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The fate and transit time of carbon in a tropical forest

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The fate and transit time of carbon in a tropical forest

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Data availability statement: All code and data needed to reproduce all results in this manuscript can be find in the following Git repository <https://git.bgc-jena.mpg.de/csierra/agedisttropical>. Upon acceptance, we will move the repository to a permanent archive in Zenodo (<https://zenodo.org/>) where we will obtain a doi for permanent reference.

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Abstract

Tropical forests fix large quantities of carbon from the atmosphere; however, the fate of this carbon as it travels through ecosystem compartments is poorly understood. We quantified 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. 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. Our results offer insights on whether CO₂ fertilization of tropical forests have consequences on timescales relevant for climate change mitigation.

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; Fu et al., 2018; Luyssaert et al., 2007). 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

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4 72 trees before being respired, and the time it takes for carbon that enters the soil to appear
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6 73 in the respiratory flux. This transit time distribution should capture all these different
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8 74 processes over a wide range of timescales.

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10 75 In this manuscript, we provide an estimate of the transit time distribution of carbon in
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12 76 a tropical forest ecosystem using a data assimilation technique to parameterize a dynamic
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14 77 ecosystem model. Our main hypothesis is that the shape of the transit time distribution
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16 78 reconciles estimates of the time carbon spends in ecosystems obtained from tree- and plot-
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18 79 level methods. Furthermore, we attempt to provide here the formal theory to not only
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20 80 obtain the transit time distribution, but also metrics to characterize the fate of carbon
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22 81 inputs through the entire ecosystem as well as the age of carbon in ecosystem pools. This
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24 82 theory is then used to present an alternative interpretation of the link between GPP,
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26 83 autotrophic respiration (R_a), and net primary production (NPP).

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30 84 **2 Theory**

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33 85 The time that carbon spends in ecosystems can be obtained using the concept of transit
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35 86 time (Bolin and Rodhe, 1973; Thompson and Randerson, 1999; Rasmussen et al., 2016;
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37 87 Sierra et al., 2017). It characterizes the time carbon atoms spend in an ecosystem, from
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39 88 the time of carbon fixation by photosynthesis until release to the atmosphere through
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43 90 To compute transit times, we will consider a special case of the general mathematical
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45 91 representation of ecosystem carbon dynamics that follows the compartmental system
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47 92 representation proposed in Sierra et al. (2018). Since we are concerned in this manuscript
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49 93 with tropical old-growth forests at equilibrium, we will represent carbon dynamics in
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51 94 multiple pools using a linear autonomous compartmental system of the form

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

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58 95 where the vector \mathbf{u} represents total carbon inputs from the atmosphere to ecosystem
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60 96 pools, and the matrix \mathbf{B} represents all cycling and transfer rates of carbon within the

ecosystem. These linear autonomous compartmental systems at equilibrium have steady-state carbon stocks equivalent to

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

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 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

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

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.

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

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

where \top is the transpose operator and $-\mathbf{1}^\top$ is a row vector containing 1 (i.e., by this multiplication the column sum of \mathbf{B} is obtained). Therefore, \mathbf{z}^\top 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

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

This function represent 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

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

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 $\|\mathbf{u}\|$. The symbol $\|\cdot\|$ 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

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

where $\mathbf{X}^* = \text{diag}(x_1^*, x_2^*, \dots, x_n^*)$ 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

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

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 comparten-

tal 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°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. $u_1 = \text{GPP}$, 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 $263.9 \pm 2.0 \text{ MgC ha}^{-1}$, 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 $23.7 \pm 2.5 \text{ MgC ha}^{-1} \text{ yr}^{-1}$, from which 70 % corresponds to autotrophic respiration (Ra , $16.7 \pm 3.1 \text{ MgC ha}^{-1} \text{ yr}^{-1}$) and 30 % to heterotrophic respiration (Rh , $7.0 \pm 1.5 \text{ MgC ha}^{-1} \text{ yr}^{-1}$).

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

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a year ($k_1 = 2.978 \text{ yr}^{-1}$), 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 ± 0.01 and $2.14 \pm 0.56 \text{ yr}$, 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 ± 0.16 , 38.12 ± 3.28 , and $45.36 \pm 0.30 \text{ yr}$, respectively. Although the coarse woody debris pool has a very similar mean age ($32.95 \pm 1.24 \text{ yr}$), 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 $61.85 \pm 8.73 \text{ yr}$, 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 $43.15 \pm 3.33 \text{ yr}$, 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 $134.9 \pm 10.0 \text{ yr}$ (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 ± 0.14 yr (median transit time), while 95% of the carbon is lost in less than 68.60 ± 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 ± 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 Porce 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 CO₂ 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 CO₂. According to this interpretation, only

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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 CO₂.

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 CO₂ 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 the supplementary material.

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 CO₂ fertilization effect.

It has been hypothesized that as CO₂ 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 CO₂ 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 CO₂ 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

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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 CO₂ 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

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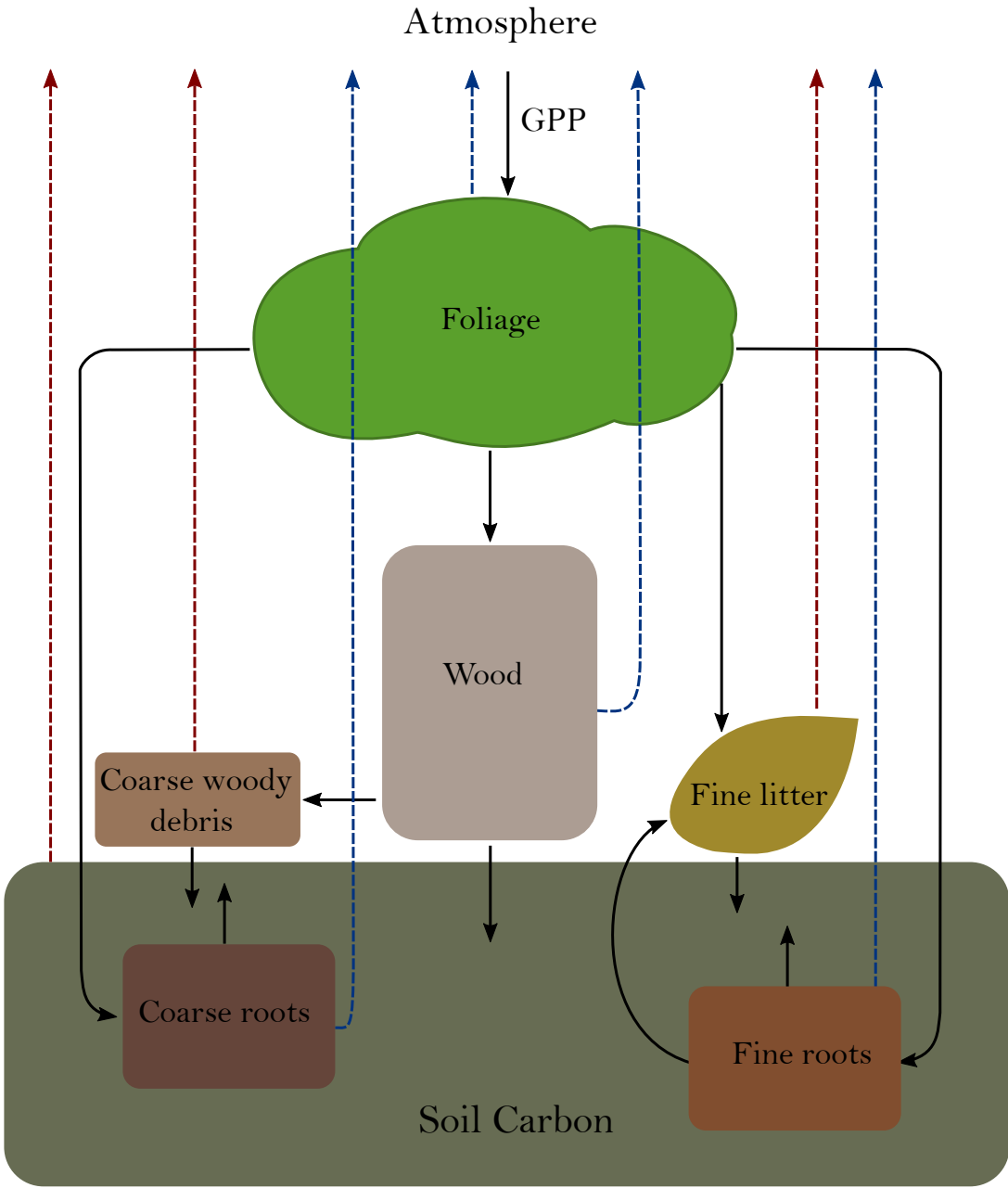


Figure 1: Structure of the compartmental model used to fit the available data from the Porce region of Colombia. Arrows represent transfers of carbon among pools (continuous line) or respiratory losses (dashed lines) to the atmosphere. Autotrophic respiration fluxes in dark blue and heterotrophic respiration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

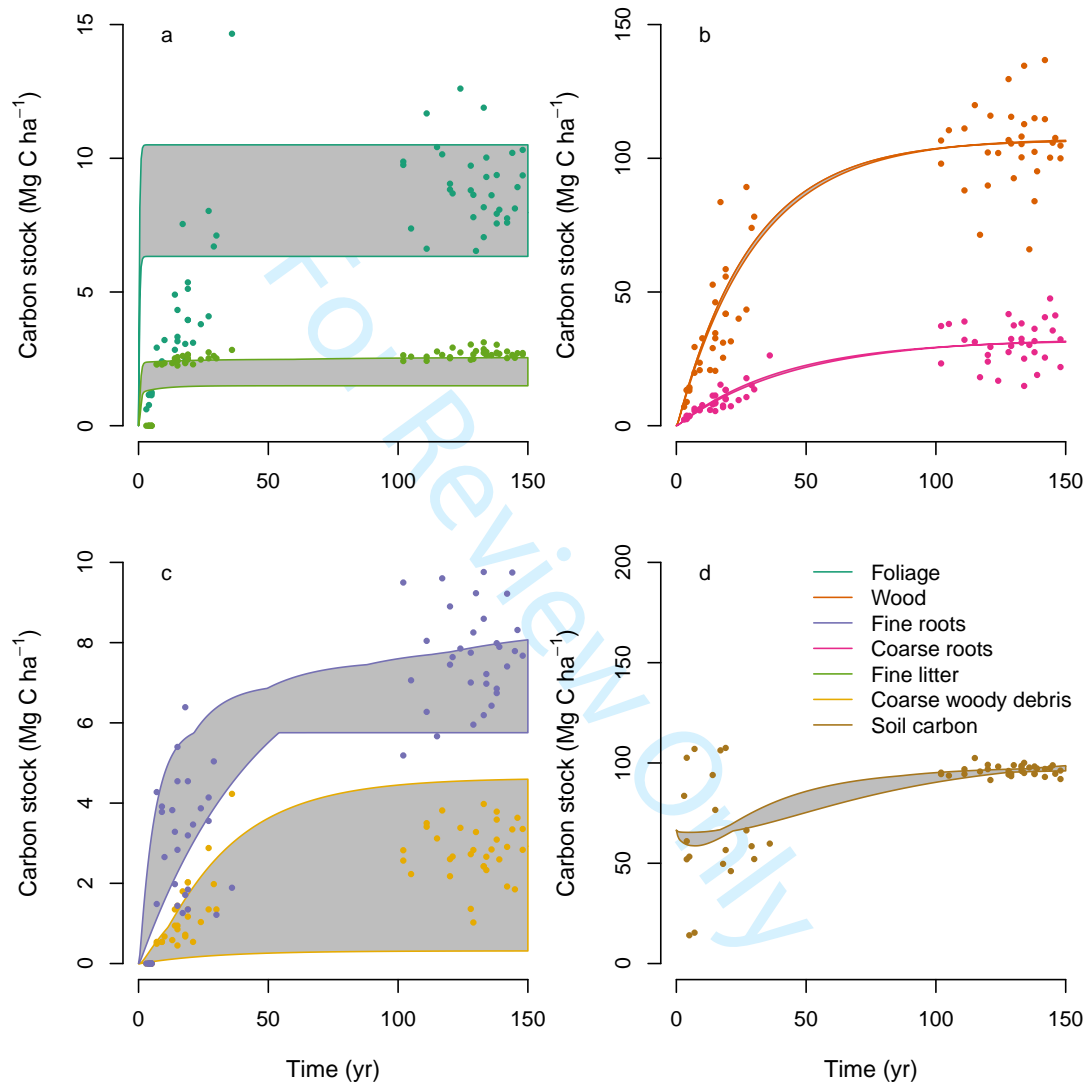


Figure 2: Observations of carbon stocks along a successional sequence and range of model predictions by fitting the model of equation (9) using observed data and random variates of GPP and old-growth carbon stocks after year 100.

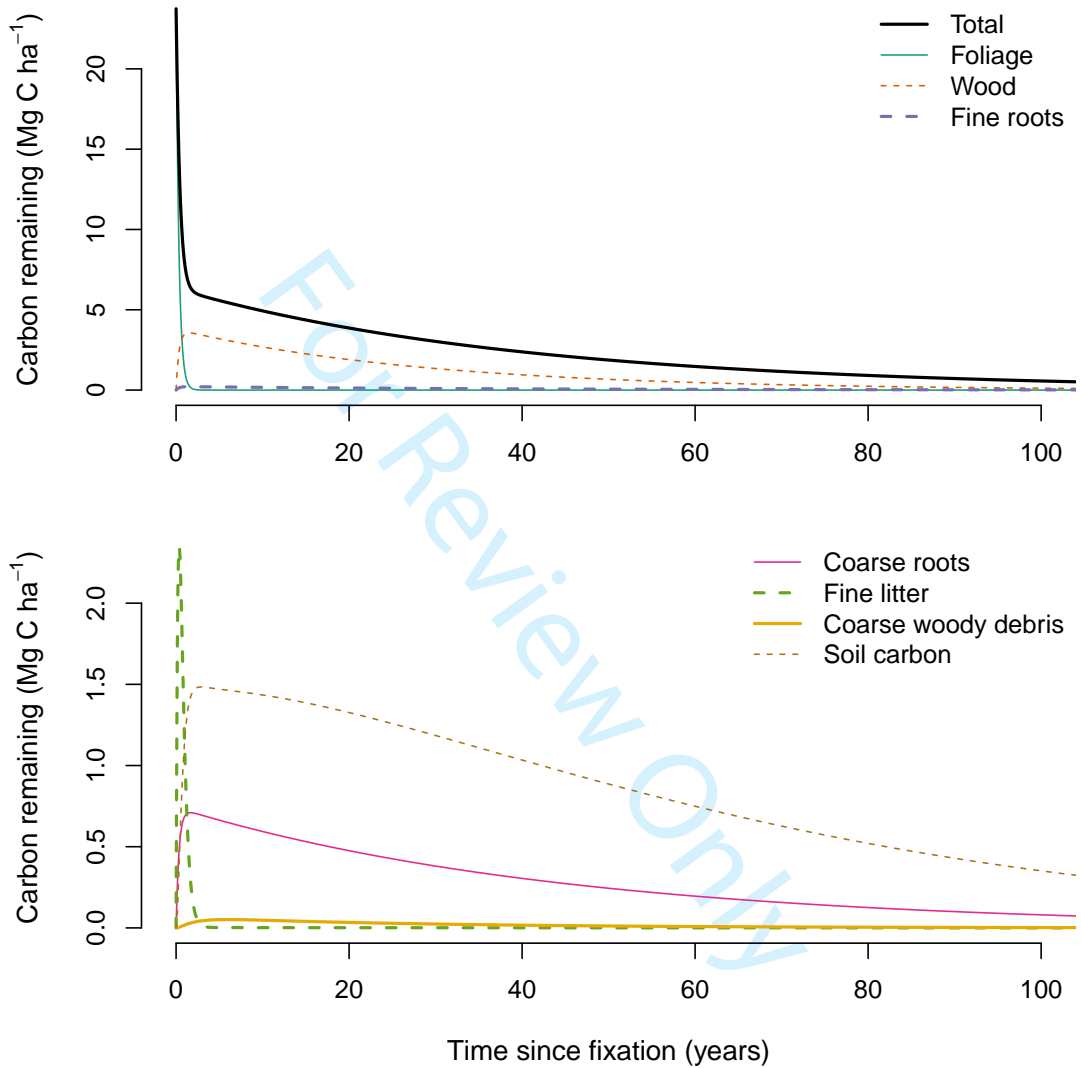


Figure 3: Fate of the annual amount of carbon fixed by photosynthesis (mean GPP = 23.98 Mg C ha⁻¹) for the forest at equilibrium as predicted by the mean values of the parameters. Carbon enters the ecosystem through the foliage compartment and it is transferred to other compartments where it spends certain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

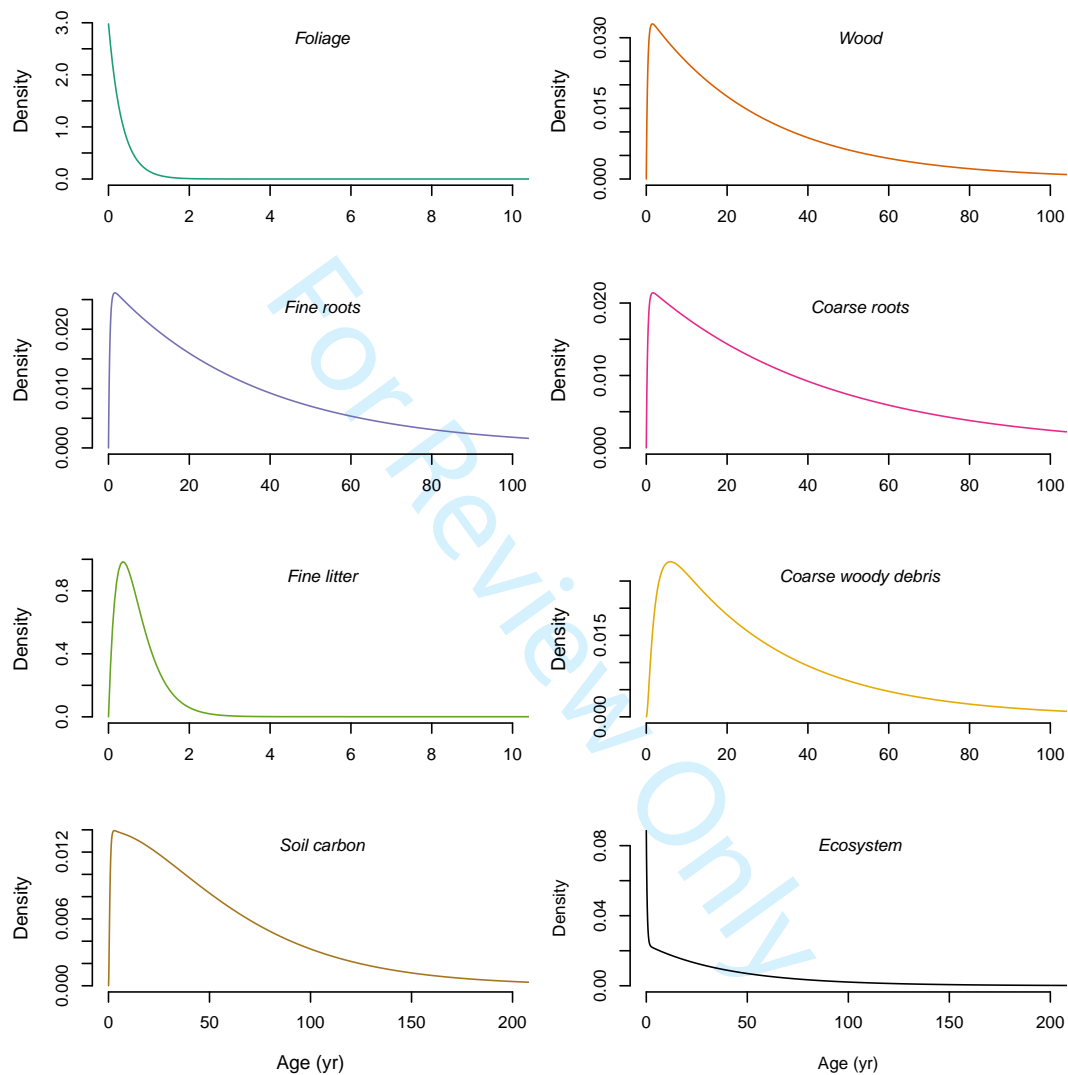


Figure 4: Age density distributions for each pool and for the entire ecosystem at equilibrium. These densities were obtained using the average parameter values from the 1000 sets of parameters after the optimization procedure. Age densities integrate to a value of 1, therefore their units are in yr^{-1}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

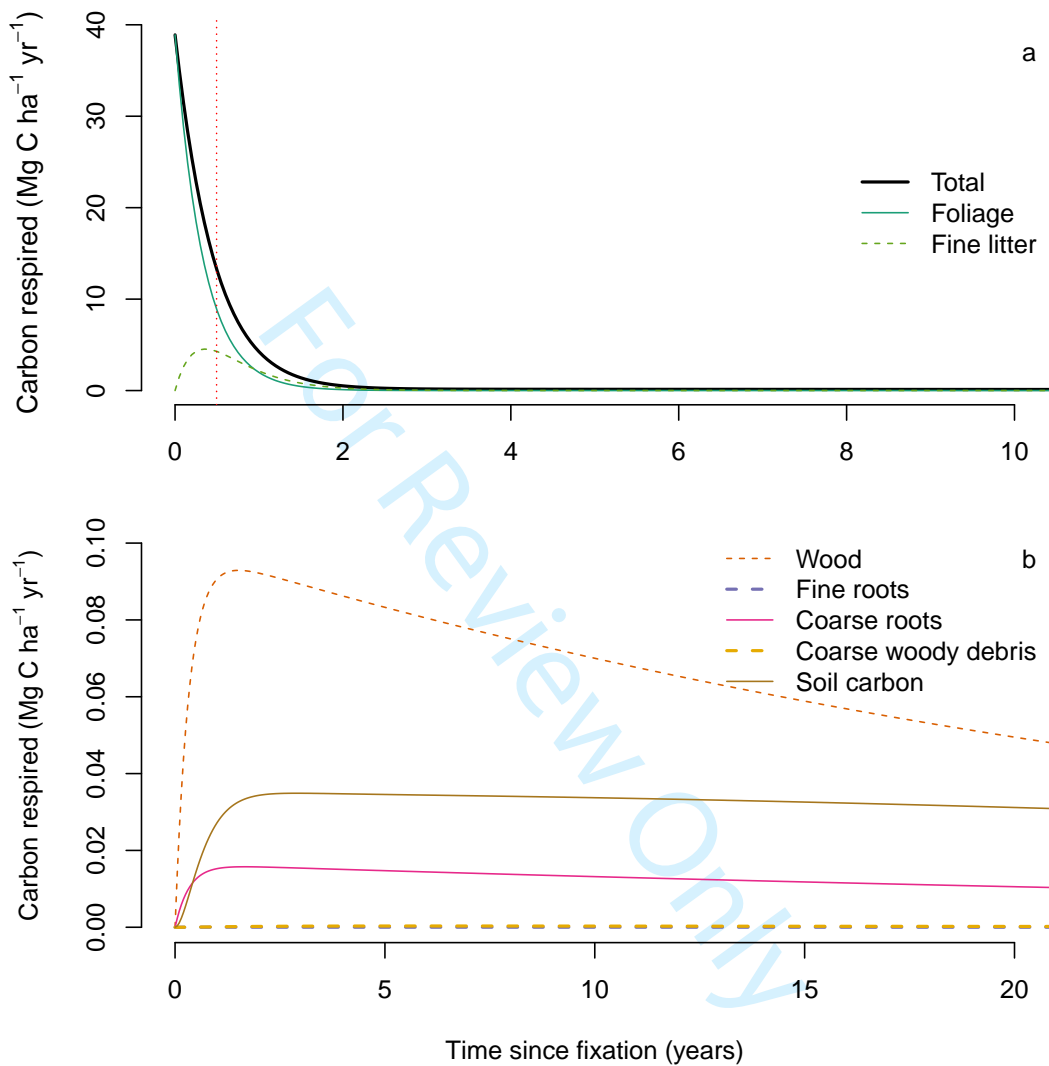


Figure 5: Transit time mass distribution and contribution of different pools to the transit time. Pool-wise mass distributions of transit times in (b) are presented on a different scale so differences among pools can be better observed. Dotted vertical line in panel a represent the median transit time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

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