Title: Carbon cycling in mature and regrowth forests globally: a macroecological synthesis based on the global forest carbon database (ForC)

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Summary

(The Summary should be no longer than 300 words and divided into the following sections: Background, Methods/Design, Review results/ Synthesis and Discussion. Up to 7 Keywords should also be provided. The total length of the article is flexible.)

Background. The fate of Earth's climate closely linked to forests, which strongly influence atmospheric carbon dioxide (CO2) and climate through their influential role in the global carbon (C) cycle. Synthetic understanding of global forest C cycles is needed to constrain model estimates of forest feedbacks to climate change and to more accurately quantify the influence of land use decisions on climate.

Methods/Design. Here, we draw from the Global Forest C 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 draw upon ## records from ## geographic locations representing ## C cycle variables to characterize ensemble C budgets for four broad forest types (tropical broadleaf evergreen, temperate broadleaf, temperate conifer, and taiga), including estimates for both mature and regrowth (age <100 years) forests. For regrowth forests, we quantify age trends for all variables.

Review Results/ Synthesis. The rate of C cycling generally increased from boreal to tropical regions, whereas C stocks showed less directional variation. The majority of flux variables, together with most live biomass pools, increased significantly with stand age, and the rate of increase again tended to increase from boreal to tropical regions.

Discussion. [Discussion section will interpret results, highlighting new and significant findings, and discuss implications. Tentative headings are "Stand level C cycling in forests globally", "Age trends in C cycling", and "Implications for climate change mitigation".]

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

Background

(The Background section needs to present the rationale for why a systematic review of this topic is needed along with a history of what has been done to date and an expectation of what new will emerge from the review, especially if quantitative meta-analyses of studies are being considered.)

Forest ecosystems globally influence climate through their critical role in the global carbon (C) cycle (Fig. 1). Their annual gross CO2 sequestration (gross primary productivity, GPP) is estimated at 59 Gt C yr-1 (Beer et al 2010), or 6.3 times average annual fossil fuel emissions from 2007-2016 (9.4 ± 0.5 Gt C yr-1; Le Quéré et al 2017). A small portion of global terrestrial GPP is retained in ecosystems (mainly forests), resulting in a C sink that averaged 3.0 ± 0.8 Gt C yr-1 from 2007-2016, offsetting 32% of anthropogenic fossil fuel emissions (Le Quéré et al 2017). The remaining ~98% of global GPP is counterbalanced by ecosystem respiration (Reco) or wildfire. Perturbation to the global GPP- Reco balance can substantially influence the growth rate of atmospheric CO2; for example, the 2015-2016 El Niño, which brought historically high temperatures and low precipitation to the tropics, released an extra 2.5 ± 0.3 Gt C to the atmosphere, resulting in the largest recorded atmospheric CO2 growth rate (Le Quéré et al 2016, Liu et al 2017). In addition, forests contain substantial C stocks that, when disturbed, release significant amounts of CO2 to the atmosphere. Although they cover only ~30% of the land surface, forests contain an estimated 92% of terrestrial biomass (Pan et al 2013) and 45% of terrestrial C (biomass and soils; Bonan 2008). Globally, gross tropical deforestation averaged 2.8 Gt C yr-1 from 2000-2007, but ~40% of this was offset by forest regrowth, resulting in a net source of ~1.1 Gt C yr-1 from tropical land use change (Pan et al 2011). This, coupled with minimal net deforestation in the extratropics and net uptake by intact forests (Pan et al 2011, Schimel et al 2015), resulted in a total gain in forest C of ~1.2-1.7 Gt C yr-1 (Le Quéré et al 2017, Schimel et al 2015), thereby substantially slowing the rate of increase of atmospheric CO2.

Given their vital role in regulating atmospheric CO2, the future of Earth's forests will strongly influence the course of climate change. If forests globally respond to the suite of contemporary and future global change drivers—including elevated CO2, climate change, and atmospheric deposition—with increased productivity and net biomass increases, they could continue to act as a significant buffer against anthropogenic emissions.

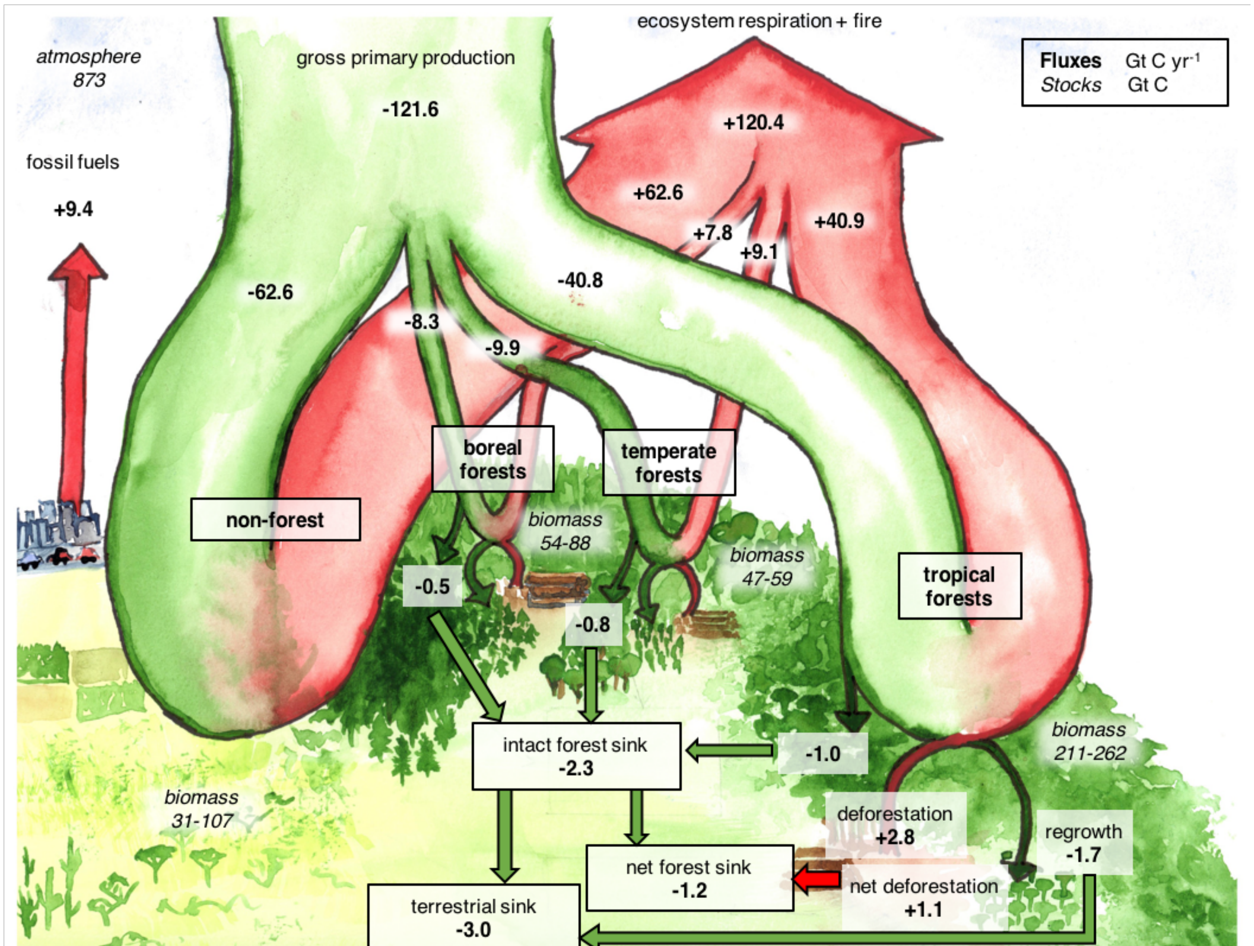

Figure 1 | The role of forests in the global carbon cycle. Values apply to the period 2000-2018. Sources are as follows: biomass- (Pan et al 2013, Baccini et al 2012) IPCC 2000; intact forest sink, net forest sink, tropical deforestation and regrowth-(Pan et al 2011); terrestrial sink- (Le Quéré et al 2017); GPP- (Beer et al 2010); respiration+fire: calculated here; fossil fuel emissions- (Le Quéré et al 2017); atmospheric CO2 (2018 value from https://scripps.ucsd.edu/programs/keelingcurve/). **see issue 19: https://github.com/forc-db/ERL-review/issues/19**

In contrast, if factors such as higher temperatures and drought stress lead to net C losses, the C sink of forests could be lost and even reversed. Global coupled climate models vary substantially in predictions regarding the future of the global forest C sink, with uncertainty in end-of-century terrestrial NEP exceeding current annual anthropogenic CO2 emissions (Friedlingstein et al 2006, Cavaleri et al 2015). Anthropogenic land use decisions will also strongly influence the future course of atmospheric CO2. In the absence of measures to reduce deforestation, this will continue to be a significant component of anthropogenic CO2 emissions. On the other hand, forest conservation, reforestation, and forest management hold strong potential to help stabilize and eventually reduce total anthropogenic CO2 emissions (estimated total of 4.4 Gt C yr-1; Griscom et al 2017; *Cook-Patton et al.*; **other refs?**) and thereby contribute towards the goals of the Paris Climate Agreement (UNFCCC 2015, Houghton et al 2015; **REFS**). Indeed, forest-based climate mitigation was a key component of Paris Climate Agreement commitments, totaling approximately one-fourth of nations' planned emissions reductions (Grassi et al 2017; IPCC1.5). Thus, forest will strongly influence the future course of climate change both through their responses to global change and through forest-related anthropogenic land use decisions.

While forests will play a critical role in the future course of climate change, there remain significant uncertainties as to current and future C cycling the world's forests. Even as the climate changes and forest age distributions shift, there are important gaps in our fundamental understanding of how C cycling varies with climate and stand age. A relative dearth of data on C cycling in secondary forests, particularly in the tropics (Anderson-Teixeira et al 2016), is problematic in that almost 2/3 of the world's forests were secondary as of 2010 (FAO 2010), implying an under-filled need to characterize age-related trends in forest C cycling. Recent studies attempting to quantify the role of forests in the global C cycle (e.g., Pan et al 2011) have been hampered by insufficient data on regrowth rates of tropical forests worldwide, C in non-living pools (i.e., dead wood, litter, soil), and source/sink status of forests in some regions. Moreover, as discussed above, model representation of forest responses to global change remain highly uncertain (Friedlingstein et al 2006, Cavaleri et al 2015), with efforts to reduce model uncertainty in part limited by ready availability of appropriate benchmark data (Clark et al 2017, Luo et al 2012). To address the need for global-scale analyses of forest C cycling, we have developed an open-access Global Forest Carbon database, ForC (https://github.com/forc-db/ForC; Anderson-Teixeira et al 2016, 2018). ForC contains data on forest ecosystem C stocks and annual fluxes (>50 variables) and associated data required for interpretation (e.g., stand history, measurement methods) amalgamated from numerous previous data compilations and directly from original publications. ForC currently contains # records from # plots and # distinct geographic areas representing all forested biogeographic and climate zones.

Here, we synthesize ForC data to provide a big-picture overview of stand-level carbon cycling of the world's major forest biomes and how it varies with stand age. We address two broad hypotheses: H1. The rate of C cycling generally decreases from tropical to boreal regions (i.e., tropical > temperate > boreal), whereas C stocks show less directional variation. H2. Both C fluxes and stocks generally increase with stand age, with particularly strong tends in autotrophic C fluxes. While components of these hypotheses have been previously addressed (e.g., REFS(Luyssaert et al 2007, Anderson et al 2006, Anderson-Teixeira et al 2013), our analysis represents by far the most comprehensive analysis of C cycling in global forests, and thereby stands to serve as a foundation for improved understanding of global forest C cycling.

Methods/ Design

(The Methods/Design section needs to describe how articles in the reviews were identified and what criteria were used for justifying inclusion in the review. While traditional reviews relying on past experience and expert knowledge are acceptable, editors should encourage reviews that are set up as so-called 'systematic reviews' (see the Cochrane Review procedure which initiated the process in the medical and health science: http://community.cochrane.org/ about-us/evidence-based-health-care).)

This review synthesizes data from the ForC database (https://github.com/forc-db/ForC; Anderson-Teixeira et al 2016, 2018). ForC amalgamates numerous intermediary data sets (e.g., REFS) 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, 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), yet these represented only approximately one-third of records in ForC v.2.0 (Anderson-Teixeira et al 2018). Since publication of ForC v.2.0, we added the following data to ForC: the Global Database of Soil Respiration Database (Bond-Lamberty and Thomson 2010; *hopefully Cook-Patton*; see GitHub list) .... We note that there remains a significant amount of relevant data that is not yet included in ForC, particularly biomass data from national forest inventories (e.g.,: REFS). The database version used for this analysis has been tagged as a new release on Github (XX) and assigned a DOI through Zenodo (DOI: XX).

For this analysis, we grouped forests into four broad biome types (tropical broadleaf, temperate broadleaf, temperate needleleaf, and boreal needleleaf) and two age classifications (young and mature). Climate zones were defined according to Köppen-Geiger zones, which were extracted based on site geographic coordinates from the ESRI Köppen-Geiger map (downloaded June 2014 from http://maps3.arcgisonline.com/ArcGIS/rest/services/A-16/Köppen-Geiger_Observed_and_Predicted_Climate_Shifts/MapServer; Rubel and Kottek 2010) and are recorded in the Koeppen field of the ForC SITES table. Tropical climates were defined to include all equatorial (A) zones, temperate climates were defined to include all warm temperate (C) zones and warmer snow climates (Dsa, Dsb, Dwa, Dwb, Dfa, and Dfb), and boreal climates were defined to include the colder snow climates (Dsc, Dsd, Dwc, Dwd, Dfc, and Dfd). Leaf type (broadleaf / needleleaf) was defined based on descriptions in original publications (prioritized) or values extracted from a global map based on satellite observations (SYNMAP; Jung et al 2006) and recorded in the dominant.veg field of the ForC MEAUREMENTS table. Stand age was obtained from the stand.age field of MEASUREMENTS table, and forests classified as "young" ($<$ 100 years) or "mature" ($\geq$ 100 years or classified as "mature", "old growth", "intact", or "undisturbed" in original publication). Records for which stand age was unknown were excluded from the analysis. These groupings were defined in March 2018, at which point they covered 91% of the primary variable records for forests of known age, or 86% of total records, in ForC (v.2.0; Anderson-Teixeira et al 2018). The most well-represented forest types excluded were boreal broadleaf and boreal and temperate mixed broadleaf-needleleaf, each with <400 records total for stands of any age.

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

Table 1. ForC variables included in this analysis. Shown are variable names and descriptions, the associated variable name(s) in the database, and number of plots with records. Complete list of variables with full definitions is available at [GitHub url].

Variable	Description	records	plots	geographic areas
Annual fluxes				
NEE	net ecosystem exchange or net ecosystem production (- indicates C sink)	n	n	n
GPP	gross primary production ($NPP + R_{auto}$ or $R_{eco} - NEE$)	n	n	n
NPP	net primary production ($ANPP + BNPP$)	n	n	n
$ANPP$	aboveground NPP	n	n	n
$ANPP_{woody}$	woody production (stem growth + branch turnover)	n	n	n
$ANPP_{stem}$	stem production	n	n	n
$ANPP_{branch}$	branch turnover	n	n	n
$ANPP_{foliage}$	foliage production, typically estimated as annual leaf litterfall	n	n	n
$ANPP_{litterfall}$	litterfall, including leaves, reproductive structures, twigs, and sometimes branches	n	n	n
$ANPP_{repro}$	production of reproductive structures (flowers, fruits, seeds)	n	n	n
$ANPP_{folivory}$	foliar biomass consumed by folivores	n	n	n
M_{woody}	aboveground biomass of trees that died	n	n	n
$BNPP$	belowground NPP ($BNPP_{coarse}$+ $BNPP_{fine}$)	n	n	n
$BNPPcoarse$	coarse root production	n	n	n
$BNPP_{fine}$	fine root production	n	n	n
R_{eco}	ecosystem respiration	n	n	n
R_{auto}	autotrophic respiration ($R_{auto-ag} + R_{root}$)	n	n	n
$R_{auto-ag}$	aboveground autotrophic respiration (i.e., leaves and stems)	n	n	n
R_{root}	root respiration	n	n	n
R_{soil}	soil respiration ($R_{het-soil} + R_{root}$)	n	n	n
$R_{het-soil}$	heterotrophic soil respiration	n	n	n
Stocks				
biomass	total live biomass	n	n	n
aboveground biomass	aboveground live biomass	n	n	n
woody aboveground biomass	woody component of aboveground biomass	n	n	n
foliage biomass	foliage biomass	n	n	n
root biomass	total root biomass	n	n	n
coarse root biomass	coarse root biomass	n	n	n
fine root biomass	fine root biomass C	n	n	n
deadwood	deadwood (standing+down)	n	n	n
standing deadwood	standing dead wood	n	n	n
down deadwood	fallen dead wood, including coarse and sometimes fine woody debris	n	n	n
organic layer	organic layer / litter/ forest floor	n	n	n