

Dear Dr. Alexey V. Eliseev:

We greatly appreciate your granting us the opportunity to revise our manuscript. We have carefully studied the comments from two referees and M. Freilich. We have revised the manuscript accordingly.

In addition to addressing those comments, we also have made the following changes.

1. We have slightly modified the title to be “**Transient Dynamics of Terrestrial Carbon Storage: Mathematical foundation and its applications**”. The original term “numeric examples” we think carries less meaning for readers than the term “its applications.”
2. We have deleted the paragraph and relevant sentences about the carbon storage potential to be used as the target quantity of research, trading, and government negotiation. We plan to explain this point in another application paper instead of in this paper.
3. We have also carefully read the manuscript and made many minor changes in the whole manuscript to improving its readability and accuracy of expression.

Hope you will find our revision and responses satisfactory.

Yiqi Luo

On behalf of all the authors

Dear Referee 1:

We greatly appreciate your comments on our manuscript. We have carefully studied your comments and revised the manuscript accordingly.

Hope you will find our revision and responses satisfactory.

Yiqi Luo  
On behalf of all the authors

Below we list our point-to-point responses to your comments:

[Comment] General remarks:

The authors present a paper showing that a matrix equation can replicate the output of a comprehensive carbon cycle model. In particular they find that the force driving the ecosystem C storage is the C storage capacity. In general the article is well written and organized and fits into the scope of the journal. Using such a simple matrix equation as a physical emulator of comprehensive models has the potential to save a lot of computing time and gains a deeper understanding of the underlying mechanisms. The authors state in their summary that this would revolutionize model evaluations.

[Response] Thanks for the positive comment.

[Comment] I have some concern about this: The matrix equation has to be fitted to a simulation of the complex model with a specified fixed climate scenario. It would be interesting to know whether this parameter set can be used for a different climate scenario. In particular some parameters in the matrix equation are time-dependent and this time-dependence might change for different climate scenarios. Then the complex model can really be replaced by the matrix equation. Otherwise the matrix equation allows only a more convenient analysis of the model output. Non-linearities in the complex model might lead to a deviation from the linearized matrix representation. It would be nice if the authors could comment on that.

[Response] The physical emulator does not result from fitting the model to simulation of the complex model. It generates by organizing the carbon balance equations in the original model into a matrix form. So the physical emulator is not climate scenario-specific. Once developed, it is applicable to all climate scenarios.

We have revised the manuscript to clarify this point. For example, we revised the title of section 2.2 to be “**TECO Model, its physical emulator, and numerical experiments**”. We completely rewrote the third paragraph in that section to describe how we have developed the physical emulator of TECO in detail as:

“To support the mathematical analysis using eq. 1, we first developed a physical emulator (i.e., the matrix representation of eq. 1) of the TECO model and then verified that the physical emulator can exactly represent simulations of the original TECO model. We first identified those parameter values in each of the C balance equations in the TECO model that are corresponding

to elements in matrices  $A$  and  $K$  in eq. 1. The time-dependent variables for  $u(t)$ , elements in vector  $B$ , and elements in matrix  $\xi(t)$  in the physical emulator were directly from outputs of the original TECO model. Then those parameter values and time-dependent variables were organized into matrices  $A$ ,  $\xi(t)$ , and  $K$ ; vectors  $X(t)$ ,  $X_0$ , and  $B$ ; and variable  $u(t)$ . Note that values of  $u(t)$ ,  $B$ , and  $\xi(t)$  could be different among different climate scenarios. Those matrices, vectors, and variable were entered to matrix calculation to compute  $X'(t)$  using eq. 1. The sum of elements in calculated  $X'(t)$  is a 100% match with simulated net ecosystem production (NEP) with the TECO model (Fig. 1b).”

Hope this paragraph explains the physical emulator clearly. In addition, we added section **6 Code availability** on page 31 and provided a webpage link to both the TECO model and its physical emulator for verification and uses.

[Comment] More specific remarks:

Abstract: The authors are talking about a 3-D parameter space. These 3 parameters, however, are not simple scalars, but are itself vectors (e.g., residence time and storage potential).

[Response] we add elements of the vectors together to get the scalars before we plotted the 3D parameter space. We clarified this point in several places in the manuscript. For example,

One paragraph on page 14 (lines 303-306) on this point is:

“Note that sums of elements in vectors  $X(t)$ ,  $X_c(t)$ ,  $X_p(t)$ , and  $X'(t)$  are corresponding, respectively, to the whole ecosystem C stock, ecosystem C storage capacity, ecosystem C storage potential, and net ecosystem production (NEP). In this paper, we do not use a separate set of symbols to represent those sums rather than express them wherever necessary. ”

Also, the legend of Figure 1 explains this point:

“Panel b compares the original TECO model outputs with those from matrix equations for net ecosystem production (NEP = the sum of elements in  $X'(t)$  from eq. 1).” “Panel c compares the original TECO model outputs with those from matrix equations for ecosystem C storage (= the sum of elements in  $X(t)$  from eq. 2).”

[Comment] Page 4: The authors state that most carbon cycle models follow a mathematical formulation of ordinary differential equations. Many of the dynamic global vegetation models (DGVM) are ab initio formulated as a time discrete model calculating, e.g., NPP on a daily level and carbon allocation to different vegetation pools on annually using some (non-linear) allocation rules. Moreover, the authors should mention these DGVMs.

[Response] Thanks for the comments. It is not very clear with “are ab initio formulated.” That leaves some uncertainty about our understanding of this comment. Nevertheless, the time steps of NPP calculation and allocation do not affect Eq. 1. Indeed, eq. 1 is mainly about C transformation within land ecosystems before the carbon is respired. NPP is input of eq. 1.

We have successfully applied Eqs. 1 and 2 to LPJ-GUESS, a DGVM, as described in line 581.

[Comment] Page 9: The authors should describe which algorithms are necessary in order to develop the matrix equation from the output of the TECO model. In particular how they determined matrix  $A$  and  $K$ .

[Response] We wrote the physical emulator of the TECO model in matlab. But it can be developed in any other computer language. Basically, we have to understand the original model and identify those carbon balance equations. Then we organize those coefficients and parameters in matrix forms to develop the physical emulator. See our responses to your comment on emulator above. We have completely revised the paragraph in Section 2.2 to describe how we developed the physical emulator of the TECO model.

We also described the physical emulator in paragraph on pages 26-27. Specifically, lines 585-588 state “the physical emulators differ for different models as the elements of each matrix could be differently parameterized or formulized in different models. Also, different models usually have different pool-flux structures, leading to different non-zero elements in the  $A$  matrix.”

[Comment] Technical comment:  
Page 29, line 586: A “to” is missing: The emulators allow us TO analyze: : :

[Response] Corrected as suggested.

[Comment] In summary the article is suitable for publication if the above-mentioned comments are incorporated.

[Response] Thank the referee for the support.

Dear Referee 2:

We greatly appreciate your time and effort to read, understand, and make comments on our manuscript. We have carefully studied your comments and revised the manuscript accordingly. Hope our responses have adequately addressed your concerns so that we can develop mutual understanding about your concerns and about what we present in the paper.

Please note the line numbers and pages numbers in this letter are all refereed in the revised, marked-up manuscript.

Yiqi Luo  
On behalf of all the authors

Below we list our point-to-point responses to your (i.e., referee 2 in this case) comments:

[Comment] In spite of words “mathematical foundation” in the title, the first mistake is contained directly in the first formula (1). Let’s rewrite it in the component form:

$$\begin{pmatrix} X_1' \\ \dots \\ X_n' \end{pmatrix} = \begin{pmatrix} B_1 \\ \dots \\ B_n \end{pmatrix} u(t) - \begin{pmatrix} A_{11} & \dots & A_{1n} \\ \dots & \dots & \dots \\ A_{n1} & \dots & A_{nn} \end{pmatrix} \begin{pmatrix} \xi_1 & 0 & 0 \\ 0 & \dots & 0 \\ 0 & 0 & \xi_n \end{pmatrix} \begin{pmatrix} K_1 & 0 & 0 \\ 0 & \dots & 0 \\ 0 & 0 & K_n \end{pmatrix} \begin{pmatrix} X_1 \\ \dots \\ X_n \end{pmatrix} \quad (1)$$

and see that in this notation all off-diagonal elements of matrix  $A$  are useless, and the system (1) is simply a set of trivial linear equations for disconnected variables. Do the authors know that matrix multiplication is non-commutative? My hypothesis is that the matrix  $A$  should be stated after other multipliers in the second member of the sum:

$$X'(t) = Bu(t) - \xi K A X(t)$$

Such a formula is at least mathematically correct and allows the following component view:

$$\begin{pmatrix} X_1' \\ \dots \\ X_n' \end{pmatrix} = u(t) \begin{pmatrix} B_1 \\ \dots \\ B_n \end{pmatrix} - \begin{pmatrix} \xi_1 & 0 & 0 \\ 0 & \dots & 0 \\ 0 & 0 & \xi_n \end{pmatrix} \begin{pmatrix} K_1 & 0 & 0 \\ 0 & \dots & 0 \\ 0 & 0 & K_n \end{pmatrix} \begin{pmatrix} A_{11} & \dots & A_{1n} \\ \dots & \dots & \dots \\ A_{n1} & \dots & A_{nn} \end{pmatrix} \begin{pmatrix} X_1 \\ \dots \\ X_n \end{pmatrix} \quad (1-a)$$

Consequently all next formulas should be corrected according to the new form of (1). It’s completely unclear why “all off-diagonal values  $a_{ji}$  are negative” (page 8).

[Response] We are grateful to you for your time and effort to examine mathematical formulas. We agree with you that it is critical to make sure the mathematical expression of biological processes should be correct before we do any analysis.

Your comment prompted us to carefully re-examine the equation. After the multiplication of  $\xi$ ,  $K$  and  $A$ , Equation 1 becomes:

$$\begin{bmatrix} X'_1 \\ X'_2 \\ \dots \\ X'_n \end{bmatrix} = \begin{bmatrix} B_1 \\ B_2 \\ \dots \\ B_n \end{bmatrix} u(t) - \begin{bmatrix} A_{11}\xi_1K_1 & A_{12}\xi_2K_2 & \dots & A_{1n}\xi_nK_n \\ A_{21}\xi_1K_1 & A_{22}\xi_2K_2 & \dots & A_{2n}\xi_nK_n \\ \dots & \dots & \dots & \dots \\ A_{n1}\xi_1K_1 & A_{n2}\xi_2K_2 & \dots & A_{nn}\xi_nK_n \end{bmatrix} \begin{bmatrix} X_1 \\ X_2 \\ \dots \\ X_n \end{bmatrix}$$

Then the carbon dynamics in pool 1 will be described by:

$$X'_1 = B_1u(t) - (A_{11}\xi_1K_1X_1 + A_{12}\xi_2K_2X_2 + \dots + A_{1n}\xi_nK_nX_n)$$

The above equation states that change in carbon content in pool 1 equals carbon influx from a fraction of NPP (i.e.,  $u(t)$  times partitioning coefficient  $B_1$ ) minus decomposition expressed by  $(A_{11}\xi_1K_1X_1 + A_{12}\xi_2K_2X_2 + \dots + A_{1n}\xi_nK_nX_n)$ . Since  $K$  is decomposition coefficient, the term  $K_1X_1$  describes that decomposition of carbon in pool 1 equals  $K_1$  times  $X_1$ , so on for  $K_2X_2$ , and  $K_nX_n$ . Environmental scalar  $\xi_i$  modifies its corresponding  $K_i$ . Transfer coefficient  $A_{1j}$  in the above equation describes carbon transfer from pool  $j$  to pool 1. In the real world, no carbon is transferred from other plant, litter, and soil pools to leaf pool. Thus  $A_{1j} = 0, j \neq 1$ .

However, not all  $A_{ij} = 0, j \neq i$ . In TECO model with carbon transfer pathways as depicted in Figure 1a, there are many zero but several non-zero elements in matrix  $A$  to represent carbon transfers among pools as:

$$A = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ -a_{41} & -a_{42} & -a_{43} & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & -a_{53} & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -a_{64} & -a_{65} & 1 & -a_{67} & -a_{68} \\ 0 & 0 & 0 & 0 & -a_{75} & -a_{76} & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & -a_{86} & -a_{87} & 1 \end{pmatrix}$$

For example,  $A_{41} \neq 0$  as it represents litterfall from leaf pool to litter pool. Some of those non-zero transfer coefficients as represented by  $A_{ij}$  are related to microbial carbon use efficiency.

Let us look at the equation you suggested (i.e., Equation 1-a). After the multiplication of  $\xi$ ,  $K$  and  $A$ , Equation 1-a will become:

$$\begin{bmatrix} X'_1 \\ X'_2 \\ \dots \\ X'_n \end{bmatrix} = u(t) \begin{bmatrix} B_1 \\ B_2 \\ \dots \\ B_n \end{bmatrix} - \begin{bmatrix} A_{11}\xi_1K_1 & A_{12}\xi_2K_2 & \dots & A_{1n}\xi_nK_n \\ A_{21}\xi_1K_1 & A_{22}\xi_2K_2 & \dots & A_{2n}\xi_nK_n \\ \dots & \dots & \dots & \dots \\ A_{n1}\xi_nK_n & A_{n2}\xi_nK_n & \dots & A_{nn}\xi_nK_n \end{bmatrix} \begin{bmatrix} X_1 \\ X_2 \\ \dots \\ X_n \end{bmatrix}$$

and the carbon dynamics in pool 1 will be described by:

$$X'_1 = B_1 u(t) - (A_{11}\xi_1 K_1 X_1 + A_{12}\xi_1 K_1 X_2 + \dots + A_{1n}\xi_1 K_1 X_n)$$

In the above equation, the term  $K_1 X_2$  or  $K_1 X_n$  biologically does not make sense as it describes the decomposition of carbon in pool 2 by coefficient  $K_1$ . The latter describes the relative rate of decomposition of pool 1. Nor does  $K_1 X_n$  biologically make sense.

Thus, we hope that you can see that our original equation still works.

The statement “all off-diagonal values  $a_{ji}$  are negative” (page 9) because carbon transfer from pool  $i$  to pool  $j$  to be positive by having negative coefficient multiplied with negative sign for this term. We have clarified this point by revising the sentences on line 175-176 as:

“In eq. 1, all the off-diagonal  $a_{ji}$  values are negative to reverse the minus sign and indicate positive C influx to the receiving pools”

[Comment] But the more essential question is concerned to its biological correctness and sense. According to (1, 1-a) matrix  $A$  consists of transfer coefficients and does not depend on system variables  $X$  making all the system non-autonomous and linear. There is no biological foundation for such strong universality of the form (1, 1-a) for all temporal and spatial scales and no mathematical proof in the paper. In particular, it's not clear how mass-balance relations are connected with that form.

[Response] Thanks for your question about the biological basis of the mathematical equation. The two paragraphs from line 143 to 161 describe the biological basis as below:

“Hundreds of models have been developed to simulate terrestrial C cycle (Manzoni and Porporato, 2009). All the models have to simulate processes of photosynthetic C input, C allocation and transformation, and respiratory C loss. It is well understood that photosynthesis is a primary pathway of C flow into land ecosystems. Photosynthetic C input is usually simulated according to carboxylation and electron transport rates (Farquhar et al., 1980). Ecosystem C influx varies with time and space mainly due to variations in leaf photosynthetic capacity, leaf area index of canopy, and a suite of environmental factors such as temperature, radiation, and relative humidity (or other water-related variables) (Potter et al., 1993; Sellers et al., 1996; Keenan et al., 2012; Walker et al., 2014, Parolari and Porporato 2016).

Photosynthetically assimilated C is partly used for plant biomass growth and partly released back into the atmosphere through plant respiration. Plant biomass in leaves and fine roots usually lives for several months up to a few years before death, while woody tissues may persist for hundreds of years in forests. Dead plant materials are transferred to litter pools and decomposed by microorganisms to be partially released through heterotrophic respiration and partially stabilized to form soil organic matter (SOM). SOM can store C in the soil for hundreds or thousands of years before it is broken down to  $\text{CO}_2$  through microbial respiration (Luo and Zhou, 2006). This series of C cycle processes has been represented in most ecosystem models with multiple pools linked by C transfers among them (Jenkinson et al., 1987; Parton et al., 1987; 1988; 1993), including those embedded in Earth system models (Ciais et al., 2013). “

Moreover, we have conducted many synthesis studies to examine different aspects of the

biological basis. The carbon input via canopy photosynthesis as described by  $\begin{bmatrix} B_1 \\ B_2 \\ \dots \\ B_n \end{bmatrix} u(t)$  has been

well accepted. Scientists in the community have questioned carbon transformation through  $A\xi KX$  in equation 1. We examine six assumptions of those carbon cycle models and the validity of our analysis in section 4.1 on pages 19-23. We would be happy to answer any specific questions you would have regarding those assumptions.

[Comment] Page 9 gives us an example of a risky statements made in the paper. Authors say that almost all world models of carbon cycle in terrestrial ecosystems have the form (1). They refer to the work (Manzoni, Porporato, 2009) and state that there is a review of 250 models of carbon cycling in it ! First, Table A2 in this work has 200 references to papers describing different versions of a smaller number of models. Second, I have a very strong doubt that all of them can be presented in the form (1) because they were made for various time scales, different set of compartments and different details of biogeochemical processes accounted for. Interesting is the fact that the model of Manzoni and Porporato (2009) themselves is nonlinear and does not look like the system (1) ! As well as another model of soil organic carbon and microbial dynamics made by Hararuk et al. (2015) also referred to by the authors !

[Response] Thanks for your comment. We agree with you that the nonlinear microbial models by Manzoni and Porporato (2009) or Hararuk et al. (2015) could not be represented by equation 1. This issue is pointed out in section 4.1 regarding those microbial models (i.e., assumption 1). We also pointed out that thousands of datasets we have reviewed do not seem to support those nonlinear microbial models as described on pages 19-20. Paper by Sierra and Müller (2015) also stated that most of the land carbon cycle models can be represented by equation 1.

Indeed, we have worked with many modeling groups and organized those carbon balance equations in their models into the matrix equations. It has been demonstraed that the matrix equation can represent those original models well as described in paragraph from lines 580-592. Please see another publication by Ahlström et al. (2015) with LPJ-GUESS for the application of eq. 1.

[Comment] In part 2.2 (pages 9-11) authors carry out comparison of the TECO terrestrial ecosystem model results and the system (1) calculations. Their statement on a 100% match of NEE calculations for TECO and (1) seem strange. If TECO is independent of the system (1) this is unbelievable result, in the opposite case the comparison has no sense.

[Response] This is the case. We organized those carbon balance equations of TECO into the matrix equation, eq. 1. Dynamics of eq. 1 should be mathematically equivalent to TECO outputs. However, they might be mismatch due to the errors from numerical simulations. Therefore, we run the matrix equation to verify that the physical emulator can exactly represent simulation outputs from the original TECO model. We have done that with CABLE (Xia et al. 2012, 2013), CLM3.5 (Rafiquee et al. 2016), CLM4.5 (Shi et al. in prep.), BEPS (Chen et al. 2016), and LPJ-GUESS (Ahlström et al. 2015). In all the cases, the matrix equation can reproduce simulations of those original models. In this paper, the matrix equation can 100% match NEP simulation, but minor mismatch in estimated C storage.



[Comment] Introducing two new definitions – the C storage capacity and C storage potential – could be a good idea of this paper if authors would explain their biological interpretation and mathematical correctness. First, we should make correspondence to (1-a) and note that

$\tau_{ch} = (\xi KA)^{-1}$  instead of (3). Second, study of existence for this inverse matrix is needed to state mathematical correctness of these definitions because inverse matrix serves as a foundation for all math terms in the following text. There is no such study in the paper. Another question arises about chasing time  $\tau_{ch}$ : why it's formula  $\tau_{ch} = (\xi KA)^{-1}$  should have physical dimension of time? There are no explanations in the text.

[Response] The biological interpretation of C storage capacity is given in Abstract (Lines 42-50), Results (lines 271-278), Discussion section 4.2, and Conclusions. For example, sentences on lines 638-641 in the Conclusion section state:

“The capacity, which is the product of C input and residence time, represents their instantaneous responses to a state of external forcing at a given time. Thus, the C storage capacity quantifies the maximum amount of C that an ecosystem can store at the given environmental condition at a point of time.”

Similarly, C storage potential is also biologically explained in Abstract, Results, Discussion, and Conclusions sections. For example, the first paragraph in section 4.3 is:

“The C storage potential represents the internal capability to equilibrate the current C storage with the capacity. Biogeochemically, the C storage potential represents re-distribution of net C pool change,  $X'(t)$ , of individual pools through a network of pools with different residence times as connected by C transfers from one pool to the others through all the pathways. The potential is conceptually equivalent to the magnitude of disequilibrium as discussed by Luo and Weng (2011).”

Thanks for your comment. We have added the time dimension for chasing time on lines 251-252 as:

“In eq. 2, we name the term  $(A\xi(t)K)^{-1}$  the chasing time,  $\tau_{ch}(t)$ , with a time unit used in exit rate  $K$ .”

[Comment] All inputs in the model (1) are supposed constant or time-dependent. In particular on page 15 plant photosynthesis is declared only time-dependent. But for some temporal scales (a year, for example) it can essentially dependent on the plant carbon content and in that case the model (1) should have another form (Parolari, Porporato, 2016).

#### Reference

Parolari A., Porporato A., Forest soil carbon and nitrogen cycles under biomass harvest: stability, transient response, and feedback. // *Ecological Modelling*, v. 329, 2016, pp. 64-76.

[Response] We have carefully studied the paper by Parolari and Porporato (2016), particularly

that paragraph on NPP on page 66. That study differentiated the productivity regime into C-limited and N-limited. The C-limit regime accounts for limitation of light, temperature and moisture whereas the N-limited regime accounts for nitrogen limitation. Both of the regimes have been discussed in relation with eq. 1. Please see sentences on lines 147-151 and lines 474-475 for more explanation. In the revised manuscript, we cited the paper and explained those environmental factors as represented by scalars on line 151.

[Comment] Therefore, since all other formulas and descriptions are based on the terms introduced above with mistakes as well as statements made without sufficient biological basis, the conclusion at page 25 (part 4.4, first sentence) about novel approach suggested by the authors to understand, evaluate, diagnose and improve carbon cycle models is represented as inadequate and seems early and premature.

[Response] We hope our responses to your comments above can help us communicate well with you and then gain mutual understanding on what we presented in this paper and what you were concerned.

We thank you for the valuable comments, some of which led us to improve the text and better communicate our points to the reader. We hope our responses above also demonstrate that our formulation did not include mistakes and that the terms we introduced were founded on sound biological principles. Thus, we stand by our conclusion that the presented approach enables one to understand, evaluate, diagnose and improve carbon cycles models.

Dear M. Freilich, maraf@mit.edu:

We greatly appreciate your comments on our manuscript. We have carefully studied your comments and revised the manuscript accordingly. Please note the line numbers and pages numbers in this letter are all refereed in the revised, marked-up manuscript.

Hope you will find our revision and responses satisfactory.

Yiqi Luo  
On behalf of all the authors

Below we list our point-to-point responses to your comments:

[Comment] Luo et al provide an excellent mathematical framework for studying the dynamics of the carbon cycle in terrestrial ecosystems. The focus on transient dynamics makes clear which aspects of carbon storage and sequestration are most important to consider in order to understand the functioning of forests are carbon reservoirs. The reduction of the models to a 3D parameter space is seemingly very useful for a mechanistic understanding of the effects of global change on terrestrial carbon storage.

[Response] We greatly appreciate your positive comments.

[Comment] The modeling assumptions could use further clarification. In particular, the assumption that short-term disturbances can be well represented by the matrix equation (assumption 5) and the assertion that this assumption is unlikely to affect the results need further support. Disturbances may be very important for the carbon cycling of terrestrial systems and can affect ecosystem dynamics and carbon cycling for decades, in addition to causing C fluxes that greatly exceed those from annual cycles.

[Response] We agree. Disturbances can substantially affect ecosystem carbon cycling

[Comment] Presumably, disturbance events could be incorporated in the time varying factors  $u(t)$  and  $_ (t)$ . However, there are a number of well-developed non-linear models for pest outbreaks that might violate the assumption that transfer between pools can be represented by a linear model (assumption 1) if outbreaks were to be incorporated into these factors.

[Response] We appreciate for your point that there are many non-linear models for pest outbreaks. Pest outbreaks affect tree mortality, which usually is in proportion to the severity of pest outbreaks. Tree mortality can be non-linearly responding to pest outbreaks as decomposition of soil organic carbon to temperature. Such non-linear responses still do not affect fundamental properties of the carbon cycle as discussed in Assumption 4 on response functions.

[Comment] While one aspect of pest outbreaks is a reduction in GPP or NPP, which may be sufficiently represented by  $u(t)$ , even a linear approximation of the rapid change in the transfer of biomass between classes cannot be represented by this model without making the matrix A of transfer coefficients also time-dependent. One way this may be overcome is by setting limits on

the timescale of applicability of this mathematical framework, so as to assume that transfer coefficients are not changing. Further, abiotic disturbances such as fire or disturbances that remove carbon from the ecosystem completely such as harvesting would be outside the scope of this model.

[Response] Matrix A can be time-dependent. Equation 1 does not explicitly include abiotic disturbances in influencing carbon cycle. Weng et al. (2012) developed a disturbance regime model that explicitly incorporates disturbances into equation 1 for their influences of terrestrial carbon cycle. This paper focuses on understanding of fundamental properties of equation 1.

To clarify this point, we have revised the second half of the paragraph on Assumption 5 (lines 485-490) as:

“Those disturbance influences can be represented in terrestrial C cycle models through changes in parameter values, environmental scalars, and/or discrete C transfers among pools of eq. 1 (Luo and Weng 2011). While eq. 1 does not explicitly incorporate disturbances for their influences on land C cycle, Weng et al. (2012) developed a disturbance regime model that combines eq. 1 with frequency distributions of disturbance severity and intervals to quantify net biome exchanges.”

[Comment] The authors show that  $X'(t)$  in this model is the net ecosystem production (NEP), but non-biotic transformation from organic and inorganic carbon is not included in NEP, nor is transfer between ecosystems. This may just require a clarification of terminology in order to include fire, other abiotic oxidation, and harvesting in the  $_-(t)$  term of the model.

[Response] Yes, you are very sharp to point out the omission of this analysis. We did not explicitly include disturbances in the analysis but state that disturbances do not alter fundamental properties of the system. As explained above, Weng et al. (2012) developed a model that explicitly combines disturbances with equation 1 to quantify net biome production on lines 488-490.

[Comment] Finally, it may be useful to clarify on what scale the results apply. Based on the assumptions about linear decay smoothing small scale fluctuations and the neglect of lateral C fluxes, it seems important to point out that this is model applies only at the ecosystem scale. The parameters are calibrated based on one grid cell of the TECO model; would the same procedure be expected to scale up to larger spatial scales?

[Response] Thanks for your comment. Equation 1 has been also applied to several global models, such as National Center for Atmosphere Research (NCAR) Community Land Model (CLM) and LPJ-GUESS. See a published paper by Ahlström et al. (2015) for the application of equation to the global model LPJ-GUESS. Fundamentally equation 1 fully represents carbon balance equations in matrix form for almost all the land carbon cycle models. Equation 1 does not do any more smoothing of small-scale fluctuations than do the original models. The paragraph on pages 26-27 about physical emulators explains it.

Yes, equation 1 does not apply to the models with lateral fluxes.

[Comment] In the conclusion, the authors state that this model is consistent with complex dynamics including tipping points, which they say are “caused by multiple environmental forcing variables interacting with relatively simple internal processes over different temporal and spatial scales.” Tipping point behavior crucially depends on non-linear dynamics and so seems inconsistent with this model. However, a clarification that this method can evaluate the transient dynamics in a given state but does not reproduce more complex behavior may be more accurate.

[Response] You are right that the eq. 1 does not cause some of the complex dynamics such as tipping points. Tipping points occur in carbon cycle mainly due to complex behaviors in external forcings. Luo and Weng (2011) and Luo et al. (2015) have explained this phenomenon in detail. While this paper could not explain this in detail again, we revised the manuscript by pointing readers to those papers for detailed discussion as on pages 29-30:

“The two components of land C storage dynamics represent interactions of external forces (via changes in the capacity) and internal capability of the land C cycle (via changes in the C storage potential) to generate complex phenomena of C cycle dynamics, such as fluctuations, directional changes, and tipping points, in the terrestrial ecosystems. From a system perspective, these complex phenomena could not be generated by relatively simple internal processes but are mostly caused by multiple environmental forcing variables interacting with internal processes over different temporal and spatial scales as explained by Luo and Weng (2011) and Luo et al. (2015). Note that while those internal processes can be mathematically represented with a relatively simple formula, their ecological and biological underpinnings can be very complex.”

1 **Transient Dynamics of Terrestrial Carbon Storage: Mathematical foundation and [its](#)**  
2 **[applications](#)**  
3

Yiqi Luo 11/20/2016 10:57 PM

Deleted: Numeric Example

4 Yiqi Luo<sup>1,2</sup>, Zheng Shi<sup>1</sup>, Xingjie Lu<sup>3</sup>, Jianyang Xia<sup>4</sup>, Junyi Liang<sup>1</sup>, Jiang Jiang<sup>1</sup>, Ying Wang<sup>5</sup>,  
5 Matthew J. Smith<sup>6</sup>, Lifan Jiang<sup>1</sup>, Anders Ahlström<sup>7,8</sup>, Benito Chen<sup>9</sup>, Oleksandra Hararuk<sup>10</sup>, Alan  
6 Hastings<sup>11</sup>, Forrest Hoffman<sup>12</sup>, Belinda Medlyn<sup>13</sup>, Shuli Niu<sup>14</sup>, Martin Rasmussen<sup>15</sup>, Katherine  
7 Todd-Brown<sup>16</sup>, Ying-Ping Wang<sup>3</sup>

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30 **Running Title:** Land carbon storage dynamics

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40 | **Abstract** Terrestrial ecosystems have absorbed roughly 30% of anthropogenic CO<sub>2</sub> emissions  
41 | over the past decades, but it is unclear whether this carbon (C) sink will endure into the future.  
42 | Despite extensive modeling, experimental, and observational studies, what fundamentally  
43 | determines transient dynamics of terrestrial C storage under global change is still not very clear.  
44 | Here we develop a new framework for understanding transient dynamics of terrestrial C storage  
45 | through mathematical analysis and numerical experiments. Our analysis indicates that the  
46 | ultimate force driving ecosystem C storage change is the C storage capacity, which is jointly  
47 | determined by ecosystem C input (e.g., net primary production, NPP) and residence time. Since  
48 | both C input and residence time vary with time, the C storage capacity is time-dependent and  
49 | acts as a moving attractor that actual C storage chases. The rate of change in C storage is  
50 | proportional to the C storage potential, the difference between the current storage and the storage  
51 | capacity. The C storage capacity represents instantaneous responses of the land C cycle to  
52 | external forcing, whereas the C storage potential represents the internal capability of the land C  
53 | cycle to influence the C change trajectory in the next time step. The influence happens through  
54 | redistribution of net C pool changes in a network of pools with different residence times.

55 | Moreover, this and our other studies have demonstrated that one matrix equation can  
56 | exactly replicate simulations of most land C cycle models (i.e., physical emulators). As a result,  
57 | simulation outputs of those models can be placed into a three-dimensional (3D) parameter space  
58 | to measure their differences. The latter can be decomposed into traceable components to track  
59 | the origins of model uncertainty. In addition, the physical emulators make data assimilation  
60 | computationally feasible so that both C flux- and pool-related datasets can be used to better  
61 | constrain model predictions of land C sequestration. Overall, this new mathematical framework  
62 | offers new approaches to understand, evaluate, diagnose, and improve land C cycle models.

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70 **1 Introduction**

71 Terrestrial ecosystems have been estimated to sequester approximately 30% of anthropogenic  
72 carbon (C) emission in the past three decades (Canadell et al., 2007). Cumulatively, land  
73 ecosystems have sequestered more than 160 Gt C from 1750 to 2015 (Le Quéré et al., 2015).  
74 Without land C sequestration, the atmospheric CO<sub>2</sub> concentration would have increased by  
75 additional 95 parts per million and result in more climate warming (Le Quéré et al., 2015).  
76 During one decade from 2005 to 2014, terrestrial ecosystems sequestered 3±0.8 Gt C per year  
77 (Le Quéré et al., 2015), which would cost billion dollars if the equivalent amount of C was  
78 sequestered using C capture and storage techniques (Smith et al., 2016). Thus, terrestrial  
79 ecosystems effectively mitigate global change through natural processes with minimal cost.  
80 Whether this terrestrial C sequestration would endure into the future, however, is not clear,  
81 making the mitigation of global change greatly uncertain. To predict future trajectories of C  
82 sequestration in the terrestrial ecosystems, it is essential to understand fundamental mechanisms  
83 that drive terrestrial C storage dynamics.

84 To predict future land C sequestration, the modeling community has developed many C  
85 cycle models. According to a review by Manzoni and Porporato (2009), approximately 250  
86 biogeochemical models have been published over a time span of 80 years to describe carbon and  
87 nitrogen mineralization. The majority of those 250 models follow some mathematical  
88 formulations of ordinary differential equations. Moreover, many of those biogeochemical models  
89 incorporate more and more processes in an attempt to simulate C cycle processes as realistically  
90 as possible (Oleson et al., 2013). As a consequence, terrestrial C cycle models have become  
91 increasingly complicated and less tractable. Almost all model intercomparison projects (MIPs),  
92 including those involved in the last three IPCC assessments, indicate that C cycle models have

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95 | consistently projected widely spread trajectories of land C sinks and were also found to fit  
96 | observations poorly (Todd-Brown et al., 2013; Luo et al., 2015). The lack of progress in  
97 | uncertainty analysis urges us to understand mathematical foundation of those terrestrial C models  
98 | so as to diagnose causes of model spreads and improve model predictive skills.

99 |         Meanwhile, many countries have made great investments on various observational and  
100 | experimental networks (or platforms) in hope to quantify terrestrial C sequestration. For  
101 | example, FLUXNET has been established about 20 years ago to quantify net ecosystem  
102 | exchange (NEE) between the atmosphere and biosphere (Baldocchi et al., 2001). Orbiting  
103 | Carbon Observatory 2 (OCO-2) satellite was launched in 2014 to quantify carbon dioxide  
104 | concentrations and distributions in the atmosphere at high spatiotemporal resolution to constrain  
105 | land surface C sequestration (Hammerling et al., 2012). Networks of global change experiments  
106 | have been designed to uncover processes that regulate ecosystem C sequestration (Rustad et al.,  
107 | 2001; Luo et al., 2011; Fraser et al., 2013; Borer et al., 2014). Massive data have been generated  
108 | from those observational systems and experimental networks. They offer an unprecedented  
109 | opportunity for advancing our understanding of ecosystem processes and constraining model  
110 | prediction of ecosystem C sequestration. Indeed, many of those networks were initiated with one  
111 | goal to improve our predictive capability. Yet the massive data have been rarely integrated into  
112 | earth system models to constrain their predictions. It is a grand challenge in our era to develop  
113 | innovative approaches to integration of big data into complex models so as to improve prediction  
114 | of future ecosystem C sequestration.

115 |         From a system perspective, ecosystem C sequestration occurs only when the terrestrial C  
116 | cycle is in a transient state, under which C influx into one ecosystem is larger than C efflux from  
117 | the ecosystem. Olson (1963) is probably among the first to examine organic matter storage in

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120 forest floors from the system perspective. His analysis approximated steady-state storage of  
121 organic matter as a balance of litter producers and decomposers for different forest types.  
122 However, global change differentially influences various C cycle processes in ecosystems and  
123 results in transient dynamics of terrestrial C storage (Luo and Weng, 2011). For example, rising  
124 atmospheric CO<sub>2</sub> concentration primarily stimulates photosynthetic C uptake while climate  
125 warming likely enhances decomposition. When ecosystem C uptake increases in a unidirectional  
126 trend under elevated [CO<sub>2</sub>], terrestrial C cycle is at disequilibrium, leading to net C storage. The  
127 net gained C is first distributed to different pools, each of which has a different turnover rate (or  
128 residence time) before C is eventually released back to the atmosphere via respiration.  
129 Distribution of net C exchange to multiple pools with different residence times is an intrinsic  
130 property of an ecosystem to gradually equalize C efflux with influx (i.e. internal recovery force  
131 toward an attractor). In contrast, global change factors that causes changes in C input and  
132 decomposition is considered external forces that create disequilibrium through altering internal C  
133 processes and pool sizes. The transient dynamics of terrestrial C cycle at disequilibrium is  
134 maintained by interactions of internal processes and external forces (Luo and Weng, 2011).  
135 Although the transient dynamics of terrestrial C storage have been conceptually discussed, we  
136 still lack a quantitative formulation to estimate transient C storage dynamics in the terrestrial  
137 ecosystems.

138 This paper was designed to address a question: what determines transient dynamics of C  
139 storage in terrestrial ecosystems from a system perspective? We first reviewed the major  
140 processes that most models have incorporated to simulate terrestrial C sequestration. The review  
141 helps establish that terrestrial C cycle can be mathematically represented by a matrix equation.  
142 We also described the Terrestrial ECOsystem (TECO) model with its numerical experiments in

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146 support of the mathematical analysis. We then presented results of mathematical analysis on  
147 determinants of the terrestrial C storage, direction and magnitude of C storage at a given time  
148 point, [and](#) numerical experiments to illustrate climate impacts on terrestrial C storage. We  
149 carefully discussed assumptions of those terrestrial C cycle models as represented by the matrix  
150 equation, the validity of this analysis, and two new concepts introduced in this study, which are  
151 the C storage capacity and C storage potential. We also discussed the potential applications of  
152 this analysis to model uncertainty analysis and data-model integration. Moreover, we proposed  
153 that the C storage potential be a targeted variable for research, trading, and government  
154 negotiation for C credit.

155

## 156 **2 Methods**

### 157 **2.1 Mathematical representation of terrestrial C cycle**

158 This study was conducted mainly with mathematical analysis. We first established the basis of  
159 this analysis, which is that the majority of terrestrial C cycle models can be represented by a  
160 matrix equation.

161        Hundreds of models have been developed to simulate terrestrial C cycle (Manzoni and  
162 Porporato, 2009). All the models have to simulate processes of photosynthetic C input, C  
163 allocation and transformation, and respiratory C loss. It is well understood that photosynthesis is  
164 a primary pathway of C flow into land ecosystems. Photosynthetic C input is usually simulated  
165 according to carboxylation and electron transport rates (Farquhar et al., 1980). Ecosystem C  
166 influx varies with time and space mainly due to variations in leaf photosynthetic capacity, leaf  
167 area index of canopy, and a suite of environmental factors such as temperature, radiation, and  
168 relative humidity (or other water-related variables) (Potter et al., 1993; Sellers et al., 1996;

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169 Keenan et al., 2012; Walker et al., 2014, [Parolari and Porporato 2016](#)).

170 Photosynthetically assimilated C is partly used for plant biomass growth and partly

171 released back into the atmosphere through plant respiration. Plant biomass in leaves and fine

172 roots usually lives for several months up to a few years before death, while woody tissues may

173 persist for hundreds of years in forests. Dead plant materials are transferred to litter pools and

174 decomposed by microorganisms to be partially released through heterotrophic respiration and

175 partially stabilized to form soil organic matter (SOM). SOM can store C in the soil for hundreds

176 or thousands of years before it is broken down to CO<sub>2</sub> through microbial respiration (Luo and

177 Zhou, 2006). This series of C cycle processes has been represented in most ecosystem models

178 with multiple pools linked by C transfers among them (Jenkinson et al., 1987; Parton et al., 1987;

179 1988; 1993), including those embedded in [Earth system models](#) (Ciais et al., 2013).

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180 The majority of the published 250 terrestrial C cycle models use ordinary differential

181 equations to describe C transformation processes among multiple plant, litter, and soil pools

182 (Manzoni and Porporato, 2009). Those ordinary differential equations can be summarized into a

183 matrix formula (Luo et al., [2001](#); 2003; Luo and Weng, 2011; Luo et al., 2015; 2016; [Sierra and](#)

184 [Müller 2015](#)) as:

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$$\begin{cases} X'(t) = Bu(t) - A\xi(t)KX(t) \\ X(t=0) = X_0 \end{cases} \quad (1)$$

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185 where  $X'(t)$  is a vector of net C pool changes at time  $t$ ,  $X(t)$  is a vector of pool sizes,  $B$  is a

186 vector of partitioning coefficients from C input to each of the pools,  $u(t)$  is C input rate,  $A$  is a

187 matrix of transfer coefficients (or microbial C use efficiency) to quantify C movement along the

188 pathways,  $K$  is a diagonal matrix of exit rates (mortality for plant pools and decomposition

189 coefficients of litter and soil pools) from donor pools,  $\xi(t)$  is a diagonal matrix of environmental

190 scalars to represent responses of C cycle to changes in temperature, moisture, nutrients, litter

191

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196 quality, and soil texture, and  $X_0$  is a vector of initial values of pool sizes of  $X$ . In eq. 1, all the  
197 off-diagonal elements of matrix  $A$ ,  $a_{ji}$ , are negative to reverse the minus sign and indicate  
198 positive C influx to the receiving pools. The equation describes net C pool change,  $X'(t)$ , as a  
199 difference between C input,  $u(t)$ , distributed to different plant pools via partitioning coefficients,  
200  $B$ , and C loss through the C transformation matrix,  $A\xi(t)K$ , among individual pools,  $X(t)$ .  
201 Elements in vector  $B$ , matrices  $A$  and  $K$  could vary with many factors, such as vegetation types,  
202 soil texture, microbial attributes, and litter chemistry. For example, vegetation succession may  
203 influence elements in vector  $B$ , matrices  $A$  and  $K$  in addition to C input,  $u(t)$ , and forcing that  
204 affects C dynamics through environmental scalars,  $\xi(t)$ .

205 After synthesis of all the possible soil C cycle models based on six principles (mass  
206 balance, substrate dependence of decomposition, heterogeneity of decay rates, internal  
207 transformations of organic matter, environmental variability effects, and substrate interactions),  
208 Sierra and Müller (2015) concluded that this form of matrix equation such as eq. 1 represents the  
209 majority of terrestrial C cycle models. Similarly, Manzoni and Porporato (2009) concluded their  
210 review of 250 models that the majority of them use ordinary differential equations, which can be  
211 summarized by eq. 1, to describe land C cycle. Our mathematical analysis in this study used  
212 matrix operations of eq. 1 to reveal determinants of transient dynamics of terrestrial C cycle,  
213 including direction and rate of C storage changes, in response to global change. We examined  
214 assumptions underlying this equation and the validity of our analysis in the Discussion section.

## 216 2.2 **TECO Model, its physical emulator, and numerical experiments**

217 We conducted numerical experiments to support the mathematical analysis and thus help  
218 understand the characteristics of terrestrial C storage dynamics using the Terrestrial ECOSystem

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226 (TECO) model. TECO has five major components: canopy photosynthesis, soil water dynamics,  
227 plant growth, litter and soil carbon decomposition and transformation, and nitrogen dynamics as  
228 described in detail by Weng and Luo (2008) and Shi et al. (2016). Canopy photosynthesis is  
229 referred from a two-leaf (sunlit and shaded) model developed by Wang and Leuning (1998). This  
230 submodel simulates canopy conductance, photosynthesis, and partitioning of available energy.  
231 The model combines the leaf photosynthesis model developed by Farquhar et al. (1980) and a  
232 stomatal conductance model (Harley et al., 1992). In the soil water dynamic submodel, soil is  
233 divided into 10 layers. The surface layer is 10 cm deep and the other 9 layers are 20 cm deep.  
234 Soil water content (SWC) in each layer results from the mass balance between water influx and  
235 efflux. The plant growth submodel simulates C allocation and phenology. Allocation of C among  
236 three plant pools, which are leaf, fine root, and wood, depends on their growth rates (Fig. 1a).  
237 Phenology dynamics are related to leaf onset, which is triggered by growing degree days, and  
238 leaf senescence, which is determined by temperature and soil moisture. The C transformation  
239 submodel estimates carbon transfer from plants to two litter pools and three soil pools (Fig. 1a).  
240 The nitrogen (N) submodel is fully coupled with C processes with one additional mineral N pool.  
241 Nitrogen is absorbed by plants from mineral soil and then partitioned among leaf, woody tissues  
242 and fine roots. Nitrogen in plant detritus is transferred among different ecosystem pools (i.e.  
243 litter, coarse wood debris, fast, slow and passive SOM) (Shi et al., 2016). The model is driven by  
244 climate data, which include air and soil temperature, vapor-pressure deficit, relative humidity,  
245 incident photosynthetically active radiation, and precipitation at hourly steps.

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246 We first calibrated TECO with eddy flux data collected at Harvard Forest from 2006-  
247 2009. The calibrated model was spun up to the equilibrium state in pre-industrial environmental  
248 conditions by recycling a 10-year climate forcing (1850-1859). Then the model was used to

251 simulate C dynamics from year 1850 to 2100 with the historical forcing scenario for 1850-2005  
252 and RCP8.5 scenario for 2006-2100 as in the Community Land Model 4.5 (Oleson et al., 2013)  
253 in the grid cell where Harvard Forest is located.

254 To support the mathematical analysis using eq. 1, we first developed a physical emulator  
255 (i.e., the matrix representation of eq. 1) of the TECO model and then verified that the physical  
256 emulator can exactly represent simulations of the original TECO model. We first identified those  
257 parameter values in each of the C balance equations in the TECO model that are corresponding  
258 to elements in matrices  $A$  and  $K$  in eq. 1. The time-dependent variables for  $u(t)$ , elements in  
259 vector  $B$ , and elements in matrix  $\xi(t)$  in the physical emulator were directly from outputs of the  
260 original TECO model. Then those parameter values and time-dependent variables were  
261 organized into matrices  $A$ ,  $\xi(t)$ , and  $K$ , vectors  $X(t)$ ,  $X_{0z}$ , and  $B$ , and variable  $u(t)$ . Note that  
262 values of  $u(t)$ ,  $B$ , and  $\xi(t)$  could be different among different climate scenarios. Those matrices,  
263 vectors, and variable were entered to matrix calculation to compute  $X'(t)$  using eq. 1. The sum  
264 of elements in calculated  $X'(t)$  is a 100% match with simulated net ecosystem production (NEP)  
265 with the TECO model (Fig. 1b).

266 Once eq. 1 was verified to exactly replicate TECO simulations, we used TECO to  
267 generate numerical experiments to support the mathematical analysis on the transient dynamics  
268 of terrestrial C storage. To analyze the seasonal patterns of C storage dynamics, we averaged 10  
269 series of three-year seasonal dynamics from 1851-1880. Then we used a 7-day moving window  
270 to further smooth the data.

271  
272 **3. Results**  
273

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288 **3.1 Determinants of C storage dynamics**

289 The transient dynamics of terrestrial carbon storage are determined by two components: the C  
290 storage capacity and the C storage potential. The two components of C storage dynamics can be  
291 mathematically derived from multiplying both sides of eq. 1 by  $(A\xi(t)K)^{-1}$  as:

292 
$$X(t) = (A\xi(t)K)^{-1}Bu(t) - (A\xi(t)K)^{-1}X'(t) \quad (2)$$

293 The first term on the right side of eq. 2 is the C storage capacity and the second term is the C  
294 storage potential. Fig. 2a shows time courses of C storage and its capacity over one year for the  
295 leaf pool of Harvard Forest.

296 In eq. 2, we name the term  $(A\xi(t)K)^{-1}$  the chasing time,  $\tau_{ch}(t)$ , with a time unit used in  
297 exit rate  $K$ . The chasing time is defined as:

298 
$$\tau_{ch}(t) = (A\xi(t)K)^{-1} \quad (3)$$

299  $\tau_{ch}(t)$  is a matrix of C residence times through the network of individual pools each with a  
300 different residence time and fractions of received C connected by pathways of C transfer.

301 Analogous to the fundamental matrix measuring life expectancies in demographic models  
302 (Caswell, 2000), the matrix,  $\tau_{ch}(t)$ , here measures expected residence time of a C atom in pool  $i$   
303 when it has entered from pool  $j$ . We call this matrix the fundamental matrix of chasing times to  
304 represent the time scale at which the net C pool change,  $X'(t)$ , is redistributed in the network.

305 Meanwhile, the residence times of individual pools in network,  $\tau_N(t)$ , can be estimated by  
306 multiplying the fundamental matrix of chasing times,  $(A\xi(t)K)^{-1}$ , with a vector of partitioning  
307 coefficients,  $B$  as:

308 
$$\tau_M(t) = (A\xi(t)K)^{-1}B \quad (4a)$$

309 Ecosystem residence time,  $\tau_E(t)$ , is the sum of the residence time of all individual pools in  
310 network as:

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317  $\tau_E(t) = (1 \ 1 \ \dots \ 1)\tau_N(t)$  (4b)

318 Thus, the C storage capacity can be defined by:

319  $X_C(t) = (A\xi(t)K)^{-1}Bu(t)$  (5a)

320 Or it can be estimated from C input,  $u(t)$ , and residence time,  $\tau_N(t)$ , as:

321  $X_C(t) = \tau_N(t)u(t)$  (5b)

322 As C input (e.g., Gross or Net Primary Productions, GPP or NPP) and residence times vary with  
 323 time, the C storage capacity varies with time. It represents instantaneous responses of the  
 324 terrestrial C cycle to the external forcing. The modeled C storage capacity in the leaf pool (Fig.  
 325 2a), for example, increases in spring, reaches the peak at summer, declines in autumn, and  
 326 becomes minimal in winter largely due to strong seasonal changes in C input (Fig. 2b). Note that  
 327 either GPP or NPP can be used as C input for analysis of transient C dynamics. Estimated  
 328 residence times, however, are smaller with GPP as C input than those with NPP as input. In this  
 329 paper, we mostly used NPP as C input as that fraction of C is distributed among pools.

330 The C storage potential at time  $t$ ,  $X_p(t)$ , can be mathematically described as:

331  $X_p(t) = (A\xi(t)K)^{-1}X'(t)$  (6a)

332 Or it can be estimated from net C pool change,  $X'(t)$ , and chasing time,  $\tau_{ch}(t)$  as:

333  $X_p(t) = \tau_{ch}(t)X'(t)$  (6b)

334 Eqs. 6a and 6b suggest that the C storage potential represents re-distribution of net C pool  
 335 change,  $X'(t)$ , of individual pools through a network of pools with different residence times as  
 336 connected by C transfers from one pool to the others through all the pathways. As time evolves,  
 337 the net C pool change,  $X'(t)$ , is redistributed again and again through the network of pools. The  
 338 network of redistribution of next C pool change, thus, represents the potential of an ecosystem to  
 339 store additional C when it is positive and lose C when it is negative. The C storage potential can

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343 also be estimated from the difference between the C storage capacity and the C storage itself at  
344 time  $t$  as:

$$345 \quad X_p(t) = X_c(t) - X(t) \quad (6c)$$

346 The C storage potential in the leaf pool, for example, is about zero in winter and early spring  
347 when the C storage capacity is very close to the storage itself (Fig. 2a). The C storage potential is  
348 positive when the capacity is larger than the storage itself from late spring to summer and early  
349 fall. As the storage capacity decreases to the point when the storage equals the capacity on the  
350 265<sup>th</sup> day of year (DOY), the C storage potential is zero. After that day, the C storage potential  
351 becomes negative.

352 Dynamics of ecosystem C storage,  $X(t)$ , can be characterized by three parameters: C  
353 influx,  $u(t)$ , residence times,  $\tau_{N_e}(t)$ , and the C storage potential  $X_p(t)$  as:

$$354 \quad X(t) = \tau_{N_e}(t)u(t) - X_p(t) \quad (7)$$

355 Eq. 7 represents a three-dimensional (3D) parameter space within which model simulation  
356 outputs can be placed to measure how and how much they diverge.

357 Note that sums of elements in vectors  $X(t)$ ,  $X_c(t)$ ,  $X_p(t)$ , and  $X'(t)$  are corresponding,  
358 respectively, to the whole ecosystem C stock, ecosystem C storage capacity, ecosystem C storage  
359 potential, and net ecosystem production (NEP). In this paper, we describe them wherever  
360 necessary rather than use a separate set of symbols to represent those sums,

### 362 3.2 Direction and rate of C storage change at a given time

363 Like studying any moving object, quantifying dynamics of land C storage needs to determine  
364 both the direction and the rate of its change at a given time. To determine the direction and rate  
365 of C storage change, we re-arranged eq. 2 to be:

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373 
$$\tau_{ch}X'(t) = X_c(t) - X(t) = X_p(t) \quad (8a)$$

374 or re-arranging eq. 6a leads to:

375 
$$X'(t) = A\xi(t)KX_p(t) \quad (8b)$$

376 As all the elements in  $\tau_{ch}$  are positive, the sign of  $X'(t)$  is the same as for  $X_p(t)$ . That means  
 377  $X'(t)$  increases when  $X_c(t) > X(t)$ , does not change when  $X_c(t) = X(t)$ , and decreases when  
 378  $X_c(t) < X(t)$  at the ecosystem scale. Thus, the C storage capacity,  $X_c(t)$ , is an attractor and  
 379 hence determines the direction toward which the C storage,  $X(t)$ , chases at any given time point.  
 380 The rate of C storage change,  $X'(t)$ , is proportional to  $X_p(t)$  and also regulated by  $\tau_{ch}$ .

381 When we study C cycle dynamics, we are interested in understanding dynamics of **not**  
 382 **only** a whole ecosystem but also individual pools. Eq. 8a can be used to derive equations to  
 383 describe C storage change for an  $i^{\text{th}}$  pool as:

384 
$$\sum_{j=1}^n f_{ij} \tau_i x'_j(t) = \sum_{j=1}^n f_{ij} \tau_i b_j u(t) - x_i(t) = x_{p,i}(t) \quad (9a)$$

385 where  $n$  is the number of pools in a C cycle model,  $f_{ij}$  is a fraction of C transferred from pool  $j$   
 386 to  $i$  through all the pathways,  $\tau_i$  measures residence times of individual pools in isolation (**in**  
 387 **contrast to  $\tau_N$  in the network**),  $x'_j$  is the net C change in the  $j^{\text{th}}$  pool,  $b_j$  is a partitioning  
 388 coefficient of C input to the  $j^{\text{th}}$  pool,  $x_i(t)$  is the C storage in the  $i^{\text{th}}$  pool, and  $x_{p,i}(t)$  is the C  
 389 storage potential in the  $i^{\text{th}}$  pool. Eq. 9a means that the C storage potential of each pool at time  $t$ ,  
 390  $x_{p,i}(t)$ , is the sum of all the individual net C pool change,  $x'_j$ , multiplied by corresponding  
 391 residence time spent in pool  $i$  coming from pool  $j$ . Through re-arrangement, eq. 9a can be solved  
 392 for each individual pool net C change as a function of C storage potential of all the pools as:

393 
$$x'_i(t) = \frac{x_{c,i,u}(t) - x_{c,i,p}(t) - x_i(t)}{f_{ii}\tau_i} \quad (9b)$$

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395 where  $x_{c,i,u}(t) = \sum_{j=1}^n f_{ij} \tau_i b_j u(t)$  for the maximal amount of C that can transfer from C input  
 396 to the  $i^{\text{th}}$  pool.  $x_{c,i,p}(t) = \sum_{j=1, j \neq i}^n f_{ij} \tau_i x'_j(t)$  for the maximal amount of C that can transfer from  
 397 all the other pools to the  $i^{\text{th}}$  pool.  $f_{ii} = 1$  for all the pools if there is no feedback of C among soil  
 398 pools.  $f_{ii} < 1$  when there are feedbacks of C among soil pools.

399 As plant pools get C only from photosynthetic C input,  $u(t)$ , but not from other pools,  
 400 the direction and rate of C storage change in the  $i^{\text{th}}$  plant pool is determined by:

$$401 \begin{cases} x'_i(t) = \frac{x_{c,i}(t) - x_i(t)}{\tau_i} = \frac{X_{p,i}(t)}{\tau_i} \\ x_{c,i}(t) = b_i u(t) \tau_i \end{cases} \quad \text{for } i = 1, 2, 3 \quad (10)$$

402 The C storage capacity of plant pools equals the product of plant C input,  $u(t)$  (i.e., net primary  
 403 production, NPP), partitioning coefficient,  $b_i$ , and residence time,  $\tau_i$ , of its own pool (Fig. 2b-d).  
 404 Thus, the C storage capacities of the leaf, root, and wood pools are high in summer and low in  
 405 winter. Plant C storage,  $x_i(t)$ , still chases the storage capacity,  $x_{c,i}(t)$ , of its own pool at a rate  
 406 that is proportional to  $X_{p,i}(t)$ . For the leaf pool, the C storage,  $x_1(t)$ , increases when  $x_{c,1}(t) >$   
 407  $x_1(t)$  (or  $x_{p,1}(t) > 0$ ) from late spring until early fall on the 265<sup>th</sup> day of year (DOY) and then  
 408 decreases when  $x_{c,1}(t) < x_1(t)$  (or  $x_{p,1}(t) < 0$ ) from DOY of 265 until 326 during fall (Fig. 2a).

409 However, the direction of C storage change in litter and soil pools are no longer solely  
 410 determined by the storage capacity,  $x_{c,i}(t)$ , of their own pools or at a rate that is proportional to  
 411  $X_{p,i}(t)$ . The C storage capacity of one litter or soil pool has two components. One component,  
 412  $x_{c,i,u}(t)$  is set by the amount of plant C input,  $u(t)$ , going through all the possible pathways,  
 413  $f_{ij} b_j$ , multiplied by residence time,  $\tau_i$ , of its own pool. The second component measures the C  
 414 exchange of one litter or soil pool with other pools according to net C pool change,  $x'_j(t)$ ,  
 415 through pathways,  $f_{ij}, j \neq i$ , weighed by residence time,  $\tau_i$ , of its own pool. For example, C  
 416 input to the litter pool is a combination of C transfer from C input through the leaf, root, and

417 wood pools (Fig. 3c, 3d, and 3e) and C transfer due to the net C pool changes in the leaf, root,  
418 and wood pools (Fig. 3f, 3g, and 3h). Thus the first capacity component of the litter pool to store  
419 C is the sum of three products of NPP, C partitioning coefficient, and network residence time,  
420 respectively, through the leaf, root, and wood pools (Fig. 3c, 3d, and 3e). The second capacity  
421 component is the sum of other three products of C transfer coefficient along all the possible  
422 pathways, network residence time, and net C pool changes, respectively, in the leaf, root, and  
423 wood pools (Fig. 3f, 3g, and 3h). Thus, C storage in the  $i^{\text{th}}$  pool,  $x_i(t)$ , chases an attractor,  
424  $(\sum_{j=1}^n f_{ij} b_j u(t) - \sum_{j=1, j \neq i}^n f_{ij} \tau_i x'_j(t)) \tau_i$ , for litter and soil pools (Fig. 4).

425 In summary, due to the network of C transfer, C storage in litter and soil pools does not  
426 chase the C storage capacities of their own pools in a multiple C pool model (Fig. 4). The  
427 capacities for individual litter and soil pools measure the amounts of C that is transferred from  
428 photosynthetic C input through plant pools to be stored in those pools. However, those litter and  
429 soil pools also exchange C with other pools according to transfer coefficients along pathways of  
430 C movement multiplying net C pool change in those pools. Integration of the C input and C  
431 exchanges together still sets as a moving attractor toward which individual pool C storage  
432 approaches (Fig. 4).

433

### 434 3.3 C storage dynamics under global change

435 In response to a global change scenario that combines historical change and simulated RCP8.5 in  
436 the TECO experiment, the modeled ecosystem C storage capacity (the sum of all elements in  
437 vector  $X_c(t)$ ) at Harvard Forest increases from 27 kg C m<sup>-2</sup> in 1850 to approximately 38 kg C m<sup>-2</sup>  
438 in 2100 with strong interannual variability (Fig. 5a). The increasing capacity results from a  
439 combination of a nearly 44% increase in NPP with a ~2% decrease in ecosystem residence times

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442 (the sum of all elements in vector  $\tau_E(t)$ ) during that period (Fig. 5b). The strong interannual  
443 variability in the modeled capacity is attributable to the variability in NPP and residence times,  
444 both of which directly respond to instantaneous variations in environmental factors. In  
445 comparison, the ecosystem C storage (the sum of all elements in vector  $X(t)$ ) itself gradually  
446 increases, lagging behind the capacity, with much dampened interannual variability (Fig. 5a).  
447 The dampened interannual variability is due to smoothing effects of pools with various residence  
448 times. In response to global change scenario RCP8.5, the ecosystem C storage potential (the sum  
449 of all elements in vector  $X_p(t)$ ) in the Harvard Forest ecosystem increases from zero at 1980 to  
450  $3.5 \text{ kg C m}^{-2}$  in 2100 with strong fluctuation over years (Fig. 5a). Over seasons, the potential is  
451 high during the summer and low in winter, similarly with the seasonal cycle of the C storage  
452 capacity.

453 Since chasing time,  $\tau_{ch}$ , is a matrix and net C pool change,  $X'(t)$ , is a vector, eq. 6a or 6b  
454 (i.e., the C storage potential) can not be analytically separated into the chasing time and net C  
455 pool change as can the capacity into C input and residence time in eq. 5a or 5b for traceability  
456 analysis. The relationships among the three quantities can be explored by regression analysis.  
457 The ecosystem C storage potential fluctuates in a similar phase with NEP from 1850 to 2100  
458 (Fig. 5c). Consequently, the C storage potential is well correlated with NEP at the whole  
459 ecosystem scale (Fig. 5d). The slope of the regression line is a statistical representation of  
460 ecosystem chasing time. In this study, we find that  $r^2$  of the relationship between the storage  
461 potential and NEP is 0.79. The regression slope is 28.1 years in comparison with the ecosystem  
462 residence time of approximately 22 years (Fig. 5b).

463 The capacity and storage itself of individual pools display similar long-term trends and  
464 interannual variability to those for the total ecosystem C storage dynamics (Fig. 6). Noticeably,

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466 the deviation of the C storage from the capacity, which is the C storage potential, is much larger  
467 for pools with long residence times than those with short residence times. For individual pools,  
468 the potential is nearly zero for those fast turnover pools and becomes very large for those pools  
469 with long residence time (Fig. 6).

470 For individual plant pools, eq. 10 describes the dependence of the C storage potential,  
471  $x_{p,i}(t)$ , on the pool-specific residence time,  $\tau_i$ ,  $i = 1, 2$ , and 3, and net C pool change of their  
472 own pools,  $x'_i(t)$ ,  $i = 1, 2$ , and 3. Thus, one value of  $x_{p,i}(t)$  is exactly corresponding to one  
473 value of  $x'_i(t)$  at slope of  $\tau_i$ , leading to the correlation coefficient in Fig. 7 being 1.00 for leaf,  
474 root, and wood pools. For a litter or soil pool, however, the C storage potential is not solely  
475 dependent on the residence time and net C pool change of its own pool but influenced by several  
476 other pools. Thus, the potential of one litter or soil pool is correlated with net C pool changes of  
477 several pools with different regression slopes (Fig. 7).

478

#### 479 **4 Discussion**

##### 480 4.1 Assumptions of the C cycle models and validity of this analysis

481 This analysis is built upon eq. 1, which represents the majority of terrestrial C cycle  
482 models developed in the past decades (Manzoni and Porporato, 2009; Sierra and Müller, 2015).  
483 Those models have several assumptions, which may influence the validity of this analysis. First,  
484 those models assume that donor pools control C transfers among pools and decomposition  
485 follows 1<sup>st</sup>-order decay functions (Assumption 1). This assumption is built upon observations  
486 from litter and SOC decomposition. Analysis of data from nearly 300 studies of litter  
487 decomposition (Zhang et al., 2008), about 500 studies of soil incubation ([Schädel et al., 2014](#);  
488 Xu et al., 2016), more than 100 studies of forest succession (Yang et al., 2011), and restoration



489 | (Matamala et al., 2008) almost all suggests that the 1<sup>st</sup>-order decay function captures  
490 | macroscopic patterns of land C dynamics. Even so, its biological, chemical and physical  
491 | underpinnings need more study (Luo et al., 2016). This assumption has recently been challenged  
492 | by a notion that microbes are actively involved in decomposition processes. To describe the  
493 | active roles of microbes in organic C decomposition, a suite of nonlinear microbial models has  
494 | been proposed using Michaelis-Menten or reverse Michaelis-Menten equations (Allison et al.,  
495 | 2010; Wieder et al., 2013). Those nonlinear models exhibit unique behaviors of modeled  
496 | systems, such as damped oscillatory responses of soil C dynamics to small perturbations and  
497 | insensitivity of the equilibrium pool sizes of litter or soil carbon to inputs (Li et al., 2014; Wang  
498 | et al., 2014; 2016). Oscillations have been documented for single enzymes at timescales between  
499 | 10<sup>-4</sup> to 10 seconds (English et al., 2006; Goldbeter, 2013; Xie, 2013). Over longer timescales  
500 | with mixtures of large diversity of enzyme-substrate complexes in soil, oscillations may be likely  
501 | averaged out so that the 1<sup>st</sup> order decay functions may well approximate these average dynamics  
502 | of organic matter decomposition (Sierra and Müller, 2015).

503 |         Second, those models all assume that multiple pools can adequately approximate  
504 | transformation, decomposition, and stabilization of SOC in the real world (Assumption 2). The  
505 | classic SOC model, CENTURY, uses three conceptual pools, active, slow, and passive SOC, to  
506 | represent SOC dynamics (Parton et al., 1987). Several models define pools that are  
507 | corresponding to measurable SOC fractions to match experimental observation with modeling  
508 | analysis (Smith et al., 2002; Stewart et al., 2008). Carbon transformation in soil over time has  
509 | also been described by a partial differential function of SOM quality (Bosatta and Ågren, 1991;  
510 | Ågren and Bosatta, 1996). The latter quality model describes the external inputs of C with  
511 | certain quality, C loss due to decomposition, and the internal transformations of the quality of

512 soil organic matter. It has been shown that multi-pool models can approximate the partial  
513 differential function or continuous quality model as the number of pools increases (Bolker et al.,  
514 1998; Sierra and Müller, 2015).

515 Assumption 3 is on partitioning coefficients of C input (i.e., elements in vector  $B$ ) and C  
516 transformation among plant, litter, and soil pools (i.e., elements in the matrix,  $A\xi(t)K$ ). Some of  
517 the terrestrial C cycle models assume that elements in vector  $B$ , and matrices  $A$  and  $K$  are  
518 constants. All the factors or processes that vary with time are represented in the diagonal matrix  
519  $\xi(t)$ . In the real world, C transformation are influenced by environmental variables (e.g.,  
520 temperature, moisture, oxygen, N, phosphorus, and acidity varying with soil profile, space, and  
521 time), litter quality (e.g., lignin, cellulose, N, or their relative content), organomineral properties  
522 of SOC (e.g., complex chemical compounds, aggregation, physiochemical binding and  
523 protection, reactions with inorganic, reactive surfaces, and sorption), and microbial attributes  
524 (e.g., community structure, functionality, priming, acclimation, and other physiological  
525 adjustments) (Luo et al., 2016). It is not practical to incorporate all of those factors and processes  
526 into one model. Only a subset of them is explicitly expressed while the majority is implicitly  
527 embedded in the C cycle models. Empirical studies have suggested that temperature, moisture,  
528 litter quality, and soil texture are primary factors that control C transformation processes of  
529 decomposition and stabilization (Burke et al., 1989; Adair et al., 2008; Zhang et al., 2008; Xu et  
530 al., 2012; Wang et al., 2013). Nitrogen influences C cycle processes mainly through changes in  
531 photosynthetic C input, C partitioning, and decomposition. It is yet to identify how other major  
532 factors and processes, such as microbial activities and organomineral protection, regulate C  
533 transformation.

534 Assumption 4 is that terrestrial C cycle models use different response functions (i.e.,  
535 different  $\xi(t)$  in eq. 1) to represent C cycle responses to external variables. As temperature  
536 modifies almost all processes in the C cycle, different formulations, including exponential,  
537 Arrhenius, and optimal response functions, have been used to describe C cycle responses to  
538 temperature changes in different models (Lloyd and Taylor, 1994; Jones et al., 2005; Sierra and  
539 Müller, 2015). Different response functions are used to connect C cycle processes with moisture,  
540 nutrient availability, soil clay content, litter quality, and other factors. Different formulations of  
541 response functions may result in substantially different model projections (Exbrayat et al., 2013)  
542 but unlikely change basic dynamics of the model behaviors.

543 Assumption 5 is that disturbance events are represented in models in different ways  
544 (Grosse et al., 2011; West et al., 2011; Goetz et al., 2012; Hicke et al., 2012). Fire, extreme  
545 drought, insect outbreaks, land management, and land cover and land use change influence  
546 terrestrial C dynamics via 1) altering rate processes, for example, gross primary productivity  
547 (GPP), growth, tree mortality, or heterotrophic respiration; 2) modifying microclimatic  
548 environments; 3) transferring C from one pool to another (e.g., from live to dead pools during  
549 storms or release to the atmosphere with fire) (Kloster et al., 2010; Thonicke et al., 2010; Luo  
550 and Weng, 2011; Prentice et al., 2011; Weng et al., 2012). Those disturbance influences can be  
551 represented in terrestrial C cycle models through changes in parameter values, environmental  
552 scalars, and/or discrete C transfers among pools of eq. 1 (Luo and Weng 2011). While eq. 1 does  
553 not explicitly incorporate disturbances for their influences on land C cycle, Weng et al. (2012)  
554 developed a disturbance regime model that combines eq. 1 with frequency distributions of  
555 disturbance severity and intervals to quantify net biome exchanges.

556 The sixth assumption that those models make is that the lateral C fluxes through erosion

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565 or local C drainage is negligible so that eq (1) can approximate terrestrial C cycle over space. If  
566 soil erosion is substantial enough to be modeled with horizontal movement of C, a third  
567 dimension should be added in addition to two-dimensional transfers in classic models.

568 Our analysis on transient dynamics of terrestrial C cycle is valid unless some of the  
569 assumptions are violated. Assumption 1 on the 1<sup>st</sup>-order decay function of decomposition  
570 appears to be supported by thousands of datasets. It is a burden on microbiologists to identify  
571 empirical evidence to support the nonlinear microbial models. Assumption 2 may not affect the  
572 validity of our analysis no matter how C pools are divided in the ecosystems. Our analysis in this  
573 study is applicable no matter whether elements are time-varying or constant in vector  $B$  and  
574 matrices  $A$  and  $K$  as in assumption 3. Neither assumption 4 nor 5 would affect the analysis in this  
575 study. The environmental scalar,  $\xi(t)$ , as related to assumption 4 can be any forms in the derived  
576 equations (e.g., eq. 2). Disturbances of fire, land use, and extreme drought change rate processes  
577 but do not alter the basic formulation of eq. 1. If soil erosion and lateral transportation of C  
578 become a major research objective, Eq. (1) can no longer be analyzed to understand the  
579 mathematical foundation underlying transient dynamics of terrestrial C cycle.

580

#### 581 **4.2 Carbon storage capacity**

582 One of the two components this analysis introduces to understand transient dynamics of  
583 terrestrial C storage is the C storage capacity (Eq. 2). Olson (1963) is probably among the first  
584 who systematically analyzed C storage dynamics at forest floor as functions of litter production  
585 and decomposition. He collected data of annual litter production and approximately steady-state  
586 organic C storage at forest floor, from which decomposition rates were estimated for a variety of  
587 ecosystems from Ghana in the tropics to alpine forests in California. Using the relationships

588 among litter production, decomposition, and C storage, Olson (1963) explored several issues,  
589 such as decay without input, accumulation with continuous or discrete annual litter fall, and  
590 adjustments in production and decay parameters during forest succession. His analysis  
591 approximated the steady-state C storage as the C input times the inverse of decomposition (i.e.,  
592 residence time). The steady-state C storage is also considered the maximal amount of C that a  
593 forest can store.

594 This study is not only built upon Olson's analysis but also expands it at least in two  
595 aspects. First, we similarly define the C storage capacity (i.e., eqs. 5a and 5b). Those equations  
596 can be applied to a whole ecosystem with multiple C pools while Olson's analysis is for one C  
597 pool. Second, Olson (1963) treated the C input and decomposition rate as yearly constants at a  
598 given location even though they varied with locations. This study considers both C input and rate  
599 of decomposition being time dependent. A dynamical system with its input and parameters being  
600 time dependent mathematically becomes a nonautonomous system (Kloeden and Rasmussen,  
601 2011). As terrestrial C cycle under [global change](#) is transient, we need to treat it a  
602 nonautonomous system to better understand the properties of transient dynamics. Olson (1963)  
603 approximated the non-autonomous system at the yearly time scale without [global change](#) so as to  
604 effectively understand properties of the steady-state C storage at the forest floor. In comparison,  
605 eqs. 5a and b are not only more general but also essential for understanding transient dynamics  
606 of the terrestrial C cycle in response to [global change](#).

607 Under the transient dynamics, the C storage capacity as defined by eqs 5a and b still sets  
608 the maximal amount of C that one ecosystem can store at time  $t$ . This capacity represents  
609 instantaneous responses of ecosystem C cycle to external forcing via changes in both C input and  
610 residence time, and thus varies within one day, over seasons of a year, and interannually over

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614 longer time scales as forcings vary. The variation of the C storage capacity can result from cyclic  
615 environmental changes (e.g., diurnal and seasonal changes), directional global change (e.g., rising  
616 atmospheric CO<sub>2</sub>, nitrogen deposition, altered precipitation, and warming), disturbance events,  
617 disturbance regime shifts, and changing vegetation dynamics (Luo and Weng, 2011). As the  
618 capacity sets the maximal amount of C storage (Fig. 2a), it is a moving attractor toward which  
619 the current C storage chases. When the capacity is larger than the C storage itself, C storage  
620 increases. Otherwise, the C storage decreases.

621

### 622 4.3 Carbon storage potential

623 The C storage potential represents the internal capability to equilibrate the current C storage with  
624 the capacity. Biogeochemically, the C storage potential represents re-distribution of net C pool  
625 change,  $X'(t)$ , of individual pools through a network of pools with different residence times as  
626 connected by C transfers from one pool to the others through all the pathways. The potential is  
627 conceptually equivalent to the magnitude of disequilibrium as discussed by Luo and Weng  
628 (2011).

629 Extensive studies have been done to quantify terrestrial C sequestration. The most  
630 commonly estimated quantities for C sequestration include net ecosystem exchange (NEE), C  
631 stocks in ecosystems (i.e., plant biomass and SOC) and their changes (Baldocchi et al., 2001; Pan  
632 et al., 2013). This study, for the first time, offers the theoretical basis to estimate the terrestrial C  
633 storage potential in at least two approaches: (1) the product of chasing time and net C pool  
634 change with eqs. 6a and 6b; and (2) the difference between the C storage capacity and the C  
635 storage itself with eqs. 6c. Since the time-varying C storage capacity is fully defined by  
636 residence time and C input at any given time, C storage potential can be estimated from three

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640 quantities: C input, residence time, and C storage.

641 To effectively quantify the C storage potential in terrestrial ecosystems, we need various  
642 data sets from experimental and observatory studies to be first assimilated into models. For  
643 example, data from Harvard Forest were first used to constrain the TECO model. The  
644 constrained model was used to explore changes in ecosystem C storage in response to global  
645 change scenario, RCP8.5. That scenario primarily stimulated NPP, which increased from 1.06 to  
646 1.8 kg C m<sup>-2</sup> yr<sup>-1</sup> in the Harvard Forest (Fig. 5b). Although climate warming decreased residence  
647 time in the Harvard Forest, the substantial increases in NPP resulted in increases in the C storage  
648 potential over time.

649

#### 650 4.4 Novel approaches to model evaluation and improvement

651 Our analysis of transient C cycle dynamics offers new approaches to understand,  
652 evaluate, diagnose, and improve land C cycle models. We have demonstrated that many global  
653 land C cycle models can be exactly represented by the matrix equation (Eqs. 1 and 2) (i.e.,  
654 physical emulators). As a consequence, outputs of all those models can be placed into a three  
655 dimensional (3D) space (Eq. 7) to measure their differences. In addition, components of land C  
656 cycle models are simulated in a mutually independent fashion so that modeled C storage can be  
657 decomposed into traceable components for traceability analysis. Moreover, the physical  
658 emulators computationally enable data assimilation to constrain complex models.

659 *Physical Emulators of land C cycle models* We have developed matrix representations  
660 (i.e., physical emulators) of CABLE, LPJ-GUESS, CLM3.5, CLM 4.0, CLM4.5, BEPS, and  
661 TECO (Xia et al., 2013; Hararuk et al., 2014; Ahlström et al., 2015; Chen et al., 2015). The  
662 emulators can exactly replicate simulations of C pools and fluxes with their original models

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664 when driven by a limited set of inputs from the full model (GPP, soil temperature, and soil  
665 moisture) (Fig. 1b and 1c). However, the physical emulators differ for different models as the  
666 elements of each matrix could be differently parameterized or formulized in different models.  
667 Also, different models usually have different pool-flux structures, leading to different non-zero  
668 elements in the  $A$  matrix. Nonetheless, the physical emulators make complex models analytically  
669 clear and, therefore, give us a way to understand the effects of forcing, model structures, and  
670 parameters on modeled ecosystem processes. They greatly simplify the task of understanding the  
671 dynamics of submodels and interactions between them. The emulators allow us to analyze model  
672 results in the 3D parameter space and the traceability framework.

673 *Parameter space of C cycle dynamics* Eq. 7 indicates that transient dynamics of modeled  
674 C storage are determined by three parameters: C input, residence time, and C storage potential.  
675 The 3D parameter space offers one novel approach to uncertainty analysis of global C cycle  
676 models. As global land models incorporate more and more processes to simulate C cycle  
677 responses to global change, it becomes very difficult to understand or evaluate complex model  
678 behaviors. As such, differences in model projections cannot be easily diagnosed and attributed to  
679 their sources (Chatfield, 1995; Friedlingstein et al., 2006; Luo et al., 2009). Eq. 7 can help  
680 diagnose and evaluate complex models by placing all modeling results within one common  
681 parameter space in spite of the fact that individual global models may have tens or hundreds of  
682 parameters to represent C cycle processes as affected by many abiotic and biotic factors (Luo et  
683 al., 2016). The 3D space can be used to measure how and how much the models diverge.

684 *Traceability analysis* The two terms on the right side of eq. 2 can be decomposed into  
685 traceable components (Xia et al., 2013) so as to identify sources of uncertainty in C cycle model  
686 projections. Model intercomparison projects (MIPs) all illustrate great spreads in projected land

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688 C sink dynamics across models (Todd-Brown et al., 2013; Tian et al., 2015). It has been  
689 extremely challenging to attribute the uncertainty to sources. Placing simulation results of a  
690 variety of C cycle models within one common parameter space can measure how much the  
691 model differences are in a common metrics (Eq. 7). The measured differences can be further  
692 attributed to sources in model structure, parameter, and forcing fields with traceability analysis  
693 (Xia et al., 2013; Rafique et al., 2014; Ahlström et al., 2015; Chen et al., 2015). The traceability  
694 analysis also can be used to evaluate effectiveness of newly incorporated modules into existing  
695 models, such as adding the N module on simulated C dynamics (Xia et al., 2013) and locate the  
696 origin of model ensemble uncertainties to external forcing vs. model structures and parameters  
697 (Ahlström et al., 2015).

698 *Constrained estimates of terrestrial C sequestration* Traditionally, global land C sink is  
699 indirectly estimated from airborne fraction of C emission and ocean uptake. Although many  
700 global land models have been developed to estimate land C sequestration, a variety of MIPs  
701 indicate that model predictions widely vary among them and do not fit observations well  
702 (Schwalm et al., 2010; Luo et al., 2015; Tian et al., 2015). Moreover, the prevailing practices in  
703 the modeling community, unfortunately, may not lead to significant enhancements in our  
704 confidence on model predictions. For example, incorporating an increasing number of processes  
705 that influence the C cycle may represent the real-world phenomena more realistically but makes  
706 the models more complex and less tractable. MIPs have effectively revealed the extent of the  
707 differences between model predictions (Schwalm et al., 2010; Keenan et al., 2012; De Kauwe et  
708 al., 2013) but provide limited insights into sources of model differences (but see Medlyn et al.  
709 | 2015). The physical emulators make data assimilation computationally feasible for global C  
710 | cycle models (Hararuk et al., 2014; 2015) and thus offer the possibility to generate independent

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713 yet constrained estimates of global land C sequestration to be compared with the indirect  
714 estimate from the airborne fraction of C emission and ocean uptake. With the emulators, we can  
715 assimilate most of the C flux- and pool-related datasets into those models to better constrain  
716 global land C sink dynamics.

717

## 718 **5 Concluding remarks**

719 In this study we theoretically explored the transient dynamics of terrestrial C storage. Our  
720 analysis indicates that transient C storage dynamics can be partitioned into two components: the  
721 C storage capacity and the C storage potential. The capacity, which is the product of C input and  
722 residence time, represents their instantaneous responses to a state of external forcing at a given  
723 time. Thus, the C storage capacity quantifies the maximum amount of C that an ecosystem can  
724 store at the given environmental condition at a point of time. Thus it varies diurnally, seasonally,  
725 and interannually as environmental condition changes.

726 The C storage potential is the difference between the capacity and the current C storage  
727 and thus measures the magnitude of disequilibrium in the terrestrial C cycle (Luo and Weng,  
728 2011). The storage potential represents the internal capability (or recovery force) of the  
729 terrestrial C cycle to influence the change in C storage in the next time step through  
730 redistribution of net C pool changes in a network of multiple pools with different residence  
731 times. The redistribution drives the current C storage towards the capacity and thus equilibrates  
732 C efflux with influx.

733 The two components of land C storage dynamics represent interactions of external forces  
734 (via changes in the capacity) and internal capability of the land C cycle (via changes in the C  
735 storage potential) to generate complex phenomena of C cycle dynamics, such as fluctuations,

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**Deleted:** We propose that the storage potential should be the targeted quantity for research, market trading, and government management for C credits.

740 directional changes, and tipping points, in the terrestrial ecosystems. From a system perspective,  
741 these complex phenomena ~~could not be generated by relatively simple internal processes but~~ are  
742 mostly caused by multiple environmental forcing variables interacting with internal processes  
743 over different temporal and spatial scales ~~as explained by Luo and Weng (2011) and Luo et al.~~  
744 ~~(2015)~~. Note that while those internal processes can be mathematically represented with a  
745 relatively simple formula, their ecological and biological underpinnings can be very complex.

746 The theoretical framework developed in this study has the potential to revolutionize  
747 model evaluation. Our analysis indicates that the matrix equation as in eq. 1 or 2 can adequately  
748 emulate most of the land C cycle models. Indeed, we have developed physical emulators of  
749 several global land C cycle models. In addition, predictions of C dynamics with complex land  
750 models can be placed in a 3D parameter space as a common metric to measure how much model  
751 predictions are different. The latter can be traced to its source components by decomposing  
752 model predictions to a hierarchy of traceable components. Moreover, the physical emulators  
753 make it computationally possible to assimilate multiple sources of data to constrain predictions  
754 of complex models.

755 The theoretical framework we developed in this study can well explain dynamics of C  
756 storage in response to cyclic seasonal change in external forcings (e.g., Figs. 2 and 3), ~~climate~~  
757 ~~change,~~ and rising atmospheric CO<sub>2</sub> (Fig. 5). It ~~can also~~ explain responses of ecosystem C  
758 storage to disturbances and other global change factors, such as nitrogen deposition, land use  
759 changes, and altered precipitation. The theoretical framework is simple and straightforward but  
760 able to characterize the direction and rate of C storage change, which are arguably among the  
761 most critical issues for quantifying terrestrial C sequestration. Future research should explicitly  
762 incorporate stochastic disturbance regime shifts (e.g., Weng et al., 2012) and vegetation

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767 dynamics (Moorcroft et al., 2001; Purves and Pacala, 2008; Fisher et al., 2010; Weng et al.,  
768 2015) into this theoretical framework to explore their theoretical issues related to  
769 biogeochemistry.

770

771 **6 Code availability**

772 Computer code of the TECO model and its physical emulator are available at

773 <http://ecolab.ou.edu/download/TECO%20Emulator.php>

774

775

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1059 | **Fig. 1** The Terrestrial ECOsystem (TECO) model and its outputs. Panel a is a schematic  
1060 | representation of C transfers among multiple pools in plant, litter and soil in the TECO model.  
1061 | TECO has feedback loops of C among soil pools. CWD = coarse wood debris, SOM = Soil  
1062 | Organic Matter. Panel b compares the original TECO model outputs with those from matrix  
1063 | equations for net ecosystem production (NEP = the sum of elements in  $X'(t)$  from eq. 1). The  
1064 | perfect match between the TECO outputs and NEP from eq. 1 is due to the fact that they are  
1065 | mathematically equivalent. Panel c compares the original TECO model outputs with those from  
1066 | matrix equations for ecosystem C storage (= the sum of elements in  $X(t)$  from eq. 2). The C  
1067 | storage values calculated with eq. 2 are close to 1:1 line with  $r^2=0.998$  with the modeled values  
1068 | (panel c). The minor mismatch in estimated C storage between the matrix equation calculation  
1069 | and TECO outputs is due to numerical errors via inverse matrix operation with some small  
1070 | numbers.

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1072 | **Fig. 2** Seasonal cycles of the C storage capacity and C storage dynamics for the leaf pool (i.e.,  
1073 | pool 1 as shown in Fig. 1). All the components are showed in panels b-d to calculate  $x_{c,1}(t) =$   
1074 |  $b_1 u(t) \tau_1$  through multiplication, where  $u(t) = NPP$  and  $\tau_1 = 1/k_1$  for leaf.

1075

1076 | **Fig. 3** Seasonal cycles of the C storage capacity and C storage dynamics for the litter pool (i.e.,  
1077 | pool 4 as shown in Fig. 1). All the components are showed to calculate

1078 |  $x_{c,4,u}(t) = \sum_{j=1}^n f_{4j} \tau_4 b_j u(t)$  in panels b-e and  $x_{c,4,p}(t) = \sum_{j=1, j \neq 4}^n f_{4j} \tau_4 x'_j(t)$  in panels f-i for  
1079 | litter.  $x_{c,4,u}(t)$  is the maximal amount of C that can transfer from C input to the litter pool.

1080 |  $x_{c,4,p}(t)$  is the maximal amount of C that can transfer from all the other pools to the litter pool.

1081 | This figure is to illustrate the network of pools through which C is distributed.

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1084 **Fig. 4** Components of the C storage capacity for litter pool (i.e., pool 4 as shown in Fig. 1).

1085 Component,  $x_{c,4,u}(t)$ , is the C from C input and component,  $x_{c,4,p}(t)$ , is the C from all the other

1086 pools to the litter pool. The sum of them is the attractor that determines the direction of C storage

1087 change in pool 4.

1088

1089 **Fig. 5** Transient dynamics of ecosystem C storage in response to [global change](#) in Harvard

1090 Forest. Panel a shows the time courses of the ecosystem C storage capacity, the ecosystem C

1091 storage potential, and ecosystem C storage (i.e., C stock) from 1850 to 2100. Panel b shows time

1092 courses of NPP(t) as C input and ecosystem residence times. Panel c shows correlated changes in

1093 ecosystem C storage potential and net ecosystem production (NEP). Panel d illustrates the

1094 regression between the C storage potential and NEP.

1095

1096 **Fig. 6** The C storage capacity ( $x_{c,i}(t)$ ), the C storage potential ( $x_{p,i}(t)$ ), and C storage ( $x_i(t)$ ) of

1097 individual pools. The potential is nearly zero for those fast turnover pools with short residence

1098 times but very large for those pools with long residence times.

1099

1100 **Fig. 7** The C storage potential of individual pools ( $x_{p,i}$ ) as influenced by net C pool change of

1101 different pools ( $x'_i$ ) in their corresponding rows. The correlation coefficients show the degree of

1102 influences of net C pool change in one pool on the C storage potential of the corresponding pool

1103 through the network of C transfer. Those empty cells indicate no pathways of C transfer between

1104 those pools as indicated in Fig. 1.

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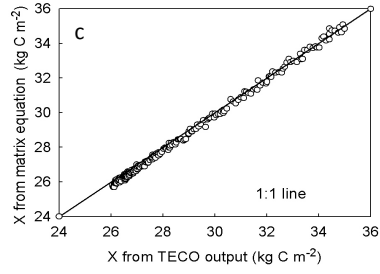
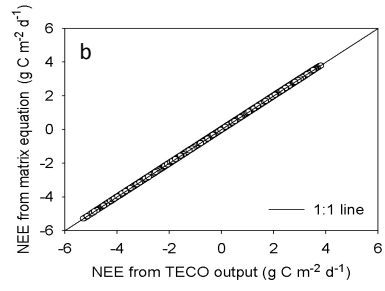
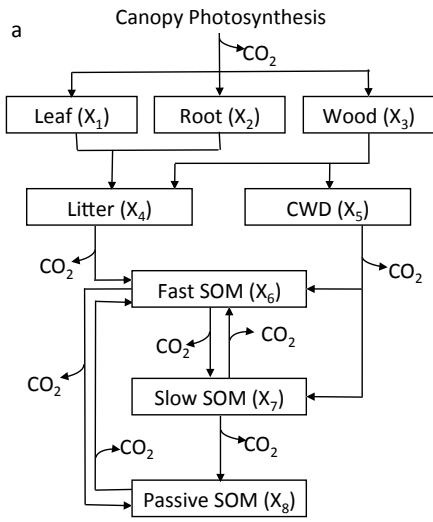


Fig. 1

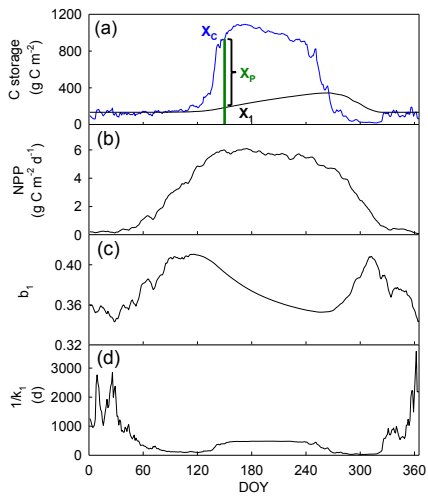
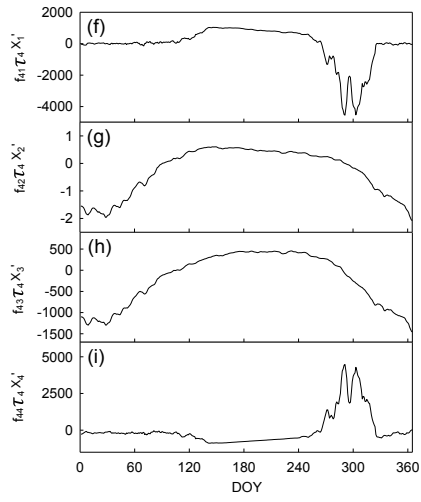
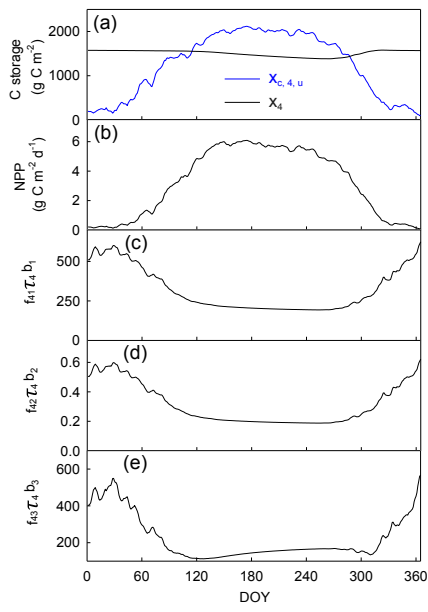


Fig. 2

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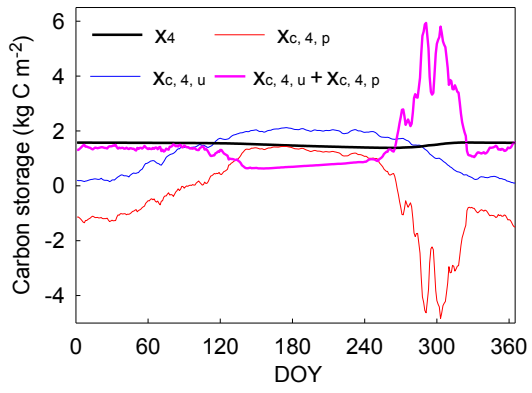




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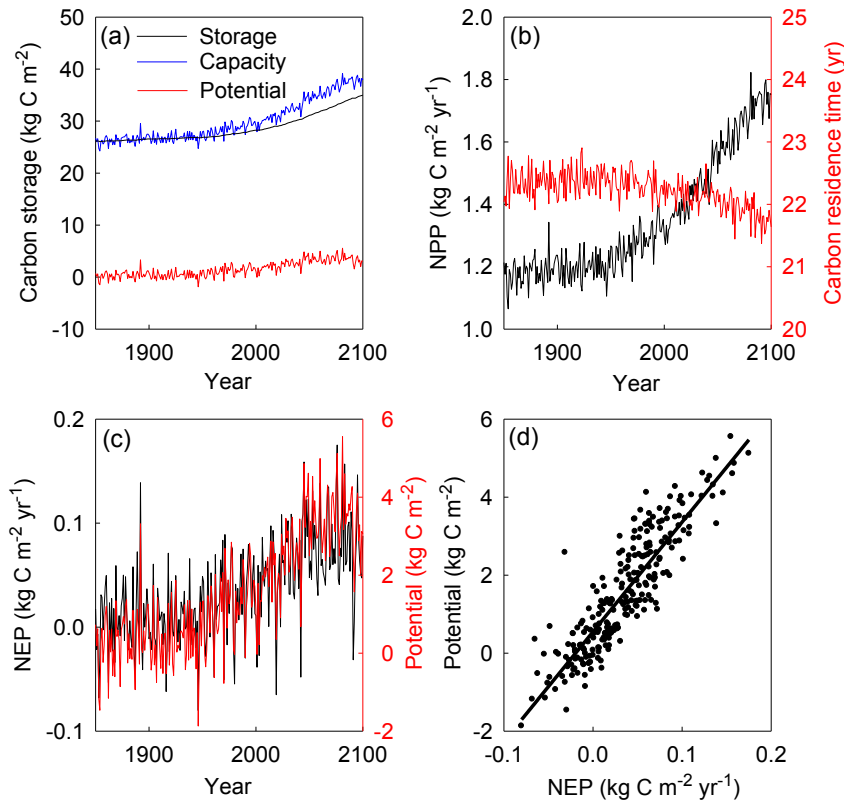
Fig. 3

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Fig. 4



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Fig. 5

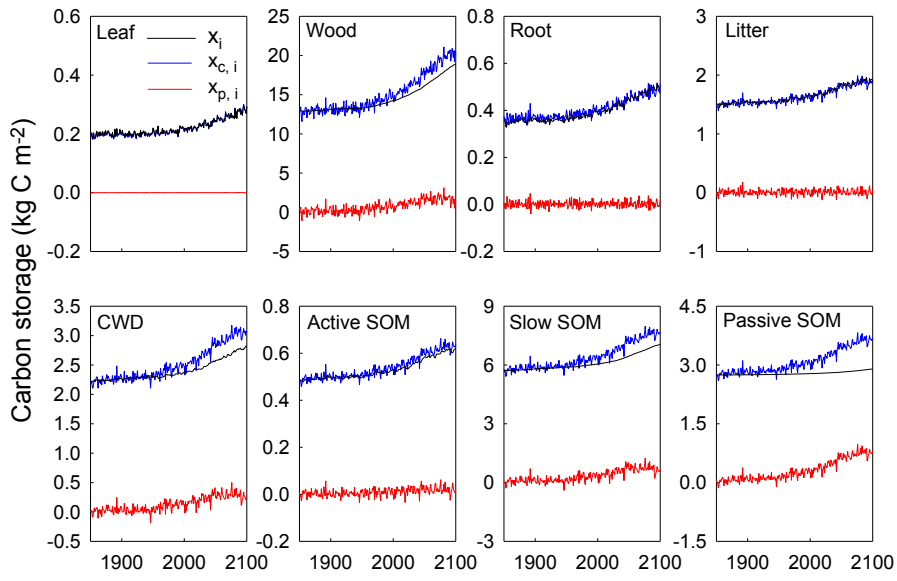
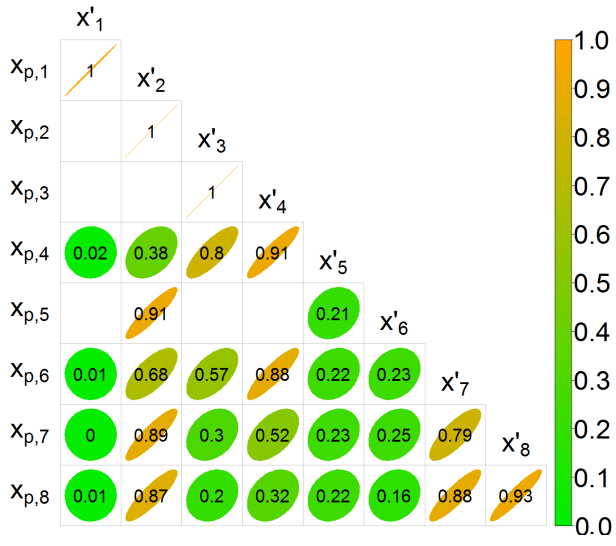


Fig. 6

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Fig. 7