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OPINION

# The muddle of ages, turnover, transit, and residence times in the carbon cycle

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## Abstract

Comparisons among ecosystem models or ecosystem dynamics along environmental gradients commonly rely on metrics that integrate different processes into a useful diagnostic. Terms such as age, turnover, residence, and transit times are often used for this purpose; however, these terms are variably defined in the literature and in many cases, calculations ignore assumptions implicit in their formulas. The aim of this opinion piece was i) to make evident these discrepancies and the incorrect use of formulas, ii) highlight recent results that simplify calculations and may help to avoid confusion, and iii) propose the adoption of simple and less ambiguous terms.

*Keywords:* carbon cycle models, carbon fluxes, carbon stocks, compartment models, dynamical systems, model diagnostics, radiocarbon, reservoir theory

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## Introduction

Carbon (C) storage in terrestrial ecosystems is the balance between two major fluxes: photosynthetic inputs and outputs through a variety of processes such as autotrophic and heterotrophic respiration, erosion, dissolved carbon runoff, and fire (Chapin *et al.*, 2006; Trumbore, 2006; Luo & Weng, 2011). Carbon stays in different ecosystem compartments for a wide range of time scales, from seconds to years in leaves, decades in wood, and centuries in stabilized soil organic matter. This large variation in the time that carbon stays in ecosystems poses challenges to study ecosystem-level processes. For instance, uncertainty in describing processes that control C outputs and their cycling rates in ecosystem compartments is a major contributor to overall uncertainty in Earth System Models (ESMs; Friedlingstein *et al.*, 2013; Friend *et al.*, 2013; Todd-Brown *et al.*, 2013; Carvalhais *et al.*, 2014).

To conceptualize all output processes into a single diagnostic metric, many different terms are commonly used in the literature, which include *turnover time*, *residence time*, (radiocarbon) *age*, *transit time*, *response time*, among others. Furthermore, these terms are commonly used as diagnostics of the capacity of ecosystems to store and cycle carbon, and therefore, we use here the term *system diagnostic times* to refer to them. However, the definitions of these terms are commonly ambiguous and inconsistent across different studies.

Despite this variety of terms, there are two main concepts that are independent of terminology: (i) the age of the mass in a system at a given time, and (ii) the age of the mass leaving the system at a given time (Eriksson, 1971; Bolin & Rodhe, 1973). Confusion between these two concepts and the different terms used arises because of a plethora of formulas for their calculation, each with specific assumptions. These assumptions are related to the way the C cycle is mathematically represented in models. For example, when assuming steady state and homogeneity of the system in which all particles have the same probability of leaving at any time (i.e. the so-called well-mixed assumption), *turnover time*, *residence time*, and *age* can be calculated similarly. Confusion starts when the assumptions are not met in reality, as in the case of the biospheric carbon cycle where the assumption of steady state is usually not met, and the system (e.g. terrestrial ecosystems) cannot be conceptualized as a single homogeneous pool.

In a timely contribution, Rasmussen *et al.* (2016) provide new formulas for the calculation of system diagnostic times in reservoir models with special application to the C cycle. This conceptual approach can help to disambiguate our current terminology. With this aim, we propose here a mathematical classification of C cycle models that helps to decide what assumptions are met for the differently proposed formulas and highlight cases in which formulas for diagnostic times do not exist yet. Furthermore, we

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differentiate between the main concepts related to diagnostic times and the different terms used in the literature with the aim to clarify current terminology.

## System diagnostic times

Although the different terms used to describe system diagnostic times in the carbon cycle are numerous and their definitions are not used consistently among different authors, we adopt here two concepts that are independent of terminology and assumptions for their calculation: *system age* and *transit time* (Fig. 1; Bolin & Rodhe, 1973). These are measurable physical variables that, for mathematical convenience, we treat as random variables in the definitions below.

## Main concepts

### *Age*

We consider the mass of carbon stored in ecosystems as composed of a finite number of particles or molecules, each characterized by an age, defined as the time elapsed from the moment the particle entered the system to a generic time $t$ (Fig. 1). If we randomly select a particle from the system, we can in principle determine its age. Therefore, the *system age* is a random variable that describes the age of particles or molecules within a system since the time of entry.

As the system age is a random variable, we can define a *system-age probability distribution* with a corresponding *mean system age*. For systems described by

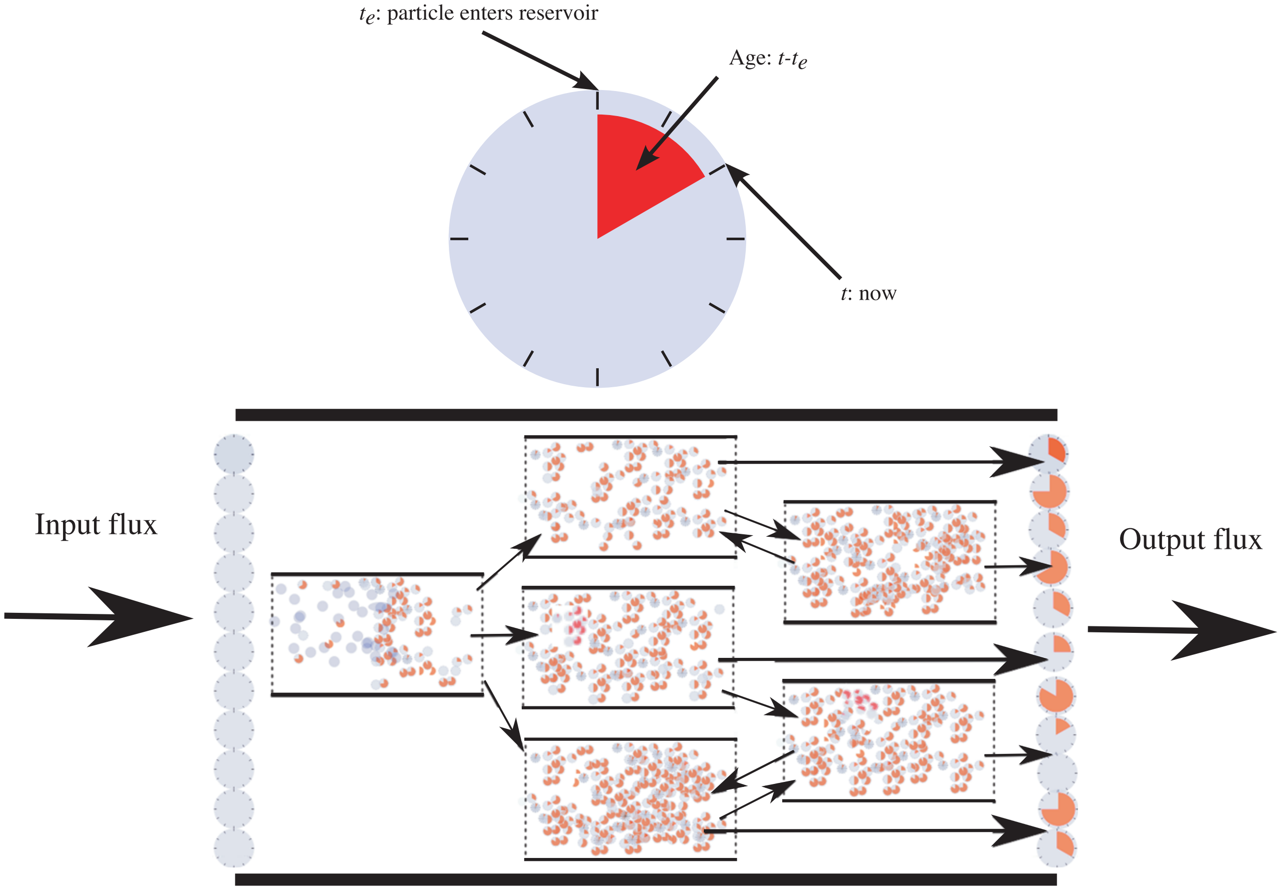


**Fig. 1** Schematic representation of the concepts of pool age, system age, and transit time with respect to the ages of particles in the system. Each particle, which can be thought of as a C molecule, is represented here as a clock that measures their age in the system. A system (e.g. a given soil volume) can be represented as a set of pools (rectangles) with mass transfer among each other (arrows), with an input flux in which particles enter with age = 0. At any given time $t$, particles in each pool have different ages and therefore each pool has a *pool-age distribution* with a corresponding *mean pool age*. For all particles in the system at any given time $t$, it is also possible to define a *system-age distribution* with a corresponding *mean system age*. Particles in the output flux have also different ages, and the age at which they leave the system is their transit time. The output flux can be characterized by a *transit-time distribution*, with a corresponding *mean transit time*. Notice that the concepts of system age and transit time do not rely on assumptions about model structure, steady state, or whether the system is autonomous.

multiple pools with different cycling rates, each pool would have a corresponding *pool-age distribution* (Fig. 1). The shapes of the pool-age and system-age distributions depend on the properties of the pool (e.g. well mixed versus piston flow), and on how the pools are arranged and exchange mass among each other (series, parallel, feedback loops).

### *Transit time*

The *transit time* is a random variable that describes the ages of the particles at the time they leave the boundaries of a system; that is, the ages of the particles in the output flux (Fig. 1). It can also be interpreted as the time it takes for a particle to transit a system. The term residence time (or exit time) is used in hydrology (e.g., Sardin *et al*., 1991; Botter *et al*., 2011) and chemical engineering (e.g., Nauman, 2008) to indicate the same quantity.

The random variable transit time can be characterized by a *transit-time probability distribution* with a corresponding *mean transit time*. As in the case of age distribution, the statistical properties of the transit-time distribution depend on the network structure and the individual pool properties.

## Common terminology

Terms such as turnover time, residence time, and radiocarbon age are used in the literature to either represent the concepts of system age or transit time, but their use is often ambiguous or misleading.

### *Turnover time*

The term turnover time commonly refers to the ratio of total carbon stock to input or output flux, and we adopt this definition here. This definition is equivalent to the concepts of system age and transit time in a set of limited cases. As mentioned earlier, turnover time, mean age, and mean transit time are identical for a system that can be represented as one homogenous pool in steady state. In autonomous multipool systems at steady state, the turnover time is equivalent to the mean transit time (see details in section *Autonomous systems* below). In all other cases, however, the turnover time differs from the concepts of system age and transit time.

The term turnover time is also used to refer to the inverse of the cycling rate for individual pools in first-order linear models (linear autonomous systems in our classification in section *Carbon cycle models as dynamical systems*). This use of the term turnover time is problematic because in systems with multiple transfers of C among pools, the inverse of the first-order cycling rate for a pool differs from the ratio of stock over output flux for the same pool, creating an ambiguity in the use and meaning of the term. Therefore, we discourage the use of the term turnover time as the inverse of a first-order cycling rate, and adopt the more general definition of the total carbon stock divided by the total input or output flux in a system.

### *Residence time*

The term residence time in carbon cycle research is often used to represent either the concept of transit time (e.g. Zhou & Luo, 2008; Luo & Weng, 2011; Galbraith *et al*., 2013), or system age (e.g. Eriksson, 1971; Martin *et al*., 2013). In other cases, residence time is simply defined as the ratio of a C stock over an input or output flux (e.g. Friend *et al*., 2013; Bloom *et al*., 2016), that is the turnover time, as defined above.

For radiocarbon-related studies, residence time is often defined as the inverse of the cycling rate obtained by fitting a one- or multiple-pool linear autonomous system to radiocarbon data (e.g. Trumbore, 1993; Baisden *et al*., 2013). Similarly, modelling studies often define residence time for individual pools as the inverse of their first-order cycling rate.

All these different uses of the term residence time make it difficult to unambiguously apply it in carbon cycle research. We therefore do not consider this term any further in this manuscript and discourage its use in further research unless clear definitions are presented that differ from those adopted for system age and transit time.

### *Radiocarbon age*

Radiocarbon is a powerful tracer for atmosphere-derived C in carbon cycle studies, as it follows the same processes at the same rates any other C atom in an ecosystem. Studies that use radiocarbon data often assume that radiocarbon-derived ages correspond to system ages, but this is only the case for a set of specific assumptions about the structure and dynamics of the system.

On timescales of centuries to thousands of years, the radioactive decay of $^{14}C$ provides a measure of the time C has been isolated from atmospheric renewal. Archaeological applications commonly report radiocarbon as *conventional radiocarbon age*, and use a special set of assumptions (closed system, homogeneously aged C) and a knowledge of past variations in atmospheric radiocarbon to convert conventional radiocarbon ages to *calendar ages* (Trumbore *et al*., 2016). However, in open systems, like the terrestrial C cycle, radiocarbon is constantly exchanged with the atmosphere, mixing newly fixed C with older C. In these cases, the mean age of the system does not correspond to radiocarbon-derived ages.

The production of excess radiocarbon by atmospheric nuclear weapons testing ('bomb' radiocarbon) allows a tracer that operates on annual to decadal timescales not normally resolvable with conventional (cosmogenically produced) radiocarbon. However, the large variations with time in the radiocarbon input function to ecosystems complicates the interpretation of radiocarbon as a direct measure of ages or transit times. Furthermore, for systems expressed by multiple pools, radiocarbon-derived age does not correspond to mean system age. Instead, rates of radiocarbon incorporation and release in different reservoirs can be compared with observed and modelled rates of C cycling; therefore, radiocarbon serves as a powerful diagnostic of model performance (Randerson *et al.*, 2002).

Radiocarbon data from terrestrial ecosystems, and in particular from soils, provide evidence that C cycling in terrestrial systems cannot be represented by a single homogeneous pool. If this were the case, the radiocarbon signature of the organic matter in the system would be equal to the signature of the carbon leaving the system. However, radiocarbon data taken from organic matter in mineral soils show marked differences from the radiocarbon signature of respired $CO_2$ in incubations as shown by the strong deviations from the 1 : 1 line in Fig. 2. In this case, radiocarbon provides direct evidence to reject the idea that organic matter in soils can be represented by a single-pool model using the well-mixed assumption. In fact, the range of ages in soil organic matter and the mechanisms that lead to its persistence are currently an active topic of research (Schmidt *et al.*, 2011). Data from the litter layer on the contrary shows a better agreement with the 1 : 1 line and supports the idea of modelling the litter layer as a single homogenous pool. However, care must be taken as in some systems, there are still important differences between the radiocarbon signature of stored C in litter and the respired $CO_2$ as shown by some outliers in Fig. 2.

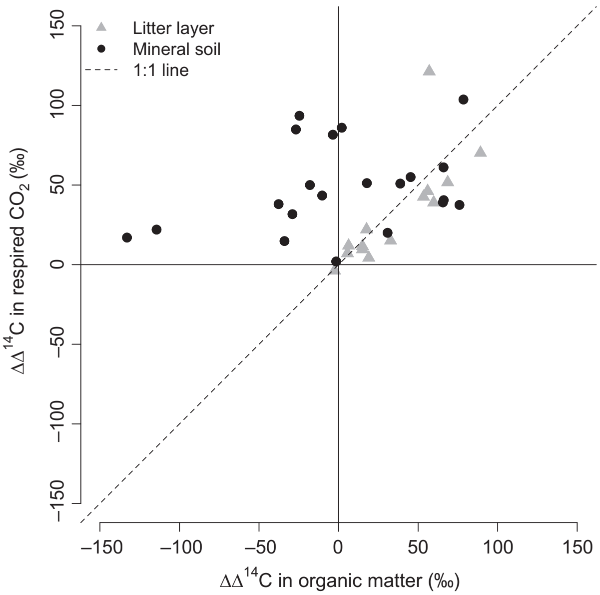


**Fig. 2** Radiocarbon signatures in bulk organic matter and in $CO_2$ evolved during incubations of litter or topsoil (mostly 0–5 or 0–10 cm) mineral soils from a range of locations (see supplemental material). To facilitate comparison for samples taken in different years, we use here the $\Delta\Delta\ ^{14}$C notation, where the $\Delta\ ^{14}$C of the atmospheric $CO_2$ (i.e. what is expected for newly fixed plant C) is subtracted. Values greater than 0‰ thus indicate radiocarbon in excess of newly fixed C, and negative values indicate OM or respired $CO_2$ have less radiocarbon than the atmosphere. For the period when most samples were taken (between 2000 and 2010), the $\Delta\ ^{14}$C of atmospheric $CO_2$ ranged from $\sim$40 to $\sim$80‰. Values greater than 0‰ thus represent C fixed mostly in the last years to decades (i.e. dominated by the excess $^{14}$C produced by nuclear weapons testing), while values below about -50‰ do not have much bomb radiocarbon and indicate predominance of C fixed hundreds to thousands of years previously.

## Carbon cycle models as dynamical systems

Models of the carbon cycle are generally based on systems of mass balance equations expressed as ordinary differential equations (ODEs), and can thus be generalized using concepts from dynamical system theory (Bolker *et al.*, 1998; Manzoni & Porporato, 2009; Luo & Weng, 2011; Raupach, 2013; Sierra & Müller, 2015). Accordingly, there are two main groups of models that can be distinguished and that have different properties: autonomous and nonautonomous systems (Fig. 3). Models that fall in the category of autonomous systems assume that inputs to the system are constant as well as all parameter values. This is similar to assuming that the environment has no effect on the cycling rates of carbon in the system. On the contrary, models described as nonautonomous dynamical systems assume that inputs and cycling rates are constantly changing due to changes in the environment.

In addition, both autonomous and nonautonomous systems may comprise one or multiple pools, and may or may not be linear. The simplest possible C cycle model is a linear ordinary differential equation that describes the change in carbon over time of one single pool as the result of constant inputs $I$ and first-order linear outputs as $dx/dt = I - kx(t)$ where $k$ is the cycling rate or first-order kinetic rate constant, in units

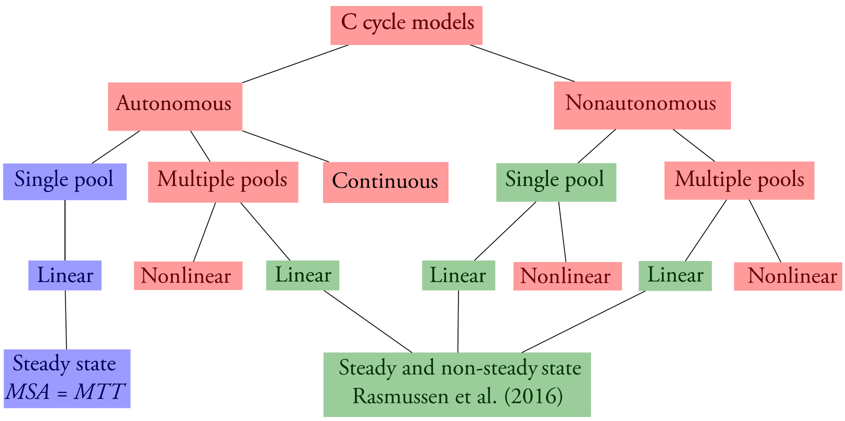


**Fig. 3** Classification of carbon cycle models according to 1) time dependencies, 2) pool structure, 3) linearity, and 4) steady-state assumption, regarding the concepts and calculation of system ages and transit times. Only in the case where the model is autonomous, single pool, linear, and at steady state, mean system age (MSA) and mean transit time (MTT) are equal and can be calculated as $1/k$ or $x/I$. For other cases of linear autonomous and nonautonomous systems, the new equations of Rasmussen *et al.* (2016) are applicable (green boxes). No general methods are available yet for nonlinear systems (red boxes).

of inverse time (Olson, 1963). For the very special case when this system is in steady state, and has been in this steady state for an infinitely long time, the concepts of age of particles in the system and age of particles leaving the system are equal (Eriksson, 1971; Bolin & Rodhe, 1973; Rasmussen *et al.*, 2016). Therefore, the terms turnover time, mean transit time, and mean age are all equal and can be calculated as the ratio of stock over input (or output) flux (e.g. $x/I$), or as the inverse of the cycling rate ($1/k$). In all other cases, these concepts and terms differ as well as formulas for their calculation (Fig. 3).

When the assumption of autonomous linear single-pool reservoir in steady state is not met (as in the soils of Fig. 2), there are important deviations of the concepts of age of particles in the system and age of particles leaving the system. Therefore, the terms age, residence, turnover, and transit time may mean completely different things depending on the assumptions met or violated.

### *Autonomous systems*

Models of the C cycle are expressed as autonomous dynamical systems when there are no time dependencies in the input fluxes and the cycling rates. It has been shown that carbon cycle models represented as linear autonomous systems are generally stable, that is, they converge in the long term to a steady state independently of the starting values of the state variables (Sierra & Müller, 2015; Rasmussen *et al.*, 2016). The assumption of no time dependencies may seem unreasonable for the C cycle where input fluxes and environmental conditions constantly change cycling rates. However, at yearly or longer time scales, variability in climatic conditions and thus input rates is generally small compared to the size of the ecosystem carbon stock, justifying the use of the autonomous system approximation. Moreover, it is useful to make this assumption to compare models, in particular with respect to the steady-state solution.

System ages and transit times at steady state for autonomous systems can serve as important diagnostics of model behaviour, for example to compare different model structures or parameterizations. Methods to calculate system diagnostic times for autonomous linear systems have been proposed before (Nir & Lewis, 1975; Thompson & Randerson, 1999; Manzoni *et al.*, 2009) using the concept of impulse response functions. This method is based on a three-step procedure. First, the system of ODEs describing the pool mass balances is converted from time to Laplace domain in the case of a sudden C input of unitary mass, resulting in a system of algebraic equations. These equations can be generally solved analytically even for complex soil models such as Century and Roth-C. Second, from this solution, the transit-time distribution is obtained as the ratio of output to input fluxes in the Laplace domain. Finally, the inverse Laplace transform is applied to return to the time domain. This method allows retrieving the entire transit-time distribution, including the higher order moments that retain important information on long-term C storage. Despite this advantage, calculation of diagnostic times can be cumbersome for complex model structures.

Rasmussen *et al.* (2016) present a much simpler method to calculate system diagnostic times for linear autonomous systems in steady state. The method only requires expressing a C cycle model in vector and matrix form (see examples in Luo & Weng, 2011; Sierra & Müller, 2015), and using simple matrix algebra, mean system age and transit time can be easily computed.

As an example, consider the five-pool carbon cycle model of Emanuel *et al.* (1981). The model is expressed in matrix and vector form as

$$\frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t} = \dot{\boldsymbol{x}} = \boldsymbol{I} + \mathbf{A} \cdot \boldsymbol{x}, \tag{1}$$

where $\boldsymbol{x}$ is a vector of carbon pools, $\boldsymbol{I}$ is a vector of photosynthetic inputs, and $\mathbf{A}$ is a matrix of cycling and transfer rates. More explicitly, input fluxes and cycling rates in the model are given by

$$\begin{pmatrix} \dot{x_1} \\ \dot{x_2} \\ \dot{x_3} \\ \dot{x_4} \\ \dot{x_5} \end{pmatrix} = \begin{pmatrix} 77 \\ 0 \\ 36 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} -2.081 & 0 & 0 & 0 & 0 \\ 0.8378 & -0.0686 & 0 & 0 & 0 \\ 0 & 0 & -0.5217 & 0 & 0 \\ 0.5676 & 0.0322 & 0.1739 & -0.5926 & 0 \\ 0 & 0.004425 & 0.087 & 0.037 & -0.009813 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{pmatrix},$$

where the pools $x_i$ represent 1: nonwoody tree parts, 2: woody tree parts, 3: nontree ground vegetation, 4: detritus/decomposers, and 5: active soil carbon. The vector of C inputs is expressed in units of Pg C yr$^{-1}$, and the matrix of cycling and transfer coefficients in units of yr$^{-1}$.

Using the formulas presented by Rasmussen *et al.* (2016), we can calculate mean transit time (MTT) and mean system age (MSA) at steady state as

$$\mathrm{MTT} = -(1, \ldots, 1) \cdot \mathbf{A}^{-1} \cdot \left( \frac{\boldsymbol{I}}{\sum \boldsymbol{I}} \right), \tag{2}$$

$$\mathrm{MSA} = -(1, \ldots, 1) \cdot \mathbf{A}^{-1} \cdot \left( \frac{\boldsymbol{x_{ss}}}{\sum \boldsymbol{x_{ss}}} \right), \tag{3}$$

where $\boldsymbol{x_{ss}} = -\mathbf{A}^{-1}\,\boldsymbol{I}$ represents the steady-state solution of the model, and the sum is over all pools. Using these formulas, we obtained MSA = 72.78 years and MTT = 15.54 years for the model above. The results with this method are almost identical as those reported in Thompson & Randerson (1999) using the impulse response function approach, with the main difference that these authors ran first the model to steady state, applied an impulsive input, and then calculated averages from the numerical output assuming the model was run long enough to approximate an integral to $t = +\infty$. Clearly, Rasmussen *et al.* (2016) method is more elegant and computationally efficient, but with the drawback that it does not provide the whole probability distribution for system ages and transit times.

It is important to note that the expression for mean transit time above (Eqn 2) is equivalent to

$$\mathrm{MTT} = \frac{\sum \boldsymbol{x_{ss}}}{\sum \boldsymbol{I}}, \tag{4}$$

where the sum is over all pools. That is, the ratio of the total stocks at steady state to the total inputs is equivalent to the mean transit time. This ratio is the *turnover time* as defined previously, and it is only equivalent to mean transit time in the autonomous case at steady state.

The formulas above can be applied to any C cycle model represented as an autonomous linear dynamical system, and analytical expressions can be easily derived. For instance, consider the simple model structures studied by Manzoni *et al.* (2009) for different types of connections among two-pool models. Using Eqns (2) and (3), we can recalculate the equations derived by Manzoni *et al.* (2009) (Table 1).

Analytical expressions for mean system age and mean transit time can also be computed for any model expressed as a linear system of the form of Eqn (1). In the supplementary material, we provide a simple python script to calculate analytical expressions of mean system age and mean transit time for an arbitrary matrix $\mathbf{A}$ and a vector $\boldsymbol{I}$ using a package for symbolic mathematics.

### *Nonautonomous (time-varying) systems*

Formulas for system-age and transit-time distribution under time-varying conditions relaxing the steady-state assumption were also developed in the context of watershed hydrology, using the formalism of the McKendrick–von Förster equation (e.g., Botter *et al.*, 2011; Calabrese & Porporato, 2015; Porporato & Calabrese, 2015; and references therein). Following a similar approach, but focusing on pool systems typically used in carbon cycle models, Rasmussen *et al.* (2016) derived formulas for mean system age and mean transit time by setting a system of differential equations for the mean age of mass in the system. This *mean-age system approach* also takes advantage of a known solution for the mass in the system, which is relatively easy to obtain for linear systems.

**Table 1** Formulas for the mean system age and mean transit time for different instances of a two-pool model with different connections among pools. For details about the model structures and alternative formulas, see Manzoni *et al.* (2009)

| Structure | $\dot{x} = I + \mathbf{A} \cdot x$ | Mean system age* | Mean transit time |
|---|---|---|---|
| Parallel | $I\begin{pmatrix} \gamma \\ 1-\gamma \end{pmatrix} + \begin{pmatrix} -k_1 & 0 \\ 0 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ | $\left(\frac{\gamma}{k_1^2} + \frac{1-\gamma}{k_2^2}\right)\left(\frac{\gamma}{k_1} + \frac{1-\gamma}{k_2}\right)^{-1}$ | $\frac{\gamma}{k_1} + \frac{(1-\gamma)}{k_2}$ |
| Series* | $I\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} -k_1 & 0 \\ \alpha_{2,1}k_1 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ | $\frac{\alpha_{21}}{k_2^2\left(\frac{\alpha_{21}}{k_2} + \frac{1}{k_1}\right)} + \frac{1}{k_1}$ | $\frac{\alpha_{21}}{k_2} + \frac{1}{k_1}$ |
| Feedback† | $I\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} -k_1 & \alpha_{1,2}k_2 \\ \alpha_{2,1}k_1 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ | $\frac{1}{1-\alpha_{12}\alpha_{21}}\left(\frac{1}{k_1} + \frac{\alpha_{21}(k_2\alpha_{12} + k_1)}{k_2(k_2 + k_1\alpha_{21})}\right)$ | $\left(\frac{1}{k_1} + \frac{\alpha_{21}}{k_2}\right)(1-\alpha_{12}\alpha_{21})^{-1}$ |

*The formula reported here for mean system age of the series model corrects a typo in Manzoni *et al.* (2009).
†The formulas for the feedback model map into Manzoni et al. (2009) for $\alpha_{21}$ = 1–*r* and $\alpha_{12}$ = 1.

The results from Rasmussen *et al.* (2016) clearly show how the computation of mean system age and mean transit time for the nonautonomous case deviates when the formulas for the autonomous case are incorrectly used. These authors forced a terrestrial C model with functions for the effect of $CO_2$ fertilization on plant production and effects of temperature increase on respiration rates. After 600 years of forcing, starting from a steady-state value, they found a difference of about 450 years between the two methods for calculating mean system ages, with an estimate of about 250 years when incorrectly using formulas for the autonomous case versus 700 years using the new formulas for the nonautonomous case. For transit times, the difference was of about 11 years, with an estimate of 24 years using the formulas for the autonomous case, and 35 years with the formulas for the nonautonomous case.

Similarly, forcing the model of Emanuel *et al.* (1981) with a time depending signal also confirms that incorrectly using the autonomous case formulas for the nonautonomous case results in large discrepancies between the two estimates of transit times (Fig. 4). In this case, we perturbed the system of Eqn (1) with a sine function for the vector $\boldsymbol{I}$, and all elements of the matrix $\mathbf{A}$ with a cosine function. The time-dependent inputs were given as

$$\boldsymbol{I}(t) = (1 + \sin(2\pi \cdot t)/2) \cdot \boldsymbol{I}, \tag{5}$$

and the time-dependent matrix of cycling and transfer rates as

$$\mathbf{A}(t) = (1 + \cos(2\pi \cdot t)) \cdot \mathbf{A}. \tag{6}$$

The trigonometric functions are useful in this example because they create a seasonal cycle in which at the end of the year, the system receives the same amount of inputs as the system with constant inputs, and the cycling rates are also on average the same as for the system with constant rates.

Comparing predictions between the correct formulas for the autonomous and nonautonomous case shows that mean ages and transit times in the nonautonomous system follow a seasonal pattern driven by the perturbing signals, and the long-term average differs from the mean ages and transit times of the autonomous system. More importantly, when incorrectly using the stock over flux approach (turnover time as defined above), the obtained curve differs dramatically from the correct mean-age and transit-time curves. The turnover time curve is closer to the correct mean transit time than to the mean age, but with a completely different seasonal cycle and a much larger amplitude.

These results have important implications for current research in the global carbon cycle. Take for instance recent calculations of turnover or residence times in influential papers such as Friend *et al.* (2013), Todd-Brown *et al.* (2013), Carvalhais *et al.* (2014), Bloom *et al.* (2016), where these metrics are obtained dividing a time-varying stock over a time-varying flux. In these publications, the method for autonomous systems in steady state is applied to the nonautonomous case out of steady state. As Rasmussen *et al.* (2016) and our results showed, there is no correspondence between the two methods, and they can largely under- or overestimate mean system ages and transit times. It is then important to ask, *how do we interpret calculations of system diagnostic times when formulas for the autonomous case are used in the nonautonomous case?*

This is a problem mostly of interpretation, because there is nothing mathematically wrong in the exercise of dividing stocks over fluxes. However, it is misleading to assume that this ratio describes the time C stays

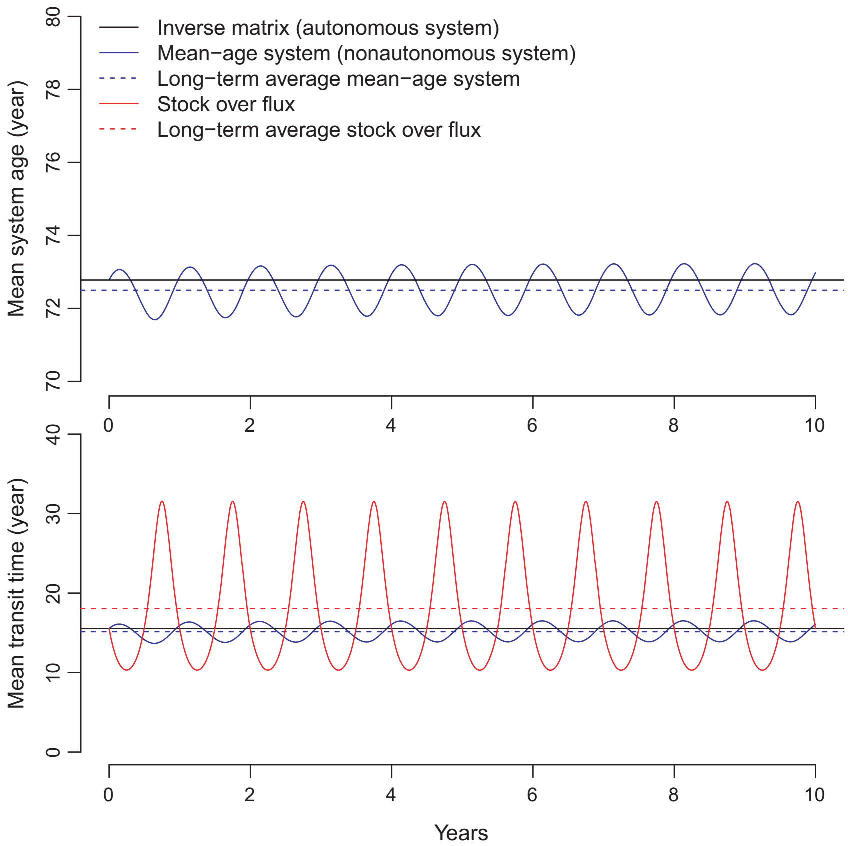


**Fig. 4** Mean system age and mean transit time in the global carbon cycle model of Emanuel *et al.* (1981) calculated for an autonomous version of the model (Eqn 1), and a nonautonomous version perturbed using the oscillating signals given by Eqns (5) and (6). The inverse matrix Eqns (2 and 3) were applied to the autonomous version of the model (black lines). The mean-age system method of Rasmussen *et al.* (2016, blue lines) and the stock-over-input method (turnover time, red lines) were applied to the nonautonomous system. Results show that incorrectly using stock-over-flux yields turnover times that dramatically deviate from the mean system age and mean transit time in nonautonomous systems.

in ecosystems. In the nonautonomous case, the history of the input fluxes and the history of changes in the cycling rates carry over to the calculation of system ages and transit times; the calculation of stock-to-flux ratios ignores this previous history.

However, a model is not inherently nonautonomous. For example, one can run a C cycle model with all parameters fixed and with constant inputs (i.e. the model is treated as an autonomous system), or with time series of environmental variables that modify parameters and inputs (i.e. the model is now described by a nonautonomous system). The distinction between autonomous and nonautonomous would be given by this simulation setup, rather than by structural differences between the two models. One approach to compare model structures and parameterizations would be calculating diagnostic times under the autonomous steady-state assumption. This approach could give helpful insights about the consequences of long-term ecological processes included in a model, without even having to find its numerical solution. Diagnostic times can be calculated from the model's matrix representation alone. Care must be taken however, in not mixing up concepts from the autonomous and nonautonomous case.

### *The nonlinear case*

Although the work of Rasmussen *et al.* (2016) has very important applications in diverse fields that use reservoir models, it only applies to linear dynamical systems. Methods to estimate diagnostic times for models expressed as nonlinear dynamical systems are not available yet. These types of systems are particularly useful to describe interactions among system compartments, for example the size of one pool controlling the rates of cycling in other pools such as in the case of the priming effect for the soil system.

For nonlinear systems, it is impossible to obtain analytical solutions in most cases, so explicit formulas for the probability functions of system age and transit time cannot be found (however see Gurtin & MacCamy, 1979, for an analytical solution of a very simple model). Instead, for a nonlinear system with a particular initial condition, it is always possible to find a numerical solution, so one can aim at algorithms that use this numerical solution and obtain numerical quantifications of system ages and transit times.

The theory developed to study hydrological reservoirs under non-steady state (e.g. Botter *et al.*, 2011; Calabrese & Porporato, 2015; Harman, 2015; Porporato & Calabrese, 2015) could be applicable to derive algorithms for the nonlinear nonautonomous case in C cycle models. This theory is general enough to be expanded to the nonlinear case, provided one has a numerical solution for the nonlinear system. However, there is an important difference on how systems are described in these hydrological models compared to carbon cycle models. Hydrologists describe the system as a one-reservoir system with one input and different outputs, and use an *age selection function* to determine what particles will leave the system at a particular time. In other words, their one-pool reservoir relaxes the assumption of equal probability for all particles of leaving a pool at any given time, but introduces a new function that must be determined. The 'continuous-quality' soil models represent the closest equivalent to hydrological models based on age selection functions. Here, a lumped model is built in which C is lost according to a distribution of first-order decay rates (Carpenter, 1981; Forney & Rothman, 2012). More sophisticated approaches include mass transfer across the quality continuum, offering an even wider and analytically tractable generalization (Ågren & Bosatta, 1996; Bosatta & Ågren, 2003).

A major challenge for future research would be to produce transit-time and system-age algorithms that can express a system one way or the other, that is, as a multiple-pool system in which mass within each pool has the same probability of leaving at any time, or as a one-pool system with a function that explicitly selects what particles leave at any given time. This would require the development of some sort of *pool algebra* that can map a system expressed as multiple pools, all with equal probability of age selection, to a representation as one single reservoir with an age selection function to determine what particles leave at any given time.

### *Diagnostic times derived from observations*

Measurements that are most often available at different observational levels, from plant organs to ecosystems, are C stocks and fluxes. It is therefore easy to divide one over the other and obtain a diagnostic time to interpret system dynamics. As discussed here, inferring mean system age and mean transit time from this ratio is possible only for a specific model structure and a set of assumptions about the configuration of the system. In fact, any derivation of a system diagnostic time must always include a set of assumptions. System diagnostic times are always model dependent, and it is not possible to obtain them from observations alone.

Nevertheless, observations of stocks, fluxes, and isotopes are fundamental to identify model structures and find their most appropriate parameter values. Once we are confident about representing a system with a specific model and parameter set, then its diagnostic times can be calculated. These diagnostic times provide a comprehensive understanding of the dynamics of a system as they integrate both a theoretical understanding of mechanisms involved in C cycling as well as empirical evidence that supports theory.

Starting from a known model structure, there are three different methodological approaches available for the calculation of system diagnostic times: (i) division of total stock over fluxes, (ii) the inverse matrix approach of Eqns (2) and (3), which is conceptually equivalent to the impulse response function approach (Nir & Lewis, 1975; Thompson & Randerson, 1999; Manzoni *et al.*, 2009), and (iii) the mean-age system approach for nonautonomous systems developed by Rasmussen *et al.* (2016). Each methodological approach must meet a certain set of assumptions that we list below:

- **Stock over flux**. The system must be linear, autonomous, in steady state, and it is assumed to have been in this state for an infinitely long time. If one single pool is assumed, MSA = MTT, but this is not true in the case of multiple pools.
- **Inverse matrix or impulse response**. Similarly, the system must be linear, autonomous in steady state, and it is assumed to have been in this state for an infinitely long time. The method is particularly useful for multiple reservoirs that exchange mass among each other, and where all cycling and transfer rates are known. An important advantage of this approach is that MSA and MTT can be computed as separate quantities. For systems with a time-varying input flux, MTT can be calculated with this approach, provided that the partitioning ratios of the input vector do not change over time (last term in Eqn 2 remains constant).
- **Mean-age system**. It assumes a linear system with known initial values for their pool content and mean ages. It also assumes that the time dependency of the inputs and cycling rates (non-autonomy) is known for all times of interest.

## Summary and conclusions

Two main concepts help as diagnostics of ecosystem processes and ecosystem models of the C cycle, the age of the mass of carbon in a system at a given time and the age of the mass in the output flux at a given time. Different formulas can be used to obtain these two diagnostics, but they depend on specific assumptions in the mathematical representation of the system. The representation of autonomous systems with no time dependencies in cycling rates and input fluxes, and the representation of nonautonomous systems with time dependencies, lead to very different calculations of mean system ages and mean transit times.

Formulas for both autonomous and nonautonomous linear systems are now available that are much simpler than previously proposed approaches, but we still lack methods for the nonlinear case.

At this point, it is evident that previous research has not only used terms such as residence time, turnover time, age, and transit time interchangeably, but worse, we have used methods for one type of system violating their inherent assumptions (i.e. methods for the linear autonomous case used for nonautonomous cases). This muddle of terms and concepts not only confuses dialogue within our discipline, but also may hinder progress.

We propose the adoption of only two terms that are less ambiguous than the others: system age and transit time, and recommend expressing the type of dynamical system for which these diagnostics are calculated. For example, one can calculate a time series of mean transit times for a C cycle model expressed as a nonautonomous system. This would be useful for example for studying effects of future climate drivers on ecosystems. Alternatively, one can study a system assuming no time dependencies and steady state to calculate the mean system age. This approach could prove useful by comparing model results with radiocarbon data where the long-time scales in some cases justify the steady-state assumption.

Although methods to calculate system age and transit time for nonlinear systems are not available yet, we envision new developments by integrating concepts from hydrological sciences. This integration could also lead to novel approaches to determine the whole probability distribution of C transit time and age in complex pool network models or simpler lumped models including a continuous range of C qualities. In both cases, we would be able to track the 'tails' of the transit-time and age distributions, which describe the fraction of C that stays longer in the system.

With clear and formal definitions of system ages and transit times, we are in a better position for comparing models against each other and against observed data; which most likely would result in scientific progress towards better understanding of the global C cycle and how it will change in the future.

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## Supporting Information

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

**Data S1.** Radiocarbon data to reproduce Fig. 2, and python code to calculate mean system age and mean transit time in linear autonomous reservoir models.