

## A general mathematical framework for representing soil organic matter dynamics

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**Abstract.** We propose here a general mathematical framework to represent soil organic matter dynamics. This framework is expressed in the language of dynamical systems and generalizes previous modeling approaches. It is based on a set of six basic principles about the decomposition of soil organic matter: (1) mass balance, (2) substrate dependence of decomposition, (3) heterogeneity of the speed of decay, (4) internal transformations of organic matter, (5) environmental variability effects, and (6) substrate interactions. We show how the majority of models previously proposed are special cases of this general model. This approach provides tools to classify models according to the main principles or concepts they include. It also helps to identify a priori the general behavior of different models or groups of models. Another important characteristic of the proposed mathematical representation is the possibility to develop particular models at any level of detail. This characteristic is described as a modeling hierarchy, in which a general model of a high degree of abstraction can accommodate specific realizations of model structure for specific modeling objectives. This framework also allows us to study general properties of groups of models such as their qualitative behavior, timescale of application, and their dynamic stability. For instance, we find conditions under which models are asymptotically stable, i.e., converge to a stable steady state in the long term, but may approach this state with or without oscillations. We also expand the concept of dynamic stability for models that include time dependencies and do not converge to a fixed steady state, but rather to a region of stability in the state-space. As an example of the application of the concept of dynamic stability, we show how this framework helps to explain the acclimation of soil respiration fluxes in soil-warming experiments.

**Key words:** *decomposition; dynamical systems; microbial carbon use efficiency; soil carbon models; soil microbial models; soil respiration; soil-warming experiments; stability analysis.*

### INTRODUCTION

Soil organic matter cycling has been the subject of research for several decades. Many attempts have been made to mathematically represent soil organic matter (SOM) decomposition with different degrees of success (Swift et al. 1979, Molina and Smith 1997, Paustian et al. 1997, Manzoni and Porporato 2009). However, the number of proposed models has increased exponentially during the last decades, revealing a lack of consensus among models and creating uncertainty about the main concepts necessary to better represent this important process (Manzoni and Porporato 2009).

The most significant contribution toward a general mathematical theory of SOM decomposition was provided by Ågren and Bosatta (1998) with their development of the continuous quality theory. These authors have shown that many soil organic matter decomposition models are discretizations or special cases of their representation of SOM by a continuous distribution of its quality that decays according to an explicit function of microbial activity (Ågren and Bosatta 1998). The continuous quality model of Ågren and Bosatta (1998) is given by the expression

$$\frac{\partial p_c(q, t)}{\partial t} = I(q, t) - f_c \frac{u(q)}{e(q)} p_c(q, t) + f_c \int D(q, q') u(q') p_c(q', t) dq' \quad (1)$$

where  $p(q, t)$  is the time-dependent distribution of

Manuscript received 27 February 2015; revised 24 April 2015; accepted 29 April 2015. Corresponding Editor: A. T. Classen.

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carbon of different qualities ( $q$ ). Details about the model can be found elsewhere (e.g., Bosatta and Ågren 1991, Ågren and Bosatta 1998); here we only would like to point out that the change of carbon over time in this model ( $\partial \rho_c(q, t)/\partial t$ ), is the result of the external inputs ( $I(q, t)$ ) minus the outputs due to decomposition (second term on the right-hand side [rhs]) and the internal transformations of the quality of the organic matter (third term on the rhs). This is an explicit representation of the law of mass balance of a heterogeneous substrate in which this heterogeneity is represented with a continuous function.

Despite the generality and range of applicability of the continuous quality framework, new emergent concepts do not necessarily fit well within this model. First, recent discussions on organic matter decomposition suggests a change in paradigm from an old view of decomposition as controlled by quality to new concepts based on the physicochemical protection and environmental constraints on decomposition (Schmidt et al. 2011). This suggests that the characterization of organic matter heterogeneity in terms of its quality does not necessarily reflect recent advances in our understanding of this process. Second, a new generation of models explicitly describe interactions between organic substrates, microbial populations, and exoenzymes (e.g., Schimel and Weintraub 2003, Allison et al. 2010, Sinsabaugh and Follstad Shah 2012, Wang et al. 2013). It is not obvious, however, how to include these new type of models and concepts within the continuous quality framework.

Here we propose an alternative theoretical framework to mathematically generalize the process of soil organic matter decomposition based on a set of basic principles that include more recent ideas. First, we derive a general model in a series of steps that include biological principles sequentially. Then, we explore some of the mathematical properties of special cases of the general model, with specific emphasis on the property of dynamical stability. As examples, we show at the end of the manuscript how this general framework, combined with the concept of dynamic stability, helps to explain results from soil-warming experiments and discuss issues of oscillatory behavior in soil carbon models.

#### DERIVATION OF GENERAL MODELS BASED ON BASIC PRINCIPLES

We propose a general mathematical model of soil organic matter decomposition based on a set of six basic principles: (1) mass balance, (2) substrate dependence, (3) heterogeneity of the speed of decomposition, (4) internal transformations of organic matter, (5) environmental variability effects, and (6) substrate interactions. These principles are simply well-known facts about the process of soil organic matter decomposition supported on an extensive amount of literature. We present in the following sections the derivation of this general model in a sequence of steps, starting from an inflexible model

that expresses only one principle and arriving to a full model that expresses the combination of all principles. At every step we will increase mathematical complexity only as much as necessary to incorporate one additional principle (Table 1). Please note that the sequence of steps we take in this derivation somehow follows the chronology of proposed models in the literature, but it is not the only logical route to derive our general model.

#### Mass balance

Mass balance is the most fundamental physical constraint on the process of decomposition (Williams 1973, Ågren and Bosatta 1998, Pastor 2008, Ågren and Andersson 2012), which, in turn, sets a basic mathematical structure on decomposition models. It states that “any mass of organic matter entering the soil must either leave the system or accumulate within the system.” This definition has the implicit assumption that the soil is an open system that exchanges mass through an observer-defined boundary (Williams 1973), typically a volume of soil.

For a complete mathematical description of the mass balance principle, we need to add other principles first (see formal treatment of mass balance in the section *Transformations of organic matter*). For the moment, however, we consider the oversimplified case of a system with constant inputs and outputs, in which accumulation (net change) of organic matter is given by the difference between inputs  $I$  and outputs  $O$ . We use as common currency the mass of carbon  $C$  in the system; therefore, we can express a simple mass balance as

$$\frac{dC}{dt} = I - O. \quad (2)$$

In soils, the external inputs  $I$  are generally dominated by carbon in the form of litterfall, root mortality, and root exudates, while carbon outputs are generally in the form of respired  $\text{CO}_2$ , dissolved organic carbon, or eroded carbon.

#### Substrate dependence of decomposition

It has been traditionally recognized that, in addition to mass balance, decomposition depends to a large extent on the amount of carbon available to decomposers (Jenny et al. 1949, Olson 1963, Swift et al. 1979, Manzoni and Porporato 2009, Don et al. 2013). In particular, *there is no decomposition without available substrate*. This implies that the outputs are a function of the available carbon in the system as

$$O = f(C). \quad (3)$$

One way to express this substrate dependence is by writing the output  $O$  as a constant proportion of the amount of carbon in the system, and inserting it into the mass balance constraint as

$$\frac{dC}{dt} = I - k \cdot C \quad (4)$$

TABLE 1. General models of soil organic matter dynamics organized by structural flexibility.

Structure, by text subsection	Principles included	Remarks
<i>Organic matter interactions</i>		
$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \mathbf{T}(\mathbf{C}, t) \cdot \mathbf{N}(\mathbf{C}, t) \cdot \mathbf{C}(t)$ $N_{i,i}(\mathbf{C}, t) \geq 0 \quad \forall i$ $T_{i,i}(\mathbf{C}, t) = -1 \quad \forall i$ $T_{i,j}(\mathbf{C}, t) \geq 0 \quad \forall i \neq j$ $\sum_i T_{i,j}(\mathbf{C}, t) \leq 1 \quad \forall i \neq j$	1) Mass balance 2) Substrate dependence 3) Heterogeneity of decomposition rates 4) Transformations of SOM 5) Environmental variability effects 6) SOM interactions	This model structure generalizes microbial models that include nonlinear interactions among state variables such as the models proposed by Schimel and Weintraub (2003), Allison et al. (2010), or Zelenov et al. (2000). This is the only model structure that allows for bifurcations. The model can be expanded to any number of microbial/enzyme and SOC pools.
<i>Environmental variability effects</i>		
$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \mathbf{T}(t) \cdot \mathbf{N}(t) \cdot \mathbf{C}(t)$ $= \mathbf{I}(t) + \mathbf{A}(t) \cdot \mathbf{C}(t)$	1) Mass balance 2) Substrate dependence 3) Heterogeneity of decomposition rates 4) Transformations of SOM 5) Environmental variability effects	The rates of decay and transfers among pools are not necessarily affected by the same functions. There might be specific functions for each element of the matrix $\mathbf{A}(t)$ . If $\dim(\mathbf{A}) \rightarrow \infty$ the system converges to the $Q$ model $\partial \rho_c(q, t) / \partial t = I(q, t) - f_c(u(q)/e(q)) \rho_c(q, t) + f_c/D(q, q') u(q') \rho_c(q', t) dq'$ . An even further generalization of the $Q$ model is then: $\partial \rho_c(q, t) / \partial t = I(q, t) - f_c(u(q, t)/e(q, t)) \rho_c(q, t) + f_c/D(q, q', t) u(q', t) \rho_c(q', t) dq'$ .
$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C}(t)$ $\mathbf{A} = \text{const}$ $\xi(t) \geq 0 \quad \forall t$	1) Mass balance 2) Substrate dependence 3) Heterogeneity of decomposition rates 4) Transformations of SOM 5) Uniform environmental variability	This is the structure of the majority of SOM decomposition models. Prominent examples include Roth-C and Century. The term $\xi(t)$ is a multiplicative function of environmental effects on decomposition rates. It accounts for effects of temperature, moisture, and oxygen concentrations.
<i>Transformations of organic matter</i>		
$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \mathbf{A} \cdot \mathbf{C}$	1) Mass balance 2) Substrate dependence 3) Heterogeneity of decomposition rates 4) Transformations of SOM	The matrix $\mathbf{A}$ contains in its main diagonal the decomposition rates and in the off-diagonals the transfer coefficients among different pools.
<i>Heterogeneity of decomposition rates</i>		
$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \mathbf{K} \cdot \mathbf{C}$ $\mathbf{K} \text{ diagonal}$	1) Mass balance 2) Substrate dependence 3) Heterogeneity of decomposition rates	The matrix $\mathbf{K}$ represents the heterogeneity of cycling rates of SOM. It is a diagonal matrix with the values of decomposition rates for discrete classes of SOM.
<i>Substrate dependence of decomposition</i>		
$\frac{d\mathbf{C}}{dt} = \mathbf{I} - k \cdot \mathbf{C}$	1) Mass balance 2) Substrate dependence	Decomposition as a substrate dependent process. A constant proportion of carbon is lost at every time step (Olson 1963).
<i>Mass balance</i>		
$\frac{d\mathbf{C}}{dt} = \mathbf{I} - \mathbf{O}$	1) Mass balance	Inputs minus outputs result in accumulation or decline in C stock which has solution $C(t) = C_0 + m \cdot t$ , where $m = I - O$ is a constant.

*Notes:* The model structure on top is flexible enough to incorporate all six principles of soil organic matter dynamics. For clarification of individual variables, see the text subsection listed; each subsection is found in the section *Derivation of general models based on basic principles*. From top to bottom, the level of flexibility is reduced and the number of principles is reduced. Abbreviations are: SOM, soil organic matter; and SOC, soil organic carbon.

where  $k > 0$ , and  $k = 0$  must be explicitly excluded since otherwise carbon would never be lost through decomposition. For this choice, Eq. 4 takes the form of the popular model described by Olson (1963), which has been very influential in shaping our understanding of soil organic matter decomposition. The model predicts accumulation of organic matter in the soil

volume up to a steady-state value ( $C^*$ ), where inputs are equal to outputs. This steady-state value is independent of the initial conditions and depends only on the amount of litter inputs to the soil and the rate of decay ( $C^* = I/k$ ). For additional details on the ecological consequences of this model, see Olson (1963).

The expression  $O = f(C) = k \cdot C$  is just only one possible form to combine the principles of mass balance and substrate dependence. Other functions that depend on the amount of carbon available are indeed biologically and mathematically possible, but this expression has proved useful in representing soil carbon dynamics over different scales.

#### *Heterogeneity of decomposition rates*

It is well recognized that soil organic matter and its inputs to the soil are heterogeneous in terms of their chemistry, and therefore, in the rates at which they decompose (Waksman et al. 1928, Hunt 1977, Minderman 1968, Ågren and Bosatta 1998, Bosatta and Ågren 1999). Depending on the chemistry of the substrate, more or fewer enzymatic steps may be required to degrade different compounds (Bosatta and Ågren 1999), which results in differences in the speed of decomposition. Similarly, organic matter in soils may get attached and occluded in mineral surfaces or protected from decomposition due to different chemical and physical mechanisms (Sollins et al. 1996, Kaiser and Guggenberger 2000, von Lützow et al. 2006, Kleber et al. 2007, Kögel-Knabner et al. 2008), thus generating heterogeneity in terms of the rates at which different proportions of the total organic matter decompose. In other words, *soil organic matter is heterogeneous in terms of its rates of decomposition*.

This heterogeneity in the speed of decomposition suggests that it is necessary to represent different components of organic matter separately. This can be achieved by representing the soil organic matter system as a set of uncoupled first-order differential equations.

If we assume that the flux of litter inputs and the mass of soil organic matter in a certain volume can be partitioned into  $m$  different components that decompose at different rates, and represent the process including the mass balance and substrate dependence equations, we can write systems of equations of the form

$$\begin{aligned}\frac{dC_1}{dt} &= I_1 - k_1 \cdot C_1 \\ \frac{dC_2}{dt} &= I_2 - k_2 \cdot C_2 \\ &\vdots \\ \frac{dC_m}{dt} &= I_m - k_m \cdot C_m.\end{aligned}\quad (5)$$

This system can be represented more compactly using notation of vectors and matrices as

$$\frac{d\mathbf{c}}{dt} = \mathbf{I} - \mathbf{K} \cdot \mathbf{C} \quad (6)$$

where  $\mathbf{K}$  is an  $m \times m$  diagonal matrix that contains in the main diagonal the value of the decomposition rates ( $k_i$ ).

For consistency with our previous publications, vectors are set uppercase bold italic; matrices are uppercase bold. An implicit assumption of this model is that each portion of organic matter decomposes independently and there are no transformations of the organic matter into different compounds. This model formulation has been used previously for partitioning soil organic matter depending on the species or the plant part delivering litter to the soil (e.g., leaves, wood, roots; Minderman 1968, Hunt 1977, Harmon et al. 2004), or the type of compound entering the soils (e.g., lignin, cellulose, waxes, et cetera; Melillo et al. 1989, Harmon et al. 2009, Forney and Rothman 2012).

This representation of heterogeneity is also associated with the concept of organic matter pools, proportions of the total soil organic matter with homogeneous properties that decompose at a pool-specific constant rate. This “pool” concept has been highly controversial given the difficulty to isolate these different soil organic matter proportions in the laboratory (Crow et al. 2007, Schmidt et al. 2011). However, the pool-based approach to modeling decomposition has been successful at reproducing patterns of organic matter decay over different scales (Manzoni and Porporato 2009).

#### *Transformations of organic matter*

The differential equations in Eq. 5 are uncoupled; i.e., there are no transfers of carbon among the different pools. If one, for example, is interested in following how organic matter changes its quality (Hunt 1977, Swift et al. 1979, Ågren and Bosatta 1998), or how it gets adsorbed to mineral surfaces (Neff and Asner 2001), Eq. 5 is inappropriate. Here, we assume that *portions of soil organic matter can be transformed in terms of their decomposition rates*. In this case, the system of equations needs to be coupled and our formulation has to be generalized further to allow transfers among different state variables. Before formulating mathematically the principle of organic matter transformation, we reconsider first the mass balance for an arbitrary pool  $i$  in more detail as

$$\frac{dC_i}{dt} = I_{\text{ext},i} + I_{\text{int},i} - O_{\text{int},i} - O_{\text{ext},i} \quad (7)$$

where we divided the total inputs to the pool between the external  $I_{\text{ext},i}$  coming from outside the system boundaries, and internal input  $I_{\text{int},i}$  coming from other pools within the system. Similarly, the total output from this pool is split between the output  $O_{\text{ext},i}$  directly leaving the system (e.g., by respiration), and  $O_{\text{int},i}$  the output of pool  $i$  to be distributed to other pools within the system. A first consequence is that for the entire system, mass balance can only be required in aggregate form as

$$\sum_i^m \frac{dC_i}{dt} = \sum_i^m I_i - \sum_i^m O_i. \quad (8)$$

For every pool  $i$ , the internal input to the pool is then the sum of distributions from internal outputs from all the source pools

$$I_{\text{int},i} = \sum_{j=1, j \neq i}^m D_{i,j} \cdot O_{\text{int},j} \quad \forall i$$

or in matrix notation as

$$\mathbf{I}_{\text{int}} = \mathbf{D} \times \mathbf{O}_{\text{int}} \quad (9)$$

where the distribution matrix  $\mathbf{D}$  has a zero diagonal and must also fulfill  $\sum_i D_{i,j} = 1$  expressing the fact that *all* internal outputs from source pools must be distributed among the sink pools. Also note that, according to our initial distinction, inputs must be positive, and therefore, no distribution coefficient can be negative  $D_{i,j} \geq 0 \quad \forall i, \forall j$ .

Now, introducing a diagonal matrix  $\mathbf{R}$  with  $0 \leq R_{i,i} \leq 1$  expressing the proportion of output of pool  $i$  removed from the system, we can write

$$\mathbf{O}_{\text{ext}} = \mathbf{R} \cdot \mathbf{O} \quad (10)$$

$$\mathbf{O}_{\text{int}} = (\mathbf{1} - \mathbf{R}) \cdot \mathbf{O}. \quad (11)$$

This is useful since we already know from Eq. 6 that  $\mathbf{O} = \mathbf{K} \cdot \mathbf{C}$ . Combining Eqs. 9, 7, 10, and 11, and dropping the subscript “ext” from external inputs, yields

$$\begin{aligned} \frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{D} \cdot \mathbf{O}_{\text{int}} - \mathbf{O}_{\text{int}} - \mathbf{O}_{\text{ext}} \\ &= \mathbf{I} + (\mathbf{D} - \mathbf{1}) \cdot \mathbf{O}_{\text{int}} - \mathbf{O}_{\text{ext}} \\ &= \mathbf{I} + (\mathbf{D} - \mathbf{1}) \cdot (\mathbf{1} - \mathbf{R}) \cdot \mathbf{O} - \mathbf{R} \cdot \mathbf{O} \\ &= \mathbf{I} + \left( (\mathbf{D} - \mathbf{1}) \cdot (\mathbf{1} - \mathbf{R}) - \mathbf{R} \right) \cdot \mathbf{O} \\ &= \mathbf{I} + \left( (\mathbf{D} - \mathbf{1}) \cdot (\mathbf{1} - \mathbf{R}) - \mathbf{R} \right) \cdot \mathbf{K} \cdot \mathbf{C} \\ &= \mathbf{I} + \mathbf{A} \cdot \mathbf{C} \end{aligned} \quad (12)$$

where  $\mathbf{1}$  is the identity matrix, and

$$\begin{aligned} \mathbf{A} &= \left( (\mathbf{D} - \mathbf{1}) \cdot (\mathbf{1} - \mathbf{R}) - \mathbf{R} \right) \cdot \mathbf{K} \\ &= \left( \mathbf{D} \cdot (\mathbf{1} - \mathbf{R}) - \mathbf{1} \right) \cdot \mathbf{K} \\ &= \mathbf{T} \cdot \mathbf{K} \end{aligned} \quad (13)$$

where  $\mathbf{T}$  contains  $-1$  in the main diagonal and transfer coefficients among pools in the off-diagonal entries. Consequently, the matrix  $\mathbf{A}$  contains in its main diagonal the decomposition rates  $-k_i$ , and in the off-diagonal, the coefficients  $a_{i,j} = T_{i,j} \cdot k_j$ . We call the matrix  $\mathbf{A}$  the decomposition operator, because it contains all the elements to decompose a certain amount of carbon in an instantaneous interval.

In component form, the system of equations can be expressed as

$$\frac{dC_1}{dt} = I_1 + \sum_{j=1}^m (T_{1,j} \cdot k_j \cdot C_j)$$

$$\frac{dC_2}{dt} = I_2 + \sum_{j=1}^m (T_{2,j} \cdot k_j \cdot C_j)$$

$\vdots$

$$\frac{dC_m}{dt} = I_m + \sum_{j=1}^m (T_{m,j} \cdot k_j \cdot C_j) \quad (14)$$

where the coefficients  $T_{i,j}$  represent the proportion of the processed carbon leaving pool  $j$  and received by pool  $i$ , and  $T_{i,i} = -1$ .

The product representation  $\mathbf{A} = \mathbf{T} \cdot \mathbf{K}$  introduces the transfer matrix  $\mathbf{T}$  that summarizes all flows of carbon among pools and out of the system, with  $\mathbf{K}$  describing the per pool processing as before. A very useful characteristic of  $\mathbf{T}$  is the relationship of its columns to the release coefficients  $R_{j,j} = -\sum_i T_{i,j}$ . These coefficients can be used to calculate the release flux out of the system as shown by Eq. 10.

Combining the principles of mass balance, substrate dependence, heterogeneity of decomposition rates, and internal transformations of soil organic matter, we can now express a general model of the form

$$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \mathbf{A} \cdot \mathbf{C} \quad (15)$$

for which the release of carbon from the system (external outputs), is consequently calculated by the expression

$$\mathbf{r} = \mathbf{R} \cdot \mathbf{K} \cdot \mathbf{C}. \quad (16)$$

Notice that this model assumes constant inputs of organic matter, constant decomposition rates, and constant transfers among different pools. We call this model linear time invariant (LTI).

#### *Environmental variability effects*

*Changes in the environment can either reduce or increase the rates of decomposition of soil organic matter* (Griffin 1963, Bunnell et al. 1977, Swift et al. 1979, Skopp et al. 1990, Davidson and Janssens 2006, Moyano et al. 2013). This has been widely acknowledged in a large number of existing models, and the most common mathematical paradigm to represent the effects of the environment in the decomposition process is with a time-dependent scalar that multiplies all decomposition rates of the matrix  $\mathbf{A}$  (Rodrigo et al. 1997, Janssens et al. 2003, Bauer et al. 2008, Luo and Weng 2011, Sierra et al. 2015). This multiplier, which we denote as  $\xi(t)$ , is usually a function of different environmental factors  $X_i$ . In general, this multiplier is the product of different functions such that

$$\xi(t) = \prod_i f_i(X_i).$$



The majority of the models, however, only include temperature,  $T$ , and moisture,  $W$ , as the main environmental factors controlling the rates of decomposition, so commonly  $\xi(t) = f_T(T) \cdot f_W(W)$ . Time dependence in this formulation is included indirectly by the time dependence of  $T$  and  $W$ .

Environmental variability can also affect the flux of carbon inputs to soil, so we now consider time-dependent inputs of organic matter to soils  $I(t)$  explicitly.

A general model of decomposition that includes the five basic principles of mass balance, substrate dependence, heterogeneity and transformations of organic matter, and environmental variability effects is therefore given by

$$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C}(t). \quad (17)$$

This model generalizes the model structure of about 65% of all models reviewed by Manzoni and Porporato (2009), and it is the structure used in the majority of Earth system models (Luo and Weng 2011, Todd-Brown et al. 2013).

Apart from mathematical convenience, there is not a particular reason for which one single function  $\xi(t)$  modifies all elements of the decomposition operator. A more general, and perhaps plausible representation, is assuming that all elements of the matrix  $\mathbf{A}$  change over time according to different functions. The decomposition operator, therefore, is not composed of constant coefficients, but rather of time-dependent functions modified by changing environmental conditions. The general model is then given by

$$\begin{aligned} \frac{d\mathbf{C}(t)}{dt} &= \mathbf{I}(t) + \mathbf{A}(t) \cdot \mathbf{C}(t) \\ &= \mathbf{I}(t) + \mathbf{T}(t) \cdot \mathbf{K}(t) \cdot \mathbf{C}(t) \end{aligned} \quad (18)$$

where the  $K_{i,i}(t)$  are functions representing the instant decomposition rates of pool  $i$  as a function of time, and  $T_{i,j}(t)$  are functions defining time-dependent transfers from pool  $j$  to  $i$ .

#### Organic matter interactions

Recent advances in our understanding of SOM decomposition suggest that *different components of the SOM system may interact, synergistically increasing or decreasing decomposition rates*. For example, the priming effect, the increase in decomposition fluxes after the addition of fresh or labile substrate (Jenkinson et al. 1985, Kuzyakov et al. 2000, Kuzyakov 2010) is an interaction among different types of organic matter that creates nonlinearities in the system of equations (Wutzler and Reichstein 2008, Blagodatsky et al. 2010). Similarly, the explicit representation of exoenzymes in catalyzing rates of decomposition requires the introduction of nonlinear elements in the system of equations. For the most part, these nonlinearities are simply multiplicative or Michaelis-Menten terms (Williams 1973, Schimel and Weintraub

2003, Manzoni and Porporato 2007, Allison et al. 2010, Blagodatsky et al. 2010). However, up to now, none of the already considered model examples account for these interactions.

To allow for interactions between different types of organic matter, the decomposition functions  $k_i(t)$  and the transfer functions  $T_{i,j}(t)$  are now allowed to be functions not only of time, but also of the carbon stocks  $C_j$  in other pools as

$$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \mathbf{T}(\mathbf{C}, t) \cdot \mathbf{N}(\mathbf{C}, t) \cdot \mathbf{C}(t) \quad (19)$$

where we renamed  $\mathbf{K}$  to  $\mathbf{N}(\mathbf{C}, t)$ , and made explicit that these matrices have a dependence on the vector of states  $\mathbf{C}$  and represents a nonlinear relationship. This model (Eq. 19), generalizes the structure of the majority of models of soil organic matter decomposition reviewed by Manzoni and Porporato (2009), and can adequately represent nonlinearities in the process of organic matter decomposition.

Considering that this general model (Eq. 19) describes a nonlinear relationship, it is fair to ask: Why do we express this general model by a matrix multiplication that normally indicates linear equations and then take the trouble to make the matrices  $\mathbf{C}$  dependent? Why do we not use a vector valued function  $\mathbf{f}(\mathbf{C}, t)$  instead? The answer is that our nonlinear model has some properties not to be expected in an arbitrary nonlinear system. First, our representation makes explicit the principle of substrate dependence of decomposition by the presence of the product with  $\mathbf{C}(t)$  at the end of the equation, which ensures that there is no decomposition if there is no carbon available to decompose. A second reason is the remarkable relationship between internal inputs and outputs represented by the product  $\mathbf{T}(\mathbf{C}, t) \cdot \mathbf{N}(\mathbf{C}, t)$ , which although first encountered in the linear model, it remarkably survives the introduced nonlinearities due to mass balance constraints. This relationship is the key requirement for the ability to compute the carbon release of the system, which would be impossible for an unrestricted nonlinear system. Therefore, the time-dependent release fluxes from this general model can be calculated as

$$\mathbf{r}(t) = \mathbf{R}(t) \cdot \mathbf{O}(t) \quad (20)$$

where  $\mathbf{R}(t)$  is a time-dependent diagonal matrix calculated from  $\mathbf{T}(\mathbf{C}, t)$ , with diagonal entries  $R_i(t) = -\sum_j T_{i,j}(t)$ , and  $\mathbf{O}(t) = \mathbf{N}(\mathbf{C}, t) \cdot \mathbf{C}(t)$ .

In the case there are no nonlinear terms in the model, the matrices  $\mathbf{T}$  and  $\mathbf{N}$  would contain functions independent on the vector of states  $\mathbf{c}$ , therefore

$$\mathbf{T}(t) \cdot \mathbf{N}(t) = \mathbf{A}(t) \quad (21)$$

establishing a direct link between the linear (Eq. 18) and the nonlinear (Eq. 19) general models.

#### Example

As an example on how this framework can represent an existing model as special case, consider a nonlinear

system with two pools: a carbon substrate  $C_S$  and microbial biomass  $C_B$  (Manzoni and Porporato 2007). This system can be represented by the coupled first-order ordinary differential equations (ODEs)

$$\begin{aligned}\frac{dC_S}{dt} &= I + k_B C_B - k_S C_B \frac{C_S}{K_M + C_S} \\ \frac{dC_B}{dt} &= \alpha k_S C_B \frac{C_S}{K_M + C_S} - k_B C_B\end{aligned}\quad (22)$$

where  $\alpha$  is the proportion of the decomposed substrate incorporated in the microbial biomass, and  $k_S$ ,  $k_B$ , and  $K_M$  are constants as follows:  $k_S$  is the maximum rate of substrate decomposition,  $k_B$  is the rate of cycling of the microbial biomass, and  $K_M$  is the half-saturation constant for the substrate concentration. This system can be represented following the general model of Eq. 19 as

$$\begin{aligned}\frac{d\mathbf{C}}{dt} &= \mathbf{I} + \mathbf{T} \cdot \mathbf{N}(\mathbf{C}) \cdot \mathbf{C} \\ &= \begin{pmatrix} I \\ 0 \end{pmatrix} + \begin{pmatrix} -1 & 1 \\ \alpha & -1 \end{pmatrix} \begin{pmatrix} \frac{k_S C_B}{K_M + C_S} & 0 \\ 0 & k_B \end{pmatrix} \begin{pmatrix} C_S \\ C_B \end{pmatrix}.\end{aligned}\quad (23)$$

The amount of carbon release from the system is given by the vector  $\mathbf{r} = \mathbf{R} \cdot \mathbf{O}$

$$\begin{aligned}\mathbf{r} &= \begin{pmatrix} 1 - \alpha & 0 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} k_S C_B \frac{C_S}{K_M + C_S} \\ k_B C_B \end{pmatrix} \\ &= \begin{pmatrix} (1 - \alpha) k_S C_B \frac{C_S}{K_M + C_S} \\ 0 \end{pmatrix}.\end{aligned}\quad (24)$$

Notice that the principle of environmental effects on decomposition is ignored in this model (no time-dependence explicitly included). However, all other principles are included in this simple model.

In Appendix A, we present a set of common models represented within the proposed framework. Many of the reviewed models include more pools or more complex representation of soil organic matter dynamics, but they all can be represented either as the linear general model of Eq. 18 or the nonlinear model of Eq. 19.

#### MATHEMATICAL PROPERTIES

The general model of Eq. 19 can accommodate many different structures of SOM decomposition models with different mathematical properties. In this section we propose a classification scheme of different families of models and explore possible qualitative behaviors. We focus, in particular, on the dynamical stability of the

models and whether or not certain groups of models can show oscillatory behavior. The concept of dynamic stability as we discuss it here must not be confused with the ecological concept of stability of soil organic matter as discussed in the work of authors such as Sollins et al. (1996), von Lützow et al. (2006), and Schmidt et al. (2011).

We propose a classification of models according to their ability to accommodate time and substrate dependences (Fig. 1). This classification scheme allows us to use different mathematical tools to study their dynamical stability properties. The concept of stability and the mathematical tools used to determine it vary depending on the characteristics of the system, mostly the time dependence of the rhs terms of Eq. 19 and the existence of nonlinear terms (Fig. 1). For example, for systems with time varying inputs it is impossible to think about the existence of a unique stable fixed point, but rather of a region of stability in the state-space.

If none of the rhs terms of Eq. 19 is time dependent, we rely mostly on concepts from dynamical system theory to determine three different types of stability: Lyapunov stability (LS), asymptotic stability (AS), or global asymptotic stability (GAS). For time-varying systems, we rely mostly on the field of control theory to determine various types of stability: bounded-input bounded-state (BIBS), bounded-input bounded-output (BIBO), or input-to-state stability (ISS) (Fig. 1).

In the following sections we analyze each case separately and specify the type of stability that can be determined for each class of models.

#### Time invariant systems

We first consider models that do not depend explicitly on time (blue region in Fig. 1), but may or may not include nonlinear terms in  $\mathbf{T}$  or  $\mathbf{N}$ .

*Linear time invariant models.*—In the case of absence of nonlinear terms in  $\mathbf{T}$  or  $\mathbf{N}$ , we can use a very well-developed theory to determine stability properties of the models and even compute an analytical solution.

Consider first the special case of a system without inputs ( $I = 0$ ):

$$\frac{d\mathbf{C}}{dt} = \mathbf{A} \cdot \mathbf{C}, \quad \mathbf{C}(t = 0) = \mathbf{C}_0 \quad (25)$$

which represents the decay of a cohort of a heterogeneous substrate under constant environmental conditions. The analytic solution to this initial value problem is given by an expression of the form

$$\mathbf{C}(t) = e^{\mathbf{A} \cdot (t-t_0)} \mathbf{C}_0 \quad (26)$$

where  $e^{\mathbf{A} \cdot (t-t_0)}$  is the matrix exponential. In order to get an intuition for the behavior of the solution, we assume for the moment that  $\mathbf{A}$  is diagonalizable. The solution can then be expressed as

$$\mathbf{C}(t) = c_1 e^{\lambda_1 t} \mathbf{v}_1 + c_2 e^{\lambda_2 t} \mathbf{v}_2 + \dots + c_m e^{\lambda_m t} \mathbf{v}_m \quad (27)$$

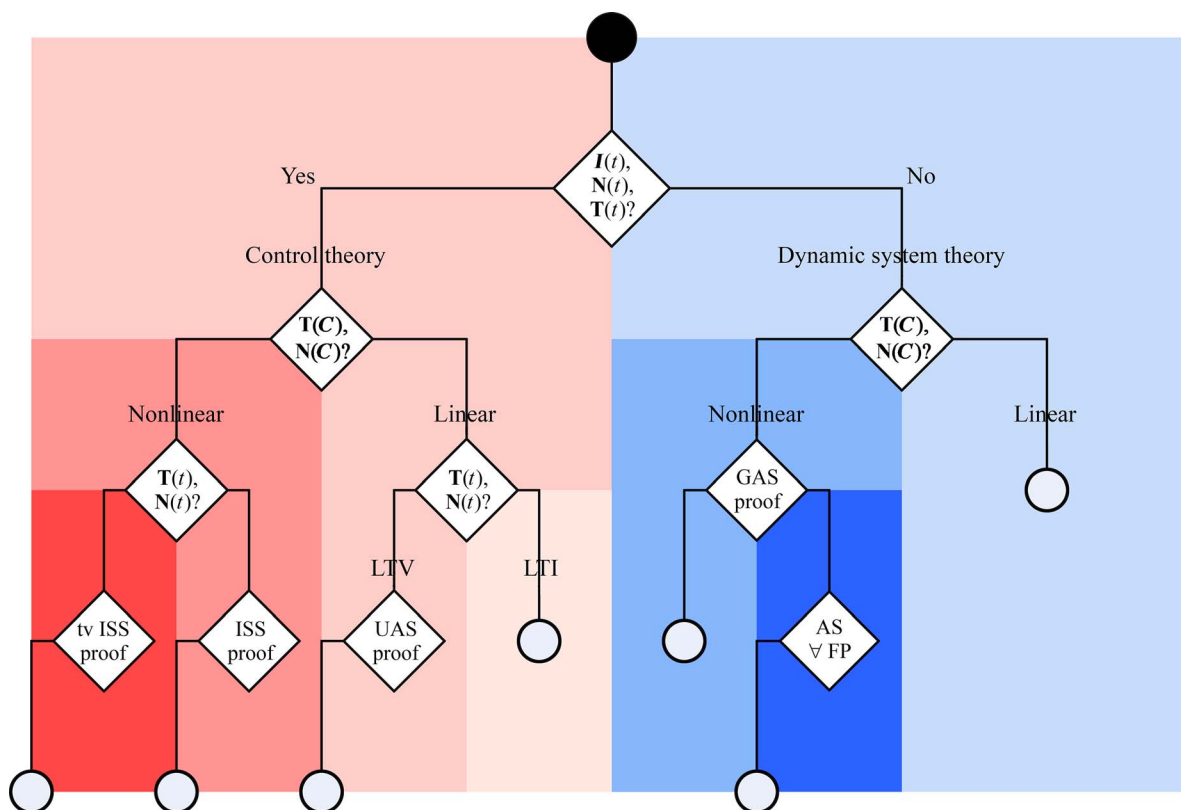


FIG. 1. Decision tree for classifying models according to different available mathematical tools and determining their dynamic stability. The decision tree starts at the top (black circle) with the general model of Eq. 19, and the first decision is made according to the time dependence of each of the equation's terms: vector of inputs,  $I(t)$ , matrix of nonlinear terms  $N(C, t)$ , and the transfer matrix  $T(C, t)$ , where  $C$  is the vector of  $C$  pools and  $t$  is time. Subsequent decisions are made according to their dependence on the vector of states, i.e., on their nonlinearity; and the results from different tests. Affirmative answers at each node move the branch to the left-hand side and negative answers to the right-hand side. Stability is determined at the end of the branch with the light-colored circle. The types of stability considered are: linear asymptotic stability, asymptotic stability for all fixed points (AS  $\forall$  FP), global asymptotic stability (GAS), uniform asymptotic stability (UAS), input to state stability (ISS), and time variant asymptotic stability (tv ISS). Linear models are abbreviated as linear time invariant (LTI) and linear time variant (LTV).

where  $c_i$  are constants that depend on initial conditions, and  $\lambda_i$  and  $v_i$  are eigenvalues and eigenvectors of the matrix  $A$ , respectively. We can then define the tuple  $\lambda$  as the set of all eigenvalues of  $A$ ; i.e.,  $\lambda = \{\lambda_1, \lambda_2, \dots, \lambda_m\}^T$ . These eigenvalues are very useful in determining the general qualitative behavior of the solutions. In particular, they can inform us about the type of stability of the system, i.e., whether the solutions of the system converge to a fixed steady state in the long term and return to it after being perturbed. In general, there are three different cases to consider: (1) If all eigenvalues have a negative real part, the system is globally asymptotically stable (GAS); i.e., it converges to zero from any start-vector. (2) If at least one eigenvalue has a positive real part, the system is not stable. (3) If at least one of the eigenvalues is equal to zero, the system may or may not be stable depending on the linear dependence of the eigenvectors (see Appendix B).

These three cases are easy to evaluate in the solution of Eq. 27. If all eigenvalues are negative, the system simply decays in the direction of the eigenvector

associated with the smallest eigenvalue (Strogatz 1994). Since the vector of initial values cannot have negative terms (negative SOM pools), a term in Eq. 27 with a positive eigenvalue will lead inevitably to exponential growth of one of the pools, which is impossible given that there are not inputs to the system. This situation (positive eigenvalues) is biologically and physically impossible for SOM decomposition models and violates the principle of mass balance. Eigenvalues can also have an imaginary part associated with oscillations of the different pools over time. To simplify our exposition, let's also assume that the elements in the main diagonal of  $A$  are organized from large to small, that is,  $\forall k_i \in \text{diag}(A), k_i \geq k_{i+1}$ . We can identify three ecologically meaningful model structures with distinctive qualitative behaviors.

1) If  $A$  is a diagonal matrix ( $A = K$ ), then  $\lambda = \text{diag}(A)$  and the absence of a positive eigenvalue is guaranteed by construction. All pools decompose independently with separate exponential functions. This model



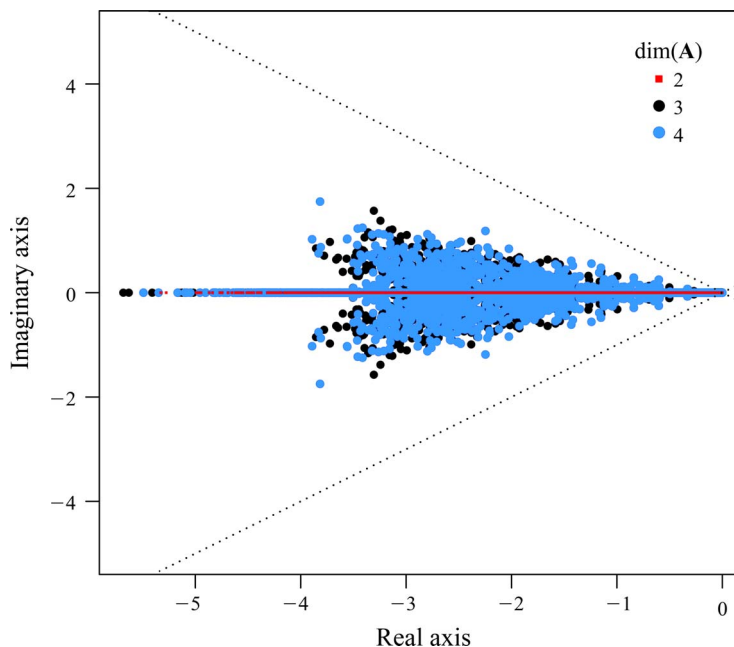


FIG. 2. Complex plane for models with feedback structure. Each point is a random realization of a model where the values of the decomposition constant  $k_i$  were sampled from a uniform distribution  $U(0, 3)$ , and values of the transfer coefficient  $\alpha_{i,j} \sim U(0, 1/m)$ , where  $m$  represents the number of dimensions or pools in the model, i.e.,  $m = \dim(\mathbf{A})$ . The simulations show that (1) the models are always stable (all eigenvalues with negative real parts), (2) two-pool models never exhibit oscillations (all eigenvalues on the real line), (3) three- and four-pool models can exhibit damped oscillations (eigenvalues as conjugate pairs).

structure is commonly denominated as parallel and implies that plant-derived organic matter is not transformed to other compounds, nor does it change its decomposition rate due to physical or chemical protection (Minderman 1968, Manzoni and Porporato 2009, Sierra et al. 2012).

- 2) If  $\mathbf{A}$  is a lower triangular matrix, fast cycling pools transfer organic matter to slow cycling pools in a structure of series or cascade (Swift et al. 1979, Manzoni and Porporato 2009, Sierra et al. 2012). Also in this case,  $\lambda = \text{diag}(\mathbf{A})$ , so imaginary eigenvalues are impossible because these are simply the values of  $k_i$ , which again insures the absence of positive eigenvalues. Also, because organic matter is always transferred from fast to slow decay classes, this model structure can be thought of as a stabilization only scheme. This model structure allows the possibility of time lags for the release of carbon if SOM is transferred sequentially to multiple pools before being released.
- 3) If  $\mathbf{A}$  has elements both above and below the main diagonal, organic matter is transferred as a feedback process in which slow cycling pools send back material to fast cycling pools. In this case,  $\lambda \neq \text{diag}(\mathbf{A})$  and it is possible to obtain imaginary eigenvalues, in which case the system can show an oscillatory behavior (Bolker et al. 1998, Wang et al. 2014). This model structure includes both stabilization and destabilization processes because organic matter is simultaneously transferred to fast and slow

cycling pools. Given that the ecological principles we identified lead to specific structures of the matrices  $\mathbf{T}$  and  $\mathbf{K}$ , it is impossible to obtain positive eigenvalues in this model structure.

By the mass balance principle, all elements of  $\text{diag}(\mathbf{A})$  are non-positive ( $-k_i \leq 0$ ). In the majority of cases, the eigenvalues of the parallel and the series type of structures are negative, which implies that these types of models have stable solutions (see Appendix B). However, in some models such as RothC (Jenkinson and Rayner 1977, Coleman and Jenkinson 1999), it is possible to obtain one eigenvalue  $\lambda_i = 0$ , which is associated with the existence of an inert pool with  $k_i = 0$ . In this case, the stability of the model cannot be determined by the eigenvalues alone, and it is necessary to determine whether the eigenvectors associated with each eigenvalue are linearly independent (see Appendix B: Theorem 1c).

We conducted a numerical experiment and calculated eigenvalues for models with feedback structure and plotted the results in the complex plane. For this analysis, we took random numbers to produce 2000 biologically meaningful realizations of the matrix  $\mathbf{A}$  with elements in the upper and lower diagonal (feedback model structure) and with two, three, or four pools (Fig. 2). The eigenvalues of these matrices show that: (1) All eigenvalues have negative real part, confirming our statement that it is impossible to build an  $\mathbf{A}$  that gives eigenvalues with positive real part from the basic

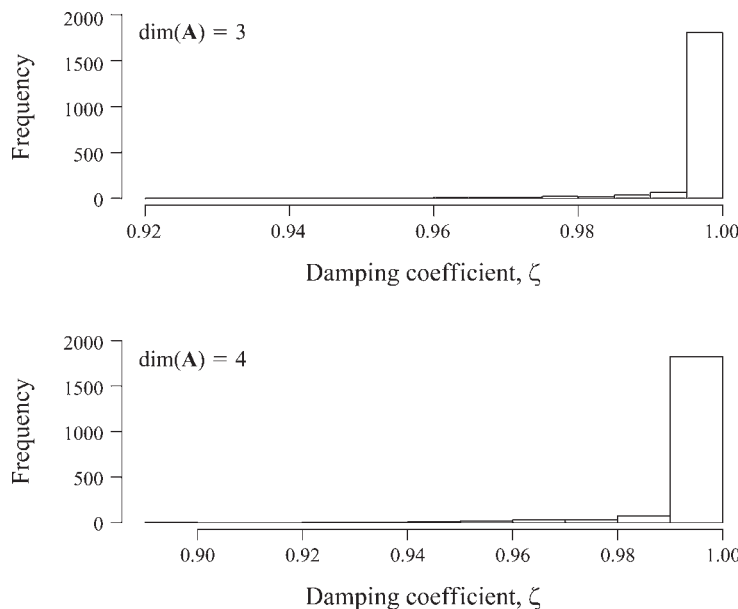


FIG. 3. Damping coefficients,  $\zeta$ , for the random realizations of the three- and four-pool models with connection in series. When  $\zeta = 0$ , the system oscillates indefinitely, and when  $\zeta = 1$ , it decays exponentially without any oscillations and returns to the equilibrium condition in the minimum amount of time.

properties of  $\mathbf{K}$  and  $\mathbf{T}$ . Therefore, the solutions of the models are always stable (provided there is not an inert pool). (2) The eigenvalues of the two-dimensional models ( $\dim(\mathbf{A}) = 2$ ) are never complex, and only decomposition operators with  $m \geq 3$  show complex eigenvalues. This implies that only models with more than three pools can potentially show oscillations and two-pool models with feedback structure (and by extension all two-pool models) cannot. (3) Oscillations seem to be more likely at fast cycling scales in comparison to slow cycling scales. This can be inferred by a higher density of complex conjugates at higher values of  $\text{Re}(\lambda)$ .

When we obtain complex eigenvalues of the form  $\lambda = \alpha \pm i\beta$ , both the real and the imaginary part of  $\lambda$  are solutions to the system of differential equation. The complex eigenvalue  $\lambda$  is associated therefore with two solutions of the form

$$\begin{aligned} C_1(t) &\propto e^{\alpha t} (v_1 \cos \beta t - v_2 \sin \beta t), \\ C_2(t) &\propto e^{\alpha t} (v_1 \cos \beta t + v_2 \sin \beta t) \end{aligned} \quad (28)$$

where  $\alpha$  controls the rate of exponential decay and  $2\pi/\beta$  the period of oscillations (Wang et al. 2014); i.e., large values of  $\beta$  are related to high oscillation frequencies. Our results from Fig. 2 suggest that, for three and four pool models, oscillation frequencies are low and the amplitude of the oscillations decreases rapidly ( $|\beta| < |\alpha|$ ).

Formally, the relation between oscillation frequencies and decay can be assessed by the damping ratio, which measures how fast or slow oscillations decay. It is given by the expression (Lallement and Inman 1995)

$$\zeta = \frac{-\alpha}{\sqrt{\alpha^2 + \beta^2}}. \quad (29)$$

When  $\zeta = 0$ , the system oscillates indefinitely, and when  $\zeta = 1$ , it decays exponentially without any oscillations and returns to the equilibrium condition in the minimum amount of time. The damping ratio for all models randomly produced in our numerical exercise shows values in the neighborhood of 1 (Fig. 3), suggesting that all these linear models, even though they have complex eigenvalues, do not show significant levels of oscillations and the decay term dominates over the oscillation term.

This information about the properties of our matrix  $\mathbf{A}$  can also give us additional insights for more complex models. Assuming now that we have a system in which there are constant inputs, we have the expression

$$\frac{d\mathbf{C}}{dt} = \mathbf{I} + \mathbf{A} \cdot \mathbf{C} \quad (30)$$

which represents the simplest structure of models that includes the principles of mass balance, substrate dependence, heterogeneity, and transformations of organic matter, but ignores the effects of environmental variability and substrate interaction on decomposition. The analytic solution of this model is given by the expression

$$\mathbf{C}(t) = e^{\mathbf{A}(t-t_0)} \mathbf{C}_0 + \left( \int_{t_0}^t e^{\mathbf{A}(t-\tau)} d\tau \right) \mathbf{I}. \quad (31)$$

From the previous analysis we concluded that the first term on the rhs decays exponentially to zero in the long term, and therefore only the second term of the rhs determines the long-term behavior of the system. In

other words, the carbon present in the system at the beginning of the simulation decomposes and only the balance between new and older carbon determines the long-term carbon stock; or, that the long-term carbon stock is independent of the initial amount of carbon at a beginning of a simulation.

The solution of the integral in Eq. 31 is given by (LeVeque 2007)

$$\int_{t_0}^t e^{\mathbf{A} \cdot (t-\tau)} d\tau = \mathbf{A}^{-1} \left( e^{\mathbf{A} \cdot (t-\tau)} - \mathbf{I} \right) \quad (32)$$

so we can assume that the long-term (asymptotic) steady-state solution of Eq. 30 is given by

$$\mathbf{C}^* = -\mathbf{A}^{-1} \cdot \mathbf{I} \quad (33)$$

under the assumption that the term  $e^{\mathbf{A} \cdot (t-\tau)}$  vanishes as  $t \rightarrow \infty$ . Notice that the same result can be simply obtained by setting the lhs of Eq. 30 equal to zero. At steady state, therefore, the carbon stores depend only on the matrix  $\mathbf{A}$  and the amount of carbon inputs to the soil. Given that the eigenvalues of  $\mathbf{A}$ , in the absence of an inert pool, always have negative real part, the steady-state solution is always stable. This means that small perturbations to the system do not change qualitatively the behavior of the system near the steady-state value (Guckenheimer and Holmes 1983, Braun 1993). In the presence of an inert pool, the system can still be stable such as the case of the RothC model, where the inert pool does not receive carbon from any other pool and it stays there forever while the other pools decompose and exchange carbon among each other. In such a case the system reaches a steady state and behaves like other linear models. An unstable behavior would be obtained if this inert pool receives carbon from other pools but does not decompose it. This situation leads to an unlimited accumulation of carbon in the inert pool and therefore in the entire system (Sierra et al. 2011). We believe the existence of completely inert pools of soil organic matter, where  $k \equiv 0$ , is unlikely in nature given the tremendous capacity of microorganisms to decompose organic materials even under extreme environmental conditions (Rothschild and Mancinelli 2001).

#### Nonlinear time invariant model (NLTI)

The qualitative properties of the nonlinear model of Eq. 19 with no time dependencies can be studied by calculating the Jacobian matrix (see Hartman-Grobman theorem in Appendix B)

$$\mathbf{J} = \begin{pmatrix} \frac{\partial \dot{C}_1}{\partial C_1} & \cdots & \frac{\partial \dot{C}_1}{\partial C_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial \dot{C}_n}{\partial C_1} & \cdots & \frac{\partial \dot{C}_n}{\partial C_n} \end{pmatrix} \quad (34)$$

where each  $\dot{C}_i$  represents an element of the  $d\mathbf{C}(t)/dt$

vector of Eq. 19. This Jacobian must be evaluated at the equilibrium point  $\mathbf{C}^*$ , where the amount of inputs equal the outputs. In nonlinear systems it is possible to obtain multiple equilibrium points, some of them may be stable and some unstable (Strogatz 1994). The eigenvalues of the Jacobian matrix evaluated at  $\mathbf{C}^*$  provide information about the type of stability in the vicinity of each equilibrium point (Guckenheimer and Holmes 1983, Braun 1993).

Similarly to the linear case, there are three main possibilities for the eigenvalues of  $\mathbf{J}$  that determine the stability and dynamic behavior of the possible nonlinear models at an equilibrium point: (1) At least one of the eigenvalues has a positive real part, (2) at least one of the eigenvalues has a zero real part, and (3) all eigenvalues have a negative real part (Guckenheimer and Holmes 1983, Braun 1993).

*Eigenvalues with positive real part.*—When at least one of the eigenvalues of the matrix  $\mathbf{J}$  evaluated at  $\mathbf{C}^*$  has a positive real part, the system in the neighborhood of  $\mathbf{C}^*$  is unstable (Guckenheimer and Holmes 1983). Contrary to the linear case, the existence of positive eigenvalues and unstable fixed points is possible in the nonlinear case. After a perturbation, a system may move from an unstable point  $\mathbf{C}^*$  to another equilibrium point that may or may not be stable.

*Eigenvalues with zero real part.*—If at least one eigenvalue of  $\mathbf{J}$  evaluated at  $\mathbf{C}^*$  has a zero real part, this fix point is said to be non-hyperbolic, and in most cases the stability of the system cannot be determined by the analysis of its eigenvalues alone (Guckenheimer and Holmes 1983, Izhikevich 2007).

These systems can sometimes represent special cases of parameterized models at a bifurcation point where a steady state could either disappear or split into many alternative steady states. For systems in which there is at least one eigenvalue equal to zero, the stability analysis must be done on a case by case basis. In some cases, however, the case of zero eigenvalues may point to potential conceptual problems with the model. For example, a version of the model proposed by Schimel and Weintraub (2003) assumes that the decomposition of soil organic carbon is only dependent on the amount of enzyme present at the microbial scale and that SOM is large and unchanging. Although this assumption is reasonable for short timescales, it ignores the principle of substrate dependence of decomposition and creates problems in the long-term behavior of the model. This assumption leads to the presence of one zero eigenvalue for the Jacobian matrix of this model (see Appendix A: Model A.5). This zero eigenvalue causes either a continuous decline of the soil organic carbon (SOC) pool with no lower limit (negative SOC values), or an infinite accumulation of  $\mathbf{C}$  under constant inputs. In this case, the zero eigenvalue is indicative of problems related to ignoring the principle of substrate dependence.

*Eigenvalues with negative real part.*—When all the eigenvalues of the matrix  $\mathbf{J}(\mathbf{C}^*)$  have negative real part,  $\mathbf{C}^*$  is stable. Almost all published nonlinear models of soil organic matter decomposition have fixed points in this category (c.f. Appendix A; Manzoni and Porporato 2007, 2009). After small perturbations, the models tend to return to this fix point with the trajectory of a stable focus (with oscillations) or a stable node (without oscillations).

Special cases of two- and three-dimensional models including nonlinear microbial interactions have been studied previously (Zelenev et al. 2000, Manzoni and Porporato 2007, Wang et al. 2014), clearly showing the oscillatory behavior of these models. However, not all possible parameter combinations in these nonlinear models show important oscillations. For example, for the two-pool nonlinear model of Eq. 22, random combinations of biologically meaningful parameter values show that the complex part of the eigenvalues can be both higher and lower than the real part (Fig. 4). Therefore, the damping ratio for this type of models cover the entire range  $0 < \xi \leq 1$  (Fig. 5), which implies that certain combinations of parameter values produce models in which oscillations are not large, but other parameter combinations produce important oscillatory behavior. A similar behavior is obtained for random combinations of parameter values for the three-pool microbial model proposed by Wieder et al. (2013; see Figs. 4 and 5).

In both the two- and three-pool microbial models, the damping ratio is proportional to the parameter  $\epsilon$ , which controls the proportion of carbon incorporated in the microbial biomass (Fig. 6). This implies that carbon use efficiency is proportional to the level of oscillations in microbial models of the Michaelis-Menten type.

#### *Systems with time dependencies*

A different set of concepts and tools are necessary to analyze the stability of models with time dependencies (left-hand side of Fig. 1). Instead of focusing on finding stability at fixed points in the state-space, we analyze the stability with respect to regions of the state-space (Fig. 7). These regions can be defined either in the input vs. output phase-plane or in the input vs. state plane.

The field of control theory provides useful concepts that help to determine stability for time-dependent systems. We will use here the concepts of bounded-input bounded-state BIBS stability, bounded-input bounded-output BIBO stability, and input-to-state stability ISS. The concepts of BIBS and BIBO help to determine upper and lower bounds on the carbon stocks and the release fluxes from the system, while ISS helps to determine functions that set upper bounds on the possible states (carbon stocks) for a time variant system.

*Linear systems with time dependencies.*—The simplest case is when  $\mathbf{A}$  is constant and  $\mathbf{I}(t)$  is time dependent, which in control theory is still considered an LTI system. In the subsection *Linear time invariant models* (above) we identified conditions for  $\mathbf{A}$  that make the system converge

to a stable fixed point under constant or no inputs. Assuming the same conditions for  $\mathbf{A}$  and with the inputs changing over time, we expect the state of the system to deviate from this fixed point and occupy certain region of the state-space. If the inputs are bounded, i.e., do not exceed an arbitrary maximum and minimum value, we expect both the outputs and the stocks to be also bounded (Fig. 7). In control theory, these types of stability are called bounded-input bounded-output BIBO, and bounded-input bounded-state BIBS stability, respectively (Sontag 2008, d'Andréa Novel and De Lara 2013). BIBS stability implies that the total stocks of the system at a time  $t$  are bounded by a function that depends on the maximum amount of inputs independently on the initial stocks (Sontag 2008). Both concepts are related, e.g., for a constant  $\mathbf{A}$  BIBS implies BIBO.

Similarly, when the elements of the decomposition operator are also time dependent,  $\mathbf{A}(t)$ , we also expect the outputs and the state of the system to be bounded if the inputs are bounded. In fact, we expect any biologically reasonable linear model to meet the BIBS and BIBO stability properties given the properties of the matrix  $\mathbf{A}$  imposed by the basic decomposition principles. We show a mathematical proof of the desired properties (BIBS, BIBO, and ISS) for some linear time-dependent systems in a separate more detailed publication (M. Müller and C. A. Sierra, *unpublished manuscript*).

*Nonlinear systems with time dependencies.*—Nonlinear systems without time dependencies may have not just one, but different equilibrium points  $\mathbf{C}^*$ . If time dependencies are introduced in any component of the model, the system may jump between regions of the state-space around different  $\mathbf{C}^*$ . In these cases, it is difficult to determine a general stability property of the model. However, nonlinear systems with time dependencies may meet the BIBS and BIBO properties as well as input-to-state stability ISS, which states that the stocks at any time  $t$  may be bounded by the input and the influence of the initial conditions decreases with time (Fig. 8; Edwards et al. 2000, Sontag 2008). However, determining ISS is not trivial and must be evaluated on case-by-case basis for different models.

#### *Timescales*

The theoretical framework proposed here facilitates the analysis of the timescale of soil organic matter cycling in models. For this purpose, it is helpful to analyze the set of eigenvalues of the matrix  $\mathbf{A}$  in the linear general model, or the eigenvalues of the Jacobian matrix  $\mathbf{J}$  of the general nonlinear model. The range in timescales for each model can be characterized by the inverse of the maximum and minimum eigenvalues as

$$\tau_{\min} = \frac{1}{\max|\operatorname{Re}(\lambda)|} \quad (35)$$

$$\tau_{\max} = \frac{1}{\min|\operatorname{Re}(\lambda)|} \quad (36)$$

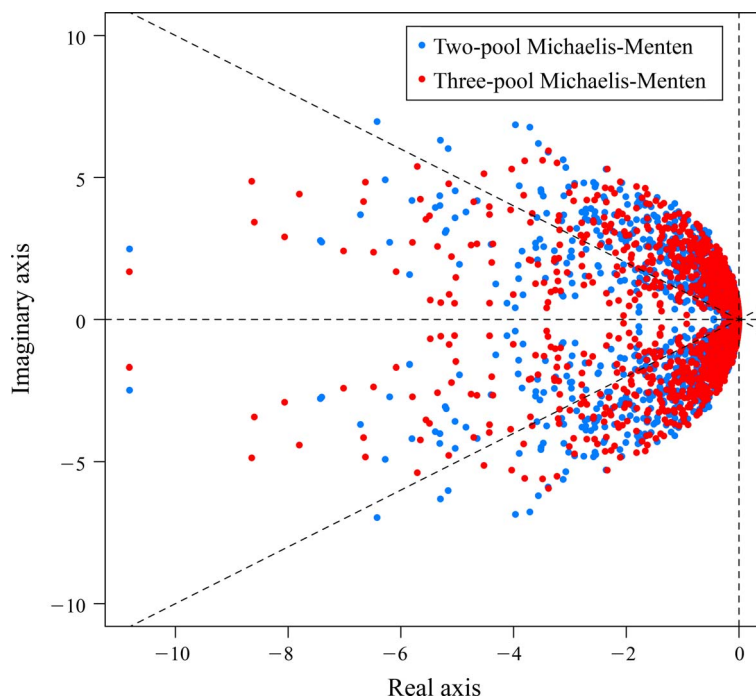


FIG. 4. Complex plane for a two- and a three-pool nonlinear Michaelis-Menten model. Each point is a random realization of a model where the parameter values are sampled randomly from the possible range of biologically meaningful values.

where  $\lambda$  includes all non-zero eigenvalues of the matrices **A** or **J**. The range characterized by  $\{\tau_{\min}, \tau_{\max}\}$  helps to compare the scale of application of different models. For example, the version of the introductory carbon balance

model (ICBM) parameterized for a bare fallow treatment (Appendix A) gives the range of timescales  $\{0.9, 125.3\}$  years, while in the RothC model this range is  $\{0.1, 57.5\}$  years. In the BACWAVE model, the real

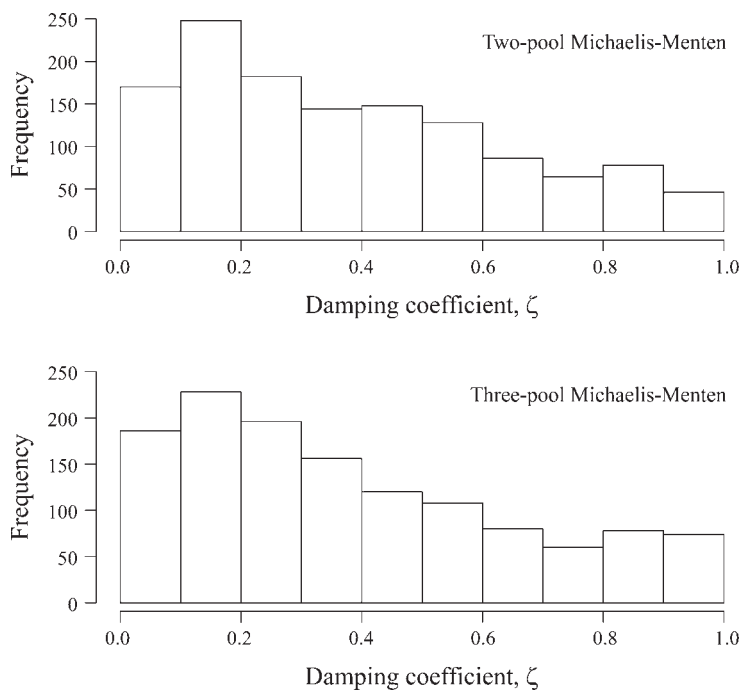


FIG. 5. Damping coefficients,  $\zeta$ , for random realizations of a two- and a three-pool Michaelis-Menten model. Parameter values were randomly sampled from the space of biologically meaningful parameter values.



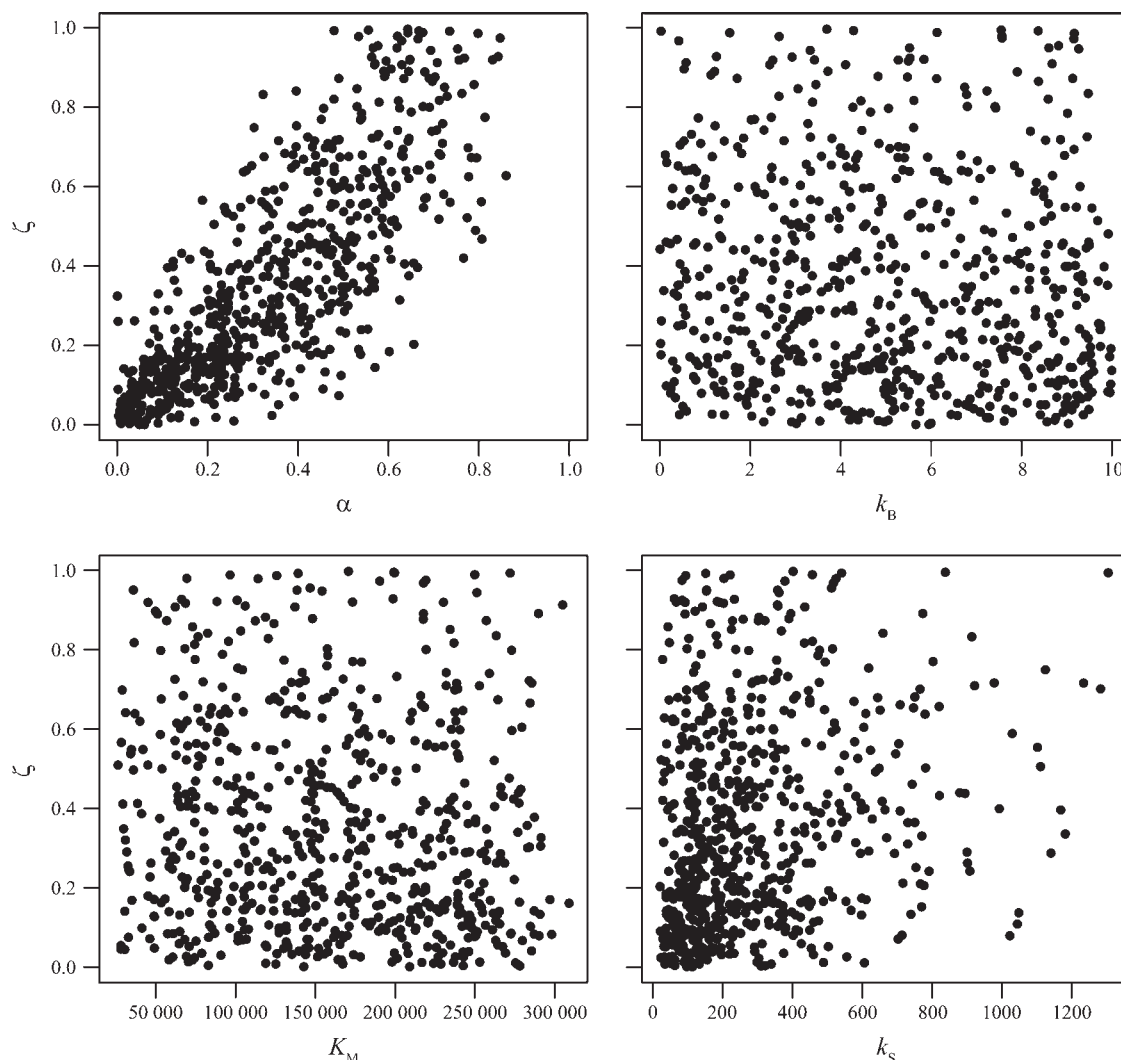


FIG. 6. Relationships between the damping ratio  $\zeta$  and the transfer coefficient  $\alpha$ , the microbial cycling rate  $k_B$ , the half-saturation constant  $K_M$ , and the maximum rate of substrate decomposition  $k_S$  of a two pool Michaelis-Menten model (see Eq. 22) for random combinations of parameter values.

part of its two eigenvalues are equal, and therefore, the timescale of this model is  $\tau_{\min} = \tau_{\max} = 2.02$  hours. These differences in timescales among models help to determine their range of application for specific research questions.

#### DISCUSSION

Here we presented a general mathematical framework to represent the process of soil organic matter decomposition as a set of general models with different properties (Table 1). We developed these general models based on simple principles, which are merely well-accepted facts about the process of organic matter decomposition. Our approach is general enough to determine the type of behaviors that different groups of models show and helps to determine envelopes of possible solutions. This framework also generalizes most previ-

ous models of soil organic matter decomposition and provides the basis for classifying models according to their main temporal behavior.

This mathematical framework builds on ideas previously proposed, in particular, it builds on the continuous quality theory of Ågren and Bosatta (1998), on the representation of ecological systems as dynamic systems (Ågren and Bosatta 1998, Bolker et al. 1998, Luo and Weng 2011), and on more recent ideas about nonlinear interactions of organic matter components (Schimel and Weintraub 2003, Manzoni and Porporato 2007).

The main results we obtained by analyzing soil organic matter decomposition models within this framework are a mathematical classification that guides the stability analysis of SOM systems, as well as special cases where the classification could be used to establish stability for general sub-classes of models (e.g., LTI) on

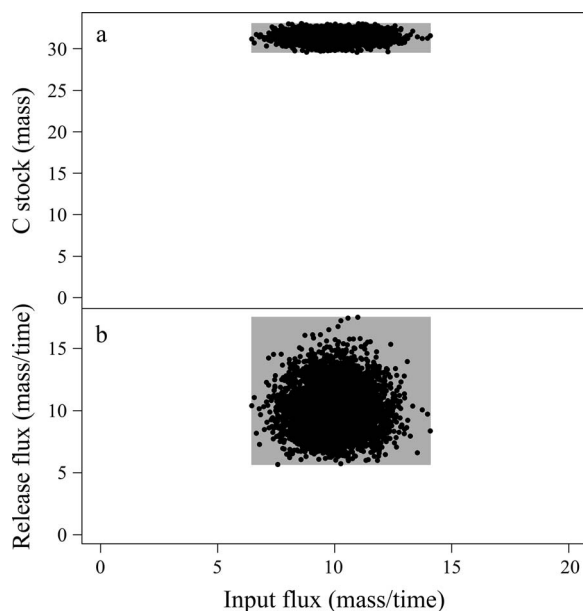


FIG. 7. Examples of (a) bounded-input bounded-state (BIBS) stability, and (b) bounded-input bounded-output (BIBO) stability. Both types of stability imply that if the inputs are bounded by a maximum and a minimum value, then the state and the outputs are also bounded by a maximum and a minimum value, respectively. The shaded regions represent the bounds imposed by these limits. Results were generated from a linear model as in Eq. 17 with random inputs and random variation in the temperature modifier  $\xi(t)$ . Input fluxes were randomly sampled from a distribution  $N \sim (10, 1)$ . Temperature values were sampled from  $N \sim (25, 5)$  and used in a modified van't Hoff function with  $Q_{10} = 1.4$ . Code to reproduce these results is provided in the Supplement.

the basis of basic ecological principles alone. Another point of interest was to determine the cases in which SOM components oscillate. We will discuss these two topics in the following sections, applying these concepts to current specific problems in SOM modeling.

#### *Dynamic stability and soil-warming experiments*

In soil-warming experiments, it has been repeatedly reported that respiration fluxes in warmed soils usually increase relative to a control non-warmed soil during a first phase of the experiment. Subsequently, respiration fluxes in the warmed soils return to pretreatment levels despite the higher temperatures (Luo et al. 2001, Melillo et al. 2002, 2011, Kirschbaum 2004, Heinemeyer et al. 2006, Bradford et al. 2008). This observed “acclimation” of soil respiration suggests that the SOM system behaves as a stable dynamical system with strong mass balance constraints in which after a perturbation, the system returns to its original state.

For any SOM decomposition model to reproduce this acclimation effect, it is only necessary that the model meets the property of dynamic stability. However, to explain experimental results on acclimation, two apparently contradictory hypotheses were proposed. One

suggested that, as temperature increases, microbial carbon use efficiency is reduced (Luo et al. 2001, Bradford et al. 2008, Allison et al. 2010). The second hypothesis suggested that a labile pool is exhausted after warming without the need to invoke changes in microbial physiology (Kirschbaum 2004, Eliasson et al. 2005). Within the theoretical framework presented here, both hypotheses are plausible. In fact, we propose that soil warming induces both changes in the efficiency of microbial C assimilation and changes in pool sizes. This result is independent on whether the SOM system shows nonlinear interactions; i.e., it can be explained by either linear or nonlinear models. In other words, the observed acclimation of respiration in warming studies can be explained by the dynamic stability property and the mass balance principle only.

Mathematically, we can explain results from warming experiments by considering time invariant models that meet the requirements for GAS. Every GAS model converges to a unique solution or stationary state in the long term, regardless of the initial conditions. If the system is perturbed, it returns in the long term either to the original state in case of a pulse perturbation, or to a different unique state in case of a permanent perturbation. Warming experiments usually modify the elements of the matrices  $\mathbf{T}$  or  $\mathbf{N}$ , i.e., decomposition and transfer rates, but do not necessarily modify the input fluxes to the soil. We can expect therefore that the system will move from the steady state at the control temperature  $C_c^*$  to a new unique steady state at the warmed

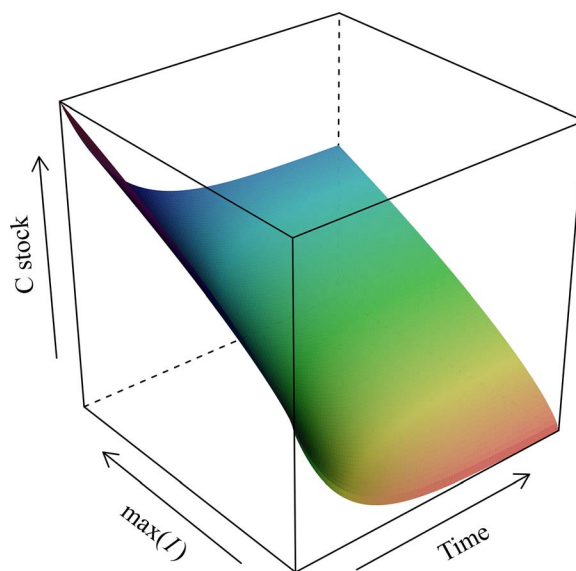


FIG. 8. Graphic representation of the concept of input-to-state stability (ISS). If a system is ISS, the C stocks are bounded by a function  $\beta(C_0, t)$  that increases as the initial stocks increase and decreases as  $t \rightarrow \infty$ , and a function  $\gamma(\max(I))$  that increases as the maximum amount of inputs increase. Notice that with no inputs the system meets the global asymptotic stability (GAS) property. Color represents the value of the C stock, from high (dark blue) to low (red).

temperature  $C_w^*$ . These different states imply differences in carbon stocks in the SOM pools, but the system must also comply with the mass balance principle at each steady state, in which the total output (respiration) flux must be equal to the total input flux

$$\sum I = \sum r \quad (37)$$

where the sum is over all pools (components of the vector). Since steady states prevail once they are reached, it is impossible to break Eq. 37 without violating basic principles of the SOM system.

To illustrate this property of the SOM system, we ran simulations for a linear and a nonlinear model in which both decomposition rates and microbial C use efficiency were modified independently and simultaneously (Fig. 9). In all cases, respiration fluxes in the warming treatments return to similar levels as the control simulation reaching different pool sizes. In the nonlinear case, due to nonlinear interactions, respiration fluxes oscillate before returning back to the original steady state. In both types of models, respiration fluxes acclimate to control levels.

#### Oscillations

Previously, it has been shown that microbial explicit models with Michaelis-Menten kinetics produce predictions with oscillatory behavior (Manzoni and Porporato 2007, Wang et al. 2014). Here we showed that, although the eigenvalues of the Jacobian matrix of these models have a nonzero complex part, the degree of oscillations depends on the specific parameterization of the model. This degree of oscillation, characterized by the damping ratio  $\zeta$ , depends on how large is the complex part of the eigenvalues with respect to the real part.

In soils, oscillatory behavior has been observed only along root tips as a consequence of microbial growth and depletion of substrate (root exudates; Semenov et al. 1999, van Bruggen et al. 2000, Zelenev et al. 2000). The period of the oscillations observed in these studies ranged between 2 to 10 hours. In contrast, the period of the oscillations obtained with the microbial explicit models recently proposed ranges between 5 to 15 years (Wang et al. 2014).

Oscillations at the level of single enzymes have been observed at timescales between  $10^{-4}$  to 10 seconds, where the Michaelis-Menten equation very well characterizes enzyme dynamics (Yang et al. 2003, English et al. 2006, Goldbeter 2013, Xie 2013). At these timescales, enzymes show dynamic disorder, i.e., stochastic changes in the conformation state that leads to temporal changes in the affinity of the enzyme for the substrate, and therefore, in their catalytic rates (English et al. 2006, Schwabe et al. 2013). A statistical distribution of waiting times can capture the stochastic nature of the fluctuations of enzyme activity at these timescales. It has been shown that the inverse of the average waiting time between molecular reactions at the single molecule level

converges to the Michaelis-Menten equation, which approaches the macroscopic behavior of the ensemble of molecules (English et al. 2006, Schwabe et al. 2013, Xie 2013). As for the time course of enzyme reactions and the conversion of substrates to products, reactions generally reach steady states in the order of seconds to minutes, depending on temperature and pH levels (Daniel and Danson 2013, Johnson 2013).

From the available biochemical evidence, it seems clear that Michaelis-Menten kinetics and related oscillations of enzymes and products operate at the level of ensembles of single enzymes and at timescales of milliseconds to seconds. In soils, with the large heterogeneity of substrate quality and concentrations and the high diversity of enzymes at the soil-core level, it seems challenging to fit one single Michaelis-Menten equation to the multitude of reactions that occur over days, weeks, seasons, and years, and over multiple spatial scales. Recent attempts to model soil organic matter dynamics with explicit Michaelis-Menten terms (e.g., Allison et al. 2010, German et al. 2012, Wieder et al. 2013) treat organic matter dynamics as a scale invariant process, leading to large periods of oscillations at larger scales (Wang et al. 2014).

It is likely, however, that soil organic matter dynamics do not follow the property of scale invariance, with interactions of organic matter only relevant at short timescales. For longer timescales and mixtures of large diversity of enzyme-substrate complexes, a macroscopic behavior may emerge in which oscillations are averaged out and linear representations of organic matter decomposition may approximate these average dynamics reasonably well. Data from long-term experiments (>50 years) show little evidence of oscillatory behavior or nonlinear dynamics related to SOM interactions (Cardinael et al. 2015); it is therefore imperative to explore scaling properties of the SOM system from short-term nonlinear dynamics to long-term trends in soil carbon cycling.

#### SUMMARY AND CONCLUSIONS

Most of our current basic understanding of the process of soil organic matter decomposition can be synthesized in six basic principles that provide the building blocks of a general model of soil organic matter dynamics. The principles of mass balance, substrate dependence of decomposition, heterogeneity and internal transformation of organic matter, and environmental effects on decomposition provide explicit forms of systems of linear ordinary differential equations that set the bounds on possible temporal behaviors these concepts may lead to in models. In addition, the principle of interactions among different classes of organic matter results in nonlinear representations of the soil organic matter system and may lead to an additional set of behaviors in which temporal oscillations are more prominent. For linear models of SOM dynamics, we exclude the possibility of unstable

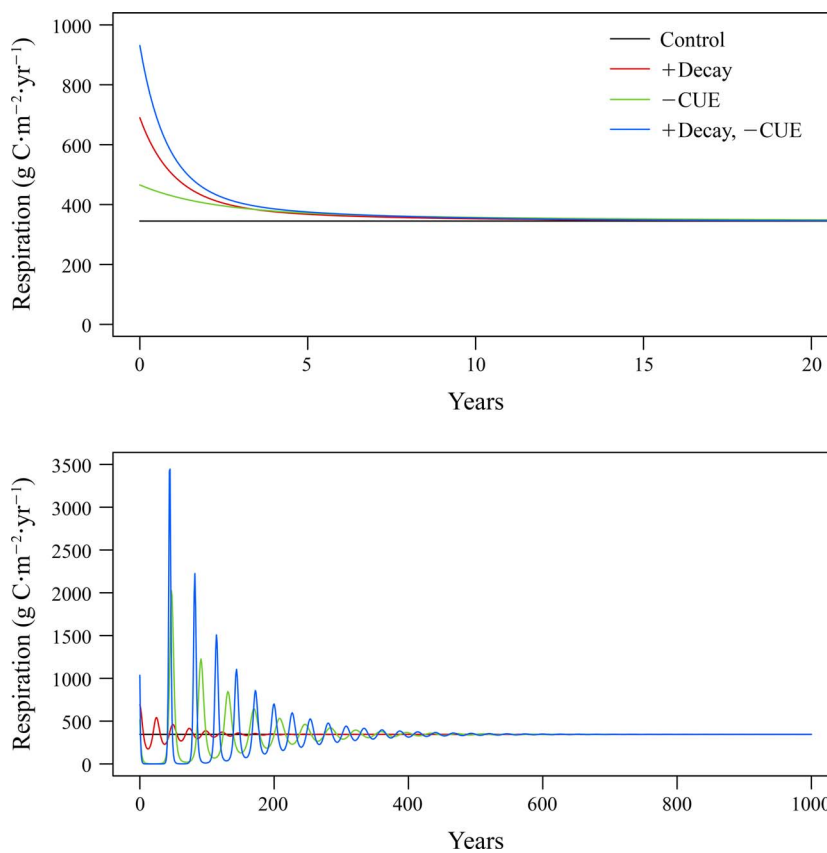


FIG. 9. Examples of stability of respiration fluxes for a linear (upper panel) and a nonlinear (lower panel) model under different assumptions about the effects of warming on soil carbon cycling. The control simulation represents a system in steady state where inputs are equal to respiration outputs. The +Decay simulation represents increases in respiration rates by a factor of 2; -CUE represents a simulation in which transfer rates (i.e., carbon use efficiency, CUE) were reduced by a factor of 0.5; and +Decay, -CUE represents a simulation in which both respiration rates and transfer rates were modified by a factor of 2 and 0.5, respectively. Code to reproduce these results is provided in the Supplement.

solutions that lead to an indefinite accumulation of matter over time. This situation is only plausible in the presence of an inert pool of organic matter that remains completely isolated from the action of microorganisms and does not decompose ( $k \equiv 0$ ), but we are skeptical that this situation actually exists in nature.

We identify two different types of dynamic stability for SOM models; for systems without time dependences, models may reach one single stability point where the stocks and fluxes reach a constant value in the long-term. Based on the first five principles we identified, we conclude all linear models reach this type of stability. For models with time dependent inputs, decomposition and transfer functions, the models may reach a region of stability in the state-space. Bounds that define these regions in the state-space and the output fluxes are set by bounds in the input fluxes. For nonlinear time-dependent models, the bounds in the carbon stocks may be set by functions that depend on the initial conditions and the maximum amount of input fluxes.

Results from soil-warming experiments in which fluxes in warm soils return to pre-warming conditions

in the long term suggest stability properties of the SOM system, which may provide additional clues for establishing stability properties for all kinds of SOM models. Interactions between different types of organic matter, such as those between exoenzymes and substrates, may lead to strong oscillations of organic matter over time, but this behavior is dependent on the carbon use efficiency of the microorganisms. The lower the efficiency, the higher the level of oscillations, which in observed enzyme-substrate reactions under laboratory conditions are expressed at timescales of milliseconds to seconds. Under the assumption of scale invariance of enzyme-substrate processes, recent representations of soil organic matter dynamics at the global scale in Earth system models show oscillations at timescales from years to decades. Long-term data sets of carbon dynamics do not provide evidence for long-term oscillatory behavior of SOM stocks and indicates a need to develop scaling relations from short-term interactions to larger spatial scales.

Our general framework includes only a set of simple basic principles that may be refined and expanded as



more research becomes available. We expect that with the theoretical development of these basic principles, more specific models can be developed that reduce current uncertainties about nonlinear interactions, multiple steady states, oscillations, and scaling.

## ACKNOWLEDGMENTS

Financial support for the development of this work was provided by the Max Planck Society and the German Research Foundation (DFG) through the Emmy Noether Program (SI 1953/2-1). We would like to thank Susan E. Trumbore for academic support and comments on an earlier version of the manuscript.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A and B and the Supplement are available online: <http://dx.doi.org/10.1890/15-0361.1.sm>