Environ. Res. Lett. 16 (2021) 053009
https://doi.org/10.1088/1748-9326/abed01

Environmental Research Letters

Topical Review

Carbon cycling in mature and regrowth forests globally

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Keywords: forest ecosystems, carbon cycle, stand age, productivity, respiration, biomass, global

Abstract

Forests are major components of the global carbon (C) cycle and thereby strongly influence atmospheric carbon dioxide (CO2) and climate. However, efforts to incorporate forests into climate models and CO2 accounting frameworks have been constrained by a lack of accessible, global-scale synthesis on how C cycling varies across forest types and stand ages. 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 11 923 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 means and standard deviations for both mature and regrowth (age < 100 years) forests and quantify trends with stand age for all variables with sufficient data. C cycling rates generally decreased from tropical to temperate to boreal in both mature and regrowth forests, whereas C stocks showed less directional variation. Mature forest net ecosystem production did not differ significantly among biomes. The majority of flux variables, together with most live biomass pools, increased significantly with the logarithm of stand age. 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 contributes to these efforts.

1. Background

Forest ecosystems are shaping the course of climate change through their influence on atmospheric carbon dioxide, CO2 (Bonan 2008, IPCC 2018, Friedlingstein et al 2019). Despite the centrality of forest carbon (C) cycling in regulating atmospheric CO2, gaps in our understanding of how C cycling varies across forest types and in relation to stand history underlie important uncertainties in climate models (Friedlingstein et al 2006, Krause et al 2018, Bonan et al 2019, Di Vittorio et al 2020) and CO2 accounting frameworks (Pan et al 2011, IPCC 2019). Improved understanding of forest C cycling globally require accessible, comprehensive, and large-scale databases with worldwide 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 (Luo et al 2012, Clark et al 2017, Fer et al 2021), quantifying the role of forests in the global C cycle (e.g. Pan et al 2011, Harris et al 2021), and using
book-keeping methods to quantify actual or potential exchanges of CO₂ between forests and the atmosphere (Griscom et al. 2017, Houghton 2020).

1.1. 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⁻¹ (Badgley et al. 2019). Most of this enormous C uptake is counterbalanced by releases to the atmosphere through ecosystem respiration (Rₑₑₑ), and fire. In recent years, total forest C uptake has exceeded releases, such that forests globally have been a C sink (Harris et al. 2021). This C sink has averaged 3.2 ± 0.6 Gt C yr⁻¹ for 2009–2018, offsetting 29% of anthropogenic fossil fuel emissions, when considering only areas remaining forested (Friedlingstein et al. 2019). However, deforestation, estimated at ~1 Gt C yr⁻¹ in recent decades (Pan et al. 2011, Tubiello et al. 2020), reduces the net forest sink to ~1.1–2.2 Gt C yr⁻¹ (Friedlingstein et al. 2019, Harris et al. 2021). Understanding, modeling, and managing forest-atmosphere CO₂ exchange is central to mitigating climate change (Cavaleri et al. 2015, Grassi et al. 2017, Griscom et al. 2017).

The future of the current forest C sink is dependent both upon forest responses to climate change and human land use decisions, with land use change itself strongly influencing the course of climate change (Friedlingstein et al. 2006). Regrowing forests (i.e. secondary forests) will play a particularly 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 a 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), there is a relative dearth of data and synthesis on other C stocks and fluxes in secondary forests. Understanding age-related trends in forest C cycling 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).

1.2. 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 among biomes (e.g. Lieth 1973, Luyssaert et al. 2007) and with stand age (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, along with appropriate measurement methods (e.g. Clark et al. 2001, Chapin et al. 2006). New technology has also enabled researchers to directly measure an expanding set of variables, notably including continuous measurements of soil CO₂ efflux (Kuziyakov 2006) and ecosystem-atmosphere CO₂ exchange (Baldocchi et al. 2001). Measurement techniques have been increasingly standardized, such as 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, including aboveground biomass (Bag, Saatchi et al. 2011, Hu et al. 2016, Spawn et al. 2020) and GPP (Li and Xiao 2019). Yet, measurement and validation of most forest C stocks and fluxes 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 questions at a global scale, researchers began synthesizing data into increasingly large databases (e.g. Lieth 1973, Luysaert 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 39 762 records from 10 608 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.

1.3. Biome differences
Forest C cycling varies enormously across biomes, categories that encapsulate major differences in
climate and vegetation. The dominant role of climate in shaping global variation among forests has been recognized since the early 19th century (Humboldt and Bonpland 1807, Holdridge 1947). Global scale data syntheses have shown that C fluxes including GPP, net primary productivity (NPP), and soil respiration ($R_{\text{soil}}$) decrease with latitude or, correspondingly, increase with mean annual temperature (figure 1(a); e.g. Lieth 1973, Luyssaert et al 2007, Hursh et al 2017, Banbury Morgan et al 2021). C stocks of mature forests show less directional variation (figure 1(c)). On average, aboveground biomass ($B_{\text{ag}}$) tends to decrease with latitude, but not as dramatically as fluxes, and with the highest biomass forests in relatively cool, moist temperate regions (Smithwick et al 2002, Keith et al 2009, Hu et al 2016). In contrast, standing and downed dead wood ($D_{\text{standing}}$ and $D_{\text{down}}$ respectively, summing to $D_{\text{tot}}$) 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).

Phenomenological analyses relating C stocks and fluxes 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 (e.g. Warner et al 2019, Cook-Patton et al 2020). The resulting models enable construction of fine-scale global maps of estimated C cycling variables. This approach can be particularly effective when it integrates satellite measurements that correlate with 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 model $B_{\text{ag}}$ at regional to global scales (e.g. Saatchi et al 2011, Hu et al 2016). However, all such analyses are ultimately constrained by the quality and coverage of ground-based estimates of forest C fluxes or stocks to train models (e.g. Schepaschenko et al 2019). While estimates of some variables (e.g. $B_{\text{ag}}$, GPP, NPP, $R_{\text{soil}}$) are widely available, many remain poorly characterized (e.g. $D_{\text{tot}}$; OL; autotrophic respiration, $R_{\text{auto}}$), even at the coarse resolution of biomes. This is a critical limitation for understanding forest C cycling and quantifying forest-based climate change mitigation potential across forest biomes or ecoregions (e.g. IPCC 2019).

1.4. Age trends and their variation across biomes

Stand age is another important axis of variation in forest C cycling (figures 1(b) and (d)). 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 (figure 1(b), Anderson-Teixeira et al 2013). Following stand-clearing disturbance, GPP, NPP, and biomass of leaves ($B_{\text{foliage}}$) and fine roots ($B_{\text{root−fine}}$) initially increase rapidly and thereafter remain relatively stable ($B_{\text{foliage}}$, $B_{\text{root−fine}}$, 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 $R_{\text{auto}}$ increases relative to GPP as forests age, corresponding to declining carbon use efficiency with stand age (DeLucia et al 2007, Collalti et al 2020). Heterotrophic respiration, most of which originates from the soil ($R_{\text{het−soil}}$), remains relatively constant with stand age (Law et al 2003, Pregitzer and Euskirchen 2004, Goulden et al 2011). As a result, net ecosystem production (NEP = GPP $− R_{\text{eco}}$, where $R_{\text{eco}}$ is total ecosystem respiration) is initially negative, increases to a maximum at intermediate ages, and thereafter declines—typically to a small positive value (Law et al 2003, Pregitzer and Euskirchen 2004, Luyssaert et al 2008, Amiro et al 2010, Goulden et al 2011). The result is that biomass accumulation is rapid in young forests, followed by a slow decline to near zero in old forests (e.g. Lichstein et al 2009, Yang et al 2011). While these trends have been the subject of fairly recent qualitative review (Anderson-Teixeira et al 2013), there is need for a synthetic, quantitative review taking advantage of the greatly expanded data now available.

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). 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, a concrete understanding of age trends in C fluxes and stocks and how these vary across biomes is critical to better understanding 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 quantifying the value
of regrowth forests for climate change mitigation (Anderson-Teixeira and DeLucia 2011, Goldstein et al 2020).

Here, we conduct a data-based review of carbon cycling from a stand to global level, and by biome and stand age, using our open-source Global Carbon Forest database (ForC; figure 2). Our goal is to provide a comprehensive synthesis on broad trends in forest C cycling that can serve as a foundation for improved understanding of global forest C cycling and highlight where key sources of uncertainty still reside.

2. Methods and design

This review synthesizes data from the ForC database (figure 2, https://github.com/forc-db/ForC, Anderson-Teixeira et al 2016, 2018). ForC amalgamates numerous intermediary data sets (e.g. Luysaert et al 2007, Bond-Lamberty and Thomson 2010, Cook-Patton et al 2020) and original studies. Original publications were referenced to check values and obtain information not contained in intermediary data sets, although this process has not been completed for all records. The database was developed with goals of understanding how C cycling in forests varies across broad geographic scales and as a function of stand age. As such, there has been a focus on incorporating data from regrowth forests (e.g. Anderson et al 2006, Bonner et al 2013, Martin et al 2013) and obtaining stand age data when possible (83% of records in ForC v2.0, 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 Soil Respiration Database (SRDB v4, 9488 records, Bond-Lamberty and Thomson 2010), with corrections and improvements to SRDB arising
from this process incorporated into SRDB v5 (Jian et al. 2020). Second, we imported (via R script) the Global Reforestation Opportunity Assessment database (GROA v1.0, 10116 records, Anderson-Teixeira et al. 2020, Cook-Patton 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 (available online at stacks.iop.org/ERL/16/053009/mmedia)). Third, we 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). We have also added data from individual publications, focusing on productivity (e.g. Taylor et al. 2017), dead wood, and ForestGEO sites (e.g. Johnson et al. 2018, Lutz 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. 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: 10.5281/zenodo.4571538).

All measurements originally expressed in units of dry organic matter (OM) were converted to units of C using the IPCC default of $C = 0.47 \times OM$ (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$_2$, 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 ($R_{het-ag}$) and total heterotrophic respiration ($R_{het}$), 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 specific variables from ForC into more broadly defined variables. Specifically, net ecosystem exchange (measured by Eddy-covariance, Baldocci et al. 2001) and biometric estimates of NEP were combined into the single variable NEP (table 1). Furthermore, for
Table 1. Carbon cycle variables included in this analysis, their sample sizes, and summary of biome differences and age trends.

| Variable                  | Description                                                                 | Records | Plots | Geographic areas | Biome differences | Age trend |
|---------------------------|-----------------------------------------------------------------------------|---------|-------|------------------|-------------------|-----------|
| **Annual fluxes**         |                                                                             |         |       |                  |                   |           |
| NEP                       | Net ecosystem production or net ecosystem exchange (+ indicates C sink)       | 329     | 146   | 88               | N.s.             | +; xB     |
| GPP                       | Gross primary production (NPP + $R_{auto}$ or NEP + $R_{eco}$)              | 303     | 115   | 84               | TrB > TeB ≥ TeN ≥ BoN | +; xB   |
| NPP                       | Net primary production (ANPP + BNPP)                                        | 214     | 112   | 74               | TrB > TeB ≥ TeN > BoN | N.s.    |
| ANPP                      | Aboveground NPP                                                            | 343     | 236   | 131              | TrB > TeB ≥ TeN > BoN | +; xB   |
| ANPPwoody                | Woody production (ANPP$_{stem}$ + ANPP$_{branch}$)                          | 64      | 53    | 37               | N.s.             | +        |
| ANPP$_{stem}$            | Woody stem production                                                      | 217     | 190   | 117              | TrB > TeN ≥ TeB ≥ BoN | N.s.    |
| ANPP$_{branch}$          | Branch turnover                                                            | 69      | 59    | 42               | TrB > TeN ≥ TeN   | N.s.     |
| ANPP$_{folioage}$        | Foliage production, typically estimated as annual leaf litterfall          | 162     | 132   | 88               | TrB > TeN ≥ TeB ≥ BoN | +        |
| ANPP$_{litterfall}$      | Litterfall, including leaves, reproductive structures, twigs, and sometimes branches | 82      | 70    | 55               | N.s.             | +        |
| ANPP$_{repro}$           | Production of reproductive structures (flowers, fruits, seeds)             | 51      | 44    | 34               | N.t.             | N.t.     |
| ANPP$_{folivory}$        | Foliar biomass consumed by folivores                                       | 20      | 12    | 11               | N.t.             | N.t.     |
| $M_{woody}$              | Woody mortality—i.e. $B_{ag}$ of trees that die                            | 18      | 18    | 18               | N.t.             | N.t.     |
| BNPP                     | Belowground NPP (BNPP$_{coarse}$ + BNPP$_{fine}$)                          | 148     | 116   | 79               | TrB > TeN ≥ TeB ≥ BoN | +        |
| BNPP$_{coarse}$          | Coarse root production                                                     | 77      | 56    | 36               | TeN ≥ TrB        | N.s.     |
| BNPP$_{fine}$            | Fine root production                                                       | 123     | 99    | 66               | N.s.             | +        |
| $R_{co}$                 | Ecosystem respiration ($R_{auto}$ + $R_{het}$)                              | 213     | 98    | 70               | TrB > TeB ≥ TeN  | +        |
| $R_{auto}$               | Autotrophic respiration ($R_{auto-ag}$ + $R_{root}$)                       | 24      | 23    | 15               | N.t.             | N.t.     |
| $R_{auto-ag}$            | Aboveground autotrophic respiration (i.e. leaves and stems)                | 2       | 2     | 1                | N.t.             | N.t.     |
| $R_{root}$               | Root respiration                                                           | 181     | 139   | 95               | TrB ≥ TeB        | +        |
| $R_{soil}$               | Soil respiration ($R_{het-soil}$ + $R_{root}$)                             | 627     | 411   | 229              | TrB > TeB ≥ TeN > BoN | N.s.   |
| $R_{het-soil}$           | Soil heterotrophic respiration                                             | 197     | 156   | 100              | TrB > TeB ≥ TeN  | N.s.     |
| $R_{het-ag}$             | Aboveground heterotrophic respiration                                      | 0       | 0     | 0                | —                | —        |
| $R_{het}$                | Heterotrophic respiration ($R_{het-ag}$ + $R_{het-soil}$)                  | 0       | 0     | 0                | —                | —        |
Table 1. (Continued.)

| Variable | Description                                                                 | Records | Plots | Geographic areas | Biome differences\(^a\) | Age trend\(^b\) |
|----------|-----------------------------------------------------------------------------|---------|-------|------------------|--------------------------|-----------------|
| **Stocks** |                                                                             |         |       |                  |                          |                 |
| \(B_{\text{tot}}\) | Total live biomass \((B_{\text{ag}} + B_{\text{root}})\) | 188     | 157   | 87               | TeB \(\geq\) TeB \(\geq\) BoN | \(\cdash\) xB  |
| \(B_{\text{ag}}\) | Aboveground live biomass \((B_{\text{ag,wood}} + B_{\text{foliage}})\) | 4466    | 4072  | 621              | TeB \(\geq\) TeN \(\geq\) TeB \(\geq\) BoN | \(\cdash\) xB  |
| \(B_{\text{ag,wood}}\) | Woody component of aboveground biomass | 115     | 102   | 64               | TeN \(\geq\) TeB \(\geq\) BoN | \(\cdash\) xB  |
| \(B_{\text{foliage}}\) | Foliage biomass | 134     | 115   | 72               | TeN \(\geq\) TeB \(\geq\) BoN \(\geq\) TeB | \(\cdash\) xB  |
| \(B_{\text{root}}\) | Total root biomass \((B_{\text{root,coarse}} + B_{\text{root,fine}})\) | 2329    | 2298  | 360              | N.s. | \(\cdash\) xB  |
| \(B_{\text{root,coarse}}\) | Coarse root biomass | 134     | 120   | 73               | TeN \(\geq\) TeB \(\geq\) BoN | \(\cdash\) xB  |
| \(B_{\text{root,fine}}\) | Fine root biomass | 226     | 180   | 109              | N.s. | \(\cdash\) xB  |
| \(DW_{\text{tot}}\) | Deadwood \((DW_{\text{standing}} + DW_{\text{down}})\) | 79      | 73    | 42               | N.t. | \(\cdash\) xB  |
| \(DW_{\text{standing}}\) | Standing dead wood | 36      | 35    | 22               | N.t. | \(\cdash\) xB  |
| \(DW_{\text{down}}\) | Fallen dead wood, including coarse and sometimes fine woody debris | 278     | 265   | 37               | N.t. | \(\cdash\) xB  |
| OL | Organic layer/litter/forest floor | 474     | 413   | 115              | N.s. | \(\cdash\) xB  |

\(^a\)TrB: tropical, TeB: temperate broadleaf, TeN: temperate needleleaf, BoN: boreal, n.s.: no significant differences, n.t.: not tested
\(^b\)\(+\) or \(-\): significant positive or negative trend, xB: significant age \(\times\) biome interaction, n.s.: no significant age trend, n.t.: not tested.
NPP, aboveground NPP (ANPP), and the litterfall component of ANPP (ANPP_{litterfall}), we combined ForC variables specifying inclusion or exclusion of minor components (e.g. measurements including or excluding fruit production, 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 threshold of 10 cm or less. All records were based on ground-based field measurements.

We grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). The climate component of the biome definitions (figure 2) was 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). Forests in dry (B) and polar (E) Köppen–Geiger zones were excluded from the analysis. We distinguished broadleaf and needle leaf forests based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYMAP, 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 needle leaf forests in the tropics. We classified forests as ‘young’ if stand age was less than 100 years, or ‘mature’ if stand age was older or if they were described as ‘mature,’ ‘old growth,’ ‘intact,’ or ‘undisturbed’ in the original publication. Assigning stands to these groupings required excluding records for which ForC lacked geographic coordinates (0.4% of sites in the full database) or records of stand age or forest maturity (5.7% of records in the full database). We also excluded records with stand age of zero years (0.8% of records in full database). In total, our analysis retained 11,923 records. Numbers of records by biome and age class are provided in table S1.

We calculated the means and standard deviations of each mature forest C cycle variable by biome over geographically distinct areas to produce biome-specific schematics. We first defined relationships among variables (e.g. 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 the means of component variables summed to within one standard deviation of the mean 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 a fixed effect and plot nested within geographic area as random effects on the intercept. When biome had a significant effect, we used Tukey’s pairwise comparison to see which biomes were significantly different from one another. This analysis was run for variables and biomes with records for at least seven distinct geographic areas per biome (table 1).

To test for age trends in young (<100 years) 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 and biomes with records for at least three distinct geographic areas per biome, excluding any biomes that failed this criterion (table 1). When the effect of stand age was significant at p ≤ 0.05, and when each biome had records for stands of at least ten different ages, a biome × 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, particularly for NEP (figure 1(b)); however, data limitations did not support fitting of functions with more parameters or reliable comparisons of different functional forms. Within the data constraints, we deemed a logarithmic function to be the appropriate functional form for most 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 R C 2020).

3. Review results and synthesis

3.1. Data coverage

Of the 39,762 records in ForC v3.0, 11,923 met our strict criteria for inclusion in this study (figure 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 (figures 3–6 and S1–S4), ForC contained sufficient mature forest data for inclusion in our statistical
analyses (i.e. records from ≥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 years), ForC contained sufficient data for inclusion in our statistical analyses (i.e. records from ≥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.

3.2. C cycling in mature forests
Average C cycles for mature tropical broadleaf, temperate broadleaf, temperate conifer, and boreal forests 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 ≥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 ($B_{\text{root}}$) was less than the combined average value of coarse and fine root biomass ($B_{\text{root}}-\text{coarse}$ and $B_{\text{root}}-\text{fine}$, respectively). This lack of closure was driven by very high estimates of $B_{\text{root}}-\text{coarse}$ from high-biomass forests of the US Pacific Northwest, a geographic region with a disproportionately large number of records for this variable (figure S25).

There were sufficient data to assess differences among biomes in mature forest values for 15 flux variables, and 12 of these variables exhibited statistically significant differences among biomes (table 1). In all cases of significant differences (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, figures 7 and S5–S19). Differences between tropical and boreal forests were consistently 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. For two of the variables without significant differences among biomes (ANPP_litterfall and BNPP_litter; figures S12 and S15, 9

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 ± std over geographically distinct areas (clusters of plots within 25 km of each other). 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 data availability (figures S5–S30). Mature forests are defined as ≥100 years old and with no known major natural or anthropogenic disturbance in that time.
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 ± std over geographically distinct areas (clusters of plots within 25 km of each other). 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 data availability (figures S5–S30). Mature forests are defined as ≥100 years old and with no known major natural or anthropogenic disturbance in that time.

respectively), the same general trends applied but were not statistically significant.

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 (figures 7 and S5). For all biomes, NEP was positive, with 95% confidence intervals excluding zero. BNPP$\text{root-coarse}$ also exhibited significant differences among biomes with the highest means outside the tropics, in this case in temperate conifer forest, a biome for which all records came from high-biomass forests in the US Pacific Northwest (EPP$\text{tot}$; differences significant in mixed effects model but not in post-hoc pairwise comparison).

Biome differences were less consistent across C stocks than fluxes (figures 8 and 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 ($B_{\text{tot}}$, $B_{\text{ag}}$, $B_{\text{ag-wood}}$, $B_{\text{root}}$, $B_{\text{root-coarse}}$; table 1). For $B_{\text{tot}}$ and $B_{\text{ag}}$, 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 $B_{\text{tot}}$ analysis because of insufficient data; figures S20 and S21). However, maximum values for these variables—along with all other stocks including live or standing woody biomass ($B_{\text{ag-wood}}$, $B_{\text{root}}$), $B_{\text{root-coarse}}$, $D W_{\text{tot}}$, $D W_{\text{standing}}$—consistently occurred in temperate biomes (figures 1(c), 8 and S20–S30). For variables for which temperate conifer forest records were disproportionately from high-biomass forests in the US Pacific Northwest ($B_{\text{ag-wood}}$, $B_{\text{foliage}}$, and $B_{\text{root-coarse}}$), temperate conifer forests had significantly higher stocks than other biomes.

3.3. C cycling in young forests

C fluxes commonly increased significantly with stand age (tables 1 and S2, figures 7, 9 and S5–S30). For $C$ contained 16 C flux variables with sufficient data to analyze age trends in young forests (see methods). Of these, ten increased significantly with log10(age): NEP, GPP, ANPP, ANPP$\text{woody}$, ANPP$\text{foliage}$, ANPP$\text{litterfall}$, BNPP, BNPP$\text{fine}$, $R_{\text{eco}}$, and $R_{\text{root}}$. The remaining six—NPP, ANPP$\text{stem}$, ANPP$\text{branch}$, BNPP$\text{coarse}$, $R_{\text{soil}}$, and $R_{\text{het-soil}}$—displayed no significant relationship to stand age.

Differences among biomes in regrowth forest $C$ fluxes typically paralleled those observed for mature forests, with $C$ cycling generally most rapid in the tropics and slowest in boreal forests (table 1, figures 7
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\(^{-1}\)). Presented are mean ± std over geographically distinct areas (clusters of plots within 25 km of each other). 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 data availability (figures S5–S30). Mature forests are defined as ⩾100 years old and with no known major natural or anthropogenic disturbance in that time. 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.

and S5–S30). The single exception was ANPP\(_{stem}\), 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 (figure 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 were less successful for young than mature forests (figure 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 \(CO_2\) efflux (respiration) portion of the budget (negative values in figure 9). In contrast, the \(CO_2\) 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\(^{-1}\) yr\(^{-1}\)). 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 (figure 9). Although age trends of young forests often converged towards mature forest averages, there were some discrepancies, most notably including a tendency for higher fluxes in regrowth boreal forests than in their mature counterparts (figures 7, 9 and S5–S30).

In terms of C stocks, ten variables (all but standing deadwood, DW\(_{standing}\) ) had sufficient data to test for age trends (table 1, figures 8 and S20–S30). All of these displayed a significant overall increase with the logarithm of 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 (figures 8, 9 and 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 in tropical forests (figures 8, 9 and S20–S30). Similarly, OL declined slightly with age in temperate broadleaf forests, contrasting an increase in the other three biomes (figures 8, 9 and 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 (figure 9).

4. 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 decreased from tropical to boreal climates in both mature and regrowth forests (figures 1 and 7–9). In contrast, mature forest C stocks (biomass, dead wood, and organic layer) and NEP, which are defined by the differences between in- and out-fluxes, exhibited little systematic variation across biomes (figures 1, 3–6 and 8). Consistent with theory and previous studies (figures 1(b) and (d)), the majority of autotrophic C fluxes, together with most live biomass pools, increased significantly with stand age (table 1; figures 7–9 and S5–S30). 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 (figure 9).

4.1. C cycling across biomes

Our analysis revealed that 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 both regrowth and mature forests (figures 1(a) and 7–9). For mature forests, this is consistent with a large body of previous work demonstrating that C fluxes generally decline with latitude and 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. 2021). 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 aligning with theoretical expectations (figure 1(a)), is novel to this analysis (but see Banbury Morgan et al. 2021 for nine autotrophic fluxes).

The notable exception to the pattern of fluxes decreasing from tropical to boreal regions was NEP (the difference between GPP and \( R_{\text{eco}} \)), which showed no significant differences across biomes, albeit with the highest mean in temperate broadleaf forests (figure 7(f)). 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 $R_{eco}$ represents net CO$_2$ sequestration (or release) by the ecosystem. NEP tends to be relatively small in mature forest stands, which accumulate carbon slowly relative to younger stands, if at all (figures 1(a) and (b), Luysaert et al 2008, Amiro et al 2010, Besnard et al 2018). The lack of pronounced differences across biomes is therefore consistent with both theory and previous research (e.g. Luysaert et al 2007). 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 $R_{soil}$ 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; figures 7 and 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 (figures 8(a) and 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$_{tot}$, OL, and soil C (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

![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. The scatterplots show age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of log10(age) and biome. The fitted lines indicate the effect of age (solid lines: significant at $p < 0.05$, dashed lines: non-significant), and non-parallel lines indicate a significant log10(age) × biome interaction (interaction effects were tested only if the main age effect was significant and data were available for at least ten stand ages per biome—i.e. for GPP, ANPP, $R_{soil}$, and NEP). The boxplots illustrate variation among biomes in 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 tests of differences across biomes (mature forests, indicated by a dash instead of a letter above the box plot). Individual figures for each flux with sufficient data, along with maps showing geographic distribution of the data, are given in the supplement (figures S5–S19).]
Figure 8. Age trends and biome differences in some of the major forest C stocks: (a) $B_{ag}$, (b) $B_{fol}$, (c) $B_{root-fine}$, (d) $DW_{standing}$, (e) $DW_{down}$, and (f) OL. The scatterplots show age trends in forests up to 100 years old, as characterized by a linear mixed effects model with fixed effects of log10(age) and biome. The fitted lines indicate the effect of age (solid lines: significant at $p < 0.05$, dashed lines: non-significant), and non-parallel lines indicate a significant log10(age) × biome interaction (all variables but $DW_{down}$). The boxplots illustrate variation among biomes in 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 tests of differences across biomes (mature forests, indicated by a dash instead of a letter above the box plot). Individual figures for each stock with sufficient data, along with maps showing geographic distribution of the data, are given in the supplement (figures S20–S30).

Consistently increase with stand age (figures 1(d), 8 and 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 (figures 7, 9 and S5–S19), suggesting that regrowth forests follow latitudinal trends in carbon cycling similar to those of mature forests (e.g. Banbury Morgan et al 2021).

In contrast to C fluxes and biomass accumulation rates in regrowth forests, stocks showed less systematic variation across biomes (cf figure 1(c)). For aboveground biomass, which is the variable in ForC with the 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 Northern hemisphere (Hu et al 2016). The highest-biomass forests on Earth are, however, found in coastal temperate climates of both the southern and northern hemispheres (figures 1(c) and 8(a), Smithwick et al 2002, Keith et al 2009, Larjavaara and Muller-Landau 2012, 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 the anomalous results described here (e.g. lack of complete C budget closure, an anomalous trend across biomes for BNPP$_{coarse}$). Thus, biome differences should always be interpreted relative to the geographic distribution of sampling, which only rarely adequately represents the majority of forested area within a biome.
Figure 9. Age trends in C cycling. The selection of variables for plotting seeks to maximize sample size and broad geographic representation while representing all C cycle elements. Error bars on mature forest flux estimates indicate ±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: \( B_{\text{bag}} - B_{\text{foliage}} = \max(0, B_{\text{bag}} - B_{\text{foliage}}) \), \( B_{\text{root coarse}} = \max(0, B_{\text{root coarse}} - B_{\text{root fine}}) \), \( D_{\text{standing}} = \max(0, D_{\text{NPP}} - D_{\text{down}}) \). For tropical forests: \( \text{ANPP}_{\text{woody}} = \max(0, \text{ANPP}_{\text{foliage}} - \text{ANPP}_{\text{woody}}) \), \( R_{\text{auto - ag}} = R_{\text{auto}} - R_{\text{root}} \), where \( R_{\text{auto}} = \text{NPP}(1/CUE - 1) \) and CUE = 0.46 (Collalti et al 2020). For non-tropical forests: \( \text{ANPP}_{\text{woody}} = \min(\text{ANPP}_{\text{stem}}, \text{ANPP}_{\text{woody}}) \), \( R_{\text{auto - ag}} = R_{\text{eco}} - R_{\text{soil}} \). Note that there remain substantial uncertainties in the functional form of age trends and discrepancies in closure among related variables.

Whereas aboveground biomass can be remotely sensed (albeit with significant uncertainties, Ploton et al 2020) and receives substantial research attention, far less is known about geographical variation in deadwood and organic layer (OL) carbon 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\(^{-1}\) in some stands (figures 8 and 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 (figures 8 and S27–S29; but see below for age trends), pointing to a need for more widespread quantification of both standing and downed deadwood. For C 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 (figures 1(c), 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.

4.2. Age trends in C cycling

Our study reveals that most autotrophic C fluxes quickly increase and then decelerate as stands age (figures 7 and 9), consistent with current understanding of age trends in forest C cycling (figures 1(b); e.g. Magnani et al 2007, Amiro et al 2010, Anderson-Teixeira et al 2013). 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 (figure 1(b)). 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 (figures 1(b), d and 7–9). In contrast, soil heterotrophic respiration (R_het–soil) and total soil respiration (R_tot)—and therefore R_eco—are expected to be non-zero following stand-clearing disturbance (figure 1(b)). These may decrease with a reduction of root respiration (R_root only) and C exudates or increase in response to an influx of dead roots, DW, and OL (Bond-Lamberty et al 2004, Maurer et al 2016, Ribeiro-Kumara et al 2020), with the latter being strongly dependent upon the type of stand initiating disturbance (discussed below). This study detects no significant overall age trends in either R_het–soil or R_tot, 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 (figure 7). This finding is consistent with previous studies showing an increase in NEP across relatively young stand ages (Baldocchi et al 2001, Pregitzer and Euskirchen 2004, Luyssaert et al 2008). However, NEP is theoretically expected to peak in intermediate-aged stands and thereafter decline, consistent with decelerating C accumulation as stands age (figure 9, Odum 1969), and such declines have been documented (Law et al 2003, Luyssaert et al 2008). The fact that NEP values estimated by our models for 100 year-old stands were not systematically different from those of mature stands (Luyssaert et al 2008, Lichstein et al 2009, McGarvey et al 2014). 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). This contrasts with more variable age trends in deadwood and the organic layer (figure 9), which depend strongly on the type of disturbance. Disturbances that remove most woody material (e.g. clearcut logging, agriculture) result in negligible deadwood in young stands, followed by a buildup over time (e.g. tropical stands in figures 8 and 9, Vargas et al 2008). In contrast, natural disturbances (e.g. fire, drought, typhoons/hurricanes) 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 figures 8 and 9, Carmona et al 2002). Further study and synthesis of non-living C stocks across biomes, stand ages, and disturbance types will be valuable in giving a more comprehensive picture.

4.3. C variable coverage and budget closure

The large number of C cycle variables covered by ForC, and the relatively high consistency among them (figures 3–6 and 9), provide confidence that our reported mature forest means provide useful baselines for analysis. However, there is wide variation around these means, implying that any given stand could deviate substantially, and the sample means presented here probably 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 (figures 3–6 and 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 (see Houghton 2020). The one instance where the C budgets do 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; figure 5) rather than issues of methodological accuracy. The overall high degree of closure implies that ForC gives a 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 (Harmon et al 2011, Williams et al 2014, Phillips et al 2017), 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, this is 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). In addition, variation in the type and severity of stand-initiating disturbances introduces significant heterogeneity in both initial values and age trends of C cycle variables (e.g. Cook-Patton et al 2020). While this review provides the 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. ForC currently has sparse—if any—coverage of fluxes to herbivores and higher consumers, along with woody mortality ($M_{woody}$) and DW (table 1, figures S27–S29). We note that there are considerable opportunities to expand data on $M_{woody}$ and DW$_{standing}$ through calculations from existing forest census data. 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 (figure 2), a common problem in the carbon-cycle community (Schimel et al 2015, Xu and Shang 2016). 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 impact forest C cycling (e.g. Chaplin-Kramer et al 2015, Remy et al 2016, Reimann and Hutyra 2017, Smith et al 2019, Ordway and Asner 2020, Reimann et al 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 (figure 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, Reimann and Hutyra 2017, Piponiot et al 2019, Smith 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 (see Cook-Patton et al 2020). Additional research and synthesis are needed to fill these critical gaps in our understanding of forest C cycling.

4.4 Relevance for climate change prediction and mitigation

The future of forest C cycling (Song et al 2019) will shape trends in atmospheric CO$_2$ 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 meet two significant challenges.

First, improved representation of forest C cycling in models is essential to improving predictions of the future course of climate change. By definition, future projections extend our existing observations and understanding to conditions that do not currently exist on Earth (Bonan and Doney 2018, Gustafson et al 2018, McDowell 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. We recommend that researchers use these resources to identify and summarize data specific to the analysis at hand. Integration of ForC with predictive models will be valuable to improving model accuracy and reliability (Fer et al 2021).

Second, ForC can serve as a pipeline through which information can flow efficiently from forest researchers to decision-makers and practitioners working to implement forest conservation strategies at global, national, or landscape scales. This is already happening: ForC has contributed to updating the IPCC guidelines for carbon accounting in forests (IPCC 2019, Requena Suarez et al 2019), mapping C accumulation potential from natural forest regrowth globally (Cook-Patton et al 2020), and informing ecosystem conservation priorities (Goldstein et al 2020).
It is also interesting to consider the complementary utility of global-scale but spatially discontinuous databases such as ForC and wall-to-wall remote sensing products. The latter provide insight, with substantial uncertainty, into aboveground carbon stocks and GPP, but are less useful for constraining belowground stocks or carbon fluxes in general (Anav et al 2015, Bond-Lamberty et al 2016). Combining observational data and remote observations may provide a much more comprehensive and accurate picture of global forest C cycling, particularly when used in formal data assimilation systems (Liu et al 2018, Konings et al 2019). Biomass is the largest C stock in most forests, and most of the emphasis has traditionally been on this variable. Remote-sensing driven aboveground biomass estimates (e.g. Saatchi et al 2011), calibrated based on high-quality ground-based data (Chave et al 2019, Schepaschenko et al 2019), provide the most promising approach, but significant uncertainties remain (Ploton et al 2020). Note, however, that factors such as stand age and disturbance history are difficult, if not impossible, to detect remotely, and can only be characterized for recent decades (Hansen et al 2013, Curtis et al 2018, Song et al 2018). Ground-based data such as those in ForC are therefore valuable in defining age-based trajectories in biomass, as in Cook-Patton et al (2020), and thus constraining variables such as carbon sink potential (Lyysyyset et al 2008).

In contrast, carbon allocation within forest ecosystems and respiration fluxes cannot be remotely sensed. Efforts such as the Global Carbon Project (Friedlingstein et al 2019) and NASA’s Carbon Monitoring System (Liu et al 2018) typically compute respiration as residuals of all other terms (Harmon et al 2011, Bond-Lamberty et al 2016). This means that the errors on respiration outputs are likely to be large and certainly poorly constrained, offering a unique opportunity for databases such as ForC and SRDB (Jian et al 2020) to provide observational benchmarks. For example, Konings et al (2019) produced a top-down estimate of global heterotrophic respiration that can both be compared with extant bottom-up estimates (Bond-Lamberty 2018) and used as an internal consistency check on other parts of the carbon cycle (Phillips et al 2017).

5. Conclusions

As climate change accelerates, understanding and managing the carbon dynamics of forests—including stocks and fluxes that satellites cannot observe—is critical to forecasting, mitigation, and adaptation. The C data in ForC, as summarized here, are valuable to these efforts. Notably, the fact that tropical forests tend to have both the highest rates of C sequestration in young stands (figure 8, Cook-Patton et al 2020), fueled by their generally high C flux rates (table 1, figure 7), and the highest mean biomass (figure 8, table 1, Hu et al 2016, Jian et al 2020) reinforces the idea that conservation and restoration of these forests is a priority for climate change mitigation, along with high-biomass old-growth temperate stands (Grassi et al 2017, Goldstein et al 2020). It is also important to note the trade-off in climate mitigation potential of restoration of young forests, with high rates of CO2 sequestration (NEP, Cook-Patton et al 2020), versus conservation and management of mature forests, with low NEP but high C stocks that, if lost through disturbance, could not be recovered on time scales most relevant to avoiding dangerous climate change (i.e. 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).

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.

The data that support the findings of this study are openly available at the following URL/DOI: https://forc-db.github.io/.

Acknowledgments

Thanks to all researchers whose data are included in ForC and this analysis, to Jennifer McGarvey and Ian McGregor for help with the database, and to Norbert Kunert for helpful discussion. Three anonymous reviewers provided helpful feedback. Funding sources included a Smithsonian Scholarly Studies grant to KAT and HML and a Smithsonian Working Land and Seascapes grant to KAT 2010.

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