



## The fate and transit time of carbon in a tropical forest

Journal:	<i>Ecology</i>
Manuscript ID	ECY20-1216
Wiley - Manuscript type:	Articles
Date Submitted by the Author:	15-Oct-2020
Complete List of Authors:	Sierra, Carlos; Max-Planck-Institute for Biogeochemistry, Estupiñán-Suárez, Lina; Max Planck Institute for Biogeochemistry Chanca, Ingrid; Max Planck Institute for Biogeochemistry
Substantive Area:	Whole-System Analysis < Ecosystems < Substantive Area, Climate Change < Ecosystems < Substantive Area, Theory < Substantive Area
Organism:	
Habitat:	
Geographic Area:	Global < Geographic Area, Northern South America (Colombia, Venezuela) < South America < Geographic Area
Key words/phrases:	global carbon cycle, tropical forests, model-data assimilation, transit times, ecosystem respiration, carbon use efficiency
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	of the NPP:GPP ratio based on the fate and respiratory pathway at which carbon returns to the atmosphere after fixation.

# The fate and transit time of carbon in a tropical forest

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## Statement of authorship:

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.

Abstract

Tropical forests fix large quantities of carbon from the atmosphere on an annual basis, and despite much research quantifying stocks and fluxes of carbon in these ecosystems, the fate of the fixed carbon as it travels through ecosystem compartments is poorly understood. Using a model-data assimilation approach, we quantified the fate of carbon (trajectory of photosynthetically fixed carbon through a network of ecosystem compartments) and its transit time (the time it takes carbon to pass through the entire ecosystem, from fixation to respiratory release) for an old-growth tropical forest ecosystem in Colombia. We show that on average, 50% of the carbon fixed at any given time is respired in less than 0.5 years, and 95% is respired in less than 69 years. The transit time distribution shows that carbon in ecosystems is respired on a range of timescales that span decades, but fast metabolic processes in vegetation dominate the return of carbon to the atmosphere. These fast processes are not well captured by estimates of the mean residence time of biomass based on data from inventory plots, or the ratio of gross primary production to the total carbon stock. We show here that the shape of the transit time distribution helps to better understand timescales of carbon storage in ecosystems and can be used to infer whether CO<sub>2</sub> fertilization of tropical forests have consequences on timescales relevant for climate change mitigation. In addition, the transit time distribution provides a new approach to interpret other ecosystem level metrics such as the ratio of net primary production (NPP) to gross primary production (GPP). We propose here an alternative interpretation of the NPP:GPP ratio based on the fate and respiratory pathway at which carbon returns to the atmosphere after fixation.

**Keywords:** global carbon cycle, tropical forests, model-data assimilation, transit times, ecosystem respiration, carbon use efficiency.

# 1 Introduction

The terrestrial biosphere photosynthesizes annually about  $120 \pm 7 \text{ PgC yr}^{-1}$ , 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  $30 \text{ MgC ha}^{-1} \text{ yr}^{-1}$  (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; Luyssaert et al., 2007; Fu et al., 2018). It is likely that between 50 to 70% of the GPP flux in tropical ecosystems is lost as autotrophic respiration (Waring et al., 1998; Gifford, 2003; DeLucia et al., 2007; Chambers et al., 2004); 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 is removed from radiative effects in the atmosphere (Noble et al., 2000; Neubauer and Megonigal, 2015; 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 (Vargas et al., 2009; Muhr et al., 2013, 2018). In fact, observational studies with temperate trees as well as modeling studies have shown that trees can respire carbon of a wide range of ages, from days- to decades-old carbon (Carbone et al., 2013; Trumbore et al., 2015; Ceballos-Núñez et al., 2018; Herrera-Ramírez et al., 2020). Therefore, one would expect that respiration in tropical ecosystems is composed by a mixture of carbon of different ages (Trumbore, 2006; Trumbore and 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 (Keel et al., 2006; Hopkins et al., 2012).

In contrast to isotopic labelling studies, data from permanent plots across the tropics suggest that carbon stays in woody biomass, 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 (Sierra et al., 2009; Chambers et al., 2013). 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 and Rodhe, 1973; Rasmussen et al., 2016; Sierra et al., 2017). 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. 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 should capture all these different processes over a wide range of timescales.

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 ( $R_a$ ), and net primary production (NPP).

## 2 Theory

The time that carbon spends in ecosystems can be obtained using the concept of transit time (Bolin and Rodhe, 1973; Thompson and Randerson, 1999; Rasmussen et al., 2016; Sierra et al., 2017). It characterizes the time carbon atoms spend in an ecosystem, from the time of carbon fixation by 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 in multiple pools using a linear autonomous compartmental system of the form

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

103 where the vector  $\mathbf{u}$  represents total carbon inputs from the atmosphere to ecosystem pools,  
 104 and the matrix  $\mathbf{B}$  represents all cycling and transfer rates of carbon within the ecosystem.  
 105 These linear autonomous compartmental systems at equilibrium have steady-state carbon  
 106 stocks equivalent to

$$\mathbf{x}^* = -\mathbf{B}^{-1} \cdot \mathbf{u}. \quad (2)$$

107 At this equilibrium point, where inputs from photosynthesis are balanced by losses from  
 108 ecosystem respiration, it is possible to compute the fate of carbon inputs entering at an  
 109 arbitrary time  $t_0$  using the matrix exponential of the compartmental matrix (Sierra et al.,  
 110 2020). Explicitly, the mass of carbon remaining in the ecosystem after photosynthetic fixation  
 111 can be obtained as

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

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

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

$$\mathbf{z}^\top = -\mathbf{1}^\top \cdot \mathbf{B}, \quad (4)$$

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



122 amount of respiratory losses as

$$\begin{aligned} R(t) &= \mathbf{z}^\top \cdot \mathbf{M}(t) \\ &= -\mathbf{1}^\top \cdot \mathbf{B} \cdot e^{(t-t_0)\mathbf{B}} \cdot \mathbf{u} \end{aligned} \quad (5)$$

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

$$f_T(\tau) = -\mathbf{1}^\top \cdot \mathbf{B} \cdot e^{\tau\mathbf{B}} \cdot \frac{\mathbf{u}}{\|\mathbf{u}\|}, \quad (6)$$

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

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

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

$$\mathbf{f}_a(\tau) = (\mathbf{X}^*)^{-1} \cdot e^{\tau\mathbf{B}} \cdot \mathbf{u} \quad (7)$$

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

$$f_A(\tau) = -\mathbf{1}^\top \cdot \mathbf{B} \cdot e^{\tau\mathbf{B}} \cdot \frac{\mathbf{x}^*}{\|\mathbf{x}^*\|}. \quad (8)$$

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

### 3 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 region in Colombia. We used carbon stock data collected at the Porce region of Colombia ( $6^{\circ} 45' 37''$  N,  $75^{\circ} 06' 28''$  W, 800–1000 m elevation above sea level, 2078 mm mean annual precipitation,  $21.3^{\circ}\text{C}$  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 (Sierra et al., 2007a; Yepes et al., 2010; del Valle et al., 2011; Sierra et al., 2012). The landscape also contains elements of old-growth forests with no evidence of previous disturbance. 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 and Ryu, 2016). In particular, we used the average  $\pm$  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  $22.89 \pm 2.46 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ . Average GPP for the same period at 10 km and 8 day resolution from Tramontana et al. (2016) gives a value of  $24.4 \pm 1.02 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ . A combined estimate of GPP for the region with uncertainty propagation gives a value of  $23.98 \pm 2.36 \text{ MgC ha}^{-1} \text{ yr}^{-1}$  (see code in supplementary material).

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; i.e.  $u_1 =$

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

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

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 aboveground tree biomass and palm biomass reported in Sierra et al. (2012) were aggregated and transformed to foliage biomass using a fraction of foliage of 0.08 as reported in Zapata (2001). 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 aboveground biomass multiplied by a fraction of wood biomass of 0.92, based on measurements reported by Zapata (2001).

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 1000 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

1000 sets of parameter values for the model using the Levenberg-Marquardt optimization algorithm (Soetaert and Petzoldt, 2010).

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). All computations were performed in R version 4.0, and code to reproduce all results is available as supplementary material at <https://git.bgc-jena.mpg.de/csierra/agedisttropical>.

## 4 Results

### 4.1 Model-data assimilation

We obtained 1000 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 1

Observations of carbon stocks along the successional sequence, together with average 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 during succession consistent with previous analyses for this chronosequence (Sierra et al., 2007a; Yepes et al., 2010; del Valle et al., 2011; Sierra et al., 2012).

The model predicts a steady-state carbon stock of  $263.9 \pm 2.0$  MgC ha<sup>-1</sup>, which is within the upper range of the observations of total carbon stocks (with soil carbon up to 30 cm depth) of  $252.4 \pm 20.2$  for the primary forests of the region (Sierra et al., 2007a).

At equilibrium, total ecosystem respiration ( $Re$ ) is predicted as  $23.7 \pm 2.5$  MgC ha<sup>-1</sup>

yr<sup>-1</sup>, from which 70 % corresponds to autotrophic respiration ( $Ra$ ,  $16.7 \pm 3.1$  MgC ha<sup>-1</sup> yr<sup>-1</sup>) and 30 % to heterotrophic respiration ( $Rh$ ,  $7.0 \pm 1.5$  MgC ha<sup>-1</sup> yr<sup>-1</sup>).

## 4.2 Fate of gross primary production

Using the set of average parameter values (Table 1), we obtained a representative function for the fate of carbon once it enters the ecosystem; i.e., 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 ( $k_1 = 2.978$  yr<sup>-1</sup>), 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 1); 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  $0.34 \pm 0.01$  and  $2.14 \pm 0.56$  yr, 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  $29.15 \pm 0.16$ ,  $38.12 \pm 3.28$ , and  $45.36 \pm 0.30$  yr, respectively. Although the coarse woody debris pool has a very similar mean age ( $32.95 \pm 1.24$  yr), the shape of the distribution is very different 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  $61.85 \pm 8.73$  yr, and a relatively long tail indicating that some carbon can stay for relatively long times in the soil.

The mean age for the entire ecosystem was predicted by the model as  $43.15 \pm 3.33$  yr, but clearly there is carbon that can be much older than this mean value. The model predicts that 95% of the carbon stored in the ecosystem is younger than  $134.9 \pm 10.0$  yr (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 less than  $0.50 \pm 0.14$  yr (median transit time), while 95% of the carbon is lost in less than  $68.60 \pm 5.53$  yr. The mean transit time for the system, which can also be obtained dividing carbon stocks at equilibrium by GPP, was  $11.24 \pm 1.20$  yr. 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 that passes quickly through the ecosystem and contributes to 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 timescales, 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 timescales 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 aboveground 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 coarse woody debris after tree mortality) and stabilization in slow cycling pools such as soil carbon.

For the old-growth tropical forests of the Porco region, we estimated a mean transit time of carbon of 11 yr, 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) timescales. These processes are not well captured by mean transit (residence) time estimates such as those obtained from inventory plots, 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  $R_a$  and  $R_h$  (Chambers et al., 2004). In particular, we obtained an estimate of NPP of  $7.0 \pm 1.5 \text{ MgC ha}^{-1} \text{ yr}^{-1}$  by subtracting  $R_a$  from GPP. Commonly, NPP is quantified in tropical forests by measuring litter production 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  $R_a$  (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  $12.76 \pm 1.36 \text{ MgC ha}^{-1} \text{ yr}^{-1}$  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.

The ratio NPP:GPP, often called carbon use efficiency (CUE) (Gifford, 2003; Chambers et al., 2004; DeLucia et al., 2007; Malhi et al., 2015), gives a value of 0.3 for these tropical forests. According to common interpretation, this ratio 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). However, we believe that this 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 for  $\text{CO}_2$  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 (Gifford, 2003; DeLucia et al., 2007), 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 timescales 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

$$\begin{aligned}\frac{\text{NPP}}{\text{GPP}} &= \frac{\text{GPP} - Ra}{\text{GPP}} = 1 - \frac{Ra}{\text{GPP}}, \\ &= \frac{Ra + Rh - Ra}{\text{GPP}} = \frac{Rh}{\text{GPP}},\end{aligned}\tag{10}$$

assuming that at equilibrium GPP and ecosystem respiration are equal, so  $\text{GPP} = Ra + Rh$ .

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, but rather on the partitioning of pathways that lead to oxidation of carbon-based molecules and return of carbon to the atmosphere as  $\text{CO}_2$ . According to this interpretation, only 30% of GPP 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  $\text{CO}_2$ .

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; for instance, radiocarbon measurements in carbon pools and in respired  $\text{CO}_2$  would provide independent measurements to confirm the predictions of the age distributions presented in Figure (4) (Trumbore and Barbosa De Camargo, 2013). Additional details about confrontation of model predictions with radiocarbon data can be found in Appendix A.

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 such as the CO<sub>2</sub> fertilization effect.

It has been hypothesized that as CO<sub>2</sub> concentrations increase in the atmosphere, primary production in tropical forest may increase (Phillips et al., 1998; Lewis, 2006; Grace et al., 2014; Hubau et al., 2020). If this were the case, the transit time distribution can help us to predict for how long the extra carbon would stay in an ecosystem. Depending on how long the extra carbon stays, forests can contribute to mitigate climate change at policy relevant timescales (Körner, 2017). Based on the transit time distribution we obtained, we would expect that any increase in GPP would lead to rapid losses within one year, and extremely small proportions of extra carbon would stay for years or decades. Our results and interpretation are consistent with results from Jiang et al. (2020), who found that most extra-carbon in a CO<sub>2</sub> fertilization experiment at a temperate forest was lost rapidly as respiration. This is indeed expected in the context of the shape of the transit time distribution, and if applicable to other old-growth forests worldwide, we would expect that extra carbon from CO<sub>2</sub> fertilization would be lost quickly, and would not remain stored at timescales relevant for climate change mitigation.

## 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 timescales 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 timescales; 50% of this carbon is respired in less than 0.5 yr and 95% is respired in less than 69 yr, with a mean transit time of 11 yr. From the annual GPP 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, i.e. 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.

In the context of global change and increases in atmospheric CO<sub>2</sub> concentrations, the transit time distribution may offer useful insights on whether additional photosynthates produced by increases in GPP will remain stored in ecosystems at timescales relevant for mitigating climate change.

## 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 has been previously published, and collection was funded by Empresas Públicas de Medellín and Universidad

385 Nacional de Colombia sede Medellín. Additional support was provided the German Re-  
 386 search Foundation (SI 1953/2-2). J. I. del Valle and D. Herrera provided useful comments  
 387 on previous versions of this manuscript.

## 388 **Appendix A: Radiocarbon as a tool for model testing**

389 Measurements of radiocarbon in ecosystem carbon pools can be used to test the adequacy  
 390 of model predictions. In particular, the pool age distributions predicted by the model and  
 391 presented in Figure (4), can be compared with radiocarbon measurements as an independent  
 392 variable for model confirmation. For this purpose, Chanca et al. (in preparation) developed  
 393 an algorithm to obtain distributions of radiocarbon in ecosystem pools to obtain the expected  
 394 variability in radiocarbon values as predicted by the model (Figure A). Because of the radio-  
 395 carbon ‘bomb spike’ effect of the 20th century, radiocarbon values change significantly from  
 396 year to year, and their incorporation in biomass pools is time dependent.

397 For example, for the year 2010, we predict that for pools with fast cycling rates and  
 398 narrow age distributions such as the foliage and fine litter pools, radiocarbon values are well  
 399 constraint within a narrow range. For slow cycling pools such as soil carbon and coarse woody  
 400 debris, the range in radiocarbon values is much wider (Figure A). For these slow cycling pools,  
 401 the number of samples required to characterize well the variability in radiocarbon would be  
 402 much higher.

403 Empirical measurements of radiocarbon in ecosystem pools can be used to build fre-  
 404 quency distributions that can then be inverted to obtain approximations of age distributions.  
 405 Through this method, it is possible to independently test our model predictions.

## 406 **References**

407 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck,  
 408 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., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I., and Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, 329(5993):834–838.

Bolin, B. and 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., and 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., and 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.

Chambers, J., Tribuzy, E., Toledo, L., Crispim, B., Higuchi, N., dos Santos, J., Araujo, A., Kruijt, B., Nobre, A., and 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., and 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*.

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

del Valle, J. I., Restrepo, H., and Londoño, M. (2011). Recuperación de la biomasa mediante

- 433 la sucesión secundaria, cordillera central de los andes, colombia. *Revista de Biología*  
434 *Tropical*, 59(3):1337–1358.
- 435 DeLucia, E. H., Drake, J. E., Thomas, R. B., and Gonzalez-Meler, M. (2007). Forest carbon  
436 use efficiency: is respiration a constant fraction of gross primary production? *Global*  
437 *Change Biology*, 13(6):1157–1167.
- 438 Fu, Z., Gerken, T., Bromley, G., Araújo, A., Bonal, D., Burban, B., Ficklin, D., Fuentes,  
439 J. D., Goulden, M., Hirano, T., Kosugi, Y., Liddell, M., Nicolini, G., Niu, S., Rouspard,  
440 O., Stefani, P., Mi, C., Tofte, Z., Xiao, J., Valentini, R., Wolf, S., and Stoy, P. C. (2018).  
441 The surface-atmosphere exchange of carbon dioxide in tropical rainforests: Sensitivity  
442 to environmental drivers and flux measurement methodology. *Agricultural and Forest*  
443 *Meteorology*, 263:292 – 307.
- 444 Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D., Doughty, C. E., Fisher, R. A.,  
445 Lewis, S. L., Peh, K. S.-H., Phillips, O. L., Quesada, C. A., Sonké, B., and Lloyd, J.  
446 (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*,  
447 6(1):139–157.
- 448 Gifford, R. M. (2003). Plant respiration in productivity models: conceptualisation, repre-  
449 sentation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*,  
450 30(2):171–186.
- 451 Grace, J., Mitchard, E., and Gloor, E. (2014). Perturbations in the carbon budget of the  
452 tropics. *Global Change Biology*, 20(10):3238–3255.
- 453 Herrera-Ramírez, D., Muhr, J., Hartmann, H., Römermann, C., Trumbore, S., and Sierra,  
454 C. A. (2020). Probability distributions of nonstructural carbon ages and transit times  
455 provide insights into carbon allocation dynamics of mature trees. *New Phytologist*,  
456 226(5):1299–1311.

- Hopkins, F. M., Torn, M. S., and Trumbore, S. E. (2012). Warming accelerates decomposition of decades-old carbon in forest soils. *Proceedings of the National Academy of Sciences*, 109(26):E1753–E1761.
- Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., Amani, C. A., Baker, T. R., Banin, L. F., Baya, F., Begne, S. K., Bennett, A. C., Benedet, F., Bitariho, R., Bocko, Y. E., Boeckx, P., Boundja, P., Brienén, R. J. W., Brncic, T., Chezeaux, E., Chuyong, G. B., Clark, C. J., Collins, M., Comiskey, J. A., Coomes, D. A., Dargie, G. C., de Haulleville, T., Kamdem, M. N. D., Doucet, J.-L., Esquivel-Muelbert, A., Feldpausch, T. R., Fofanah, A., Foli, E. G., Gilpin, M., Gloor, E., Gonmadje, C., Gourlet-Fleury, S., Hall, J. S., Hamilton, A. C., Harris, D. J., Hart, T. B., Hockemba, M. B. N., Hladik, A., Ifo, S. A., Jeffery, K. J., Jucker, T., Yakusu, E. K., Kearsley, E., Kenfack, D., Koch, A., Leal, M. E., Levesley, A., Lindsell, J. A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J. C., Makana, J.-R., Malhi, Y., Marshall, A. R., Martin, J., Martin, E. H., Mbayu, F. M., Medjibe, V. P., Mihindou, V., Mitchard, E. T. A., Moore, S., Munishi, P. K. T., Bengone, N. N., Ojo, L., Ondo, F. E., Peh, K. S. H., Pickavance, G. C., Poulsen, A. D., Poulsen, J. R., Qie, L., Reitsma, J., Rovero, F., Swaine, M. D., Talbot, J., Taplin, J., Taylor, D. M., Thomas, D. W., Toirambe, B., Mukendi, J. T., Tuagben, D., Umunay, P. M., van der Heijden, G. M. F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J. T., and Zemagho, L. (2020). Asynchronous carbon sink saturation in african and amazonian tropical forests. *Nature*, 579(7797):80–87.
- Jiang, C. and 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.
- Jiang, M., Medlyn, B. E., Drake, J. E., Duursma, R. A., Anderson, I. C., Barton, C. V. M.,

Boer, M. M., Carrillo, Y., Castañeda-Gómez, L., Collins, L., Crous, K. Y., De Kauwe,  
M. G., dos Santos, B. M., Emmerson, K. M., Facey, S. L., Gherlenda, A. N., Gimeno,  
T. E., Hasegawa, S., Johnson, S. N., Kännaste, A., Macdonald, C. A., Mahmud, K.,  
Moore, B. D., Nazaries, L., Neilson, E. H. J., Nielsen, U. N., Niinemets, Ü., Noh, N. J.,  
Ochoa-Hueso, R., Pathare, V. S., Pendall, E., Pihlblad, J., Piñeiro, J., Powell, J. R., Power,  
S. A., Reich, P. B., Renchon, A. A., Riegler, M., Rinnan, R., Rymer, P. D., Salomón, R. L.,  
Singh, B. K., Smith, B., Tjoelker, M. G., Walker, J. K. M., Wujeska-Klaue, A., Yang,  
J., Zaehle, S., and Ellsworth, D. S. (2020). The fate of carbon in a mature forest under  
carbon dioxide enrichment. *Nature*, 580(7802):227–231.

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., Nabel, J. E.  
M. S., Nelson, J. A., O’Sullivan, M., Pallandt, M., Papale, D., Peters, W., Pongratz,  
J., Rödenbeck, C., Sitch, S., Tramontana, G., Walker, A., Weber, U., and 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., and Körner, C. (2006). Canopy CO<sub>2</sub> enrichment permits  
tracing the fate of recently assimilated carbon in a mature deciduous forest. *New Phytol-*  
*ogist*, 172(2):319–329.

Körner, C. (2017). A matter of tree longevity. *Science*, 355(6321):130–131.

Lewis, S. L. (2006). Review. tropical forests and the changing earth system. *Philo-*  
*sophical Transactions of the Royal Society B: Biological Sciences*, 361(1465):195–210.  
10.1098/rstb.2005.1711.

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., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grunwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Mahli, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E. J., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M., Seufert, G., Sierra, C. A., Smith, M.-L., Tang, J., Valentini, R., Vesala, T., and Janssens, I. A. (2007). CO<sub>2</sub> 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., and 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., and Aragão, L. E. O. C. (2013). The production, storage, and flow of carbon in amazonian forests. In *Amazonia and Global Change*, pages 355–372. American Geophysical Union (AGU).

Metzler, H. and 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., and Trumbore, S. E. (2013). Carbon dioxide emitted from live stems of tropical trees is several years old. *Tree Physiology*, 33(7):743–752.

- 533 Muhr, J., Trumbore, S., Higuchi, N., and Kunert, N. (2018). Living on borrowed time –  
 534 amazonian trees use decade-old storage carbon to survive for months after complete stem  
 535 girdling. *New Phytologist*, 220(1):111–120.
- 536 Neubauer, S. C. and Megonigal, J. P. (2015). Moving beyond global warming potentials to  
 537 quantify the climatic role of ecosystems. *Ecosystems*, 18(6):1000–1013.
- 538 Noble, I., Apps, M., Houghton, R., Lashof, D., Makundi, W., Murdiyarso, D., Murray, B.,  
 539 Sombroek, W., , and Valentini, R. (2000). Implications of different definitions and generic  
 540 issues. In Watson, R. T., Noble, I. R., Bolin, B., Ravindranath, N. H., Verardo, D. J.,  
 541 and Dokken, D. J., editors, *Land Use, Land Use Change, and Forestry*, pages 53–156.  
 542 Cambridge University Press.
- 543 Phillips, O., Malhi, Y., Higuchi, N., Laurance, W., Núñez, P., Vásquez, R., Laurance, S.,  
 544 Ferreira, L., Stern, M., Brown, S., and Grace, J. (1998). Changes in the carbon balance  
 545 of tropical forests: evidence from long term plots. *Science*, 282:439–442.
- 546 Rasmussen, M., Hastings, A., Smith, M. J., Agosto, F. B., Chen-Charpentier, B. M., Hoff-  
 547 man, F. M., Jiang, J., Todd-Brown, K. E. O., Wang, Y., Wang, Y.-P., and Luo, Y. (2016).  
 548 Transit times and mean ages for nonautonomous and autonomous compartmental systems.  
 549 *Journal of Mathematical Biology*, 73(6):1379–1398.
- 550 Ryu, Y., Baldocchi, D. D., Kobayashi, H., van Ingen, C., Li, J., Black, T. A., Beringer, J.,  
 551 van Gorsel, E., Knohl, A., Law, B. E., and Rouspard, O. (2011). Integration of modis  
 552 land and atmosphere products with a coupled-process model to estimate gross primary  
 553 productivity and evapotranspiration from 1 km to global scales. *Global Biogeochemical*  
 554 *Cycles*, 25(4).
- 555 Sierra, C., del Valle, J., and Restrepo, H. (2012). Total carbon accumulation in a tropical  
 556 forest landscape. *Carbon Balance and Management*, 7(1):12.

- Sierra, C. A., Ceballos-Núñez, V., Metzler, H., and 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., and Schulze, E.-D. (2020). The climate benefit of carbon sequestration. *Biogeosciences Discussions*, 2020:in review.
- 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., and 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., and 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., and 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., and 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. and 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. and Randerson, J. T. (1999). Impulse response functions of terrestrial carbon cycle models: method and application. *Global Change Biology*, 5(4):371–394. 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., and 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. and Barbosa De Camargo, P. (2013). Soil carbon dynamics. In *Amazonia and Global Change*, pages 451–462. American Geophysical Union (AGU).
- Trumbore, S., Czimczik, C. I., Sierra, C. A., Muhr, J., and Xu, X. (2015). Non-structural carbon dynamics and allocation relate to growth rate and leaf habit in california oaks. *Tree Physiology*, 35(11):1206–1222.
- Vargas, R., Trumbore, S. E., and 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., and Williams, M. (1998). Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol*, 18(2):129–134.
- Yepes, A. P., del Valle, J. I., Jaramillo, S. L., and Orrego, S. A. (2010). Recuperación estructural en bosques sucesionales andinos de porce (antioquia, colombia). *Revista de Biología Tropical*, 58:427–445.
- Zapata, M. (2001). Ecuaciones de biomasa aérea para los bosques primarios del área de influencia de la central hidroeléctrica Porce II.

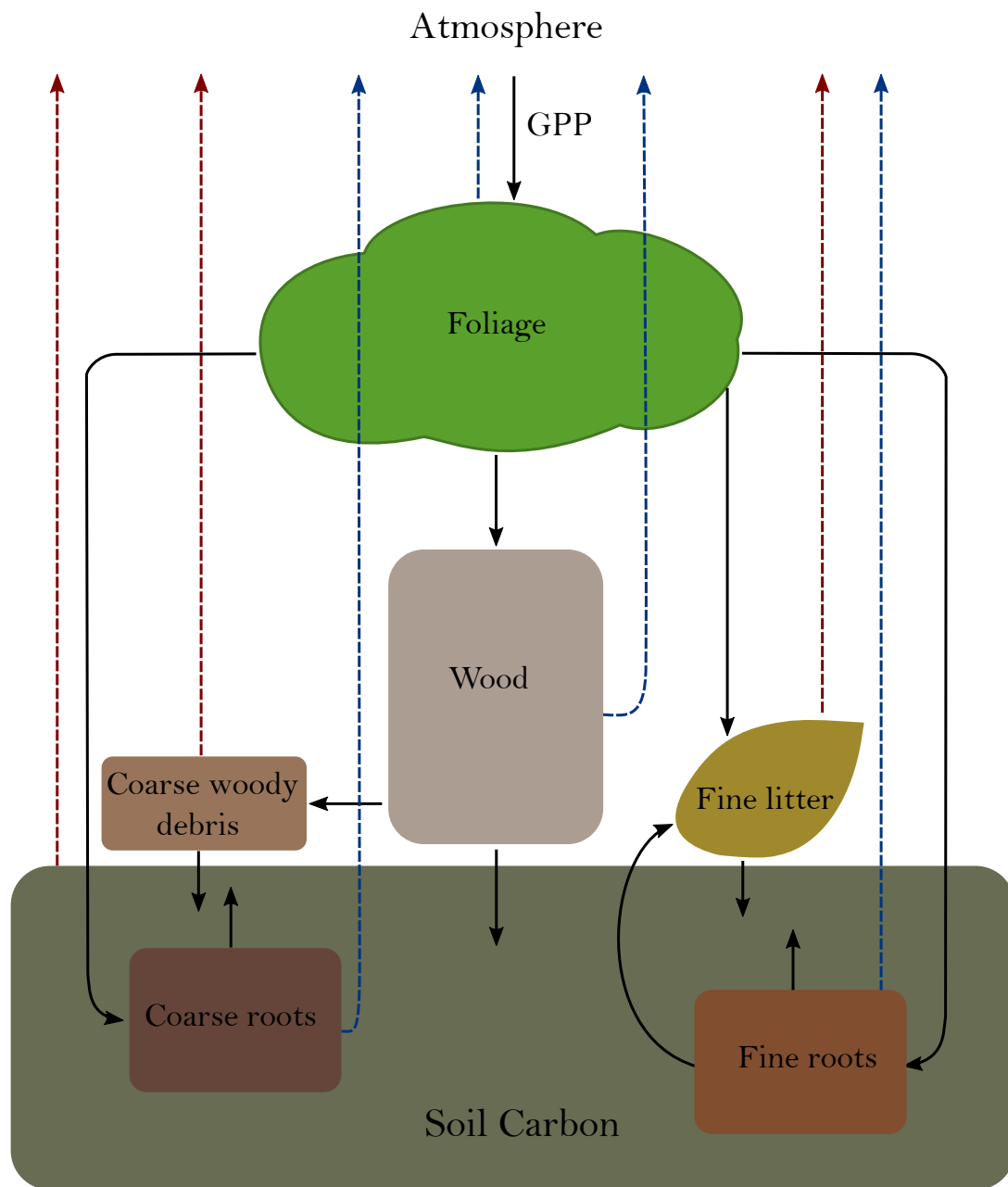


Figure 1: Structure of the compartmental model used to fit the available data from the Porce region of Colombia. Arrows represent transfers of carbon among pools (continuous line) or respiratory losses (dashed lines) to the atmosphere. Autotrophic respiration fluxes in dark blue and heterotrophic respiration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

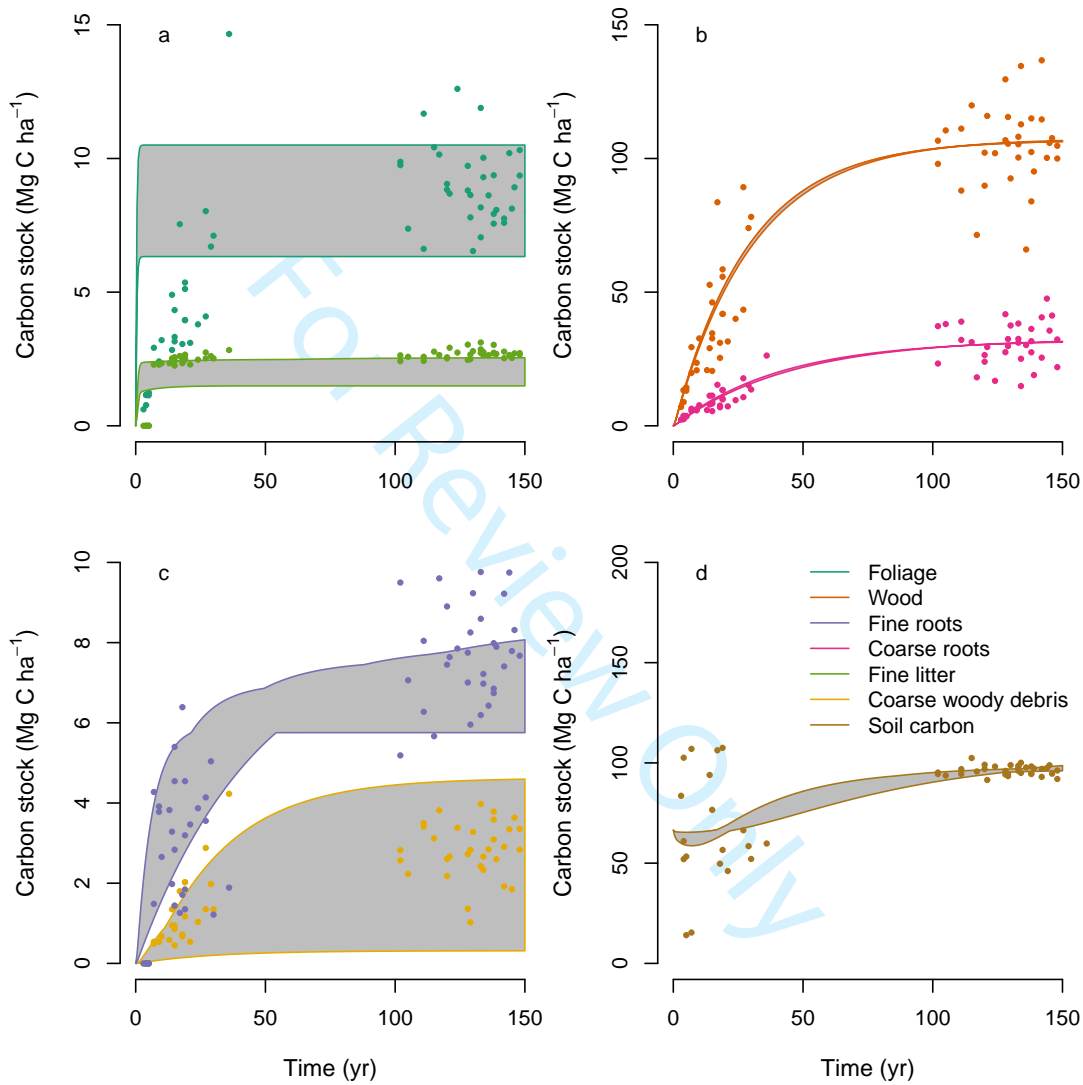


Figure 2: Observations of carbon stocks along a successional sequence and range of model predictions by fitting the model of equation (9) using observed data and random variates of GPP and old-growth carbon stocks after year 100.

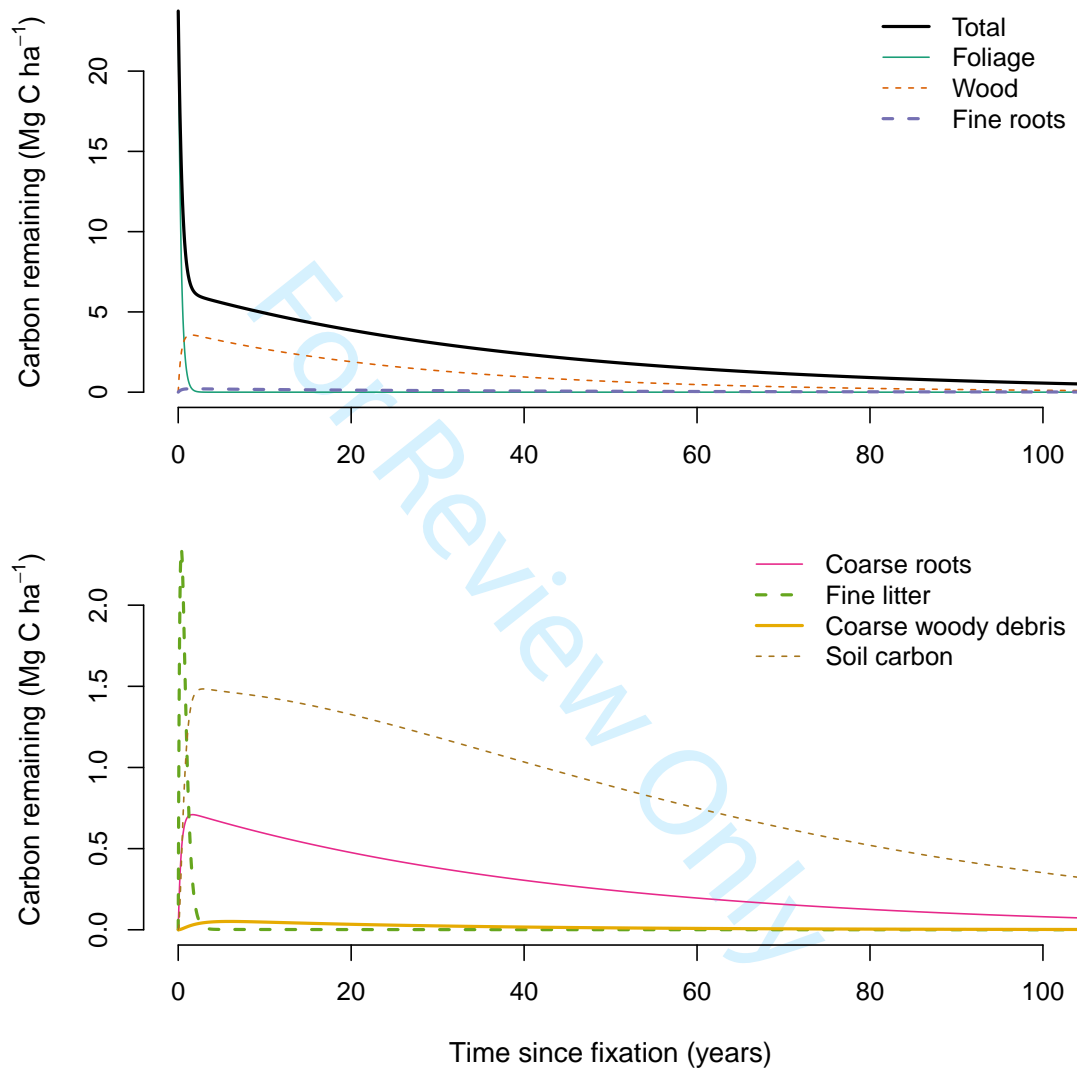


Figure 3: Fate of the annual amount of carbon fixed by photosynthesis (mean GPP = 23.98 Mg C ha<sup>-1</sup>) for the forest at equilibrium as predicted by the mean values of the parameters. Carbon enters the ecosystem through the foliage compartment and it is transferred to other compartments where it spends certain amount of time before being released back to the atmosphere. After 100 years, most carbon is lost from all pools.

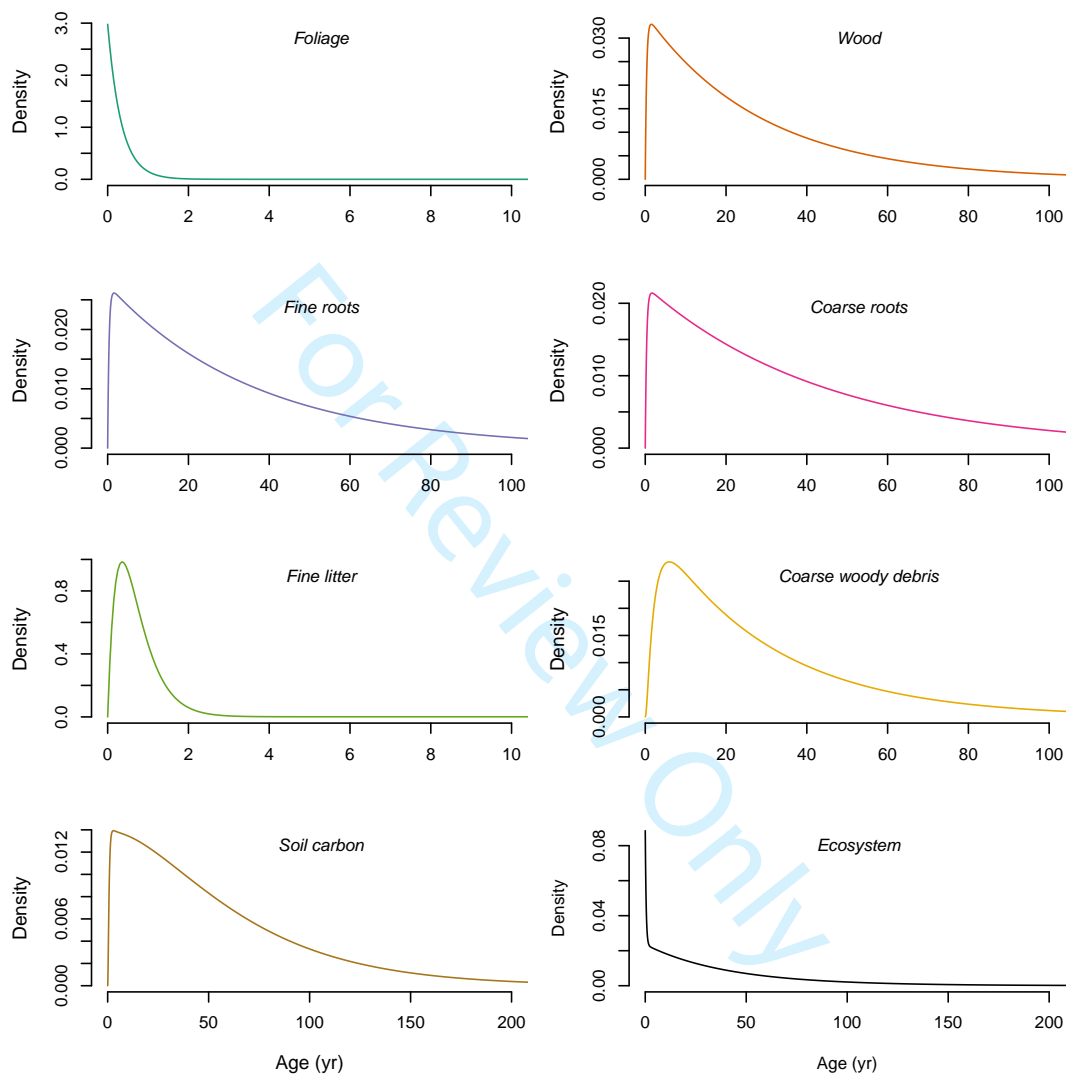


Figure 4: Age density distributions for each pool and for the entire ecosystem at equilibrium. These densities were obtained using the average parameter values from the 1000 sets of parameters after the optimization procedure. Age densities integrate to a value of 1, therefore their units are in  $\text{yr}^{-1}$ . Axes for each panel are different to facilitate the display of each distribution.



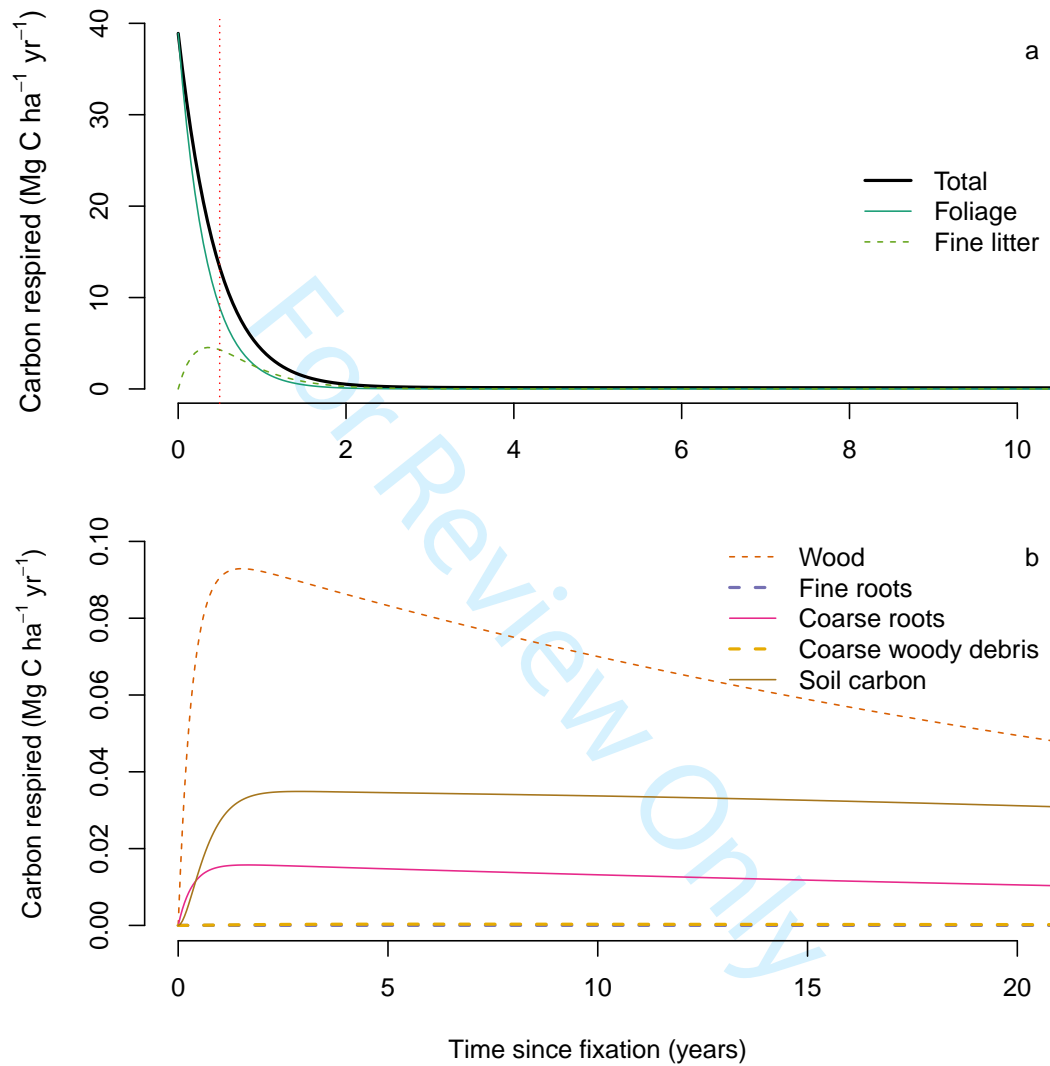


Figure 5: Transit time mass distribution and contribution of different pools to the transit time. Pool-wise mass distributions of transit times in (b) are presented on a different scale so differences among pools can be better observed. Dotted vertical line in panel a represent the median transit time (50% quantile) of the distribution, equivalent to 0.5 yr. 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.

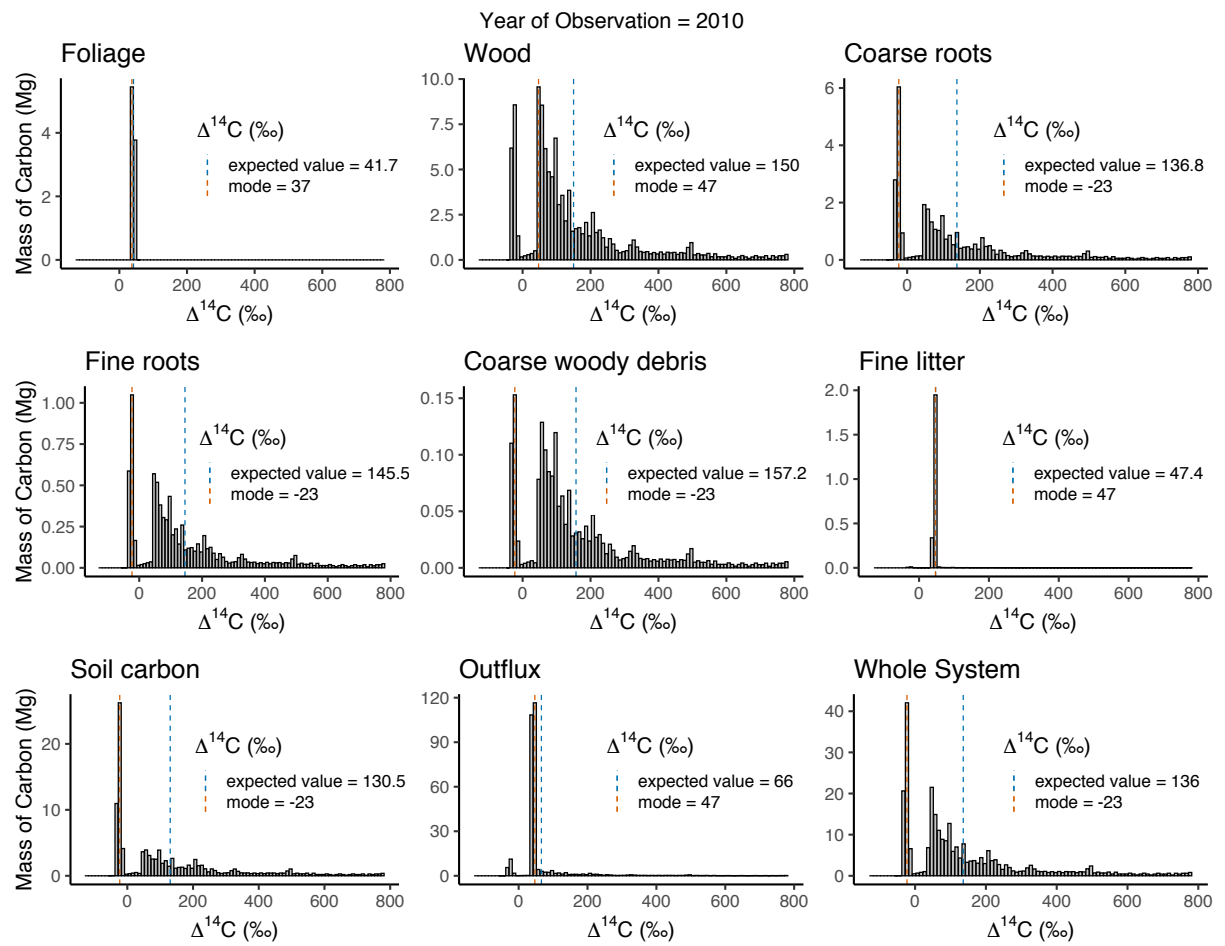


Figure A: Expected distributions of radiocarbon for each of the pools obtained by taking pool age distributions and predicting the corresponding radiocarbon values from atmospheric  $^{14}\text{CO}_2$ . These radiocarbon distributions are time-dependent, and therefore we present here only the predictions corresponding to calendar year 2010.

Table 1: Mean and standard deviation (SD) of parameter values obtained from the 1000 iterations of the optimization procedure.

Parameter	Mean	SD
$k_1$	2.978	0.041
$k_2$	0.035	0.000
$k_3$	0.027	0.011
$k_4$	0.022	0.000
$k_5$	2.594	0.520
$k_6$	0.519	0.789
$k_7$	0.024	0.015
$\alpha_{2,1}$	0.158	0.017
$\alpha_{3,1}$	0.009	0.003
$\alpha_{4,1}$	0.031	0.003
$\alpha_{5,1}$	0.251	0.061
$\alpha_{5,3}$	0.997	0.005
$\alpha_{6,2}$	0.249	0.172
$\alpha_{6,4}$	0.001	0.000
$\alpha_{7,5}$	0.256	0.144
$\alpha_{7,6}$	0.988	0.045