

RESEARCH REVIEW

Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db)

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Abstract

Tropical forests play a critical role in the global carbon (C) cycle, storing ~45% of terrestrial C and constituting the largest component of the terrestrial C sink. Despite their central importance to the global C cycle, their ecosystem-level C cycles are not as well-characterized as those of extra-tropical forests, and knowledge gaps hamper efforts to quantify C budgets across the tropics and to model tropical forest-climate interactions. To advance understanding of C dynamics of pantropical forests, we compiled a new database, the Tropical Forest C database (TropForC-db), which contains data on ground-based measurements of ecosystem-level C stocks and annual fluxes along with disturbance history. This database currently contains 3568 records from 845 plots in 178 geographically distinct areas, making it the largest and most comprehensive database of its type. Using TropForC-db, we characterized C stocks and fluxes for young, intermediate-aged, and mature forests. Relative to existing C budgets of extra-tropical forests, mature tropical broadleaf evergreen forests had substantially higher gross primary productivity (GPP) and ecosystem respiration (R_{eco}), their autotrophic respiration (R_a) consumed a larger proportion (~67%) of GPP, and their woody stem growth ($ANPP_{stem}$) represented a smaller proportion of net primary productivity (NPP, ~32%) or GPP (~9%). In regrowth stands, aboveground biomass increased rapidly during the first 20 years following stand-clearing disturbance, with slower accumulation following agriculture and in deciduous forests, and continued to accumulate at a slower pace in forests aged 20–100 years. Most other C stocks likewise increased with stand age, while potential to describe age trends in C fluxes was generally data-limited. We expect that TropForC-db will prove useful for model evaluation and for quantifying the contribution of forests to the global C cycle. The database version associated with this publication is archived in Dryad (DOI: 10.5061/dryad.t516f) and a dynamic version is maintained at <https://github.com/forc-db>.

Keywords: biomass, carbon cycle, net ecosystem exchange, productivity, regeneration, secondary, tropical forest

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Introduction

Tropical forests, including both regrowth and intact forests, play a critical role in the global carbon (C) cycle. They store an estimated 45% of terrestrial C and account for over one-third of terrestrial gross primary production (GPP; Bonan, 2008; Beer *et al.*, 2010). Tropical forests also constitute the largest component of the terrestrial C sink. In recent years (early 2000's), forest regrowth on ~557 Mha of abandoned agricultural land in tropical regions has represented an estimated sink of 1.4–1.7 Pg C yr⁻¹ (Pan *et al.*, 2011; Grace *et al.*, 2014; Lewis *et al.*, 2015)—an amount equal to ~20% of annual fossil fuel emissions or over half of the estimated

terrestrial land sink over a similar period (2000–2009; Le Quéré *et al.*, 2013). At the same time, intact tropical forests have on average been increasing in biomass over recent decades (Phillips, 1998; Lewis *et al.*, 2009; Muller-Landau *et al.*, 2014), sequestering an estimated 0.5–1.0 Pg C yr⁻¹ in the early 2000's (Pan *et al.*, 2011; Grace *et al.*, 2014; Lewis *et al.*, 2015). Moreover, natural disturbance-recovery cycles result in substantial ecosystem-atmosphere CO₂ exchange. For instance, in the Amazon alone, natural disturbances release an estimated 1.3 Pg C yr⁻¹, which is more than compensated for by CO₂ sequestration through tree growth (Espírito-Santo *et al.*, 2014). Thus, CO₂ exchanges between the tropical forest biome and the atmosphere meaningfully influence atmospheric CO₂.

In the present era of global change, tropical forests play a central role in determining the rate of increase

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in atmospheric CO₂. Tropical deforestation is of key significance; from 1990 to 2007, CO₂ emissions from tropical deforestation were $\sim 3 \text{ Pg C yr}^{-1}$, equivalent to $\sim 40\%$ of global fossil fuel emissions (Pan *et al.*, 2011). Efforts to reduce tropical deforestation (e.g., REDD+; UNFCCC, 2008, 2015), if successful, will contribute substantially to reduction of anthropogenic CO₂ emissions (Houghton *et al.*, 2015). At the same time, tropical forests are changing in response to climate change and other global change pressures, and this will alter their CO₂ exchange with the atmosphere (e.g., Malhi *et al.*, 2014; Anderson-Teixeira *et al.*, 2015). Although currently C sinks, intact tropical forests could become net C sources if, for example, drought and other disturbances substantially increase tree mortality (e.g., Lewis *et al.*, 2011; Brien *et al.*, 2015). Climate change is likely to increase the frequency and intensity of some natural disturbances (e.g., storms; droughts; IPCC, 2013; Trenberth *et al.*, 2014), and regional C balances will be strongly influenced by tropical forest regrowth dynamics, which are also likely to be altered by climate change (Anderson-Teixeira *et al.*, 2013). Altered disturbance-recovery dynamics have the potential to have a much stronger influence on regional C balances than metabolically driven changes (Kurz *et al.*, 2008; Running, 2008; Anderson-Teixeira *et al.*, 2013). The net response of the tropical forest biome to global change pressures will influence the future trajectory of atmospheric CO₂, yet remains highly uncertain.

Despite the importance of tropical forests to the global C cycle, their C cycles are not as well understood as those of extra-tropical forests, and important gaps in our knowledge of their ecosystem-level C cycles hamper scientific and societal efforts to quantify C budgets across the tropics and to model tropical forest-climate interactions. More data are required to understand C cycling in tropical forest ecosystems, how it compares to C cycling in extra-tropical forests, and how it is influenced by environmental variation (U.S. DOE, 2012; Bustamante *et al.*, 2016; Malhi *et al.*, 2015). Modeling the role of tropical forests in Earth's changing climate system presents a significant challenge (U.S. DOE, 2012), and regrowth forests in particular remain poorly represented in Earth system models (ESMs; Arora & Boer, 2010; Schwalm *et al.*, 2010). Improved data on how C stocks and fluxes of tropical forests are affected by disturbance history and climate is needed to parameterize, test, and validate ESMs (Friedlingstein *et al.* 1999; Bonan, 2008; Schwalm *et al.*, 2010). Moreover, high uncertainty regarding C stocks and fluxes of tropical forests—particularly regrowth forests—introduces substantial uncertainty into the global forest C balance (Pan *et al.*, 2011). On a practical level, national inventories

of C stocks and fluxes are central to international climate change mitigation efforts (e.g., greenhouse gas accounting under the Kyoto Protocol), yet the IPCC guidelines for national greenhouse gas inventories (IPCC, 2006) present estimates of tropical forest C stocks and accumulation rates that are based on a very small subset of available data. Improved data on C stocks and fluxes of tropical forests are therefore key to more accurate quantification of the role of tropical forests the global C cycle.

Pantropical data on C stocks and fluxes of tropical forests are critical to understanding the C dynamics of tropical forests, how these compare to the better-characterized C dynamics of extra-tropical forests, and the role of tropical forests in the global C cycle. Relevant data have been collected at many locations throughout the world (Table 1), yet appropriate synthesis has been lacking. Recent global compilations of forest C data are scant on tropical forests (Luysaert *et al.*, 2007; Liu *et al.*, 2014; Michaletz *et al.*, 2014)—in part because tropical data are relatively less abundant, but also because there has not been a focused effort to identify and incorporate relevant tropical forest data. Moreover, most existing forest C databases have limited information about disturbance history—information that is key to analyzing trajectories of forest recovery.

Here, we present a new database on C dynamics of tropical forests, the Tropical Forest C database (TropForC-db) and use it to synthesize knowledge to date about tropical forest C dynamics and identify key uncertainties. TropForC-db synthesizes data on ground-based measurements of C stocks and flows along with site disturbance history for forests throughout the tropics. It focuses on C stocks and annual C fluxes, drawing upon existing data compilations and data from original studies identified using a literature search. We use this database, which is the largest and most comprehensive of its type, to characterize C stocks and annual fluxes for young, intermediate-aged, and mature/intact forests—comparing the latter to existing budgets for extra-tropical forests—and to examine patterns of C accumulation following stand-clearing disturbance.

Materials & methods

Overview of TropForC-db

TropForC-db is the tropical component of ForC-db, which is a global C database that is currently under development and maintained at <https://github.com/forc-db>. Its structure is derived from and compatible with that of BETY-db (www.betydb.org; LeBauer *et al.*, 2010). In brief, the database consists of a series of cross-referenced data tables describing (1)

Table 1 List of studies with data included in TropForC-db, by region

Region	Studies included
Global/ multiregional*	Clark <i>et al.</i> , 2001b, 2013; IPCC, 2003, 2006; Anderson <i>et al.</i> , 2006; Litton <i>et al.</i> , 2007; Luyssaert <i>et al.</i> , 2007; Baldocchi, 2008; Martin <i>et al.</i> , 2013; Liu <i>et al.</i> , 2014; Yu <i>et al.</i> , 2014
Afrotropics	Bartholomew <i>et al.</i> , 1953; Egunjobi & Bada, 1979; DeAngelis <i>et al.</i> , 1981; Kadeba, 1991; Esser <i>et al.</i> , 1997; Nye & Greenland, 1998; Laclau <i>et al.</i> , 2000; Clark <i>et al.</i> , 2001b; Olson <i>et al.</i> , 2001; Clark <i>et al.</i> , 2013; Nygård <i>et al.</i> , 2004; Onyekwelu, 2004, 2007; Veenendaal <i>et al.</i> , 2004; Harmand <i>et al.</i> , 2004; Epron <i>et al.</i> , 2006; Lewis <i>et al.</i> , 2009
Australasia	Edwards & Grubb, 1977; Chen <i>et al.</i> , 2003; Hutley <i>et al.</i> , 2005; Leuning <i>et al.</i> , 2005; Mialet-Serra <i>et al.</i> , 2005; Roupsard <i>et al.</i> , 2006; Beringer <i>et al.</i> , 2007; Navarro <i>et al.</i> , 2008; Clark <i>et al.</i> , 2013; Stocker, 2013
Indo-Malaya	Hozumi <i>et al.</i> , 1969; Ogawa <i>et al.</i> , 1965; Kunstadter <i>et al.</i> , 1978; Nakane, 1980; Yamakura <i>et al.</i> , 1986a,b; Behera <i>et al.</i> , 1990; Dang & Wu, 1992; Chen <i>et al.</i> , 1993, 2010; Peng & Zhang, 1994; Luo, 1996; Pinard & Putz, 1996; Zhang & Ding, 1996; Esser <i>et al.</i> , 1997; Wen <i>et al.</i> , 1997; Kira, 1998; Wen <i>et al.</i> , 1999; Yi <i>et al.</i> , 2000; Clark <i>et al.</i> , 2001b, 2013; Ito & Oikawa, 2002; Fang <i>et al.</i> , 2003; Hoshizaki <i>et al.</i> , 2004; Swamy <i>et al.</i> , 2004; Adachi <i>et al.</i> , 2006; Jepsen, 2006; Yan <i>et al.</i> , 2006; Hirano <i>et al.</i> , 2007, 2009; Terakunpisut <i>et al.</i> , 2007; Hirata <i>et al.</i> , 2008; Kato & Tang, 2008; Kosugi <i>et al.</i> , 2008; Ramachandran & Byrappa Gowdu Viswanathan, 2009; Chen, 2010; Kenzo <i>et al.</i> , 2010; Van Do <i>et al.</i> , 2010; Zhang <i>et al.</i> , 2010; Aththorick <i>et al.</i> , 2012; Chan <i>et al.</i> , 2013; Proctor, 2013; Yu <i>et al.</i> , 2013
Neotropics	Snedaker, 1970; Ewel, 1971; Golley, 1975; Klinge <i>et al.</i> , 1975; Folster <i>et al.</i> , 1976; Scott, 1977; Crow, 1980; Tanner, 1980; Klinge & Herrera, 1983; Williams-Linera, 1983; Uhl & Jordan, 1984; Bongers <i>et al.</i> , 1985; Frangi & Lugo, 1985; Uhl, 1987; Saldarriaga <i>et al.</i> , 1988; Lugo <i>et al.</i> , 1990; Lugo, 1992; Guimaraes, 1993; Overman <i>et al.</i> , 1994; de Salomão, 1994; Szott <i>et al.</i> , 1994; Aide <i>et al.</i> , 1995; Brown <i>et al.</i> , 1995; Alves <i>et al.</i> , 1997; Delaney <i>et al.</i> , 1997; Lucas <i>et al.</i> , 1998, 2002; Malhi <i>et al.</i> , 1998, 1999, 2004; Gehring <i>et al.</i> , 1999, 2005; Grimm & Fassbender, 1999; Hughes <i>et al.</i> , 1999, 2000, 2002; Jordan <i>et al.</i> , 1999; Parrotta, 1999; Clark & Clark, 2000; Montagnini, 2000; Sorrensen, 2000; Steininger, 2000; Chambers <i>et al.</i> , 2001, 2004; Chave <i>et al.</i> , 2001; Clark <i>et al.</i> , 2001b, 2013; Keller <i>et al.</i> , 2001, 2004; Maass & Martinez-Yrizar, 2001; Weaver, 2001; Zarin <i>et al.</i> , 2001; Araújo, 2002; Carswell <i>et al.</i> , 2002; Davidson <i>et al.</i> , 2002, 2004; Falge <i>et al.</i> , 2002; Fehse <i>et al.</i> , 2002; Kraenzel <i>et al.</i> , 2003; Loescher <i>et al.</i> , 2003; Read & Lawrence, 2003; Saleska, 2003; Santos <i>et al.</i> , 2003; Baker <i>et al.</i> , 2004; Feldpausch <i>et al.</i> , 2004; Li <i>et al.</i> , 2004; Miller <i>et al.</i> , 2004; Rice <i>et al.</i> , 2004; Silver <i>et al.</i> , 2004; Stape <i>et al.</i> , 2004; Vourlitis <i>et al.</i> , 2004; Vieira <i>et al.</i> , 2005; Cleveland & Townsend, 2006; Trumbore <i>et al.</i> , 2006; Hutrya <i>et al.</i> , 2007; Marín-Spiotta <i>et al.</i> , 2007; Palace <i>et al.</i> , 2007; Sierra <i>et al.</i> , 2007a,b, 2012; Terakunpisut <i>et al.</i> , 2007; Vargas <i>et al.</i> , 2008; Aragão <i>et al.</i> , 2009; Letcher & Chazdon, 2009; Girardin <i>et al.</i> , 2010; Schöngart & Wittmann, 2010; Van Do <i>et al.</i> , 2010; Fonseca <i>et al.</i> , 2011; Moser <i>et al.</i> , 2011; Mascaro <i>et al.</i> , 2012; Clark, 2013; Orihuela-Belmonte <i>et al.</i> , 2013; Araujo-Murakami <i>et al.</i> , 2014; Becknell & Powers, 2014; Broadbent <i>et al.</i> , 2014; da Costa <i>et al.</i> , 2014; del Aguila-Pasquel <i>et al.</i> , 2014; Doughty <i>et al.</i> , 2014; Rocha <i>et al.</i> , 2014
Oceania	Webb & Fa'aumu, 1999; Clark <i>et al.</i> , 2001b, 2013; Giardina <i>et al.</i> , 2003, 2004; Ryan <i>et al.</i> , 2004; Schuur, 2005

*These data compilations were used to identify original studies relevant to our database.

sites, (2) plots and their history, (3) measurements of C cycle variables, (4) variables, (5) disturbance/history event type, (6) plant functional types (PFTs)/species, (7) methodologies, and (8) allometries (Table 2).

Records of plot locations within the database were designed to preserve maximum possible location information given in original publications and to allow grouping of related plots. Specifically, plots were grouped by site and area, where site is the most precisely described location with unique site conditions (e.g., latitude/longitude, elevation, edaphic conditions), and area groups one or more geographically proximate plots. Each plot was described in terms of its history and dominant vegetation. Plot most commonly refers to a contiguous sampling area; however, when an original study presented only average values for noncontiguous replicate plots, they are treated as a single plot within our database. Depending on the level of site detail given by the original publication, a plot may be treated as a unique site or may share site data with other plots. Geographically proximate sites were grouped into areas, where area was defined as a group of sites where no site is >0.25° latitude or longitude distant from another site in the

group. This groups chronosequences—i.e., plots differing in time since a stand-clearing disturbance—within a single area. Thus, 'areas' group plots suitable for direct comparison, whereas 'sites' link plots to the most precisely described geographic, climatic, and edaphic data.

Each plot was described in terms of known history of events affecting the entire plot and relevant to understanding the C cycle. Events recorded included major natural and anthropogenic disturbances (e.g., fires, major storms, harvest, tillage), initiation of forest growth (e.g., initiation of natural succession, planting), management (e.g., fertilization, thinning), and experimental manipulation (e.g., irrigation). Smaller-scale natural disturbances such as tree fall were not included. We used 'stand age' to refer to the age of the oldest cohort of trees within the plot; however, we note that the database does include records from some large, heterogeneous plots containing multiple stands that may vary in age (e.g., CTFs-ForestGEO plots; Anderson-Teixeira *et al.*, 2015). Thus, some mature/intact plots contain, but are not dominated by, stands of younger age. When not reported directly, stand age was estimated based on the year of initiation of forest

Table 2 Overview of TropForC-db structure and content

Table	Description	Content
1) Sites	Geographic, climatic, and edaphic site data	Site ; city, state, country, geographic coordinates, elevation, climate data, and soil descriptors from original publications or subsequent compilations; area (as grouped here). Additional data acquired or derived from global maps and included in the sites table are biogeographic zone, FAO ecozone, Köppen-Geiger climate zone, Site ; plot ; plot area; date (with its certainty) and level* of known events (disttype) of relevance to the C cycle. When plots have no known disturbance history, the year to which an absence of disturbance is known with confidence is recorded.
2) Plots & history	Known history of each plot or set of replicate plots	Site ; plot ; dominant vegetation type (PFT/species)†; stand age at time of measurement; variable name ; method_id ; measurement dates and their certainty, sample size; measured values and their uncertainty, covariates that are important to interpreting trait data, including allometric_equation , citation
3) Measurements	Records of ecosystem-level measurements relevant to C cycling	Variable name , units, description, equations, notes, and associated covariates
4) Variables	Definitions of variables	Disturbance category, disttype , description, units (when applicable)
5) Disturbance Type	Definition of disturbance, management or regeneration history event types.	PFT (plant functional type), description
6) Plant functional types/species	Definitions of species/PFT codes	method_id ; method citation, variable, notes
7) Methodology	Description of methodologies	allometric_equation ; citation for equation source; notes
8) Allometries	Sources and description of allometric equations	

*Level is recorded for some event types. For example, for harvest, a level of 100% indicates clear cut.

†For dominant vegetation type, the PFT or species that encompasses all trees in the stand is recorded. PFT categories range in their specificity; for example, 'broadleaf evergreen trees' would be applied to a stand dominated entirely by evergreen trees, whereas 'broadleaf trees' would be applied to a mixed evergreen/deciduous stand. A single species is recorded only in the case of monoculture plantations. Species and PFT are recorded in the measurements table (as opposed to the sites or treatments & history tables) because species composition changes over time.

Bold indicates variables that link data tables.

regrowth. When stand age was reported, we used it to calculate the year of establishment of the oldest trees within a plot, which was recorded as part of the plot's history. Particularly for late successional or old growth stands, this may differ from the year of initiation of forest regrowth following disturbance.

Measurements of ecosystem-level C stocks and annual fluxes were included. Most variables were defined as in Chapin *et al.* (2006) or Luyssaert *et al.* (2007). Definitions of the variables presented here are given in Tables 3 and 4, and complete definitions of all variables and equations relating the variables are included in the data files (Anderson-Teixeira *et al.*, 2016). Measurement records included the sites and plots at which measurements were made, dominant plant functional type or species (in the case of plantations), stand age, measurement methods and dates, reported measurement values and error, and covariates important to interpretation of the measurement (e.g., minimum DBH, allometries used; Table 2). A single plot was commonly linked to measurements of multiple variables, and a single variable could be measured multiple times in the same plot.

Complete metadata are given in an associated data publication in Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.t516f>; Anderson-Teixeira *et al.*, 2016).

Data sources

We used previous data compilations on ecosystem-level C stocks and annual fluxes for regrowth or mature tropical forests to identify original publications relevant to the database (Table 1). We referred to the original publications to check data presented in these original compilations and to obtain additional information (e.g., plot history). In addition, in fall 2013–spring 2014, we used Google Scholar to search the literature for additional studies focused on regrowth forests and those quantifying dead wood. Data compilations and individual studies included in the database are listed in Table 1. The search for relevant data was substantive but not comprehensive; we are aware of relevant data that were not included in the database as of September 2015.

Plots were included in TropForC-db if located within the tropics (latitude $\leq 23.5^\circ$) and tree-dominated (including savannas with woody vegetation). Peat forests were included. The data compilation effort focused on unmanaged forests, but managed or plantation forests were included when their data were included in a previous compilation.

We focused the search around ecosystem-level measurements of biomass, dead wood, and major annual C fluxes

Table 3 TropForC-db C flux variables included in Figs 3–5. Shown are variable names and descriptions, the associated variable name(s) in the database, number of records (*n*), and number of plots (*n* plots) in the database. All units are Mg C ha⁻¹ yr⁻¹. Complete list of variables is available in Anderson-Teixeira *et al.* (2016)

Variable	Description	Variable name(s)	<i>n</i>	<i>n</i> plots
Ecosystem C balance				
NEE or NEP	Annual net ecosystem exchange (– indicates C sink) or net ecosystem production (+ indicates C sink)	NEE_annual, NEP_annual	84	29
Production				
GPP	Annual gross primary production	GPP_annual, GPP_C_annual	93	48
NPP	Annual net primary production	NPP_[1-5](_C)	71	42
ANPP	Aboveground NPP	ANPP_[1-2](_C)	116	71
ANPP _{stem}	Annual stem production; <i>i.e.</i> , annual stem aboveground biomass increment	ANPP_stem(_C)	201	185
ANPP _{foliage}	Annual foliage production, typically estimated as annual leaf litterfall	ANPP_foliage(_C)	73	58
ANPP _{litterfall}	Annual litterfall, including leaves, reproductive structures, and sometimes woody material	ANPP_litterfall_[1-2](_C)	19	16
ANPP _{folivory}	Annual productivity consumed by folivores	ANPP_folivory(_C)	112	62
BNPP	Total annual belowground NPP	BNPP_root(_C)	46	37
BNPP _{coarse}	Annual coarse root production	BNPP_coarse root(_C)	44	41
BNPP _{fine}	Annual fine root production	BNPP_fine root(_C)	42	37
Respiration				
R _{eco}	Annual ecosystem respiration	Reco_annual	66	26
R _a	Annual autotrophic respiration	R_auto_annual	14	13
R _{soil}	Annual soil respiration	Rsoil_annual	49	33
R _{h,soil}	Annual heterotrophic soil respiration	Rsoil_het_annual	2	2
R _h	Annual heterotrophic respiration	R_het_annual	29	25
Other flux variables			132	123

(Tables 3 and 4), also including a number of other relevant variables when reported in studies including data on focal variables (see metadata of Anderson-Teixeira *et al.*, 2016 for complete list). While the database does include soil carbon data, we did not attempt to make a comprehensive compilation of soil carbon data. Marín-Spiotta & Sharma (2013) provides a recent compilation of pan-tropical data on soil carbon in forests of different ages and disturbance histories.

Data were obtained from tables or extracted from figures using WEBPLOTDIGITIZER v.3.8 (Rohatgi, 2015). All data were converted to standardized units: Mg [dry biomass or C] ha⁻¹ for stocks and Mg [dry biomass or C] ha⁻¹ yr⁻¹ for fluxes. The database preserves measurements in biomass or C as reported by the original study. For analyses presented here, we converted biomass to C using the approximation that biomass is 47% C (IPCC, 2006).

Additional geographic and climatic data for all sites were extracted from global databases. Biogeographic zones were delineated using the map of Olson *et al.* (2001), and FAO ecozone classification was obtained from FAO's GeoNetwork (<http://www.fao.org:80/geonetwork>). Climate zone was extracted 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).

Analyses

For the purpose of the descriptive statistics reported here, we grouped forests into three age classes determined based on benchmarks related to biomass recovery and alignment with existing international standards (IPCC, 2006): young (age ≤ 20), intermediate-aged (20 < age < 100), and mature (age ≥ 100)/intact. The 20-year cut-off between young and intermediate ages was selected because this is the age at which the most rapidly recovering tropical forest stands observed to date achieve the aboveground biomass of nearby undisturbed stands (Martin *et al.*, 2013) and because this cut-off aligns with IPCC guidelines for national greenhouse gas inventories (IPCC, 2006). The cut-off between intermediate-aged and mature/intact forests—100 years—was intended as a roughly appropriate cut-off to differentiate stands in which forest C stocks remain significantly affected by past disturbance from those in which C stocks are relatively stable. Estimates of the average age at which biomass of secondary forests equals that of undisturbed forests range from 50 to 200 years (Martin *et al.*, 2013 and references therein), and this threshold is likely to vary significantly among forests and by the C stock under consideration (e.g., aboveground biomass/root biomass/total ecosystem C; Martin *et al.*, 2013). Forests with no known history of stand-clearing or substantial anthropogenic distur-

Table 4 TropForC-db C stock variables included in Figs 3–5. Shown are variable names and descriptions, the associated variable name(s) in the database, number of records (*n*), and number of plots (*n* plots) in the database. All units are Mg C ha⁻¹. Complete list of variables is available in Anderson-Teixeira *et al.* (2016)

Variable	Description	Variable name(s)	<i>n</i>	<i>n</i> plots
Living				
Biomass	Total live biomass C	Biomass_total; C_total	180	105
Aboveground biomass	Aboveground live biomass C	Biomass_ag; C_ag	1051	672
Foliage biomass	Foliage biomass C	Biomass_ag; C_ag	157	115
Root biomass	Total root biomass C	Biomass_root_total; C_root_total	258	149
Coarse root biomass	Coarse root biomass C	Biomass_root_coarse; C_root_coarse	48	30
Fine root biomass	Fine root biomass C	Biomass_root_fine; C_root_fine	82	53
Nonliving				
Dead wood	Dead wood, including standing dead wood and coarse woody debris.	(C_)Deadwood, Downdeadwood, Standingdeadwood	135	105
Organic layer	Organic layer ('forest floor') C.	(C_)Organic layer	106	79
Other stock variables			204	154

balance within 100 years of the measurement were classified as mature/intact; thus, mature unmanaged and old-growth forests were grouped together for these analyses.

Statistics were computed both for all records in the database and for the subset of unmanaged tropical broadleaf evergreen forests. We use the term 'unmanaged' to refer only to the regrowth phase; stands that were naturally regenerating following agriculture or other management were included in this category. Plantations were excluded. Broadleaf evergreen forests were as delineated by satellite remote sensing (Fig. 1; Jung *et al.*, 2006), which does not preclude the presence of some deciduous trees.

Descriptive statistics were calculated for 17 focal variables (Tables S2–S7) for plots grouped by age class. When there were multiple records for a variable for a plot, these values were averaged prior to computing other statistics. The effect of age class was assessed using ANOVA, and pairwise differences between age classes was assessed using a two-sided t-test. Furthermore, for young and intermediate age categories with data from ≥ 4 areas, we tested for an effect of age within young and intermediate age classes using a mixed-effects model where age was a fixed effect and plot nested within area was a random effect. When the effect of age was statistically significant at $P \leq 0.05$, we reported the slope and intercept of this relationship in place of a mean (Tables S2, S3, S5 and S6).

For aboveground biomass in regrowth stands, we analyzed the interactive effects of stand age and other variables using mixed effects models. Specifically, we applied a linear mixed effects model using the package 'lme4' in R v.3.1.2 (R Core Team, 2013) where the random effect was stand nested within area, and fixed effects were age and its interaction with regeneration type and/or FAO ecozone. Regeneration type was a categorical variable; sites were classified as plantation or natural regeneration following cultivation, grazing, or other disturbance. Regeneration type or ecozone categories with < 20 records were excluded from the analysis. For young stands, regeneration type

included natural regeneration following cultivation, natural regeneration following pasture, natural regeneration following other disturbance, and plantations; while ecozone included tropical rainforest, moist deciduous forest, mountain system, and dry forests (all dry forest plots were plantations). For intermediate forests, regeneration type included natural regeneration following cultivation or pasture; while ecozone included tropical rainforest and moist deciduous forest. Models were run both with all forests and with naturally regenerating forests only.

Results

Database content

As of September 2015, TropForC-db contained 3568 records from 845 plots in 178 geographically distinct areas. These were represented by 503 site records (Fig. 1). 57.9% of measurements and 55.1% of plots were from unmanaged broadleaf evergreen forests. Geographically, 69.7% of records and 70.4% of plots were from the Neotropics, 12.7% of records and 10.8% of plots were from Indo-Malaya, 9.3% of records and 13.5% of plots were from the Afrotropics, 3.7% of records and 1.8% of plots were from Australasia, and 4.6% of records and 3.6% of plots were from Oceania (Fig. 1; Table S1). Climatically, 40.5% of records and 40.9% of plots were classified as equatorial (Af in Köppen-Geiger climate zone), 19.8% of records and 23.2% of plots were classified as tropical monsoon (Am), 25.4% of records and 26.6% of plots were classified as tropical wet-dry (Aw/As), 0.3% of records and 0.9% of plots were classified as hot semiarid (Bsh), and 14% of records and 8.3% of plots were classified as subtropical (Cfa, Cfb, or Cwa).

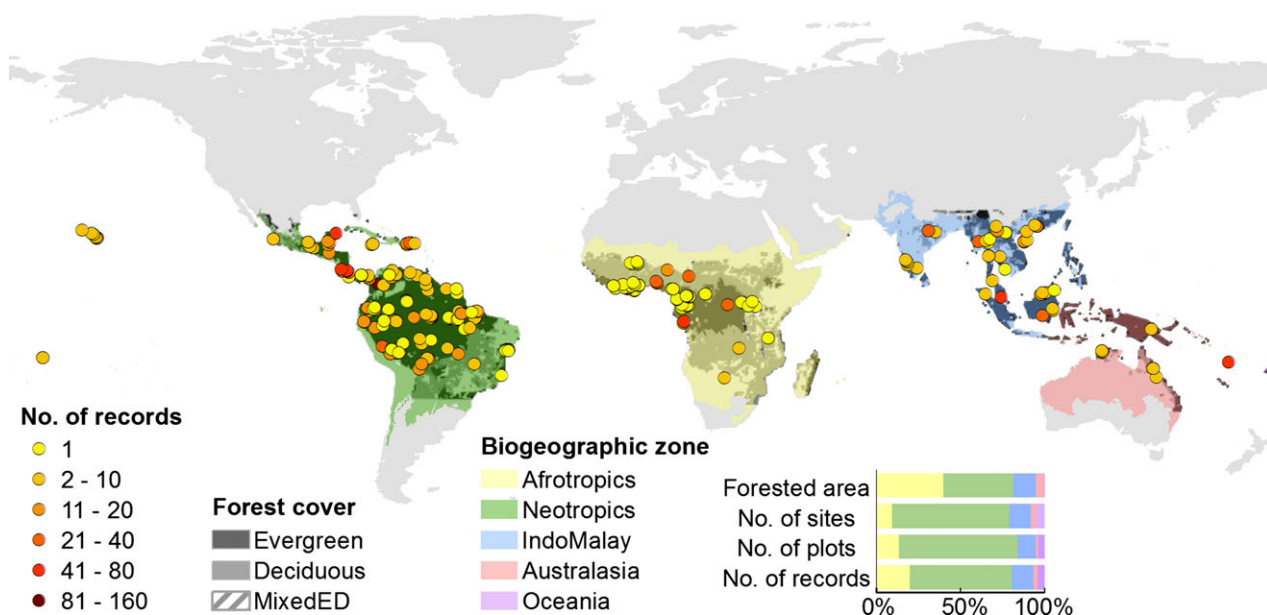


Fig. 1 Geographical distributions of sites included in TropForC-db. Map shows satellite-derived coverage of evergreen and deciduous forest (from SYNMAP; Jung *et al.*, 2006). Inset shows distribution of sites, plots, and records among biogeographic regions (*sensu* Olson *et al.*, 2001).

In terms of stand age, mature forests were relatively well-represented (44.9% of plots/41.9% of records). For regrowth forests, the number of records for regrowth plots decreased with increasing stand age (Fig. 2), with young forests represented by 42.7% of plots/41% of records and intermediate-aged stands represented by 9.7% of plots/13.7% of records. Over 1/3 of plots represented naturally regenerating forests following cultivation (19.4% of plots/17.7% of all records), grazing (13.8% of plots/11.4% of records), or other disturbance types (5.1% of plots/7.4% of records; Fig. 2). The remainder represented plantations (14.1% of plots/19.1% of records), or unknown regeneration types (47.6% of plots/44.4% of records, many of which were mature/intact).

In terms of the variables represented, the database contained a total of 2222 records for C stocks from 1463 plots and 1226 records for C fluxes from 875 plots (Tables 3 and 4). Aboveground biomass had by far the most records ($n = 1051$ records from 672 plots; 29.4% of total). Other variables measured at >100 plots included stem aboveground net primary productivity ($ANPP_{stem}$), total biomass, foliage biomass, total root biomass, and dead wood (including standing dead wood and coarse woody debris; Tables 3 and 4). There were 26 variables measured in ≥ 25 plots, and 21 variables with fewer records (Anderson-Teixeira *et al.*, 2016). Mature/intact and young forests were better represented in terms of the number of variables measured (36 variables each), while intermediate-aged stands had records

for fewer variables (26 variables). The three age classes were approximately equally represented in terms of aboveground biomass records (34% young; 33.5% intermediate-aged, 25.6% mature/intact; remainder age unknown). There was very low representation of C fluxes in young and intermediate-aged stands (17.9% and 6.7% of C flux records, respectively); for instance, the database contains only one set of eddy flux measurements in a naturally regenerating tropical forest (a young stand) and only one measurement each of belowground and total NPP in naturally regenerating intermediate-aged tropical forest stands.

C stocks and fluxes of mature forests

Carbon stocks and fluxes of mature/intact unmanaged tropical broadleaf evergreen forests are summarized in Fig. 3 and are also presented in Tables S4 (stocks) and S7 (fluxes). This ensemble C budget was internally consistent; that is, none of the C fluxes shown in Fig. 3 differed significantly from the sum of its component C flux terms (Fig. 3; analyses not shown).

Descriptive statistics for all mature/intact forests (not limited to unmanaged broadleaf evergreen) are presented in the Supporting Information (Tables S2–S7).

C cycling in regrowth forests

C stocks commonly exhibited significant age trends both across and within age categories (Figs 3–6).

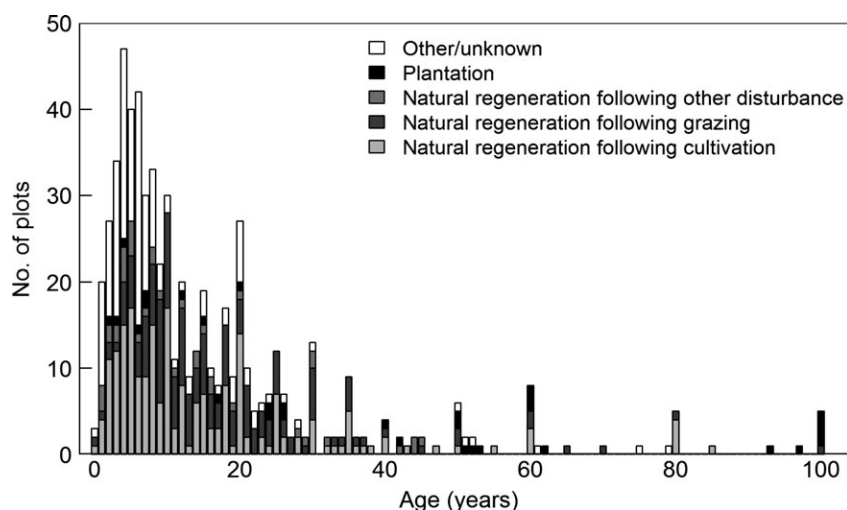


Fig. 2 Histogram of stand age distribution for young and intermediate stands within TropForC-db, broken down by regeneration types, in the order as shown in the legend. The database also contains 380 mature forest plots (old-growth or age >100; not shown here).

Trends were similar when all forests were included and when analyses were limited to unmanaged broad-leaf evergreen forests; here, we present results for the latter; those for all forests are presented in Tables S2–S4. Aboveground, total root, and total biomass all accumulated as forests aged and were highest on average in mature forest stands, with at least marginally significant differences (all $P < 0.07$) in all pairwise comparisons among young, intermediate and mature age classes (Figs 3–5; Tables S2–S4). Foliage biomass accumulated with age within the young forest age class: foliage C = $0.9 \pm 0.8 + \text{age} \times 0.3 \pm 0.03$ ($P < 0.001$; $n = 41$ records from 29 plots in seven areas), but did not vary significantly with age in intermediate-aged forests. Mean foliage biomass of mature forests was significantly higher than those of young forests ($4.2 \pm 0.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; $n = 18$ records from 14 plots in five areas), while that of intermediate forests did not significantly differ from either young or mature forests (Tables S2–S4). Fine root biomass differed significantly among age classes ($P < 0.05$, mixed effects model with age class as the only fixed effect and plot nested within area as the random effect); however, pairwise comparison of plot means between age classes using t-tests were nonsignificant (Tables S2–S4).

Aboveground biomass increased with stand age (Tables S2–S4; S8–S11), and was also significantly affected by regrowth type and FAO ecozone in young stands (Fig. 6a; Tables S8–S11). Specifically, in young stands, aboveground biomass increased with age ($P < 0.001$), and there was a significant age \times regeneration type interaction ($P < 0.001$), with the steepest slope for plantations and the shallowest slope following cultivation (Fig. 6a; Tables S8 and S9). When the analysis

was limited to naturally regenerating forests (*i.e.*, plantations excluded), aboveground biomass in young stands was significantly influenced by age ($P < 0.001$) and its interactions with both regeneration type ($P = 0.02$) and FAO ecozone ($P = 0.04$; Table S8), where biomass accumulated more rapidly in tropical rainforests and mountain systems than in moist deciduous forests (Table S10). For intermediate-aged stands, aboveground biomass again increased with stand age ($P < 0.001$), but was not significantly influenced by its interactions with regeneration type (natural regeneration following cultivation or pasture) or FAO ecozone (tropical rainforest or moist deciduous forest; all $P > 0.5$; Table S8).

Dead wood C also varied with stand age (Fig. 6b). It was highly variable in young stands, and there was no significant effect of age within the first 20 years of stand development. In intermediate-aged stands, stocks were lower and less variable, but increased with stand age (dead wood C = $0.6 \pm 2.3 + \text{age} \times 0.1 \pm 0.04$; $P = 0.02$). In mature stands, dead wood C was higher—averaging $18 \pm 4 \text{ Mg C ha}^{-1}$ —and quite variable, ranging from 7 to 46 Mg C ha^{-1} ($n = 9$ records from nine plots in five areas).

Potential to describe age trends in C fluxes was limited by the small number of records of C flux for young and intermediate-aged stands (Figs 3–5; Tables S1, S5–S7). The database contained only one NEE record for an unmanaged regrowth stand (4 years postfire). This forest was a stronger C sink (NEE = $-4.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, where negative sign indicates C sink) than was typical for mature stands (average -1.85 ± 0.69), but not outside the range of observed values (-5.6 to $+1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). There were a few significant trends in com-

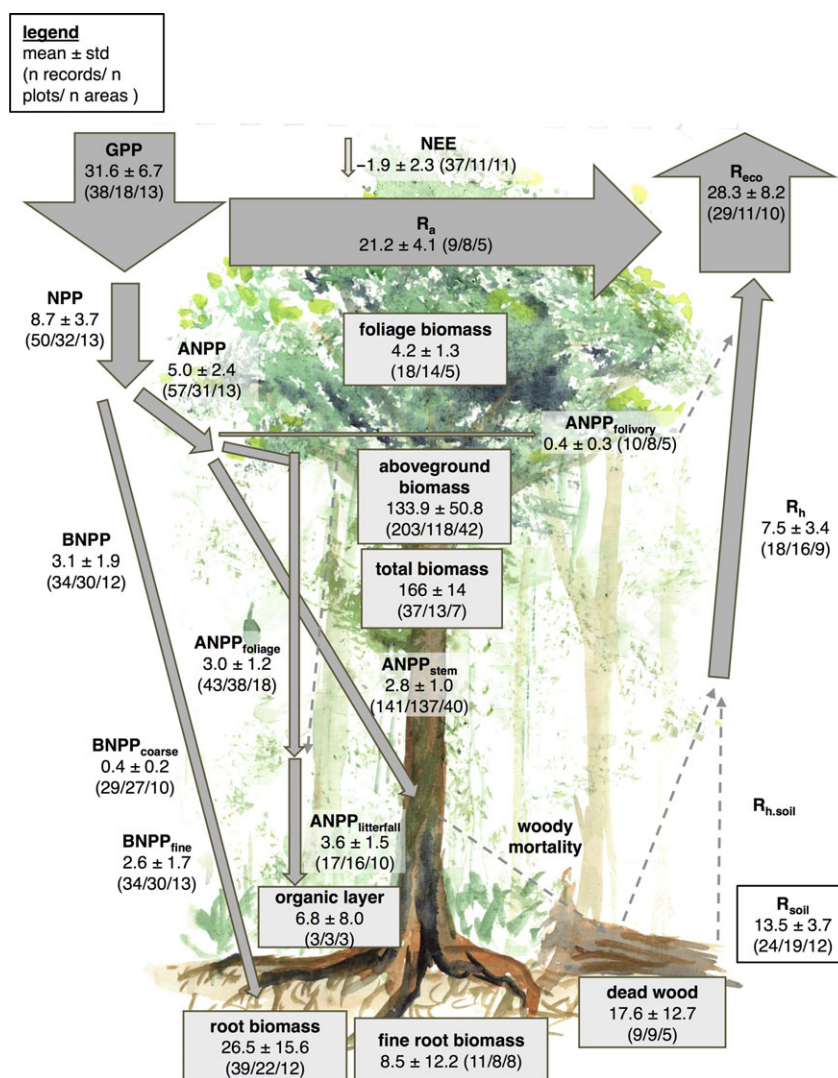


Fig. 3 Diagram of major C stocks and flows in mature (>100 year)/intact tropical broadleaf evergreen forests. Variables are as described in Tables 3 and 4, and detailed descriptive statistics are given in Tables S4 and S7. All units are Mg C ha^{-1} (stocks) or $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ (flux). Arrow width is scaled according to magnitude of flux. Dashed arrows indicate fluxes for which no data are included in the database.

ponents of ANPP. First, $\text{ANPP}_{\text{stem}}$ in unmanaged broadleaf evergreen forests declined across the age classes, with a significant difference between young and mature stands (Tables S5–S7): young stands averaged $3.9 \pm 0.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, intermediate-aged stands averaged $2.5 \pm 0.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, and mature stands averaged $2.7 \pm 0.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Figs 3–5). Second, ANPP increased with age in young unmanaged broadleaf evergreen stands: $-1.44 \pm 3.79 + \text{age} \times 1.34 \pm 0.33$ ($P = 0.02$). Finally, $\text{ANPP}_{\text{litterfall}}$ did not differ among age classes (Tables S5–S7), but did increase with age within the intermediate-age category (Tables S5–S7). There was no detectable age trend in

GPP, NPP, foliage ANPP, BNPP, fine root productivity, or soil or ecosystem respiration for unmanaged broadleaf evergreen forests (Tables S5–S7).

Discussion

Trop ForC-db and the status of tropical forest C data coverage

TropForC-db is the largest existing compilation of data on ground-based measurements of C stocks and fluxes in tropical forests. As such, it is valuable for new and more comprehensive analyses of C cycling in mature

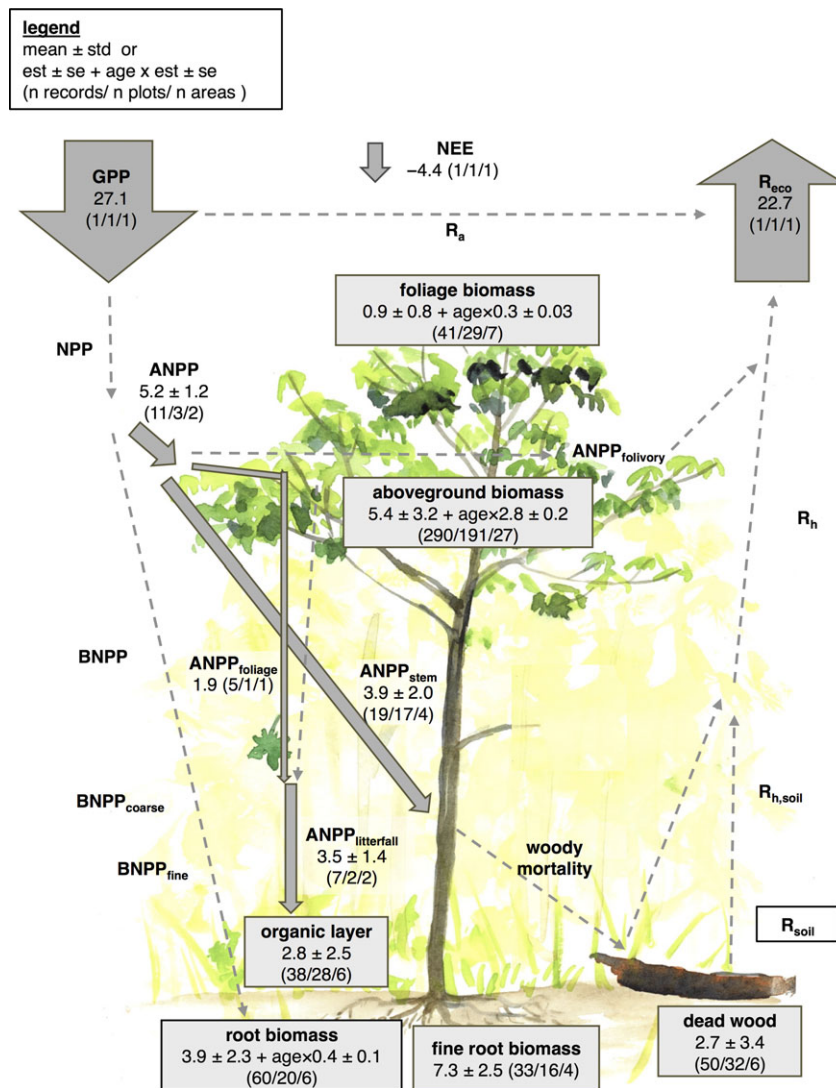


Fig. 4 Diagram of major C stocks and flows in young (<20 year) naturally regenerating tropical broadleaf evergreen forests. For variables with a significant age trend, regression parameters are given. Detailed descriptive statistics are given in Tables S2 and S5. Other numbers and symbols are as in Fig. 3.

and regrowth tropical forests, some of which are included here (e.g., Figs 3–6; Tables S2–S7). While the database represents a substantive effort to assemble existing data on tropical forest C stocks and fluxes, it is by no means complete in terms of including all available and relevant data. We encourage future studies that draw upon TropForC-db to seek out additional available data for the variables or forest types of interest and to contribute these data to the database at <https://github.com/forc-db>.

While the >3000 records included in TropForC-db represent a substantial body of data on tropical forest C stocks and fluxes, there remain important limitations in terms of data coverage, standardization, and uncertainty. Aboveground biomass is the variable with most

records (Tables 3 and 4), yet coverage within TropForC-db remains sparse for many parts of the tropics—particularly for deciduous forests and parts of Africa, Indomalaya, and Oceania (Fig. 1; Table S1). Moreover, biomass estimates are highly influenced by allometries, which are rarely available on a species- or region-specific basis in the tropics (Chave *et al.*, 2014). Measurements of other C stocks are more sparsely distributed and are also associated with sometimes-high uncertainty and lack of methods standardization; for example, root biomass measurements are labor-intensive and differ in sampling design, root size cut-offs, and sampling depth. Measurements of NPP and components thereof are more sparsely distributed. Moreover, there is variability in terms of how the components of

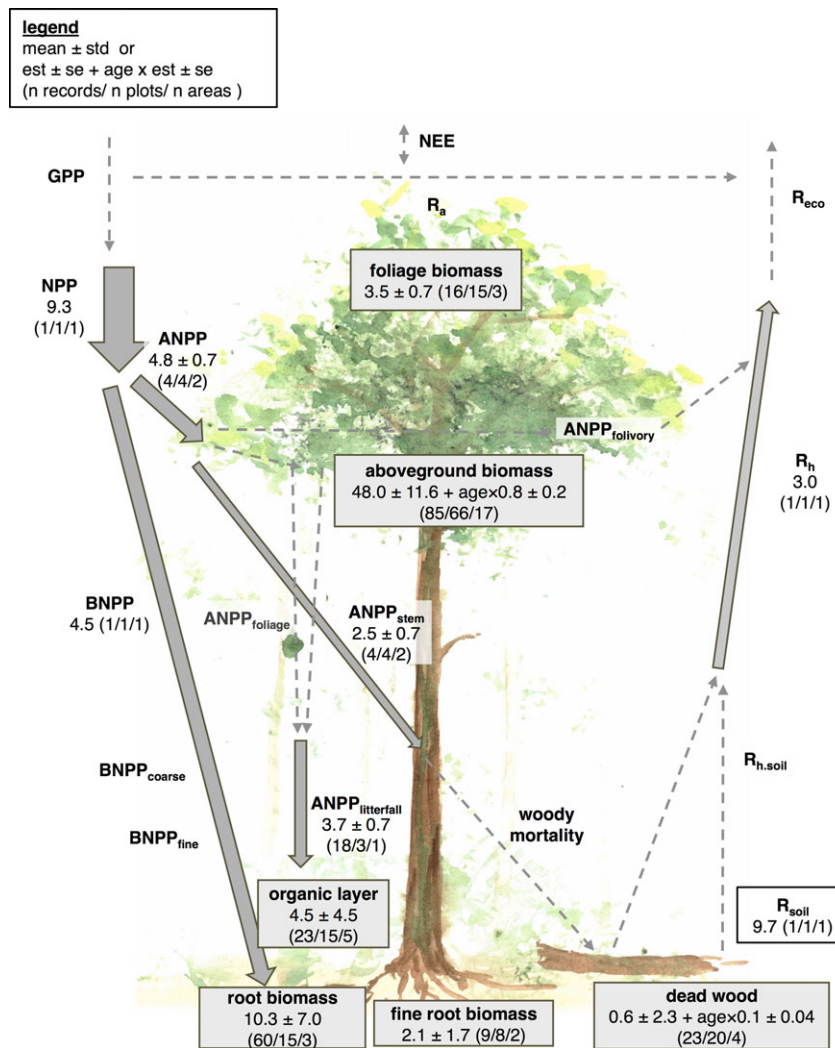


Fig. 5 Diagram of major C stocks and flows in intermediate-aged (20–100 year) naturally regenerating tropical broadleaf evergreen forests. For variables with a significant age trend, regression parameters are given. Detailed descriptive statistics are given in Tables S3 and S6. Other numbers and symbols are as in Fig. 3.

NPP are measured and which are included in estimates of total NPP, ANPP, or BNPP (*e.g.*, see multiple NPP variables and associated definitions in Anderson-Teixeira *et al.*, 2016; Luyssaert *et al.*, 2007). Measuring NPP in forests is challenging; many measurement methods are associated with high uncertainty, and some smaller yet potentially significant components of NPP—*e.g.*, herbivory, volatile organic C (VOC) production—are rarely quantified (Clark *et al.*, 2001a). Finally, measurements of ecosystem-atmosphere CO₂ exchange—NEE, GPP, and R_{eco}—are particularly challenging in tropical forests (Kruijt *et al.*, 2004), which are highly underrepresented in terms of eddy flux measurements (Schimel *et al.*, 2015). For C flux variables, coverage is particularly sparse in regrowth forests. Future research aimed at filling some of these gaps will be of great value.

C cycling in mature forests

TropForC-db allows the most comprehensive analysis to date of C cycling in mature tropical forests, including an ensemble C budget for mature unmanaged broadleaf evergreen forests (Fig. 3). The observed closure of this ensemble C budget is not necessarily to be expected, given that the averages reported here are derived from different sets of plots, that a variety of methodologies are employed (often ignoring smaller component fluxes), and that C flux measurements involve many methodological challenges. In part, the observed closure is attributable to high variability in the data; nevertheless, it suggests that the averages presented here are broadly accurate (or, less parsimoniously, that systematic biases cancel).

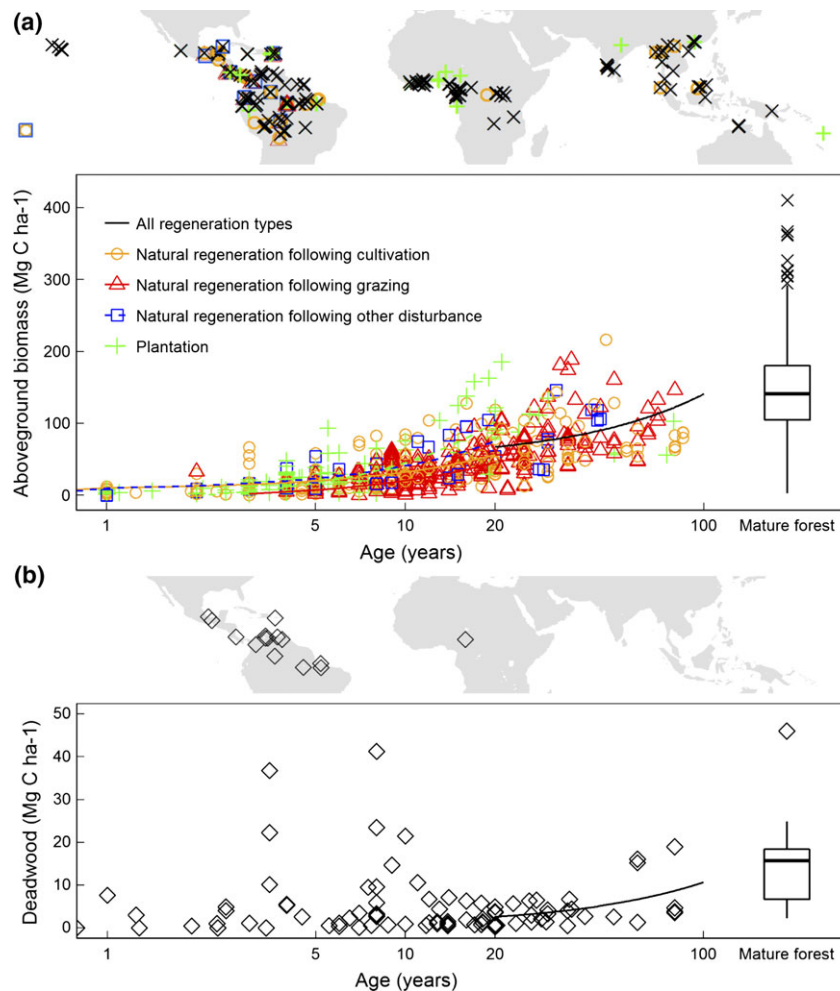


Fig. 6 Age trends in (a) aboveground biomass and (b) dead wood for forest regeneration following stand-clearing disturbances. Maps show the sites from which data were obtained. Forests are grouped by young, intermediate-aged, and mature/intact, showing separate statistical fits for each age class. Regression lines indicate mixed model where age and regeneration type (aboveground biomass in young stands only) are fixed effects and plot nested within area is a random effect (Tables S5–S7, S9 and S11).

It is important to bear in mind that this ensemble C budget is unlikely to be completely accurate for any given stand; rather, there is substantial variation around these means. Thus, for best estimates of C stocks or fluxes for a particular forest type or for calculation of C allocation parameters, we recommend recomputation of values based on specifically selected subsets of the database—as opposed to reliance on the means presented here.

Our ensemble estimates of C fluxes in mature unmanaged broadleaf evergreen forests (Fig. 3) are generally consistent with previous work characterizing tropical forest C budgets (e.g., Luyssaert *et al.*, 2007; Malhi, 2012). In terms of C fluxes, the only meaningful differences involve modest differences in GPP and net ecosystem productivity ($NEP \approx -NEE$; see Chapin *et al.*, 2006) from the means presented in Luyssaert *et al.* (2007), where our means are significantly lower than

this previous average but are not significantly lower than the 25th percentile of observations. Specifically, our average GPP, $31.6 \pm 1.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, is lower than Luyssaert *et al.*'s estimate of $35.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, and our average for NEP, $1.9 \pm 0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, is lower than Luyssaert *et al.*'s estimate of $4.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Our revised estimate of average NEP is closer to pantropical averages for C stock changes, being larger but not significantly so. Specifically, average C stock changes for pantropical forests have been estimated at $\sim 0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for 1990–2007 (Pan *et al.*, 2011), and a pantropical weighted average for changes in C stocks of aboveground biomass alone is $0.34 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (95% CI: $0.23\text{--}0.45 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Muller-Landau *et al.*, 2014). If our average NEP is not upwardly biased, this indicates that intact tropical forests are a somewhat stronger C sink than recently estimated (Pan *et al.*, 2011).

The ensemble C budget of mature unmanaged broadleaf evergreen forests differs from those of extra-tropical forests in three important ways. First, gross C fluxes into and out of the ecosystem, GPP and R_{eco} , are much larger than in extra-tropical forests, where they rarely exceed $20 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Luyssaert *et al.*, 2007). The high productivity is driven primarily by longer growing seasons, as opposed to higher productivity during the growing season (e.g., Hirata *et al.*, 2008; Malhi, 2012). Second, the ratio of NPP to GPP, or carbon use efficiency (CUE), is lower than average values observed for any forest biome globally. While the ratio of average NPP to average GPP is not the same as an average CUE, our $\text{NPP/GPP} = 0.28$ is in line with CUE's observed $0.27\text{--}0.46$ throughout the tropics (Malhi, 2012). This is on the low end of what has been observed in forests globally (DeLucia *et al.*, 2007; Litton *et al.*, 2007; Luyssaert *et al.*, 2007; Campioli *et al.*, 2015), but this finding is consistent with the fact that CUE tends to decline with both stand age and the ratio of leaf to total biomass (DeLucia *et al.*, 2007). A number of mechanisms may cause this low CUE, including high respiratory costs associated with high temperatures, greater maintenance costs associated with large tree size, greater C costs of defense, or 'idling respiration' of excess C (Chambers *et al.*, 2004; DeLucia *et al.*, 2007; Malhi, 2012). Third, the proportion of NPP allocated to stem productivity ($\text{ANPP}_{\text{stem}}$)—as opposed to root or leaf productivity (BNPP and $\text{ANPP}_{\text{foliage}}$, respectively)—is lower in the tropics than in other forest biomes (Luyssaert *et al.*, 2007). Specifically, $\text{ANPP}_{\text{stem}}$ equaled $\sim 32\%$ of total NPP in our C budget (Fig. 3; slightly higher than the 25% estimates of Malhi *et al.*, 2011 and Malhi, 2012), compared to values ranging from 34% in boreal semiarid evergreen forests to 76% in boreal humid evergreen forests (Luyssaert *et al.*, 2007). This may reflect the fact that the database of Luyssaert *et al.* (2007) includes some regrowth forests, which tend to allocate more C to $\text{ANPP}_{\text{stem}}$ (Figs 3–5), or it may indicate greater proportional allocation to leaves and roots in the tropics. Together, lower CUE and lower $\text{ANPP}_{\text{stem}}:\text{NPP}$ mean that $\text{ANPP}_{\text{stem}}$ of unmanaged broadleaf evergreen forests is similar to that of many extra-tropical forests (Luyssaert *et al.*, 2007; Huston & Wolverton, 2009). Thus, tropical forests metabolize far more C than extra-tropical forests, with most of the difference accounted for by high R_d and greater C allocation to functions other than woody growth.

Observed patterns of C allocation within mature unmanaged broadleaf evergreen forests (Fig. 3) have important implications for making inferences about forest productivity from commonly measured variables. The most commonly measured C fluxes in tropical forests are the largest components of ANPP: woody

productivity ($\text{ANPP}_{\text{stem}}$) and litterfall ($\text{ANPP}_{\text{foliage}}/\text{ANPP}_{\text{litterfall}}$; Table 3). In mature unmanaged broadleaf evergreen forests, $\text{ANPP}_{\text{stem}}$ equals approximately 32% of NPP and 9% of GPP, $\text{ANPP}_{\text{litterfall}}$ equals approximately 41% of NPP and 11% of GPP, and total ANPP equals approximately 57% of NPP and 16% of GPP (Fig. 3). Thus, measurements of ANPP and its components capture only a modest proportion of total productivity, and shifting C allocation in response to environmental variability implies that these are not good proxies for total productivity (Doughty *et al.*, 2015; Malhi *et al.*, 2015). We therefore caution against using these to infer responses of NPP or GPP to climatic variation. Nevertheless, understanding the responses of $\text{ANPP}_{\text{stem}}$ in particular to climatic variation is critical in that this C has a long residence time.

C cycling in regrowth forests

Aboveground biomass accumulation accounts for the majority of C sequestration by regrowth forests, and understanding the rate at which it accumulates is thereby critical to accurately characterizing the role of tropical regrowth forests in the global C cycle. The slopes of biomass-age mixed effects models are primarily derived from chronosequence data and as such do not necessarily equal to biomass accumulation rates—especially, for example, when the intercepts for young stands deviate substantively from zero. Therefore, these are not directly comparable to values used in global forest C inventories (e.g., Pan *et al.*, 2011; Grace *et al.*, 2014) or IPCC accounting (IPCC, 2006). However, our analyses yield insight into the relative influence of various factors on aboveground biomass accumulation rate. Among many variables examined—including climate variables, vegetation type, ecoregion, and biogeographic zone (analyses not shown)—regeneration type was the most important driver of regeneration rate (Fig. 6a). Specifically, in young forests, biomass accumulated most rapidly in plantations, as has been previously observed (Anderson *et al.*, 2006; Bonner *et al.*, 2013). Conversely, biomass accumulation was slowest following agricultural abandonment, which is consistent with previous work demonstrating that forest regrowth rate declines with increasing frequency and intensity of past agricultural disturbance (Uhl *et al.*, 1988; Fearnside & Guimaraes, 1996; Hughes *et al.*, 1999; Steininger, 2000; Lawrence, 2005; Lawrence *et al.*, 2010; Bonner *et al.*, 2013; de Mesquita *et al.*, 2015). The importance of regeneration type suggests that future tropical forest C inventories could be improved by accounting for disturbance history (Fig. 6a; Bonner *et al.*, 2013), along with seed availability or forest cover in the surrounding landscape (not analyzed here, but see Bonner

et al., 2013; de Mesquita *et al.*, 2015). Our analysis revealed that biomass accumulation in naturally regenerating young stands was higher in tropical rainforests and tropical mountain systems (this category included many lowland forests in our dataset) than tropical deciduous forests (Table S10), which is in broad agreement with previous studies showing an effect of precipitation on biomass accumulation rate and with IPCC values (Brown & Lugo, 1982; IPCC, 2006; Marín-Spiotta *et al.*, 2008; Poorter *et al.*, 2016). In summary, aboveground biomass increases rapidly with stand age during the first 20 years following stand-clearing disturbance, with slower accumulation in deciduous forests and following agriculture.

While biomass accumulation decelerates in intermediate-aged stands, there remains a significant effect of age on aboveground biomass for stands aged 20–100 years (Fig. 6a; Table S3). The ongoing accumulation of biomass in intermediate-aged stands implies that C inventories, which commonly lump regrowth forests >20 years old with mature/intact forests (IPCC, 2006), could be improved by distinguishing older regrowth forests from mature/intact forests, when feasible. By age 100, regrowth forests on average have similar aboveground biomass to mature/intact forests (Fig. 6a). However, the time required for biomass to recover to the levels of adjacent undisturbed forests is variable (Martin *et al.*, 2013), and successional processes may continue to drive biomass accumulation even in forests with no known history of stand-clearing disturbance (Chave *et al.*, 2008).

Beyond aboveground biomass, which accounts for approximately 60–90% of C sequestration in tropical regrowth forests, other C stocks also increase as forests age (Figs 3–5, Tables S2–S4). Carbon accumulation in leaves, roots, and dead wood follows different temporal patterns than aboveground biomass (see also Martin *et al.*, 2013). Foliage biomass accumulates rapidly in young forests, and does not increase markedly thereafter—a pattern that is common in forests globally (Anderson-Teixeira *et al.*, 2013). Total root biomass effectively tracks aboveground biomass (Tables S2–S4), whereas we detected no age-related trends in fine root biomass. Dead wood accumulation lags behind live biomass accumulation, as has been observed in temperate forest stand development (Harmon, 2009). Following decomposition of legacy dead wood in young stands, dead wood accumulation also contributes to the C sink of regrowth forests, sequestering on average $0.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in intermediate-aged forests, and likely continuing to accumulate beyond stand age 100 (Fig. 6b), as has been observed in temperate forests (Janisch & Harmon, 2002; McGarvey *et al.*, 2014). These findings—combined with eddy covariance measurements

indicating that mature unmanaged broadleaf evergreen forests are C sinks (Fig. 3), indicate that tropical forests continue to accumulate C beyond 100 years of age.

Carbon accumulation in regrowth forests is fueled by GPP and its allocation among various C flux terms. However, scant data on C fluxes in tropical regrowth forests (Figs 4–5; Table S1) and the fact that comparisons are being made across forests that vary in many factors other than age limit generalizations about age trends in C fluxes. Our analysis detected no differences across young, intermediate-aged, and mature forests in NEE, respiration (R_{eco} , R_h , R_{soil} , etc.), GPP, NPP, BNPP, or most major components of NPP (ANPP, $\text{ANPP}_{\text{foliage}}$, $\text{ANPP}_{\text{litterfall}}$, BNPP, $\text{BNPP}_{\text{fine}}$). For many of these variables, existing age trends would not be detectable because of data limitations. However, the lack of detectable age trends in some of these variables is also broadly consistent with observations from higher-latitude forests, where GPP and NPP quickly plateau as forests age, sometimes followed by a modest decline, and where heterotrophic respiration, R_h , appears to be roughly invariant with stand age (Anderson-Teixeira *et al.*, 2013 and refs therein). Contrasting with the lack of an age trend in ANPP, the decline in $\text{ANPP}_{\text{stem}}$ from young to mature stands indicates decreasing C allocation to stem growth as stands age, eventually declining to an average of only ~6% of GPP in mature/intact unmanaged broadleaf evergreen forests (Figs 3–5). Additional measurements of C flux in regrowth tropical forests will be required to clarify how patterns of C flux and allocation change as stands age.

Implications & future directions

TropForC-db is the largest database on ground-based measurement of ecosystem level C stocks and fluxes in tropical forests, and as such allows us to provide the most comprehensive synthesis to date of C cycling in tropical regrowth and mature forests (Figs 3–6). Our findings refine estimates of average C stocks and fluxes using a more comprehensive pantropical data set and complement findings of previous work.

Moving forward, we anticipate that TropForC-db will be of value for various initiatives seeking to understand and manage the role of tropical forests in the global C cycle. Specifically, the data will be useful for synthetic analyses seeking to better understand tropical forest C stocks and flows, how these are shaped by past disturbance, and how they are influenced by environmental factors. It will also be of value for model calibration, benchmarking, and improvement, and will be integrated into the BETYdb/PEcAn ecosystem modeling system (LeBauer *et al.*, 2010, 2012). Finally, TropForC-db can be used to provide more accurate

estimates of C stocks and fluxes for regional to global scale tropical forest C inventories (e.g., IPCC, 2006; Pan *et al.*, 2011). For instance, estimates of biomass accumulation rates in regrowth forests used by previous studies estimating regional to global scale tropical forest C balances (e.g., Houghton *et al.*, 2000; Achard *et al.*, 2004; Pan *et al.*, 2011) and current IPCC greenhouse gas inventory guidelines (IPCC, 2006) are underlain by only a subset of the data in TropForC-db.

We anticipate ongoing development of the database. In addition to archiving of the data associated with this publication (Anderson-Teixeira *et al.*, 2016), we plan to maintain a dynamic instance of the database including forests globally (ForC-db), which can be accessed <https://github.com/forc-db>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Classification of plots and areas included in the TropForC-db database.

Table S2. Descriptive statistics on C stocks for young (<20) tropical forest stands.

Table S3. Descriptive statistics on C stocks for intermediate-aged (20 < age<100) tropical forest stands.

Table S4. Descriptive statistics on C stocks for mature (age>100)/intact tropical forest stands.

Table S5. Descriptive statistics on C fluxes for young (<20) tropical forest stands.

Table S6. Descriptive statistics on C fluxes for intermediate-aged (20 < age<100) tropical forest stands.

Table S7. Descriptive statistics on C fluxes for mature (age > 100)/intact tropical forest stands.

Table S8. Linear mixed-effects models for aboveground biomass in young and intermediate- aged stands.

Table S9. Parameter estimates for linear mixed-effects model for aboveground biomass in young stands, where age and its interaction with regeneration type are fixed effects.

Table S10. Parameter estimates for linear mixed-effects model for aboveground biomass in naturally regenerating young stands, where age and its interactions with regeneration type and FAO ecozone are fixed effects.

Table S11. Parameter estimates for linear mixed-effects model for aboveground biomass in naturally regenerating intermediate-aged, where age is the fixed effect.