 90.3% of the total records eligible for inclusion. For this analysis, we combined  
38 202 some of *ForC*'s specific variables into more broadly defined variables. Specifically, net ecosystem exchange  
39 203 (measured by eddy-covariance; Baldocchi *et al* 2001) and biometric estimates of *NEP* were combined into  
40 204 the single variable *NEP* (Table 1). Furthermore, for *NPP*, aboveground *NPP* (*ANPP*), and the litterfall  
41 205 component of *ANPP* (*ANPP<sub>litterfall</sub>*), *ForC* variables specifying inclusion of different components were  
42 206 combined (e.g., measurements including or excluding fruit and flower production and herbivory).  
43 207 Throughout *ForC*, for all measurements drawing from tree census data (e.g., biomass, productivity), trees  
44 208 were censused down to a minimum diameter breast height (DBH) threshold of 10 cm or less. All records were  
45 209 measured directly or derived from field measurements.

46 210 211 We grouped forests into four broad biome types based on climate zones and dominant vegetation type  
47 212 (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age

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		
<b>Annual fluxes</b>						
<i>NEP</i>	net ecosystem production or net ecosystem exchange (+ indicates C sink)	329	146	88	n.s.	+; xB
<i>GPP</i>	gross primary production ( $NPP + R_{auto}$ or $NEP + R_{eco}$ )	303	115	84	TrB > TeB $\geq$ TeN $\geq$ BoN	+; xB
<i>NPP</i>	net primary production ( $ANPP + BNPP$ )	214	112	74	TrB > TeB $\geq$ TeN $>$ BoN	n.s.
<i>ANPP</i>	aboveground <i>NPP</i>	343	236	131	TrB > TeB $\geq$ TeN $>$ BoN	+; xB
<i>ANPP<sub>woody</sub></i>	woody production ( $ANPP_{stem} + ANPP_{branch}$ )	64	53	37	n.s.	+
<i>ANPP<sub>stem</sub></i>	woody stem production	217	190	117	TrB > TeN $\geq$ TeB $\geq$ BoN	n.s.
<i>ANPP<sub>branch</sub></i>	branch turnover	69	59	42	TrB > TeB $\geq$ TeN	n.s.
<i>ANPP<sub>foliage</sub></i>	foliage production, typically estimated as annual leaf litterfall	162	132	88	TrB > TeB $\geq$ TeN $>$ BoN	+
<i>ANPP<sub>litterfall</sub></i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	82	70	55	n.s.	+
<i>ANPP<sub>repro</sub></i>	production of reproductive structures (flowers, fruits, seeds)	51	44	34	n.t.	n.t.
<i>ANPP<sub>folivory</sub></i>	foliar biomass consumed by folivores	20	12	11	n.t.	n.t.
<i>M<sub>woody</sub></i>	woody mortality—i.e., $B_{ag}$ of trees that die	18	18	18	n.t.	n.t.
<i>BNPP</i>	belowground NPP ( $BNPP_{coarse} + BNPP_{fine}$ )	148	116	79	TrB > TeN $\geq$ TeB $\geq$ BoN	+
<i>BNPP<sub>coarse</sub></i>	coarse root production	77	56	36	TeN $\geq$ TrB	n.s.
<i>BNPP<sub>fine</sub></i>	fine root production	123	99	66	n.s.	+
<i>R<sub>eco</sub></i>	ecosystem respiration ( $R_{auto} + R_{het}$ )	213	98	70	TrB > TeB $\geq$ TeN	+
<i>R<sub>auto</sub></i>	autotrophic respiration ( $(R_{auto-ag} + R_{root})$ )	24	23	15	n.t.	n.t.
<i>R<sub>auto-ag</sub></i>	aboveground autotrophic respiration (i.e., leaves and stems)	2	2	1	n.t.	n.t.
<i>R<sub>root</sub></i>	root respiration	181	139	95	TrB $\geq$ TeB	+
<i>R<sub>soil</sub></i>	soil respiration ( $R_{het-soil} + R_{root}$ )	627	411	229	TrB > TeB $>$ TeN $\geq$ BoN	n.s.
<i>R<sub>het-soil</sub></i>	soil heterotrophic respiration	197	156	100	TrB > TeB $\geq$ TeN	n.s.
<i>R<sub>het-ag</sub></i>	aboveground heterotrophic respiration	0	0	0	-	-
<i>R<sub>het</sub></i>	heterotrophic respiration ( $(R_{het-ag} + R_{het-soil})$ )	0	0	0	-	-
<b>Stocks</b>						
<i>B<sub>tot</sub></i>	total live biomass ( $B_{ag} + B_{root}$ )	188	157	87	TrB $\geq$ TeB $>$ BoN	+; xB
<i>B<sub>ag</sub></i>	aboveground live biomass ( $B_{ag-wood} + B_{foliage}$ )	4466	4072	621	TrB $\geq$ TeN $\geq$ TeB $>$ BoN	+; xB
<i>B<sub>ag-wood</sub></i>	woody component of aboveground biomass	115	102	64	TeN > TrB $\geq$ BoN	+; xB
<i>B<sub>foliage</sub></i>	foliage biomass	134	115	72	TeN > TrB $\geq$ BoN $\geq$ TeB	+; xB
<i>B<sub>root</sub></i>	total root biomass ( $B_{root-coarse} + B_{root-fine}$ )	2329	2298	360	n.s.	+; xB
<i>B<sub>root-coarse</sub></i>	coarse root biomass	134	120	73	TeN > TeB $\geq$ BoN	+; xB
<i>B<sub>root-fine</sub></i>	fine root biomass	226	180	109	n.s.	+; xB
<i>DW<sub>tot</sub></i>	deadwood ( $DW_{standing} + DW_{down}$ )	79	73	42	n.t.	+; xB
<i>DW<sub>standing</sub></i>	standing dead wood	36	35	22	n.t.	n.t.
<i>DW<sub>down</sub></i>	fallen dead wood, including coarse and sometimes fine woody debris	278	265	37	n.t.	+; xB
<i>OL</i>	organic layer / litter / forest floor	474	413	115	n.s.	+; xB

\* TrB: Tropical, TeB: Temperate Broadleaf, TeN: Temperate Needleleaf, BoN: Boreal, n.s.: no significant differences, n.t.: not tested

† + or -: significant positive or negative trend, xB: significant age x biome interaction, n.s.: no significant age trend, n.t.: not tested

213 classifications (young and mature). Climate zones (Fig. 2) were defined based on site geographic coordinates  
 214 according to Köppen-Geiger zones (Rubel and Kottke 2010). We defined the tropical biome as including all

equatorial (A) zones, temperate biomes as including all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and the boreal biome as including 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. We defined leaf type (broadleaf / needleleaf) based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYNMAP; Jung *et al* 2006). For young tropical forests imported from *GROA* but not yet classified by leaf type, we assumed that all were broadleaf, consistent with the rarity of naturally regenerating needleleaf forests in the tropics. We also classified forests as “young” (< 100 years) or “mature” ( $\geq 100$  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 geographic coordinates (0.4% of sites in full database) or records of stand age (5.7% of records in full database). We also excluded records of stand age = 0 year (0.8% of records in full database). In total, our analysis retained 11923 records. Numbers of records by biome and age class are given in Table S1.

Data were summarized to produce schematics of C cycling for mature forests of each biome. To obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot. Values were then averaged across geographically distinct areas, defined as 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.

We tested whether the C budgets described above “closed”—*i.e.*, whether they were internally consistent. Specifically, we first defined relationships among variables: for example,  $NEP = GPP - R_{eco}$ ,  $BNPP = BNPP_{coarse} + BNPP_{fine}$ ,  $DW_{tot} = DW_{standing} + DW_{down}$ . Henceforth, we refer to the variables on the left side of the equation as “aggregate” fluxes or stocks, and those that are summed as “component” fluxes or stocks, noting that the same variable can take both aggregate and component positions in different relationships. We considered the C budget for a given relationship “closed” when component variables summed to within one standard deviation of the aggregate variable.

To test for differences across mature forest biomes, we also examined how stand age impacted fluxes and stocks, employing a mixed effects model (“lmer” function in “lme4” R package; Bates *et al* 2015) 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. This analysis was run for variables with records for at least seven distinct geographic areas in more than one biome, excluding any biomes that failed this criteria (Table 1).

To test for age trends in young (<100yrs) forests, 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. This analysis was run for variables with records for at least three distinct geographic areas in more than one biome, excluding any biomes that failed this criteria (Table 1). 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  $\times$  stand.age interaction was included in the model. We note that the logarithmic function fit in this analysis does not always correspond to theoretical expectations (Fig. 1); however, data limitations did not support fitting of functions with more parameters or reliable comparison of different functional forms. Within the data constraints, we deemed a logarithmic function to be the most appropriate functional form for the majority of variables.

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3     256 To facilitate the accessibility of our results and data, and to allow for rapid updates as additional data  
4     257 become available, we automated all database manipulation, analyses, and figure production in R (Team  
5     258 2020).

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8     259 **Review Results/ Synthesis**

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10     260 **Data Coverage**

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12     261 Of the 39762 records in *ForC* v3.0, 11923 met our strict criteria for inclusion in this study (Fig. 2). These  
13     262 records were distributed across 5062 plots in 865 distinct geographic areas. Of the 23 flux and 11 stock  
14     263 variables mapped in our C cycle diagrams (Figs. 3-6, S1-S4), *ForC* contained sufficient mature forest data for  
15     264 inclusion in our statistical analyses (*i.e.*, records from  $\geq 7$  distinct geographic areas) for 20 fluxes and 9 stocks  
16     265 in tropical broadleaf forests, 15 fluxes and 8 stocks in temperate broadleaf forests, 14 fluxes and 7 stocks in  
17     266 temperate conifer forests, and 8 fluxes and 7 stocks in boreal forests. For regrowth forests (<100 yrs), *ForC*  
18     267 contained sufficient data for inclusion in our statistical analyses (*i.e.*, records from  $\geq 3$  distinct geographic  
19     268 areas) for 11 fluxes and 10 stocks in tropical broadleaf forests, 16 fluxes and 10 stocks in temperate broadleaf  
20     269 forests, 16 fluxes and 10 stocks in temperate conifer forests, and 14 fluxes and 9 stocks in boreal forests.

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23     270 **C cycling in mature forests**

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25     271 Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq$   
26     272 100 years old and with no known major natural or anthropogenic disturbance are presented in Figures 3-6  
27     273 (and available in tabular format in the *ForC* release accompanying this publication:  
28  
29     274 [ForC/numbers\\_and\\_facts/ForC\\_variable\\_averages\\_per\\_Biome.csv](#)).

30  
31     275 For variables with records from  $\geq 7$  distinct geographic areas, these ensemble C budgets met our criteria for  
32     276 budget “closure”. That is, component variables summed to within one standard deviation of their respective  
33     277 aggregate variables in all but one instance. In the temperate conifer biome, the average composite measure of  
34     278 root biomass ( $B_{root}$ ) was less than the combined average value of coarse and fine root biomass ( $B_{root-coarse}$   
35     279 and  $B_{root-fine}$ , respectively). This lack of closure was driven by very high estimates of  $B_{root-coarse}$  from  
36     280 high-biomass forests of the US Pacific Northwest (Fig. S25).

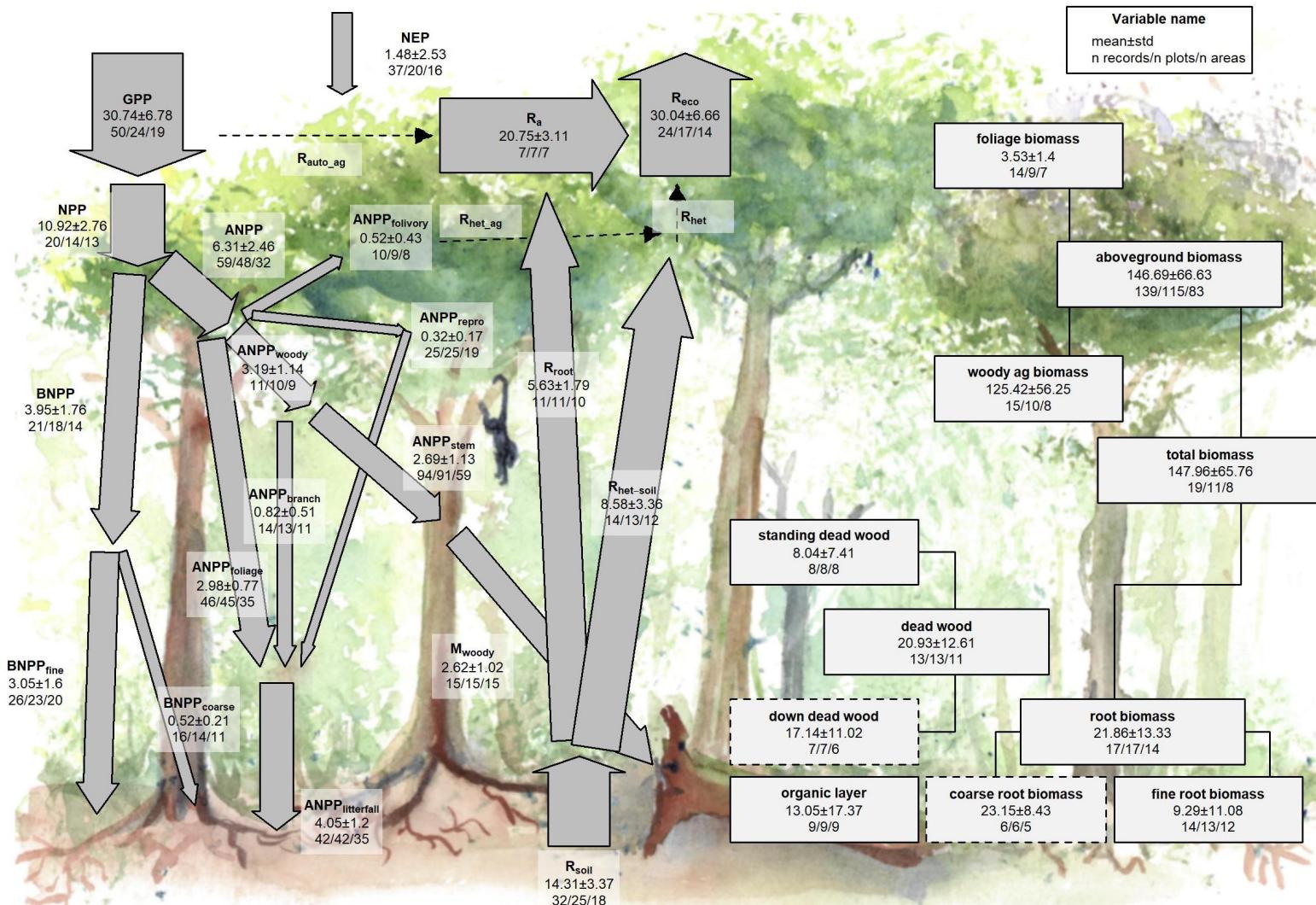


Figure 3 | C cycle diagram for mature tropical broadleaf forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

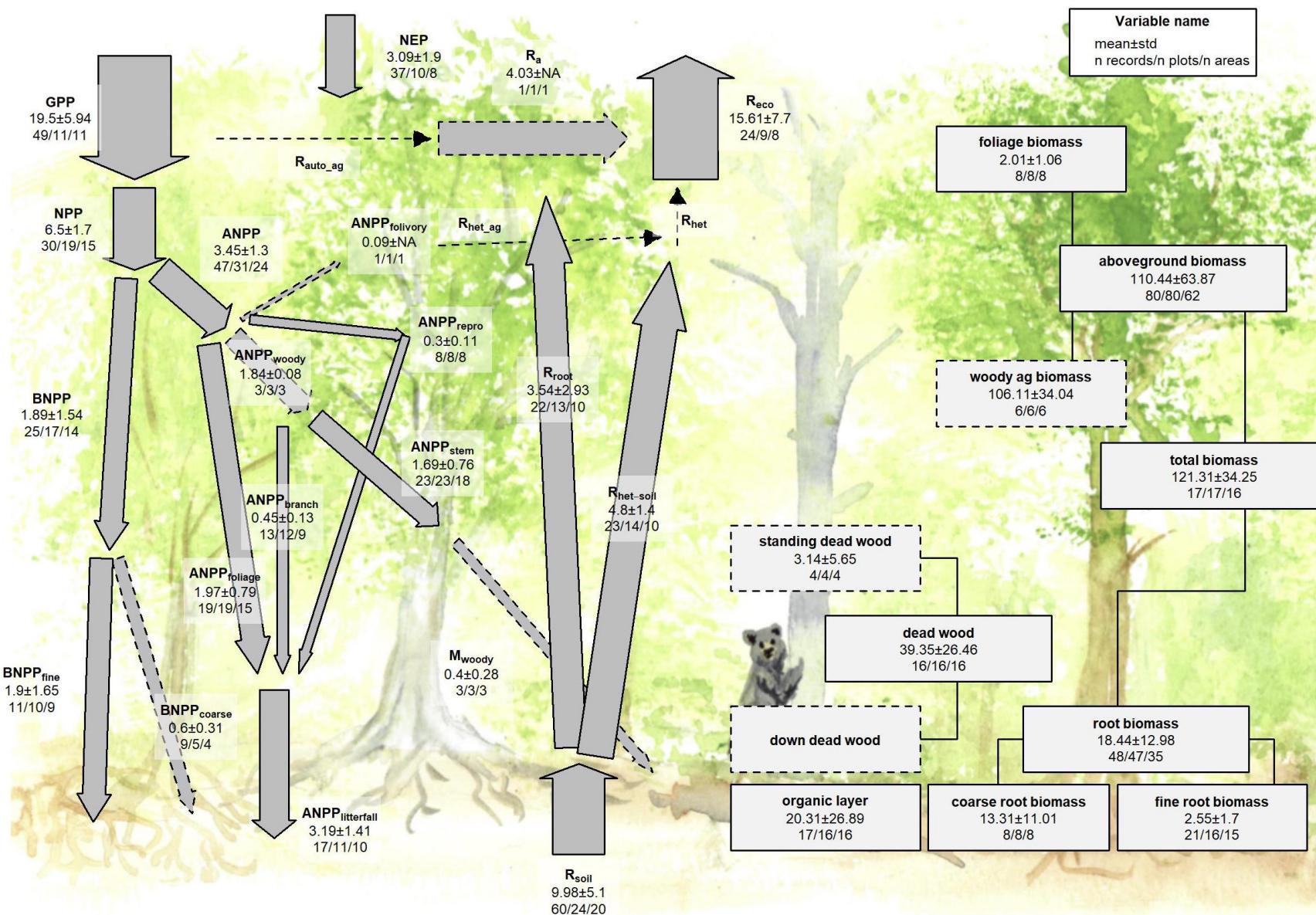


Figure 4 | C cycle diagram for mature temperate broadleaf forests. Arrows indicate fluxes ( $Mg C ha^{-1} yr^{-1}$ ); boxes indicate stocks ( $Mg C ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

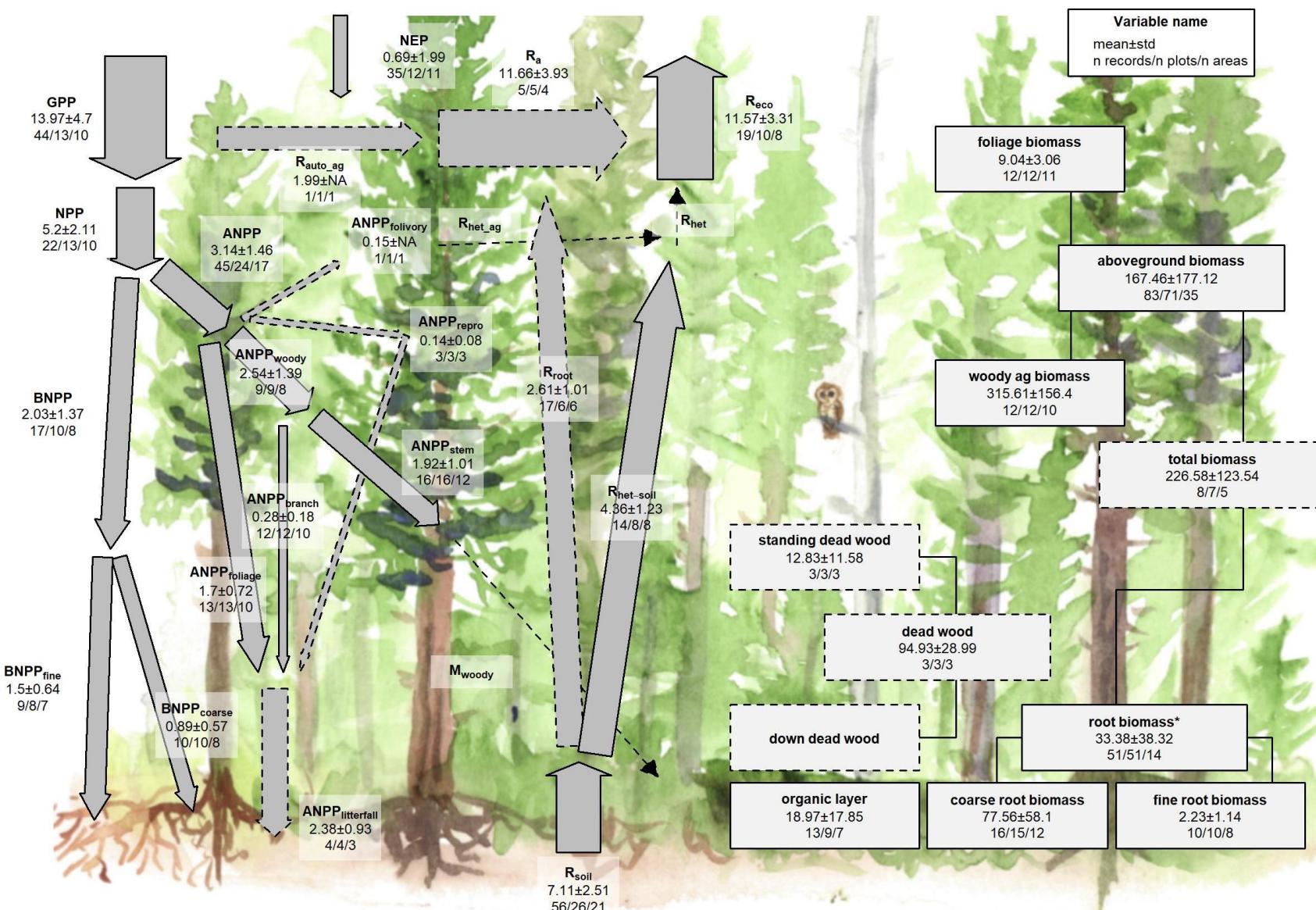


Figure 5 | C cycle diagram for mature temperate conifer forests. Arrows indicate fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ); boxes indicate stocks ( $\text{Mg C ha}^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30). The temperate conifer biome in particular is subject to high variability, with highest fluxes and stocks in the high-biomass forests of the US Pacific Northwest. An asterisk after a variable name indicates lack of C cycle closure.

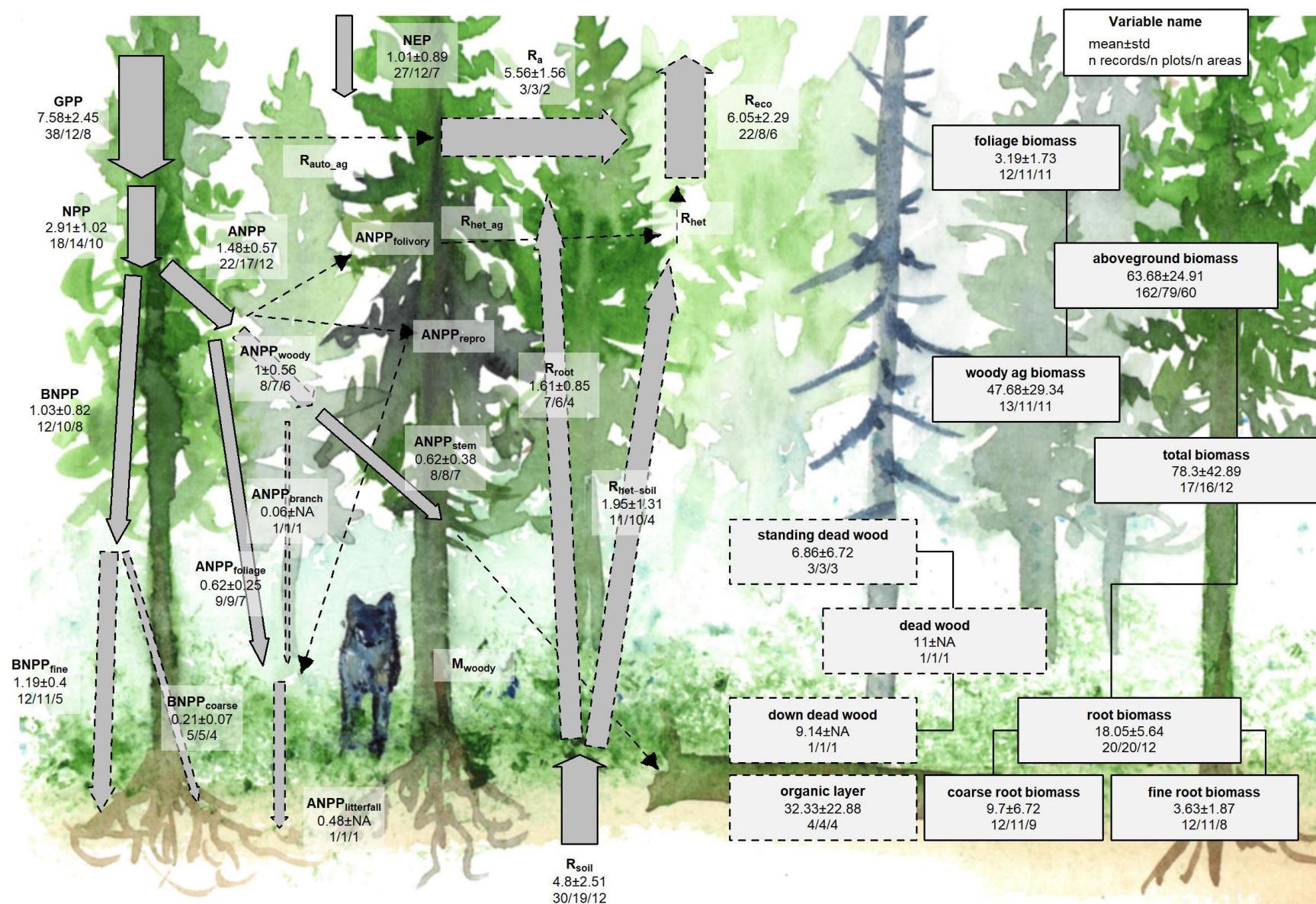


Figure 6 | C cycle diagram for mature boreal conifer forests. Arrows indicate fluxes ( $Mg C ha^{-1} yr^{-1}$ ); boxes indicate stocks ( $Mg C ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

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3 There were sufficient data to assess differences among biomes in mature forest values for 15 flux variables, and  
4 significant differences among biomes were detected for 12 variables (Table 1). In all of these cases—including  
5 C fluxes into, within, and out of the ecosystem—C fluxes were highest in tropical forests, intermediate in  
6 temperate (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 7, S5-S19). Differences  
7 between tropical and boreal forests were always significant, with temperate forests intermediate and  
8 significantly different from one or both. Fluxes tended to be numerically greater in temperate broadleaf than  
9 temperate conifer forests, but the difference was never statistically significant. This pattern held for the  
10 following variables:  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{stem}$ ,  $ANPP_{branch}$ ,  $ANPP_{foliage}$ ,  $BNPP$ ,  $R_{eco}$ ,  $R_{root}$ ,  
11  $R_{soil}$ , and  $R_{het-soil}$ . For two of the variables without significant differences among biomes ( $ANPP_{litterfall}$   
12 and  $BNPP_{fine}$ ; Figs. S12 and S15, respectively), the same general trends applied but were not statistically  
13 significant. Another exception was for  $BNPP_{root-coarse}$ , where all records came from high-biomass forests in  
14 the US Pacific Northwest, resulting in marginally higher values for the temperate conifer biome (Fig. S14;  
15 differences significant in mixed effects model but not in post-hoc pairwise comparison).  
16  
17 The most notable exception to the pattern of decreasing flux per unit area from tropical to boreal biomes  
18 was  $NEP$ , with no significant differences across biomes but with the largest average in temperate broadleaf  
19 forests, followed by tropical, boreal, and temperate conifer forests (Figs. 7, S5). For all biomes,  $NEP$  was  
20 positive, with 95% confidence intervals excluding zero.  
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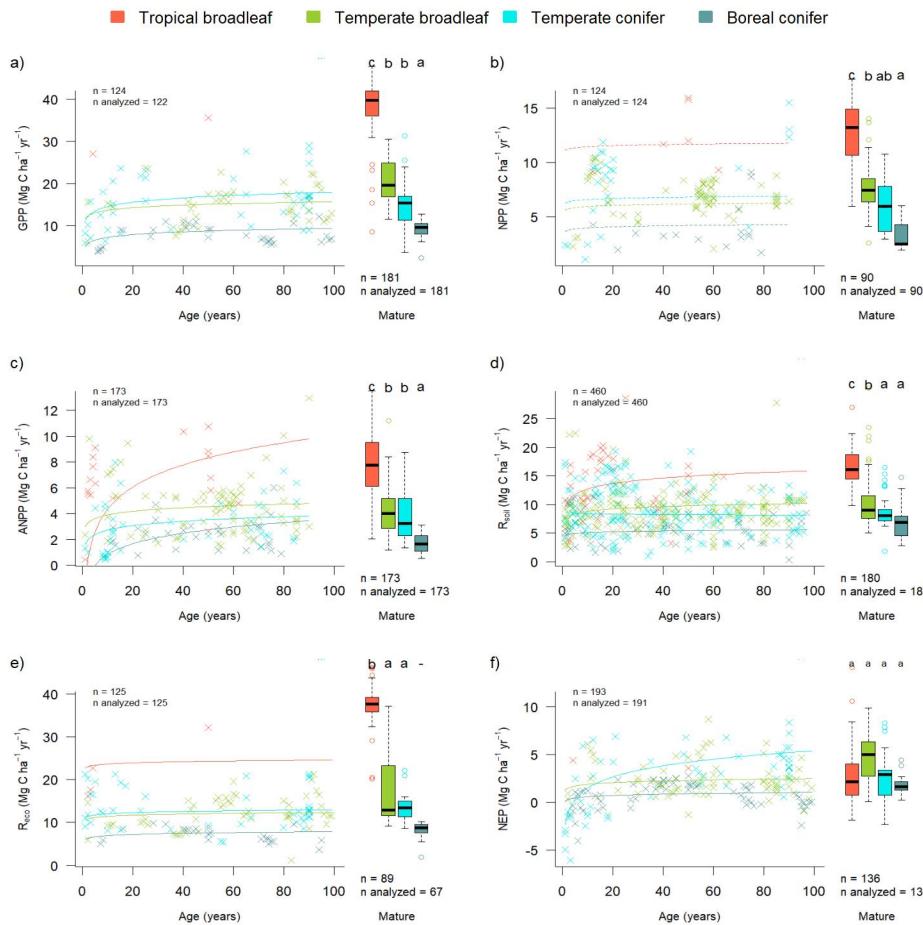


Figure 7 | Age trends and biome differences in some of the major C fluxes: (a)  $GPP$ , (b)  $NPP$ , (c)  $ANPP$ , (d)  $R_{soil}$ , (e)  $R_{reco}$ , and (f)  $NEP$ . In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of  $\log_{10}(\text{age})$  and biome. The fitted line indicates the effect of age (solid lines: significant at  $p < 0.05$ , dashed lines: non-significant), and non-parallel lines indicate a significant  $\log_{10}(\text{age}) \times \text{biome}$  interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each flux with sufficient data, along with maps showing geographic distribution of the data, are given in the Supplement (Figs. S5-S19).

Biome differences were less consistent across C stocks than fluxes (Figs. 8, S20-S30). There were sufficient data to assess mature forest biome differences for nine stock variables, and significant differences among biomes were detected for five variables ( $B_{tot}$ ,  $B_{ag}$ ,  $B_{ag-wood}$ ,  $B_{foliage}$ ,  $B_{root-coarse}$ ; Table 1). For  $B_{tot}$  and  $B_{ag}$ , tropical broadleaf forests had the highest mean biomass and boreal forests the lowest, with intermediate means for temperate broadleaf and needleleaf forests (temperate needleleaf excluded from  $B_{tot}$  analysis because of insufficient data; Figs. S20, S21). However, maximum values for these variables – along with all other stocks including live or standing woody biomass ( $B_{ag-wood}$ ,  $B_{root}$ ,  $B_{root-coarse}$ ,  $DW_{tot}$ ,  $DW_{standing}$ ) – consistently occurred in temperate biomes (Figs. 1, 8, S20-S30). For variables that were disproportionately sampled in such high-biomass forests ( $B_{ag-wood}$ ,  $B_{foliage}$ , and  $B_{root-coarse}$ ; disproportionately sampled in the US Pacific Northwest), temperate conifer forests had significantly higher stocks than the other biomes.

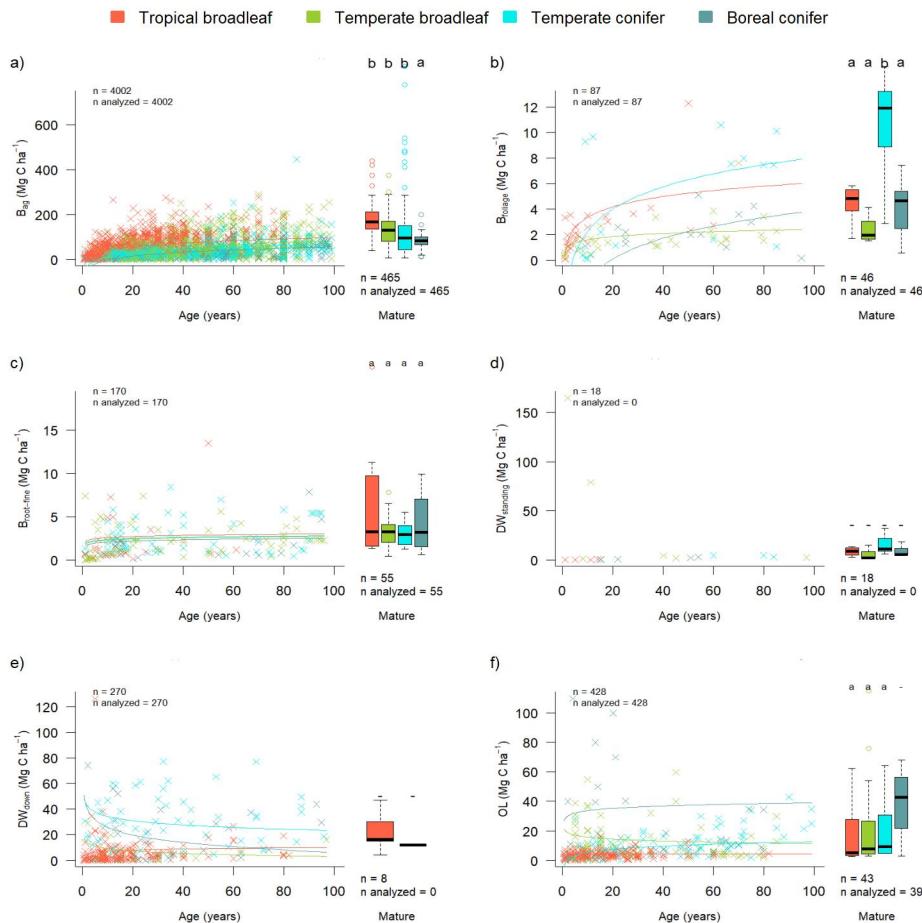
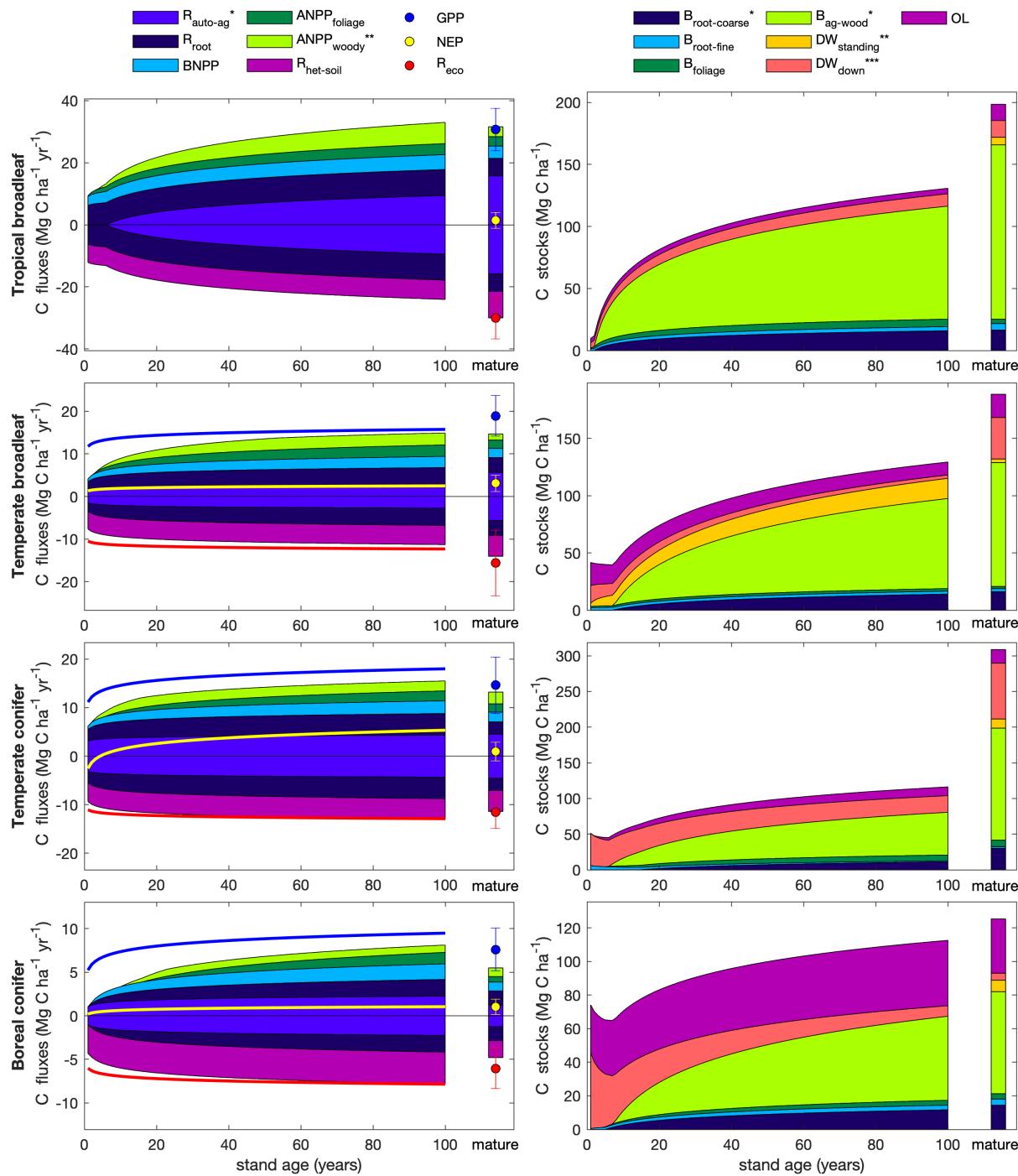


Figure 8 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of  $\log_{10}(\text{age})$  and biome. The fitted line indicates the effect of age (solid lines: significant at  $p < 0.05$ , dashed lines: non-significant), and non-parallel lines indicate a significant  $\log_{10}(\text{age}) \times \text{biome}$  interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each stock with sufficient data, along with maps showing geographic distribution of the data, are given in the Supplement (Figs. S20-S30).

## 42 C cycling in young forests

43 C fluxes commonly increased significantly with stand age (Tables 1, S2, Figs. 7, 9, S5-S30). *ForC* contained  
 44 16 C flux variables with sufficient data for analyses of age trends in young forests (see Methods). Of these,  
 45 ten increased significantly with  $\log_{10}[\text{age}]$ : *NEP*, *GPP*, *ANPP*, *ANPP<sub>woody</sub>*, *ANPP<sub>foliage</sub>*,  
 46 *ANPP<sub>litterfall</sub>*, *BNPP*, *BNPP<sub>fine</sub>*, *R<sub>eco</sub>*, and *R<sub>root</sub>*. The remaining six – *NPP*, *ANPP<sub>stem</sub>*, *ANPP<sub>branch</sub>*,  
 47 *BNPP<sub>coarse</sub>*, *R<sub>soil</sub>*, and *R<sub>het-soil</sub>* – displayed no significant relationship to stand age.  
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 49 Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling  
 50 generally most rapid in the tropics and slowest in boreal forests (Table 1, Figs. 7, S5-S30). The single  
 51 exception was *ANPP<sub>stem</sub>*, for which temperate broadleaf and conifer forests had flux rates similar to tropical  
 52 forests. Notably, and in contrast to the lack of biome differences in *NEP* for mature forests (Fig. 7), the  
 53 tendency for temperate forests to have greater fluxes than boreal forests held for *NEP* in regrowth forests  
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319 (tropical forests excluded because of insufficient data).



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51 Figure 9 | Age trends in C cycling. Selection of variables for plotting seeks to maximize sample size and broad geographic  
52 representation while representing all elements of C cycle. Error bars on mature forest flux estimates indicate  $\pm 1$  standard  
53 deviation. Asterisks indicate variables whose age trends were calculated based on other variables (\* young and mature  
54 forests; \*\* young forests only; \*\*\* mature forests only), as follows. For all forests:  $B_{ag-wood} = \max(0, B_{ag} - B_{foliage})$ ,  
55  $B_{root-coarse} = \max(0, B_{root} - B_{root-fine})$ ,  $DW_{standing} = \max(0, DW_{tot} - DW_{down})$ . For tropical forests:  $ANPP_{woody} =$   
56  $\max(0, ANPP - ANPP_{foliage})$ ,  $R_{auto-ag} = R_{auto} - R_{root}$ , where  $R_{auto} = NPP(1/CUE - 1)$  and  $CUE=0.46$  (Collati et  
57 al. 2020). For non-tropical forests:  $ANPP_{woody} = \min(ANPP_{stem}, ANPP_{woody})$ ,  $R_{auto-ag} = R_{eco} - R_{soil}$ . Note that there  
58 remain substantial uncertainties as to the functional form of age trends and discrepancies in closure among related variables.  
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“Closure” and internal consistency of the C flux budget was less successful for young than mature forests (Figs. 9). Summed regression equations for  $R_{soil-het}$  and  $R_{root}$  were generally very close to  $R_{soil}$ . In assessing the C budget of young forests, we calculated  $R_{auto-ag}$  as the difference between  $R_{eco}$  and  $R_{soil}$  (except for tropical forests, which had insufficient  $R_{eco}$  data), effectively guaranteeing near-closure of the CO<sub>2</sub> efflux (respiration) portion of the budget (negative values in Figs. 9). In contrast, the CO<sub>2</sub> influx portion of the budget generally did not “close”: the sum of  $R_{auto}$  ( $R_{root} + R_{auto-ag}$ , as described above) and components of  $NPP$  consistently fell short of  $GPP$ , particularly in young stands (range across forest types and ages: 0.9-7.6 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). Moreover, there was not consistent budget closure among the components of  $NPP$ , and substantially different age trends resulting from the sum of components versus total  $NPP$  (Figs. 9). Although age trends of young forests often converged towards mature forest averages, there were also some discrepancies between young forest trends and mature forest averages (Figs. 7, 9, S5-S30), most notably including a tendency for higher fluxes in regrowth boreal forests than in their mature counterparts (Fig. 9).

In terms of C stocks, ten variables (all but standing deadwood,  $DW_{standing}$ ) had sufficient data to test for age trends (Table 1, Figs. 8, S20-S30). All of these displayed a significant overall increase with  $\log_{10}[stand.age]$ . Age × biome interactions were also significant for all ten of these C stock variables (Table S2), with living C stocks tending to accumulate more rapidly during the early stages of forest regrowth in tropical forests (Figs. 8, 9, S20-S30). In the case of two non-living C stocks ( $DW_{down}$  and  $OL$ ), age × biome interactions were such that age trends were positive in some biomes and negative in others. Specifically,  $DW_{down}$  declined with age in temperate and boreal forests, compared to an increase with age in tropical forests (Figs. 8, 9, S29). Similarly,  $OL$  declined slightly with age in temperate broadleaf forests, contrasting an increase in the other three biomes (Figs. 8, 9, S30). Again, there were some discrepancies between young forest trends and mature forests, most notably including generally higher C stocks in mature forests relative to their 100-year counterparts, particularly for temperate conifer forests (with discrepancies again driven by differences in geographic representation) and, to a lesser extent, tropical broadleaf forests (Fig. 9).

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3     **344 Discussion**  
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6     345 *ForC* v3.0 provided unprecedented coverage of most major variables, yielding a broad picture of C cycling in  
7     346 the world's major forest biomes. Carbon cycling rates generally increased from boreal to tropical regions and  
8     347 with stand age (Figs. 1, 9). Specifically, most C fluxes were highest in tropical forests, intermediate in  
9     348 temperate (broadleaf or conifer) forests, and lowest in boreal forests – a pattern that generally held for  
10     349 regrowth as well as mature forests (Figs. 1, 7- 8, 9). The notable exception was mature forest *NEP*, which,  
11     350 as the difference between *GPP* and *R<sub>eco</sub>*, was statistically indistinguishable across biomes (Fig. 7f). There  
12     351 was also little directional variation in mean mature forest C stocks (biomass, dead wood, and organic layer)  
13     352 across biomes, although maximum values for the majority of stocks (all including live or standing woody  
14     353 biomass) occurred in temperate biomes (Figs. 1, 3-6, 8). Consistent with theory and previous studies (Fig.  
15     354 1), the majority of flux variables, together with most live biomass pools, increased significantly with stand  
16     355 age (Table 1; Figs. 7- 9, S5-S30). Together, these results indicate that, moving from cold to tropical climates  
17     356 and from young to old stands, there is a general acceleration of C cycling, whereas C stocks and *NEP* of  
18     357 mature forests, which are defined by the differences between in- and out- fluxes, do not vary systematically  
19     358 across biomes. Together, these results refine and expand our understanding of C cycling in mature forests,  
20     359 while providing the first global-scale analysis of age trends in multiple forest C stocks and fluxes (Figs. 9).  
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25     **360 C cycling across biomes**  
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28     361 Our analysis reveals that carbon cycling is most rapid in the tropics and slowest in boreal regions, including  
29     362 C fluxes into (*GPP*), within (e.g., *NPP* and its components), and out of (e.g., *R<sub>soil</sub>*, *R<sub>eco</sub>*) the ecosystem.  
30     363 For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes  
31     364 generally decline with latitude – or increase with temperature – on a global scale (e.g., Luyssaert *et al* 2007,  
32     365 Gillman *et al* 2015, Li and Xiao 2019, Banbury Morgan *et al* n.d.). This consistency is not surprising,  
33     366 particularly given commonality in the data analyzed or used for calibration. The finding that these patterns  
34     367 hold consistently across numerous fluxes, while consistent with theoretical expectations (Fig. 1), is  
35     368 novel to this analysis (but see Banbury Morgan *et al* n.d. for nine autotrophic fluxes).  
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37     369 The notable exception to the pattern of fluxes decreasing from tropical to boreal regions is *NEP*, which  
38     370 showed no significant differences across biomes, albeit with the highest mean in temperate broadleaf forests  
39     371 (Fig. 7f). Unlike the other C flux variables, *NEP* does not characterize the rate at which C cycles through  
40     372 the ecosystem, but, as the balance between *GPP* and *R<sub>eco</sub>*, represents net CO<sub>2</sub> sequestration (or release) by  
41     373 the ecosystem (Fig. 1). *NEP* tends to be relatively small in mature forest stands, which accumulate carbon  
42     374 slowly relative to younger stands, if at all (Fig. 1; Luyssaert *et al* 2008, Amiro *et al* 2010, Besnard *et al*  
43     375 2018). It is therefore consistent with theory – and with previous research (Luyssaert *et al* 2007) – that there  
44     376 are no pronounced differences across biomes. Rather, variation in *NEP* of mature forests appears to be  
45     377 controlled less by climate and more by other factors including moderate disturbances (Curtis and Gough  
46     378 2018) or disequilibrium of *R<sub>soil</sub>* relative to C inputs (e.g., in peatlands where anoxic conditions inhibit  
47     379 decomposition; Wilson *et al* 2016). The fact that mature temperate broadleaf forests have a higher mean  
48     380 than the other biomes may reflect the fact that most of these forests are older secondary forests that, while  
49     381 classified here as mature, are still accumulating carbon (Curtis and Gough 2018).  
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52     382 In contrast to the patterns observed for *NEP* in mature stands, *NEP* of stands between 20 and 100 years of  
53     383 age varied across biomes, being lowest in boreal forests, intermediate in temperate broadleaf forests, and  
54     384 highest in temperate conifer forests (with insufficient data to assess tropical forests; Figs. 7, S5). This is  
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3 consistent with findings that live biomass accumulation rates ( $\Delta B_{ag}$  or  $\Delta B_{tot}$ ) during early secondary  
4 succession decrease with latitude (Figs. 8a, S20-S30; Anderson *et al* 2006, Cook-Patton *et al* 2020). Note,  
5 though, that *NEP* includes not only  $\Delta B_{tot}$ , but also changes in *DW<sub>tot</sub>*, *OL*, and soil carbon (not analyzed  
6 here). Biome differences in the accumulation rates of *DW*, *OL*, and soil C have not been detected, in part  
7 because these variables do not consistently increase with stand age (Figs. 1, 8, S27-S30, and see discussion  
8 below; Cook-Patton *et al* 2020).

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11 For regrowth forests, little was previously known about cross-biome differences in carbon fluxes, and we are  
12 not aware of any previous large-scale comparisons of C fluxes that have been limited to regrowth forests.  
13 Thus, this analysis was the first to examine flux trends in regrowth forests across biomes. The observed  
14 tendency for young forest fluxes to decrease from tropical to boreal regions paralleled patterns in mature  
15 forests (Figs. 7, 9, S5-S19), suggesting that regrowth forests follow latitudinal trends in carbon cycling  
16 similar to those of mature forests (e.g., Banbury Morgan *et al* n.d.).

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19 In contrast to C fluxes and biomass accumulation rates in regrowth forests, stocks showed less systematic  
20 variation across biomes (c.f. Fig. 1). For aboveground biomass, which is the variable in *ForC* with broadest  
21 geographical representation, the modest trend of declining biomass from tropical to boreal regions mirrors  
22 observations from spaceborne lidar that reveal a decline in aboveground biomass (for all forests, including  
23 secondary) with latitude across the N hemisphere (Hu *et al* 2016). The highest- biomass forests on Earth are,  
24 however, found in coastal temperate climates of both the southern and northern hemisphere (Figs. 1, 8a;  
25 Keith *et al* 2009, Smithwick *et al* 2002, Hu *et al* 2016). Disproportionate representation of forests in one such  
26 region—the US Pacific Northwest—biased estimates of temperate conifer fluxes and stocks for some variables  
27 and was responsible for all of the anomalous results described here (e.g., lack of complete C budget closure,  
28 anomalous trend across biomes for *BNPP<sub>coarse</sub>*). Thus, biome differences should always be interpreted  
29 relative to the geographic distribution of sampling, which only rarely covers the majority of forested area  
30 within a biome.

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33 Whereas aboveground biomass can be remotely sensed (albeit with significant uncertainties; Ploton *et al*  
34 2020) and receives significant research attention, far less is known about geographical variation in deadwood  
35 and organic layer (*OL*) across biomes, which has proved a limitation for C accounting efforts (Pan *et al*  
36 2011). Although these stocks can be important—exceeding 100 Mg C ha<sup>-1</sup> in some stands (Figs. 8, S27-S29),  
37 this study is the first to synthesize deadwood data on a global scale (but see Cook-Patton *et al* 2020 for  
38 young forests). Unfortunately, data remain too sparse for statistical comparison across biomes (Figs. 8,  
39 S27-S29; but see below for age trends), pointing to a need for more widespread quantification of both  
40 standing and downed deadwood. *ForC* coverage of *OL* stocks is more comprehensive, revealing no significant  
41 differences across temperate and tropical biomes, but a tendency towards higher *OL* in boreal forests,  
42 consistent with the idea that proportionally slower decomposition in colder climates results in more buildup  
43 of organic matter (Fig. 1; Allen *et al* 2002, Anderson-Teixeira *et al* 2011). Further research on non-living C  
44 stocks in the world's forests will be essential to completing the picture.

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51 **Age trends in C cycling**

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53 Our study reveals that most C fluxes quickly increase and then decelerate as stands age (Figs. 7, 9),  
54 consistent with current understanding of age trends in forest C cycling (Fig. 1; e.g., Anderson-Teixeira *et al*  
55 2013, Amiro *et al* 2010, Magnani *et al* 2007). While limited records in very young (*i.e.*, <5 year old) stands  
56 resulted in poor resolution of the earliest phases of this increase for many variables (sometimes detecting no  
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3 age trend; Table 1), any autotrophic C flux (e.g.,  $GPP$ ,  $NPP$  and its components,  $R_{auto}$ ) would be minimal  
4 immediately following a stand-clearing disturbance (Fig. 1). These would be expected to increase rapidly,  
5 along with the most metabolically active components of biomass, foliage and fine roots, which also increase  
6 rapidly with stand age (Figs. 1, 7-9). In contrast, soil heterotrophic respiration ( $R_{het-soil}$ ) and total soil  
7 respiration ( $R_{soil}$ )—and therefore  $R_{eco}$  are expected to be non-zero following stand-clearing disturbance (Fig.  
8 1), although these may decrease with a reduction of root respiration ( $R_{soil}$  only) and C exudates or increase  
9 in response to an influx of dead roots and litter (Ribeiro-Kumara *et al* 2020, Maurer *et al* 2016,  
10 Bond-Lamberty *et al* 2004). In this study, we detect no significant age trends in either  $R_{het-soil}$  or  $R_{soil}$ ,  
11 consistent with previous findings (Law *et al* 2003, Pregitzer and Euskirchen 2004, Goulden *et al* 2011).

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14 Notably, net carbon sequestration ( $NEP$ ) exhibits an overall increase with age across the first 100 years of  
15 stand development, with more pronounced patterns in temperate than boreal forests (Fig. 7). This finding is  
16 consistent with previous studies showing an increase in  $NEP$  across relatively young stand ages (Pregitzer  
17 and Euskirchen 2004, Baldocchi *et al* 2001, Luyssaert *et al* 2008). However,  $NEP$  has been observed to  
18 decline from intermediate to old stands (Law *et al* 2003, Luyssaert *et al* 2008), whereas the  $NEP$  values  
19 estimated by our models for 100-year-old stands were not systematically different from those of mature  
20 stands (lower for temperate broadleaf, higher for temperate conifer, and equal for boreal; Fig. 9). This lack  
21 of a consistent age-related decrease may be driven by differences in geographical representation across age  
22 classes or by the fitting of an inappropriate functional form. A decrease in  $NEP$  would be consistent with  
23 the observed deceleration of C accumulation as stands age (Fig. 9), although both biomass and non-living C  
24 stocks will often continue to increase well beyond the 100-yr threshold used here to delimit young and  
25 mature stands (Luyssaert *et al* 2008, McGarvey *et al* 2014, Lichstein *et al* 2009). Additional data, including  
26 on age trends of deadwood, the organic layer, and soil C will be important to parsing the timing and extend  
27 of an age-related  $NEP$  decrease across forest biomes.

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33 In terms of stocks, our study reveals consistent increases in live biomass stocks with stand age, a pattern that  
34 is well-known and expected (e.g., Lichstein *et al* 2009, Yang *et al* 2011), contrasting with more variable age  
35 trends in deadwood and the organic layer (Fig. 9). The latter are particularly sensitive to the type of  
36 disturbance, where disturbances that remove most organic material (e.g., logging, agriculture) result in  
37 negligible deadwood in young stands, followed by a buildup over time (e.g., tropical stands in Figs. 8, 9; e.g.,  
38 Vargas *et al* 2008). In contrast, natural disturbances (e.g., fire, drought) can produce large amounts of  
39 deadwood (mostly  $DW_{standing}$ ) that slowly decomposes as the stand recovers, resulting in declines across  
40 young stand ages (e.g., temperate and boreal stands in Figs. 8, 9; Carmona *et al* 2002). Again, further study  
41 and synthesis of non-living C stocks across biomes and stand ages will be valuable to giving a more  
42 comprehensive picture.

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46 **C variable coverage and budget closure**

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48 The large number of C cycle variables covered by ForC, and the relatively high consistency among them  
49 (Figs. 3-6, 9), provide confidence that our reported mature forest means provide useful baselines for analysis –  
50 with the caveats that they are unlikely to be accurate representations of C cycling for any particular forest,  
51 and that these sample means almost certainly do not represent true biome means (particularly for temperate  
52 conifer forests where high-biomass stands are over-represented in *ForC*).

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55 In this analysis, the C cycle budgets for mature forests usually come close to closure—that is, the sums of  
56 component variables do not differ from the larger fluxes by more than one standard deviation (Figs. 3-6, 9).

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3 On the one hand, this reflects the general fact that ecosystem-scale measurements tend to close the C budget  
4 more easily and consistently than, for example, for energy balance (Stoy *et al* 2013). On the other, however,  
5 *ForC* derives data from multiple heterogeneous sources, and standard deviations within each biome are high;  
6 as a result, the standard for C closure is relatively loose (*c.f.* Houghton 2020). The one instance where the C  
7 budgets does not close according to our criteria is likely due to differences in the representation of forest  
8 types (*i.e.*, disproportionate representation of US Pacific NW for  $B_{root-coarse}$  relative to  $B_{root}$ ; Fig. 5)  
9 rather than issues of methodological accuracy. The overall high degree of closure implies that *ForC* gives an  
10 at least roughly consistent picture of C cycling within biomes for mature forests. This is an important and  
11 useful test, because it allows for consistency checks within the C cycle, for example leveraging separate and  
12 independently-measured fluxes to constrain errors in another (Phillips *et al* 2017, Williams *et al* 2014,  
13 Harmon *et al* 2011), or producing internally consistent global data products (Wang *et al* 2018).

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17 In contrast, age trends for young forests generally remain less clearly defined, in large part because their data  
18 records remain relatively sparse (*i.e.*, have low representation of different geographical regions for any given  
19 age) for most variables, particularly in the tropics (Anderson-Teixeira *et al* 2016). While this review provides  
20 a first analysis of age trends in forest C cycling for multiple variables at a global scale, improved resolution of  
21 these trends will require additional data.

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24 There are of course notable holes in the *ForC* variable coverage that limit the scope of our inferences here.  
25 Notably, *ForC* currently has sparse—if any—coverage of fluxes to herbivores and higher consumers, along with  
26 the woody mortality ( $M_{woody}$ ) and DW (Table 1, Figs. S27-S29). *ForC* does not include soil carbon, which  
27 is covered by other efforts (*e.g.*, Köchy *et al* 2015). *ForC* is not intended to replace databases that are  
28 specialized for particular parts of the C cycle analyses, *e.g.*, aboveground biomass (Spawn *et al* 2020),  
29 land-atmosphere fluxes (Baldocchi *et al* 2001), soil respiration (Jian *et al* 2020), or the human footprint in  
30 global forests (Magnani *et al* 2007).

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33 Importantly, *ForC* and the analyses presented here cover the forests that have received research attention,  
34 which are not a representative sample of the world’s existing forests, either geographically or in terms of  
35 human impacts (Martin *et al* 2012). Geographically, all variables are poorly covered in Africa and Siberia  
36 (Fig. 2), a common problem in the carbon-cycle community (Xu and Shang 2016, Schimel *et al* 2015). In  
37 terms of human impacts, research efforts tend to focus on interior forest ecosystems (Martin *et al* 2012),  
38 often in permanently protected areas (*e.g.*, Davies *et al* 2021). Studies of regrowth forests tend to focus on  
39 sites where recurring anthropogenic disturbance is not a confounding factor. Yet, fragmentation and  
40 degradation impact a large and growing proportion of Earth’s forests (FAO and UNEP 2020). Fragmentation  
41 and the creation of edges strongly impacts forest C cycling (*e.g.*, Chaplin-Kramer *et al* 2015, Remy *et al*  
42 2016, Reinmann and Hutyra 2017, Smith *et al* 2019, Reinmann *et al* 2020, Ordway and Asner 2020). Partial  
43 logging and other forms of non- stand clearing anthropogenic disturbance also alter forest C cycling (*e.g.*,  
44 Huang and Asner 2010, Piponiot *et al* 2016), but are under-studied (Sist *et al* 2015) and excluded from this  
45 analysis. Fragmented and degraded forests do not fit the idealized conceptual framework around which this  
46 review is structured (Fig. 1), yet their representation in models, sustainability assessments, and C accounting  
47 systems is critical to accurate accounting of C cycling in Earth’s forests (*e.g.*, Huang and Asner 2010,  
48 Reinmann and Hutyra 2017, Smith *et al* 2019, Piponiot *et al* 2019). Finally, plantation forests account for  
49 approximately 3% of Earth’s forests (FAO and UNEP 2020) but are not included in this analysis. While it is  
50 known that these tend to accumulate biomass faster than naturally regenerating forests (Anderson *et al* 2006,  
51 Bonner *et al* 2013), their global scale C cycling patterns remain less clearly understood (*c.f.* Cook-Patton *et*  
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3 509 Additional research and synthesis are needed to fill these critical gaps in our understanding of forest  
4 510 C cycling.  
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## 7 511 Relevance for climate change prediction and mitigation

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10 512 The future of forest C cycling (Song *et al* 2019) will shape trends in atmospheric CO<sub>2</sub> and the course of  
11 513 climate change (Schimel *et al* 2015). Our findings, and more generally the data contained in *ForC* and  
12 514 summarized here, can help to meet two major challenges.

13 515 First, improved representation of forest C cycling in models is essential to improving predictions of the future  
14 516 course of climate change, for the simple reason that by definition future projections extend our existing  
15 517 observations and understanding to conditions that do not currently exist on Earth (McDowell *et al* 2018,  
16 518 Bonan and Doney 2018, Gustafson *et al* 2018). To ensure that models are giving the right answers for the  
17 519 right reasons (Sulman *et al* 2018), it is important to benchmark against multiple components of the C cycle  
18 520 that are internally consistent with each other (Collier *et al* 2018, Wang *et al* 2018). *ForC*'s tens of thousands  
19 521 of records are readily available in a standardized format, along with all code used in the analyses presented  
20 522 here, and we recommend that researchers use these resources to identify and summarize data specific to the  
21 523 analysis at hand. Integration of *ForC* with models will be valuable to improving the accuracy and reliability  
22 524 of models (Fer *et al* 2021).

23 525 Second, *ForC* can serve as a pipeline through which information can flow efficiently from forest researchers to  
24 526 decision-makers working to implement forest conservation strategies at global, national, or landscape scales.  
25 527 This is already happening: *ForC* has contributed to updating the IPCC guidelines for carbon accounting in  
26 528 forests (IPCC 2019, Requena Suarez *et al* 2019), mapping C accumulation potential from natural forest  
27 529 regrowth globally (Cook-Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al*  
28 530 2020).

29 531 It is also interesting to consider the complementary utility of global-scale but spatially discontinuous  
30 532 databases such as *ForC* and remote wall-to-wall remote sensing products. The latter provide insight into  
31 533 aboveground carbon stocks, but less constraint on belowground stocks or carbon fluxes in general  
32 534 (Bond-Lamberty *et al* 2016, Anav *et al* 2015). Combining observational data and remote observations may  
33 535 provide a much more comprehensive and accurate picture of global forest C cycling, particularly when used  
34 536 in formal data assimilation systems (Konings *et al* 2019, Liu *et al* 2018). Biomass is the largest C stock in  
35 537 most forests, and most of the emphasis has traditionally been on this variable. Remote-sensing driven  
36 538 aboveground biomass estimates (e.g., Saatchi *et al* 2011), calibrated based on high-quality ground-based data  
37 539 (Schepaschenko *et al* 2019, Chave *et al* 2019), provide the most promising approach, but significant  
38 540 uncertainties remain (Ploton *et al* 2020). Note, however, that factors such as stand age and disturbance  
39 541 history are difficult, if not impossible, to detect remotely, and can only be characterized for very recent  
40 542 decades (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). Ground-based data such as *ForC* are  
41 543 therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al* (2020), and thus  
42 544 constraining variables such as carbon sink potential (Luyssaert *et al* 2008).

43 545 In contrast, carbon allocation within forest ecosystems and respiration fluxes cannot be remotely sensed.  
44 546 Efforts such as the Global Carbon Project (Friedlingstein *et al* 2019) and NASA's Carbon Monitoring  
45 547 System (Liu *et al* 2018) typically compute respiration as residuals of all other terms (Bond-Lamberty *et al*  
46 548 2016, Harmon *et al* 2011). This means that the errors on respiration outputs are likely to be large and

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3     549 certainly poorly constrained, offering a unique opportunity for databases such as ForC and SRDB (Jian *et al*  
4     550 2020) to provide observational benchmarks. For example, Konings *et al* (2019) produced a unique top-down  
5     551 estimate of global heterotrophic respiration that can both be compared with extant bottom-up estimates  
6     552 (Bond-Lamberty 2018) and used as an internal consistency check on other parts of the carbon cycle (Phillips  
7     553 *et al* 2017).  
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10     554 **Conclusions**  
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13     555 As climate change accelerates, understanding and managing the carbon dynamics of forests— including  
14     556 dynamics and fluxes that cannot be observed by satellites—is critical to forecasting, mitigation, and  
15     557 adaptation. The C data in *ForC*, as summarized here, will be valuable to these efforts. Notably, the fact that  
16     558 tropical forests tend to have both the highest rates of C sequestration in young stands (Fig. 8; Cook-Patton  
17     559 *et al* 2020), fueled by their generally high C flux rates (Table 1; Fig. 7), and the highest mean biomass (Fig.  
18     560 8; Table 1; Hu *et al* 2016, Jian *et al* 2020) reinforces the concept that conservation and restoration of these  
19     561 forests is a priority for climate change mitigation, along with high-biomass old-growth temperate stands  
20     562 (Grassi *et al* 2017, Goldstein *et al* 2020). It is also important to note the trade-off in climate mitigation  
21     563 potential of restoration of young forests, with high rates of CO<sub>2</sub> sequestration (*NEP*; Cook-Patton *et al*  
22     564 2020), versus conservation and management of mature forests, with low *NEP* but high C stocks that could  
23     565 not be recovered on a time scale relevant to climate change mitigation (Goldstein *et al* 2020). Generally  
24     566 speaking, the conservation of mature forests will yield greater climate benefits (Anderson-Teixeira and  
25     567 DeLucia 2011), but both approaches are critical to avoiding catastrophic climate change (IPCC 2018).  
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29     568 **Data availability statement**  
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32     569 The data that support the findings of this study are openly available. Materials required to fully reproduce  
33     570 these analyses, including data, R scripts, and image files, are archived in Zenodo (DOI: TBD]. Data, scripts,  
34     571 and results presented here are also available through the open-access *ForC* GitHub repository  
35     572 (<https://github.com/forc-db/ForC>), where many will be updated as the database develops.  
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38     573 **References**  
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40

- 41     574 Allen A, Brown J and Gillooly J 2002 Global biodiversity, biochemical kinetics, and the energetic-equivalence  
42     575 rule *SCIENCE* **297** 1545–8  
43     576 Amiro B D, Barr A G, Barr J G, Black T A, Bracho R, Brown M, Chen J, Clark K L, Davis K J, Desai A R,  
44     577 Dore S, Engel V, Fuentes J D, Goldstein A H, Goulden M L, Kolb T E, Lavigne M B, Law B E, Margolis  
45     578 H A, Martin T, McCaughey J H, Misson L, Montes-Helu M, Noormets A, Randerson J T, Starr G and  
46     579 Xiao J 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America *J. Geophys.*  
47     580 *Res.* **115** G00K02  
48  
49     581 Anav A, Friedlingstein P, Beer C, Ciais P, Harper A, Jones C, Murray-Tortarolo G, Papale D, Parazoo N C,  
50     582 Peylin P, Piao S, Sitch S, Viovy N, Wiltshire A and Zhao M 2015 Spatiotemporal patterns of terrestrial  
51     583 gross primary production: A review *Reviews of Geophysics* **53** 785–818  
52  
53     584 Andela N, Morton D C, Giglio L, Chen Y, van der Werf G R, Kasibhatla P S, DeFries R S, Collatz G J,  
54     585 Hantson S, Kloster S, Bachelet D, Forrest M, Lasslop G, Li F, Mangeon S, Melton J R, Yue C and  
55     586 Randerson J T 2017 A human-driven decline in global burned area *Science* **356** 1356–62  
56  
57  
58  
59  
60

- 1  
2  
3 587 Anderson K J, Allen A P, Gillooly J F and Brown J H 2006 Temperature-dependence of biomass  
4 588 accumulation rates during secondary succession *Ecology Letters* **9** 673–82  
5  
6 589 Anderson-Teixeira K, Herrmann V, CookPatton, Ferson A and Lister K 2020 Forc-db/GROA: Release with  
7 590 Cook-Patton et al. 2020, *Nature*.  
8  
9 591 Anderson-Teixeira K J, Davies S J, Bennett A C, Gonzalez-Akre E B, Muller-Landau H C, Joseph Wright S,  
10 592 Abu Salim K, Almeyda Zambrano A M, Alonso A, Baltzer J L, Bassett Y, Bourg N A, Broadbent E N,  
11 593 Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Butt N, Cao M, Cardenas D, Chuyong G B,  
12 594 Clay K, Cordell S, Dattaraja H S, Deng X, Dettman M, Du X, Duque A, Erikson D L, Ewango C E N,  
13 595 Fischer G A, Fletcher C, Foster R B, Giardina C P, Gilbert G S, Gunatilleke N, Gunatilleke S, Hao Z,  
14 596 Hargrove W W, Hart T B, Hau B C H, He F, Hoffman F M, Howe R W, Hubbell S P, Inman-Narahari F  
15 597 M, Jansen P A, Jiang M, Johnson D J, Kanzaki M, Kassim A R, Kenfack D, Kibet S, Kinnaird M F,  
16 598 Korte L, Kral K, Kumar J, Larson A J, Li Y, Li X, Liu S, Lum S K Y, Lutz J A, Ma K, Maddalena D M,  
17 599 Makana J-R, Malhi Y, Marthews T, Mat Serudin R, McMahon S M, McShea W J, Memiaghe H R, Mi X,  
18 600 Mizuno T, Morecroft M, Myers J A, Novotny V, de Oliveira A A, Ong P S, Orwig D A, Ostertag R, den  
19 601 Ouden J, Parker G G, Phillips R P, Sack L, Sainge M N, Sang W, Sri-ngernyuang K, Sukumar R, Sun  
20 602 I-F, Sungpalee W, Suresh H S, Tan S, Thomas S C, Thomas D W, Thompson J, Turner B L, Uriarte M,  
21 603 Valencia R, et al 2015 CTFS-ForestGEO : A worldwide network monitoring forests in an era of global  
22 604 change *Global Change Biology* **21** 528–49  
23  
24  
25  
26  
27 605 Anderson-Teixeira K J, Delong J P, Fox A M, Brese D A and Litvak M E 2011 Differential responses of  
28 606 production and respiration to temperature and moisture drive the carbon balance across a climatic  
29 607 gradient in New Mexico *Global Change Biology* **17** 410–24  
30  
31 608 Anderson-Teixeira K J and DeLucia E H 2011 The greenhouse gas value of ecosystems *Global Change Biology*  
32 609 **17** 425–38  
33  
34 610 Anderson-Teixeira K J, Miller A D, Mohan J E, Hudiburg T W, Duval B D and DeLucia E H 2013 Altered  
35 611 dynamics of forest recovery under a changing climate *Global Change Biology* **19** 2001–21  
36  
37 612 Anderson-Teixeira K J, Wang M M H, McGarvey J C, Herrmann V, Tepley A J, Bond-Lamberty B and  
38 613 LeBauer D S 2018 ForC : A global database of forest carbon stocks and fluxes *Ecology* **99** 1507–7  
39  
40 614 Anderson-Teixeira K J, Wang M M H, McGarvey J C and LeBauer D S 2016 Carbon dynamics of mature  
41 615 and regrowth tropical forests derived from a pantropical database (TropForC-db) *Global Change Biology*  
42 616 **22** 1690–709  
43  
44 617 Badgley G, Anderegg L D L, Berry J A and Field C B 2019 Terrestrial gross primary production: Using  
45 618 NIRV to scale from site to globe *Global Change Biology* **25** 3731–40  
46  
47 619 Baldocchi D, Falge E, Gu L, Olson R, Hollinger D, Running S, Anthony P, Bernhofer C, Davis K, Evans R,  
48 620 Fuentes J, Goldstein A, Katul G, Law B, Lee X, Malhi Y, Meyers T, Munger W, Oechel W, Paw K T,  
49 621 Pilegaard K, Schmid H P, Valentini R, Verma S, Vesala T, Wilson K and Wofsy S 2001 FLUXNET : A  
50 622 New Tool to Study the Temporal and Spatial Variability of EcosystemScale Carbon Dioxide, Water  
51 623 Vapor, and Energy Flux Densities *Bulletin of the American Meteorological Society* **82** 2415–34  
52  
53  
54 624 Banbury Morgan B, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau H C and Anderson-Teixeira  
55 625 K J Global patterns of forest autotrophic carbon fluxes *Global Change Biology*

- 1  
2  
3 626 Bates D, Mächler M, Bolker B and Walker S 2015 Fitting Linear Mixed-Effects Models Using **Lme4** *Journal*  
4 627 *of Statistical Software* **67**  
5  
6 628 Besnard S, Carvalhais N, Arain M A, Black A, de Bruin S, Buchmann N, Cescatti A, Chen J, Clevers J G P  
7 629 W, Desai A R, Gough C M, Havrankova K, Herold M, Hörtnagl L, Jung M, Knohl A, Kruijt B, Krupkova  
8 630 L, Law B E, Lindroth A, Noormets A, Roupsard O, Steinbrecher R, Varlagin A, Vincke C and Reichstein  
9 631 M 2018 Quantifying the effect of forest age in annual net forest carbon balance *Environmental Research*  
10 632 *Letters* **13** 124018  
11  
12 633 Bonan G B 2008 Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests  
13 634 *Science* **320** 1444–9  
14  
15 635 Bonan G B and Doney S C 2018 Climate, ecosystems, and planetary futures: The challenge to predict life in  
16 636 Earth system models *Science* **359**  
17  
18 637 Bonan G B, Lombardozzi D L, Wieder W R, Oleson K W, Lawrence D M, Hoffman F M and Collier N 2019  
19 638 Model Structure and Climate Data Uncertainty in Historical Simulations of the Terrestrial Carbon Cycle  
20 639 (1850) *Global Biogeochemical Cycles* **33** 1310–26  
21  
22  
23 640 Bond-Lamberty B 2018 New Techniques and Data for Understanding the Global Soil Respiration Flux  
24 641 *Earth's Future* **6** 1176–80  
25  
26 642 Bond-Lamberty B, Epron D, Harden J, Harmon M E, Hoffman F, Kumar J, David McGuire A and Vargas R  
27 643 2016 Estimating heterotrophic respiration at large scales: Challenges, approaches, and next steps  
28 644 *Ecosphere* **7**  
29  
30 645 Bond-Lamberty B and Thomson A 2010 A global database of soil respiration data *Biogeosciences* **7** 1915–26  
31  
32 646 Bond-Lamberty B, Wang C and Gower S T 2004 Contribution of root respiration to soil surface CO<sub>2</sub> flux in  
33 647 a boreal black spruce chronosequence *Tree Physiology* **24** 1387–95  
34  
35 648 Bonner M T L, Schmidt S and Shoo L P 2013 A meta-analytical global comparison of aboveground biomass  
36 649 accumulation between tropical secondary forests and monoculture plantations *Forest Ecology and*  
37 650 *Management* **291** 73–86  
38  
39 651 Carmona M R, Armesto J J, Aravena J C and Pérez C A 2002 Coarse woody debris biomass in successional  
40 652 and primary temperate forests in Chiloé Island, Chile *Forest Ecology and Management* **164** 265–75  
41  
42 653 Cavalieri M A, Reed S C, Smith W K and Wood T E 2015 Urgent need for warming experiments in tropical  
43 654 forests *Global Change Biology* **21** 2111–21  
44  
45 655 Chapin F, Woodwell G, Randerson J, Rastetter E, Lovett G, Baldocchi D, Clark D, Harmon M, Schimel D,  
46 656 Valentini R, Wirth C, Aber J, Cole J, Goulden M, Harden J, Heimann M, Howarth R, Matson P, McGuire  
47 657 A, Melillo J, Mooney H, Neff J, Houghton R, Pace M, Ryan M, Running S, Sala O, Schlesinger W and  
48 658 Schulze E D 2006 Reconciling Carbon-cycle Concepts, Terminology, and Methods *Ecosystems* **9** 1041–50  
49  
50 659 Chaplin-Kramer R, Ramler I, Sharp R, Haddad N, Gerber J, West P, Mandle L, Engstrom P, Baccini A, Sim  
51 660 S, Mueller C and King H 2015 Degradation in carbon stocks near tropical forest edges *Nature*  
52 661 *Communications* **6**  
53  
54 662 Chave J, Davies S J, Phillips O L, Lewis S L, Sist P, Schepaschenko D, Armston J, Baker T R, Coomes D,  
55 663 Disney M, Duncanson L, Héault B, Labrière N, Meyer V, Réjou-Méchain M, Scipal K and Saatchi S  
56  
57  
58  
59  
60

- 1  
2  
3 664 2019 Ground Data are Essential for Biomass Remote Sensing Missions *Surveys in Geophysics*  
4  
5 665 Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan M S, Delitti W B C, Duque A, Eid T,  
6 Fearnside P M, Goodman R C, Henry M, Martínez-Yrízar A, Mugasha W A, Muller-Landau H C,  
7 Mencuccini M, Nelson B W, Ngomanda A, Nogueira E M, Ortiz-Malavassi E, Pélassier R, Ploton P, Ryan  
8 C M, Saldarriaga J G and Vieilledent G 2014 Improved allometric models to estimate the aboveground  
9 biomass of tropical trees *Global Change Biology* n/a-a  
10 669  
11 670 Clark D A, Asao S, Fisher R, Reed S, Reich P B, Ryan M G, Wood T E and Yang X 2017 Field data to  
12 benchmark the carbon-cycle models for tropical forests *Biogeosciences Discussions* 1-44  
13  
14 672 Clark D A, Brown S, Kicklighter D W, Chambers J, Thominson J R and Ni J 2001 Measuring net primary  
15 production in forests: Concepts and field methods *Ecological Applications* **11** 356-70  
16  
17 674 Collalti A, Ibrom A, Stockmarr A, Cescatti A, Alkama R, Fernández-Martínez M, Matteucci G, Sitch S,  
18 Friedlingstein P, Ciais P, Goll D S, Nabel J E M S, Pongratz J, Arneth A, Haverd V and Prentice I C  
19 676 2020 Forest production efficiency increases with growth temperature *Nature Communications* **11** 5322  
20  
21 677 Collier N, Hoffman F M, Lawrence D M, Keppel-Aleks G, Koven C D, Riley W J, Mu M and Randerson J T  
22 678 2018 The International Land Model Benchmarking (ILAMB) System: Design, Theory, and  
23 Implementation *Journal of Advances in Modeling Earth Systems* **10** 2731-54  
24  
25 679  
26 680 Cook-Patton S C, Leavitt S M, Gibbs D, Harris N L, Lister K, Anderson-Teixeira K J, Briggs R D, Chazdon  
27 R L, Crowther T W, Ellis P W, Griscom H P, Herrmann V, Holl K D, Houghton R A, Larrosa C, Lomax  
28 G, Lucas R, Madsen P, Malhi Y, Paquette A, Parker J D, Paul K, Routh D, Roxburgh S, Saatchi S, van  
29 den Hoogen J, Walker W S, Wheeler C E, Wood S A, Xu L and Griscom B W 2020 Mapping carbon  
30 accumulation potential from global natural forest regrowth *Nature* **585** 545-50  
31  
32 681  
33 682  
34 683  
35 684  
36 685  
37 686  
38 687  
39 688  
40 689  
41 690  
42 691  
43 692  
44 693  
45 694  
46 695  
47 696  
48 697  
49 698  
50 699  
51 700  
52 701  
53 702  
54  
55  
56  
57  
58  
59  
60  
Corman J R, Collins S L, Cook E M, Dong X, Gherardi L A, Grimm N B, Hale R L, Lin T, Ramos J,  
Reichmann L G and Sala O E 2019 Foundations and Frontiers of Ecosystem Science: Legacy of a Classic  
Paper (Odum 1969) *Ecosystems* **22** 1160-72  
Curtis P G, Slay C M, Harris N L, Tyukavina A and Hansen M C 2018 Classifying drivers of global forest  
loss *Science* **361** 1108-11  
Curtis P S and Gough C M 2018 Forest aging, disturbance and the carbon cycle *New Phytologist*  
Davies S J, Abiem I, Abu Salim K, Aguilar S, Allen D, Alonso A, Anderson-Teixeira K, Andrade A, Arellano  
G, Ashton P S, Baker P J, Baker M E, Baltzer J L, Basset Y, Bissengou P, Bohlman S, Bourg N A,  
Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Cao M, Cárdenas D, Chang L-W, Chang-Yang  
C-H, Chao K-J, Chao W-C, Chapman H, Chen Y-Y, Chisholm R A, Chu C, Chuyong G, Clay K, Comita  
L S, Condit R, Cordell S, Dattaraja H S, de Oliveira A A, den Ouden J, Detto M, Dick C, Du X, Duque  
Á, Ediriweera S, Ellis E C, Obiang N L E, Esufali S, Ewango C E N, Fernando E S, Filip J, Fischer G A,  
Foster R, Giambelluca T, Giardina C, Gilbert G S, Gonzalez-Akre E, Gunatilleke I A U N, Gunatilleke C  
V S, Hao Z, Hau B C H, He F, Ni H, Howe R W, Hubbell S P, Huth A, Inman-Narahari F, Itoh A, Janík  
D, Jansen P A, Jiang M, Johnson D J, Jones F A, Kanzaki M, Kenfack D, Kiratiprayoon S, Král K,  
Krizel L, Lao S, Larson A J, Li Y, Li X, Litton C M, Liu Y, Liu S, Lum S K Y, Luskin M S, Lutz J A,  
Luu H T, Ma K, Makana J-R, Malhi Y, Martin A, McCarthy C, McMahon S M, McShea W J, Memiaghe  
H, Mi X, Mitre D, Mohamad M, et al 2021 ForestGEO: Understanding forest diversity and dynamics

- 1  
2  
3     703 through a global observatory network *Biological Conservation* **253** 108907  
4  
5     704 DeLucia E H, Drake J, Thomas R B and Gonzalez-Meler M A 2007 Forest carbon use efficiency: Is  
6         705 respiration a constant fraction of gross primary production? *Global Change Biology* **13** 1157–67  
7  
8     706 Di Vittorio A V, Shi X, Bond-Lamberty B, Calvin K and Jones A 2020 Initial Land Use/Cover Distribution  
9         707 Substantially Affects Global Carbon and Local Temperature Projections in the Integrated Earth System  
10         708 Model *Global Biogeochemical Cycles* **34**  
11  
12     709 FAO 2010 *Global Forest Resources Assessment 2010* (Rome, Italy: Food and Agriculture Organization of the  
13         710 United Nations)  
14  
15     711 FAO and UNEP 2020 *The State of the World's Forests 2020: Forests, biodiversity and people* (Rome, Italy:  
16         712 FAO and UNEP)  
17  
18     713 Fer I, Gardella A K, Shiklomanov A N, Campbell E E, Cowdery E M, Kauwe M G D, Desai A, Duveneck M  
19         714 J, Fisher J B, Haynes K D, Hoffman F M, Johnston M R, Kooper R, LeBauer D S, Mantooth J, Parton  
20         715 W J, Poulter B, Quaife T, Raiho A, Schaefer K, Serbin S P, Simkins J, Wilcox K R, Viskari T and Dietze  
21         716 M C 2021 Beyond ecosystem modeling: A roadmap to community cyberinfrastructure for ecological  
22         717 data-model integration *Global Change Biology* **27** 13–26  
23  
24     718 Friedlingstein P, Cox P, Betts R, Bopp L, von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I, Bala  
25         719 G, John J, Jones C, Joos F, Kato T, Kawamiya M, Knorr W, Lindsay K, Matthews H D, Raddatz T,  
26         720 Rayner P, Reick C, Roeckner E, Schnitzler K-G, Schnur R, Strassmann K, Weaver A J, Yoshikawa C and  
27         721 Zeng N 2006 ClimateCarbon Cycle Feedback Analysis: Results from the C4MIP Model Intercomparison  
28         722 *Journal of Climate* **19** 3337–53  
29  
30     723 Friedlingstein P, Jones M W, O'Sullivan M, Andrew R M, Hauck J, Peters G P, Peters W, Ponratz J, Sitch  
31         724 S, Quéré C L, Bakker D C E, Canadell J G, Ciais P, Jackson R B, Anthoni P, Barbero L, Bastos A,  
32         725 Bastrikov V, Becker M, Bopp L, Buitenhuis E, Chandra N, Chevallier F, Chini L P, Currie K I, Feely R  
33         726 A, Gehlen M, Gilfillan D, Gkritzalis T, Goll D S, Gruber N, Gutekunst S, Harris I, Haverd V, Houghton  
34         727 R A, Hurtt G, Ilyina T, Jain A K, Joetzer E, Kaplan J O, Kato E, Klein Goldewijk K, Korsbakken J I,  
35         728 Landschützer P, Lauvset S K, Lefèvre N, Lenton A, Lienert S, Lombardozzi D, Marland G, McGuire P C,  
36         729 Melton J R, Metzl N, Munro D R, Nabel J E M S, Nakaoka S-I, Neill C, Omar A M, Ono T, Peregon A,  
37         730 Pierrot D, Poulter B, Rehder G, Resplandy L, Robertson E, Rödenbeck C, Séférian R, Schwinger J,  
38         731 Smith N, Tans P P, Tian H, Tilbrook B, Tubiello F N, Werf G R van der, Wiltshire A J and Zaehle S  
39         732 2019 Global Carbon Budget 2019 *Earth System Science Data* **11** 1783–838  
40  
41     733 Gillman L N, Wright S D, Cusens J, McBride P D, Malhi Y and Whittaker R J 2015 Latitude, productivity  
42         734 and species richness *Global Ecology and Biogeography* **24** 107–17  
43  
44     735 Goldstein A, Turner W R, Spawn S A, Anderson-Teixeira K J, Cook-Patton S, Fargione J, Gibbs H K,  
45         736 Griscom B, Hewson J H, Howard J F, Ledezma J C, Page S, Koh L P, Rockström J, Sanderman J and  
46         737 Hole D G 2020 Protecting irrecoverable carbon in Earth's ecosystems *Nature Climate Change* **10** 287–95  
47  
48     738 Goulden M L, McMillan A M S, Winston G C, Rocha A V, Manies K L, Harden J W and Bond-Lamberty B  
49         739 P 2011 Patterns of NPP, GPP, respiration, and NEP during boreal forest succession *Global Change  
50         740 Biology* **17** 855–71

- 1  
2  
3 741 Grassi G, House J, Dentener F, Federici S, den Elzen M and Penman J 2017 The key role of forests in  
4 meeting climate targets requires science for credible mitigation *Nature Climate Change* **7** 220–6  
5  
6 743 Griscom B W, Adams J, Ellis P W, Houghton R A, Lomax G, Miteva D A, Schlesinger W H, Shoch D,  
7 Siikamäki J V, Smith P, Woodbury P, Zganjar C, Blackman A, Campari J, Conant R T, Delgado C,  
8 Elias P, Gopalakrishna T, Hamsik M R, Herrero M, Kiesecker J, Landis E, Laestadius L, Leavitt S M,  
9 Minnemeyer S, Polasky S, Potapov P, Putz F E, Sanderman J, Silvius M, Wollenberg E and Fargione J  
10 746 2017 Natural climate solutions *Proceedings of the National Academy of Sciences* **114** 11645–50  
11 747  
12  
13 748 Gustafson E J, Kubiske M E, Miranda B R, Hoshika Y and Paoletti E 2018 Extrapolating plot-scale CO<sub>2</sub>  
14 and ozone enrichment experimental results to novel conditions and scales using mechanistic modeling  
15 750 *Ecological Processes* **7** 31  
16  
17 751 Hansen M C, Potapov P V, Moore R, Hancher M, Turubanova S A, Tyukavina A, Thau D, Stehman S V,  
18 Goetz S J, Loveland T R, Kommareddy A, Egorov A, Chini L, Justice C O and Townshend J R G 2013  
19 753 High-Resolution Global Maps of 21st-Century Forest Cover Change *Science* **342** 850–3  
20  
21 754 Harmon M E, Bond-Lamberty B, Tang J and Vargas R 2011 Heterotrophic respiration in disturbed forests:  
22 A review with examples from North America *Journal of Geophysical Research* **116**  
23  
24 756 Harmon M E, Franklin J F, Swanson F J, Sollins P, Gregory S V, Lattin J D, Anderson N H, Cline S P,  
25 Aumen N G, Sedell J R, Lienkaemper G W, Cromack K and Cummins K W 1986 Ecology of Coarse  
26 Woody Debris in Temperate Ecosystems *Advances in Ecological Research* vol 15, ed A MacFadyen and E  
27 758 D Ford (Academic Press) pp 133–302  
28 759  
29  
30 760 Harris N L, Gibbs D A, Baccini A, Birdsey R A, Bruun S de, Farina M, Fatoyinbo L, Hansen M C, Herold M,  
31 Houghton R A, Potapov P V, Suarez D R, Roman-Cuesta R M, Saatchi S S, Slay C M, Turubanova S A  
32 762 and Tyukavina A 2021 Global maps of twenty-first century forest carbon fluxes *Nature Climate Change*  
33 763 1–7  
34  
35 764 Holdridge L R 1947 Determination of World Plant Formations From Simple Climatic Data *Science* **105** 367–8  
36  
37 765 Houghton R A 2020 Terrestrial fluxes of carbon in GCP carbon budgets *Global Change Biology* **26** 3006–14  
38  
39 766 Hu T, Su Y, Xue B, Liu J, Zhao X, Fang J and Guo Q 2016 Mapping Global Forest Aboveground Biomass  
40 767 with Spaceborne LiDAR, Optical Imagery, and Forest Inventory Data *Remote Sensing* **8** 565  
41  
42 768 Huang M and Asner G P 2010 Long-term carbon loss and recovery following selective logging in Amazon  
43 forests *Global Biogeochemical Cycles* **24**  
44  
45 770 Humboldt A von and Bonpland A 1807 *Essay on the Geography of Plants*  
46  
47 771 Hursh A, Ballantyne A, Cooper L, Maneta M, Kimball J and Watts J 2017 The sensitivity of soil respiration  
48 to soil temperature, moisture, and carbon supply at the global scale *Global Change Biology* **23** 2090–103  
49  
50 773 IPCC 2019 *Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories*  
51  
52 774 IPCC 2018 *Global Warming of 1.5C. An IPCC Special Report on the impacts of global warming of 1.5C  
53 above pre-industrial levels and related global greenhouse gas emission pathways, in the context of  
54 strengthening the global response to the threat of climate change, sustainable development, and efforts to  
55 eradicate poverty* [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A.  
56  
57  
58  
59  
60

- 1  
2  
3     778     *Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I.*  
4     779     *Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)].*
- 5  
6     780     Jian J, Vargas R, Anderson-Teixeira K, Stell E, Herrmann V, Horn M, Kholod N, Manzon J, Marchesi R,  
7     781     Paredes D and Bond-Lamberty B 2020 *A restructured and updated global soil respiration database*  
8     782     (SRDB-V5) (Data, Algorithms, and Models)
- 9  
10     783     Johnson C, Zarin D and Johnson A 2000 Post-disturbance aboveground biomass accumulation in global  
11     784     secondary forests *Ecology* **81** 1395–401
- 12  
13     785     Johnson D J, Needham J, Xu C, Massoud E C, Davies S J, Anderson-Teixeira K J, Bunyavejchewin S,  
14     786     Chambers J Q, Chang-Yang C-H, Chiang J-M, Chuyong G B, Condit R, Cordell S, Fletcher C, Giardina  
15     787     C P, Giambelluca T W, Gunatilleke N, Gunatilleke S, Hsieh C-F, Hubbell S, Inman-Narahari F, Kassim  
16     788     A R, Katabuchi M, Kenfack D, Litton C M, Lum S, Mohamad M, Nasardin M, Ong P S, Ostertag R,  
17     789     Sack L, Swenson N G, Sun I F, Tan S, Thomas D W, Thompson J, Umaña M N, Uriarte M, Valencia R,  
18     790     Yap S, Zimmerman J, McDowell N G and McMahon S M 2018 Climate sensitive size-dependent survival  
19     791     in tropical trees *Nature Ecology & Evolution* **1**
- 20  
21  
22     792     Jung M, Henkel K, Herold M and Churkina G 2006 Exploiting synergies of global land cover products for  
23     793     carbon cycle modeling *Remote Sensing of Environment* **101** 534–53
- 24  
25     794     Keith H, Mackey B G and Lindenmayer D B 2009 Re-evaluation of forest biomass carbon stocks and lessons  
26     795     from the world's most carbon-dense forests *Proceedings of the National Academy of Sciences* **106**  
27     796     11635–40
- 28  
29  
30     797     Konings A G, Bloom A A, Liu J, Parazoo N C, Schimel D S and Bowman K W 2019 Global satellite-driven  
31     798     estimates of heterotrophic respiration *Biogeosciences* **16** 2269–84
- 32  
33     799     Köchy M, Hiederer R and Freibauer A 2015 Global distribution of soil organic carbon Part 1: Masses and  
34     800     frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world *SOIL* **1**  
35     801     351–65
- 36  
37     802     Krause A, Pugh T A M, Bayer A D, Li W, Leung F, Bondeau A, Doelman J C, Humpenöder F, Anthoni P,  
38     803     Bodirsky B L, Ciais P, Müller C, Murray-Tortarolo G, Olin S, Popp A, Sitch S, Stehfest E and Arneth A  
39     804     2018 Large uncertainty in carbon uptake potential of land-based climate-change mitigation efforts *Global  
40     805     Change Biology* **24** 3025–38
- 41  
42     806     Kuzyakov Y 2006 Sources of CO<sub>2</sub> efflux from soil and review of partitioning methods *Soil Biology and  
43     807     Biochemistry* **38** 425–48
- 44  
45     808     Law B E, Sun O J, Campbell J, Tuyl S V and Thornton P E 2003 Changes in carbon storage and fluxes in a  
46     809     chronosequence of ponderosa pine *Global Change Biology* **9** 510–24
- 47  
48     810     Li X and Xiao J 2019 Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A Global,  
49     811     Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2 *Remote Sensing* **11** 2563
- 50  
51     812     Lichstein J W, Wirth C, Horn H S and Pacala S W 2009 Biomass Chronosequences of United States Forests:  
52     813     Implications for Carbon Storage and Forest Management *Old-Growth Forests Ecological Studies* ed C  
53     814     Wirth, G Gleixner and M Heimann (Springer Berlin Heidelberg) pp 301–41
- 54  
55     815     Lieth H 1973 Primary production: Terrestrial ecosystems *Human Ecology* **1** 303–32
- 56  
57  
58  
59  
60

- 1  
2  
3 816 Liu J, Bowman K, Parazoo N C, Bloom A A, Wunch D, Jiang Z, Gurney K R and Schimel D 2018 Detecting  
4 817 drought impact on terrestrial biosphere carbon fluxes over contiguous US with satellite observations  
5 818 *Environmental Research Letters* **13** 095003
- 6 819 Luo Y Q, Randerson J T, Abramowitz G, Bacour C, Blyth E, Carvalhais N, Ciais P, Dalmonech D, Fisher J  
7 820 B, Fisher R, Friedlingstein P, Hibbard K, Hoffman F, Huntzinger D, Jones C D, Koven C, Lawrence D, Li  
8 821 D J, Mahecha M, Niu S L, Norby R, Piao S L, Qi X, Peylin P, Prentice I C, Riley W, Reichstein M,  
9 822 Schwalm C, Wang Y P, Xia J Y, Zaehle S and Zhou X H 2012 A framework for benchmarking land  
10 823 models *Biogeosciences* **9** 3857–74
- 11 824 Lutz J A, Furniss T J, Johnson D J, Davies S J, Allen D, Alonso A, Anderson-Teixeira K J, Andrade A,  
12 825 Baltzer J, Becker K M L, Blomdahl E M, Bourg N A, Bunyavejchewin S, Burslem D F R P, Cansler C A,  
13 826 Cao K, Cao M, Cárdenas D, Chang L-W, Chao K-J, Chao W-C, Chiang J-M, Chu C, Chuyong G B, Clay  
14 827 K, Condit R, Cordell S, Dattaraja H S, Duque A, Ewango C E N, Fischer G A, Fletcher C, Freund J A,  
15 828 Giardina C, Germain S J, Gilbert G S, Hao Z, Hart T, Hau B C H, He F, Hector A, Howe R W, Hsieh  
16 829 C-F, Hu Y-H, Hubbell S P, Inman-Narahari F M, Itoh A, Janík D, Kassim A R, Kenfack D, Korte L,  
17 830 Král K, Larson A J, Li Y, Lin Y, Liu S, Lum S, Ma K, Makana J-R, Malhi Y, McMahon S M, McShea W  
18 831 J, Memiaghe H R, Mi X, Morecroft M, Musili P M, Myers J A, Novotny V, Oliveira A de, Ong P, Orwig  
19 832 D A, Ostertag R, Parker G G, Patankar R, Phillips R P, Reynolds G, Sack L, Song G-Z M, Su S-H,  
20 833 Sukumar R, Sun I-F, Suresh H S, Swanson M E, Tan S, Thomas D W, Thompson J, Uriarte M, Valencia  
21 834 R, Vicentini A, Vrška T, Wang X, Weiblen G D, Wolf A, Wu S-H, Xu H, Yamakura T, Yap S and  
22 835 Zimmerman J K 2018 Global importance of large-diameter trees *Global Ecology and Biogeography* **27**  
23 836 849–64
- 24 837 Luyssaert S, Inglima I, Jung M, Richardson A D, Reichstein M, Papale D, Piao S L, Schulze E-D, Wingate L,  
25 838 Matteucci G, Aragao L, Aubinet M, Beer C, Bernhofer C, Black K G, Bonal D, Bonnefond J-M,  
26 839 Chambers J, Ciais P, Cook B, Davis K J, Dolman A J, Gielen B, Goulden M, Grace J, Granier A, Grelle  
27 840 A, Griffis T, Grünwald T, Guidolotti G, Hanson P J, Harding R, Hollinger D Y, Hutyra L R, Kolari P,  
28 841 Kruijt B, Kutsch W, Lagergren F, Laurila T, Law B E, Maire G L, Lindroth A, Loustau D, Malhi Y,  
29 842 Mateus J, Migliavacca M, Misson L, Montagnani L, Moncrieff J, Moors E, Munger J W, Nikinmaa E,  
30 843 Ollinger S V, Pita G, Rebmann C, Roupsard O, Saigusa N, Sanz M J, Seufert G, Sierra C, Smith M-L,  
31 844 Tang J, Valentini R, Vesala T and Janssens I A 2007 CO<sub>2</sub> balance of boreal, temperate, and tropical  
32 845 forests derived from a global database *Global Change Biology* **13** 2509–37
- 33 846 Luyssaert S, Schulze E D, Borner A, Knohl A, Hessenmoller D, Law B E, Ciais P and Grace J 2008  
34 847 Old-growth forests as global carbon sinks *Nature* **455** 213
- 35 848 Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis P G,  
36 849 Kolari P, Kowalski A S, Lankreijer H, Law B E, Lindroth A, Loustau D, Manca G, Moncrieff J B,  
37 850 Rayment M, Tedeschi V, Valentini R and Grace J 2007 The human footprint in the carbon cycle of  
38 851 temperate and boreal forests *Nature* **447** 849–51
- 39 852 Martin L J, Blossey B and Ellis E 2012 Mapping where ecologists work: Biases in the global distribution of  
40 853 terrestrial ecological observations *Frontiers in Ecology and the Environment* **10** 195–201
- 41 854 Martin P A, Newton A C and Bullock J M 2013 Carbon pools recover more quickly than plant biodiversity  
42 855 in tropical secondary forests *Proceedings of the Royal Society B: Biological Sciences* **280** 20132236–6

- 1  
2  
3 Maurer G E, Chan A M, Trahan N A, Moore D J P and Bowling D R 2016 Carbon isotopic composition of  
4 forest soil respiration in the decade following bark beetle and stem girdling disturbances in the Rocky  
5 Mountains *Plant, Cell & Environment* **39** 1513–23  
6  
7 McDowell N G, Allen C D, Anderson-Teixeira K, Aukema B H, Bond-Lamberty B, Chini L, Clark J S,  
8 Dietze M, Grossiord C, Hanbury-Brown A, Hurt G C, Jackson R B, Johnson D J, Kueppers L, Lichstein  
9 J W, Ogle K, Poulter B, Pugh T A M, Seidl R, Turner M G, Uriarte M, Walker A P and Xu C 2020  
10 Pervasive shifts in forest dynamics in a changing world *Science* **368**  
11  
12 McDowell N G, Michaletz S T, Bennett K E, Solander K C, Xu C, Maxwell R M and Middleton R S 2018  
13 Predicting Chronic Climate-Driven Disturbances and Their Mitigation *Trends in Ecology & Evolution* **33**  
14 15–27  
15  
16 McGarvey J C, Thompson J R, Epstein H E and Shugart H H 2014 Carbon storage in old-growth forests of  
17 the Mid-Atlantic: Toward better understanding the eastern forest carbon sink *Ecology* **96** 311–7  
18  
19 Novick K A, Biederman J A, Desai A R, Litvak M E, Moore D J P, Scott R L and Torn M S 2018 The  
20 AmeriFlux network: A coalition of the willing *Agricultural and Forest Meteorology* **249** 444–56  
21  
22 Odum E 1969 The strategy of ecosystem development *Science* **164** 262–70  
23  
24 Ordway E M and Asner G P 2020 Carbon declines along tropical forest edges correspond to heterogeneous  
25 effects on canopy structure and function *Proceedings of the National Academy of Sciences* **117** 7863–70  
26  
27 Pan Y, Birdsey R A, Fang J, Houghton R, Kauppi P E, Kurz W A, Phillips O L, Shvidenko A, Lewis S L,  
28 Canadell J G, Ciais P, Jackson R B, Pacala S, McGuire A D, Piao S, Rautiainen A, Sitch S and Hayes D  
29 2011 A Large and Persistent Carbon Sink in the World's Forests *Science* **333** 988–93  
30  
31 Pastorello G, Trotta C, Canfora E, Chu H, Christianson D, Cheah Y-W, Poindexter C, Chen J, Elbashandy  
32 A, Humphrey M, Isaac P, Polidori D, Ribeca A, van Ingen C, Zhang L, Amiro B, Ammann C, Arain M A,  
33 Ardö J, Arkebauer T, Arndt S K, Arriga N, Aubinet M, Aurela M, Baldocchi D, Barr A, Beamesderfer E,  
34 Marchesini L B, Bergeron O, Beringer J, Bernhofer C, Berveiller D, Billesbach D, Black T A, Blanken P  
35 D, Bohrer G, Boike J, Bolstad P V, Bonal D, Bonnefond J-M, Bowling D R, Bracho R, Brodeur J,  
36 Brümmer C, Buchmann N, Burban B, Burns S P, Buysse P, Cale P, Cavagna M, Cellier P, Chen S, Chini  
37 I, Christensen T R, Cleverly J, Collalti A, Consalvo C, Cook B D, Cook D, Coursolle C, Cremonese E,  
38 Curtis P S, D'Andrea E, da Rocha H, Dai X, Davis K J, De Cinti B, de Grandcourt A, De Ligne A, De  
39 Oliveira R C, Delpierre N, Desai A R, Di Bella C M, di Tommasi P, Dolman H, Domingo F, Dong G,  
40 Dore S, Duce P, Dufrêne E, Dunn A, Dušek J, Eamus D, Eichelmann U, ElKhidir H A M, Eugster W,  
41 Ewenz C M, Ewers B, Famulari D, Fares S, Feigenwinter I, Feitz A, Fensholt R, Filippa G, Fischer M,  
42 Frank J, Galvagno M, Gharun M, et al 2020 The FLUXNET2015 dataset and the ONEFlux processing  
43 pipeline for eddy covariance data *Scientific Data* **7** 225  
44  
45 Phillips C L, Bond-Lamberty B, Desai A R, Lavoie M, Risk D, Tang J, Todd-Brown K and Vargas R 2017  
46 The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling *Plant*  
47 and *Soil* **413** 1–25  
48  
49 Piponiot C, Rödig E, Putz F E, Rutishauser E, Sist P, Ascarrunz N, Blanc L, Derroire G, Descroix L, Guedes  
50 M C, Coronado E H, Huth A, Kanashiro M, Licona J C, Mazzei L, d'Oliveira M V N, Peña-Claros M,  
51 Rodney K, Shenkin A, Souza C R de, Vidal E, West T A P, Wortel V and Héroult B 2019 Can timber  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 provision from Amazonian production forests be sustainable? *Environmental Research Letters* **14** 064014  
4  
5 Piponiot C, Sist P, Mazzei L, Peña-Claros M, Putz F E, Rutishauser E, Shenkin A, Ascarrunz N, de Azevedo  
6 C P, Baraloto C, França M, Guedes M, Honorio Coronado E N, d’Oliveira M V, Ruschel A R, da Silva K  
7 E, Doff Sotta E, de Souza C R, Vidal E, West T A and Héault B 2016 Carbon recovery dynamics  
8 following disturbance by selective logging in Amazonian forests *eLife* **5** e21394  
9  
10 Ploton P, Mortier F, Réjou-Méchain M, Barbier N, Picard N, Rossi V, Dormann C, Cornu G, Viennois G,  
11 Bayol N, Lyapustin A, Gourlet-Fleury S and Pélassier R 2020 Spatial validation reveals poor predictive  
12 performance of large-scale ecological mapping models *Nature Communications* **11** 4540  
13  
14 Poorter L, Bongers F, Aide T M, Zambrano A M A, Balvanera P, Becknell J M, Boukili V, Brancalion P H S,  
15 Broadbent E N, Chazdon R L, Craven D, Almeida-Cortez J S de, Cabral G A L, Jong B H J de, Denslow  
16 J S, Dent D H, DeWalt S J, Dupuy J M, Durán S M, Espírito-Santo M M, Fandino M C, César R G, Hall  
17 J S, Hernandez-Stefanoni J L, Jakovac C C, Junqueira A B, Kennard D, Letcher S G, Licona J-C,  
18 Lohbeck M, Marín-Spiotta E, Martínez-Ramos M, Massoca P, Meave J A, Mesquita R, Mora F, Muñoz  
19 R, Muscarella R, Nunes Y R F, Ochoa-Gaona S, Oliveira A A de, Oriuela-Belmonte E, Peña-Claros M,  
20 Pérez-García E A, Piotto D, Powers J S, Rodríguez-Velázquez J, Romero-Pérez I E, Ruíz J, Saldarriaga J  
21 G, Sanchez-Azofeifa A, Schwartz N B, Steininger M K, Swenson N G, Toledo M, Uriarte M, Breugel M  
22 van, Wal H van der, Veloso M D M, Vester H F M, Vicentini A, Vieira I C G, Bentos T V, Williamson G  
23 B and Rozendaal D M A 2016 Biomass resilience of Neotropical secondary forests *Nature* **530** 211–4  
24  
25 Pregitzer K S and Euskirchen E S 2004 Carbon cycling and storage in world forests: Biome patterns related  
26 to forest age *Global Change Biology* **10** 2052–77  
27  
28 Pugh T A M, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V and Calle L 2019 Role of forest  
29 regrowth in global carbon sink dynamics *Proceedings of the National Academy of Sciences* **116** 4382–7  
30  
31 Reinmann A B and Hutyra L R 2017 Edge effects enhance carbon uptake and its vulnerability to climate  
32 change in temperate broadleaf forests *Proceedings of the National Academy of Sciences* **114** 107–12  
33  
34 Reinmann A B, Smith I A, Thompson J R and Hutyra L R 2020 Urbanization and fragmentation mediate  
35 temperate forest carbon cycle response to climate *Environmental Research Letters* **15** 114036  
36  
37 Remy E, Wuyts K, Boeckx P, Ginzburg S, Gundersen P, Demey A, Van Den Bulcke J, Van Acker J and  
38 Verheyen K 2016 Strong gradients in nitrogen and carbon stocks at temperate forest edges *Forest Ecology  
39 and Management* **376** 45–58  
40  
41 Requena Suarez D, Rozendaal D M A, Sy V D, Phillips O L, Alvarez-Dávila E, Anderson-Teixeira K,  
42 Araujo-Murakami A, Arroyo L, Baker T R, Bongers F, Brienen R J W, Carter S, Cook-Patton S C,  
43 Feldpausch T R, Griscom B W, Harris N, Héault B, Coronado E N H, Leavitt S M, Lewis S L, Marimon  
44 B S, Mendoza A M, N’dja J K, N’Guessan A E, Poorter L, Qie L, Rutishauser E, Sist P, Sonké B,  
45 Sullivan M J P, Vilanova E, Wang M M H, Martius C and Herold M 2019 Estimating aboveground net  
46 biomass change for tropical and subtropical forests: Refinement of IPCC default rates using forest plot  
47 data *Global Change Biology* **25** 3609–24  
48  
49 Ribeiro-Kumara C, Köster E, Aaltonen H and Köster K 2020 How do forest fires affect soil greenhouse gas  
50 emissions in upland boreal forests? A review *Environmental Research* **184** 109328  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 933 Saatchi S S, Harris N L, Brown S, Lefsky M, Mitchard E T A, Salas W, Zutta B R, Buermann W, Lewis S L,  
4 934 Hagen S, Petrova S, White L, Silman M and Morel A 2011 Benchmark map of forest carbon stocks in  
5 935 tropical regions across three continents *Proceedings of the National Academy of Sciences* **108** 9899–904
- 6 936 Schepaschenko D, Chave J, Phillips O L, Lewis S L, Davies S J, Réjou-Méchain M, Sist P, Scipal K, Perger  
7 937 C, Herault B, Labrière N, Hofhansl F, Affum-Baffoe K, Aleinikov A, Alonso A, Amani C,  
8 938 Araujo-Murakami A, Armston J, Arroyo L, Ascarrunz N, Azevedo C, Baker T, Balazy R, Bedeau C,  
9 939 Berry N, Bilous A M, Bilous S Y, Bissiengou P, Blanc L, Bobkova K S, Braslavskaya T, Brienen R,  
10 940 Burslem D F R P, Condit R, Cuni-Sánchez A, Danilina D, Torres D del C, Derroire G, Descroix L, Sotta  
11 941 E D, d’Oliveira M V N, Dresel C, Erwin T, Evdokimenko M D, Falck J, Feldpausch T R, Foli E G, Foster  
12 942 R, Fritz S, Garcia-Abril A D, Gornov A, Gornova M, Gothard-Basséché E, Gourlet-Fleury S, Guedes M,  
13 943 Hamer K C, Susanty F H, Higuchi N, Coronado E N H, Hubau W, Hubbell S, Ilstedt U, Ivanov V V,  
14 944 Kanashiro M, Karlsson A, Karminov V N, Killeen T, Koffi J-C K, Konovalova M, Kraxner F, Krejza J,  
15 945 Krisnawati H, Krivobokov L V, Kuznetsov M A, Lakyda I, Lakyda P I, Licona J C, Lucas R M, Lukina  
16 946 N, Lussetti D, Malhi Y, Manzanera J A, Marimon B, Junior B H M, Martinez R V, Martynenko O V,  
17 947 Matsala M, Matyashuk R K, Mazzei L, Memiaghe H, Mendoza C, Mendoza A M, Morozuk O V,  
18 948 Mukhortova L, Musa S, Nazimova D I, Okuda T, Oliveira L C, et al 2019 The Forest Observation System,  
19 949 building a global reference dataset for remote sensing of forest biomass *Scientific Data* **6** 1–11
- 20 950 Schimel D, Hargrove W, Hoffman F and MacMahon J 2007 NEON: A hierarchically designed national  
21 951 ecological network *Frontiers in Ecology and the Environment* **5** 59–9
- 22 952 Schimel D, Stephens B B and Fisher J B 2015 Effect of increasing CO<sub>2</sub> on the terrestrial carbon cycle  
23 953 *Proceedings of the National Academy of Sciences* **112** 436–41
- 24 954 Sist P, Rutishauser E, Peña-Claros M, Shenkin A, Hérault B, Blanc L, Baraloto C, Baya F, Benedet F, Silva  
25 955 K E da, Descroix L, Ferreira J N, Gourlet-Fleury S, Guedes M C, Harun I B, Jalonén R, Kanashiro M,  
26 956 Krisnawati H, Kshatriya M, Lincoln P, Mazzei L, Medjibé V, Nasi R, d’Oliveira M V N, Oliveira L C de,  
27 957 Picard N, Pietsch S, Pinard M, Priyadi H, Putz F E, Rodney K, Rossi V, Roopsind A, Ruschel A R,  
28 958 Shari N H Z, Souza C R de, Susanty F H, Sotta E D, Toledo M, Vidal E, West T A P, Wortel V and  
29 959 Yamada T 2015 The Tropical managed Forests Observatory: A research network addressing the future of  
30 960 tropical logged forests *Applied Vegetation Science* **18** 171–4
- 31 961 Smith I A, Hutyra L R, Reinmann A B, Thompson J R and Allen D W 2019 Evidence for Edge  
32 962 Enhancements of Soil Respiration in Temperate Forests *Geophysical Research Letters* **46** 4278–87
- 33 963 Smithwick E A H, Harmon M E, Remillard S M, Acker S A and Franklin J F 2002 Potential upper bounds of  
34 964 carbon stores in forests of the Pacific Northwest *Ecological Applications* **12** 1303–17
- 35 965 Song J, Wan S, Piao S, Knapp A K, Classen A T, Vicca S, Ciais P, Hovenden M J, Leuzinger S, Beier C,  
36 966 Kardol P, Xia J, Liu Q, Ru J, Zhou Z, Luo Y, Guo D, Adam Langley J, Zscheischler J, Dukes J S, Tang  
37 967 J, Chen J, Hofmockel K S, Kueppers L M, Rustad L, Liu L, Smith M D, Templar P H, Quinn Thomas R,  
38 968 Norby R J, Phillips R P, Niu S, Fatichi S, Wang Y, Shao P, Han H, Wang D, Lei L, Wang J, Li X, Zhang  
39 969 Q, Li X, Su F, Liu B, Yang F, Ma G, Li G, Liu Y, Liu Y, Yang Z, Zhang K, Miao Y, Hu M, Yan C,  
40 970 Zhang A, Zhong M, Hui Y, Li Y and Zheng M 2019 A meta-analysis of 1,119 manipulative experiments  
41 971 on terrestrial carbon-cycling responses to global change *Nature Ecology & Evolution* **3** 1309–20

- 1  
2  
3     972 Song X-P, Hansen M C, Stehman S V, Potapov P V, Tyukavina A, Vermote E F and Townshend J R 2018  
4         973 Global land change from 1982 to 2016 *Nature* **560** 639–43  
5  
6     974 Spawn S A, Sullivan C C, Lark T J and Gibbs H K 2020 Harmonized global maps of above and belowground  
7         975 biomass carbon density in the year 2010 *Scientific Data* **7** 112  
8  
9     976 Stoy P C, Mauder M, Foken T, Marcolla B, Boegh E, Ibrom A, Arain M A, Arneth A, Aurela M, Bernhofer  
10         977 C, Cescatti A, Dellwik E, Duce P, Gianelle D, van Gorsel E, Kiely G, Knohl A, Margolis H, McCaughey  
11         978 H, Merbold L, Montagnani L, Papale D, Reichstein M, Saunders M, Serrano-Ortiz P, Sottocornola M,  
12         979 Spano D, Vaccari F and Varlagin A 2013 A data-driven analysis of energy balance closure across  
13         980 FLUXNET research sites: The role of landscape scale heterogeneity *Agricultural and Forest Meteorology*  
14         981 **171-172** 137–52  
15  
16  
17     982 Sulman B N, Moore J A M, Abramoff R, Averill C, Kivlin S, Georgiou K, Sridhar B, Hartman M D, Wang  
18         983 G, Wieder W R, Bradford M A, Luo Y, Mayes M A, Morrison E, Riley W J, Salazar A, Schimel J P,  
19         984 Tang J and Classen A T 2018 Multiple models and experiments underscore large uncertainty in soil  
20         985 carbon dynamics *Biogeochemistry* **141** 109–23  
21  
22  
23     986 Taylor P G, Cleveland C C, Wieder W R, Sullivan B W, Doughty C E, Dobrowski S Z and Townsend A R  
24         987 2017 Temperature and rainfall interact to control carbon cycling in tropical forests ed L Liu *Ecology*  
25         988 Letters **20** 779–88  
26  
27  
28     989 Team R C 2020 R : A language and environment for statistical computing. R Foundation for Statistical  
29         990 Computing, Vienna, Austria. URL <http://www.R-project.org/>.  
30  
31     991 Tubiello F N, Pekkarinen A, Marklund L, Wanner N, Conchedda G, Federici S, Rossi S and Grassi G 2020  
32         992 Carbon Emissions and Removals by Forests: New Estimates 1990–2020 *Earth System Science*  
33         993 *Data Discussions* 1–21  
34  
35     994 van der Werf G R, Randerson J T, Giglio L, van Leeuwen T T, Chen Y, Rogers B M, Mu M, van Marle M J  
36         995 E, Morton D C, Collatz G J, Yokelson R J and Kasibhatla P S 2017 Global fire emissions estimates  
37         996 during 1997 *Earth System Science Data* **9** 697–720  
38  
39     997 Vargas R, Allen M F and Allen E B 2008 Biomass and carbon accumulation in a fire chronosequence of a  
40         998 seasonally dry tropical forest *Global Change Biology* **14** 109–24  
41  
42     999 Wang Y, Ciais P, Goll D, Huang Y, Luo Y, Wang Y-P, Bloom A A, Broquet G, Hartmann J, Peng S,  
43         1000 Penuelas J, Piao S, Sardans J, Stocker B D, Wang R, Zaehle S and Zechmeister-Boltenstern S 2018  
44         1001 GOLUM-CNP v1.0: A data-driven modeling of carbon, nitrogen and phosphorus cycles in major  
45         1002 terrestrial biomes *Geoscientific Model Development* **11** 3903–28  
46  
47     1003 Warner D L, Bond-Lamberty B, Jian J, Stell E and Vargas R 2019 Spatial Predictions and Associated  
48         1004 Uncertainty of Annual Soil Respiration at the Global Scale *Global Biogeochemical Cycles* **33** 1733–45  
49  
50     1005 Williams C A, Collatz G J, Masek J, Huang C and Goward S N 2014 Impacts of disturbance history on  
51         1006 forest carbon stocks and fluxes: Merging satellite disturbance mapping with forest inventory data in a  
52         1007 carbon cycle model framework *Remote Sensing of Environment* **151** 57–71  
53  
54     1008 Wilson R M, Hopple A M, Tfaily M M, Sebestyen S D, Schadt C W, Pfeifer-Meister L, Medvedeff C,  
55         1009 McFarlane K J, Kostka J E, Kolton M, Kolka R K, Kluber L A, Keller J K, Guilderson T P, Griffiths N  
56  
57  
58  
59  
60

1  
2  
3 1010 A, Chanton J P, Bridgham S D and Hanson P J 2016 Stability of peatland carbon to rising temperatures  
4 1011 *Nature Communications* **7** 13723  
5

6 1012 Xu M and Shang H 2016 Contribution of soil respiration to the global carbon equation *Journal of Plant*  
7 1013 *Physiology* **203** 16–28  
8

9 1014 Yang Y, Luo Y and Finzi A C 2011 Carbon and nitrogen dynamics during forest stand development: A  
10 1015 global synthesis *New Phytologist* **190** 977  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
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25  
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**Title:** Carbon cycling in mature and regrowth forests globally  
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## Summary

*Background.* Forests are major components of the global carbon (C) cycle and thereby strongly influence atmospheric carbon dioxide (CO<sub>2</sub>) and climate. However, efforts to incorporate forests into climate models and CO<sub>2</sub> accounting frameworks have been constrained by a lack of accessible, global-scale synthesis on how C cycling varies across forest types and stand ages.

*Methods/Design.* Here, we draw from the Global Forest Carbon Database, ForC, to provide a macroscopic overview of C cycling in the world's forests, giving special attention to stand age-related variation. Specifically, we use 11923 ForC records for 34 C cycle variables from 865 geographic locations to characterize ensemble C budgets for four broad forest types – tropical broadleaf evergreen, temperate broadleaf, temperate conifer, and boreal. We calculate statistics for both mature and regrowth (age <100 years) forests, and quantify trends with stand age in regrowth forests for all variables with sufficient data.

*Review Results/ Synthesis.* The rate of C cycling generally decreased from tropical to boreal regions in both mature and regrowth forests, whereas C stocks showed less directional variation. Net ecosystem production of mature forests was indistinguishable across biomes. The majority of flux variables, together with most live biomass pools, increased significantly with stand age when fit with logarithmic functions.

*Discussion.* As climate change accelerates, understanding and managing the carbon dynamics of forests is critical to forecasting, mitigation, and adaptation. This comprehensive and synthetic global overview of C stocks and fluxes across biomes and stand ages will help to advance these efforts.

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

## Background

Forest ecosystems are shaping the course of climate change through their influence on atmospheric carbon dioxide (CO<sub>2</sub>; Bonan 2008, Friedlingstein *et al* 2019, IPCC 2018). Despite the centrality of forest C cycling in regulating atmospheric CO<sub>2</sub>, important uncertainties in climate models (Friedlingstein *et al* 2006, Krause *et al* 2018, Bonan *et al* 2019, Di Vittorio *et al* 2020) and CO<sub>2</sub> accounting frameworks (Pan *et al* 2011, IPCC 2019) can be traced to lack of understanding on how C cycling varies across forest types and in relation to stand history. This requires accessible, comprehensive, and large-scale databases with global coverage, which runs contrary to the traditional way forest C stocks and fluxes have been measured and published. Large-scale synthesis is critical to benchmarking model performance with global data (Clark *et al* 2017, Luo *et al* 2012), quantifying the role of forests in the global C cycle (*e.g.*, Pan *et al* 2011), and using book-keeping methods to quantify actual or potential exchanges of CO<sub>2</sub> between forests and the atmosphere (Griscom *et al* 2017, Houghton 2020).

### Forests in the global C cycle: current and future

A robust understanding of forest impacts on global C cycling is essential. Total annual photosynthesis in forests (gross primary productivity, GPP) is estimated at approximately 69 Gt C yr<sup>-1</sup> (Badgley *et al* 2019), more than seven times the average annual fossil fuel emissions during 2009-2018 ( $9.5 \pm 0.5$  Gt C yr<sup>-1</sup>; Friedlingstein *et al* 2019). Most of this enormous C uptake is counterbalanced by releases to the atmosphere through ecosystem respiration ( $R_{eco}$ ) and fire, with forests globally dominant as sources of both soil respiration (Warner *et al* 2019) and fire (van der Werf *et al* 2017). In recent years, total forest C uptake has exceeded releases, such that globally forests have been a C sink (Harris *et al* 2021). Considering only areas remaining in forest, this C sink has averaged  $3.2 \pm 0.6$  Gt C yr<sup>-1</sup> for 2009-2018, offsetting 29% of anthropogenic fossil fuel emissions (Friedlingstein *et al* 2019). However, deforestation, estimated at  $\sim 1$  Gt C yr<sup>-1</sup> in recent decades (Pan *et al* 2011, Tubiello *et al* 2020), reduces the net forest sink to  $\sim 1.1\text{-}2.2$  Gt C yr<sup>-1</sup> (Friedlingstein *et al* 2019, Harris *et al* 2021).

The future of the current forest C sink is dependent both upon forest responses to climate change itself and human land use decisions, which will feedback and strongly influence the course of climate change (Friedlingstein *et al* 2006). Regrowing forests in particular will play an important role (Pugh *et al* 2019), as almost two-thirds of the world's forests were secondary as of 2010 (FAO 2010). As anthropogenic and climate-driven disturbances impact an growing proportion of Earth's forests (Andela *et al* 2017, McDowell *et al* 2020), understanding the carbon dynamics of regrowth forests is increasingly important (Anderson-Teixeira *et al* 2013). Although age trends in aboveground biomass have been well-studied and synthesized globally (Cook-Patton *et al* 2020), a relative dearth of data and synthesis on other C stocks and fluxes in secondary forests points to an under-filled need to characterize age-related trends in forest C cycling. Such understanding is particularly critical for reducing uncertainty regarding the potential for carbon uptake and climate change mitigation by regrowth forests (Krause *et al* 2018, Cook-Patton *et al* 2020). Understanding, modeling, and managing forest-atmosphere CO<sub>2</sub> exchange is thus central to

efforts to mitigate climate change (Grassi *et al* 2017, Griscom *et al* 2017, Cavalieri *et al* 2015).

### Evolution of forest C cycle research

For more than half a century, researchers have sought to understand how forest carbon cycling varies across stands, including those of different biomes (e.g., Lieth 1973, Luyssaert *et al* 2007) and stand ages (e.g., Odum 1969, Luyssaert *et al* 2008). Over this time, an increasingly refined conceptual understanding of the elements of ecosystem C cycles has developed, as a growing number of variables have been defined (e.g., Chapin *et al* 2006), along with appropriate measurement methods (e.g., Clark *et al* 2001). New technology has also enabled researchers to directly measure an expanding set of variables, notably including the development of continuous measurements of soil CO<sub>2</sub> efflux (Kuzyakov 2006) and ecosystem-atmosphere CO<sub>2</sub> exchange (Baldocchi *et al* 2001). Measurement techniques have been increasingly standardized; for example, of the biomass allometries that strongly influence estimates of most C cycle variables (e.g., Chave *et al* 2014). Further standardization has been made possible through research networks such as ForestGEO (Anderson-Teixeira *et al* 2015, Davies *et al* 2021), NEON (Schimel *et al* 2007), and FLUXNET (Baldocchi *et al* 2001, Novick *et al* 2018). Remote sensing technology has become increasingly useful for global- or regional-scale estimates of a few critical variables (e.g., aboveground biomass,  $B_{ag}$ ; Saatchi *et al* 2011, Hu *et al* 2016, Spawn *et al* 2020, gross primary productivity, GPP; Li and Xiao 2019), yet measurement and validation of most forest C stocks and fluxes necessarily requires intensive on-the-ground data collection.

Alongside these conceptual and methodological developments, there has been a proliferation of measurements across the world's forests. The result of decades of research on forest C cycling is tens of thousands of records distributed across thousands of scientific articles, varying in data formats, units, measurement methods, etc. To address global-scale questions, researchers began synthesizing data into increasingly large databases (e.g., Lieth 1973, Luyssaert *et al* 2007, Bond-Lamberty and Thomson 2010, Anderson-Teixeira *et al* 2016, 2018, Cook-Patton *et al* 2020). The current largest, most comprehensive database on forest C cycling is *ForC* (Anderson-Teixeira *et al* 2016, 2018), which contains published estimates of forest ecosystem C stocks and annual fluxes (>50 variables), with different variables capturing distinct ecosystem pools (e.g., woody, foliage, and root biomass; dead wood) and flux types (e.g., gross and net primary productivity; soil, root, and ecosystem respiration). These data represent ground-based measurements, and *ForC* contains associated data required for interpretation (e.g., stand history, measurement methods). Since its most recent publication (*ForC v2.0-Ecology*; Anderson-Teixeira *et al* 2018), *ForC* has grown 129%, primarily through the incorporation of two additional large databases that also synthesized published forest C data: the Global Soil Respiration Database (SRDB; Bond-Lamberty and Thomson 2010, Jian *et al* 2020) and the Global Reforestation Opportunity Assessment database (GROA; Cook-Patton *et al* 2020). Following these additions, *ForC* currently contains 39762 records from 10608 plots and 1532 distinct geographic areas representing all forested biogeographic and climate zones, making it ideal for assessing how forest C cycling varies across biomes and with respect to stand age.

### Biome differences

Forest C cycling varies enormously across biomes, which categorize the world's forests according to major differences in climate, vegetation, *etc.* Since the early 19th century, it has been recognized that climate plays a dominant role in shaping differences among forests on a global scale (Humboldt and Bonpland 1807, Holdridge 1947). Global scale data syntheses have shown that C fluxes including *GPP*, net primary productivity (*NPP*), and soil respiration ( $R_{soil}$ ) decrease with latitude or, correspondingly, increase with mean annual temperature (Fig. 1; e.g., Lieth 1973, Luyssaert *et al* 2007, Hursh *et al* 2017, Banbury Morgan *et al* n.d.). C stocks of mature forests show less directional variation (Fig. 1). On average, aboveground biomass ( $B_{ag}$ ) tends to decrease with latitude, but not as dramatically as fluxes, and with the highest  $B_{ag}$  forests in relatively cool, moist temperate regions (Keith *et al* 2009, Smithwick *et al* 2002, Hu *et al* 2016). In contrast, standing and downed dead wood ( $DW_{standing}$  and  $DW_{down}$ , respectively, summing to  $DW_{tot}$ ) and the organic layer (*OL*) tend to accumulate more in colder climates where decomposition is slow relative to *NPP* (Harmon *et al* 1986, Allen *et al* 2002).

Correlative analyses relating C cycle variables to climate and other environmental variables have recently been taken to a new level through use of machine-learning algorithms that relate ground-based C cycle data to global maps of environmental covariates, making it possible to create fine-scale global maps of C cycling (e.g., Warner *et al* 2019, Cook-Patton *et al* 2020). This approach can be particularly effective when paired with satellite measurements that correlate to C cycle variables of interest; for example, solar-induced chlorophyll fluorescence is useful for fine-scale mapping of gross primary productivity (*GPP*; Li and Xiao 2019), while LiDAR, radar, and optical imagery are being used to estimate  $B_{ag}$  at regional to global scales (e.g., Saatchi *et al* 2011, Hu *et al* 2016). Any such analysis is however constrained by the quality and coverage of ground-based estimates of forest C fluxes or stocks (e.g., Schepaschenko *et al* 2019). While estimates of some variables (e.g.,  $B_{ag}$ , *GPP*, *NPP*,  $R_{soil}$ ) are widely available, many remain poorly characterized (e.g.,  $DW_{tot}$ ; *OL*; autotrophic respiration,  $R_{auto}$ ) –even at the coarse resolution of biomes. This is a critical limitation not only for understanding forest C cycling, but also for quantifying forest-based climate change mitigation across forest biomes or ecozones (e.g., IPCC 2019).

### Age trends and their variation across biomes

Stand age is another important axis of variation in forest C cycling (Fig. 1). In 1969, E.P. Odum's "The Strategy of Ecosystem Development" laid out predictions as to how forest energy flows and organic matter stocks vary with stand age (Odum 1969). Although the conceptualization of the C cycle in this paper was simplistic by current standards, the paper was foundational in framing the theory around which research on the subject still revolves (Corman *et al* 2019), and the basic framework still holds, albeit with modest modifications (Fig. 1; Anderson-Teixeira *et al* 2013). Following stand-clearing disturbance, *GPP*, *NPP*, and biomass of leaves ( $B_{foliage}$ ) and fine roots ( $B_{root-fine}$ ) increase rapidly and thereafter remain relatively stable ( $B_{foliage}$ ,  $B_{root-fine}$ , sometimes *GPP*) or decline slightly (*NPP*, sometimes *GPP*; e.g., Law *et al* 2003, Pregitzer and Euskirchen 2004, Amiro *et al* 2010, Goulden *et al* 2011). The decline in *NPP* occurs because  $R_{auto}$  increases relative to *GPP* as

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3 forests age, corresponding to declining carbon use efficiency with stand age (DeLucia *et al* 4  
4 2007, Collalti *et al* 2020). Heterotrophic respiration, most of which originates from the soil 5  
5 ( $R_{het-soil}$ ) remains relatively constant with stand age (Law *et al* 2003, Pregitzer and 6  
6 Euskirchen 2004, Goulden *et al* 2011), with the result that net ecosystem production 7  
7 ( $NEP = GPP - R_{eco}$ , where  $R_{eco}$  is total ecosystem respiration) is initially negative, 8  
8 increases to a maximum at intermediate ages, and declines—typically to a small positive 9  
9 value—thereafter (Law *et al* 2003, Pregitzer and Euskirchen 2004, Amiro *et al* 2010, 10  
10 Goulden *et al* 2011, Luyssaert *et al* 2008). The result is that biomass accumulates rapidly in 11  
11 young forests, followed by a slow decline to near zero in old forests (e.g., Lichstein *et al* 12  
12 2009, Yang *et al* 2011). While these trends have been subject of fairly recent qualitative 13  
13 review (Anderson-Teixeira *et al* 2013), there is need for a synthetic, quantitative review 14  
14 taking advantage of the greatly expanded data now available.  
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17 In the past few decades, researchers have started asking how age trends—mostly in  $B_{ag}$  or  
18 total biomass ( $B_{tot}$ ) accumulation—vary across biomes. Early research on this theme  
19 showed that biomass accumulation rates during secondary succession increase with  
20 temperature on a global scale (Johnson *et al* 2000, Anderson *et al* 2006) and with water  
21 availability in the neotropics (Poorter *et al* 2016). Most recently, Cook-Patton *et al* (2020)  
22 reinforced these earlier findings with a much larger dataset and created a high-resolution  
23 global map of estimated potential C accumulation rates. However, there has been little  
24 synthesis of cross-biome differences in variables other than biomass and its accumulation  
25 rate (but see Cook-Patton *et al* (2020) for DW, OL, and soil C accumulation in young  
26 stands). Given the important role of secondary forests in the current and future global C  
27 cycle, concrete understanding of age trends in C fluxes and stocks and how these vary  
28 across biomes is critical to better understanding of the global C cycle. Accurate estimates of  
29 C sequestration rates by regrowth forests are also critical for national greenhouse gas  
30 accounting under the IPCC framework (IPCC 2019, Requena Suarez *et al* 2019) and to  
31 quantifying the value of regrowth forests for climate change mitigation (Anderson-Teixeira  
32 and DeLucia 2011, Goldstein *et al* 2020).  
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35 Here, we conduct a data-based review of carbon cycling from a stand to global level, and by  
36 biome and stand age, using the largest global compilation of forest carbon data, which is  
37 available in our open source Global Carbon Forest database (*ForC*; Fig. 2). Our goal is to  
38 provide a comprehensive synthesis on broad trends in forest C cycling that can serve as a  
39 foundation for improved understanding of global forest C cycling and highlight where key  
40 sources of uncertainty still reside.  
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## 43 Methods/ Design

44 This review synthesizes data from the *ForC* database (Fig. 2; <https://github.com/forc-db/ForC>; Anderson-Teixeira *et al* 2016, 2018). *ForC* amalgamates numerous intermediary  
45 data sets (e.g., Luyssaert *et al* 2007, Bond-Lamberty and Thomson 2010, Cook-Patton *et al*  
46 2020) and original studies. Original publications were referenced to check values and  
47 obtain information not contained in intermediary data sets, although this process has not  
48 been completed for all records. The database was developed with goals of understanding  
49 how C cycling in forests varies across broad geographic scales and as a function of stand  
50 age. As such, there has been a focus on incorporating data from regrowth forests (e.g.,  
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Anderson *et al* 2006, Martin *et al* 2013, Bonner *et al* 2013) and obtaining stand age data when possible (83% of records in v.2.0; Anderson-Teixeira *et al* 2018). Particular attention was given to developing the database for tropical forests (Anderson-Teixeira *et al* 2016), which represented roughly one-third of records in *ForC* v2.0 (Anderson-Teixeira *et al* 2018). Since publication of *ForC* v2.0, we imported three large additional databases into *ForC* via a combination of R scripts and manual edits. First, we imported (via R script) the Global Database of Soil Respiration Database (*SRDB* v4, 9488 records; Bond-Lamberty and Thomson 2010), and corrections and improvements to *SRDB* arising from this process were incorporated in *SRDB* v5 (Jian *et al* 2020). Second, we imported (via R script) the Global Reforestation Opportunity Assessment database (*GROA* v1.0, 10116 records; Cook-Patton *et al* 2020, Anderson-Teixeira *et al* 2020), which itself had drawn on an earlier version of *ForC*. Because all records in *GROA* were checked against original publications, these records were given priority over duplicates in *ForC* (Appendix S1). Third, we incorporated records of annual *NEP*, *GPP*, and *R<sub>eco</sub>* from the FLUXNET2015 dataset (Pastorello *et al* 2020), treating these records as authoritative when they duplicated earlier records (Appendix S1). We have also added data from individual publications, with a particular focus on productivity (e.g., Taylor *et al* 2017), dead wood, and ForestGEO sites (e.g., Lutz *et al* 2018, Johnson *et al* 2018). A record of data sets added to *ForC* over the course of its development is available at [https://github.com/forc-db/ForC/blob/master/database\\_management\\_records/ForC\\_data\\_additions\\_log.csv](https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv). The database version used for this analysis has been tagged as a new release on Github (v3.0) and assigned a DOI through Zenodo (DOI: TBD).

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 2018). Duplicate or otherwise conflicting records were purged as described in Appendix S1, resulting in a total of 22265 records (56% 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 plots with any record of managements manipulating CO<sub>2</sub>, temperature, hydrology, nutrients, or biota, as well as any plots whose site or plot name contained the terms “plantation”, “planted”, “managed”, “irrigated”, or “fertilized” (13.9% of duplicate-purged records). We also removed stands that had undergone any notable anthropogenic thinning or partial harvest (5.6% of duplicate-purged records). 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 (5.7% of duplicate-purged records). In total, this resulted in 17349 records (43.6% 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 (Table 1). These different flux and stock variables represent different pools (e.g., aboveground biomass, root biomass, dead wood) and levels of combination (e.g., total net primary productivity, *NPP*, versus the individual elements of *NPP* such as foliage, roots, and branches). We did not analyze soil carbon, which is not a focus of the *ForC* database. Note that two flux variables, aboveground heterotrophic respiration (*R<sub>het-ag</sub>*) and total respiration (*R<sub>het</sub>*), were included for conceptual completeness but had no records in *ForC*.

(Table 1). Records for our focal variables represented 90.3% of the total records eligible for inclusion. For this analysis, we combined some of ForC's specific variables into more broadly defined variables. Specifically, net ecosystem exchange (measured by eddy-covariance; Baldocchi *et al* 2001) and biometric estimates of *NEP* were combined into the single variable *NEP* (Table 1). Furthermore, for *NPP*, aboveground *NPP* (*ANPP*), and the litterfall component of *ANPP* (*ANPP<sub>litterfall</sub>*), *ForC* variables specifying inclusion of different components were combined (*e.g.*, measurements including or excluding fruit and flower production and herbivory). Throughout *ForC*, for all measurements drawing from tree census data (*e.g.*, biomass, productivity), trees were censused down to a minimum diameter breast height (DBH) threshold of 10 cm or less. All records were measured directly or derived from field measurements.

We grouped forests into four broad biome types based on climate zones and dominant vegetation type (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones (Fig. 2) were defined based on site geographic coordinates according to Köppen-Geiger zones (Rubel and Kottek 2010). We defined the tropical biome as including all equatorial (A) zones, temperate biomes as including all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and the boreal biome as including 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. We defined leaf type (broadleaf / needleleaf) based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYNMAP; Jung *et al* 2006). For young tropical forests imported from *GROA* but not yet classified by leaf type, we assumed that all were broadleaf, consistent with the rarity of naturally regenerating needleleaf forests in the tropics. We also classified forests as "young" (< 100 years) or "mature" ( $\geq 100$  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 geographic coordinates (0.4% of sites in full database) or records of stand age (5.7% of records in full database). We also excluded records of stand age = 0 year (0.8% of records in full database). In total, our analysis retained 11923 records. Numbers of records by biome and age class are given in Table S1.

Data were summarized to produce schematics of C cycling for mature forests of each biome. To obtain the values reported in the C cycle schematics, we first averaged any repeated measurements within a plot. Values were then averaged across geographically distinct areas, defined as 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.

We tested whether the C budgets described above "closed"—*i.e.*, whether they were internally consistent. Specifically, we first defined relationships among variables: for example,  $NEP = GPP - R_{eco}$ ,  $BNPP = BNPP_{coarse} + BNPP_{fine}$ ,  $DW_{tot} = DW_{standing} + DW_{down}$ ). Henceforth, we refer to the variables on the left side of the equation as "aggregate" fluxes or stocks, and those that are summed as "component" fluxes or stocks, noting that the same variable can take both aggregate and component positions in different

relationships. We considered the C budget for a given relationship “closed” when component variables summed to within one standard deviation of the aggregate variable.

To test for differences across mature forest biomes, we also examined how stand age impacted fluxes and stocks, employing a mixed effects model (“lmer” function in “lme4” R package; Bates *et al* 2015) 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. This analysis was run for variables with records for at least seven distinct geographic areas in more than one biome, excluding any biomes that failed this criteria (Table 1).

To test for age trends in young (<100yrs) forests, we employed a mixed effects model with biome and log10[stand age] as fixed effects and plot nested within geographic area as a random effect on the intercept. This analysis was run for variables with records for at least three distinct geographic areas in more than one biome, excluding any biomes that failed this criteria (Table 1). 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  $\times$  stand.age interaction was included in the model. We note that the logarithmic function fit in this analysis does not always correspond to theoretical expectations (Fig. 1); however, data limitations did not support fitting of functions with more parameters or reliable comparison of different functional forms. Within the data constraints, we deemed a logarithmic function to be the most appropriate functional form for the majority of variables.

To facilitate the accessibility of our results and data, and to allow for rapid updates as additional data become available, we automated all database manipulation, analyses, and figure production in R (Team 2020).

## Review Results/ Synthesis

### Data Coverage

Of the 39762 records in *ForC* v3.0, 11923 met our strict criteria for inclusion in this study (Fig. 2). These records were distributed across 5062 plots in 865 distinct geographic areas. Of the 23 flux and 11 stock variables mapped in our C cycle diagrams (Figs. 3-6, S1-S4), *ForC* contained sufficient mature forest data for inclusion in our statistical analyses (*i.e.*, records from  $\geq 7$  distinct geographic areas) for 20 fluxes and 9 stocks in tropical broadleaf forests, 15 fluxes and 8 stocks in temperate broadleaf forests, 14 fluxes and 7 stocks in temperate conifer forests, and 8 fluxes and 7 stocks in boreal forests. For regrowth forests (<100 yrs), *ForC* contained sufficient data for inclusion in our statistical analyses (*i.e.*, records from  $\geq 3$  distinct geographic areas) for 11 fluxes and 10 stocks in tropical broadleaf forests, 16 fluxes and 10 stocks in temperate broadleaf forests, 16 fluxes and 10 stocks in temperate conifer forests, and 14 fluxes and 9 stocks in boreal forests.

### C cycling in mature forests

Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests  $\geq 100$  years old and with no known major natural or anthropogenic disturbance are presented in Figures 3-6 (and available in tabular format in the *ForC* release accompanying this publication:

[ForC/numbers\\_and\\_facts/ForC\\_variable\\_averages\\_per\\_Biome.csv](#)).

For variables with records from  $\geq 7$  distinct geographic areas, these ensemble C budgets met our criteria for budget “closure”. That is, component variables summed to within one standard deviation of their respective aggregate variables in all but one instance. In the temperate conifer biome, the average composite measure of root biomass ( $B_{root}$ ) was less than the combined average value of coarse and fine root biomass ( $B_{root-coarse}$  and  $B_{root-fine}$ , respectively). This lack of closure was driven by very high estimates of  $B_{root-coarse}$  from high-biomass forests of the US Pacific Northwest (Fig. S25).

There were sufficient data to assess differences among biomes in mature forest values for 15 flux variables, and significant differences among biomes were detected for 12 variables (Table 1). In all of these cases—including C fluxes into, within, and out of the ecosystem—C fluxes were highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and lowest in boreal forests (Table 1, Figs. 7, S5-S19). Differences between tropical and boreal forests were always significant, with temperate forests intermediate and significantly different from one or both. Fluxes tended to be numerically greater in temperate broadleaf than temperate conifer forests, but the difference was never statistically significant. This pattern held for the following variables:  $GPP$ ,  $NPP$ ,  $ANPP$ ,  $ANPP_{stem}$ ,  $ANPP_{branch}$ ,  $ANPP_{foliage}$ ,  $BNPP$ ,  $R_{eco}$ ,  $R_{root}$ ,  $R_{soil}$ , and  $R_{het-soil}$ . For two of the variables without significant differences among biomes ( $ANPP_{litterfall}$  and  $BNPP_{fine}$ ; Figs. S12 and S15, respectively), the same general trends applied but were not statistically significant. Another exception was for  $BNPP_{root-coarse}$ , where all records came from high-biomass forests in the US Pacific Northwest, resulting in marginally higher values for the temperate conifer biome (Fig. S14; differences significant in mixed effects model but not in post-hoc pairwise comparison).

The most notable exception to the pattern of decreasing flux per unit area from tropical to boreal biomes was  $NEP$ , with no significant differences across biomes but with the largest average in temperate broadleaf forests, followed by tropical, boreal, and temperate conifer forests (Figs. 7, S5). For all biomes,  $NEP$  was positive, with 95% confidence intervals excluding zero.

Biome differences were less consistent across C stocks than fluxes (Figs. 8, S20-S30). There were sufficient data to assess mature forest biome differences for nine stock variables, and significant differences among biomes were detected for five variables ( $B_{tot}$ ,  $B_{ag}$ ,  $B_{ag-wood}$ ,  $B_{foliage}$ ,  $B_{root-coarse}$ ; Table 1). For  $B_{tot}$  and  $B_{ag}$ , tropical broadleaf forests had the highest mean biomass and boreal forests the lowest, with intermediate means for temperate broadleaf and needleleaf forests (temperate needleleaf excluded from  $B_{tot}$  analysis because of insufficient data; Figs. S20, S21). However, maximum values for these variables – along with all other stocks including live or standing woody biomass ( $B_{ag-wood}$ ,  $B_{root}$ ,

*B<sub>root-coarse</sub>*, *DW<sub>tot</sub>*, *DW<sub>standing</sub>*) – consistently occurred in temperate biomes (Figs. 1, 8, S20-S30). For variables that were disproportionately sampled in such high-biomass forests (*B<sub>ag-wood</sub>*, *B<sub>foliage</sub>*, and *B<sub>root-coarse</sub>*; disproportionately sampled in the US Pacific Northwest), temperate conifer forests had significantly higher stocks than the other biomes.

### C cycling in young forests

C fluxes commonly increased significantly with stand age (Tables 1, S2, Figs. 7, 9, S5-S30). *ForC* contained 16 C flux variables with sufficient data for analyses of age trends in young forests (see Methods). Of these, ten increased significantly with *log10[age]*: *NEP*, *GPP*, *ANPP*, *ANPP<sub>woody</sub>*, *ANPP<sub>foliage</sub>*, *ANPP<sub>litterfall</sub>*, *BNPP*, *BNPP<sub>fine</sub>*, *R<sub>eco</sub>*, and *R<sub>root</sub>*. The remaining six – *NPP*, *ANPP<sub>stem</sub>*, *ANPP<sub>branch</sub>*, *BNPP<sub>coarse</sub>*, *R<sub>soil</sub>*, and *R<sub>het-soil</sub>* – displayed no significant relationship to stand age.

Differences in C fluxes across biomes typically paralleled those observed for mature forests, with C cycling generally most rapid in the tropics and slowest in boreal forests (Table 1, Figs. 7, S5-S30). The single exception was *ANPP<sub>stem</sub>*, for which temperate broadleaf and conifer forests had flux rates similar to tropical forests. Notably, and in contrast to the lack of biome differences in *NEP* for mature forests (Fig. 7), the tendency for temperate forests to have greater fluxes than boreal forests held for *NEP* in regrowth forests (tropical forests excluded because of insufficient data).

“Closure” and internal consistency of the C flux budget was less successful for young than mature forests (Figs. 9). Summed regression equations for *R<sub>soil-het</sub>* and *R<sub>root</sub>* were generally very close to *R<sub>soil</sub>*. In assessing the C budget of young forests, we calculated *R<sub>auto-ag</sub>* as the difference between *R<sub>eco</sub>* and *R<sub>soil</sub>* (except for tropical forests, which had insufficient *R<sub>eco</sub>* data), effectively guaranteeing near-closure of the CO<sub>2</sub> efflux (respiration) portion of the budget (negative values in Figs. 9). In contrast, the CO<sub>2</sub> influx portion of the budget generally did not “close”: the sum of *R<sub>auto</sub>* (*R<sub>root</sub>* + *R<sub>auto-ag</sub>*, as described above) and components of *NPP* consistently fell short of *GPP*, particularly in young stands (range across forest types and ages: 0.9-7.6 Mg C ha<sup>-1</sup> yr<sup>-1</sup>). Moreover, there was not consistent budget closure among the components of *NPP*, and substantially different age trends resulting from the sum of components versus total *NPP* (Figs. 9). Although age trends of young forests often converged towards mature forest averages, there were also some discrepancies between young forest trends and mature forest averages (Figs. 7, 9, S5-S30), most notably including a tendency for higher fluxes in regrowth boreal forests than in their mature counterparts (Fig. 9).

In terms of C stocks, ten variables (all but standing deadwood, *DW<sub>standing</sub>*) had sufficient data to test for age trends (Table 1, Figs. 8, S20-S30). All of these displayed a significant overall increase with *log10[stand. age]*. Age × biome interactions were also significant for all ten of these C stock variables (Table S2), with living C stocks tending to accumulate more rapidly during the early stages of forest regrowth in tropical forests (Figs. 8, 9, S20-S30). In the case of two non-living C stocks (*DW<sub>down</sub>* and *OL*), age × biome interactions were such that age trends were positive in some biomes and negative in others. Specifically, *DW<sub>down</sub>* declined with age in temperate and boreal forests, compared

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3 to an increase with age in tropical forests (Figs. 8,9, S29). Similarly, *OL* declined slightly  
4 with age in temperate broadleaf forests, contrasting an increase in the other three biomes  
5 (Figs. 8, 9, S30). Again, there were some discrepancies between young forest trends and  
6 mature forests, most notably including generally higher C stocks in mature forests relative  
7 to their 100-year counterparts, particularly for temperate conifer forests (with  
8 discrepancies again driven by differences in geographic representation) and, to a lesser  
9 extent, tropical broadleaf forests (Fig. 9).  
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## Discussion

ForC v3.0 provided unprecedented coverage of most major variables, yielding a broad picture of C cycling in the world's major forest biomes. Carbon cycling rates generally increased from boreal to tropical regions and with stand age (Figs. 1, 9). Specifically, most C fluxes were highest in tropical forests, intermediate in temperate (broadleaf or conifer) forests, and lowest in boreal forests – a pattern that generally held for regrowth as well as mature forests (Figs. 1, 7- 8, 9). The notable exception was mature forest *NEP*, which, as the difference between *GPP* and *R<sub>eco</sub>*, was statistically indistinguishable across biomes (Fig. 7f). There was also little directional variation in mean mature forest C stocks (biomass, dead wood, and organic layer) across biomes, although maximum values for the majority of stocks (all including live or standing woody biomass) occurred in temperate biomes (Figs. 1, 3-6, 8). Consistent with theory and previous studies (Fig. 1), the majority of flux variables, together with most live biomass pools, increased significantly with stand age (Table 1; Figs. 7- 9, S5-S30). Together, these results indicate that, moving from cold to tropical climates and from young to old stands, there is a general acceleration of C cycling, whereas C stocks and *NEP* of mature forests, which are defined by the differences between in- and out- fluxes, do not vary systematically across biomes. Together, these results refine and expand our understanding of C cycling in mature forests, while providing the first global-scale analysis of age trends in multiple forest C stocks and fluxes (Figs. 9).

### C cycling across biomes

Our analysis reveals that carbon cycling is most rapid in the tropics and slowest in boreal regions, including C fluxes into (*GPP*), within (e.g., *NPP* and its components), and out of (e.g., *R<sub>soil</sub>*, *R<sub>eco</sub>*) the ecosystem. For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes generally decline with latitude – or increase with temperature – on a global scale (e.g., Luyssaert *et al* 2007, Gillman *et al* 2015, Li and Xiao 2019, Banbury Morgan *et al* n.d.). This consistency is not surprising, particularly given commonality in the data analyzed or used for calibration. The finding that these patterns hold consistently across numerous fluxes, while consistent with theoretical expectations (Fig. 1), is novel to this analysis (but see Banbury Morgan *et al* n.d. for nine autotrophic fluxes).

The notable exception to the pattern of fluxes decreasing from tropical to boreal regions is *NEP*, which showed no significant differences across biomes, albeit with the highest mean in temperate broadleaf forests (Fig. 7f). Unlike the other C flux variables, *NEP* does not characterize the rate at which C cycles through the ecosystem, but, as the balance between *GPP* and *R<sub>eco</sub>*, represents net CO<sub>2</sub> sequestration (or release) by the ecosystem (Fig. 1). *NEP* tends to be relatively small in mature forest stands, which accumulate carbon slowly relative to younger stands, if at all (Fig. 1; Luyssaert *et al* 2008, Amiro *et al* 2010, Besnard *et al* 2018). It is therefore consistent with theory – and with previous research (Luyssaert *et al* 2007) – that there are no pronounced differences across biomes. Rather, variation in *NEP* of mature forests appears to be controlled less by climate and more by other factors including moderate disturbances (Curtis and Gough 2018) or disequilibrium of *R<sub>soil</sub>* relative to C inputs (e.g., in peatlands where anoxic conditions inhibit decomposition; Wilson *et al* 2016). The fact that mature temperate broadleaf forests have a higher mean

than the other biomes may reflect the fact that most of these forests are older secondary forests that, while classified here as mature, are still accumulating carbon (Curtis and Gough 2018).

In contrast to the patterns observed for *NEP* in mature stands, *NEP* of stands between 20 and 100 years of age varied across biomes, being lowest in boreal forests, intermediate in temperate broadleaf forests, and highest in temperate conifer forests (with insufficient data to assess tropical forests; Figs. 7, S5). This is consistent with findings that live biomass accumulation rates ( $\Delta B_{ag}$  or  $\Delta B_{tot}$ ) during early secondary succession decrease with latitude (Figs. 8a, S20-S30; Anderson *et al* 2006, Cook-Patton *et al* 2020). Note, though, that *NEP* includes not only  $\Delta B_{tot}$ , but also changes in *DW<sub>tot</sub>*, *OL*, and soil carbon (not analyzed here). Biome differences in the accumulation rates of *DW*, *OL*, and soil C have not been detected, in part because these variables do not consistently increase with stand age (Figs. 1, 8, S27-S30, and see discussion below; Cook-Patton *et al* 2020).

For regrowth forests, little was previously known about cross-biome differences in carbon fluxes, and we are not aware of any previous large-scale comparisons of C fluxes that have been limited to regrowth forests. Thus, this analysis was the first to examine flux trends in regrowth forests across biomes. The observed tendency for young forest fluxes to decrease from tropical to boreal regions paralleled patterns in mature forests (Figs. 7, 9, S5-S19), suggesting that regrowth forests follow latitudinal trends in carbon cycling similar to those of mature forests (e.g., Banbury Morgan *et al* n.d.).

In contrast to C fluxes and biomass accumulation rates in regrowth forests, stocks showed less systematic variation across biomes (c.f. Fig. 1). For aboveground biomass, which is the variable in *ForC* with broadest geographical representation, the modest trend of declining biomass from tropical to boreal regions mirrors observations from spaceborne lidar that reveal a decline in aboveground biomass (for all forests, including secondary) with latitude across the N hemisphere (Hu *et al* 2016). The highest- biomass forests on Earth are, however, found in coastal temperate climates of both the southern and northern hemisphere (Figs. 1, 8a; Keith *et al* 2009, Smithwick *et al* 2002, Hu *et al* 2016). Disproportionate representation of forests in one such region—the US Pacific Northwest— inflated estimates of temperate conifer fluxes and stocks for some variables and was responsible for all of the anomalous results described here (e.g., lack of complete C budget closure, anomalous trend across biomes for *BNPP<sub>coarse</sub>*). Thus, biome differences should always be interpreted relative to the geographic distribution of sampling, which only rarely covers the majority of forested area within a biome.

Whereas aboveground biomass can be remotely sensed (albeit with significant uncertainties; Ploton *et al* 2020) and receives significant research attention, far less is known about geographical variation in deadwood and organic layer (*OL*) across biomes, which has proved a limitation for C accounting efforts (Pan *et al* 2011). Although these stocks can be important—exceeding 100 Mg C ha<sup>-1</sup> in some stands (Figs. 8, S27-S29), this study is the first to synthesize deadwood data on a global scale (but see Cook-Patton *et al* 2020 for young forests). Unfortunately, data remain too sparse for statistical comparison across biomes (Figs. 8, S27-S29; but see below for age trends), pointing to a need for more widespread quantification of both standing and downed deadwood. *ForC* coverage of *OL*

stocks is more comprehensive, revealing no significant differences across temperate and tropical biomes, but a tendency towards higher  $OL$  in boreal forests, consistent with the idea that proportionally slower decomposition in colder climates results in more buildup of organic matter (Fig. 1; Allen *et al* 2002, Anderson-Teixeira *et al* 2011). Further research on non-living C stocks in the world's forests will be essential to completing the picture.

## Age trends in C cycling

Our study reveals that most C fluxes quickly increase and then decelerate as stands age (Figs. 7, 9), consistent with current understanding of age trends in forest C cycling (Fig. 1; e.g., Anderson-Teixeira *et al* 2013, Amiro *et al* 2010, Magnani *et al* 2007). While limited records in very young (*i.e.*, <5 year old) stands resulted in poor resolution of the earliest phases of this increase for many variables (sometimes detecting no age trend; Table 1), any autotrophic C flux (e.g.,  $GPP$ ,  $NPP$  and its components,  $R_{auto}$ ) would be minimal immediately following a stand-clearing disturbance (Fig. 1). These would be expected to increase rapidly, along with the most metabolically active components of biomass, foliage and fine roots, which also increase rapidly with stand age (Figs. 1, 7-9). In contrast, soil heterotrophic respiration ( $R_{het-soil}$ ) and total soil respiration ( $R_{soil}$ )—and therefore  $R_{eco}$  are expected to be non-zero following stand-clearing disturbance (Fig. 1), although these may decrease with a reduction of root respiration ( $R_{soil}$  only) and C exudates or increase in response to an influx of dead roots and litter (Ribeiro-Kumara *et al* 2020, Maurer *et al* 2016, Bond-Lamberty *et al* 2004). In this study, we detect no significant age trends in either  $R_{het-soil}$  or  $R_{soil}$ , consistent with previous findings (Law *et al* 2003, Pregitzer and Euskirchen 2004, Goulden *et al* 2011).

Notably, net carbon sequestration ( $NEP$ ) exhibits an overall increase with age across the first 100 years of stand development, with more pronounced patterns in temperate than boreal forests (Fig. 7). This finding is consistent with previous studies showing an increase in  $NEP$  across relatively young stand ages (Pregitzer and Euskirchen 2004, Baldocchi *et al* 2001, Luyssaert *et al* 2008). However,  $NEP$  has been observed to decline from intermediate to old stands (Law *et al* 2003, Luyssaert *et al* 2008), whereas the  $NEP$  values estimated by our models for 100-year-old stands were not systematically different from those of mature stands (lower for temperate broadleaf, higher for temperate conifer, and equal for boreal; Fig. 9). This lack of a consistent age-related decrease may be driven by differences in geographical representation across age classes or by the fitting of an inappropriate functional form. A decrease in  $NEP$  would be consistent with the observed deceleration of C accumulation as stands age (Fig. 9), although both biomass and non-living C stocks will often continue to increase well beyond the 100-yr threshold used here to delimit young and mature stands (Luyssaert *et al* 2008, McGarvey *et al* 2014, Lichstein *et al* 2009). Additional data, including on age trends of deadwood, the organic layer, and soil C will be important to parsing the timing and extend of an age-related  $NEP$  decrease across forest biomes.

In terms of stocks, our study reveals consistent increases in live biomass stocks with stand age, a pattern that is well-known and expected (e.g., Lichstein *et al* 2009, Yang *et al* 2011), contrasting with more variable age trends in deadwood and the organic layer (Fig. 9). The latter are particularly sensitive to the type of disturbance, where disturbances that remove

most organic material (e.g., logging, agriculture) result in negligible deadwood in young stands, followed by a buildup over time (e.g., tropical stands in Figs. 8, 9; e.g., Vargas *et al* 2008). In contrast, natural disturbances (e.g., fire, drought) can produce large amounts of deadwood (mostly  $DW_{standing}$ ) that slowly decomposes as the stand recovers, resulting in declines across young stand ages (e.g., temperate and boreal stands in Figs. 8, 9; Carmona *et al* 2002). Again, further study and synthesis of non-living C stocks across biomes and stand ages will be valuable to giving a more comprehensive picture.

### C Variable coverage and budget closure

The large number of C cycle variables covered by ForC, and the relatively high consistency among them (Figs. 3-6, 9), provide confidence that our reported mature forest means provide useful baselines for analysis – with the caveats that they are unlikely to be accurate representations of C cycling for any particular forest, and that these sample means almost certainly do not represent true biome means (particularly for temperate conifer forests where high-biomass stands are over-represented in ForC).

In this analysis, the C cycle budgets for mature forests usually come close to closure—that is, the sums of component variables do not differ from the larger fluxes by more than one standard deviation (Figs. 3-6, 9). On the one hand, this reflects the general fact that ecosystem-scale measurements tend to close the C budget more easily and consistently than, for example, for energy balance (Stoy *et al* 2013). On the other, however, ForC derives data from multiple heterogeneous sources, and standard deviations within each biome are high; as a result, the standard for C closure is relatively loose (*c.f.* Houghton 2020). The one instance where the C budgets does not close according to our criteria is likely due to differences in the representation of forest types (*i.e.*, disproportionate representation of US Pacific NW for  $B_{root-coarse}$  relative to  $B_{root}$ ; Fig. 5) rather than issues of methodological accuracy. The overall high degree of closure implies that ForC gives an at least roughly consistent picture of C cycling within biomes for mature forests. This is an important and useful test, because it allows for consistency checks within the C cycle, for example leveraging separate and independently-measured fluxes to constrain errors in another (Phillips *et al* 2017, Williams *et al* 2014, Harmon *et al* 2011), or producing internally consistent global data products (Wang *et al* 2018).

In contrast, age trends for young forests generally remain less clearly defined, in large part because their data records remain relatively sparse (*i.e.*, have low representation of different geographical regions for any given age) for most variables, particularly in the tropics (Anderson-Teixeira *et al* 2016). While this review provides a first analysis of age trends in forest C cycling for multiple variables at a global scale, improved resolution of these trends will require additional data.

There are of course notable holes in the ForC variable coverage that limit the scope of our inferences here. Notably, ForC currently has sparse—if any—coverage of fluxes to herbivores and higher consumers, along with the woody mortality ( $M_{woody}$ ) and  $DW$  (Table 1, Figs. S27-S29). ForC does not include soil carbon, which is covered by other efforts (e.g., Köchy *et al* 2015). ForC is not intended to replace databases that are specialized for particular parts of the C cycle analyses, *e.g.*, aboveground biomass (Spawn *et al* 2020), land-

atmosphere fluxes (Baldocchi *et al* 2001), soil respiration (Jian *et al* 2020), or the human footprint in global forests (Magnani *et al* 2007).

Importantly, *ForC* and the analyses presented here cover the forests that have received research attention, which are not a representative sample of the world's existing forests, either geographically or in terms of human impacts (Martin *et al* 2012). Geographically, all variables are poorly covered in Africa and Siberia (Fig. 2), a common problem in the carbon-cycle community (Xu and Shang 2016, Schimel *et al* 2015). In terms of human impacts, research efforts tend to focus on interior forest ecosystems (Martin *et al* 2012), often in permanently protected areas (e.g., Davies *et al* 2021). Studies of regrowth forests tend to focus on sites where recurring anthropogenic disturbance is not a confounding factor. Yet, fragmentation and degradation impact a large and growing proportion of Earth's forests (FAO and UNEP 2020). Fragmentation and the creation of edges strongly impacts forest C cycling (e.g., Chaplin-Kramer *et al* 2015, Remy *et al* 2016, Reinmann and Hutyra 2017, Smith *et al* 2019, Reinmann *et al* 2020, Ordway and Asner 2020). Partial logging and other forms of non- stand clearing anthropogenic disturbance also alter forest C cycling (e.g., Huang and Asner 2010, Piponiot *et al* 2016), but are under-studied (Sist *et al* 2015) and excluded from this analysis. Fragmented and degraded forests do not fit the idealized conceptual framework around which this review is structured (Fig. 1), yet their representation in models, sustainability assessments, and C accounting systems is critical to accurate accounting of C cycling in Earth's forests (e.g., Huang and Asner 2010, Reinmann and Hutyra 2017, Smith *et al* 2019, Piponiot *et al* 2019). Finally, plantation forests account for approximately 3% of Earth's forests (FAO and UNEP 2020) but are not included in this analysis. While it is known that these tend to accumulate biomass faster than naturally regenerating forests (Anderson *et al* 2006, Bonner *et al* 2013), their global scale C cycling patterns remain less clearly understood (c.f. Cook-Patton *et al* 2020). Additional research and synthesis are needed to fill these critical gaps in our understanding of forest C cycling.

### Relevance for climate change prediction and mitigation

The future of forest C cycling (Song *et al* 2019) will shape trends in atmospheric CO<sub>2</sub> and the course of climate change (Schimel *et al* 2015). Our findings, and more generally the data contained in *ForC* and summarized here, can help to meet two major challenges.

First, improved representation of forest C cycling in models is essential to improving predictions of the future course of climate change, for the simple reason that by definition future projections extend our existing observations and understanding to conditions that do not currently exist on Earth (McDowell *et al* 2018, Bonan and Doney 2018, Gustafson *et al* 2018). To ensure that models are giving the right answers for the right reasons (Sulman *et al* 2018), it is important to benchmark against multiple components of the C cycle that are internally consistent with each other (Collier *et al* 2018, Wang *et al* 2018). *ForC*'s tens of thousands of records are readily available in a standardized format, along with all code used in the analyses presented here, and we recommend that researchers use these resources to identify and summarize data specific to the analysis at hand. Integration of *ForC* with models will be valuable to improving the accuracy and reliability of models (Fer *et al* 2021).

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3 Second, *ForC* can serve as a pipeline through which information can flow efficiently from  
4 forest researchers to decision-makers working to implement forest conservation strategies  
5 at global, national, or landscape scales. This is already happening: *ForC* has contributed to  
6 updating the IPCC guidelines for carbon accounting in forests (IPCC 2019, Requena Suarez  
7 *et al* 2019), mapping C accumulation potential from natural forest regrowth globally (Cook-  
8 Patton *et al* 2020), and informing ecosystem conservation priorities (Goldstein *et al* 2020).  
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11 It is also interesting to consider the complementary utility of global-scale but spatially  
12 discontinuous databases such as *ForC* and remote wall-to-wall remote sensing products.  
13 The latter provide insight into aboveground carbon stocks, but less constraint on  
14 belowground stocks or carbon fluxes in general (Bond-Lamberty *et al* 2016, Anav *et al*  
15 2015). Combining observational data and remote observations may provide a much more  
16 comprehensive and accurate picture of global forest C cycling, particularly when used in  
17 formal data assimilation systems (Konings *et al* 2019, Liu *et al* 2018). Biomass is the largest  
18 C stock in most forests, and most of the emphasis has traditionally been on this variable.  
19 Remote-sensing driven **aboveground** biomass estimates (e.g., Saatchi *et al* 2011), calibrated  
20 based on high-quality ground-based data (Schepaschenko *et al* 2019, Chave *et al* 2019),  
21 **provide the most promising approach, but significant uncertainties remain (Ploton *et al***  
22 **2020).** Note, however, that factors such as stand age and disturbance history are difficult, if  
23 **not impossible,** to detect remotely, and can only be characterized for very recent decades  
24 (Hansen *et al* 2013, Song *et al* 2018, Curtis *et al* 2018). Ground-based data such as *ForC* are  
25 therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton *et al*  
26 (2020), and thus constraining variables such as carbon sink potential (Luyssaert *et al*  
27 2008).  
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30 In contrast, carbon allocation within forest ecosystems and respiration fluxes cannot be  
31 remotely sensed. Efforts such as the Global Carbon Project (Friedlingstein *et al* 2019) and  
32 NASA's Carbon Monitoring System (Liu *et al* 2018) typically compute respiration as  
33 residuals of all other terms (Bond-Lamberty *et al* 2016, Harmon *et al* 2011). This means  
34 that the errors on respiration outputs are likely to be large and certainly poorly  
35 constrained, offering a unique opportunity for databases such as *ForC* and SRDB (Jian *et al*  
36 2020) to provide observational benchmarks. For example, Konings *et al* (2019) produced a  
37 unique top-down estimate of global heterotrophic respiration that can both be compared  
38 with extant bottom-up estimates (Bond-Lamberty 2018) and used as an internal  
39 consistency check on other parts of the carbon cycle (Phillips *et al* 2017).  
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## 42 Conclusions

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45 As climate change accelerates, understanding and managing the carbon dynamics of  
46 forests– including dynamics and fluxes that cannot be observed by satellites–is critical to  
47 forecasting, mitigation, and adaptation. The C data in *ForC*, as summarized here, will be  
48 valuable to these efforts. Notably, the fact that tropical forests tend to have both the highest  
49 rates of C sequestration in young stands (Fig. 8; Cook-Patton *et al* 2020), fueled by their  
50 generally high C flux rates (Table 1; Fig. 7), and the highest mean biomass (Fig. 8; Table 1;  
51 Hu *et al* 2016, Jian *et al* 2020) reinforces the concept that conservation and restoration of  
52 these forests is a priority for climate change mitigation, along with high-biomass old-  
53 growth temperate stands (Grassi *et al* 2017, Goldstein *et al* 2020). It is also important to  
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note the trade-off in climate mitigation potential of restoration of young forests, with high rates of CO<sub>2</sub> sequestration (*NEP*; Cook-Patton *et al* 2020), versus conservation and management of mature forests, with low *NEP* but high C stocks that could not be recovered on a time scale relevant to climate change mitigation (Goldstein *et al* 2020). Generally speaking, the conservation of mature forests will yield greater climate benefits (Anderson-Teixeira and DeLucia 2011), but both approaches are critical to avoiding catastrophic climate change (IPCC 2018).

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## Data availability statement

The data that support the findings of this study are openly available. 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.

## References

- Allen A, Brown J and Gillooly J 2002 Global biodiversity, biochemical kinetics, and the energetic-equivalence rule *SCIENCE* **297** 1545–8
- Amiro B D, Barr A G, Barr J G, Black T A, Bracho R, Brown M, Chen J, Clark K L, Davis K J, Desai A R, Dore S, Engel V, Fuentes J D, Goldstein A H, Goulden M L, Kolb T E, Lavigne M B, Law B E, Margolis H A, Martin T, McCaughey J H, Misson L, Montes-Helu M, Noormets A, Randerson J T, Starr G and Xiao J 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America *J. Geophys. Res.* **115** G00K02
- Anav A, Friedlingstein P, Beer C, Ciais P, Harper A, Jones C, Murray-Tortarolo G, Papale D, Parazoo N C, Peylin P, Piao S, Sitch S, Viovy N, Wiltshire A and Zhao M 2015 Spatiotemporal patterns of terrestrial gross primary production: A review *Reviews of Geophysics* **53** 785–818
- Andela N, Morton D C, Giglio L, Chen Y, van der Werf G R, Kasibhatla P S, DeFries R S, Collatz G J, Hantson S, Kloster S, Bachelet D, Forrest M, Lasslop G, Li F, Mangeon S, Melton J R, Yue C and Randerson J T 2017 A human-driven decline in global burned area *Science* **356** 1356–62
- Anderson K J, Allen A P, Gillooly J F and Brown J H 2006 Temperature-dependence of biomass accumulation rates during secondary succession *Ecology Letters* **9** 673–82

1  
2  
3 Anderson-Teixeira K, Herrmann V, CookPatton, Ferson A and Lister K 2020 Forc-db/GROA:  
4 Release with Cook-Patton et al. 2020, *Nature*.  
5

6 Anderson-Teixeira K J, Davies S J, Bennett A C, Gonzalez-Akre E B, Muller-Landau H C,  
7 Joseph Wright S, Abu Salim K, Almeyda Zambrano A M, Alonso A, Baltzer J L, Basset Y,  
8 Bourg N A, Broadbent E N, Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Butt N,  
9 Cao M, Cardenas D, Chuyong G B, Clay K, Cordell S, Dattaraja H S, Deng X, Dettman M, Du X,  
10 Duque A, Erikson D L, Ewango C E N, Fischer G A, Fletcher C, Foster R B, Giardina C P,  
11 Gilbert G S, Gunatilleke N, Gunatilleke S, Hao Z, Hargrove W W, Hart T B, Hau B C H, He F,  
12 Hoffman F M, Howe R W, Hubbell S P, Inman-Narahari F M, Jansen P A, Jiang M, Johnson D J,  
13 Kanzaki M, Kassim A R, Kenfack D, Kibet S, Kinnaird M F, Korte L, Kral K, Kumar J, Larson A  
14 J, Li Y, Li X, Liu S, Lum S K Y, Lutz J A, Ma K, Maddalena D M, Makana J-R, Malhi Y, Marthews  
15 T, Mat Serudin R, McMahon S M, McShea W J, Memiaghe H R, Mi X, Mizuno T, Morecroft M,  
16 Myers J A, Novotny V, de Oliveira A A, Ong P S, Orwig D A, Ostertag R, den Ouden J, Parker G  
17 G, Phillips R P, Sack L, Sainge M N, Sang W, Sri-ngernyuang K, Sukumar R, Sun I-F,  
18 Sungpalee W, Suresh H S, Tan S, Thomas S C, Thomas D W, Thompson J, Turner B L, Uriarte  
19 M, Valencia R, et al 2015 CTFS-ForestGEO : A worldwide network monitoring forests in an  
20 era of global change *Global Change Biology* **21** 528–49  
21  
22

23  
24 Anderson-Teixeira K J, Delong J P, Fox A M, Brese D A and Litvak M E 2011 Differential  
25 responses of production and respiration to temperature and moisture drive the carbon  
26 balance across a climatic gradient in New Mexico *Global Change Biology* **17** 410–24  
27  
28

29 Anderson-Teixeira K J and DeLucia E H 2011 The greenhouse gas value of ecosystems  
30 *Global Change Biology* **17** 425–38  
31

32 Anderson-Teixeira K J, Miller A D, Mohan J E, Hudiburg T W, Duval B D and DeLucia E H  
33 2013 Altered dynamics of forest recovery under a changing climate *Global Change Biology*  
34 **19** 2001–21  
35

36 Anderson-Teixeira K J, Wang M M H, McGarvey J C, Herrmann V, Tepley A J, Bond-Lamberty  
37 B and LeBauer D S 2018 ForC : A global database of forest carbon stocks and fluxes *Ecology*  
38 **99** 1507–7  
39

40 Anderson-Teixeira K J, Wang M M H, McGarvey J C and LeBauer D S 2016 Carbon dynamics  
41 of mature and regrowth tropical forests derived from a pantropical database (TropForC-  
42 db) *Global Change Biology* **22** 1690–709  
43  
44

45 Badgley G, Anderegg L D L, Berry J A and Field C B 2019 Terrestrial gross primary  
46 production: Using NIRV to scale from site to globe *Global Change Biology* **25** 3731–40  
47

48 Baldocchi D, Falge E, Gu L, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K,  
49 Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee X, Malhi Y, Meyers T, Munger W, Oechel  
50 W, Paw K T, Pilegaard K, Schmid H P, Valentini R, Verma S, Vesala T, Wilson K and Wofsy S  
51 2001 FLUXNET : A New Tool to Study the Temporal and Spatial Variability of  
52 EcosystemScale Carbon Dioxide, Water Vapor, and Energy Flux Densities *Bulletin of the*  
53 *American Meteorological Society* **82** 2415–34  
54  
55

56  
57  
58  
59  
60

1  
2  
3 Banbury Morgan B, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau H C and  
4 Anderson-Teixeira K J Global patterns of forest autotrophic carbon fluxes *Global Change  
5 Biology*

6  
7 Bates D, Mächler M, Bolker B and Walker S 2015 Fitting Linear Mixed-Effects Models Using  
8 **Lme4** *Journal of Statistical Software* **67**  
9

10 Besnard S, Carvalhais N, Arain M A, Black A, de Bruin S, Buchmann N, Cescatti A, Chen J,  
11 Clevers J G P W, Desai A R, Gough C M, Havrankova K, Herold M, Hörtnagl L, Jung M, Knohl  
12 A, Kruijt B, Krupkova L, Law B E, Lindroth A, Noormets A, Roupsard O, Steinbrecher R,  
13 Varlagin A, Vincke C and Reichstein M 2018 Quantifying the effect of forest age in annual  
14 net forest carbon balance *Environmental Research Letters* **13** 124018  
15

16  
17 Bonan G B 2008 Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits  
18 of Forests *Science* **320** 1444–9  
19

20  
21 Bonan G B and Doney S C 2018 Climate, ecosystems, and planetary futures: The challenge  
22 to predict life in Earth system models *Science* **359**  
23

24 Bonan G B, Lombardozzi D L, Wieder W R, Oleson K W, Lawrence D M, Hoffman F M and  
25 Collier N 2019 Model Structure and Climate Data Uncertainty in Historical Simulations of  
26 the Terrestrial Carbon Cycle (1850) *Global Biogeochemical Cycles* **33** 1310–26  
27

28 Bond-Lamberty B 2018 New Techniques and Data for Understanding the Global Soil  
29 Respiration Flux *Earth's Future* **6** 1176–80  
30

31 Bond-Lamberty B, Epron D, Harden J, Harmon M E, Hoffman F, Kumar J, David McGuire A  
32 and Vargas R 2016 Estimating heterotrophic respiration at large scales: Challenges,  
33 approaches, and next steps *Ecosphere* **7**  
34

35 Bond-Lamberty B and Thomson A 2010 A global database of soil respiration data  
36 *Biogeosciences* **7** 1915–26  
37

38 Bond-Lamberty B, Wang C and Gower S T 2004 Contribution of root respiration to soil  
39 surface CO<sub>2</sub> flux in a boreal black spruce chronosequence *Tree Physiology* **24** 1387–95  
40

41 Bonner M T L, Schmidt S and Shoo L P 2013 A meta-analytical global comparison of  
42 aboveground biomass accumulation between tropical secondary forests and monoculture  
43 plantations *Forest Ecology and Management* **291** 73–86  
44

45 Carmona M R, Armesto J J, Aravena J C and Pérez C A 2002 Coarse woody debris biomass in  
46 successional and primary temperate forests in Chiloé Island, Chile *Forest Ecology and  
47 Management* **164** 265–75  
48

49 Cavalieri M A, Reed S C, Smith W K and Wood T E 2015 Urgent need for warming  
50 experiments in tropical forests *Global Change Biology* **21** 2111–21  
51

52 Chapin F, Woodwell G, Randerson J, Rastetter E, Lovett G, Baldocchi D, Clark D, Harmon M,  
53 Schimel D, Valentini R, Wirth C, Aber J, Cole J, Goulden M, Harden J, Heimann M, Howarth R,  
54

55  
56  
57  
58  
59  
60

1  
2  
3 Matson P, McGuire A, Melillo J, Mooney H, Neff J, Houghton R, Pace M, Ryan M, Running S,  
4 Sala O, Schlesinger W and Schulze E D 2006 Reconciling Carbon-cycle Concepts,  
5 Terminology, and Methods *Ecosystems* **9** 1041–50  
6

7 Chaplin-Kramer R, Ramler I, Sharp R, Haddad N, Gerber J, West P, Mandle L, Engstrom P,  
8 Baccini A, Sim S, Mueller C and King H 2015 Degradation in carbon stocks near tropical  
9 forest edges *Nature Communications* **6**  
10

11 Chave J, Davies S J, Phillips O L, Lewis S L, Sist P, Schepaschenko D, Armston J, Baker T R,  
12 Coomes D, Disney M, Duncanson L, Hérault B, Labrière N, Meyer V, Réjou-Méchain M, Scipal  
13 K and Saatchi S 2019 Ground Data are Essential for Biomass Remote Sensing Missions  
14 *Surveys in Geophysics*  
15

16 Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan M S, Delitti W B C, Duque A, Eid  
17 T, Fearnside P M, Goodman R C, Henry M, Martínez-Yrízar A, Mugasha W A, Muller-Landau  
18 H C, Mencuccini M, Nelson B W, Ngomanda A, Nogueira E M, Ortiz-Malavassi E, Pélassier R,  
19 Ploton P, Ryan C M, Saldarriaga J G and Vieilledent G 2014 Improved allometric models to  
20 estimate the aboveground biomass of tropical trees *Global Change Biology* n/a-a  
21

22 Clark D A, Asao S, Fisher R, Reed S, Reich P B, Ryan M G, Wood T E and Yang X 2017 Field  
23 data to benchmark the carbon-cycle models for tropical forests *Biogeosciences Discussions*  
24 1–44  
25

26 Clark D A, Brown S, Kicklighter D W, Chambers J, Thomlinson J R and Ni J 2001 Measuring  
27 net primary production in forests: Concepts and field methods *Ecological Applications* **11**  
28 356–70  
29

30 Collalti A, Ibrom A, Stockmarr A, Cescatti A, Alkama R, Fernández-Martínez M, Matteucci G,  
31 Sitch S, Friedlingstein P, Ciais P, Goll D S, Nabel J E M S, Pongratz J, Arneth A, Haverd V and  
32 Prentice I C 2020 Forest production efficiency increases with growth temperature *Nature  
33 Communications* **11** 5322  
34

35 Collier N, Hoffman F M, Lawrence D M, Keppel-Aleks G, Koven C D, Riley W J, Mu M and  
36 Randerson J T 2018 The International Land Model Benchmarking (ILAMB) System: Design,  
37 Theory, and Implementation *Journal of Advances in Modeling Earth Systems* **10** 2731–54  
38

39 Cook-Patton S C, Leavitt S M, Gibbs D, Harris N L, Lister K, Anderson-Teixeira K J, Briggs R  
40 D, Chazdon R L, Crowther T W, Ellis P W, Griscom H P, Herrmann V, Holl K D, Houghton R A,  
41 Larrosa C, Lomax G, Lucas R, Madsen P, Malhi Y, Paquette A, Parker J D, Paul K, Routh D,  
42 Roxburgh S, Saatchi S, van den Hoogen J, Walker W S, Wheeler C E, Wood S A, Xu L and  
43 Griscom B W 2020 Mapping carbon accumulation potential from global natural forest  
44 regrowth *Nature* **585** 545–50  
45

46 Corman J R, Collins S L, Cook E M, Dong X, Gherardi L A, Grimm N B, Hale R L, Lin T, Ramos J,  
47 Reichmann L G and Sala O E 2019 Foundations and Frontiers of Ecosystem Science: Legacy  
48 of a Classic Paper (Odum 1969) *Ecosystems* **22** 1160–72  
49

50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 Curtis P G, Slay C M, Harris N L, Tyukavina A and Hansen M C 2018 Classifying drivers of  
4 global forest loss *Science* **361** 1108–11  
5

6 Curtis P S and Gough C M 2018 Forest aging, disturbance and the carbon cycle *New*  
7 *Phytologist*  
8

9 Davies S J, Abiem I, Abu Salim K, Aguilar S, Allen D, Alonso A, Anderson-Teixeira K, Andrade  
10 A, Arellano G, Ashton P S, Baker P J, Baker M E, Baltzer J L, Basset Y, Bissiengou P, Bohlman  
11 S, Bourg N A, Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Cao M, Cárdenas D,  
12 Chang L-W, Chang-Yang C-H, Chao K-J, Chao W-C, Chapman H, Chen Y-Y, Chisholm R A, Chu  
13 C, Chuyong G, Clay K, Comita L S, Condit R, Cordell S, Dattaraja H S, de Oliveira A A, den  
14 Ouden J, Detto M, Dick C, Du X, Duque Á, Ediriweera S, Ellis E C, Obiang N L E, Esufali S,  
15 Ewango C E N, Fernando E S, Filip J, Fischer G A, Foster R, Giambelluca T, Giardina C, Gilbert  
16 G S, Gonzalez-Akre E, Gunatilleke I A U N, Gunatilleke C V S, Hao Z, Hau B C H, He F, Ni H,  
17 Howe R W, Hubbell S P, Huth A, Inman-Narahari F, Itoh A, Janík D, Jansen P A, Jiang M,  
18 Johnson D J, Jones F A, Kanzaki M, Kenfack D, Kiratiprayoon S, Král K, Krizel L, Lao S, Larson  
19 A J, Li Y, Li X, Litton C M, Liu Y, Liu S, Lum S K Y, Luskin M S, Lutz J A, Luu H T, Ma K, Makana  
20 J-R, Malhi Y, Martin A, McCarthy C, McMahon S M, McShea W J, Memiaghe H, Mi X, Mitre D,  
21 Mohamad M, et al 2021 ForestGEO: Understanding forest diversity and dynamics through a  
22 global observatory network *Biological Conservation* **253** 108907  
23

24 DeLucia E H, Drake J, Thomas R B and Gonzalez-Meler M A 2007 Forest carbon use  
25 efficiency: Is respiration a constant fraction of gross primary production? *Global Change*  
26 *Biology* **13** 1157–67  
27

28 Di Vittorio A V, Shi X, Bond-Lamberty B, Calvin K and Jones A 2020 Initial Land Use/Cover  
29 Distribution Substantially Affects Global Carbon and Local Temperature Projections in the  
30 Integrated Earth System Model *Global Biogeochemical Cycles* **34**  
31

32 FAO 2010 *Global Forest Resources Assessment 2010* (Rome, Italy: Food and Agriculture  
33 Organization of the United Nations)  
34

35 FAO and UNEP 2020 *The State of the World's Forests 2020: Forests, biodiversity and people*  
36 (Rome, Italy: FAO and UNEP)  
37

38 Fer I, Gardella A K, Shiklomanov A N, Campbell E E, Cowdery E M, Kauwe M G D, Desai A,  
39 Duvaneck M J, Fisher J B, Haynes K D, Hoffman F M, Johnston M R, Kooper R, LeBauer D S,  
40 Mantooth J, Parton W J, Poulter B, Quaife T, Raiho A, Schaefer K, Serbin S P, Simkins J,  
41 Wilcox K R, Viskari T and Dietze M C 2021 Beyond ecosystem modeling: A roadmap to  
42 community cyberinfrastructure for ecological data-model integration *Global Change*  
43 *Biology* **27** 13–26  
44

45 Friedlingstein P, Cox P, Betts R, Bopp L, von Bloh W, Brovkin V, Cadule P, Doney S, Eby M,  
46 Fung I, Bala G, John J, Jones C, Joos F, Kato T, Kawamiya M, Knorr W, Lindsay K, Matthews H  
47 D, Raddatz T, Rayner P, Reick C, Roeckner E, Schnitzler K-G, Schnur R, Strassmann K,  
48 Weaver A J, Yoshikawa C and Zeng N 2006 ClimateCarbon Cycle Feedback Analysis: Results  
49 from the C4MIP Model Intercomparison *Journal of Climate* **19** 3337–53  
50

51  
52  
53  
54  
55  
56  
57  
58  
59  
60

Friedlingstein P, Jones M W, O'Sullivan M, Andrew R M, Hauck J, Peters G P, Peters W, Pongratz J, Sitch S, Quéré C L, Bakker D C E, Canadell J G, Ciais P, Jackson R B, Anthoni P, Barbero L, Bastos A, Bastrikov V, Becker M, Bopp L, Buitenhuis E, Chandra N, Chevallier F, Chini L P, Currie K I, Feely R A, Gehlen M, Gilfillan D, Gkritzalis T, Goll D S, Gruber N, Gutekunst S, Harris I, Haverd V, Houghton R A, Hurt G, Ilyina T, Jain A K, Joetzjer E, Kaplan J O, Kato E, Klein Goldewijk K, Korsbakken J I, Landschützer P, Lauvset S K, Lefèvre N, Lenton A, Lienert S, Lombardozzi D, Marland G, McGuire P C, Melton J R, Metzl N, Munro D R, Nabel J E M S, Nakaoka S-I, Neill C, Omar A M, Ono T, Peregón A, Pierrot D, Poulter B, Rehder G, Resplandy L, Robertson E, Rödenbeck C, Séférian R, Schwinger J, Smith N, Tans P P, Tian H, Tilbrook B, Tubiello F N, Werf G R van der, Wiltshire A J and Zaehle S 2019 Global Carbon Budget 2019 *Earth System Science Data* **11** 1783–838

Gillman L N, Wright S D, Cusens J, McBride P D, Malhi Y and Whittaker R J 2015 Latitude, productivity and species richness *Global Ecology and Biogeography* **24** 107–17

Goldstein A, Turner W R, Spawn S A, Anderson-Teixeira K J, Cook-Patton S, Fargione J, Gibbs H K, Griscom B, Hewson J H, Howard J F, Ledezma J C, Page S, Koh L P, Rockström J, Sanderman J and Hole D G 2020 Protecting irrecoverable carbon in Earth's ecosystems *Nature Climate Change* **10** 287–95

Goulden M L, McMillan A M S, Winston G C, Rocha A V, Manies K L, Harden J W and Bond-Lamberty B P 2011 Patterns of NPP, GPP, respiration, and NEP during boreal forest succession *Global Change Biology* **17** 855–71

Grassi G, House J, Dentener F, Federici S, den Elzen M and Penman J 2017 The key role of forests in meeting climate targets requires science for credible mitigation *Nature Climate Change* **7** 220–6

Griscom B W, Adams J, Ellis P W, Houghton R A, Lomax G, Miteva D A, Schlesinger W H, Shoch D, Siikamäki J V, Smith P, Woodbury P, Zganjar C, Blackman A, Campari J, Conant R T, Delgado C, Elias P, Gopalakrishna T, Hamsik M R, Herrero M, Kiesecker J, Landis E, Laestadius L, Leavitt S M, Minnemeyer S, Polasky S, Potapov P, Putz F E, Sanderman J, Silvius M, Wollenberg E and Fargione J 2017 Natural climate solutions *Proceedings of the National Academy of Sciences* **114** 11645–50

Gustafson E J, Kubiske M E, Miranda B R, Hoshika Y and Paoletti E 2018 Extrapolating plot-scale CO<sub>2</sub> and ozone enrichment experimental results to novel conditions and scales using mechanistic modeling *Ecological Processes* **7** 31

Hansen M C, Potapov P V, Moore R, Hancher M, Turubanova S A, Tyukavina A, Thau D, Stehman S V, Goetz S J, Loveland T R, Kommareddy A, Egorov A, Chini L, Justice C O and Townshend J R G 2013 High-Resolution Global Maps of 21st-Century Forest Cover Change *Science* **342** 850–3

Harmon M E, Bond-Lamberty B, Tang J and Vargas R 2011 Heterotrophic respiration in disturbed forests: A review with examples from North America *Journal of Geophysical Research* **116**

1  
2  
3 Harmon M E, Franklin J F, Swanson F J, Sollins P, Gregory S V, Lattin J D, Anderson N H,  
4 Cline S P, Aumen N G, Sedell J R, Lienkaemper G W, Cromack K and Cummins K W 1986  
5 Ecology of Coarse Woody Debris in Temperate Ecosystems *Advances in Ecological Research*  
6 vol 15, ed A MacFadyen and E D Ford (Academic Press) pp 133–302  
7  
8

9 Harris N L, Gibbs D A, Baccini A, Birdsey R A, Bruun S de, Farina M, Fatoyinbo L, Hansen M C,  
10 Herold M, Houghton R A, Potapov P V, Suarez D R, Roman-Cuesta R M, Saatchi S S, Slay C M,  
11 Turubanova S A and Tyukavina A 2021 Global maps of twenty-first century forest carbon  
12 fluxes *Nature Climate Change* 1–7  
13  
14

15 Holdridge L R 1947 Determination of World Plant Formations From Simple Climatic Data  
16 *Science* **105** 367–8  
17  
18

19 Houghton R A 2020 Terrestrial fluxes of carbon in GCP carbon budgets *Global Change  
Biology* **26** 3006–14  
20  
21

22 Hu T, Su Y, Xue B, Liu J, Zhao X, Fang J and Guo Q 2016 Mapping Global Forest Aboveground  
23 Biomass with Spaceborne LiDAR, Optical Imagery, and Forest Inventory Data *Remote  
Sensing* **8** 565  
24  
25

26 Huang M and Asner G P 2010 Long-term carbon loss and recovery following selective  
27 logging in Amazon forests *Global Biogeochemical Cycles* **24**  
28  
29

30 Humboldt A von and Bonpland A 1807 *Essay on the Geography of Plants*  
31  
32

33 Hursh A, Ballantyne A, Cooper L, Maneta M, Kimball J and Watts J 2017 The sensitivity of  
34 soil respiration to soil temperature, moisture, and carbon supply at the global scale *Global  
Change Biology* **23** 2090–103  
35  
36

37 IPCC 2019 *2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas  
Inventories*  
38  
39

40 IPCC 2018 *Global Warming of 1.5C. An IPCC Special Report on the impacts of global warming  
41 of 1.5C above pre-industrial levels and related global greenhouse gas emission pathways, in  
42 the context of strengthening the global response to the threat of climate change, sustainable  
43 development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D.  
44 Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors,  
45 J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T.  
Waterfield (eds.)].*  
46  
47

48 Jian J, Vargas R, Anderson-Teixeira K, Stell E, Herrmann V, Horn M, Kholod N, Manzon J,  
49 Marchesi R, Paredes D and Bond-Lamberty B 2020 *A restructured and updated global soil  
respiration database (SRDB-V5)* (Data, Algorithms, and Models)  
50  
51

52 Johnson C, Zarin D and Johnson A 2000 Post-disturbance aboveground biomass  
53 accumulation in global secondary forests *Ecology* **81** 1395–401  
54  
55

56 Johnson D J, Needham J, Xu C, Massoud E C, Davies S J, Anderson-Teixeira K J,  
57 Bunyavejchewin S, Chambers J Q, Chang-Yang C-H, Chiang J-M, Chuyong G B, Condit R,  
58  
59  
60

Cordell S, Fletcher C, Giardina C P, Giambelluca T W, Gunatilleke N, Gunatilleke S, Hsieh C-F, Hubbell S, Inman-Narahari F, Kassim A R, Katabuchi M, Kenfack D, Litton C M, Lum S, Mohamad M, Nasardin M, Ong P S, Ostertag R, Sack L, Swenson N G, Sun I F, Tan S, Thomas D W, Thompson J, Umaña M N, Uriarte M, Valencia R, Yap S, Zimmerman J, McDowell N G and McMahon S M 2018 Climate sensitive size-dependent survival in tropical trees *Nature Ecology & Evolution* **1**

Jung M, Henkel K, Herold M and Churkina G 2006 Exploiting synergies of global land cover products for carbon cycle modeling *Remote Sensing of Environment* **101** 534–53

Keith H, Mackey B G and Lindenmayer D B 2009 Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests *Proceedings of the National Academy of Sciences* **106** 11635–40

Konings A G, Bloom A A, Liu J, Parazoo N C, Schimel D S and Bowman K W 2019 Global satellite-driven estimates of heterotrophic respiration *Biogeosciences* **16** 2269–84

Köchy M, Hiederer R and Freibauer A 2015 Global distribution of soil organic carbon Part 1: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world *SOIL* **1** 351–65

Krause A, Pugh T A M, Bayer A D, Li W, Leung F, Bondeau A, Doelman J C, Humpenöder F, Anthoni P, Bodirsky B L, Ciais P, Müller C, Murray-Tortarolo G, Olin S, Popp A, Sitch S, Stehfest E and Arneth A 2018 Large uncertainty in carbon uptake potential of land-based climate-change mitigation efforts *Global Change Biology* **24** 3025–38

Kuzyakov Y 2006 Sources of CO<sub>2</sub> efflux from soil and review of partitioning methods *Soil Biology and Biochemistry* **38** 425–48

Law B E, Sun O J, Campbell J, Tuyl S V and Thornton P E 2003 Changes in carbon storage and fluxes in a chronosequence of ponderosa pine *Global Change Biology* **9** 510–24

Li X and Xiao J 2019 Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A Global, Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2 *Remote Sensing* **11** 2563

Lichstein J W, Wirth C, Horn H S and Pacala S W 2009 Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management *Old-Growth Forests Ecological Studies* ed C Wirth, G Gleixner and M Heimann (Springer Berlin Heidelberg) pp 301–41

Lieth H 1973 Primary production: Terrestrial ecosystems *Human Ecology* **1** 303–32

Liu J, Bowman K, Parazoo N C, Bloom A A, Wunch D, Jiang Z, Gurney K R and Schimel D 2018 Detecting drought impact on terrestrial biosphere carbon fluxes over contiguous US with satellite observations *Environmental Research Letters* **13** 095003

Luo Y Q, Randerson J T, Abramowitz G, Bacour C, Blyth E, Carvalhais N, Ciais P, Dalmonech D, Fisher J B, Fisher R, Friedlingstein P, Hibbard K, Hoffman F, Huntzinger D, Jones C D,

1  
2  
3 Koven C, Lawrence D, Li D J, Mahecha M, Niu S L, Norby R, Piao S L, Qi X, Peylin P, Prentice I  
4 C, Riley W, Reichstein M, Schwalm C, Wang Y P, Xia J Y, Zaehle S and Zhou X H 2012 A  
5 framework for benchmarking land models *Biogeosciences* **9** 3857–74  
6

7 Lutz J A, Furniss T J, Johnson D J, Davies S J, Allen D, Alonso A, Anderson-Teixeira K J,  
8 Andrade A, Baltzer J, Becker K M L, Blomdahl E M, Bourg N A, Bunyavejchewin S, Burslem D  
9 F R P, Cansler C A, Cao K, Cao M, Cárdenas D, Chang L-W, Chao K-J, Chao W-C, Chiang J-M,  
10 Chu C, Chuyong G B, Clay K, Condit R, Cordell S, Dattaraja H S, Duque A, Ewango C E N,  
11 Fischer G A, Fletcher C, Freund J A, Giardina C, Germain S J, Gilbert G S, Hao Z, Hart T, Hau B  
12 C H, He F, Hector A, Howe R W, Hsieh C-F, Hu Y-H, Hubbell S P, Inman-Narahari F M, Itoh A,  
13 Janík D, Kassim A R, Kenfack D, Korte L, Král K, Larson A J, Li Y, Lin Y, Liu S, Lum S, Ma K,  
14 Makana J-R, Malhi Y, McMahon S M, McShea W J, Memiaghe H R, Mi X, Morecroft M, Musili P  
15 M, Myers J A, Novotny V, Oliveira A de, Ong P, Orwig D A, Ostertag R, Parker G G, Patankar R,  
16 Phillips R P, Reynolds G, Sack L, Song G-Z M, Su S-H, Sukumar R, Sun I-F, Suresh H S,  
17 Swanson M E, Tan S, Thomas D W, Thompson J, Uriarte M, Valencia R, Vicentini A, Vrška T,  
18 Wang X, Weiblen G D, Wolf A, Wu S-H, Xu H, Yamakura T, Yap S and Zimmerman J K 2018  
19 Global importance of large-diameter trees *Global Ecology and Biogeography* **27** 849–64  
20  
21  
22

23 Luyssaert S, Inglima I, Jung M, Richardson A D, Reichstein M, Papale D, Piao S L, Schulze E-  
24 D, Wingate L, Matteucci G, Aragao L, Aubinet M, Beer C, Bernhofer C, Black K G, Bonal D,  
25 Bonnefond J-M, Chambers J, Ciais P, Cook B, Davis K J, Dolman A J, Gielen B, Goulden M,  
26 Grace J, Granier A, Grelle A, Griffis T, Grünwald T, Guidolotti G, Hanson P J, Harding R,  
27 Hollinger D Y, Hutyra L R, Kolari P, Kruijt B, Kutsch W, Lagergren F, Laurila T, Law B E,  
28 Maire G L, Lindroth A, Loustau D, Malhi Y, Mateus J, Migliavacca M, Misson L, Montagnani L,  
29 Moncrieff J, Moors E, Munger J W, Nikinmaa E, Ollinger S V, Pita G, Rebmann C, Roupsard O,  
30 Saigusa N, Sanz M J, Seufert G, Sierra C, Smith M-L, Tang J, Valentini R, Vesala T and  
31 Janssens I A 2007 CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a  
32 global database *Global Change Biology* **13** 2509–37  
33  
34

35 Luyssaert S, Schulze E D, Borner A, Knohl A, Hessenmoller D, Law B E, Ciais P and Grace J  
36 2008 Old-growth forests as global carbon sinks *Nature* **455** 213  
37  
38

39 Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P,  
40 Jarvis P G, Kolari P, Kowalski A S, Lankreijer H, Law B E, Lindroth A, Loustau D, Manca G,  
41 Moncrieff J B, Rayment M, Tedeschi V, Valentini R and Grace J 2007 The human footprint in  
42 the carbon cycle of temperate and boreal forests *Nature* **447** 849–51  
43  
44

45 Martin L J, Blossey B and Ellis E 2012 Mapping where ecologists work: Biases in the global  
46 distribution of terrestrial ecological observations *Frontiers in Ecology and the Environment*  
47 **10** 195–201  
48

49 Martin P A, Newton A C and Bullock J M 2013 Carbon pools recover more quickly than plant  
50 biodiversity in tropical secondary forests *Proceedings of the Royal Society B: Biological  
51 Sciences* **280** 20132236–6  
52

53 Maurer G E, Chan A M, Trahan N A, Moore D J P and Bowling D R 2016 Carbon isotopic  
54 composition of forest soil respiration in the decade following bark beetle and stem girdling  
55 disturbances in the Rocky Mountains *Plant, Cell & Environment* **39** 1513–23  
56  
57  
58  
59  
60

1  
2  
3 McDowell N G, Allen C D, Anderson-Teixeira K, Aukema B H, Bond-Lamberty B, Chini L,  
4 Clark J S, Dietze M, Grossiord C, Hanbury-Brown A, Hurtt G C, Jackson R B, Johnson D J,  
5 Kueppers L, Lichstein J W, Ogle K, Poulter B, Pugh T A M, Seidl R, Turner M G, Uriarte M,  
6 Walker A P and Xu C 2020 Pervasive shifts in forest dynamics in a changing world *Science*  
7 **368**  
8  
9

10 McDowell N G, Michaletz S T, Bennett K E, Solander K C, Xu C, Maxwell R M and Middleton R  
11 S 2018 Predicting Chronic Climate-Driven Disturbances and Their Mitigation *Trends in*  
12 *Ecology & Evolution* **33** 15–27  
13

14 McGarvey J C, Thompson J R, Epstein H E and Shugart H H 2014 Carbon storage in old-  
15 growth forests of the Mid-Atlantic: Toward better understanding the eastern forest carbon  
16 sink *Ecology* **96** 311–7  
17

18 Novick K A, Biederman J A, Desai A R, Litvak M E, Moore D J P, Scott R L and Torn M S 2018  
19 The AmeriFlux network: A coalition of the willing *Agricultural and Forest Meteorology* **249**  
20 444–56  
21  
22

23 Odum E 1969 The strategy of ecosystem development *Science* **164** 262–70  
24

25 Ordway E M and Asner G P 2020 Carbon declines along tropical forest edges correspond to  
26 heterogeneous effects on canopy structure and function *Proceedings of the National*  
27 *Academy of Sciences* **117** 7863–70  
28

29 Pan Y, Birdsey R A, Fang J, Houghton R, Kauppi P E, Kurz W A, Phillips O L, Shvidenko A,  
30 Lewis S L, Canadell J G, Ciais P, Jackson R B, Pacala S, McGuire A D, Piao S, Rautiainen A,  
31 Sitch S and Hayes D 2011 A Large and Persistent Carbon Sink in the World's Forests *Science*  
32 **333** 988–93  
33  
34

35 Pastorello G, Trotta C, Canfora E, Chu H, Christianson D, Cheah Y-W, Poindexter C, Chen J,  
36 Elbashandy A, Humphrey M, Isaac P, Polidori D, Ribeca A, van Ingen C, Zhang L, Amiro B,  
37 Ammann C, Arain M A, Ardö J, Arkebauer T, Arndt S K, Arriga N, Aubinet M, Aurela M,  
38 Baldocchi D, Barr A, Beamesderfer E, Marchesini L B, Bergeron O, Beringer J, Bernhofer C,  
39 Berveiller D, Billesbach D, Black T A, Blanken P D, Bohrer G, Boike J, Bolstad P V, Bonal D,  
40 Bonnefond J-M, Bowling D R, Bracho R, Brodeur J, Brümmer C, Buchmann N, Burban B,  
41 Burns S P, Buysse P, Cale P, Cavagna M, Cellier P, Chen S, Chini I, Christensen T R, Cleverly J,  
42 Collalti A, Consalvo C, Cook B D, Cook D, Coursolle C, Cremonese E, Curtis P S, D'Andrea E,  
43 da Rocha H, Dai X, Davis K J, De Cinti B, de Grandcourt A, De Ligne A, De Oliveira R C,  
44 Delpierre N, Desai A R, Di Bella C M, di Tommasi P, Dolman H, Domingo F, Dong G, Dore S,  
45 Duce P, Dufrêne E, Dunn A, Dušek J, Eamus D, Eichelmann U, ElKhidir H A M, Eugster W,  
46 Ewenz C M, Ewers B, Famulari D, Fares S, Feigenwinter I, Feitz A, Fensholt R, Filippa G,  
47 Fischer M, Frank J, Galvagno M, Gharun M, et al 2020 The FLUXNET2015 dataset and the  
48 ONEFlux processing pipeline for eddy covariance data *Scientific Data* **7** 225  
49  
50

51 Phillips C L, Bond-Lamberty B, Desai A R, Lavoie M, Risk D, Tang J, Todd-Brown K and  
52 Vargas R 2017 The value of soil respiration measurements for interpreting and modeling  
53 terrestrial carbon cycling *Plant and Soil* **413** 1–25  
54  
55

56  
57  
58  
59  
60

1  
2  
3 Piponiot C, Rödig E, Putz F E, Rutishauser E, Sist P, Ascarrunz N, Blanc L, Derroire G,  
4 Descroix L, Guedes M C, Coronado E H, Huth A, Kanashiro M, Licona J C, Mazzei L, d'Oliveira  
5 M V N, Peña-Claros M, Rodney K, Shenkin A, Souza C R de, Vidal E, West T A P, Wortel V and  
6 Héault B 2019 Can timber provision from Amazonian production forests be sustainable?  
7 *Environmental Research Letters* **14** 064014  
8  
9

10 Piponiot C, Sist P, Mazzei L, Peña-Claros M, Putz F E, Rutishauser E, Shenkin A, Ascarrunz N,  
11 de Azevedo C P, Baraloto C, França M, Guedes M, Honorio Coronado E N, d'Oliveira M V,  
12 Ruschel A R, da Silva K E, Doff Sotta E, de Souza C R, Vidal E, West T A and Héault B 2016  
13 Carbon recovery dynamics following disturbance by selective logging in Amazonian forests  
14 *eLife* **5** e21394  
15  
16

17 Ploton P, Mortier F, Réjou-Méchain M, Barbier N, Picard N, Rossi V, Dormann C, Cornu G,  
18 Viennois G, Bayol N, Lyapustin A, Gourlet-Fleury S and Pélissier R 2020 Spatial validation  
19 reveals poor predictive performance of large-scale ecological mapping models *Nature Communications* **11** 4540  
20  
21

22 Poorter L, Bongers F, Aide T M, Zambrano A M A, Balvanera P, Becknell J M, Boukili V,  
23 Brancalion P H S, Broadbent E N, Chazdon R L, Craven D, Almeida-Cortez J S de, Cabral G A  
24 L, Jong B H J de, Denslow J S, Dent D H, DeWalt S J, Dupuy J M, Durán S M, Espírito-Santo M  
25 M, Fandino M C, César R G, Hall J S, Hernandez-Stefanoni J L, Jakovac C C, Junqueira A B,  
26 Kennard D, Letcher S G, Licona J-C, Lohbeck M, Marín-Spiotta E, Martínez-Ramos M,  
27 Massoca P, Meave J A, Mesquita R, Mora F, Muñoz R, Muscarella R, Nunes Y R F, Ochoa-  
28 Gaona S, Oliveira A A de, Orihuela-Belmonte E, Peña-Claros M, Pérez-García E A, Piotto D,  
29 Powers J S, Rodríguez-Velázquez J, Romero-Pérez I E, Ruíz J, Saldarriaga J G, Sanchez-  
30 Azofeifa A, Schwartz N B, Steininger M K, Swenson N G, Toledo M, Uriarte M, Breugel M van,  
31 Wal H van der, Veloso M D M, Vester H F M, Vicentini A, Vieira I C G, Bentos T V, Williamson  
32 G B and Rozendaal D M A 2016 Biomass resilience of Neotropical secondary forests *Nature*  
33 **530** 211–4  
34  
35

36 Pregitzer K S and Euskirchen E S 2004 Carbon cycling and storage in world forests: Biome  
37 patterns related to forest age *Global Change Biology* **10** 2052–77  
38  
39

40 Pugh T A M, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V and Calle L 2019 Role of  
41 forest regrowth in global carbon sink dynamics *Proceedings of the National Academy of  
42 Sciences* **116** 4382–7  
43  
44

45 Reinmann A B and Hutyra L R 2017 Edge effects enhance carbon uptake and its  
46 vulnerability to climate change in temperate broadleaf forests *Proceedings of the National  
47 Academy of Sciences* **114** 107–12  
48

49 Reinmann A B, Smith I A, Thompson J R and Hutyra L R 2020 Urbanization and  
50 fragmentation mediate temperate forest carbon cycle response to climate *Environmental  
51 Research Letters* **15** 114036  
52

53 Remy E, Wuyts K, Boeckx P, Ginzburg S, Gundersen P, Demey A, Van Den Bulcke J, Van  
54 Acker J and Verheyen K 2016 Strong gradients in nitrogen and carbon stocks at temperate  
55 forest edges *Forest Ecology and Management* **376** 45–58  
56  
57  
58  
59  
60

1  
2  
3 Requena Suarez D, Rozendaal D M A, Sy V D, Phillips O L, Alvarez-Dávila E, Anderson-  
4 Teixeira K, Araujo-Murakami A, Arroyo L, Baker T R, Bongers F, Brienen R J W, Carter S,  
5 Cook-Patton S C, Feldpausch T R, Griscom B W, Harris N, Héault B, Coronado E N H, Leavitt  
6 S M, Lewis S L, Marimon B S, Mendoza A M, N'dja J K, N'Guessan A E, Poorter L, Qie L,  
7 Rutishauser E, Sist P, Sonké B, Sullivan M J P, Vilanova E, Wang M M H, Martius C and  
8 Herold M 2019 Estimating aboveground net biomass change for tropical and subtropical  
9 forests: Refinement of IPCC default rates using forest plot data *Global Change Biology* **25**  
10 3609–24  
11  
12

13 Ribeiro-Kumara C, Köster E, Aaltonen H and Köster K 2020 How do forest fires affect soil  
14 greenhouse gas emissions in upland boreal forests? A review *Environmental Research* **184**  
15 109328  
16  
17

18 Saatchi S S, Harris N L, Brown S, Lefsky M, Mitchard E T A, Salas W, Zutta B R, Buermann W,  
19 Lewis S L, Hagen S, Petrova S, White L, Silman M and Morel A 2011 Benchmark map of  
20 forest carbon stocks in tropical regions across three continents *Proceedings of the National  
21 Academy of Sciences* **108** 9899–904  
22

23 Schepaschenko D, Chave J, Phillips O L, Lewis S L, Davies S J, Réjou-Méchain M, Sist P, Scipal  
24 K, Perger C, Herault B, Labrière N, Hofhansl F, Affum-Baffoe K, Aleinikov A, Alonso A, Amani  
25 C, Araujo-Murakami A, Armston J, Arroyo L, Ascarrunz N, Azevedo C, Baker T, Bałazy R,  
26 Bedeau C, Berry N, Bilous A M, Bilous S Y, Bissiengou P, Blanc L, Bobkova K S, Braslavskaya  
27 T, Brienen R, Burslem D F R P, Condit R, Cuni-Sánchez A, Danilina D, Torres D del C,  
28 Derroire G, Descroix L, Sotta E D, d'Oliveira M V N, Dresel C, Erwin T, Evdokimenko M D,  
29 Falck J, Feldpausch T R, Foli E G, Foster R, Fritz S, Garcia-Abril A D, Gornov A, Gornova M,  
30 Gothard-Bassébé E, Gourlet-Fleury S, Guedes M, Hamer K C, Susanty F H, Higuchi N,  
31 Coronado E N H, Hubau W, Hubbell S, Ilstedt U, Ivanov V V, Kanashiro M, Karlsson A,  
32 Karminov V N, Killeen T, Koffi J-C K, Konovalova M, Kraxner F, Krejza J, Krisnawati H,  
33 Krivobokov L V, Kuznetsov M A, Lakyda I, Lakyda P I, Licona J C, Lucas R M, Lukina N,  
34 Lussetti D, Malhi Y, Manzanera J A, Marimon B, Junior B H M, Martinez R V, Martynenko O V,  
35 Matsala M, Matyashuk R K, Mazzei L, Memiaghe H, Mendoza C, Mendoza A M, Morozuk O V,  
36 Mukhortova L, Musa S, Nazimova D I, Okuda T, Oliveira L C, et al 2019 The Forest  
37 Observation System, building a global reference dataset for remote sensing of forest  
38 biomass *Scientific Data* **6** 1–11  
39  
40

41 Schimel D, Hargrove W, Hoffman F and MacMahon J 2007 NEON: A hierarchically designed  
42 national ecological network *Frontiers in Ecology and the Environment* **5** 59–9  
43  
44

45 Schimel D, Stephens B B and Fisher J B 2015 Effect of increasing CO<sub>2</sub> on the terrestrial  
46 carbon cycle *Proceedings of the National Academy of Sciences* **112** 436–41  
47  
48

49 Sist P, Rutishauser E, Peña-Claros M, Shenkin A, Héault B, Blanc L, Baraloto C, Baya F,  
50 Benedet F, Silva K E da, Descroix L, Ferreira J N, Gourlet-Fleury S, Guedes M C, Harun I B,  
51 Jalonen R, Kanashiro M, Krisnawati H, Kshatriya M, Lincoln P, Mazzei L, Medjibé V, Nasi R,  
52 d'Oliveira M V N, Oliveira L C de, Picard N, Pietsch S, Pinard M, Priyadi H, Putz F E, Rodney  
53 K, Rossi V, Roopsind A, Ruschel A R, Shari N H Z, Souza C R de, Susanty F H, Sotta E D,  
54 Toledo M, Vidal E, West T A P, Wortel V and Yamada T 2015 The Tropical managed Forests  
55  
56  
57  
58  
59  
60

1  
2  
3 Observatory: A research network addressing the future of tropical logged forests *Applied*  
4 *Vegetation Science* **18** 171–4  
5

6 Smith I A, Hutyra L R, Reinmann A B, Thompson J R and Allen D W 2019 Evidence for Edge  
7 Enhancements of Soil Respiration in Temperate Forests *Geophysical Research Letters* **46**  
8 4278–87  
9

10 Smithwick E A H, Harmon M E, Remillard S M, Acker S A and Franklin J F 2002 Potential  
11 upper bounds of carbon stores in forests of the Pacific Northwest *Ecological Applications*  
12 **12** 1303–17  
13

14 Song J, Wan S, Piao S, Knapp A K, Classen A T, Vicca S, Ciais P, Hovenden M J, Leuzinger S,  
15 Beier C, Kardol P, Xia J, Liu Q, Ru J, Zhou Z, Luo Y, Guo D, Adam Langley J, Zscheischler J,  
16 Dukes J S, Tang J, Chen J, Hofmockel K S, Kueppers L M, Rustad L, Liu L, Smith M D, Templer  
17 P H, Quinn Thomas R, Norby R J, Phillips R P, Niu S, Fatichi S, Wang Y, Shao P, Han H, Wang  
18 D, Lei L, Wang J, Li X, Zhang Q, Li X, Su F, Liu B, Yang F, Ma G, Li G, Liu Y, Liu Y, Yang Z, Zhang  
19 K, Miao Y, Hu M, Yan C, Zhang A, Zhong M, Hui Y, Li Y and Zheng M 2019 A meta-analysis of  
20 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change  
21 *Nature Ecology & Evolution* **3** 1309–20  
22

23 Song X-P, Hansen M C, Stehman S V, Potapov P V, Tyukavina A, Vermote E F and  
24 Townshend J R 2018 Global land change from 1982 to 2016 *Nature* **560** 639–43  
25

26 Spawn S A, Sullivan C C, Lark T J and Gibbs H K 2020 Harmonized global maps of above and  
27 belowground biomass carbon density in the year 2010 *Scientific Data* **7** 112  
28

29 Stoy P C, Mauder M, Foken T, Marcolla B, Boegh E, Ibrom A, Arain M A, Arneth A, Aurela M,  
30 Bernhofer C, Cescatti A, Dellwik E, Duce P, Gianelle D, van Gorsel E, Kiely G, Knohl A,  
31 Margolis H, McCaughey H, Merbold L, Montagnani L, Papale D, Reichstein M, Saunders M,  
32 Serrano-Ortiz P, Sottocornola M, Spano D, Vaccari F and Varlagin A 2013 A data-driven  
33 analysis of energy balance closure across FLUXNET research sites: The role of landscape  
34 scale heterogeneity *Agricultural and Forest Meteorology* **171–172** 137–52  
35

36 Sulman B N, Moore J A M, Abramoff R, Averill C, Kivlin S, Georgiou K, Sridhar B, Hartman M  
37 D, Wang G, Wieder W R, Bradford M A, Luo Y, Mayes M A, Morrison E, Riley W J, Salazar A,  
38 Schimel J P, Tang J and Classen A T 2018 Multiple models and experiments underscore  
39 large uncertainty in soil carbon dynamics *Biogeochemistry* **141** 109–23  
40

41 Taylor P G, Cleveland C C, Wieder W R, Sullivan B W, Doughty C E, Dobrowski S Z and  
42 Townsend A R 2017 Temperature and rainfall interact to control carbon cycling in tropical  
43 forests ed L Liu *Ecology Letters* **20** 779–88  
44

45 Team R C 2020 R : A language and environment for statistical computing. R Foundation for  
46 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.  
47

48 Tubiello F N, Pekkarinen A, Marklund L, Wanner N, Conchedda G, Federici S, Rossi S and  
49 Grassi G 2020 Carbon Emissions and Removals by Forests: New Estimates  
50 1990&ndash;2020 *Earth System Science Data Discussions* 1–21  
51

52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 van der Werf G R, Randerson J T, Giglio L, van Leeuwen T T, Chen Y, Rogers B M, Mu M, van  
4 Marle M J E, Morton D C, Collatz G J, Yokelson R J and Kasibhatla P S 2017 Global fire  
5 emissions estimates during 1997 *Earth System Science Data* **9** 697–720  
6

7 Vargas R, Allen M F and Allen E B 2008 Biomass and carbon accumulation in a fire  
8 chronosequence of a seasonally dry tropical forest *Global Change Biology* **14** 109–24  
9

10 Wang Y, Ciais P, Goll D, Huang Y, Luo Y, Wang Y-P, Bloom A A, Broquet G, Hartmann J, Peng  
11 S, Penuelas J, Piao S, Sardans J, Stocker B D, Wang R, Zaehle S and Zechmeister-Boltenstern  
12 S 2018 GOLUM-CNP v1.0: A data-driven modeling of carbon, nitrogen and phosphorus  
13 cycles in major terrestrial biomes *Geoscientific Model Development* **11** 3903–28  
14

15 Warner D L, Bond-Lamberty B, Jian J, Stell E and Vargas R 2019 Spatial Predictions and  
16 Associated Uncertainty of Annual Soil Respiration at the Global Scale *Global Biogeochemical  
17 Cycles* **33** 1733–45  
18

19 Williams C A, Collatz G J, Masek J, Huang C and Goward S N 2014 Impacts of disturbance  
20 history on forest carbon stocks and fluxes: Merging satellite disturbance mapping with  
21 forest inventory data in a carbon cycle model framework *Remote Sensing of Environment*  
22 **151** 57–71  
23

24 Wilson R M, Hopple A M, Tfaily M M, Sebestyen S D, Schadt C W, Pfeifer-Meister L,  
25 Medvedeff C, McFarlane K J, Kostka J E, Kolton M, Kolka R K, Kluber L A, Keller J K,  
26 Guilderson T P, Griffiths N A, Chanton J P, Bridgman S D and Hanson P J 2016 Stability of  
27 peatland carbon to rising temperatures *Nature Communications* **7** 13723  
28

29 Xu M and Shang H 2016 Contribution of soil respiration to the global carbon equation  
30 *Journal of Plant Physiology* **203** 16–28  
31

32 Yang Y, Luo Y and Finzi A C 2011 Carbon and nitrogen dynamics during forest stand  
33 development: A global synthesis *New Phytologist* **190** 977  
34

35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
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3 **Table 1. Carbon cycle variables included in this analysis, their sample sizes, and summary of biome**  
4 **differences and age trends.**

Variable	Description	n records			biome differences*	age trend**
		records	plots	geographic areas		
<b>Annual Fluxes</b>						
<i>NEP</i>	net ecosystem production or net ecosystem exchange (+ indicates C sink)	329	146	88	n.s.	+; xB
<i>GPP</i>	gross primary production ( <i>NPP</i> + <i>R<sub>auto</sub></i> or <i>NEP+R<sub>eco</sub></i> )	303	115	84	TrB > TeB ≥ TeN ≥ BoN	+; xB
<i>NPP</i>	net primary production ( <i>ANPP</i> + <i>BNPP</i> )	214	112	74	TrB > TeB ≥ TeN > BoN	n.s.
<i>ANPP</i>	aboveground <i>NPP</i>	343	236	131	TrB > TeB ≥ TeN > BoN	+; xB
<i>ANPP<sub>woody</sub></i>	woody production ( <i>ANPP<sub>stem</sub></i> + <i>ANPP<sub>branch</sub></i> )	64	53	37	n.s.	+
<i>ANPP<sub>stem</sub></i>	woody stem production	217	190	117	TrB > TeN ≥ TeB ≥ BoN	n.s.
<i>ANPP<sub>branch</sub></i>	branch turnover	69	59	42	TrB > TeB ≥ TeN	n.s.
<i>ANPP<sub>foliage</sub></i>	foliage production, typically estimated as annual leaf litterfall	162	132	88	TrB > TeB ≥ TeN > BoN	+
<i>ANPP<sub>litterfall</sub></i>	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	82	70	55	n.s.	+
<i>ANPP<sub>repro</sub></i>	production of reproductive structures (flowers, fruits, seeds)	51	44	34	n.t.	n.t.
<i>ANPP<sub>folivory</sub></i>	foliar biomass consumed by folivores	20	12	11	n.t.	n.t.
<i>M<sub>woody</sub></i>	woody mortality--i.e., <i>B<sub>ag</sub></i> of trees that die	18	18	18	n.t.	n.t.
<i>BNPP</i>	belowground NPP ( <i>BNPP<sub>coarse</sub></i> + <i>BNPP<sub>fine</sub></i> )	148	116	79	TrB > TeN ≥ TeB ≥ BoN	+
<i>BNPP<sub>coarse</sub></i>	coarse root production	77	56	36	TeN ≥ TrB	n.s.
<i>BNPP<sub>fine</sub></i>	fine root production	123	99	66	n.s.	+
<i>R<sub>eco</sub></i>	ecosystem respiration ( <i>R<sub>auto</sub></i> + <i>R<sub>het</sub></i> )	213	98	70	TrB > TeB ≥ TeN	+
<i>R<sub>auto</sub></i>	autotrophic respiration ( <i>R<sub>auto-ag</sub></i> + <i>R<sub>root</sub></i> )	24	23	15	n.t.	n.t.
<i>R<sub>auto-ag</sub></i>	aboveground autotrophic respiration (i.e., leaves and stems)	2	2	1	n.t.	n.t.
<i>R<sub>root</sub></i>	root respiration	181	139	95	TrB ≥ TeB	+
<i>R<sub>soil</sub></i>	soil respiration ( <i>R<sub>het-soil</sub></i> + <i>R<sub>root</sub></i> )	627	411	229	TrB > TeB > TeN ≥ BoN	n.s.
<i>R<sub>het-soil</sub></i>	soil heterotrophic respiration	197	156	100	TrB > TeB ≥ TeN	n.s.
<i>R<sub>het-ag</sub></i>	aboveground heterotrophic respiration	0	0	0	-	-
<i>R<sub>het</sub></i>	heterotrophic respiration ( <i>R<sub>het-ag</sub></i> + <i>R<sub>het-soil</sub></i> )	0	0	0	-	-
<b>Stocks</b>						
<i>B<sub>tot</sub></i>	total live biomass ( <i>B<sub>ag</sub></i> + <i>B<sub>root</sub></i> )	188	157	87	TrB ≥ TeB > BoN	+; xB
<i>B<sub>ag</sub></i>	aboveground live biomass ( <i>B<sub>ag-wood</sub></i> + <i>B<sub>foliage</sub></i> )	4466	4072	621	TrB ≥ TeN ≥ TeB > BoN	+; xB
<i>B<sub>ag-wood</sub></i>	woody component of aboveground biomass	115	102	64	TeN > TrB ≥ BoN	+; xB
<i>B<sub>foliage</sub></i>	foliage biomass	134	115	72	TeN > TrB ≥ BoN ≥ TeB	+; xB
<i>B<sub>root</sub></i>	total root biomass ( <i>B<sub>root-coarse</sub></i> + <i>B<sub>root-fine</sub></i> )	2329	2298	360	n.s.	+; xB
<i>B<sub>root-coarse</sub></i>	coarse root biomass	134	120	73	TeN > TeB ≥ BoN	+; xB
<i>B<sub>root-fine</sub></i>	fine root biomass	226	180	109	n.s.	+; xB
<i>DW<sub>tot</sub></i>	deadwood ( <i>DW<sub>standing</sub></i> + <i>DW<sub>down</sub></i> )	79	73	42	n.t.	+; xB
<i>DW<sub>standing</sub></i>	standing dead wood	36	35	22	n.t.	n.t.
<i>DW<sub>down</sub></i>	fallen dead wood, including coarse and sometimes fine woody debris	278	265	37	n.t.	+; xB
OL	organic layer / litter/ forest floor	474	413	115	n.s.	+; xB

53 \* **TrB:** Tropical, **TeB:** Temperate Broadleaf, **TeN:** Temperate Needleleaf, **BoN:** Boreal, n.s.: no significant differences, n.t.: not tested

54 \*\* + or -: significant positive or negative trend, xB: significant age x biome interaction, n.s.: no significant age trend, n.t.: not tested

### Figure Legends

Figure 1 | Schematic diagram summarizing current understanding of biome differences and age trends in forest C cycling. Variables are defined in Table 1. Age trends, which represent idealized dynamics following a disturbance that removes all living vegetation, are an updated version of the classic figure from Odum (1969), with heavy lines corresponding to those in Odum's figure and *NEP* corresponding to Odum's 'net production'. Here, *NEP* consists primarily of woody aboveground net primary production ( $ANPP_{woody}$ ), while  $ANPP_{woody,turnover}$  is the sum of woody mortality and branch turnover. Dotted lines refer to decomposition of potential 'legacy' organic material produced prior to the disturbance and remaining at the site (e.g., standing and fallen dead wood,  $DW_{tot}$ ; soil organic matter). Error bars on C stocks plot represent within-biome variability, wherein mean biomass is highest in the tropics, but maximum biomass is highest in temperate regions.

Figure 2 | 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 (shading differences; data from Jung et al. 2006) and biomes (color differences). Distribution of sites, plots, and records among biomes is shown in the inset.

Figure 3 | C cycle diagram for mature tropical broadleaf forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

Figure 4 | C cycle diagram for mature temperate broadleaf forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

Figure 5 | C cycle diagram for mature temperate conifer forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30). The temperate conifer biome in particular is subject to high variability, with

highest fluxes and stocks in the high-biomass forests of the US Pacific Northwest. An asterisk after a variable name indicates lack of C cycle closure.

Figure 6 | C cycle diagram for mature boreal conifer forests. Arrows indicate fluxes ( $Mg\ C\ ha^{-1}\ yr^{-1}$ ); boxes indicate stocks ( $Mg\ C\ ha^{-1}$ ), with variables as defined in Table 1. Presented are mean  $\pm$  std, where geographically distinct areas are treated as the unit of replication. Dashed shape outlines indicate variables with records from <7 distinct geographic areas, and dashed arrows indicate fluxes with no data. To illustrate the magnitude of different fluxes, arrow width is proportional to the square root of the corresponding flux. Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).

Figure 7 | 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. In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of  $\log_{10}(\text{age})$  and biome. The fitted line indicates the effect of age (solid lines: significant at  $p<0.05$ , dashed lines: non-significant), and non-parallel lines indicate a significant  $\log_{10}(\text{age}) \times$  biome interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each flux with sufficient data, along with maps showing geographic distribution of the data, are given in the Supplement (Figs. S5-S19).

Figure 8 | Age trends and biome differences in some of the major forest C stocks: (a) aboveground biomass, (b) foliage, (c) fine roots, (d) dead wood. In each panel, the left scatterplot shows age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of  $\log_{10}(\text{age})$  and biome. The fitted line indicates the effect of age (solid lines: significant at  $p<0.05$ , dashed lines: non-significant), and non-parallel lines indicate a significant  $\log_{10}(\text{age}) \times$  biome interaction. The boxplot illustrates distribution across mature forests, with different letters indicating significant differences between biomes. Data from biomes that did not meet the sample size criteria (see Methods) are plotted, but lack regression lines (young forests) or test of differences across biomes (mature forests). Individual figures for each stock with sufficient data, along with maps showing geographic distribution of the data, are given in the Supplement (Figs. S20-S30).

Figure 9 | Age trends in C cycling. Selection of variables for plotting seeks to maximize sample size and broad geographic representation while representing all elements of C cycle. Error bars on mature forest flux estimates indicate  $\pm 1$  standard deviation. Asterisks indicate variables whose age trends were calculated based on other variables (\* young and mature forests; \*\* young forests only; \*\*\* mature forests only), as follows. For all forests:  $B_{ag-wood} = \max(0, B_{ag} - B_{foliage})$ ,  $B_{root-coarse} = \max(0, B_{root} - B_{root-fine})$ ,  $DW_{standing} = \max(0, DW_{tot} - DW_{down})$ . For tropical forests:  $ANPP_{woody} = \max(0, ANPP - ANPP_{foliage})$ ,  $R_{auto-ag} = R_{auto} - R_{root}$ , where  $R_{auto} = NPP(1/CUE - 1)$  and  $CUE=0.46$  (Collati et al. 2020). For non-tropical forests:  $ANPP_{woody} =$

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3  $\min(ANPP_{stem}, ANPP_{woody})$ ,  $R_{auto-ag} = R_{eco} - R_{soil}$ . Note that there remain substantial  
4 uncertainties as to the functional form of age trends and discrepancies in closure among  
5 related variables.  
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Figure 1.

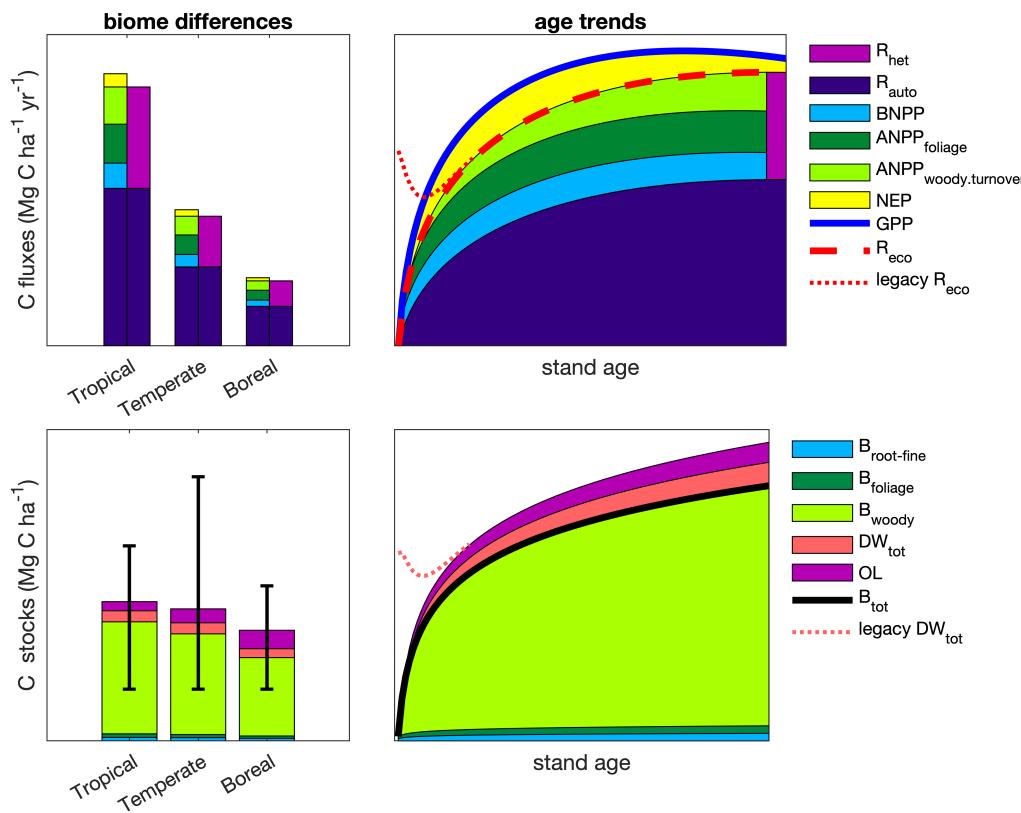


Figure 2.

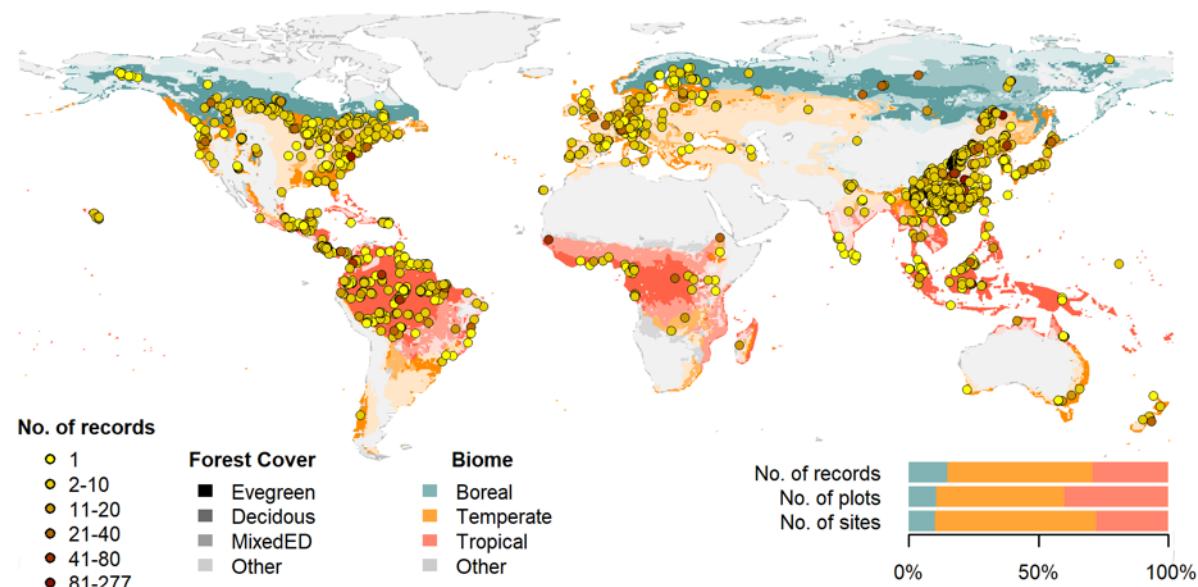


Figure 3.

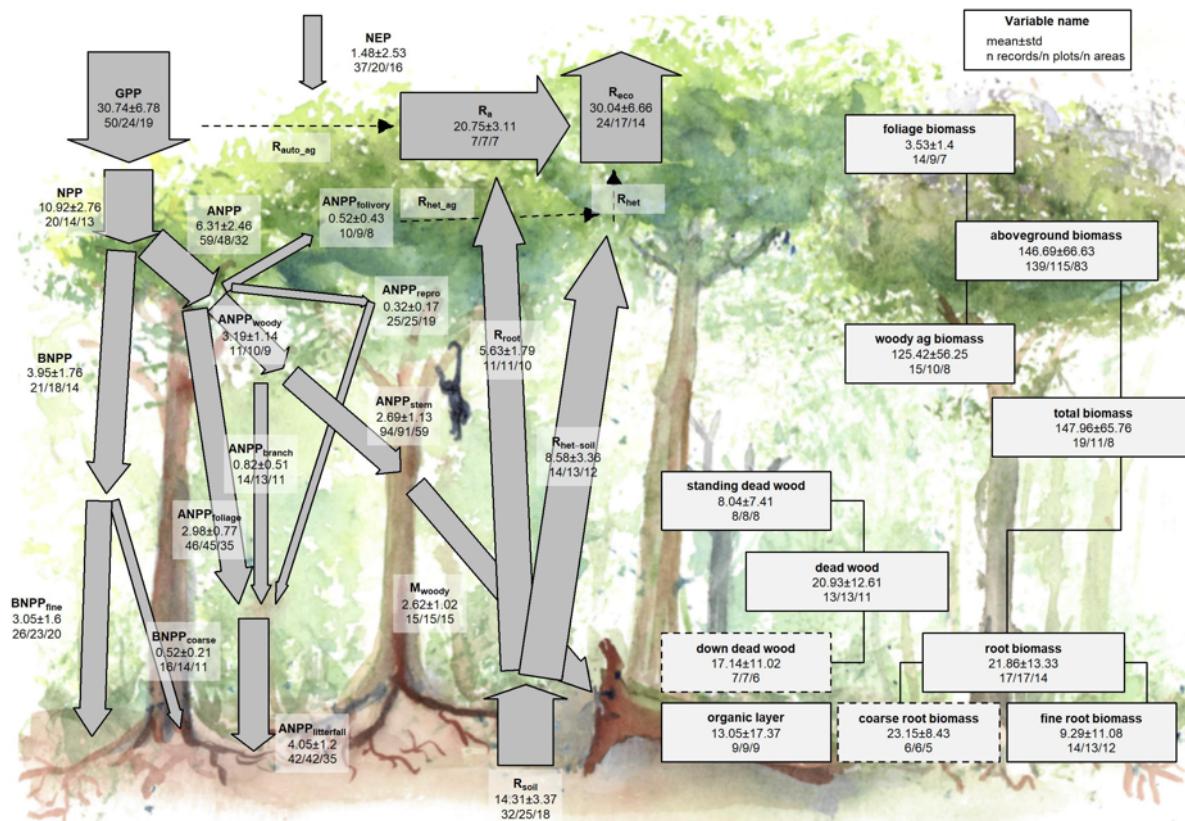


Figure 4.

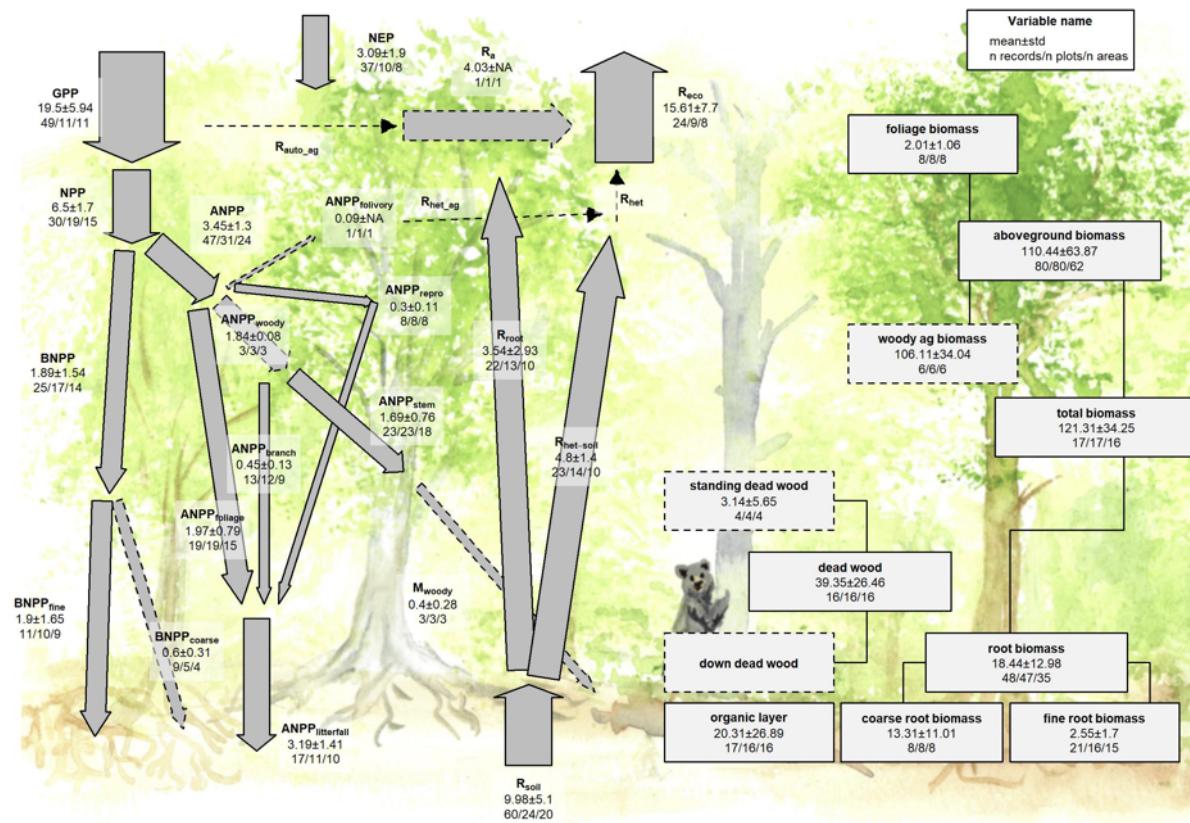


Figure 5.

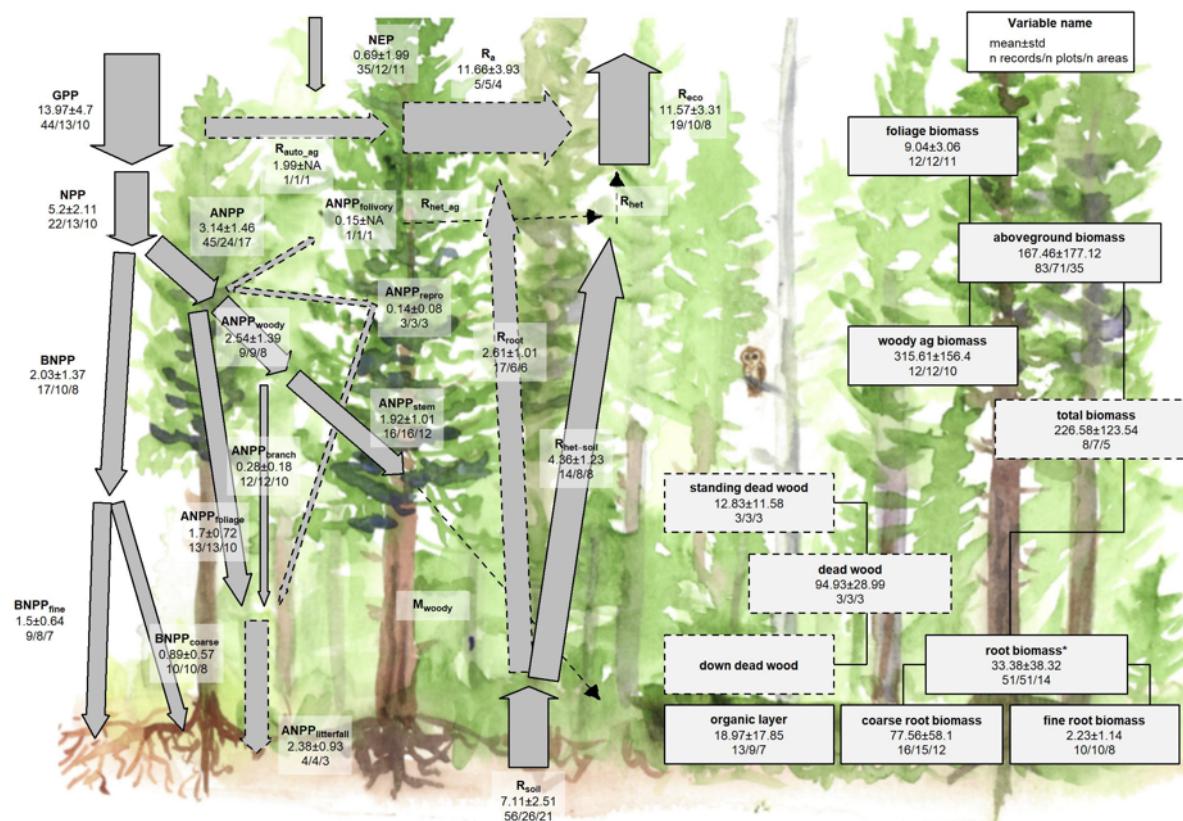


Figure 6.

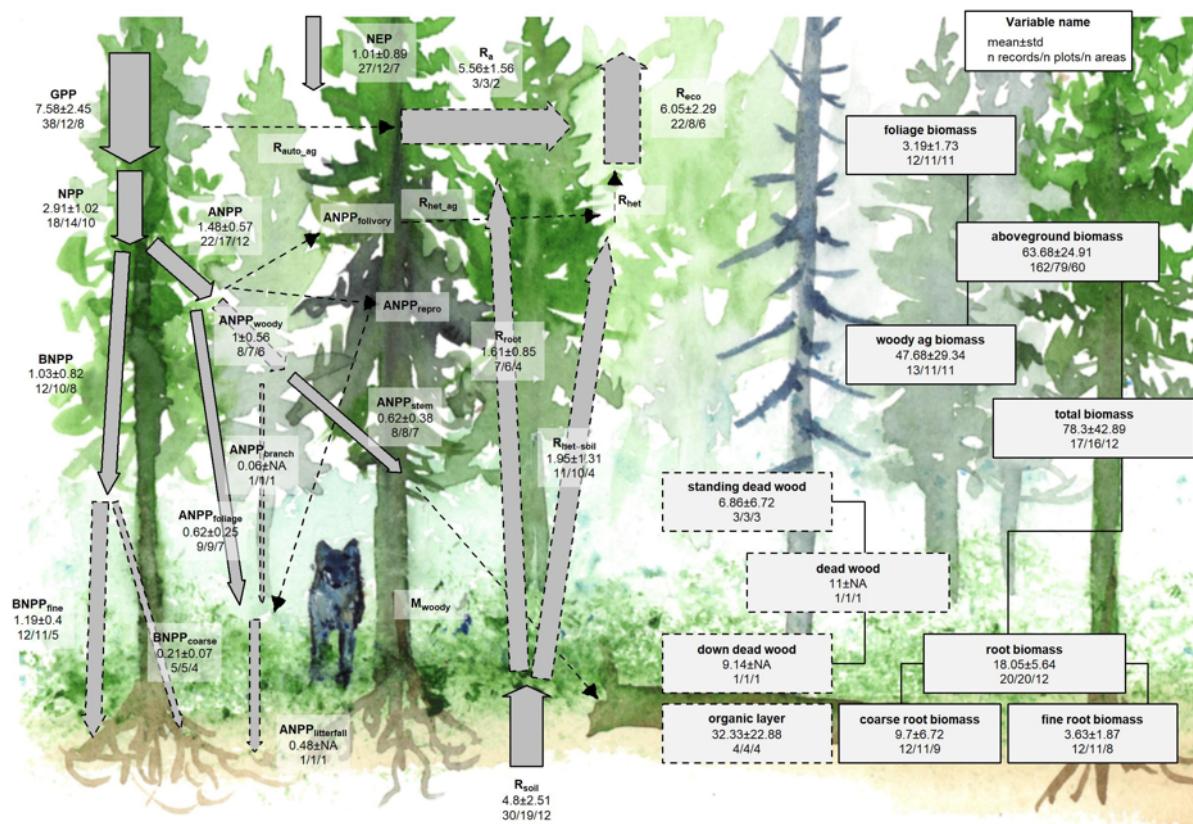


Figure 7.

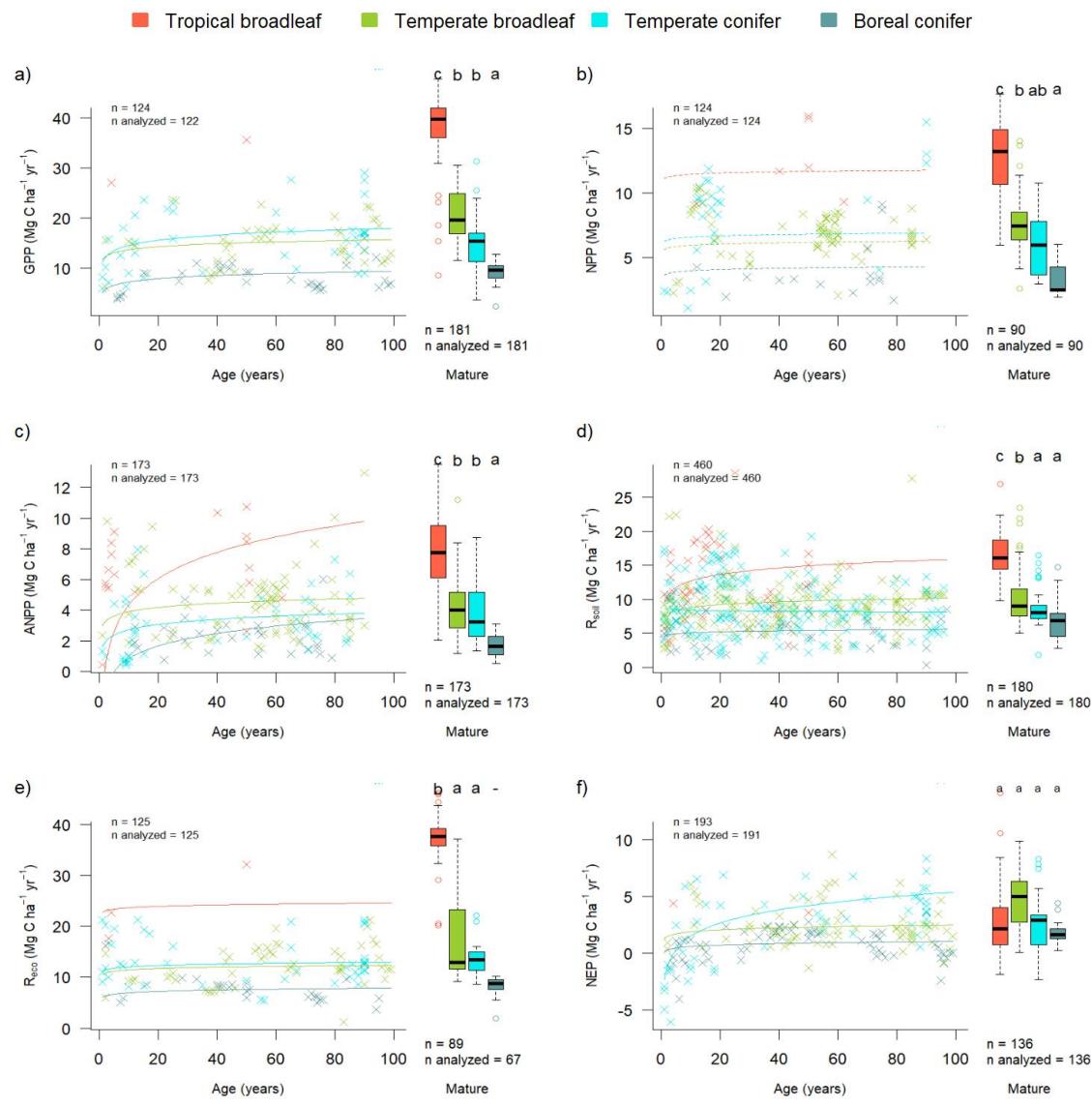


Figure 8.

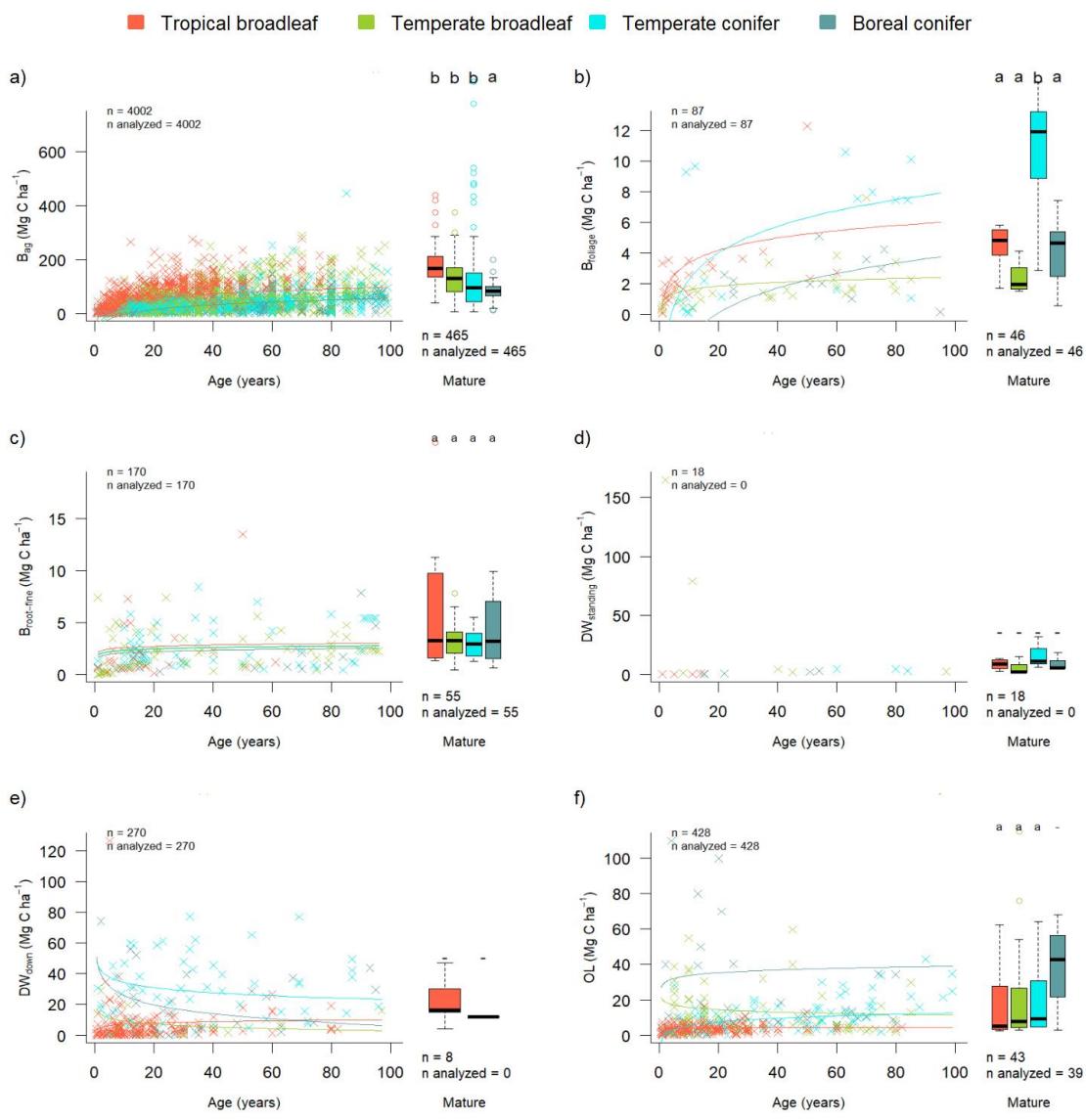
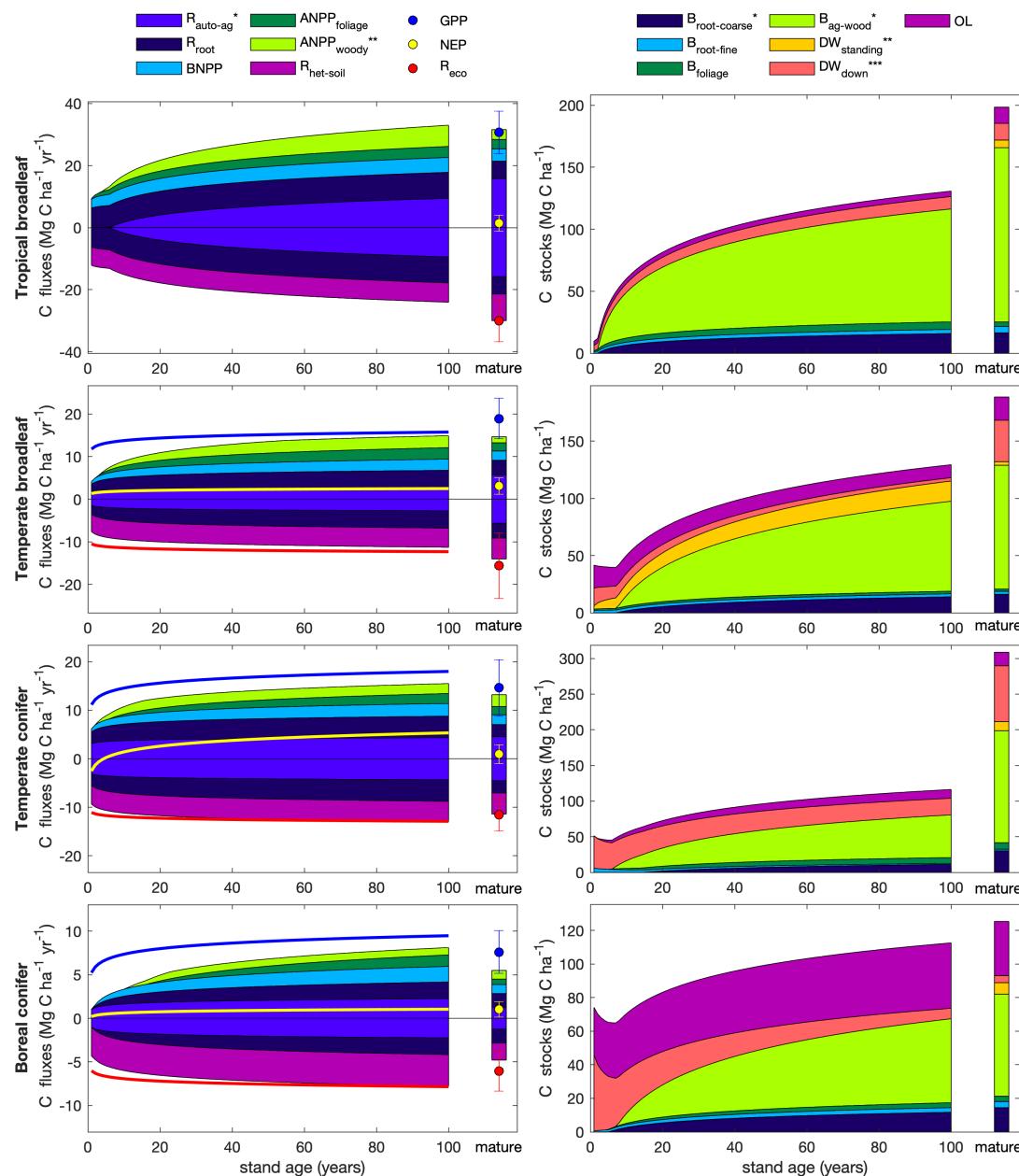


Figure 9.



**Title:** Response to reviews

Re: "Carbon cycling in mature and regrowth forests globally" by Anderson-Teixeira, Kristina; Herrmann, Valentine; Banbury Morgan , Rebecca ; Bond-Lamberty, Benjamin; Cook-Patton, Susan; Ferson , Abigail; Muller-Landau, Helene; Wang, Maria Article reference: ERL-109898

**LETTER TO EDITOR:**

Dear Editor:

We are please to submit a revised version of our manuscript, "Carbon cycling in mature and regrowth forests globally" (ERL-109898), for consideration for publication in *Environmental Research Letters*. We have addressed all points raised by the reviewers, as detailed below. The most substantive changes included the following:

- We changed the figure set in accordance with comments from R3. Specifically, we (1) added a schematic figure, somewhat in the style of Odum (1969), to help with conceptual framing of the review; (2) added a figure synthesizing changes in fluxes through time for each biome; (3) removed maps from age trend diagrams (maps still available in supplementary information), which makes the figures less busy/ easier to read; and (4) moved C cycle diagrams for young forests to the supplementary information.
- We improved conceptual framework and "review" nature of the work by adding background information to the introduction, including the schematic figure mentioned above. We also shifted emphasis more towards the ecological questions (trends across biomes and with age), while retaining (with less emphasis) the analysis of database representativeness.

Thank you for considering this revised version, and we look forward to your response.

Sincerely,

Kristina Anderson-Teixeira (on behalf of all coauthors)

**REFeree REPORT(S) & RESPONSES:****Referee: 2****COMMENTS TO THE AUTHOR(S)**

The manuscript provides an important contribution to carbon cycle research. It provides an update to a previously published data base of forest carbon stocks and fluxes (ForC) and analyses the dataset across forests biomes and in relation to stand age. This is a valuable dataset for assessing the current state of the carbon cycle and comparing across biomes. The dataset presents carbon cycle modelers with an opportunity to rigorously compare their models with observations. Figures 2-5, 8-11 are excellent summaries of the dataset. Yet I have some concerns and clarifications that must be addressed.

1. It is not clear what the various sources of data are. Perhaps this is because the authors have already  
described data sources in previous documentation of the dataset. However, I think some summary is  
needed for readers new to the dataset. I need to know what I am looking at when I see the various  
numbers in Figures 2-5, 8-11.

In addition to addressing the specific questions below, we have added a link to a spreadsheet recording the datasets that have been incorporated, which is maintained in the open-access GitHub repository: “A record of data sets added to *ForC* is available at [https://github.com/forc-db/ForC/blob/master/database\\_management\\_records/ForC\\_data\\_additions\\_log.csv](https://github.com/forc-db/ForC/blob/master/database_management_records/ForC_data_additions_log.csv).”

- a. For example, is Fluxnet the source of GPP and Reco? The authors state that “ForC amalgamates numerous intermediary data sets” (line 119) and cite Luyssaert et al (2007). Is that the source of GPP and Reco, or have the fluxes been updated to newer Fluxnet data products? Similarly for the soil respiration data. Is this the data from Bond-Lamberty and Thomson (2010) or has it been updated?

We now clarify as follows:

**FLUXNET:**

Methods: “Third, we manually incorporated records of annual  $NEP$ ,  $GPP$ , and  $R_{eco}$  from the FLUXNET2015 dataset (Pastorello *et al* 2020), treating these records as authoritative when they duplicated earlier records (Appendix S1).”

Appendix S1: “For eddy-covariance variables ( $NEP$ ,  $GPP$ ,  $R_{eco}$ ), we retained the record associated with the most recent publication (most often Pastorello *et al* 2020), as these data are commonly re-assessed using new analysis methods.”

**SRDB:**

Methods: “First, we imported (via R script) the Global Database of Soil Respiration Database (SRDB v4, 9488 records; Bond-Lamberty and Thomson 2010), and corrections and improvements to SRDB arising from this process were incorporated in SRDB v5 (Jian *et al* 2020).”

- b. I need information on how Figures 2-5, 8-11 were prepared. Carbon stocks and fluxes such as NPP, litterfall, etc. are probably plot data. There is a detailed discussion of how the data were filtered to

remove, for example, disturbance effects (lines 140-149). The GPP, Reco, and soil respiration databases seem to me to be different and may not be collocated with the plot data. Was disturbance filtering applied to the GPP, Reco, and soil respiration databases, too?

All records analyzed here have been fully incorporated into the ForC format and treated as described. We believe this should now be clearer where we describe the importation of new datasets: “Since publication of ForC v2.0, we imported three large additional databases [SRDB, GROA, FLUXNET15] into *ForC* via a combination of R scripts and manual edits. . .”

- c. If Luyssaert et al (2007) is a source of data, is there circularity in the comparison with latitudinal trends found in other datasets, for which Luyssaert et al is cited (lines 317-318)?

We don't see this as circular; we are reaffirming earlier results with an expanded dataset. To make it clear that we are not claiming to provide an independent test, we have edited this text as follows: “For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes generally decline with latitude (or increase with temperature) on a global scale (e.g., Luyssaert *et al* 2007, Gillman *et al* 2015, Li and Xiao 2019, Banbury Morgan *et al* n.d.). This consistency is not surprising, particularly given commonality in the data analyzed or used for calibration.”

2. Figures 2-5, 8-11 are excellent summaries of the dataset. Yet there is much unexplained in the figure and the reported data values. No guidance is given on how to use the data, and especially how to resolve discrepancies in the data.
  - a. For example, Figure 2 lists foliage and woody aboveground biomass in tropical broadleaf forests. These do not sum to aboveground biomass ( $3.53 + 125.42 = 128.95$  Mg C/ha vs 146.69). Nor do coarse root biomass and fine root biomass sum to root biomass ( $23.15 + 9.29 = 32.44$  vs. 21.86). Total biomass (147.96) is not the sum of aboveground (146.69) and root (21.86).

We acknowledge and discuss lack of closure in various places throughout the results and discussion. To ensure that this is clear from the figures, we have added the following statement to the captions of Figures 3-6 (formerly 2-5): “Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).” We have also added a similar statement to the captions of Figures S1-S4 (formerly 8-11). We also make a related statement in the captions of new figures 9-12: “Note that there remain substantial uncertainties as to the functional form of age trends and discrepancies in closure among related variables.”

- b. Figure 4 for temperate conifer forests has large discrepancies in carbon stocks: e.g., 315.61 Mg C/ha for woody aboveground biomass, but only 167.46 for aboveground biomass and 226.58 for total biomass. The authors have a detailed discussion about lack of closure for root biomass, but do not discuss aboveground biomass. Presumably, this is because the data fall within the closure criteria, but what are we to make of the inconsistent data?

This is partially addressed by the response above, and covered in the results and discussion. In addition, to help explain the fact that lack of closure is particularly pronounced in temperate conifer forests, we have included errorbars in on the new schematic figure (Fig. 1)

indicating that temperate forests have particularly high variation in C stocks.

I understand that the data comes from many different sources and so may not always be compatible and that they have large standard deviations, but how are we to interpret and use the various data entries? For example, what has higher confidence: the component variables or the aggregate variables? What is the best estimate for aboveground biomass or root biomass? The authors take great pride in that component variables sum to within one standard deviation of the aggregate variables in all but one instance (lines 225-226, 301-302, 309-310). This is somewhat remarkable! But users of the dataset need guidance on how to interpret and use the data.

We have done two things to address this comment. First, to ensure accurate interpretation, we added the following statement to the captions of Figures 3-6 (formerly 2-5): “Mean component fluxes do not necessarily add up to the mean total fluxes because different sets of sites are included depending on availability of data (Figs. S5-S30).” Second, we have added the following guidance on using the data to the discussion: “*ForC*’s tens of thousands of records are readily available in a standardized format, along with all code used in the analyses presented here, and we recommend that researchers use these resources to identify and summarize data specific the analysis at hand.”

3. There is a general sloppiness to the manuscript that makes me think the authors did not proofread the manuscript carefully.

We have proofread more carefully this time.

a. Line 58: The authors say GPP is estimated to be >69 Gt C/year, and cite Badgley et al. (2019). This statement is factually correct, but is quite misleading. Badgley et al. "estimate global annual terrestrial photosynthesis to be 147 Pg C/year (95% credible interval 131-163 Pg C/year)". The value of 69 Gt C is less than one-half that reported by Badgley. What are the authors trying to say? Such a large discrepancy does not instill confidence in the other numbers reported in the manuscript.

The 147 Pg C/year figure refers to *total* annual terrestrial photosynthesis, including non-forests. Table S4 in Badgley *et al* (2019) breaks this down by biome. The >69 Gt C/yr figure was obtained by summing the forest biomes, not including savannas/ mixed biomes.

b. Line 81: “rare exceptions that span regions or continents” is repeated twice.

Fixed.

c. Figure 1: Explain the gray scale for “forest cover”. It seems like this refers to gradations of the various biomes, but the figure caption does not provide an explanation.

We have added an explanation.

d. Line 162: Clarify what is meant by “the minimum diameter breast height (DBH) threshold for tree census was <10cm”?

We have reworded this sentence for improved clarity: “Throughout ForC, for all measurements drawing from tree census data (*e.g.*, biomass, productivity), trees were censused down to a minimum diameter breast height (DBH) threshold of 10 cm or less.”

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3 e. Table 1: (i) The definition of GPP refers to NEE, but this is never defined. The preceding entry  
4 defines NEP not NEE. (ii) The description of the biome labels is inaccurate. The table uses “TrB” but  
5 the note refers to “Tr”. The table uses “BoN”, but the note refers to “B”.  
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7 We have fixed both of these.  
8

- 9 f. Line 210: I am confused by the statement that of the 39762 records in ForC v3.0, 11923 were included  
10 in this study. Previously (lines 135-149), the authors described creating “ForC-simplified” with 17349  
11 records. Clarify the difference between ForC-simplified and ForC v3.0.  
12  
13 It appears that reference to ForC-simplified (essentially an automatically generated  
14 rearrangement of ForC that is purged of duplicates and organized for easy analysis) makes  
15 the process more confusing, and isn't necessary, so we eliminated mention of it.  
16  
17 g. Line 212: The authors refer to ForC, where in the previous sentence they referred to ForC v3.0, and  
18 previously used ForC-simplified. Clarify what database is used in the analyses.  
19  
20 As in the response above, we have eliminated unnecessary/confusing mention of  
21 ForC-simplified. The version used is ForC v3.0 (to be released with DOI upon acceptance of  
22 this manuscript). We do not feel it is necessary to state the version number every time ForC  
23 is mentioned.  
24  
25 4. This is not a review article in the traditional sense that a review is a critical assessment of recent  
26 papers in the field of carbon cycle research or identifies future research priorities. Instead, the paper  
27 documents a database and shows the utility of the database for carbon cycle research. My comments  
28 on the review aspect of the manuscript are:  
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30 a. Yes, there is a need for this database; but  
31 b. No, this is not a critical and authoritative review of the carbon cycle; and  
32 c. The authors reference many other publications and datasets, but they do not critically evaluate their  
33 own dataset or other datasets.  
34  
35 We'd define this as a “quantitative review”—i.e., one that quantitatively synthesizes previous  
36 studies. However, we agree that the previous version did little to critically review the  
37 corresponding literature. To improve in this area, we have expanded and reorganized the  
38 introduction into four sub-sections (“Forests in the global C cycle: current and future”,  
39 “Evolution of forest C cycle research”, “Biome differences”, and “Age trends and their  
40 variation across biomes”). The latter three sections are mostly or entirely new relative to the  
41 previous version, and briefly review the development and current status of the science on  
42 each topic. We have also added a schematic figure (Fig. 1) to summarize current  
43 understanding of each topic and help with conceptual framing of the review. We also shifted  
44 emphasis more towards the ecological questions (trends across biomes and with age), while  
45 retaining (with less emphasis) the analysis of database representativeness.  
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## Referee: 3

COMMENTS TO THE AUTHOR(S)

This paper uses a database recently created and updated by the author team – For C – to understand how forest carbon stocks and pools varies across broad biome classifications (e.g. boreal, temperate, and tropical) and stand age. The find that the rate of C cycling is faster in warmer climates, and that many C fluxes and pools increase with stand age (at least up to 100 years of age).

There were several things I really liked about this paper. First, I applaud the author's ambition in creating (and maintaining) this database, which has already been used in multiple high-profile papers. It is a novel idea to curate all the C fluxes and pools together in one virtual location, and the carbon cycle budgets illustrated in Figures 2-5, and 8-11, will likely function as useful “reality checks” against which both empirical and modeling results can be assessed. I also appreciated the focus on understanding how carbon cycles varies with stand age, as this is an important unknown that limits understanding of the usefulness of reforestation as a natural climate solution (among other unknowns). Overall I found the manuscript to be clearly written.

### Thank you.

However, I also found that many aspects of the paper gave me considerable pause.

First, the paper covers an awful lot of ground. It strikes me that each of the three research questions (bottom of page 4) could easily motivate an entire paper on their own. By attempting to address all three in one (relatively short) manuscript, it is not possible to discuss in any detail the mechanisms and processes that determine the results. There are no process-oriented hypotheses or frameworks against which the results are evaluated.

**We agree that this covers a lot of ground, which corresponds with our vision of producing a comprehensive synthesis of broad trends. We envision that smaller questions can (and hopefully will) be broken off for more detailed analysis in the future.**

**At the same time, we agreed that the manuscript could be improved with more of a conceptual framework.** To improve in this area, we have expanded and reorganized the introduction into four sub-sections (“Forests in the global C cycle: current and future”, “Evolution of forest C cycle research”, “Biome differences”, and “Age trends and their variation across biomes”). The latter three sections are mostly or entirely new relative to the previous version, and briefly review the development and current status of the science on each topic. We have also added a schematic figure (Fig. 1) to summarize current understanding of each topic and help with conceptual framing of the review. We also shifted emphasis more towards the ecological questions (trends across biomes and with age), while retaining (with less emphasis) the analysis of database representativeness.

For example, concerning expectations about how various C cycles and pools vary with stand age? There is a fairly extensive literature on this topic . . . Odum’s classic paper on the topic (“The Strategy of Ecosystem Development, 1969) has been cited thousands of times. But this literature is not referenced or cited in the current manuscript. Odum’s hypothesis suggests that NEP (arguably the most important flux, at least from a climate mitigation perspective) should increase initially with stand age and then eventually decrease as forests continue to mature. However, this framework/literature is not referenced, and the way the results are presented make it difficult to understand whether those expectations were borne out in the data. On that note, I didn’t understand why the authors chose to show flux trends explicitly as a function of age up to 100 years (Figure 6), but then group all the forests >100 years old into a single “bar). Why not plot the mature

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3 forests explicitly on the flux versus age axis? This would allow a clearer assessment of whether flux trends  
4 with age are really linear. It would also help the reader understand better one of the most striking results  
5 from this manuscript: that NEP of mature forests is indistinguishable across biomes. The authors describe  
6 this as unsurprising, but I think it is a bit unexpected, especially given the results of some of the more  
7 synthetic work from FLUXNET (e.g. Luyssaert et al. 2007). The authors explain this result in a couple of  
8 sentences (Page 25, lines 22-26), speculating that the result is driver by “moderate disturbances” or  
9 “disequilibrium of  $R_{soil}$  relative to C inputs). A deeper dive into the results, combined with some mechanistic  
10 grounding, might reveal to what extent this result represents a climate-age interaction that is predicted from  
11 the existing theory.  
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14 We greatly appreciated the suggestion to engage with Odum’s framework. We now cite and  
15 discuss Odum (1969) in the introduction, and designed the age trends portion of the  
16 schematic figure to correspond to Odum’s classic Fig. 1 (updated with more details and  
17 current terminology).

18 Regarding the question of showing flux trends as a function of age beyond 100 years, this  
19 unfortunately doesn’t make sense within the context of the database because tropical forests  
20 can rarely be aged beyond 100 years (if that). This is because tropical trees rarely form  
21 annual rings, which are used to age (older) extratropical forests. It would not make sense to  
22 treat tropical and extra-tropical forests differently.

23 Regarding the NEP result for mature forests, we agree that a better conceptual framework  
24 (now implemented) should help set the stage for explaining this result. We have modified  
25 the discussion paragraph on this to cite the schematic figure and also to note that this result  
26 does agree with Luyssaert *et al* (2007) (although that study did not standardize for age).  
27 The paragraph now reads as follows:

28 “The notable exception to the pattern of fluxes decreasing from tropical to boreal regions is  
29 NEP, which showed no significant differences across biomes (Fig. 6f). Unlike the other C  
30 flux variables, NEP does not characterize the rate at which C cycles through the ecosystem,  
31 but is the balance between C sequestration ( $GPP$ ) and respiratory losses ( $R_{eco}$ ) and  
32 represents net CO<sub>2</sub> sequestration (or release) by the ecosystem (Fig. 1). NEP tends to be  
33 relatively small in mature forest stands (discussed further below), which accumulate carbon  
34 slowly relative to younger stands, if at all (Luyssaert *et al* 2008, Amiro *et al* 2010, Besnard *et*  
35 *al* 2018). It is therefore unsurprising that there are no pronounced differences across biomes  
36 (in agreement with Luyssaert *et al* 2007), suggesting that variation in NEP of mature forests  
37 is controlled less by climate and more by other factors including moderate disturbances  
38 (Curtis and Gough 2018) or disequilibrium of  $R_{soil}$  relative to C inputs (e.g., in peatlands  
39 where anoxic conditions inhibit decomposition; Wilson *et al* 2016).”

40 Finally, I wondered about the interacting effects of changing climate (rising CO<sub>2</sub>, warming temperatures)  
41 and stand age, especially in determining trends in the pools. Mature forests will have experienced a much  
42 wider range of climate conditions than younger stands. How does this complicate the comparison of live  
43 biomass across forest of different age?

44 This is an excellent question, and one that is of great interest to the lead author (e.g.,  
45 Anderson-Teixeira *et al* 2013); however, we think it is unlikely to have much influence at this

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3 relatively coarse scale of analysis, especially given that much of the data in ForC was  
4 collected in the 20th century. Sorting this out would require carefully designed studies, and  
5 probably would not be possible using ForC data at this point.  
6

7 Second, I had some questions about the representativeness of the dataset. While I appreciate that the  
8 authors choose to use distinct geographic areas as the unit of analysis (avoiding some issues of  
9 pseudo-replication from many observations from a single site), I still wondered about the extent to which the  
10 distinct geographic areas were representative of the climate space within each biome. For example, if mean  
11 annual climate versus presentation for all boreal, temperate and tropical locations are shown in a scatterplot  
12 (for example, using reanalysis data), and then mean annual temperature and precipitation of the observations  
13 are shown on top, how much of the “climate space” is covered by the dataset?  
14

15 An analysis of this type would need to be fairly involved, including a separate analysis for  
16 each variable. While do-able (we have previously published a plot similar to that described  
17 for the entire database), such an analysis would only begin to cover important aspects of  
18 representativeness (MAT and MAP, but not seasonality, soils, floristic composition, etc.).  
19 We feel that, in this case, the insights gained from the analysis would not justify the strain  
20 on time and resources that it would require. We have, however, given additional attention to  
21 the issue of representativeness in the revision. Specifically, we have done the following:  
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- 23 • Set the stage for discussion of within-biome variability by including error bars on our  
24 schematic figure (Fig. 1).
- 25 • Ensured that the issue is clearly and transparently presented in the figures—for example,  
26 by adding the following statement to the captions of Figures 3-6 (formerly 2-5): “Note  
27 that variables differ in geographical representation, resulting in potential imbalances  
28 (Figs. S5-S30). Probability that estimates reflect true biome means scales with the  
29 number of distinct geographical areas represented.”
- 30 • Revisited our presentation of representativeness issues in the results and discussion,  
31 revising text to ensure clear communication of the concept that biome differences were  
32 influenced by geographical representation within the biome. For example, our discussion  
33 of stock differences across biome differences now reads: “...For  $B_{tot}$  and  $B_{ag}$ , tropical  
34 broadleaf forests had the highest mean biomass and boreal forests the lowest, with  
35 temperate broadleaf and needleleaf ( $B_{ag}$  only) intermediate. However, maximum values  
36 for stocks including live or standing woody biomass ( $B_{tot}$ ,  $B_{ag}$ ,  $B_{ag-wood}$ ,  $B_{root}$ ,  $B_{root-coarse}$ ,  
37  $DW_{tot}$ ,  $DW_{standing}$ ) consistently occurred in temperate biomes (Figs. 1, 8, S20-S30). For  
38 variables that were disproportionately sampled in such high-biomass forests ( $B_{ag-wood}$ ,  
39  $B_{foliage}$ , and  $B_{root-coarse}$ ; disproportionately sampled in the US Pacific Northwest),  
40 temperate conifer forests had significantly higher stocks than the other biomes.”

41 Third, I found the presentation of the results made it difficult to see clearly the major differences in C fluxes  
42 and pools across biomes and age classes. The illustrated C budgets (the majority of the figures, 8 in total)  
43 are visually very appealing, but the reader has to do a lot of flipping back and forth to see how any  
44 particular flux or pool varies across biomes and age class. Figure 6 is more synthetic, but each panel is very  
45 small and the differences from one group to the next are hard to see. It is also difficult to compare results for  
46 young forests (as scatterplots) with the box plots for the mature forests. My advice is to move some of the  
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3 budgets to SI, and include in the main manuscript more figures that clearly illustrate the most interesting  
4 trends with biome, and to allow an expansion of the results in Figure 6 (for example, by first showing  
5 scatterplots of all forests, young and old, as a function of stand age), and then perhaps another that is a box  
6 plot comparison of mature versus old forests in each biome.  
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9 We have done a major re-arrangement of figures, including the following: (1) added a  
10 schematic figure, somewhat in the style of Odum (1969), to help with conceptual framing of  
11 the review; (2) added a figure synthesizing changes in fluxes through time for each biome;  
12 (3) removed maps from age trend diagrams (maps still available in SI), which makes the  
13 figures less busy/ easier to read; and (4) moved C cycle diagrams for young forests to SI.  
14 The result is that (1) the main manuscript contains only the more informative illustrated C  
15 budgets (mature forests); (2) the figures showing age trends and biome differences in 6 C  
16 flux and stock variables (Figs. 7-8, formerly 6-7) are much easier to read; and (3) the new  
17 figure 9 provides an overall synthesis of results, focusing on the most trusted variables.  
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20 Regarding the suggestion of showing age of old forests as a scatterplot, this is unfortunately  
21 not possible give unknown ages of most mature tropical forests, as explained above.  
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24 A few other comments:

25 Page 6, first paragraph: I wondered about the extent to which filtering the data for “managed” affected the  
26 results. In the Eastern US, for example, its difficult to find any forests on public land that aren’t managed to  
27 some extent (for example, through periodic selective harvests), and many of them regenerated from “planted”  
28 stands back in the 1930s. I would be curious to know if including “managed” forests substantially altered  
29 results.  
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32 The binary age classification (two ages, less than 100 years or greater than 100 years) was difficult to accept,  
33 as forests that are in the 80-100 year age range are often considered to be mature (at least in the temperate  
34 zone). I realize that even with a dataset as rich as For C, data availability will limit stratification into too  
35 many bins. Nonetheless, at least for some measurements, I wonder if it’s possible to consider a greater  
36 number of age classes (for example, young, maturing, and mature).  
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39 We prefer not to separate forests of known age into categories, but rather to represent age as  
40 a continuous variable, when possible. In large part this is motivated by the fact that  
41 appropriate age thresholds for various categories would vary across biomes, given differences  
42 in biomass accumulation rates. While our ideal would be to have no categorical divisions,  
43 unknown stand ages—particularly in the tropics—force us to divide the data into the  
44 categories used here.  
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47 To provide a better representation of age trends, we created new figure 9. Although it does  
48 not break forests into additional age categories, it does address what seems to be at the core  
49 of this concern, which is a concise representation of differences across the full range of stand  
50 ages.  
51

52 The consistency check (e.g. do component fluxes/pools sum to within one standard deviation of the  
53 aggregate flux or pool) seems like it is destined to provide a favorable assessment of the degree of closure so  
54 long as the data within each grouping represent a wide range of natural climatic and soil variability. As long  
55 as the aggregate variable has a large standard deviation, the results are likely guaranteed to be “consistent.”  
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3 It seems this metric would benefit from some simulations (perhaps with artificially generated data) to  
4 understand exactly how poor closure needs to be at the site-level to generate an inconsistent results when  
5 aggregated across sites.  
6

7 We agree that such an analysis would be valuable, but time and resource constraints place it  
8 beyond the scope of what is currently feasible in this already very large analysis. We also  
9 note that the focus is now shifted towards the ecological questions (trends across biomes and  
10 with age), dropping as a main focus the original question on database representativeness and  
11 C cycle closure.  
12

13 We believe that the current consistency check is valuable as a first pass for identifying cases  
14 of extreme mis-matches, and therefore retain it as is. However, we agree that it is not the  
15 ideal test, and that it is not very stringent (given high standard deviations) and have  
16 therefore toned down claims that the budgets are “closed”/“internally consistent”  
17 throughout the manuscript (e.g., removed from abstract). We note that the discussion  
18 already stated that our criteria for closure was relatively loose (and this statement is  
19 unchanged in the revised version): “On the other, however, *ForC* derives data from multiple  
20 heterogeneous sources, and standard deviations within each biome are high; as a result, the  
21 standard for C closure is relatively loose (*c.f.* Houghton 2020).”  
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## 24 Referee: 4 25 26

27 COMMENTS TO THE AUTHOR(S) General: This paper presents the findings of a rather comprehensive  
28 modeling analysis of C fluxes and stocks in the world’s major forest biomes. An important strength of this  
29 work is its reliance on a fairly large empirical data set to calculate a comprehensive suite of fluxes and stocks  
30 to close (or come close) C budgets in these systems. Another unique component of this work is the contrasts  
31 of young vs mature forests in each biome. An important contribution of this work is its highlighting of gaps  
32 in data (e.g., deadwood) and non-random distribution of empirical data (though this, of course is  
33 well-known) and how these factors influence C accounting efforts. Overall, the paper is well written with  
34 beautiful figures and the analyses and data sets are sound. I think this work makes an important and timely  
35 contribution to fields of C cycle science, forest ecology, and ecosystem ecology and is likely to be of interest  
36 to many ERL readers. I have no fundamental concerns with this manuscript. However, in addition to the  
37 detailed comments/suggestions below, I think it would greatly benefit the paper if the authors could include  
38 some discussion of how the forest ecosystems they characterize here compare to the forest ecosystems that  
39 actually exist. The data here represent generally interior forest ecosystems, which of course are incredibly  
40 important. But, work over the last 5 years or so highlights the extent to which forest fragmentation  
41 influences a large proportion of the world’s forests (Haddad et al., 2015). Fragmentation and the creation of  
42 edges has been shown to have important implications for C stocks and fluxes with regional and global  
43 implications (e.g., (Chaplin-Kramer et al., 2015; Remy et al., 2016; Reinmann & Hutyra, 2017; Smith et al.,  
44 2019; Ordway & Asner, 2020; Reinmann et al., 2020: FULL REFS BELOW). Logging and other forms of  
45 management also influence a large proportion of the world’s forests. I am not suggesting this be included in  
46 modeling efforts here, but in placing this work in the broader context of C stocks and fluxes of the world’s  
47 forests I think it would do the scientific community a great service to more explicitly recognize what is being  
48 modeled and perhaps the proportion of the world’s forests these data might represent... even if discussed in a  
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3 qualitative sense.  
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5 Thank you. We have added the following paragraph (citing the references given above) on  
6 representation of forest types in the Discussion section “C variable coverage and budget  
7 closure”:

8 Importantly, *ForC* and the analyses presented here cover the forests that have received  
9 research attention, which are not a representative sample of the world’s existing  
10 forests—geographically or in terms of human impacts (Martin *et al* 2012). Geographically, all  
11 variables are poorly covered in Africa and Siberia (Fig. 1), a common problem in the  
12 carbon-cycle community (Xu and Shang 2016, Schimel *et al* 2015). In terms of human  
13 impacts, research efforts tend to focus on interior forest ecosystems (Martin *et al* 2012),  
14 often in permanently protected areas (e.g., Davies *et al* 2021). Studies of regrowth forests  
15 tend to focus on sites where recurring anthropogenic disturbance is not a confounding factor.  
16 Yet, fragmentation and degradation impact a large and growing proportion of Earth’s forests  
17 (FAO and UNEP 2020). Fragmentation and the creation of edges strongly impacts forest C  
18 cycling (e.g., Chaplin-Kramer *et al* 2015, Remy *et al* 2016, Reinmann and Hutyra 2017,  
19 Smith *et al* 2019, Reinmann *et al* 2020, Ordway and Asner 2020). Partial logging and other  
20 forms of non- stand clearing anthropogenic disturbance also strongly impact forest C cycling  
21 (e.g., Huang and Asner 2010, Piponiot *et al* 2016) but are under-studied (Sist *et al* 2015)  
22 and excluded from this analysis. Fragmented and degraded forests do not fit the idealized  
23 conceptual framework around which this review is structured (Fig. 1), yet their  
24 representation in models, sustainability assessments, and C accounting systems is critical to  
25 accurate accounting of C cycling in Earth’s forests (e.g., Huang and Asner 2010, Reinmann  
26 and Hutyra 2017, Smith *et al* 2019, Piponiot *et al* 2019). Finally, plantation forests account  
27 for approximately 3% of Earth’s forests (FAO and UNEP 2020) but are not included in this  
28 analysis. While it is known that these tend to accumulate biomass faster than naturally  
29 regenerating forests (Anderson *et al* 2006, Bonner *et al* 2013), their global scale C cycling  
30 patterns remain less clearly understood (c.f. Cook-Patton *et al* 2020). Additional research  
31 and synthesis are needed to fill these critical gaps in our understanding of forest C cycling.  
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34 Introduction:  
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37 L81: “exceptions” in sentence twice.  
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39 Fixed.  
40

41 L97: Typo “Since the its most”  
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43 Fixed.  
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45 Methods:  
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47 L144: If there is a non-trivial proportion of the world’s forests (especially in certain biomes) is plantation or  
48 planted forests, does removing such plots from the dataset bias the results of a global modeling product?  
49

50 We have added a statement on plantation forests in the paragraph representation of forest  
51 types: Finally, plantation forests account for approximately 3% of Earth’s forests (FAO and  
52 UNEP 2020) but are not included in this analysis. While it is known that these tend to  
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3 accumulate biomass faster than naturally regenerating forests (Anderson *et al* 2006, Bonner  
4 *et al* 2013), their global scale C cycling patterns remain less clearly understood (c.f.  
5 Cook-Patton *et al* 2020)."

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7 Results:  
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9 L243-245: I think this is per unit forest area, correct? If so, I think it would be helpful to specify that here.  
10 Also, the reader should be referred to Figs 2-5, not just 5, right?

11  
12 Fixed.

13  
14 L270-271: The wording of the sentence "There were sufficient data to model...." Seems a bit awkward.  
15 Should it read "... WHICH were also significant...?"?

16  
17 We have reworded this sentence to read, "Age × biome interactions were also significant for  
18 all ten of these C stock variables (Table S2), with living C stocks tending to accumulate  
19 more rapidly during the early stages of forest regrowth in tropical forests (Figs. 8, S20-S30)."

20  
21 Discussion: You might consider reiterating in the first paragraph of the Discussion section that your findings  
22 indicate that Temperate Broadleaf Forests are actually the most productive forest biome in terms of NEP. I  
23 think this is a surprising finding (we normally think of Tropical forests as being more productive) that  
24 warrants attention.

25  
26 We have added the following sentence to the first paragraph of the discussion: "The notable  
27 exception was mature forest NEP, which, as the difference between GPP and  $R_{eco}$ , was  
28 statistically indistinguishable across biomes (Fig. 7f)." Given that there is no significant  
29 difference among biomes, we prefer not to discuss temperate broadleaf forests as higher.

30  
31 L297: The fact that ForC does not include soil C is important. It is not a flaw in the model or the approach  
32 here, but throughout you discuss C stocks, which many would interpret as being inclusive of soil C. I think  
33 the authors should consider clearly indicating in the Methods section, and perhaps reiterating in the Results  
34 and Discussion, that stocks here are defined as litter layer, biomass, and necromass, but excludes C in soil.

35  
36 We have added the following statement to the methods section: "We did not analyze soil  
37 carbon, which is not a focus of the *ForC* database." We also now note this in the first  
38 paragraph of the discussion "There was also little directional variation in mean mature forest  
39 C stocks (biomass, dead wood, and organic layer) across biomes, although maximum values  
40 for the majority of stocks (all including live or standing woody biomass) occurred in  
41 temperate biomes (Figs. 1, 2-5, 8)."

42  
43 L322-323: As you point out in the Results section, while there are no statistically sig differences in NEP  
44 across biomes, there are large differences in the means. Is this an artifact of the data sources used  
45 (i.e. distribution and number of sites with empirical data)? Can you speak a little more to this point in this  
46 section?

47  
48 We have modified sentences in this paragraph to address this: "The notable exception to the  
49 pattern of fluxes decreasing from tropical to boreal regions is NEP, which showed no  
50 significant differences across biomes, albeit with the highest mean in temperate broadleaf  
51 forests (Fig. 7f). ... The fact that mature temperate broadleaf forests have a higher mean  
52 than the other biomes may reflect the fact that most of these forests are older secondary  
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3 forests that, while classified here as mature, are still accumulating carbon (Curtis and Gough  
4 2018).  
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6 L382: You might consider changing text to “increases with age AT LEAST up to the 100-yr threshold  
7 examined here” so that it does not come across as suggesting that NEP only increases for the first hundred  
8 years of stand development, which we know is not true.  
9

10 Reworded to read, “Notably, net carbon sequestration (NEP) exhibits an overall increase  
11 with age across the first 100 years of stand development...”.  
12

13 L445-450: I come back to the data in Figs 2-5 and text in the results section (L243-245), which indicates no  
14 sig differences in NEP, but highest means in temperate forests. Of course, the high biomass in tropical  
15 forests makes them critical to protect from a C storage perspective, but if NEP (i.e. rates of C sequestration)  
16 are highest, at least as a mean, in temperate broadleaf forests how should those ecosystems factor into  
17 conservation priorities. Related to this point, is the high NEP of temperate forests driven by the relatively  
18 young nature of temperate broadleaf forests in the eastern U.S., where a lot of data exist?  
19

20 This question is now addressed earlier in the discussion (see response to comment on  
21 L322-323). The higher NEP of mature temperate forests contributes to their value for  
22 climate change mitigation, but does not make them more valuable than higher-biomass  
23 tropical forests (for example) that have already sequestered C that would become committed  
24 to eventual release as CO<sub>2</sub> emissions if the forest were to be cleared (with the rapidity of  
25 that release depending on mode of clearing, wood product decay...). That trade-off is  
26 explored to some extent in one of the references given in this paragraph (Anderson-Teixeira  
27 and DeLucia 2011), but seems too complex to get into here.  
28

29 References mentioned above:  
30

- 31 Chaplin-Kramer R., Ramler I., Sharp R., Haddad N. M., Gerber J. S., West P. C., ... King H. (2015).  
32 Degradation in carbon stocks near tropical forest edges. *Nature Communications*, 6, 1–6.  
33 <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.1038%2Fncomms10158&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e44e fe93b78cdd5fc5d11c%7C0%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=maYY3mHl%2F%2FX0jgkAOK5Kc9K1TpaoTVkFM52HsOxeMjU%3D&reserved=0>.  
34 Haddad N. M., Brudvig L. a., Cloibert J., Davies K. F., Gonzalez A., Holt W. M., ... Townshend J. R.  
35 (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, (March),  
36 e1500052. <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.4028%2Fwww.scientific.net%2FAMM.315.108&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e44fe93b78cdd5fc5d11c%7C0%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=1L35xf2RdBj6Y9PjsYhSY5tct4RhnJLE8Jd50QJdzBM%3D&reserved=0>.  
37 Ordway E. M. & Asner G. P. (2020). Carbon declines along tropical forest edges correspond to  
38 heterogeneous effects on canopy structure and function. *Proceedings of the National Academy of Sciences of  
39 the United States of America*, 117(14), 7863–7870.  
40 <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.1073%2Fpnas.191456>

1  
2  
3 420117&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e4  
4 4efe93b78cdd5fc5d11c%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoi  
5 MC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=DnTMc4L  
6 CIoRcHMLUEAcpvNOn%2FeJLO3%2Bh8pXVYSUb%2BI4%3D&reserved=0.  
7  
8

9 Reinmann A. B. & Hutyra L. R. (2017). Edge effects enhance carbon uptake and its vulnerability to climate  
10 change in temperate broadleaf forests. Proceedings of the National Academy of Sciences, 114(1), 107–112.  
11 <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.1073%2Fpnas.1612369114&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e44efe93b78cdd5fc5d11c%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=GncJJ%2FLa2f96c0tjkl5RZZv2JLJFoAoQnOTm0b%2BYyNo%3D&reserved=0>.  
12  
13  
14  
15  
16  
17

18 Reinmann A. B., Smith I. A., Thompson J. R. & Hutyra L. R. (2020). Urbanization and fragmentation  
19 mediate temperate forest carbon cycle response to climate. Environmental Research Letters, 15, 114036.  
20  
21

22 Remy E., Wuyts K., Boeckx P., Ginzburg S., Gundersen P., Demey A., ... Verheyen K. (2016). Strong  
23 gradients in nitrogen and carbon stocks at temperate forest edges. Forest Ecology and Management,  
24 376(2016), 45–58. <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.1016%2Fforeco.2016.05.040&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e44efe93b78cdd5fc5d11c%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=u2ylmC4K4VIxHWamrCnk%2BNfu%2FsZDUkSPfABgfN%2BCzT4%3D&reserved=0>.  
25  
26  
27  
28  
29

30 Smith I. A., Hutyra L. R., Reinmann A. B. & Thompson J. R. (2019). Evidence for Edge Enhancements of  
31 Soil Respiration in Temperate Forests Geophysical Research Letters. Geophysical Research Letters, 46, 1–10.  
32 <https://nam02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.1029%2F2019GL082459&data=04%7C01%7Cteixeirak%40si.edu%7Cd27c53d6ec434c8ae42108d8a03017cf%7C989b5e2a14e44efe93b78cdd5fc5d11c%7C0%7C637435475707545147%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C1000&sdata=92jjRZSUzQrNX6SGIV%2BZRfHIUN%2B6AL96%2FJI4PIK3a8%3D&reserved=0>.  
33  
34  
35  
36  
37  
38

### References

- Amiro B D, Barr A G, Barr J G, Black T A, Bracho R, Brown M, Chen J, Clark K L, Davis K J, Desai A R, Dore S, Engel V, Fuentes J D, Goldstein A H, Goulden M L, Kolb T E, Lavigne M B, Law B E, Margolis H A, Martin T, McCaughey J H, Misson L, Montes-Helu M, Noormets A, Randerson J T, Starr G and Xiao J 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America *J. Geophys. Res.* **115** G00K02
- Anderson K J, Allen A P, Gillooly J F and Brown J H 2006 Temperature-dependence of biomass accumulation rates during secondary succession *Ecology Letters* **9** 673–82
- Anderson-Teixeira K J and DeLucia E H 2011 The greenhouse gas value of ecosystems *Global Change Biology* **17** 425–38
- Anderson-Teixeira K J, Miller A D, Mohan J E, Hudiburg T W, Duval B D and DeLucia E H 2013 Altered dynamics of forest recovery under a changing climate *Global Change Biology* **19** 2001–21
- Badgley G, Anderegg L D L, Berry J A and Field C B 2019 Terrestrial gross primary production: Using NIRV to scale from site to globe *Global Change Biology* **25** 3731–40
- Banbury Morgan B, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau H C and Anderson-Teixeira K J Global patterns of forest autotrophic carbon fluxes *Global Change Biology*
- Besnard S, Carvalhais N, Arain M A, Black A, de Bruin S, Buchmann N, Cescatti A, Chen J, Clevers J G P W, Desai A R, Gough C M, Havrankova K, Herold M, Hörtnagl L, Jung M, Knohl A, Kruijt B, Krupkova L, Law B E, Lindroth A, Noormets A, Roupsard O, Steinbrecher R, Varlagin A, Vincke C and Reichstein M 2018 Quantifying the effect of forest age in annual net forest carbon balance *Environmental Research Letters* **13** 124018
- Bond-Lamberty B and Thomson A 2010 A global database of soil respiration data *Biogeosciences* **7** 1915–26
- Bonner M T L, Schmidt S and Shoo L P 2013 A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations *Forest Ecology and Management* **291** 73–86
- Chaplin-Kramer R, Ramler I, Sharp R, Haddad N, Gerber J, West P, Mandle L, Engstrom P, Baccini A, Sims S, Mueller C and King H 2015 Degradation in carbon stocks near tropical forest edges *Nature Communications* **6**
- Cook-Patton S C, Leavitt S M, Gibbs D, Harris N L, Lister K, Anderson-Teixeira K J, Briggs R D, Chazdon R L, Crowther T W, Ellis P W, Griscom H P, Herrmann V, Holl K D, Houghton R A, Larrosa C, Lomax G, Lucas R, Madsen P, Malhi Y, Paquette A, Parker J D, Paul K, Routh D, Roxburgh S, Saatchi S, van den Hoogen J, Walker W S, Wheeler C E, Wood S A, Xu L and Griscom B W 2020 Mapping carbon accumulation potential from global natural forest regrowth *Nature* **585** 545–50
- Curtis P S and Gough C M 2018 Forest aging, disturbance and the carbon cycle *New Phytologist*
- Davies S J, Abiem I, Abu Salim K, Aguilar S, Allen D, Alonso A, Anderson-Teixeira K, Andrade A, Arellano G, Ashton P S, Baker P J, Baker M E, Baltzer J L, Basset Y, Bissengou P, Bohlman S, Bourg N A, Brockelman W Y, Bunyavejchewin S, Burslem D F R P, Cao M, Cárdenas D, Chang L-W, Chang-Yang C-H, Chao K-J, Chao W-C, Chapman H, Chen Y-Y, Chisholm R A, Chu C, Chuyong G, Clay K, Comita

1  
2  
3 L S, Condit R, Cordell S, Dattaraja H S, de Oliveira A A, den Ouden J, Detto M, Dick C, Du X, Duque  
4 Á, Ediriweera S, Ellis E C, Obiang N L E, Esufali S, Ewango C E N, Fernando E S, Filip J, Fischer G A,  
5 Foster R, Giambelluca T, Giardina C, Gilbert G S, Gonzalez-Akre E, Gunatilleke I A U N, Gunatilleke C  
6 V S, Hao Z, Hau B C H, He F, Ni H, Howe R W, Hubbell S P, Huth A, Inman-Narahari F, Itoh A, Janík  
7 D, Jansen P A, Jiang M, Johnson D J, Jones F A, Kanzaki M, Kenfack D, Kiratiprayoon S, Král K,  
8 Krizel L, Lao S, Larson A J, Li Y, Li X, Litton C M, Liu Y, Liu S, Lum S K Y, Luskin M S, Lutz J A,  
9 Luu H T, Ma K, Makana J-R, Malhi Y, Martin A, McCarthy C, McMahon S M, McShea W J, Memiaghe  
10 H, Mi X, Mitre D, Mohamad M, et al 2021 ForestGEO: Understanding forest diversity and dynamics  
11 through a global observatory network *Biological Conservation* **253** 108907

12  
13 FAO and UNEP 2020 *The State of the World's Forests 2020: Forests, biodiversity and people* (Rome, Italy:  
14 FAO and UNEP)

15 Gillman L N, Wright S D, Cusens J, McBride P D, Malhi Y and Whittaker R J 2015 Latitude, productivity  
16 and species richness *Global Ecology and Biogeography* **24** 107–17

17 Houghton R A 2020 Terrestrial fluxes of carbon in GCP carbon budgets *Global Change Biology* **26** 3006–14

18 Huang M and Asner G P 2010 Long-term carbon loss and recovery following selective logging in Amazon  
19 forests *Global Biogeochemical Cycles* **24**

20 Jian J, Vargas R, Anderson-Teixeira K, Stell E, Herrmann V, Horn M, Kholod N, Manzon J, Marchesi R,  
21 Paredes D and Bond-Lamberty B 2020 *A restructured and updated global soil respiration database*  
22 (*SRDB-V5*) (Data, Algorithms, and Models)

23 Li X and Xiao J 2019 Mapping Photosynthesis Solely from Solar-Induced Chlorophyll Fluorescence: A Global,  
24 Fine-Resolution Dataset of Gross Primary Production Derived from OCO-2 *Remote Sensing* **11** 2563

25 Luyssaert S, Inglima I, Jung M, Richardson A D, Reichstein M, Papale D, Piao S L, Schulze E-D, Wingate L,  
26 Matteucci G, Aragao L, Aubinet M, Beer C, Bernhofer C, Black K G, Bonal D, Bonnefond J-M,  
27 Chambers J, Ciais P, Cook B, Davis K J, Dolman A J, Gielen B, Goulden M, Grace J, Granier A, Grelle  
28 A, Griffis T, Grünwald T, Guidolotti G, Hanson P J, Harding R, Hollinger D Y, Hutyra L R, Kolari P,  
29 Kruijt B, Kutsch W, Lagergren F, Laurila T, Law B E, Maire G L, Lindroth A, Loustau D, Malhi Y,  
30 Mateus J, Migliavacca M, Misson L, Montagnani L, Moncrieff J, Moors E, Munger J W, Nikinmaa E,  
31 Ollinger S V, Pita G, Rebmann C, Roupsard O, Saigusa N, Sanz M J, Seufert G, Sierra C, Smith M-L,  
32 Tang J, Valentini R, Vesala T and Janssens I A 2007 CO<sub>2</sub> balance of boreal, temperate, and tropical  
33 forests derived from a global database *Global Change Biology* **13** 2509–37

34 Luyssaert S, Schulze E D, Borner A, Knohl A, Hessenmoller D, Law B E, Ciais P and Grace J 2008  
35 Old-growth forests as global carbon sinks *Nature* **455** 213

36 Martin L J, Blossey B and Ellis E 2012 Mapping where ecologists work: Biases in the global distribution of  
37 terrestrial ecological observations *Frontiers in Ecology and the Environment* **10** 195–201

38 Odum E 1969 The strategy of ecosystem development *Science* **164** 262–70

39 Ordway E M and Asner G P 2020 Carbon declines along tropical forest edges correspond to heterogeneous  
40 effects on canopy structure and function *Proceedings of the National Academy of Sciences* **117** 7863–70

41 Pastorello G, Trotta C, Canfora E, Chu H, Christianson D, Cheah Y-W, Poindexter C, Chen J, Elbashandy  
42

A, Humphrey M, Isaac P, Polidori D, Ribeca A, van Ingen C, Zhang L, Amiro B, Ammann C, Arain M A, Ardö J, Arkebauer T, Arndt S K, Arriga N, Aubinet M, Aurela M, Baldocchi D, Barr A, Beamesderfer E, Marchesini L B, Bergeron O, Beringer J, Bernhofer C, Berveiller D, Billesbach D, Black T A, Blanken P D, Bohrer G, Boike J, Bolstad P V, Bonal D, Bonnefond J-M, Bowling D R, Bracho R, Brodeur J, Brümmer C, Buchmann N, Burban B, Burns S P, Buysse P, Cale P, Cavagna M, Cellier P, Chen S, Chini I, Christensen T R, Cleverly J, Collalti A, Consalvo C, Cook B D, Cook D, Coursolle C, Cremonese E, Curtis P S, D'Andrea E, da Rocha H, Dai X, Davis K J, De Cinti B, de Grandcourt A, De Ligne A, De Oliveira R C, Delpierre N, Desai A R, Di Bella C M, di Tommasi P, Dolman H, Domingo F, Dong G, Dore S, Duce P, Dufrêne E, Dunn A, Dušek J, Eamus D, Eichelmann U, ElKhidir H A M, Eugster W, Ewenz C M, Ewers B, Famulari D, Fares S, Feigenwinter I, Feitz A, Fenstolt R, Filippa G, Fischer M, Frank J, Galvagno M, Gharun M, et al 2020 The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data *Scientific Data* **7** 225

Piponiot C, Rödig E, Putz F E, Rutishauser E, Sist P, Ascarrunz N, Blanc L, Derroire G, Descroix L, Guedes M C, Coronado E H, Huth A, Kanashiro M, Licona J C, Mazzei L, d'Oliveira M V N, Peña-Claros M, Rodney K, Shenkin A, Souza C R de, Vidal E, West T A P, Wortel V and Hérault B 2019 Can timber provision from Amazonian production forests be sustainable? *Environmental Research Letters* **14** 064014

Piponiot C, Sist P, Mazzei L, Peña-Claros M, Putz F E, Rutishauser E, Shenkin A, Ascarrunz N, de Azevedo C P, Baraloto C, França M, Guedes M, Honorio Coronado E N, d'Oliveira M V, Ruschel A R, da Silva K E, Doff Sotta E, de Souza C R, Vidal E, West T A and Hérault B 2016 Carbon recovery dynamics following disturbance by selective logging in Amazonian forests *eLife* **5** e21394

Reinmann A B and Hutyra L R 2017 Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests *Proceedings of the National Academy of Sciences* **114** 107–12

Reinmann A B, Smith I A, Thompson J R and Hutyra L R 2020 Urbanization and fragmentation mediate temperate forest carbon cycle response to climate *Environmental Research Letters* **15** 114036

Remy E, Wyts K, Boeckx P, Ginzburg S, Gundersen P, Demey A, Van Den Bulcke J, Van Acker J and Verheyen K 2016 Strong gradients in nitrogen and carbon stocks at temperate forest edges *Forest Ecology and Management* **376** 45–58

Schimel D, Stephens B B and Fisher J B 2015 Effect of increasing CO<sub>2</sub> on the terrestrial carbon cycle *Proceedings of the National Academy of Sciences* **112** 436–41

Sist P, Rutishauser E, Peña-Claros M, Shenkin A, Hérault B, Blanc L, Baraloto C, Baya F, Benedet F, Silva K E da, Descroix L, Ferreira J N, Gourlet-Fleury S, Guedes M C, Harun I B, Jalonan R, Kanashiro M, Krisnawati H, Kshatriya M, Lincoln P, Mazzei L, Medjibé V, Nasi R, d'Oliveira M V N, Oliveira L C de, Picard N, Pietsch S, Pinard M, Priyadi H, Putz F E, Rodney K, Rossi V, Roopsind A, Ruschel A R, Shari N H Z, Souza C R de, Susanty F H, Sotta E D, Toledo M, Vidal E, West T A P, Wortel V and Yamada T 2015 The Tropical managed Forests Observatory: A research network addressing the future of tropical logged forests *Applied Vegetation Science* **18** 171–4

Smith I A, Hutyra L R, Reinmann A B, Thompson J R and Allen D W 2019 Evidence for Edge Enhancements of Soil Respiration in Temperate Forests *Geophysical Research Letters* **46** 4278–87

Wilson R M, Hopple A M, Tfaily M M, Sebestyen S D, Schadt C W, Pfeifer-Meister L, Medvedeff C, McFarlane K J, Kostka J E, Kolton M, Kolka R K, Kluber L A, Keller J K, Guilderson T P, Griffiths N

1  
2  
3 A, Chanton J P, Bridgham S D and Hanson P J 2016 Stability of peatland carbon to rising temperatures  
4 *Nature Communications* **7** 13723  
5

6 Xu M and Shang H 2016 Contribution of soil respiration to the global carbon equation *Journal of Plant*  
7 *Physiology* **203** 16–28  
8  
9  
10  
11  
12  
13  
14  
15  
16  
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