

1 **Soil organic matter persistence as a stochastic process:**
2 **age and transit time distributions of carbon in soils**

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Abstract

The question of why some organic matter is more persistent than other that decomposes quickly in soils has motivated a large amount of research in recent years. Persistence is commonly characterized as turnover or mean residence time of soil organic matter (SOM). However, turnover and residence times are ambiguous measures of persistence, because they could either represent the concepts of age or transit time. To disambiguate these concepts and propose a metric to assess SOM persistence, we calculated age and transit time distributions for a wide range of soil organic carbon (SOC) models. Furthermore, we show how age and transit time distributions can be obtained from a stochastic approach that takes a deterministic model of mass transfers among different pools and creates an equivalent stochastic model at the level of atoms. Using this approach we show: 1) age distributions have relatively old mean values and long tails in relation to transit time distributions, suggesting that carbon stored in soils is on average much older than carbon in the release flux. 2) The difference between mean ages and mean transit times is large, with estimates of SOC persistence in the order of centuries or millennia when assessed using ages, and in the order of decades when using transit or turnover times. 3) The age distribution is an appropriate metric to characterize persistence of SOM. An important implication of our analysis is that random chance is a factor that helps to explain why some organic matter persists for millennia in soil.

1 Introduction

The observation that soil organic matter (SOM) persists in soils for a wide range of times independent of its quality has challenged previous views in SOM cycling research [Kleber, 2010; Schmidt *et al.*, 2011; Dungait *et al.*, 2012; Gleixner, 2013; Paul, 2016]. It has been reported that easily degradable compounds can persist for years to decades in soils [Kiem and Kögel-Knabner, 2003; Kleber, 2010], while highly aromatic organic compounds such as lignin or charcoal can degrade in a matter of years, much faster than previously believed [Gleixner *et al.*, 1999; Kleber, 2010; Heim and Schmidt, 2007; Lehmann *et al.*, 2015]. To explain this variability, current research on mechanisms of SOM cycling and stabilization focus on physical and chemical protection rather than molecular structure to explain SOM persistence [Schmidt *et al.*, 2011; Lehmann and Kleber, 2015].

The term persistence however, has been vaguely defined. In most cases, persistence is associated with the turnover or mean residence time of carbon in SOM [Schmidt *et al.*,

2011; *Derrien and Amelung*, 2011; *Lehmann et al.*, 2015]. These two terms are problematic to use as definitions of persistence for three main reasons: 1) they are ambiguously used in many studies, in some cases referring to the concept of age and in others to the concept of transit times (see below), 2) in some cases their calculation relies on the assumption of a single homogenous pool at steady-state while a range of timescales for C has been clearly reported [*Trumbore*, 2000, 2009], and 3) measures of central tendency do not provide information on the distribution of the maximum age that could be observed in a soil (Figure 1). This highlights the need for a more precise definition of SOM persistence.

Turnover and residence times are ambiguous terms because they may indicate concepts related to the age of carbon within the soil system or the age of carbon in the flux out of soils (e.g. CO₂ respiration or dissolved organic carbon leaching) [*Sierra et al.*, 2017]. Less ambiguous are the concepts of system age and transit times [*Bolin and Rodhe*, 1973; *Bruun et al.*, 2004; *Derrien and Amelung*, 2011; *Manzoni et al.*, 2009; *Sierra et al.*, 2017]. System age can be defined as the age of particles or atoms in a system, in this case a soil, since the time the atom entered the system until the time of observation. Transit time can be defined as the time elapsed since the atom entered until it leaves in the output flux. It is well established that both system age and transit time are equal in single-pool systems at steady-state. For systems with multiple pools that cycle at different time scales, these quantities are generally different.

System age and transit time can be characterized by a distribution that measures the proportion of atoms or particles in a soil that have less than a certain age [*Eriksson*, 1971; *Bolin and Rodhe*, 1973]. These distributions can also be interpreted in a probabilistic sense, suggesting that the problem of persistence could also be approached from a stochastic point of view.

In this manuscript, we assess age and transit time distributions to determine which is most appropriate to characterize the persistence of SOM. We focus on carbon cycling, but the ideas and theory presented can be applied to any other biogeochemical element [*Spohn and Sierra*, 2018]. To evaluate the applicability of these distributions, we calculate estimates of ages and transit times of carbon for a particular set of models, and estimates at the global scale using output from Earth system models. We take a mostly theoretical approach, starting from a general stochastic model for the definition of ages

and using a set of examples from the literature to calculate ages and transit times at a set of single sites and at the global scale. Through this analysis, we show that 1) ages of carbon in soils can be explained by stochastic processes that can be directly linked to mechanisms of SOM (de)stabilization, 2) ages and transit times differ considerably in soils, with ages being much older than transit times and 3) across models, SOM age distributions have a long tail of old C, suggesting a small fraction of SOM persists in soils for centuries to millennia. Finally, based on these findings we suggest that age distributions are a strong indicator of SOM persistence in soils.

2 Conceptual framework

2.1 A stochastic interpretation of SOM dynamics

Soils are constituted by a mixture of carbon atoms of mostly plant origin that have accumulated over a period of time. For each atom, the time elapsed since it entered the soil is defined here as *age*. If we were able to measure the age a of every single atom in a given amount of soil, we would be able to produce a frequency distribution of the ages of carbon. To be able to construct this frequency distribution, we would need to group C atoms in age bins of some size Δa and count how many atoms belong to each age class. If we make the size of these age bins very small, we would obtain a series of $a + \delta a$ intervals that define what is commonly known as a probability density function (pdf). This pdf measures the probability that certain amount of carbon is below or above certain age. Once we have a pdf of carbon ages, we can characterize the age structure of SOC by simple measures such as the mean, the median, and quantiles (Figure 1).

To arrive at a pdf of SOC ages, we need to take the atom perspective further. Consider a carbon atom that ~~is part of~~ belongs to a dead plant part just entering the soil. This C atom will stay in the soil until something will happen; for instance, the plant part may be broken down by physical mechanisms or by macro-organisms. The molecules that contain the atom may be transformed by exo-enzymes, they might be absorbed by mineral surfaces, or they might be ingested by a microorganism. All these different possibilities are the well-studied mechanisms of soil carbon (de)stabilization [Sollins *et al.*, 1996; von Lützow *et al.*, 2008; Schmidt *et al.*, 2011; Lehmann and Kleber, 2015]. In this context however, we consider these mechanisms to set a probability on a C atom of changing its location and its state. Depending on the context, i.e. to what macro-molecule the

atom belongs to, or the environment determined by factors such as pH, temperature, moisture, redox potential, etc., the probability of the C atom changing its state would be determined. However, we assume that none of these mechanisms operate at the age level. This means that mechanisms of (de)stabilization operate based on the physical, chemical, and biological properties of the organic matter, but not on the age since it entered the soil. We assume that SOM processing is independent of age, and therefore atoms are processed randomly with respect to age, but deterministically based on physical, chemical, and biological mechanisms.

Once the probabilities for the change of state of carbon atoms are determined, it is possible to use them to compute for how long a particle may stay in a specific state, and how long it will take for the particle to leave the system [Metzler and Sierra, 2018]. In the following section, we show how to perform these computations.

2.2 Computation of age distributions

To characterize SOM persistence using age distributions, it is necessary to use models that incorporate different (de)stabilization mechanisms. Over several decades, researchers have proposed a large variety of SOM models that account for biological, physical, and chemical mechanisms of SOM (de)stabilization [Manzoni and Porporato, 2009]. A large number of these models can be represented as systems of linear differential equations [Sierra and Müller, 2015] of the form

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

where the rate of change of carbon over time in n different pools is represented by the n -dimensional vector $\dot{\mathbf{x}}(t)$. Constant inputs of carbon to each soil pool are represented by the n -dimensional vector \mathbf{u} , and rates of carbon processing, stabilization, and destabilization are represented in the $n \times n$ dimensional matrix \mathbf{B} . The diagonal entries of \mathbf{B} contain the rates at which carbon is processed in each of the pools, and if we organize them from fast to slow from left to right, we can interpret all lower diagonal entries as the rates of carbon stabilization; and the upper diagonal entries as the rates of carbon destabilization [Sierra and Müller, 2015; Sierra et al., 2011]. By adding all rows from each column of \mathbf{B} , one obtains a vector \mathbf{z} with the fraction of the decomposed carbon that is released from the system either as respired or dissolved carbon. This vector can

be computed as $\mathbf{z}^T = -\mathbf{1}^T \cdot \mathbf{B}$, where T represents the transpose operator. At steady-state, the model of equation (1) has the general solution $\mathbf{x}^* = -\mathbf{B}^{-1} \cdot \mathbf{u}$.

Metzler and Sierra [2018] showed that it is possible to build a stochastic model from the deterministic compartmental model of equation (1). The stochastic model corresponds to a continuous-time absorbing Markov chain with transition rate matrix \mathbf{Q} as

$$\mathbf{Q} = \begin{pmatrix} \mathbf{B} & \mathbf{0} \\ \mathbf{z}^T & 0 \end{pmatrix}. \quad (2)$$

This transition rate matrix contains as elements the probabilities that carbon atoms move across different pools (\mathbf{B}) and get released from the entire system (\mathbf{z}^T) to an absorbing state where the atom cannot return back to the system. This transition rate matrix also clearly establishes the relation between deterministic models of differential equations and stochastic models at the level of atoms, and can be used to compute age and transit time distributions.

The age pdf for this type of linear models at steady-state can be computed by the following expression [*Metzler and Sierra*, 2018]

$$f(a) = -\mathbf{1}^T \cdot \mathbf{B} \cdot e^{a \cdot \mathbf{B}} \cdot \frac{\mathbf{x}^*}{\sum \mathbf{x}^*}, \quad a \geq 0, \quad (3)$$

where a is the random variable age, $\mathbf{1}^T$ is the transpose of the n -dimensional vector containing ones, $e^{a \cdot \mathbf{B}}$ is the matrix exponential computed for each value of a , and $\sum \mathbf{x}^*$ is the sum of the stocks of all pools at steady-state.

The mean, i.e. expected value, of the age pdf can be computed by the expression

$$\mathbb{E}(a) = -\mathbf{1}^T \cdot \mathbf{B}^{-1} \cdot \frac{\mathbf{x}^*}{\sum \mathbf{x}^*}. \quad (4)$$

2.3 Computation of transit time distributions

Although we propose age distributions to characterize persistence of SOM, it is also useful to compute transit time distributions of soil organic matter for comparison purposes, and to get an idea of the age structure of the carbon that is released from soils.

The pdf of the transit time variable τ for models of the form of equation (1) is given by [*Metzler and Sierra*, 2018]

$$f(\tau) = -\mathbf{1}^T \cdot \mathbf{B} \cdot e^{\tau \cdot \mathbf{B}} \cdot \frac{\mathbf{u}}{\sum \mathbf{u}}, \quad \tau \geq 0, \quad (5)$$

and the mean transit time by

$$\mathbb{E}(\tau) = -\mathbf{1}^T \cdot \mathbf{B}^{-1} \cdot \frac{\mathbf{u}}{\sum \mathbf{u}}. \quad (6)$$

It is important to note that the mean transit time can also be obtained dividing the stock of mass at steady-state by either the input or the output flux. This metric is also called the turnover time, and it is used in many applications to characterize time scales of carbon cycling in ecosystems [Sierra *et al.*, 2017].

Notice that the computation of the transit time density distribution and its mean depends directly on the elements of the matrix \mathbf{B} and on the proportional distribution of the inputs as stated in the vector $\mathbf{u}/\sum \mathbf{u}$ (equations 5 and 6). In other words, transit times depend on the cycling rates of each pool and the transfer rates among them as embedded in the compartmental matrix, and on how the external inputs are distributed to the different pools. However, transit times do not depend on the total amount of inputs to the system.

Ages however, depend on the cycling and transfer rates encoded in the compartmental matrix \mathbf{B} , and on the proportional distribution of the carbon stocks at steady-state as expressed in $\mathbf{x}^*/\sum \mathbf{x}^*$ (equation 3 and 4). Since the steady state \mathbf{x}^* does depend on the total amount of inputs, the age distribution and its mean do depend on the total amount of inputs and its distribution to different pools.

2.4 Computation of quantiles

Quantiles for the age and transit time probability density functions (equations 3 and 5) are computed numerically by taking the inverse of their cumulative distribution function $F(y)$, and finding the smallest y such that $F(y) \geq q$, where $q \in (0, 1)$ are the cut points for which quantiles are desired; e.g. $q = 0.5$ represents the Q_{50} quantile (median) of the distribution.

2.5 Hypothetical relation between ages and transit times

Following Bolin and Rodhe [1973], we examine the relations between ages and transit times of soil organic carbon, which fall into three categories: I) the age and the tran-

sit time distributions are equal, II) ages are younger than transit times, III) ages are older than transit time (Figure 2). The type I relation implies that the soil organic matter system is well mixed and all carbon atoms in soil have the same probability of being mineralized and released as CO₂ or as dissolved organic carbon. When plotting ages versus transit times of carbon, type I systems would lie along the 1:1 line (Figure 2).

If the transit time is longer than the age (type II), the system retains carbon for a relatively long time before it is released. This type of behavior is common in systems in which physical transport or recycling are dominant mechanisms. For example, when a physical transport pathway moves carbon atoms sequentially before they are released, or when carbon is continuously recycled by microorganisms and only released outside the system after a long time. In these cases, the age of atoms in the release flux is older than the age of atoms stored inside the system, and a plot of ages versus transit times would occupy the region above the 1:1 line (Figure 2). We can also think about the type II relation as representative of a sequential process with multiple steps in the degradation of organic matter, in which fresh OM is transformed into multiple products before it is mineralized and released from the soil in a final step. Or alternatively, we could also think of soil as a chromatography column with new C added at the top and oldest C released from the bottom in dissolved form.

Finally, for a type III relation, ages are older than transit times, and occupy the lower region below the 1:1 line (Figure 2). A relationship in this region implies that most carbon atoms enter and leave the system in a relatively short time, but those atoms that remain in the system stay there for a long time. This situation can happen when input and output fluxes occur at relatively close distance between each other, and storage is physically separated from them; or, when specific mechanisms favor the processing and release of material close to the input source [Bolin and Rodhe, 1973].

3 Methods

Equations 3 to 6 as well as additional formulas for the quantiles of these distributions described in Metzler and Sierra [2018] were implemented in the R package SoilR [Sierra et al., 2014].

We applied these formulas to a variety of SOC models reported in the literature (Table 1). We selected popular SOC models such as RothC and Century [Jenkinson et al.,

1990; *Parton et al.*, 1987], using reference parameter values reported in their original publications; i.e. parameter values that are not affected by the temperature and moisture modifiers implemented in these models. For RothC, we excluded its inert pool because it has a decomposition rate equal to zero and therefore the age is infinitely large at steady-state and the matrix \mathbf{B} is not invertible [*Metzler and Sierra*, 2018]. We also selected the Yasso07 model because it has been parameterized using an extensive dataset of litter decomposition experiments [*Tuomi et al.*, 2009], and it has been implemented as part of the MPI Earth system model [*Goll et al.*, 2015]. Also, the ICBM model was selected due to its simplicity and yet enough complexity to represent stabilization of SOC [*Andren and Katterer*, 1997].

In addition, we selected a set of models used for global-scale applications. First, we selected three different parameterizations of the Community Land Model version 4 (CLM4cn), for needleleaf, deciduous, and tropical forest plant functional types (PFT). These parameterizations differ mostly on the amount and distribution of C inputs to the soil [*Wieder et al.*, 2014]. Second, we used three versions of reduced complexity models constructed from the output of three Earth system models [*He et al.*, 2016]: the Community Earth System Model, version 1–Biogeochemistry (CESM1-BGC, here CESM), L’Institut Pierre-Simon Laplace Coupled Model, version 5, coupled with NEMO, low resolution (IPSL-CM5A-LR, here IPSL), and the Meteorological Research Institute Earth System Model, version 1 (MRI-ESM1, here MRI). For these reduced complexity models, we had sets of parameter values for a fixed 3-pool structure and for each individual grid cell, corrected to match radiocarbon values observed in a dataset of soil radiocarbon profiles as reported in *He et al.* [2016]. We used the global mean of these parameter values to compare age and transit time distributions among all models, and used the complete set of gridded values to calculate mean, 50, and 95% quantiles of the age and transit time distributions. For each model, we plotted the relation between age and transit time and tested whether relation type I, II, or III (Figure 2) hold.

4 Results

4.1 Age distributions of SOC in models

Despite large differences in mean ages, the shape of the age distribution was relatively similar across models. All models produced age distributions of SOC in which

Table 1. Models used for the calculation of age and transit time distributions. Their matrix representation can be found in the Appendix.

Model	Description	Number of pools	Reference
RothC	Rothamsted soil carbon model. This implementation excludes the inert pool.	4	<i>Jenkinson et al. [1990]</i>
Century	Implementation of the Century model as originally described for temperate grasslands	5	<i>Parton et al. [1987]</i>
Yasso07	Model of litter decomposition parameterized from a global- scale database	5	<i>Tuomi et al. [2009]</i>
ICBM	Introductory carbon model, parameters for an experimen- tal treatment without N and straw additions, interpreted as a control treatment	2	<i>Andren and Katterer [1997]</i>
CLM4cn-Needleleaf	Community land model version 4 with parameterization for needleleaf evergreen forest	8	<i>Wieder et al. [2014]</i>
CLM4cn-Deciduous	Community land model version 4 with parameterization for deciduous forest	8	<i>Wieder et al. [2014]</i>
CLM4cn-Tropical	Community land model version 4 with parameterization for tropical forest	8	<i>Wieder et al. [2014]</i>
CESM	Reduced complexity model ob- tained from the output of the CESM model	3	<i>He et al. [2016]</i>
IPSL	Reduced complexity model ob- tained from the output of the IPSL model	3	<i>He et al. [2016]</i>
MRI	Reduced complexity model ob- tained from the output of the MRI model	3	<i>He et al. [2016]</i>

most of the carbon is stored in relatively young ages, but with relatively long tails of old C (Figure 3). The mean ages with corresponding 50 and 95% quantiles from these distributions presented large differences among models, from a few decades to thousands of years (Table 2). The lower values for the mean and quantiles of the age distributions were obtained for the CLM4cn model with parameters for the needleleaf PFT; while the highest values for the mean and quantiles of the distributions were obtained for the average parameter values of the IPSL model (Table 2).

Interestingly, relatively similar distributions were obtained within two groups of models, the reduced complexity models obtained from the three Earth system models CESM, IPSL, and MRI, and the three parameterizations of CLM4cn. For the latter group, these results suggest that different parameterizations of carbon inputs for the PFTs in this model have little influence on the SOC age distribution and therefore on the predicted persistence of organic matter.

The Century and RothC models presented large differences in their age distributions, even though they are commonly considered as relatively similar models. One important reason that explains this difference is that we excluded the inert pool from RothC for the computations. This pool is, by definition, considered to not decompose or exchange material with other pools. Its decomposition rate is equal to zero, and therefore the age of the material is infinitely large at steady-state ($+\infty$). After removing this pool from the calculations, the mean age is approximately 50 years with an upper 95% quantile of about 164 years.

For all models, the median of the age distribution (Age Q_{50}) was always lower than the mean age. Given that the age distributions have long tails (Figure 3), the mean age is more sensitive to the skewness of the distribution than the median. As a measure of central tendency, the median may be a better metric to characterize the age of these distributions.

4.2 Transit time distributions for all models

The transit time distributions obtained for all models showed that most of the carbon leaving the soil is of relatively young ages (Figure 4). Compared to the age distributions, there were less differences in the shapes of the transit time distributions among models. However, there were still large differences in the mean and the quantiles of the

Table 2. Mean, 50, and 95 percent quantiles (Q_{50} and Q_{95}) of the age and transit time distributions for all models

Model	Mean age	Age Q_{50}	Age Q_{95}	Mean trans. time	Trans. time Q_{50}	Trans. time Q_{95}
RothC	49.70	30.80	163.70	9.30	0.40	58.40
Century	4082.40	814.50	17981.40	382.50	49.20	1027.60
Yasso07	275.40	180.80	878.60	22.50	1.50	91.20
ICBM	134.30	90.70	416.00	18.70	0.90	130.50
CLM4cn-Needleleaf	22.50	13.10	76.00	6.20	0.80	35.30
CLM4cn-Deciduous	22.80	13.40	76.50	6.10	0.60	35.10
CLM4cn-Tropical	23.50	14.40	77.40	5.80	0.30	34.90
CESM	4210.60	2647.50	13933.10	41.30	2.10	18.80
IPSL	8942.60	1202.40	39236.50	39.40	4.00	49.90
MRI	7554.00	1252.20	32846.50	69.50	5.30	158.40

transit time distributions, which vary from a few years to a few centuries (Table 2). Although the lowest mean transit time was predicted by the CLM4cn model, the lowest value of the 95% quantile was predicted by the CESM Earth system model. The highest mean and 95% quantile of the transit time distributions was predicted by the Century model.

The median of the transit time distribution (Q_{50}) was always much lower than the mean transit time, reflecting the fact that most of the output flux is dominated by carbon of very young age in all models, but with a very small contribution of extremely old carbon. Given the long tails of these transit time distributions, the mean transit times were biased towards older values for characterizing central tendency. This bias was extreme for the CESM model where the mean transit time was even older than the 95% quantile of the distribution (Table 2). For characterizing central tendency of the transit time distribution, the median transit time may be a better metric than the mean.

4.3 Relation between age and transit time

Overall, the age distribution for each model is very different from the transit time distribution. To analyze the relation between these two distributions for all models, we

plotted their sequence of quantiles, from 5 to 95%, in 5% increments (Figure 5). Two important results emerge from this analysis. First, for all models and across the entire quantile sequence, ages are always older than transit times. This gives strong support to the hypothetical relation of type III, and although clear from the multiple-pool structure of all models, it rejects the idea that SOC in these models behaves as a one single well-mixed reservoir, or as a retention system in which material is sequentially processed or highly recycled before it leaves the system. This type III relation is also consistent with recent research that suggests that multiple biological, physical, and chemical mechanisms contribute to the (de)stabilization of SOM, and that the probability of a carbon atom being mineralized at any given time would depend on the combined effect of these mechanisms without a specific progression of degradation steps, or sequential physical movement [Lehmann and Kleber, 2015].

The second main result is that variability in the initial part of the distributions (5% quantile) is much larger for transit times than for ages. This can be observed in Figure (5) as a larger spread along the vertical direction towards the left part of the graph. On the contrary, the variability is much larger in terms of the 95% quantile of the age than of the transit time distributions. In other words, the upper tail of the distributions is much more variable for age than for transit time.

4.4 Global distribution of SOC age and transit time

The three reduced complexity Earth system models showed a global distribution of mean and median ages as well as mean and median transit times that support the type III relation across all grid cells (Figures 6 and 7, supplementary figures). On a global scale, the spread of mean ages was much larger than the spread of mean transit times; suggesting that the age of SOC has a large degree of geographic variability, much larger than what can be estimated from mean transit times alone. Similarly, ~~for~~ the median age, ~~which had~~ had a larger variability than the median transit time (Figure 7).

The average of the mean age across all grid cells for the CESM, IPSL, and MRI models was 4162, 8916, and 7312 years, respectively. However, mean ages can be as high as 25,000 years for some grid cells (see supplementary figures for details on the spatial distribution). The average of the median ages was much lower than the average of the mean age, which were 2582, 1488, and 1887 years, respectively. The average of the 95%

quantiles across all grid cells for the CESM, IPSL, and MRI models were 13867, 39056, and 31802 years, respectively; but for some grid cells the 95% quantile was as high as 80,000 years.

These mean ages and quantiles of the age distributions suggest that some SOC persists on a millennial time scale across global soils. These values contrast with estimates of mean transit times across grid cells. For the CESM, IPSL, and MRI models, average mean transit times across grid cells were 40, 39, and 67 years, with average 50% quantiles as 2, 4, and 6 years, and 95% quantiles as 26, 56, and 157 years, respectively. This difference between age and transit time at the global scale confirms that using transit times as a metric of the persistence of SOM yields much different results than an age-based approach.

5 Discussion

5.1 Age distributions as a measure of SOC persistence

We computed age and transit time probability density functions with corresponding mean and quantiles to assess the time that SOC persists in soils. Our results show that transit time distributions differ substantially from age distributions for all models. This is due to the fact that the transit time distribution characterizes the age structure of the output flux from the system, whereas the age distribution characterizes the age structure of the carbon stored within the system. Taken together, these two distributions provide important insights into soil C dynamics. However, based on an assessment of these distributions, we suggest the age distribution as a more appropriate characterization of SOM persistence in soils for two reasons: 1) across all models, we found carbon age distributions with a very long tail of old C that represent storage in slow pools. This suggests that a fraction of SOM persists in soils on timescales of centuries to millennia. 2) Transit times represent the carbon that enters the soil and gets quickly processed and released, with small contributions from carbon that has been stored in slow cycling pools. As a result, transit times do not provide a good indication of how long C persists in soils.

The difference between age and transit time distributions is very important to consider in the context of the debate of SOM persistence [Schmidt *et al.*, 2011; Dungait *et al.*, 2012; Lehmann and Kleber, 2015]. If persistence is ambiguously defined as age, residence,

or turnover time, we may not be able to appropriately study how mechanisms of (de)stabilization contribute to the long-term storage of carbon in soils. For instance, if we characterize persistence as the turnover time from models (stock over flux) and compare against radiocarbon-derived ages measured in bulk soils, we would be comparing transit times versus ages, which obviously would yield contradictory results. For this reason, we advocate a more precise definition of SOM persistence, and consider the age distribution of C as an adequate metric for this purpose.

5.2 How long does carbon persist in soils?

Our results showed that age distributions depend on both model structure and the specific set of parameters in each model. The influence of model structure can be further decomposed between the relative split of the inputs to the different pools, and the rates and transfers of carbon among pools. Furthermore, persistence is a model derived quantity and cannot be obtained by measurements alone. Radiocarbon is a useful tracer that can help to assess persistence [Trumbore, 2000, 2009], but to be able to translate isotopic ratios to ages, one must use a model [Trumbore *et al.*, 2016]. The choice of model (structure and parameters) would therefore influence the estimates of persistence that could be predicted for a particular soil.

The set of models we analyzed suggest that carbon persists on the order of centuries to millennia in soils. These time-scales contrast with estimates of turnover or mean residence times of soil carbon, which are generally in the order of decades [Carvalhais *et al.*, 2014; Wang *et al.*, 2018]. This apparent contradiction can be easily explained by the fact that the stock to flux ratio approximates the mean transit time and not the mean age. Furthermore, we found that the mean ages and mean transit times are not good metrics to characterize the central tendency of the distributions. Instead, the medians of these distributions better provide an idea of the central tendency of time scales of carbon cycling.

Geographically, ages are highly variable according to the reduced complexity models we analyzed. They are much more variable than transit times, and can reach 95% quantiles of up to 80,000 years. A future research challenge is to study specific mechanisms that contribute to SOC persistence and how they change across biomes or environmental gradients. Radiocarbon, in combination with models, are promising tools

for this purpose. The radiocarbon value of bulk soil is a good indicator of the age of SOC, while radiocarbon in respired CO₂ or leached in DOC is a good indicator of SOC transit time. If they both are measured across large environmental gradients, we may be able to better explain how different environmental drivers affect the time at which soil organic matter persists.

Radiocarbon measurements however, have a few caveats that must be taken into account for their interpretation. For example, radiocarbon in SOM can also be influenced by the incorporation of fossil C derived from parent rocks into soil organisms and therefore into organic matter [Seifert *et al.*, 2013]. Radiocarbon in SOM can also reflect the time spent of C in vegetation pools such as tree-stems and thus the derived age from these measurements must account for this time lag.

5.3 Is random chance a relevant factor in explaining SOC persistence?

The obtained probability density functions of SOC age suggest that a stochastic interpretation of persistence is feasible. In a previous study [Metzler and Sierra, 2018], we found that deterministic pool models expressed as systems of differential equations such as those studied here, have a stochastic counterpart that correspond to the concept of continuous-time absorbing Markov chains (see also correspondence between equations 1 and 2). The rates that are used to represent decomposition of entire masses in the deterministic case, can be interpreted as probabilities at the atom level. Given this duality in interpretation, we can consider random chance at the atomic level as a relevant factor in explaining SOM persistence. This interpretation is an important implication of our approach.

This stochastic interpretation does not mean that carbon atoms randomly persist in soils. On the contrary, the probability that an atom persists depends directly on the mechanisms of SOM (de)stabilization. These mechanisms set fixed probabilities for the atoms to move among different pools, to get consumed by microorganisms, or to leave the soil system in gas, liquid, or solid phase.

In our framework, we assume that these probabilities are based on physical, chemical, and biological processes, but not on age itself. For example, we assume that microbes consume an organic substrate based on the chemical or physical properties of the substrate, but not on the age of the carbon in the substrate. In this way, carbon consump-

tion by microorganisms is random with respect to age, but not with respect to its chemical properties or its physical location within the soil matrix. If this is not the case, we would have to study how microorganisms can detect the age of a carbon substrate and make a decision to consume this substrate with respect to age. We consider this case unlikely, and not supported by previous literature on soil microbial ecology.

Random chance is therefore a relevant factor that helps to explain why some carbon atoms persist for centuries or millennia in soils. It is a factor that has not been previously discussed in the literature of soil carbon (de)stabilization mechanisms [Schmidt *et al.*, 2011; Dungait *et al.*, 2012; Lehmann and Kleber, 2015], but we think it is key to explain observations and interpret model results. Some authors have emphasized the need to consider the probability that enzyme and substrates meet, and the probability that the product can be consumed by microorganisms [Don *et al.*, 2013; Gleizner, 2013; Spohn and Kuzyakov, 2014], and many previously proposed models have considered stochastic processes in modeling decomposition [Manzoni and Porporato, 2009]. These stochastic interpretations of decomposition are important and must be considered in the context of the dual interpretation of models, at the atomic level from a stochastic point of view, and at the deterministic level from a macro-scale perspective.

5.4 Implications for global change studies

Ages and transit time distributions are concepts that can be used beyond the realm of soil carbon (de)stabilization mechanisms to address other questions relevant for global change studies. For instance, they could be used to assess the effect of global change factors such as increased atmospheric CO₂ concentrations and air temperature change on the time scale of ecosystem carbon cycling [Lu *et al.*, 2018]. As we showed here, these distributions are also very useful to compare models with diverse structures and parameterizations. In particular, the quantiles of these distributions can be very helpful in predicting how models predict the behavior of carbon of different ages, something that it is not possible to determine from mean ages or mean transit times alone. Furthermore, the bias in the means of the distributions we identified here advocate for approaches that characterize the central tendency of the age and transit time using the 50% quantile (median), which can only be obtained if the pdf of the distributions is known.

441 *Thompson and Randerson* [1999] also describe the utility of *impulse response func-*
 442 *tions* and *storage response functions* for a number of global change applications such as
 443 model inter-comparisons and validation as well as to convolve these functions and ob-
 444 tain isotope dynamics. These functions are equivalent to the transit time distribution
 445 and the system age distribution, respectively [*Metzler and Sierra*, 2018]. Therefore, it
 446 is possible to use the transit time and system age distributions to directly model the iso-
 447 topic disequilibrium of carbon in global soils as well as radiocarbon dynamics. Taking
 448 advantage of the radiocarbon ‘bomb-spike’, transit time distributions can be used to as-
 449 sess the speed at which this tracer of the global carbon cycle has been assimilated in soils
 450 worldwide.

451 6 Summary and conclusions

452 Persistence of soil organic matter can be characterized using the age distribution
 453 of carbon in soils. It provides information on the proportional distribution of carbon across
 454 the age range, and offers insights on the maximum ages of carbon that could be observed
 455 in a soil. The age distribution differs from the transit time distribution, which provides
 456 information on the age of carbon in the output flux. Since metrics such as turnover or
 457 residence time are commonly calculated using approaches such as dividing stocks over
 458 fluxes, and since these metrics are in most cases indicative of the transit time rather than
 459 the age, persistence of SOM cannot be reliably estimated from these metrics. Instead,
 460 approaches to estimate soil carbon age such as isotopic measurements on the bulk SOM
 461 and soil fractions should better approximate the age distribution of carbon and the as-
 462 sociated concept of persistence.

463 At the carbon atom level, random chance is an important factor that helps to ex-
 464 plain persistence of soil organic matter. We can interpret mechanisms of stabilization
 465 and destabilization of soil organic matter as processes that determine the probability of
 466 carbon atoms to change state, moving across different pools in the soil or being consumed
 467 and mineralized by microorganisms. We assume that organic matter processing does not
 468 depend on the age of the carbon, but rather on physical, chemical, and biological pro-
 469 cesses that set probabilities of carbon processing. The emergent outcome is a mix of car-
 470 bon of different ages, but with defined age distributions. We believe it is important to
 471 include random chance in the discussion of understanding persistence of organic mat-
 472 ter in soils.

Radiocarbon measurements in bulk soils are important to understand SOC persistence. Our current best estimates of SOC in models corrected by radiocarbon measurements [He *et al.*, 2016], indicate that SOC persists for centuries to millennia. This differs from estimates based on turnover times that are in the order of decades, but this difference can be explained by the fact that turnover times are indicative of transit times rather than age.

Both age and transit time distributions are useful concepts to integrate the diversity of mechanisms that control organic matter cycling. There is still a long way to determine how different interacting mechanisms produce different age and transit time distributions in soils. More efforts to integrate measurements with models should help us to integrate these different processes and understand why organic matter persists in soils for millennia.

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References

- Andren, O., and T. Katterer (1997), ICBM: The introductory carbon balance model for exploration of soil carbon balances, *Ecological Applications*, 7(4), 1226–1236.
- Bolin, B., and H. Rodhe (1973), A note on the concepts of age distribution and transit time in natural reservoirs, *Tellus*, 25(1), 58–62.
- Bruun, S., J. Six, and L. S. Jensen (2004), Estimating vital statistics and age distributions of measurable soil organic carbon fractions based on their pathway of formation and radiocarbon content, *Journal of Theoretical Biology*, 230(2), 241–250.
- Carvalhais, N., M. Forkel, M. Khomik, J. Bellarby, M. Jung, M. Migliavacca, M. u, S. Saatchi, M. Santoro, M. Thurner, U. Weber, B. Ahrens, C. Beer, A. Cescatti,

- 504 J. T. Randerson, and M. Reichstein (2014), Global covariation of carbon turnover
505 times with climate in terrestrial ecosystems, *Nature*, *514*, 213–217.
- 506 Derrien, D., and W. Amelung (2011), Computing the mean residence time of soil
507 carbon fractions using stable isotopes: impacts of the model framework, *European*
508 *Journal of Soil Science*, *62*(2), 237–252.
- 509 Don, A., C. Rödenbeck, and G. Gleixner (2013), Unexpected control of soil carbon
510 turnover by soil carbon concentration, *Environmental Chemistry Letters*, pp. 1–7,
511 doi:10.1007/s10311-013-0433-3.
- 512 Dungait, J. A. J., D. W. Hopkins, A. S. Gregory, and A. P. Whitmore (2012), Soil
513 organic matter turnover is governed by accessibility not recalcitrance, *Global*
514 *Change Biology*, *18*(6), 1781–1796, doi:10.1111/j.1365-2486.2012.02665.x.
- 515 Eriksson, E. (1971), Compartment models and reservoir theory, *Annual Review of*
516 *Ecology and Systematics*, *2*(1), 67–84.
- 517 Gleixner, G. (2013), Soil organic matter dynamics: a biological perspective derived
518 from the use of compound-specific isotopes studies, *Ecological Research*, *28*(5),
519 683–695, doi:10.1007/s11284-012-1022-9.
- 520 Gleixner, G., R. Bol, and J. Balesdent (1999), Molecular insight into soil carbon
521 turnover, *Rapid Communications in Mass Spectrometry*, *13*(13), 1278–1283, doi:
522 10.1002/(SICI)1097-0231(19990715)13:13<1278::AID-RCM649>3.0.CO;2-N.
- 523 Goll, D. S., V. Brovkin, J. Liski, T. Raddatz, T. Thum, and K. E. O. Todd-Brown
524 (2015), Strong dependence of co2 emissions from anthropogenic land cover change
525 on initial land cover and soil carbon parametrization, *Global Biogeochemical Cy-*
526 *cles*, *29*(9), 1511–1523, doi:10.1002/2014GB004988, 2014GB004988.
- 527 He, Y., S. E. Trumbore, M. S. Torn, J. W. Harden, L. J. S. Vaughn, S. D. Alli-
528 son, and J. T. Randerson (2016), Radiocarbon constraints imply reduced car-
529 bon uptake by soils during the 21st century, *Science*, *353*(6306), 1419–1424, doi:
530 10.1126/science.aad4273.
- 531 Heim, A., and M. W. I. Schmidt (2007), Lignin turnover in arable soil and grass-
532 land analysed with two different labelling approaches, *European Journal of Soil*
533 *Science*, *58*(3), 599–608, doi:10.1111/j.1365-2389.2006.00848.x.
- 534 Jenkinson, D. S., S. P. S. Andrew, J. M. Lynch, M. J. Goss, and P. B. Tinker
535 (1990), The turnover of organic carbon and nitrogen in soil [and discussion],
536 *Philosophical Transactions: Biological Sciences*, *329*(1255), 361–368.

- Kiem, R., and I. Kögel-Knabner (2003), Contribution of lignin and polysaccharides to the refractory carbon pool in c-depleted arable soils, *Soil Biology and Biochemistry*, 35(1), 101 – 118, doi:[https://doi.org/10.1016/S0038-0717\(02\)00242-0](https://doi.org/10.1016/S0038-0717(02)00242-0).
- Kleber, M. (2010), What is recalcitrant soil organic matter?, *Environmental Chemistry*, 7(4), 320–332.
- Lehmann, J., and M. Kleber (2015), The contentious nature of soil organic matter, *Nature*, 528, 60 EP –.
- Lehmann, J., S. Abiven, M. Kleber, G. Pan, B. P. Singh, S. P. Sohi, and A. R. Zimmerman (2015), Persistence of biochar in soil, in *Biochar for Environmental Management: Science, Technology and Implementation*, edited by J. Lehmann and S. Joseph, Earthscan, London.
- Lu, X., Y.-P. Wang, Y. Luo, and L. Jiang (2018), Ecosystem carbon transit versus turnover times in response to climate warming and rising atmospheric CO₂ concentration, *Biogeosciences Discussions*, 2018, 1–22, doi:10.5194/bg-2018-175.
- Manzoni, S., and A. Porporato (2009), Soil carbon and nitrogen mineralization: Theory and models across scales, *Soil Biology and Biochemistry*, 41(7), 1355 – 1379, doi:<http://dx.doi.org/10.1016/j.soilbio.2009.02.031>.
- Manzoni, S., G. G. Katul, and A. Porporato (2009), Analysis of soil carbon transit times and age distributions using network theories, *J. Geophys. Res.*, 114.
- Metzler, H., and C. A. Sierra (2018), Linear autonomous compartmental models as continuous-time Markov chains: Transit-time and age distributions, *Mathematical Geosciences*, 50(1), 1–34, doi:10.1007/s11004-017-9690-1.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima (1987), Analysis of factors controlling soil organic matter levels in great plains grasslands, *Soil Sci. Soc. Am. J.*, 51(5), 1173–1179.
- Paul, E. A. (2016), The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization, *Soil Biology and Biochemistry*, 98, 109 – 126, doi:<http://dx.doi.org/10.1016/j.soilbio.2016.04.001>.
- Schmidt, M. W. I., M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, M. Kleber, I. Kögel-Knabner, J. Lehmann, D. A. C. Manning, P. Nannipieri, D. P. Rasse, S. Weiner, and S. E. Trumbore (2011), Persistence of soil organic matter as an ecosystem property, *Nature*, 478(7367), 49–56.

- Seifert, A.-G., S. Trumbore, X. Xu, D. Zhang, and G. Gleixner (2013), Variable effects of plant colonization on black slate uptake into microbial PLFAs, *Geochimica et Cosmochimica Acta*, 106, 391 – 403, doi:https://doi.org/10.1016/j.gca.2012.12.011.
- Sierra, C. A., and M. Müller (2015), A general mathematical framework for representing soil organic matter dynamics, *Ecological Monographs*, 85, 505–524, doi:10.1890/15-0361.1.
- Sierra, C. A., M. E. Harmon, and S. S. Perakis (2011), Decomposition of heterogeneous organic matter and its long-term stabilization in soils, *Ecological Monographs*, 81(4), 619–634, doi:10.1890/11-0811.1.
- Sierra, C. A., M. Müller, and S. E. Trumbore (2014), Modeling radiocarbon dynamics in soils: SoilR version 1.1, *Geoscientific Model Development*, 7(5), 1919–1931, doi:10.5194/gmd-7-1919-2014.
- Sierra, C. A., M. Müller, H. Metzler, S. Manzoni, and S. E. Trumbore (2017), The muddle of ages, turnover, transit, and residence times in the carbon cycle, *Global Change Biology*, 23(5), 1763–1773, doi:10.1111/gcb.13556.
- Sollins, P., P. Homann, and B. A. Caldwell (1996), Stabilization and destabilization of soil organic matter: mechanisms and controls, *Geoderma*, 74(1-2), 65–105, doi: DOI: 10.1016/S0016-7061(96)00036-5.
- Spohn, M., and Y. Kuzyakov (2014), Spatial and temporal dynamics of hotspots of enzyme activity in soil as affected by living and dead roots—a soil zymography analysis, *Plant and Soil*, 379(1), 67–77, doi:10.1007/s11104-014-2041-9.
- Spohn, M., and C. A. Sierra (2018), How long do elements cycle in terrestrial ecosystems?, *Biogeochemistry*, 139(1), 69–83, doi:10.1007/s10533-018-0452-z.
- Thompson, M. V., and J. T. Randerson (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.
- Trumbore, S. (2000), Age of soil organic matter and soil respiration: radiocarbon constraints on belowground c dynamics, *Ecological Applications*, 10(2), 399–411.
- Trumbore, S. (2009), Radiocarbon and soil carbon dynamics, *Annual Review of Earth and Planetary Sciences*, 37(1), 47–66.
- Trumbore, S. E., C. A. Sierra, and C. E. Hicks Pries (2016), Radiocarbon nomenclature, theory, models, and interpretation: Measuring age, determining cycling

- 602 rates, and tracing source pools, in *Radiocarbon and Climate Change: Mechanisms,*
 603 *Applications and Laboratory Techniques*, edited by A. E. Schuur, E. Druffel, and
 604 E. S. Trumbore, pp. 45–82, Springer International Publishing.
- 605 Tuomi, M., T. Thum, H. Järvinen, S. Fronzek, B. Berg, M. Harmon, J. Trofymow,
 606 S. Sevanto, and J. Liski (2009), Leaf litter decomposition—estimates of global
 607 variability based on yasso07 model, *Ecological Modelling*, *220*(23), 3362 – 3371,
 608 doi:10.1016/j.ecolmodel.2009.05.016.
- 609 von Lützow, M., I. Kögel-Knabner, B. Ludwig, E. Matzner, H. Flessa, K. Ekschmitt,
 610 G. Guggenberger, B. Marschner, and K. Kalbitz (2008), Stabilization mechanisms
 611 of organic matter in four temperate soils: Development and application of a con-
 612 ceptual model, *Journal of Plant Nutrition and Soil Science*, *171*(1), 111–124.
- 613 Wang, J., J. Sun, J. Xia, N. He, M. Li, and S. Niu (2018), Soil and vegetation car-
 614 bon turnover times from tropical to boreal forests, *Functional Ecology*, *32*(1),
 615 71–82, doi:10.1111/1365-2435.12914.
- 616 Wieder, W. R., J. Boehnert, and G. B. Bonan (2014), Evaluating soil biogeochem-
 617 istry parameterizations in earth system models with observations, *Global Biogeo-*
 618 *chemical Cycles*, *28*(3), 211–222, doi:10.1002/2013GB004665.

Figure 1. Soil organic matter age for two hypothetical soils with similar mean age, but with different density functions. In both cases, the mean age is 200 years (purple vertical line), but for the exponentially distributed soil the 95% quantile $Q_{95} = 599$ years, while for the normally distributed soil (blue line) $Q_{95} = 282$ years. In asymmetric distributions with long tails such as the exponential or the phase-type, the mean is more sensitive to the skewness than the median. In this example, the 50% quantile $Q_{50} = 139$ years (vertical solid red line) for the exponential distribution.

Figure 2. Possible relations between ages and transit times of organic matter in soils. Axes in arbitrary time units, e.g. days, months, years.

Figure 3. Age density distribution functions of soil organic carbon calculated for the models described in Table (1).

Figure 4. Transit time density distribution functions of soil organic carbon calculated for the models described in Table (1).

Figure 5. Sequence of quantiles, from 5 to 95% by 5% increments, for the age and transit time distributions of soil organic carbon calculated for the models of Table (1). Dashed line represents the 1:1 line. Notice that axes are in logarithmic scale.

Figure 6. Mean age and mean transit times of soil organic carbon predicted for each grid cell by the three versions of the reduced complexity Earth system models CESM, IPSL, and MRI, corrected by observations of radiocarbon in soil profiles as described in *He et al.* [2016]. Dashed line represents the 1:1 line.

639 **Figure 7.** Median age and median transit times (Q_{50}) of soil organic carbon predicted for
640 each grid cell by the three versions of the reduced complexity Earth system models CESM, IPSL,
641 and MRI, corrected by observations of radiocarbon in soil profiles as described in *He et al.* [2016].
642 Dashed line represents the 1:1 line.

Appendix

Matrix representation of analyzed models

Each model was represented as a compartmental system of the form of equation (1). Below, we present the specific form of the matrix \mathbf{B} and the vector \mathbf{u} with the parameter values used for each model.

RothC

$$\mathbf{B} = \begin{pmatrix} -10.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & -0.30 & 0.00 & 0.00 \\ 1.02 & 0.03 & -0.59 & 0.00 \\ 1.20 & 0.04 & 0.08 & -0.02 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 1.00 \\ 0.70 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (7)$$

Century

$$\mathbf{B} = \begin{pmatrix} -0.069637 & 0.000000 & 0.000000 & 0.000000 & 0.000000 \\ 0.000000 & -0.350000 & 0.000000 & 0.000000 & 0.000000 \\ 0.031337 & 0.192500 & -0.071750 & 0.001596 & 0.000058 \\ 0.020891 & 0.000000 & 0.042189 & -0.003800 & 0.000000 \\ 0.000000 & 0.000000 & 0.000287 & 0.000114 & -0.000130 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 0.08 \\ 0.02 \\ 0.00 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (8)$$

Yasso07

$$\mathbf{B} = \begin{pmatrix} -0.6600 & 1.3760 & 0.0035 & 0.2046 & 0.0000 \\ 0.2244 & -4.3000 & 0.0000 & 0.0000 & 0.0000 \\ 0.0231 & 0.0215 & -0.3500 & 0.0022 & 0.0000 \\ 0.0003 & 0.1290 & 0.3220 & -0.2200 & 0.0000 \\ 0.0264 & 0.1720 & 0.0140 & 0.0088 & -0.0033 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 10.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (9)$$

651

ICBM

$$\mathbf{B} = \begin{pmatrix} -0.9360 & 0.0000 \\ 0.1170 & -0.0071 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 0.06 \\ 0.00 \end{pmatrix} \quad (10)$$

652

CLM4cn

This model contains one single \mathbf{B} matrix for all plant functional types (PFTs):

$$\mathbf{B} = \begin{pmatrix} -434.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 \\ 0.0000 & -26.4700 & 0.0000 & 0.2776 & 0.0000 & 0.0000 & 0.0000 & 0.0000 \\ 0.0000 & 0.0000 & -5.1450 & 0.0876 & 0.0000 & 0.0000 & 0.0000 & 0.0000 \\ 0.0000 & 0.0000 & 0.0000 & -0.3652 & 0.0000 & 0.0000 & 0.0000 & 0.0000 \\ 264.7400 & 0.0000 & 0.0000 & 0.0000 & -26.4700 & 0.0000 & 0.0000 & 0.0000 \\ 0.0000 & 11.9115 & 0.0000 & 0.0000 & 19.0584 & -5.1450 & 0.0000 & 0.0000 \\ 0.0000 & 0.0000 & 3.6529 & 0.0000 & 0.0000 & 2.7783 & -0.5114 & 0.0000 \\ 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.0000 & 0.2301 & -0.0365 \end{pmatrix} \quad (11)$$

For the needleleaf, deciduous, and tropical PFTs, the vector \mathbf{u} is given by, respectively

$$\mathbf{u} = \begin{pmatrix} 95.75 \\ 191.50 \\ 95.75 \\ 200.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 105.50 \\ 211.00 \\ 105.50 \\ 180.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 362.25 \\ 724.50 \\ 362.25 \\ 360.00 \\ 0.00 \\ 0.00 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (12)$$

653

654

For the following reduced complexity models, the average of parameters across all grid cells is given by the following matrices

655

CESM

$$\mathbf{B} = \begin{pmatrix} -0.3595 & 0.0000 & 0.0000 \\ 0.0226 & -0.0180 & 0.0000 \\ 0.0000 & 0.0020 & -0.0002 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 0.31 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (13)$$

656

IPSL

$$\mathbf{B} = \begin{pmatrix} -0.19021 & 0.00000 & 0.00000 \\ 0.01160 & -0.00459 & 0.00000 \\ 0.00000 & 0.00009 & -0.00006 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 0.63 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (14)$$

657

MRI

$$\mathbf{B} = \begin{pmatrix} -0.14629 & 0.00000 & 0.00000 \\ 0.01110 & -0.00288 & 0.00000 \\ 0.00000 & 0.00010 & -0.00007 \end{pmatrix} \quad \mathbf{u} = \begin{pmatrix} 0.76 \\ 0.00 \\ 0.00 \end{pmatrix} \quad (15)$$