Received: 1 December 2020 | Accepted: 1 June 2021

DOI: 10.1111/1365-2745.13723

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

The fate and transit time of carbon in a tropical forest

Carlos A. Sierra[1,2] | Lina M. Estupinan-Suarez[1] | Ingrid Chanca[1]

[1]Max Planck Institute for Biogeochemistry, Jena, Germany

[2]Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Carlos A. Sierra
Email: csierra@bgc-jena.mpg.de

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: 01LK1602A

Handling Editor: Gabriela Bielefeld Nardoto

Abstract

1. Tropical forests fix large quantities of carbon from the atmosphere every year; however, the fate of this carbon as it travels through ecosystem compartments is poorly understood. In particular, there is a large degree of uncertainty regarding the time carbon spends in an ecosystem before it is respired and returns to the atmosphere as CO_2.
2. We estimated the fate of carbon (trajectory of photosynthetically fixed carbon through a network of compartments) and its transit time (time it takes carbon to pass through the entire ecosystem, from fixation to respiration) for an old-growth tropical forest located in the foothills of the Andes of Colombia.
3. We show that on average, 50% of the carbon fixed at any given time is respired in < 0.5 years, and 95% is respired in < 69 years. The transit time distribution shows that carbon in ecosystems is respired on a range of time-scales that span decades, but fast metabolic processes in vegetation dominate the return of carbon to the atmosphere.
4. *Synthesis*. The transit time distribution integrates multiple ecosystem processes occurring at a wide range of time-scales. It reconciles measurements of the age of respired CO_2 with estimates of mean residence time in woody biomass, and provides a new approach to interpret other ecosystem level metrics such as the ratio of net primary production to gross primary production.

KEYWORDS

carbon use efficiency, ecosystem respiration, global carbon cycle, model data assimilation, transit times, tropical forests

1 | INTRODUCTION

The terrestrial biosphere photosynthesizes annually about 120 ± 7 PgC/year, a flux that is largely driven by productivity in the tropics (Beer et al., 2010; Jung et al., 2020) where gross primary production (GPP) is often larger than $30\,MgC\,ha^{-1}\,year^{-1}$ (Fu et al., 2018). Most of this photosynthetically fixed carbon is assumed to return quickly to the atmosphere, with ecosystem respiration (*Re*) being often as large as the GPP flux (Chambers et al., 2004; Fu et al., 2018; Luyssaert et al., 2007). It is likely that between 50% and 70% of the GPP flux in tropical ecosystems is lost as autotrophic respiration (Chambers et al., 2004; DeLucia et al., 2007; Doughty et al., 2018; Gifford, 2003; Waring et al., 1998); however, it is uncertain if the respiratory flux is composed mostly of recent photosynthates or of carbon that spends years to decades stored in the ecosystem.

The time that carbon fixed as GPP spends in an ecosystem is of relevance to understand feedbacks between ecosystems and the climate system. During the time carbon is stored in ecosystems as

organic compounds, it does not contribute to the greenhouse effect in the atmosphere (Neubauer & Megonigal, 2015; Noble et al., 2000; Sierra et al., 2020). Therefore, whether respired carbon from ecosystem is young or old, gives an idea of the time photosynthetically fixed carbon remains stored. This lapse of time when carbon is removed from the atmosphere is particularly relevant for tropical ecosystems given their dominance in the global GPP flux.

Studies with tropical trees have shown that healthy mature trees respire mostly recent carbon assimilates (< 2 years-old carbon), but can respire decades-old carbon under stress (Muhr et al., 2013, 2018; Vargas et al., 2009). In fact, observational studies with temperate trees as well as modelling studies have shown that trees can respire carbon of a wide range of ages, from days- to decades-old carbon (Carbone et al., 2013; Ceballos-Núñez et al., 2018; Herrera-Ramírez et al., 2020; Trumbore et al., 2015). Therefore, one would expect that respiration in tropical ecosystems is composed by a mixture of carbon of different ages (Trumbore, 2006; Trumbore & Barbosa De Camargo, 2013), but such a mixture is difficult to quantify. Isotopic labelling experiments in temperate ecosystems have shown that respired carbon is mostly young, but with a high degree of mixing difficult to characterize from the isotopic data alone (Hopkins et al., 2012; Keel et al., 2006).

In contrast to isotopic labelling studies, data from permanent plots across the tropics suggest that carbon stays in the woody biomass pool, on average, by about 50 years or more (Galbraith et al., 2013; Malhi et al., 2013). Plot-level estimates of the time carbon stays in the woody biomass of tropical forests are commonly obtained by dividing wood biomass carbon stocks over stem growth. This approach relies on three main assumptions: (1) the forests are in a dynamic equilibrium in which inputs of carbon are balanced by losses from mortality and respiration, (2) the obtained mean value characterizes an unknown underlying distribution of the time carbon spends in an ecosystem and (3) the woody biomass pool is representative of the dynamics of the entire ecosystem, so dynamics in detritus and soil carbon pools can be ignored. Assumption 1 is reasonable for old-growth tropical forests because it is expected that over the long-term, climate variability, disturbances and internal forest dynamics would balance the net carbon flux around a mean value of zero, but with important variability in fluxes from year to year (Chambers et al., 2013; Sierra et al., 2009). A deeper exploration of Assumptions 2 and 3 may help to explain the large difference between tree- and plot-level estimates of the time carbon spends in tropical ecosystems.

The fate of carbon through an ecosystem and the time it spends there, from photosynthesis until respiration, is well captured by the concept of transit time (Bolin & Rodhe, 1973; Rasmussen et al., 2016; Sierra et al., 2017; Thompson & Randerson, 1999). This concept quantifies the time it takes carbon atoms to travel through the entire ecosystem and links three main ecosystem processes: photosynthesis, storage and respiration. It can be expressed as a probability mass function that quantifies the time it takes to respire a proportion of carbon fixed at a given time. Under the assumption of equilibrium, the total carbon stock divided by the total input or output flux provides an estimate of the mean of the transit time distribution (Sierra et al., 2017). Therefore, estimates of the entire transit time distribution of carbon in tropical forests would help us to better understand not only the mean time carbon spends in the woody biomass, but also the time recent photosynthates spend in trees before being respired, and the time it takes for carbon that enters the soil to appear in the respiratory flux. This transit time distribution captures all these different processes over a wide range of time-scales.

In this manuscript, we provide an estimate of the transit time distribution of carbon in a tropical forest ecosystem using a data assimilation technique to parameterize a dynamic ecosystem model. Our main hypothesis is that the shape of the transit time distribution reconciles estimates of the time carbon spends in ecosystems obtained from tree- and plot-level methods. Furthermore, we attempt to provide here the formal theory to not only obtain the transit time distribution, but also metrics to characterize the fate of carbon inputs through the entire ecosystem as well as the age of carbon in ecosystem pools. This theory is then used to present an alternative interpretation of the link between GPP, autotrophic respiration (*Ra*) and net primary production (NPP).

2 | THEORY

The time that carbon spends in ecosystems can be obtained using the concept of transit time (Bolin & Rodhe, 1973; Rasmussen et al., 2016; Sierra et al., 2017; Thompson & Randerson, 1999). It characterizes the time carbon atoms spend in an ecosystem, from the time of carbon fixation through photosynthesis until release to the atmosphere through respiration in the absence of fire.

To compute transit times, we will consider a special case of the general mathematical representation of ecosystem carbon dynamics that follows the compartmental system representation proposed in Sierra et al. (2018). Since we are concerned in this manuscript with tropical old-growth forests at equilibrium, we will represent carbon dynamics with differential equations in multiple pools using a linear autonomous compartmental system of the form

$$\frac{d\boldsymbol{x}}{dt} = \dot{\boldsymbol{x}}(t) = \boldsymbol{u} + \mathbf{B}\boldsymbol{x}(t), \tag{1}$$

where the vector $\boldsymbol{u}$ represents total carbon inputs from the atmosphere to ecosystem pools, and the matrix $\mathbf{B}$ represents all cycling and transfer rates of carbon within the ecosystem. Linear first order models of differential equations are the most common representation of carbon dynamics in ecosystem and land surface models (Ceballos-Núñez et al., 2020; Huang et al., 2018; Luo & Weng, 2011; Luo et al., 2017). These linear autonomous compartmental systems at equilibrium have steady-state carbon stocks equivalent to

$$\boldsymbol{x}^* = -\mathbf{B}^{-1}\boldsymbol{u}. \tag{2}$$

At this equilibrium point, where inputs from photosynthesis are balanced by losses from ecosystem respiration, it is possible to compute

the *fate* of carbon inputs entering at an arbitrary time t_0, defined as the trajectory of photosynthetically fixed carbon through the network of ecosystem compartments. This fate of carbon can be computed using the matrix exponential of the compartmental matrix (Sierra et al., 2020). Explicitly, the mass of carbon remaining in the ecosystem after photosynthetic fixation can be obtained as

$$\boldsymbol{M}(t) = e^{(t-t_0)\mathbf{B}}\,\boldsymbol{u}, \tag{3}$$

where $e^{(t-t_0)\mathbf{B}}$ is the matrix exponential. In other words, photosynthetic inputs are lost from the ecosystem according to an exponential term that takes into account possible transfers of matter among compartments that are encapsulated in the matrix $\mathbf{B}$.

Carbon that is lost from each pool and that is not transferred to other pools is lost from the system as respiration. Therefore, the rate of respiratory losses can be obtained as the sum of all column elements of the compartmental matrix as

$$\boldsymbol{z}^{\intercal} = -\mathbf{1}^{\intercal}\mathbf{B}, \tag{4}$$

where $\intercal$ is the transpose operator and $-\mathbf{1}^{\intercal}$ is a row vector containing 1 (i.e. by this multiplication the column sum of $\mathbf{B}$ is obtained). Therefore, $\boldsymbol{z}^{\intercal}$ is a row vector of rates of carbon loss from each pool. Total respiratory losses are thus proportional to the amount of carbon stored at any time t. If we focus on the fate of inputs entering at t_0, we can thus obtain the amount of respiratory losses as

$$\begin{aligned} R(t) &= \boldsymbol{z}^{\intercal}\boldsymbol{M}(t) \\ &= -\mathbf{1}^{\intercal}\mathbf{B}\,e^{(t-t_0)\mathbf{B}}\,\boldsymbol{u}. \end{aligned} \tag{5}$$

This function represents how carbon that enters at a particular time t_0 is lost from the system. This equation is virtually similar to the *transit time* distribution function derived by Metzler and Sierra (2018) and expressed as

$$f_T(\tau) = -\mathbf{1}^{\intercal}\mathbf{B}\,e^{\tau\mathbf{B}}\frac{\boldsymbol{u}}{\|\boldsymbol{u}\|}. \tag{6}$$

Assuming that $\tau = t - t_0$, we can see that Equations (5) and (6) are identical, with the only difference that $f_T(\tau)$ is a density function that integrates to the value of one, while $R(t)$ is a mass function that integrates to the total input mass $\|\boldsymbol{u}\|$. The symbol $\|\ \|$ represents the sum of all elements inside the vector.

We can see now that the transit time distribution can be interpreted as the time it takes for carbon entering the ecosystem as GPP to appear in the respiratory flux.

Rasmussen et al. (2016) have previously shown that the mean transit time is composed by the contribution to respiration of ecosystem carbon pools with specific mean ages. It is therefore of interest to compute the age distribution for each individual pool and for the entire ecosystem. According to Metzler and Sierra (2018), the vector of density distributions of age for individual pools can be obtained as

$$\boldsymbol{f_a}(\tau) = (\mathbf{X}^*)^{-1}\,e^{\tau\mathbf{B}}\,\boldsymbol{u}, \tag{7}$$

where $\mathbf{X}^* = \mathrm{diag}\left(x_1^*, x_2^*, \ldots, x_n^*\right)$ is the diagonal matrix with the steady-state vector of carbon stocks as components. The age distribution function for the entire system is given by

$$f_A(\tau) = -\mathbf{1}^{\intercal}\mathbf{B}\,e^{\tau\mathbf{B}}\frac{\boldsymbol{x}^*}{\|\boldsymbol{x}^*\|}. \tag{8}$$

These age distributions can help us to better understand how carbon of different ages contributes to the total respiratory flux in an ecosystem.

3 | MATERIALS AND METHODS

To obtain the transit time distribution of carbon for an old-growth tropical forest ecosystem, we implemented a model data assimilation procedure that integrates a compartmental dynamical model with carbon stock and flux data from a tropical pre-montane region in Colombia. We used carbon stock data collected at the Porce region of Colombia (6°45′37″N, 75°06′28″W, 800–1,000-m elevation above sea level, 2,078-mm mean annual precipitation, 21.3°C mean annual temperature), where intensive studies have been conducted to obtain carbon accumulation over time along a sequence of secondary forests recovering from grazing and agricultural land use (del Valle et al., 2011; Sierra et al., 2007a, 2012; Yepes et al., 2010). The landscape also contains elements of old-growth forests with no evidence of previous disturbance. The most relevant species in the old-growth forests, according to their abundance, density and dominance (importance value index), are *Oenocarpus bataua* Mart., *Pourouma cecropiaefolia* Mart., *Jacaranda copaia* (Aubl.) D. Don, *Anacardium excelsum* (Bertero and Balb. ex Kunth), and *Euterpe* sp. (Yepes et al., 2010).

We used data previously collected on above- and below-ground biomass, the biomass of fine and coarse roots, the mass of fine litter and coarse woody debris, and soil carbon stocks up to 30-cm depth (Table 1). We used data from 33 plots from secondary forests where we have a comprehensive inventory of all major carbon stocks, using locally derived biomass equations for trees, palms and coarse roots, and measurements of individual trees with diameter at breast height > 1 cm (del Valle et al., 2011; Sierra et al., 2007a; Yepes et al., 2010). We also used estimates of carbon stocks for the old-growth forests were similar measurements were conducted.

Together, these observations were used in a data assimilation procedure to fit a linear compartmental system of the form of Equation (1), using as carbon inputs satellite-derived estimates of GPP for the region as reported in Tramontana et al. (2016) and Ryu et al. (2011) (updated in Jiang & Ryu, 2016). In particular, we used the average ± standard deviation of GPP for the period between 2001 and 2015 from Jiang and Ryu (2016) at 1 km and 8-day resolution, which gives a value of $22.89 \pm 2.46\,\mathrm{MgC\,ha^{-1}\,year^{-1}}$. Average GPP for the same period at 10 km and 8 day resolution from Tramontana et al. (2016) gives a value of $24.4 \pm 1.02\,\mathrm{MgC\,ha^{-1}\,year^{-1}}$. A combined estimate of GPP for the region with uncertainty propagation gives a value of $23.98 \pm 2.36\,\mathrm{MgC\,ha^{-1}\,year^{-1}}$ (see code in Supporting Information).

TABLE 1 Summary of field data used for obtaining ecosystem carbon pools from the study area

Ecosystem C pool	Field measurement	Method
Foliage and Wood	Tree above-ground biomass	Local biomass equations and plot inventories
	Palm above-ground biomass	Local biomass equations and plot inventories
	Herbaceous vegetation	Sampling quadrants within plots
Fine roots	Fine root biomass	Soil core sampling, root diameter < 5 mm
Coarse roots	Coarse root biomass	Local biomass equations and plot inventories
Fine litter	Fine litter mass	Sampling quadrants within plots
Coarse woody debris	Coarse woody debris mass	Subplot sampling
Soil carbon	Soil organic carbon from 0 to 15 and 15 to 30-cm depth	Soil core sampling

Note. Specific details about sampling plots, biomass equations and replication can be found in Sierra et al. (2007a, 2012). All data are provided in Supporting Information.

The model has seven pools, x_1: foliage, x_2: wood, x_3: fine roots, x_4: coarse roots, x_5: fine litter, x_6: coarse woody debris, and x_7: soil carbon from 0 to 30 cm depth (Figure 1). In the model, all carbon fixed as GPP enters through the foliage compartment; that is, $u_1 = \mathrm{GPP}$, and from there carbon is transferred to the x_2, x_3, and x_4 pools according to transfer coefficients $\alpha_{i,j}$ that represent the proportional transfers of material from pool j to pool i. We make the implicit assumption that photosynthetically fixed carbon stored as non-structural carbohydrates in the foliage can be mobilized and allocated to wood, fine and coarse roots. Transfers from the vegetation pools to the litter and soil pools were also represented using transfer coefficients $\alpha_{i,j}$. In particular, the dynamic model has the form

$$\begin{pmatrix}\dot{x}_1\\ \dot{x}_2\\ \dot{x}_3\\ \dot{x}_4\\ \dot{x}_5\\ \dot{x}_6\\ \dot{x}_7\end{pmatrix} = \begin{pmatrix}\mathrm{GPP}\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\end{pmatrix} + \begin{pmatrix} -k_1 & 0 & 0 & 0 & 0 & 0 & 0\\ \alpha_{2,1}k_1 & -k_2 & 0 & 0 & 0 & 0 & 0\\ \alpha_{3,1}k_1 & 0 & -k_3 & 0 & 0 & 0 & 0\\ \alpha_{4,1}k_1 & 0 & 0 & -k_4 & 0 & 0 & 0\\ \alpha_{5,1}k_1 & 0 & \alpha_{5,3}k_3 & 0 & -k_5 & 0 & 0\\ 0 & \alpha_{6,2}k_2 & 0 & \alpha_{6,4}k_4 & 0 & -k_6 & 0\\ 0 & 0 & 0 & 0 & \alpha_{7,5}k_5 & \alpha_{7,6}k_6 & -k_7\end{pmatrix}\begin{pmatrix}x_1\\ x_2\\ x_3\\ x_4\\ x_5\\ x_6\\ x_7\end{pmatrix}, \quad (9)$$

where the cycling rates for each pool i are denoted as k_i, and the transfer coefficients from a pool j to a pool i are denoted as $\alpha_{i,j}$.

Measurements of above-ground tree biomass and palm biomass were aggregated and transformed to foliage biomass using a fraction of foliage of 0.08 (Zapata & del Valle, 2001). This foliage fraction is based on site-level measurements used for the development of local biomass equations (Sierra et al., 2007a). Measurements of biomass of herbaceous vegetation were added to this foliage biomass pool. To obtain values for the wood biomass pool, we used the aggregated values of tree and palm above-ground biomass multiplied by a fraction of wood biomass of 0.92.

The data assimilation procedure used random variates of GPP and carbon stocks in old-growth forests sampled from a normal distribution of mean values with their corresponding standard deviation. We used 1,000 random variates for GPP and 33 random variates (equivalent to the original sample size) for the old-growth carbon stocks, which were used to find 1,000 sets of parameter values for the model using the Levenberg-Marquardt optimization algorithm (Soetaert & Petzoldt, 2010). The algorithm finds parameter values that minimize the difference between model predictions and the join set of observations of carbon stocks for all pools.

Using the average of the entire set of parameter values, we computed representative distributions of age and transit time using Equations (7), (8) and (6). We also obtained estimates of autotrophic (*Ra*) and heterotrophic respiration (*Rh*) by splitting the vector of respiration for all pools (Equation 5) between autotrophic pools (foliage, wood, fine and coarse roots) and heterotrophic pools (fine litter, coarse woody debris, soil carbon), respectively. With these

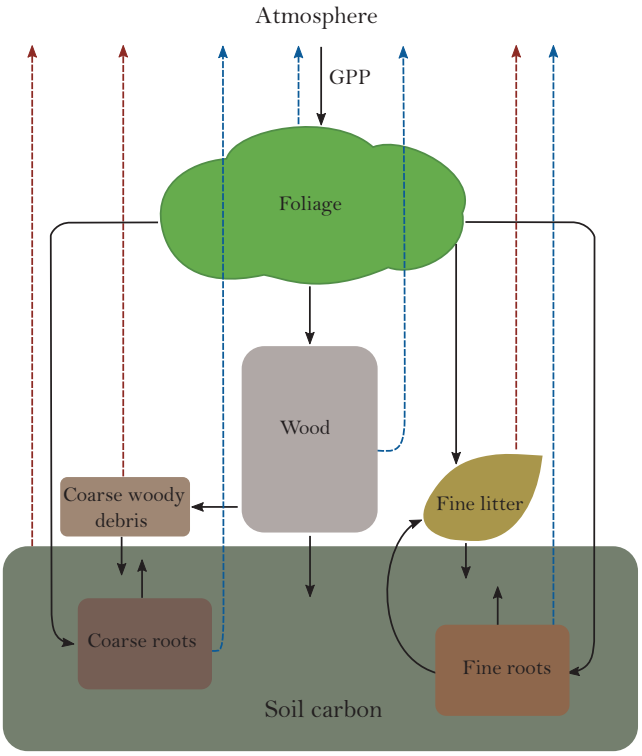

FIGURE 1 Structure of the compartmental model used to fit the available data from the Porce region of Colombia. Arrows represent transfers of carbon among pools (continuous line) or respiratory losses (dashed lines) to the atmosphere. Autotrophic respiration fluxes in dark blue and heterotrophic respiration fluxes in dark red

respiration estimates, we then computed net primary production NPP as the difference GPP − *Ra*.

All computations were performed in R version 4.0, and code to reproduce all results is available from Zenodo: http://doi.org/10.5281/zenodo.4893606 (Sierra, 2021).

4 | RESULTS

4.1 | Model data assimilation

We obtained 1,000 sets of parameter values of the dynamic model that provide the best fit between predictions and observations, taking into account the uncertainty and variability in GPP and steady-state carbon stocks. These parameter sets were used to compute uncertainty ranges for the predictions of the dynamic model, and to obtain one average parameter set considered as representative for the entire ensemble of parameters. Averages of the obtained parameter values, together with their uncertainty, are shown in Table 2.

TABLE 2 Mean and standard deviation (*SD*) of parameter values obtained from the 1,000 iterations of the optimization procedure

Parameter	Description	Mean	*SD*
k_1	Cycling rate in foliage	2.978	0.041
k_2	Cycling rate in wood	0.035	0.000
k_3	Cycling rate in fine roots	0.027	0.011
k_4	Cycling rate in coarse roots	0.022	0.000
k_5	Cycling rate in fine litter	2.594	0.520
k_6	Cycling rate in coarse woody debris	0.519	0.789
k_7	Cycling rate in soil carbon	0.024	0.015
$\alpha_{2,1}$	Proportion transferred from foliage to wood	0.158	0.017
$\alpha_{3,1}$	Proportion transferred from foliage to fine roots	0.009	0.003
$\alpha_{4,1}$	Proportion transferred from foliage to coarse roots	0.031	0.003
$\alpha_{5,1}$	Proportion transferred from foliage to fine litter	0.251	0.061
$\alpha_{5,3}$	Proportion transferred from fine roots to fine litter	0.997	0.005
$\alpha_{6,2}$	Proportion transferred from wood to coarse woody debris	0.249	0.172
$\alpha_{6,4}$	Proportion transferred from coarse roots to coarse woody debris	0.001	0.000
$\alpha_{7,5}$	Proportion transferred from fine litter to soil carbon	0.256	0.144
$\alpha_{7,6}$	Proportion transferred from coarse woody debris to soil carbon	0.988	0.045

Note. Values of cycling rates are given in units of year^{-1}, and values of transfer coefficients are unitless (proportion between 0 and 1).

Observations of carbon stocks along the successional sequence, together with possible values of GPP and carbon stocks in old-growth forests, provided relatively good fit to a linear autonomous compartmental system with seven pools (Figure 2). The variability in model predictions was much lower for the wood and the coarse root biomass pools than for other ecosystem pools. Except for soil carbon, the model predicts rapid accumulation of carbon in all compartment during succession consistent with previous analyses for this chronosequence (del Valle et al., 2011; Sierra et al., 2007a, 2012; Yepes et al., 2010).

The model predicts a steady-state carbon stock of 263.9 ± 2.0 MgC/ha, which is within the upper range of the observations of total carbon stocks (with soil carbon up to 30-cm depth) of 252.4 ± 20.2 for the primary forests of the region (Sierra et al., 2007a).

At equilibrium, total ecosystem respiration (*Re*) is predicted as $23.7 \pm 2.5\,\text{MgC}\,\text{ha}^{-1}\,\text{year}^{-1}$, from which 70% corresponds to autotrophic respiration (*Ra*, $16.7 \pm 3.1\,\text{MgC}\,\text{ha}^{-1}\,\text{year}^{-1}$) and 30% to heterotrophic respiration (*Rh*, $7.0 \pm 1.5\,\text{MgC}\,\text{ha}^{-1}\,\text{year}^{-1}$).

4.2 | Fate of gross primary production

Using the set of average parameter values (Table 2), we obtained a representative function for the fate of carbon once it enters the ecosystem; that is, the amount of remaining carbon after photosynthetic fixation computed using Equation (3) (Figure 3). The model predicts that once carbon is fixed and incorporated in the foliage mass, it is lost within a third of a year ($k_1 = 2.978$/year), due to autotrophic respiration (55%) and to transfers to other pools (45%). In particular, about 25% of the losses from the foliage pool are transferred to the fine root pool ($\alpha_{5,1}$), and about 16% to the wood pool ($\alpha_{2,1}$) (Table 2); however, carbon is lost quickly from the fine litter pool while it stays for longer in the wood pool (Figure 3).

Within a few years after fixation, carbon is transferred to the soil pool where it can remain for some decades. However, the model predicts that 100 years after photosynthetic fixation, most of the carbon is lost and very small proportions remain in situ.

4.3 | Age and transit time distributions

We obtained probability distributions for the age of carbon in individual pools and for the entire ecosystem using Equations (7) and (8), respectively (Figure 4). These distributions show that carbon in foliage and fine litter is mostly young (mean ages of 0.34 ± 0.01 and 2.14 ± 0.56 year, respectively), while other pools contain carbon with a wide mix of ages. Despite different biomass values among them, the wood, fine- and coarse-root biomass pools have relatively similar age distributions (Figure 4), with mean age values of 29.15 ± 0.16, 38.12 ± 3.28 and 45.36 ± 0.30 years, respectively. Although the coarse woody debris pool has a very similar mean age (32.95 ± 1.24 years), the shape of the distribution is very different

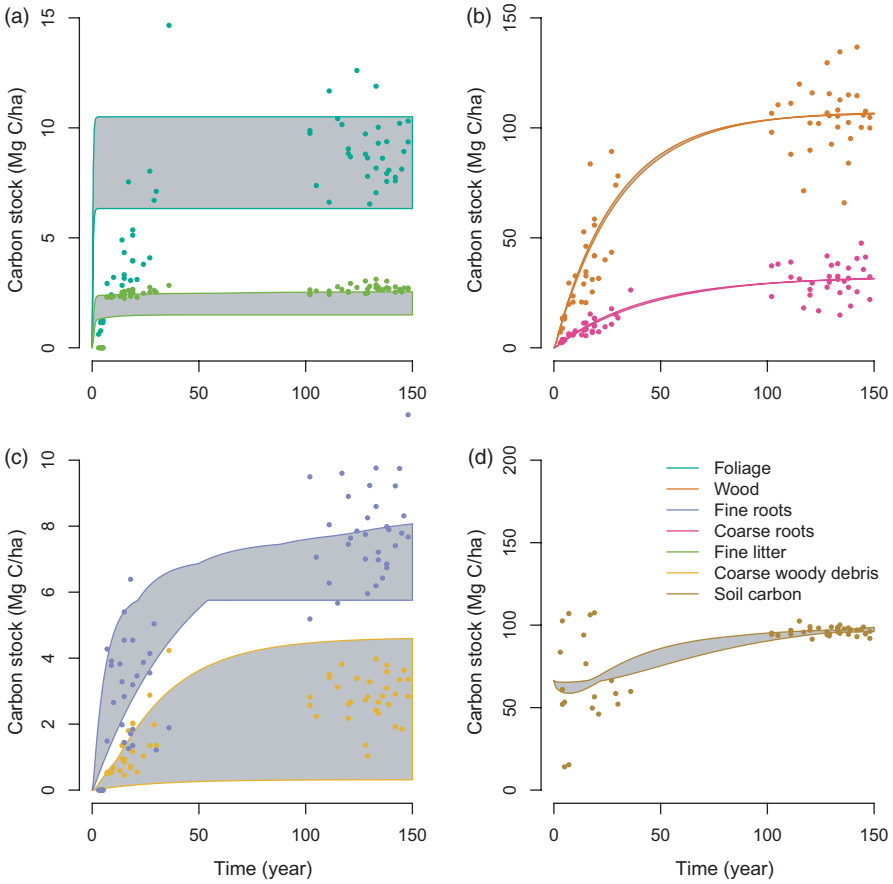

FIGURE 2 Observations of carbon stocks (points) along a successional sequence and range of model predictions by fitting the model of Equation (9). Grey areas represent the entire range of 1,000 predictions produced by the model. (a) Foliage and fine litter pools, (b) wood and coarse root pools, (c) fine roots and coarse woody debris, (d) soil carbon to 30-cm depth

than the distribution of other pools, with an age delay of a few years due to the time carbon spends in wood and coarse roots before entering this pool. The pool with the oldest mean age was the soil carbon pool, with a mean value of 61.85 ± 8.73 years, and a relatively long tail indicating that some carbon can stay for hundreds of years in the soil.

The mean age of carbon for the entire ecosystem was predicted by the model as 43.15 ± 3.33 years, and the median age was 28.6 ± 2.4 years, but clearly there is carbon that can be much older than these mean or median values. The model predicts that 95% of the carbon stored in the ecosystem is younger than 134.9 ± 10.0 years (95% quantile of the system age distribution).

We also obtained the transit time distribution of carbon for these forests at equilibrium (Figure 5a). The obtained distribution shows that 50% of the carbon that is fixed at any given year is lost in < 0.50 ± 0.14 year (median transit time), while 95% of the carbon is lost in < 68.60 ± 5.53 years. The mean transit time for the system, which can also be obtained dividing carbon stocks at equilibrium by GPP, was 11.24 ± 1.20 years. The difference between the mean and the median transit time is large, which indicates that estimates of ecosystem transit times based on the stock-over-flux approach do not provide a good overview of the fast dynamics of carbon losses that occur early after carbon fixation by photosynthesis. Most of the carbon passes quickly through the ecosystem and is responsible for the fast transit time is contributed by the foliage and fine litter pools (Figure 5a). Carbon with long transit times is contributed mostly by the soil carbon, coarse roots and wood biomass pools.

5 | DISCUSSION

Our results indicate that carbon fixed during photosynthesis in a tropical forest returns back to the atmosphere at a wide range of time-scales, a property that is captured by the transit time distribution. We found that in old-growth tropical forests of the Porce region in Colombia, most of the fixed carbon is respired very quickly, with 50% of total GPP returning back to the atmosphere in half of a year after fixation. Smaller proportions of the annually fixed carbon are transferred to other ecosystem pools, and they are also gradually lost from the system. Quantiles of the transit time distribution show that 95% of the annual photosynthesis is lost in less than 69 years, and very small proportions may remain in wood, coarse roots or soil carbon for longer times.

The concept of transit time distribution as presented here, helps to reconcile different types of studies on the time-scales at which carbon is cycled in tropical forests. Previous studies with healthy tropical trees using radiocarbon techniques have shown that respired carbon is generally a few years old (Muhr et al., 2013, 2018), while mean residence time estimates based on the above-ground biomass of inventory plots are around 50 years or higher (Galbraith et al., 2013; Malhi et al., 2013, 2015). However, these different estimates can be better explained in the context of an underlying distribution of transit (residence) times that can capture the fast dynamics of respiratory processes as well as the slow dynamics due to carbon transfers among compartments (e.g. from live biomass to

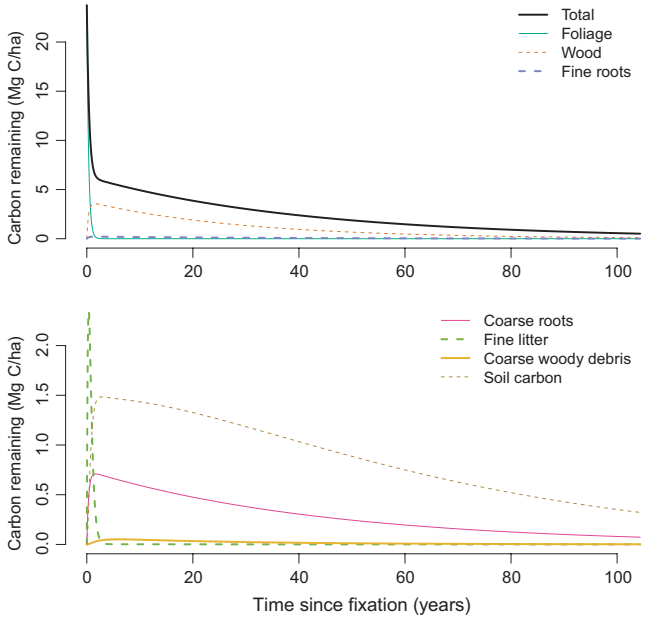

FIGURE 3 Fate of the annual amount of carbon fixed by photosynthesis (mean GPP = 23.98 MgC ha^{-1}) for the forest at equilibrium as predicted by the mean values of the parameters of the model. Carbon enters the ecosystem through the foliage compartment and it is transferred to other compartments where it spends certain amount of time before being released back to the atmosphere. After 100 years, most carbon is lost from all pools, although small proportions can remain in the soil pool for a few hundred years. The figure is split in two panels due to differences in scale of the vertical axis

coarse woody debris after tree mortality) and stabilization in slow cycling pools such as soil carbon. Previous radiocarbon studies in tropical soils have shown that soil carbon and heterotrophic respiration is mostly young, with small proportions that can persist in soils for hundreds of years (Trumbore, 1993; Trumbore & Barbosa De Camargo, 2013), in agreement with our results.

For the old-growth tropical forests of the Porce region, we estimated a mean transit time of carbon of 11 years, but the underlying transit time distribution showed, at one extreme, fast carbon losses within the first year after fixation, and at the other extreme, small amounts being respired only after several decades. Therefore, the transit time distribution has a shape with a strong initial decline, suggesting that most metabolic processes responsible for sustaining biomass stocks operate at short (intra-annual) time-scales (Figure 5). These processes are not well captured by mean transit (residence) time estimates such as those obtained from inventory plots alone, or dividing total carbon stocks by GPP.

The model data assimilation approach introduced here allowed us to estimate important ecosystem-level metrics that are very difficult to obtain from measurements alone such as *Ra* and *Rh* (Chambers et al., 2004). In particular, we obtained an estimate of NPP of 7.0 ± 1.5 MgC ha^{-1} year^{-1} by subtracting *Ra* from GPP. Commonly, NPP is quantified in tropical forests by measuring litter production, fine-root growth and changes in biomass from inventory plots, but this type of estimates can largely deviate from NPP as defined by the difference between GPP and *Ra* (Clark et al., 2001). Due to this deviation, plot-based estimates are often called NPP* to differentiate them from the flux-based definition of NPP (Clark et al., 2001). Indeed, the inventory-based estimate of NPP* for old-growth forests of the Porce region was reported as 12.76 ± 1.36 MgC ha^{-1} year^{-1} in Sierra et al. (2007b). This large difference between NPP and NPP* can be due to overestimations of the inventory-based methods such as the accounting of ingrowth of new trees to inventory plots; or due to overestimations of GPP from the satellite-based products, which can lead to large estimates of autotrophic respiration in the data assimilation procedure. Independent of the reason for the disagreement, our results confirm the assertion by Clark et al. (2001) that these two type of approaches can give largely different estimates of net primary production.

We obtained an average value of 0.3 for the ratio NPP:GPP for the forests at equilibrium, a ratio that is often called carbon use efficiency (CUE) (Chambers et al., 2004; DeLucia et al., 2007; Gifford, 2003; Malhi et al., 2015). According to common interpretation, this ratio would suggests that 30% of the photosynthetically fixed carbon is used for biomass production. Similar values for CUE with similar interpretations are also given by Chambers et al. (2004) and Malhi et al. (2013), although larger variability in CUE is reported in Doughty et al. (2018). However, we believe that this common interpretation of CUE has problems since, as our transit time distribution showed, autotrophic respiration is composed of carbon that spends some time in biomass before being respired. The amount of time carbon stays in plant cells can vary from hours to decades, but photosynthates have to be metabolized from living cells (biomass) for CO_2 production to occur. Thus, autotrophic respiration originates from biomass already produced; however, most of this metabolism occurs very quickly as the transit time distribution suggests, giving the false impression that a large proportion of carbon was not used to produce biomass. As other authors have shown (DeLucia et al., 2007; Gifford, 2003), estimates of CUE depend largely on whether estimates are made on short or long periods of time, and the transit time distribution provides good support for avoiding an interpretation of this ratio out of the context of the time-scales involved.

We prefer to interpret the ratio NPP:GPP as the proportion of total photosynthesized carbon metabolized and respired by heterotrophs, and not by autotrophs. This interpretation emerges by the simple relations

$$\frac{\mathrm{NPP}}{\mathrm{GPP}} = \frac{\mathrm{GPP}-Ra}{\mathrm{GPP}} = 1-\frac{Ra}{\mathrm{GPP}}, \quad = \frac{Ra+Rh-Ra}{\mathrm{GPP}} = \frac{Rh}{\mathrm{GPP}}, \tag{10}$$

assuming that at equilibrium, GPP and ecosystem respiration are equal, so GPP = *Ra* + *Rh* (Gifford, 2003; Raich & Nadelhoffer, 1989).

For the old-growth forests of the Porce region, we can thus infer that 30% of total photosynthate is respired by heterotrophic organisms, and 70% by autotrophic organisms. This interpretation has little to do with an efficiency concept for biomass production,

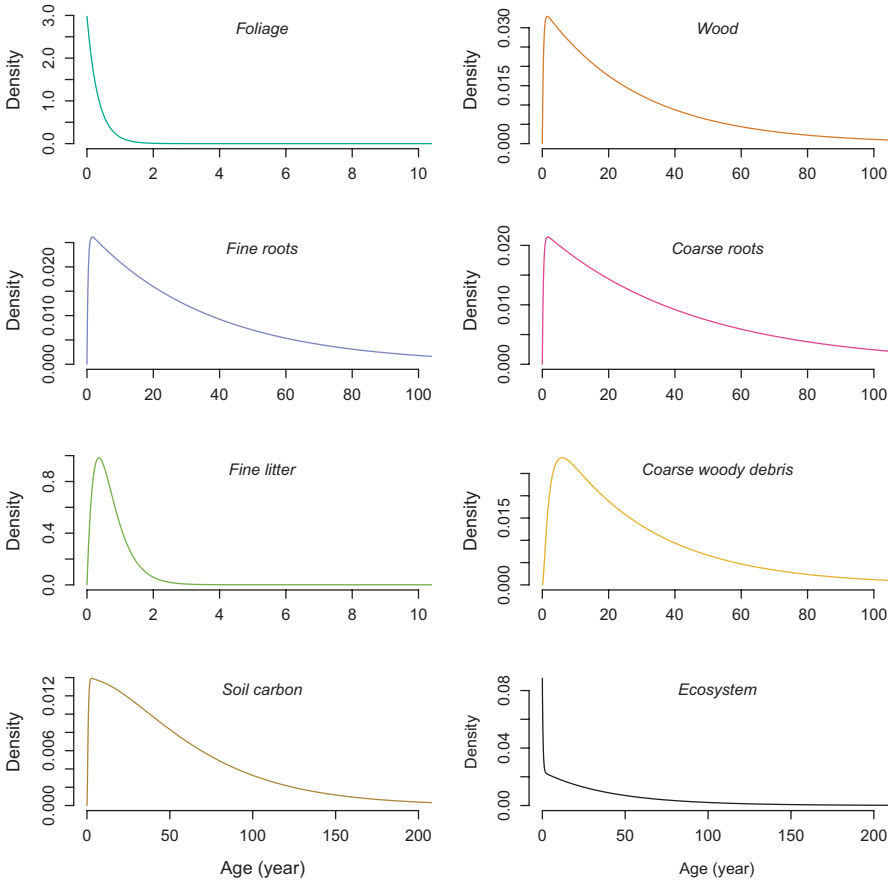

FIGURE 4 Age density distributions for each pool and for the entire ecosystem at equilibrium. These densities were obtained using the average parameter values from the 1,000 sets of parameters after the optimization procedure. Age densities integrate to a value of 1, therefore their units are in year^{-1}. Axes for each panel are different to facilitate the display of each distribution

but rather on the partitioning of pathways that leads to oxidation of carbon-based molecules and return of carbon to the atmosphere as CO_2. According to this interpretation, only 30% of GPP in old-growth forests of the Porce region follows a path through the network of compartments from where it can be respired by heterotrophs. A large proportion of the photosynthetically fixed carbon (70%), follows short paths through this compartmental network, with autotrophs responsible for its return as CO_2.

A major source of uncertainty for these predictions of respiration, NPP and their ratios, arises from the choice of model structure for the data assimilation procedure. We chose here a parsimonious model structure with constant first-order rates of carbon cycling and transfers among compartments. A different model structure may predict different shapes of the transit time distribution and the respiratory fluxes that compose it. Independent datasets may help to better identify appropriate model structures. Radiocarbon measurements in carbon pools and in respired CO_2 provide an ideal independent measurement-based constraint that would help to confirm the model predictions of age and transit time distributions. Radiocarbon in carbon stocks and CO_2 can be obtained easily from our compartmental model (see Supporting Information), and offers an opportunity to reduce the range of uncertainties in our predictions.

Despite model-related uncertainties, we believe the approach introduced here provides an alternative view of ecosystem carbon cycling that can help to interpret existing approaches and paradigms currently used to study the carbon cycle in tropical forests (e.g. Malhi et al., 2015). Data assimilation is a useful approach to incorporate existing observations into ecosystem models, and obtain metrics that cannot be obtained by measurements alone. If applied to the existing networks of tropical forest plots, combined with satellite- and eddy covariance-based measurements of primary production, data assimilation techniques can provide a better understanding of mechanisms and emergent properties of the carbon cycle in the tropics. The transit time distribution is a very powerful metric that integrates multiple processes of ecosystem carbon cycling across multiple temporal scales. Estimates of this distribution across tropical forests can thus help us to determine the fate of the large masses of carbon that are annually drawn down from the atmosphere into the tropics, and potential consequences of global change on the carbon cycle.

6 | CONCLUSIONS

We provide here the first estimation of the fate of carbon after photosynthesis, and of the transit time distribution of carbon for a tropical forest ecosystem, using a combination of model data assimilation methods and the theory of time-scales for compartmental dynamical systems. We estimate that for old-growth forests of the Porce region of Colombia, the annual photosynthetic carbon flux returns back to the atmosphere at a wide range of time-scales; 50% of this carbon is respired in < 0.5 year and 95% is respired in < 69 year, with a mean transit time of 11 year. From the annual GPP

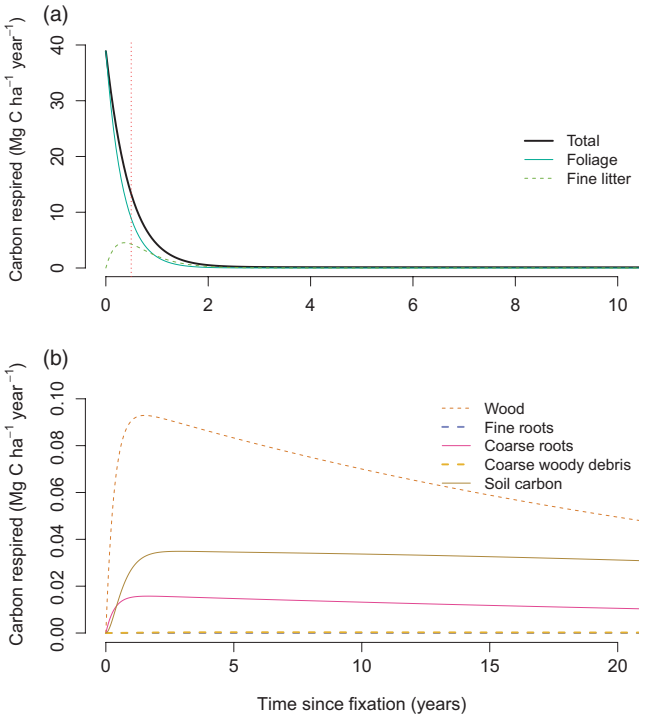

FIGURE 5 Transit time mass distribution and contribution of different pools to the transit time. Pool-wise mass distributions of transit times in (b) are presented on a different scale so differences among pools can be better observed. Dotted vertical line in panel (a) represents the median transit time (50% quantile) of the distribution, equivalent to 0.5 year. Units in vertical axis represent a rate at which carbon fixed at a certain time is respired. The integral over the entire transit time distribution is equal to total ecosystem respiration

flux, about 70% of the carbon follows a pathway across the network of ecosystem carbon compartments that leads to respiration by autotrophs, while 30% follows a pathway that leads to respiration by heterotrophs.

In comparison with traditional methods that estimate mean residence times in biomass, we offer here a new perspective to integrate multiple ecosystem processes using the age of respired carbon, that is, the transit time distribution, as a unifying concept. This approach also provides a new perspective for interpreting the ratio NPP:GPP, not as an efficiency of biomass production, but as the proportion of photosynthetic products that are not respired by autotrophs.

ACKNOWLEDGEMENTS

This work was motivated by scientific research at the Amazon Tall Tower Observatory (ATTO), partly funded by the German Federal Ministry of Education and Research (grant number 01LK1602A) and the Max Planck Society. Data used here have been previously published, and collection was funded by Empresas Públicas de Medellín and Universidad Nacional de Colombia sede Medellín. Additional support was provided by the German Research Foundation (SI 1953/2-2). J. I. del Valle and D. Herrera provided useful comments on previous versions of this manuscript. Open access funding enabled and organized by Projekt DEAL.

AUTHORS' CONTRIBUTIONS

C.A.S. conceived the analysis and led this study; L.M.E.-S. obtained gross primary production data and computed average values for the site; I.C. computed radiocarbon distributions.

DATA AVAILABILITY STATEMENT

All code and data needed to reproduce all results in this manuscript have been permanently archived in Zenodo with the digital object identifier https://doi.org/10.5281/zenodo.4893606 (Sierra, 2021).

ORCID

Carlos A. Sierra http://orcid.org/0000-0003-0009-4169
Lina M. Estupinan-Suarez https://orcid.org/0000-0002-2359-9496
Ingrid Chanca https://orcid.org/0000-0003-0933-5838

REFERENCES

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K. W., Roupsard, O., … Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, *329*(5993), 834–838.

Bolin, B., & Rodhe, H. (1973). A note on the concepts of age distribution and transit time in natural reservoirs. *Tellus*, *25*(1), 58–62.

Carbone, M. S., Czimczik, C. I., Keenan, T. F., Murakami, P. F., Pederson, N., Schaberg, P. G., Xu, X., & Richardson, A. D. (2013). Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytologist*, *200*(4), 1145–1155.

Ceballos-Núñez, V., Richardson, A. D., & Sierra, C. A. (2018). Ages and transit times as important diagnostics of model performance for predicting carbon dynamics in terrestrial vegetation models. *Biogeosciences*, *15*(5), 1607–1625.

Ceballos-Núñez, V., Müller, M., & Sierra, C. A. (2020). Towards better representations of carbon allocation in vegetation: A conceptual framework and mathematical tool. *Theoretical Ecology*, *13*(3), 317–332.

Chambers, J., Tribuzy, E., Toledo, L., Crispim, B., Higuchi, N., dos Santos, J., Araujo, A., Kruijt, B., Nobre, A., & Trumbore, S. E. (2004). Respiration from a tropical forest ecosystem: Partitioning of sources and low carbon use efficiency. *Ecological Applications*, *14*(4), S72–S88.

Chambers, J. Q., Negron-Juarez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G. H. P. M., Trumbore, S. E., & Higuchi, N. (2013). The steady-state mosaic of disturbance and succession across an old-growth central amazon forest landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(10), 3949–3954.

Clark, D., Brown, S., Klicklighter, D., Chambers, J., Tomlinson, J., & Ni, J. (2001). Measuring net primary production in forests: Concepts and field methods. *Ecological Applications*, *11*(2), 356–370.

delValle, J. I., Restrepo, H., & Londoño, M. (2011). Recuperación de la biomasa mediante la sucesión secundaria, cordillera central de los andes, colombia. *Revista de Biología Tropical*, *59*(3), 1337–1358.

DeLucia, E. H., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, *13*(6), 1157–1167.

Doughty, C. E., Goldsmith, G. R., Raab, N., Girardin, C. A. J., Farfan-Amezquita, F., Huaraca-Huasco, W., Silva-Espejo, J. E., Araujo-Murakami, A., da Costa, A. C. L., Rocha, W., Galbraith, D., Meir, P., Metcalfe, D. B., & Malhi, Y. (2018). What controls variation in carbon use efficiency among amazonian tropical forests? *Biotropica*, *50*(1), 16–25.

Fu, Z., Gerken, T., Bromley, G., Araújo, A., Bonal, D., Burban, B., Ficklin, D., Fuentes, J. D., Goulden, M., Hirano, T., Kosugi, Y., Liddell, M., Nicolini, G., Niu, S., Roupsard, O., Stefani, P., Mi, C., Tofte, Z., Xiao, J., … Stoy, P. C. (2018). The surface-atmosphere exchange of carbon dioxide in tropical rainforests: Sensitivity to environmental drivers and flux measurement methodology. *Agricultural and Forest Meteorology*, *263*, 292–307.

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D., Doughty, C. E., Fisher, R. A., Lewis, S. L., Peh, K. S.-H., Phillips, O. L., Quesada, C. A., Sonké, B., & Lloyd, J. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, *6*(1), 139–157.

Gifford, R. M. (2003). Plant respiration in productivity models: Conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, *30*(2), 171–186.

Herrera-Ramírez, D., Muhr, J., Hartmann, H., Römermann, C., Trumbore, S., & Sierra, C. A. (2020). Probability distributions of nonstructural carbon ages and transit times provide insights into carbon allocation dynamics of mature trees. *New Phytologist*, *226*(5), 1299–1311.

Hopkins, F. M., Torn, M. S., & Trumbore, S. E. (2012). Warming accelerates decomposition of decades-old carbon in forest soils. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(26), E1753–E1761.

Huang, Y., Lu, X., Shi, Z., Lawrence, D., Koven, C. D., Xia, J., Du, Z., Kluzek, E., & Luo, Y. (2018). Matrix approach to land carbon cycle modeling: A case study with the community land model. *Global Change Biology*, *24*(3), 1394–1404.

Jiang, C., & Ryu, Y. (2016). Multi-scale evaluation of global gross primary productivity and evapotranspiration products derived from breathing earth system simulator (bess). *Remote Sensing of Environment*, *186*, 528–547.

Jung, M., Schwalm, C., Migliavacca, M., Walther, S., Camps-Valls, G., Koirala, S., Anthoni, P., Besnard, S., Bodesheim, P., Carvalhais, N., Chevallier, F., Gans, F., Goll, D. S., Haverd, V., Köhler, P., Ichii, K., Jain, A. K., Liu, J., Lombardozzi, D., … Reichstein, M. (2020). Scaling carbon fluxes from eddy covariance sites to globe: Synthesis and evaluation of the fluxcom approach. *Biogeosciences*, *17*(5), 1343–1365.

Keel, S. G., Siegwolf, R. T. W., & Körner, C. (2006). Canopy CO_2 enrichment permits tracing the fate of recently assimilated carbon in a mature deciduous forest. *New Phytologist*, *172*(2), 319–329.

Luo, Y., Shi, Z., Lu, X., Xia, J., Liang, J., Jiang, J., Wang, Y., Smith, M. J., Jiang, L., Ahlström, A., Chen, B., Hararuk, O., Hastings, A., Hoffman, F., Medlyn, B., Niu, S., Rasmussen, M., Todd-Brown, K., & Wang, Y.-P. (2017). Transient dynamics of terrestrial carbon storage: Mathematical foundation and its applications. *Biogeosciences*, *14*(1), 145–161.

Luo, Y., & Weng, E. (2011). Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends in Ecology & Evolution*, *26*(2), 96–104.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., … Janssens, I. A. (2007). CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, *13*(12), 2509–2537.

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., del Aguila-Pasquel, J., Aragão, L. E. O. C., Araujo-Murakami, A., Brando, P., da Costa, A. C. L., Silva-Espejo, J. E., Farfán Amézquita, F., Galbraith, D. R., Quesada, C. A., Rocha, W., Salinas-Revilla, N., Silvério, D., Meir, P., … Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland amazonian forests. *Global Change Biology*, *21*(6), 2283–2295.

Malhi, Y., Saatchi, S., Girardin, C., & Aragão, L. E. O. C. (2013). The production, storage, and flow of carbon in amazonian forests. In M. Keller, M. Bustamante, J. Gash, & P. S. Dias (Eds.), *Amazonia and global change* (pp. 355–372). American Geophysical Union (AGU).

Metzler, H., & Sierra, C. A. (2018). Linear autonomous compartmental models as continuous-time Markov chains: Transit-time and age distributions. *Mathematical Geosciences*, *50*(1), 1–34.

Muhr, J., Angert, A., Negrón-Juárez, R. I., Muñoz, W. A., Kraemer, G., Chambers, J. Q., & Trumbore, S. E. (2013). Carbon dioxide emitted from live stems of tropical trees is several years old. *Tree Physiology*, *33*(7), 743–752.

Muhr, J., Trumbore, S., Higuchi, N., & Kunert, N. (2018). Living on borrowed time – Amazonian trees use decade-old storage carbon to survive for months after complete stem girdling. *New Phytologist*, *220*(1), 111–120.

Neubauer, S. C., & Megonigal, J. P. (2015). Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, *18*(6), 1000–1013.

Noble, I., Apps, M., Houghton, R., Lashof, D., Makundi, W., Murdiyarso, D., Murray, B., Sombroek, W., & Valentini, R. (2000). Implications of different definitions and generic issues. In R. T. Watson, I. R. Noble, B. Bolin, N. H. Ravindranath, D. J. Verardo, & D. J. Dokken (Eds.), *Land use, land use change, and forestry* (pp. 53–156). Cambridge University Press.

Raich, J., & Nadelhoffer, K. (1989). Belowground carbon allocation in forest ecosystems: Global trends. *Ecology*, *70*(5), 1346–1354.

Rasmussen, M., Hastings, A., Smith, M. J., Agusto, F. B., Chen-Charpentier, B. M., Hoffman, F. M., Jiang, J., Todd-Brown, K. E. O., Wang, Y., Wang, Y.-P., & Luo, Y. (2016). Transit times and mean ages for nonautonomous and autonomous compartmental systems. *Journal of Mathematical Biology*, *73*(6), 1379–1398.

Ryu, Y., Baldocchi, D. D., Kobayashi, H., van Ingen, C., Li, J., Black, T. A., Beringer, J., van Gorsel, E., Knohl, A., Law, B. E., & Roupsard, O. (2011). Integration of modis land and atmosphere products with a coupled-process model to estimate gross primary productivity and evapotranspiration from 1 km to global scales. *Global Biogeochemical Cycles*, *25*(4).

Sierra, C. A. (2021). The fate and transit time of carbon in a tropical forest. *Zenodo*, https://doi.org/10.5281/zenodo.4893606

Sierra, C., del Valle, J., & Restrepo, H. (2012). Total carbon accumulation in a tropical forest landscape. *Carbon Balance and Management*, *7*(1), 12.

Sierra, C. A., Ceballos-Núñez, V., Metzler, H., & Müller, M. (2018). Representing and understanding the carbon cycle using the theory of compartmental dynamical systems. *Journal of Advances in Modeling Earth Systems*, *10*(8), 1729–1734.

Sierra, C. A., Crow, S. E., Heimann, M., Metzler, H., & Schulze, E.-D. (2020). The climate benefit of carbon sequestration. *Biogeosciences Discussions*, *18*(3), 1029–1048.

Sierra, C. A., del Valle, J. I., Orrego, S. A., Moreno, F. H., Harmon, M. E., Zapata, M., Colorado, G. J., Herrera, M. A., Lara, W., Restrepo, D. E., Berrouet, L. M., Loaiza, L. M., & Benjumea, J. F. (2007a). Total carbon stocks in a tropical forest landscape of the Porce region. *Colombia*. *Forest Ecology and Management*, *243*(2–3), 299–309.

Sierra, C. A., Harmon, M. E., Moreno, F. H., Orrego, S. A., & del Valle, J. I. (2007b). Spatial and temporal variability of net ecosystem production in a tropical forest: Testing the hypothesis of a significant carbon sink. *Global Change Biology*, *13*(4), 838–853.

Sierra, C. A., Loescher, H. W., Harmon, M. E., Richardson, A. D., Hollinger, D. Y., & Perakis, S. S. (2009). Interannual variation of carbon fluxes from three contrasting evergreen forests: The role of forest dynamics and climate. *Ecology*, *90*(10), 2711–2723.

Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., & Trumbore, S. E. (2017). The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology*, *23*(5), 1763–1773.

Soetaert, K., & Petzoldt, T. (2010). Inverse modelling, sensitivity and Monte Carlo analysis in R using package FME. *Journal of Statistical Software*, *33*(3), 1–28.

Thompson, M. V., & Randerson, J. T. (1999). Impulse response functions of terrestrial carbon cycle models: Method and application. *Global Change Biology*, *5*(4), 371–394. doi:10.1046/j.1365-2486.1999.00235.x.

Tramontana, G., Jung, M., Schwalm, C. R., Ichii, K., Camps-Valls, G., Ráduly, B., Reichstein, M., Arain, M. A., Cescatti, A., Kiely, G., Merbold, L., Serrano-Ortiz, P., Sickert, S., Wolf, S., & Papale, D. (2016). Predicting carbon dioxide and energy fluxes across global fluxnet sites with regression algorithms. *Biogeosciences*, *13*(14), 4291–4313.

Trumbore, S. (2006). Carbon respired by terrestrial ecosystems – Recent progress and challenges. *Global Change Biology*, *12*(2), 141–153.

Trumbore, S., & Barbosa De Camargo, P. (2013). Soil carbon dynamics. In M. Keller, M. Bustamante, J. Gash, & P. S. Dias (Eds.), *Amazonia and global change* (pp. 451–462). American Geophysical Union (AGU).

Trumbore, S., Czimczik, C. I., Sierra, C. A., Muhr, J., & Xu, X. (2015). Nonstructural carbon dynamics and allocation relate to growth rate and leaf habit in California oaks. *Tree Physiology*, *35*(11), 1206–1222.

Trumbore, S. E. (1993). Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochemical Cycles*, *7*(2), 275–290.

Vargas, R., Trumbore, S. E., & Allen, M. F. (2009). Evidence of old carbon used to grow new fine roots in a tropical forest. *New Phytologist*, *182*(3), 710–718.

Waring, R. H., Landsberg, J. J., & Williams, M. (1998). Net primary production of forests: A constant fraction of gross primary production? *Tree Physiology*, *18*(2), 129–134.

Yepes, A. P., del Valle, J. I., Jaramillo, S. L., & Orrego, S. A. (2010). Recuperación estructural en bosques sucesionales andinos de porce (Antioquia, Colombia). *Revista de Biología Tropical*, *58*, 427–445.

Zapata, M., & del Valle, J. I. (2001). *Ecuaciones de biomasa aérea para los bosques primarios del área de influencia de la central hidroeléctrica Porce II*. Universidad Nacional de Colombia.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sierra, C. A., Estupinan-Suarez, L. M., & Chanca, I. (2021). The fate and transit time of carbon in a tropical forest. *Journal of Ecology*, 109, 2845–2855. https://doi.org/10.1111/1365-2745.13723