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COMMENTARY

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Key Points:
- Models of the carbon cycle can be represented as nonautonomous compartmental systems
- This representation helps to bridge the gap between simulation and understanding
- It can also help to address a new set of questions in carbon cycle science

Supporting Information:
- Supporting Information S1
- Supporting Information S2

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Representing and Understanding the Carbon Cycle Using the Theory of Compartmental Dynamical Systems

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Abstract Models representing exchange of carbon between the atmosphere and the terrestrial biosphere include a large variety of processes and mechanisms, and have increased in complexity in the last decades. These models are no exception of the simulation versus understanding conundrum previously articulated for models of the physical climate, which states that increasing detail in process representation in models, and the simulations they produce, hinders understanding of holistic system behavior. However, recent theoretical progress on the mathematical representation of the carbon cycle in ecosystems may help to provide a general framework for the qualitative understanding of models without compromising detail in process representation. Here we (1) briefly review recent ideas on the theory of transient dynamics of the terrestrial carbon cycle and its matrix representation, pointing out issues of interpretation, (2) show that these ideas can be further generalized in the mathematical concept of nonautonomous compartmental systems, and (3) provide thoughts on how this framework can be used to address a new set of questions in carbon cycle science.

1. Introduction

The global carbon cycle consists of a variety of complex processes that requires the development of models for its understanding and prediction of future dynamics. The history of carbon cycle modeling is rich, and for many decades, different models with different levels of complexity have been proposed (Bolin et al., 1983; Cramer et al., 2001; Friedlingstein et al., 2014; Prentice et al., 2007; Raupach et al., 2005). The terrestrial carbon cycle, in particular, has been described with a large numbers of models that vary in their degree of complexity, number of processes represented, scales of application, and implementation in different computing languages (Prentice et al., 2007; Raupach et al., 2005). It is therefore difficult to compare different models, and for this reason researchers resort to comparisons of model output to assess the performance of models (e.g., Cramer et al., 2001; Friedlingstein et al., 2014), rather than to the concepts and the mathematics directly implemented in the model.

The problem does not necessarily belong to carbon cycle models only, but climate and Earth system models in general. For instance, Held (2005) describes a conundrum in modeling the physical climate for which the high degree of complexity and sophistication of model implementations hinders understanding of general patterns of atmospheric circulation and climate dynamics. On the one hand, it is important to implement detailed representations of relevant processes in models to attain realism; but on the other hand, as the level of detail increases in a model, so does the uncertainty in parameterizations and predictions as well as our inability to understand general dynamics of the overrepresented system (Bolin et al., 1983; Held, 2005, 2014; Raupach et al., 2005).

The tension between understanding and complexity can be resolved to some extent by viewing carbon cycle models through the lens of dynamical systems, allowing carbon cycle models of varying complexity and detail to be understood in a consistent framework using well-established mathematical concepts. This approach can help increase our level of understanding of general system dynamics while simultaneously allowing complex representations of multiple processes. There has been recent progress in this direction through the representation of terrestrial carbon models in matrix form (Jiang et al., 2018; Luo et al., 2017; Sierra & Müller, 2015; Xia et al., 2013), which we can potentially use to take full advantage of the rich existing mathematical theory of dynamical systems. This would allow us to make progress not only on holistic system understanding, but also in the development of more efficient and clean codes; develop models at

different levels of complexity under one overarching theory; and facilitate comparisons of competing theories implemented in different models.

In this commentary, we will review recent progress on the mathematical representation of terrestrial carbon models as dynamical systems while highlighting issues of interpretation, propose a general representation and classification of models using the concept of compartmental systems, and highlight new research opportunities.

2. Carbon Cycle Models as Dynamical Systems

The terrestrial carbon cycle is generally conceptualized as a set of reservoirs (pools, compartments) such as foliage, wood, roots, and soils that store and exchange carbon among them in different forms (gas, dissolved, solid) (Bolin et al., 1983; Emanuel & Killough, 1984; Luo et al., 2015; Schimel, 1995). The terrestrial carbon cycle is also conceptualized as an open system defined by an observer-defined boundary that exchanges carbon with the external environment through the process of photosynthesis as the main input, and with multiple output fluxes such as autotrophic and heterotrophic respiration as well as dissolved organic forms (Luo et al., 2015; Trumbore, 2006).

Models of the terrestrial carbon cycle, and Earth system models in general, fit in the general mathematical definition of dynamical system (e.g., Lucarini et al., 2017; Luo et al., 2017; Raupach, 2013; Xia et al., 2013). According to Jost (2005, p. 1), "*A dynamical system is a system that evolves in time through the iterated application of an underlying dynamical rule. That transition rule describes the change of the actual state in terms of itself and possibly also previous states*." Independent of how complicated a model might be, we can think of it as a rule that is applied repeatedly to describe the time evolution of mass and/or energy. In early carbon cycle models, this rule is implemented as a large loop that updates the state of the system, generally C stocks in separate compartments, in discrete time steps such as days or years. Other models implement the update rules based on sets of ordinary or partial differential equations with variable time steps, which also fit the definition of dynamical systems.

The set of equations generally implemented in models are based on mass balance constraints, and can be written more compactly in matrix and vector form. Bolin (1983) was one of the first to write a simple carbon cycle model in matrix form. However, this form of representing carbon models has become more common recently by the development of the dynamic disequilibrium (Luo & Weng, 2011), traceability framework (Xia et al., 2013), and the transient dynamics theory (Jiang et al., 2018; Luo et al., 2017) of the terrestrial carbon cycle. Within these frameworks, carbon stocks in ecosystem pools $\boldsymbol{x}$ are represented as

$$\frac{d\boldsymbol{x}(t)}{dt} = \dot{\boldsymbol{x}}(t) = U(t) \cdot \boldsymbol{b} + \xi(t) \cdot \mathbf{A} \cdot \mathbf{K} \cdot \boldsymbol{x}(t), \quad \boldsymbol{x}(t=0) = \boldsymbol{x}_0, \tag{1}$$

where $\boldsymbol{x}(t)$ is a vector of carbon pool sizes; $U(t)$ is a scalar function that represents photosynthetically fixed carbon; $\boldsymbol{b}$ is a vector of partitioning coefficients of the photosynthetically fixed carbon to plant pools (e.g., leaf, root, and woody biomass). The square matrices $\mathbf{A}$ and $\mathbf{K}$ contain coefficients to calculate carbon transfers among the different pools, and the rates of carbon processing in each individual compartment, respectively. The time-dependent diagonal matrix $\xi(t)$ modifies process and transfer rates according to time-dependent environmental factors such as temperature and precipitation.

Equation (1) is a very general representation of carbon cycle models, and emerges from the similarities in which the terrestrial carbon cycle is implemented in many models. By expressing models in this general and compact form, it is possible to better understand holistic behaviors of terrestrial carbon cycle models. For instance, the framework can be applied to better trace different components of the carbon cycle (Xia et al., 2013), determine timescales of different processes (Huang et al., 2018; Yan et al., 2017), determine the predictability and dynamic disequilibrium of the carbon cycle (Luo et al., 2015; Luo & Weng, 2011), and assess carbon storage capacity and potential (Jiang et al., 2018; Luo et al., 2017; Luo & Weng, 2011).

However, it is important to highlight that the model of equation (1) is a linear representation of the carbon cycle, and nonlinear processes in which the rate of change of one state variable depends on the state of other variables cannot be represented. This can occur when, for example, carbon uptake $U(t)$ also depends on the amount of stored carbon in other ecosystem compartments such as foliage, nonstructural

Table 1
Classification of Carbon Cycle Models According to Their Dependence on the Vector of States (Linearity), and on Time (Autonomy)

	t-dependence	
x-dependence	Autonomous	Nonautonomous
Linear	$\boldsymbol{u}+\mathbf{B}\cdot\boldsymbol{x}(t)$	$\boldsymbol{u}(t)+\mathbf{B}(t)\cdot\boldsymbol{x}(t)$
Nonlinear	$\boldsymbol{u}(\boldsymbol{x})+\mathbf{B}(\boldsymbol{x})\cdot\boldsymbol{x}(t)$	$\boldsymbol{u}(\boldsymbol{x},t)+\mathbf{B}(\boldsymbol{x},t)\cdot\dot{\boldsymbol{x}}(t)$

Note. Cells are expressions for the differential equation describing $\dot{\boldsymbol{x}}(t)$ that captures the change of carbon contents with respect to time.

carbohydrates, or fine roots; or when the presence of carbon of a labile soil organic matter pool influences the rate of more recalcitrant pools such as the case of the priming effect (Sierra & Müller, 2015; Wutzler & Reichstein, 2008). Clearly, a more general framework that can accommodate nonlinear interactions among carbon cycle components is needed.

Such a general model that allows nonlinear interactions among ecosystem components can be expressed as

$$\dot{\boldsymbol{x}}(t)=\boldsymbol{u}(\boldsymbol{x}(t),t)+\mathbf{B}(\boldsymbol{x}(t),t)\cdot\boldsymbol{x}(t),\quad \boldsymbol{x}(t=0)=\boldsymbol{x}_0, \tag{2}$$

where $\boldsymbol{u}(\boldsymbol{x}(t),t)$ is a vector-valued function of external inputs to the system and $\mathbf{B}(\boldsymbol{x}(t),t)$ a matrix-valued function of cycling and transfer rates, where both can depend on the vector of states $\boldsymbol{x}(t)$ and can also change over time *t*. Note that these matrices and vectors can not only be populated by constant coefficients, but by functions that may depend on other functions and parameters.

This general representation reveals an important classification of models according to their mathematical properties (Table 1), i.e., according to model dependence on the vector of states (linearity), and time (autonomy). We call a model linear when the vector of inputs and the matrix of cycling rates are not dependent on the vector of states, and nonlinear otherwise. Similarly, we call a model autonomous when inputs and cycling rates are not explicitly time-dependent, and nonautonomous otherwise.

The model of equation (1) proposed for the disequilibrium, traceability, and transient dynamics frameworks (Jiang et al., 2018; Luo et al., 2017; Luo & Weng, 2011; Xia et al., 2013) can be classified as linear nonautonomous because there are no dependencies on the vector of states, but rates and inputs are time-dependent. We will see below that this classification is of fundamental importance to study the qualitative mathematical properties and overall behavior of ecosystem models.

3. Compartmental Systems

Carbon in and out of ecosystem reservoirs must obey mass balance constraints independent on the degree of complexity and number of functions that determine process rates in a model. These mass balance constraints impose strong attributes on the dynamical system of equation (2), and in particular on the matrix $\mathbf{B}(\boldsymbol{x}(t),t)$. We say that system (2) is compartmental if $\mathbf{B}(\boldsymbol{x}(t),t)$ has (i) all its diagonal elements nonpositive, (ii) all off-diagonal elements nonnegative, and (iii) the sum of all elements in each individual column nonpositive. These conditions must apply for all times *t* and for all possible values of $\boldsymbol{x}(t)$ predicted by the model (Anderson, 1983; Jacquez & Simon, 1993; Rasmussen et al., 2016). In the supplement, we show an example on how to compute these properties for the ecosystem model described in Weng and Luo (2011).

There is already a very rich theory on compartmental systems that can be transferred to problems related to the global carbon cycle. For instance, there are already important results on the qualitative behavior of different types of compartmental systems and necessary conditions for their stability (convergence to attractors in the long-term), identifiability (determination of model parameters from observations), and control (manipulation of the system to obtain a desired state) (Anderson, 1983; Jacquez & Simon, 1993), and the calculation of system diagnostics such as ages and transit times (Metzler et al., 2018; Metzler & Sierra, 2018; Rasmussen et al., 2016), among others. These results, however, may change dramatically depending on whether one is dealing with linear versus a nonlinear systems, or with autonomous versus nonautonomous systems.

4. Autonomous Versus Nonautonomous Systems

In the autonomous case (Table 1), mass inputs and process rates in the system are constant. This implies that the external environment (e.g., atmospheric CO_2 concentrations, temperature, and precipitation) are assumed constant. Although this may sound unrealistic or nonapplicable for most of the simulation work that is done in carbon cycle research, many concepts that are commonly used to describe system dynamics are borrowed from mathematical concepts that only apply to autonomous systems. These concepts include:

steady state, tipping point, fixed point, or impulse response function, which are quantities that do not change over time and can only be computed because the system is autonomous. Other concepts or metrics such as ages and transit times of mass in the system would also need very different formulas depending on whether one is dealing with an autonomous or a nonautonomous system (Metzler et al., 2018; Rasmussen et al., 2016; Sierra et al., 2017).

One main difference in the theory of nonautonomous systems compared to autonomous systems is that instead of thinking of concepts such as steady state defined by a single point in the state space, sets of points or trajectories define concepts such as attractors (Figure 1). Similarly, methods such as eigenvalue/eigenvector analysis to determine the qualitative behavior of a trajectory as it converges to a fix point are of little use in the analysis of nonautonomous systems. Instead, the properties of the perturbing signal are of outmost importance in the analysis of nonautonomous compartmental systems (Müller & Sierra, 2017).

Issues of interpretation are evident in the recent theory of transient dynamics of the carbon cycle (Jiang et al., 2018; Luo et al., 2017). For instance, if we adopt the notation of the linear nonautonomous system of Table 1, we can rewrite it as

$$\boldsymbol{x}(t)=\mathbf{B}^{-1}(t)\cdot\dot{\boldsymbol{x}}(t)-\mathbf{B}^{-1}(t)\cdot\boldsymbol{u}(t). \tag{3}$$

Luo et al. (2017) defined the second term of the right-hand side as an attractor and denoted it the carbon storage capacity, and the first term the carbon storage potential (notice that signs are reversed in relation to Luo et al. (2017) due to the definition of compartmental systems, in which all diagonal elements of **B** are negative or zero). This interpretation, however, is rather awkward because we are dealing with quantities that are changing all the time. The storage capacity may be reached by the system if all rates and inputs

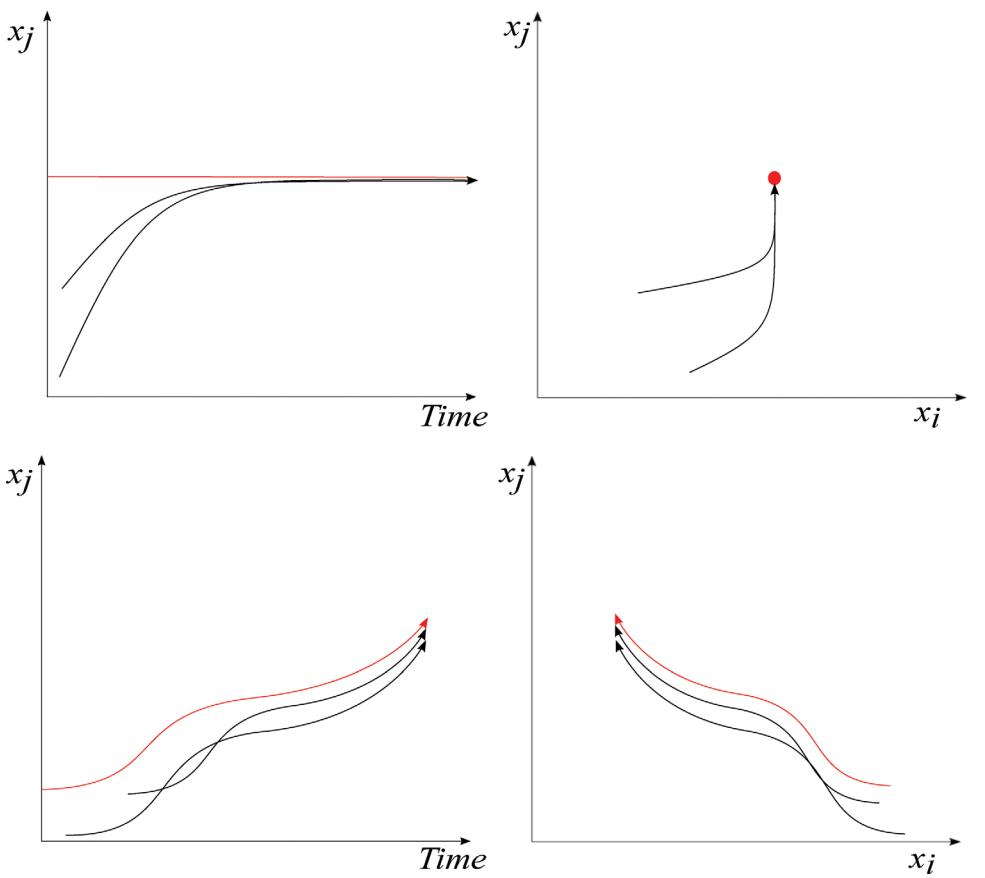

Figure 1. Trajectories for (upper plots) autonomous and (lower plots) nonautonomous linear compartmental systems (left) with respect to time and (right) in a two-dimensional state space. In the autonomous case, all trajectories converge to a fixed point in the state space (red dot) independent of their initial conditions, while in the nonautonomous case all trajectories are *forward attracting*, with a unique *pullback attracting* trajectory (red curve).

remain constant after some time, but because they are permanently changing, the storage capacity behaves more like a moving target that is never reached by the system. Similarly for the storage potential, it changes at all times and it is difficult to grasp what this value really means.

For linear nonautonomous systems, we can only say that any solution is *forward attracting* (Rasmussen et al., 2016), i.e., solutions with different initial conditions exponentially converge to each other (supporting information Figure 1), but they do not reach any fixed point in the state space. Rasmussen et al. (2016) also showed that there exist a unique *pullback attracting* solution (trajectory) to which all other trajectories are attracted to. This trajectory, which is not a point but rather a set in the state space, is the attractor of the linear nonautonomous system. Since the carbon storage capacity is not a solution trajectory, $\boldsymbol{x}(t) \neq -\mathbf{B}^{-1}(t) \cdot \boldsymbol{u}(t)$, it cannot be defined as the attractor of the system.

Nevertheless, the concepts of attractors and repellers are very powerful abstractions, which bring together mathematical concepts from dynamical system theory with concepts from ecosystem ecology, biogeochemistry and Earth system science.

5. Opportunities and Future Research

Recent work on representing the terrestrial carbon cycle as nonautonomous dynamical systems opens the door to new opportunities for increasing our understanding of general patterns and properties of the carbon cycle. Taking advantage of the fact that these systems must comply with the requirements of compartmental systems, it is possible to ask a new set of questions not necessarily explored in previous research. For instance, one could ask: what are meaningful pairs of attractors and repellers for different compartments of the global carbon cycle and how global change drivers may modify these attractors? What specific biogeochemical processes determine rates of convergence to these attractors? How are critical transitions in the state of the global carbon cycle expressed in the nonautonomous sense? These are just a few questions that this new approach to carbon cycle research can tackle.

To address these questions though, it would be helpful to represent existing and new models as compartmental dynamical systems in matrix form. This would facilitate the analysis of models within the theoretical framework of dynamical systems using a common mathematical language independent from the programming language used for model implementation.

In summary, new advances in expressing models as compartmental dynamical systems and studying their properties in the nonautonomous sense can potentially change the way we currently understand and represent processes in the carbon cycle. It can help us better understand the overall dynamics of models, even for those with complex implementations. In addition, it can help us develop new models in ways such that we can easily understand their structure and overall behavior. More importantly, it can help us address a whole new set of questions not addressed before in carbon cycle science, bridging a gap between simulation and understanding.

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References

Anderson, D. H. (1983). *Compartmental modeling and tracer kinetics*. Berlin, Germany: Springer Science & Business Media.
Bolin, B. (1983). Steady state and response characteristics of a simple model of the carbon cycle. In Bolin, B. (Eds.), *Carbon cycle modelling* (Scope 16, pp. 315–331). Hoboken, NJ: John Wiley.
Bolin, B., Keeling, C., Bacastow, R., Björkström, A., & Siegenthaler, U. (1983). Carbon cycle modelling. In Bolin, B. (Eds.), *Carbon cycle modelling* (Scope 16, pp. 1–28). Hoboken, NJ: John Wiley.
Cramer, W., Bondeau, A., Woodward, F., Prentice, I., Betts, R., Brovkin, V., et al. (2001). Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology*, *7*, 357–373.
Emanuel, W. R., & Killough, G. G. (1984). Modeling terrestrial ecosystems in the global carbon cycle with shifts in carbon storage capacity by land-use change. *Ecology*, *65*(3), 970–983. https://doi.org/10.2307/1938069
Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., et al. (2014). Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate*, *27*(2), 511–526. https://doi.org/10.1175/JCLI-D-12-00579.1
Held, I. M. (2005). The gap between simulation and understanding in climate modeling. *Bulletin of the American Meteorological Society*, *86*(11), 1609–1614. https://doi.org/10.1175/BAMS-86-11-1609
Held, I. M. (2014). Simplicity amid complexity. *Science*, *343*(6176), 1206–1207. https://doi.org/10.1126/science.1248447
Huang, Y., Lu, X., Shi, Z., Lawrence, D., Koven, C. D., Xia, J., et al. (2018). Matrix approach to land carbon cycle modeling: A case study with the community land model. *Global Change Biology*, *24*, 1394–1404. https://doi.org/10.1111/gcb.13948
Jacquez, J. A., & Simon, C. P. (1993). Qualitative theory of compartmental systems. *SIAM Review*, *35*(1), 43–79. https://doi.org/10.1137/1035003

Jiang, L., Shi, Z., Xia, J., Liang, J., Lu, X., Wang, Y., et al. (2018). Transient traceability analysis of land carbon storage dynamics: Procedures and its application to two forest ecosystems. *Journal of Advances in Modeling Earth Systems*, *9*, 2822–2835. https://doi.org/10.1002/2017MS001004

Jost, J. (2005). *Dynamical systems* (189 p.). Berlin, Germany: Springer.

Lucarini, V., Ragone, F., & Lunkeit, F. (2017). Predicting climate change using response theory: Global averages and spatial patterns. *Journal of Statistical Physics*, *166*(3), 1036–1064. https://doi.org/10.1007/s10955-016-1506-z

Luo, Y., Keenan, T. F., & Smith, M. (2015). Predictability of the terrestrial carbon cycle. *Global Change Biology*, *21*(5), 1737–1751. https://doi.org/10.1111/gcb.12766

Luo, Y., Shi, Z., Lu, X., Xia, J., Liang, J., Jiang, J., et al. (2017). Transient dynamics of terrestrial carbon storage: Mathematical foundation and its applications. *Biogeosciences*, *14*(1), 145–161. https://doi.org/10.5194/bg-14-145-2017

Luo, Y., & Weng, E. (2011). Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends in Ecology & Evolution*, *26*(2), 96–104.

Metzler, H., Müller, M., & Sierra, C. A. (2018). Transit-time and age distributions for nonlinear time-dependent compartmental systems. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(6), 1150–1155. https://doi.org/10.1073/pnas.1705296115

Metzler, H., & Sierra, C. A. (2018). Linear autonomous compartmental models as continuous-time Markov chains: Transit-time and age distributions. *Mathematical Geosciences*, *50*(1), 1–34. https://doi.org/10.1007/s11004-017-9690-1

Müller, M., & Sierra, C. A. (2017). Application of input to state stability to reservoir models. *Theoretical Ecology*, *10*, 451–475. https://doi.org/10.1007/s12080-017-0342-3

Prentice, I., Bondeau, A., Cramer, W., Harrison, S., Hickler, T., Lucht, W., et al. (2007). Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In Canadell, J. G., Pataki, D., & Pitelka, L. (Eds.), *Terrestrial ecosystems in a changing world, The IGBP Series* (pp. 175–192). Berlin, Germany: Springer.

Rasmussen, M., Hastings, A., Smith, M. J., Agusto, F. B., Chen-Charpentier, B. M., Hoffman, F. M., et al. (2016). Transit times and mean ages for nonautonomous and autonomous compartmental systems. *Journal of Mathematical Biology*, *73*(6), 1379–1398. https://doi.org/10.1007/s00285-016-0990-8

Raupach, M. R. (2013). The exponential eigenmodes of the carbon-climate system, and their implications for ratios of responses to forcings. *Earth System Dynamics*, *4*(1), 31–49. https://doi.org/10.5194/esd-4-31-2013

Raupach, M. R., Barrett, D. J., Briggs, P. R., & Kirby, J. M. (2005). Simplicity, complexity and scale in terrestrial biosphere modelling. In Franks, S. W., Sivapalan, M., Takeuchi, K., & Tachikawa, Y. (Eds.), *Predictions in ungauged basins: International perspectives on the state of the art and pathways forward* (pp. 239–274). Wallingford, UK: IAHS Press.

Schimel, D. S. (1995). Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, *1*(1), 77–91. https://doi.org/10.1111/j.1365-2486.1995.tb00008.x

Sierra, C. A., Müller, M., & Trumbore, S. E. (2012). Models of soil organic matter decomposition: the SoilR package, version 1.0. *Geosci. Model Dev.*, *5*(4), 1045–1060. https://doi.org/10.5194/gmd-5-1045-2012

Sierra, C. A., & Müller, M. (2015). A general mathematical framework for representing soil organic matter dynamics. *Ecological Monographs*, *85*, 505–524. https://doi.org/10.1890/15-0361.1

Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., & Trumbore, S. E. (2017). The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology*, *23*(5), 1763–1773. https://doi.org/10.1111/gcb.13556

Trumbore, S. (2006). Carbon respired by terrestrial ecosystems—Recent progress and challenges. *Global Change Biology*, *12*(2), 141–153. https://doi.org/10.1111/j.1365-2486.2006.01067.x

Weng, E., & Luo, Y. (2011). Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics. *Ecological Applications*, *21*(5), 1490–1505. https://doi.org/10.1890/09-1394.1

Wutzler, T., & Reichstein, M. (2008). Colimitation of decomposition by substrate and decomposers: A comparison of model formulations. *Biogeosciences*, *5*(3), 749–759.

Xia, J., Luo, Y., Wang, Y.-P., & Hararuk, O. (2013). Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biology*, *19*(7), 2104–2116. https://doi.org/10.1111/gcb.12172

Yan, Y., Zhou, X., Jiang, L., & Luo, Y. (2017). Effects of carbon turnover time on terrestrial ecosystem carbon storage. *Biogeosciences*, *14*(23), 5441–5454. https://doi.org/10.5194/bg-14-5441-2017