

Modelling processes at the ecosystem level

Based on a contribution to Plant Ecology by E.-D. Schulze et al.

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2017

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1 Introduction

Mathematical models are a fundamental tool in the study of plant ecology and whole ecosystem dynamics. They can be used to formalize our conceptual understanding of physiological and ecological processes in the form of mathematical relations, which can serve in the development of testable hypotheses. They also serve as tools for integrating different sources of information, and to predict the consequences of the model's assumptions in the future behavior of the system (Canham et al., 2003; Soetaert and Herman, 2009).

Models at the ecosystem level of organization are generally focused on describing processes related with the water, carbon, nutrient and energy balance of ecosystems (Ågren and Andersson, 2012). They generally describe the physiology of plant processes in terms of carbon, water and nutrient uptake, and the transfers of these materials to the soil system. Other ecological processes are also often included such as competition among individuals for light and nutrients, age-related mortality, or the dispersal and reproduction of species (Botkin et al., 1972; Agren et al., 1991; Bugmann, 2001; Sierra and Harmon, 2008).

In this section we will explore different classifications of models and will review the basic building blocks of ecosystem and biogeochemical models from a mathematical point of view. We will adopt a holistic approach, in which we will review the most general mathematical aspects of models ignoring specific details of each process for the sake of general understanding.

2 Classification of ecosystem models

2.1 Model dichotomies

There exists a large variety of mathematical models to represent terrestrial ecosystems and their biogeochemistry. They can be classified under different categories, which are often ambiguous or can apply equally to very dissimilar models. It is common that models are presented in dichotomies such as mechanistic versus empirical or deterministic versus stochastic, depending on a main attribute of the model that is highlighted (Jones, 1992).

A model is generally classified as empirical when a mathematical relation (e.g. a linear regression) only captures a trend observed in a given dataset and there is no explicit representation of underlying processes. These type of models are generally contrasted with mechanistic models, in which basic understanding of underlying processes is used to set the mathematical structure of the model. Compared to empirical models, mechanistic models usually contain a higher level of detail and descriptions of interactions of ecosystem components. However, empirical models can more easily accommodate measurement uncertainty and produce predictions within a given confidence interval. In addition, empirical models are usually the starting point for the development of more detailed mechanistic models and serve to guide our intuition in the development of more complex theories.

Table 1: Some dichotomies used to classify ecosystem models.

Simple	Complex
Theoretical	Applied
Qualitative	Quantitative
Mathematical	Statistical
Mechanistic	Empirical
Analytical	Numerical
Static	Dynamic
Discrete	Continuous
Population-based	Individual-based
Deterministic	Stochastic
Spatial	Point-based
Global	Regional

Another important model dichotomy is deterministic versus stochastic. Deterministic models produce exact and invariable predictions when all inputs to the model are known. This contrast with stochastic models in which random elements are included (e.g. tree mortality or disturbances) and predictions are always different, even if all model parameters are fixed. A large number of simulations are used in stochastic models to determine the plausible interval of model predictions. A very important group of stochastic models are the so called ‘gap models’ (Bugmann, 2001). They represent the dynamics of individual trees growing on a patch of forest (a forest gap), and the emergent dynamic of the system is the result of the interactions among individuals. These type of models have been very important in predicting the effects of climate change on species distributions, and it has been said they can potentially unify ecological theory (Huston and Smith, 1987; Bugmann, 2001; Shugart, 2002)

Other dichotomies such as dynamic versus static (also known as time invariant), or analytic versus numeric, are common in the classification of models. Static models are very useful to study the main characteristics of the ecosystem under steady-state conditions, while dynamic models are useful to study the transient behaviour of an ecosystem as it is altered by external factors such as climate. When models are solved using computers, they are classified as numeric while when solutions are derived mathematically they are classified as analytical.

There are many other dichotomies in the classification of models. Some of them are presented in Table 1.

2.2 Model classes

In addition to model dichotomies, it is possible to classify models in general classes associated with the scale or the main processes represented in the model. Four main classes of models are commonly distinguished in the scientific liter-

Table 2: Common characteristics of the main classes of vegetation and ecosystem models.

Class	Scale	Characteristics	Examples
Physiological	Hours to days; single plant.	Detailed calculation of photosynthesis, respiration, transpiration, and allocation. Usually high level of detail for leaf processes.	SIB, BATS, LSM, Canveg, SPA
Biogeochemical	Days to decades; ecosystem patch to globe.	Soil-plant-atmosphere interactions. Includes, photosynthesis, respiration, growth, allocation, nutrient uptake, and water and energy balances.	Century, TEM, CASA, BIOME- BGC, PnET
Gap	Seasons to decades; forest patch to biomes.	Population and community dynamics. Represent competition among different individuals and random processes such as mortality, fire or insect outbreaks.	Jabowa, SORTIE, FORET, ED, StandCarb
Biogeographical	Years to centuries; regions to globe.	Species distributions and climate control on vegetation. Potential distribution of vegetation types and biomes across the Earth.	Miami, DOLY, MAPSS, BIOME
Dynamic global vegetation	Hours to centuries; globe.	Representation of carbon, water, energy and nutrient balances at the global scale. Vegetation-climate interactions as well as disturbances and human impacts.	LPJ, ORCHIDEE, CLM, JSBACH

ature, these are: physiological, gap, biogeochemical, biogeographical, and dynamic global vegetation models. Some examples with their main characteristics are presented in Table (2). However, it should be noted that the boundary between these classes is not very clear in many cases and some of these models could be easily classified in different categories.

3 Basic approach to model development

The large majority of ecosystem and biogeochemical models are special cases of **linear dynamical systems** (Ågren and Bosatta, 1996; Pastor, 2008; Luo and Weng, 2011; Ågren and Andersson, 2012). This is a group of mathematical equations, systems of ordinary differential equations, that have very similar and

interesting properties. They are widely used for many applications in science and engineering and can reproduce complex dynamics such as those produced by the cycling of biogeochemical elements and their interactions with the environment.

The main principle behind all ecosystem models is **mass balance** (Rodhe, 2000; Ågren and Andersson, 2012). Therefore, the differential equations that conform models are all based on the idea that changes in matter and energy are the result of inputs and outputs to and from the system. For example, the changes over time in mass of a reservoir X can be expressed as

$$\frac{dX(t)}{dt} = \text{Inputs} - \text{Outputs} = I(t) - O(t). \quad (1)$$

A particular characteristic of linear dynamical systems is that the outputs from a reservoir can be expressed as a proportion k of the existing mass in that reservoir. If this proportion changes over time, we can express this proportion as $k(t)$. Each component of the ecosystem (reservoir) can then be expressed as

$$\frac{dX(t)}{dt} = I(t) - k(t) \cdot X(t). \quad (2)$$

An ecosystem model is a collection of differential equations of this type. The number of conceptual pools or reservoirs in a model determines the number of differential equations in the model. This is sometimes called the **dimension** of the model. For example, a model that explicitly represents the dynamic behavior of five pools: canopy, woody biomass, roots, litter, and soil, is represented by 5 differential equations and therefore it has dimension 5.

Using these concepts we can build now a very simple carbon model with two reservoirs, vegetation and soil (Figure 1). In this model, carbon is fixed by the vegetation V and transferred to the soil S . From both pools a fraction is also lost to the atmosphere as CO_2 by the process of respiration. We can represent the conceptual model of Figure 1 mathematically by the following linear system of differential equations:

$$\frac{dV(t)}{dt} = P - c_1 V(t) \quad (3)$$

$$\frac{dS(t)}{dt} = \alpha c_1 V(t) - c_2 S(t) \quad (4)$$

where P represents the annual amount of photosynthetically fixed carbon that enters the ecosystem; c_1 the proportion of carbon that leaves the vegetation every year both as respired CO_2 and transferred to the soil pool; α is the proportion of the carbon that leaves the vegetation that is transferred to the soil; c_2 is the proportion of carbon stored in the soil that is lost every year by heterotrophic respiration.

Although equations (3) and (4) do not explicitly show a calculation of respiration, the amount of respired carbon from each pool can be calculated easily as

$$r_1(t) = (1 - \alpha)c_1 V(t) \quad (5)$$

$$r_2(t) = c_2 S(t) \quad (6)$$

where r_1 and r_2 represent the amount of respiration from the vegetation and the soil pools, respectively. Notice that only a fraction $(1 - \alpha)$ of the carbon leaving the vegetation pool is respired, while all carbon that leaves the soil pool is respired.

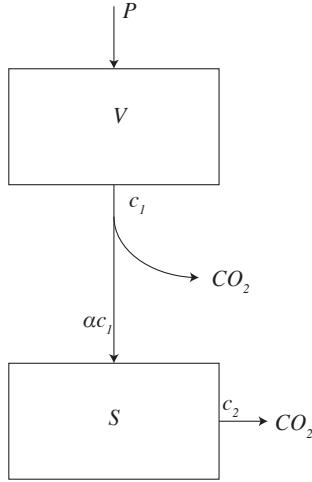


Figure 1: Simple two-pool model of carbon transfers between vegetation (V), soil (S) and the atmosphere (not explicitly represented). P are inputs from gross primary production; c_1 and c_2 are coefficients of carbon flow out of each reservoir. Fluxes out of the system are represented as respiration losses in the form of CO_2 .

There is a lot of complexity from real ecosystems that is not included in equations (3) and (4). For example, this model does not explicitly represent plant hydrological processes, the uptake and use of nutrients, or the allocation of carbon to different plant parts. To explicitly represent these processes it would be necessary to partition the vegetation and soil pools into many more components, and include many more differential equations. In fact, most ecosystem models are a collection of a large number of equations that describe particular processes in vegetation and soils.

To analyze mathematical properties of an ecosystem model, it is much easier to represent them in terms of vectors and matrices than writing a long list of differential equations. In vector and matrix notation, the model of equations (3) and (4) can be expressed as

$$\begin{pmatrix} \frac{dV}{dt} \\ \frac{dS}{dt} \end{pmatrix} = \begin{pmatrix} P \\ 0 \end{pmatrix} + \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix} \cdot \begin{pmatrix} V \\ S \end{pmatrix}, \quad (7)$$

which by matrix multiplication and summation yields the exact system of equations as equations (3) and (4). Even more compactly, this model can be written

as

$$\begin{pmatrix} \frac{dV}{dt} \\ \frac{dS}{dt} \end{pmatrix} = \begin{pmatrix} P \\ 0 \end{pmatrix} + \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix} \cdot \begin{pmatrix} V \\ S \end{pmatrix}$$

$$\frac{dx}{dt} = p + \mathbf{C} \cdot x, \quad (8)$$

where the italic boldface letters correspond to vectors and uppercase boldface correspond to matrices. We will use this notation to present a general model of ecosystem carbon cycling and analyze its parts and general properties.

4 General ecosystem carbon model

4.1 The linear model of Luo and Weng (2011)

Using vector and matrix notation, Luo and Weng (2011) proposed a model that generalizes a large majority of models of carbon cycling in terrestrial ecosystems. The model is given by

$$\frac{dx(t)}{dt} = U(t) \cdot b + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C} \cdot x(t) \quad (9)$$

where $x(t)$ is a vector of carbon pool sizes; $U(t)$ represents photosynthetically fixed carbon; b is a vector of partitioning coefficients of the photosynthetically fixed carbon to plant pools (e.g. leaf, root, and woody biomass). The matrices \mathbf{A} and \mathbf{C} contain coefficients to calculate carbon transfers among the different pools and the amount of carbon release by respiration (Figure 2).

Each element of equation (9) represents an ecosystem process, which we will explore with more detail in the following sections.

4.1.1 Carbon uptake: $U(t)$

The first component of our general model is a function $U(t)$ that determines the amount of carbon uptake in the ecosystem as a function of time. This function represents the total amount of fixed carbon by photosynthesis at the ecosystem level. Most models describe photosynthesis using the biochemical model proposed by Farquhar et al. (1980) and Farquhar and Caemmerer (1982). This model contains equations that represent the rate of ribulose biphosphate (RuBP)-saturated carboxylation, the ratio of photorespiration to carboxylation, and the rates of electron transport/photophosphorylation and dark respiration (See section by A. Arneth). However, these processes occur at the cellular level in the leaf, and need to be scaled up to the entire leaf, the canopy, the individual plant, and the ecosystem (Bugmann, 2001).

Many of the early ecosystem models represented photosynthesis at the leaf level and scaled up directly to the ecosystem level using information on the leaf area index. This type of models are sometimes referred to as ‘big leaf’ models. Other models try to represent the vegetation canopy more explicitly

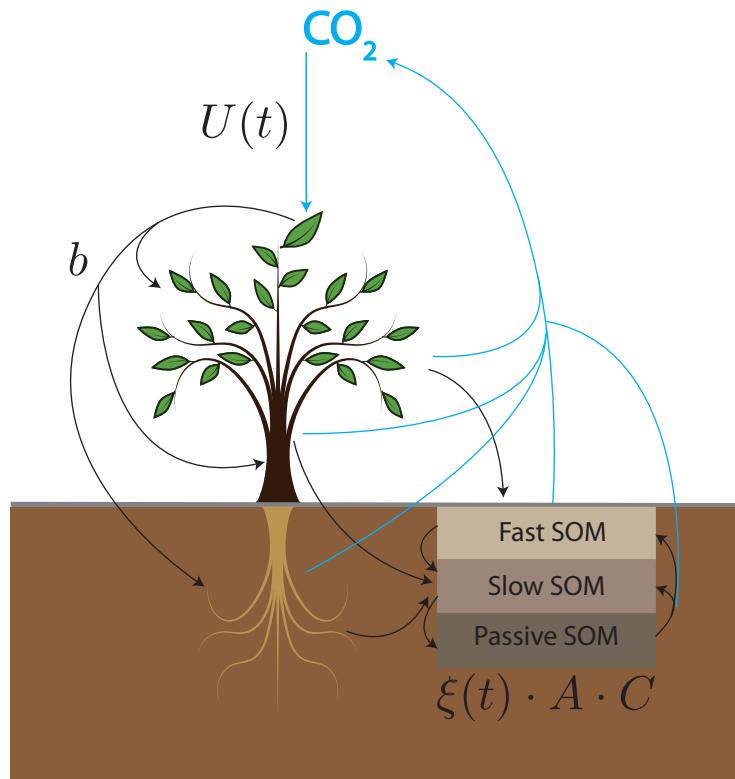


Figure 2: Graphical representation of the components of equation (9). CO_2 fixation by plants is included in the term $U(t)$ and allocation of fixed carbon to plant pools is represented by the vector b . Cycling rates and transfers among different ecosystem compartments are represented by the matrix product $\mathbf{A} \cdot \mathbf{C}$, which can be modified by the environmental scalar $\xi(t)$.

accounting for the distribution of leaves on a vertical profile and their angle of sun exposure (Jones, 1992). Other models represent carbon uptake individually for each tree on a forest patch ('gap models') doing an explicit scaling from leaves and individual trees to the ecosystem level (Bugmann, 2001; Moorcroft et al., 2001; Shugart, 2002).

4.1.2 Carbon allocation: \mathbf{b}

Once carbon is fixed by plants it needs to be allocated to different plant parts with different function and dynamics. This is accomplished in our general model by the vector \mathbf{b} , which contains coefficients that determine the proportion of the total inputs $U(t)$ that are allocated to different vegetation pools.

Models differ widely in the type of vegetation pools they represent; they can be as simple as foliage, stem and roots, or finer pools such as sugars, starch, structural carbon, etc. Allocation schemes in models could also be based on simple fixed ratios, on allometric scaling rules or could also be based on an optimization principle in which carbon is allocated dynamically driven by resource availability (Malhi et al., 2011; Franklin et al., 2012).

In models based on an optimization principle, allocation may depend on the availability of light, water, and nutrients. In general, an optimization rule is applied to the partitioning of carbon to photosynthetic, woody, and uptake pools (Franklin et al., 2012). For example, a balance between water loss and carbon uptake may dictate the proportion of carbon allocated to foliage and fine roots (Schulze et al., 1983), or soil available nitrogen may control foliage to root ratios (Reynolds and Chen, 1996). In other models, the allocation strategy is not prescribed, but rather emerges by the abiotic constraints on plant performance (Kleidon and Mooney, 2000; Pavlick et al., 2013).

4.1.3 Cycling rates in ecosystem pools: \mathbf{C}

Organic compounds allocated to different plant parts reside there for a certain amount of time. In deciduous trees, carbon resides in the leaves for the duration of the growing season while carbon in the stems reside there for decades. These differences in cycling rates are accounted for in the matrix \mathbf{C} of the general model. The diagonal of this matrix contains the rates at which carbon cycles in each pool in units of per time ($1/[time]$); therefore, the inverse of these rates represents the *turnover time* of carbon in each compartment.

In vegetation, cycling rates may depend on species composition or geographical location, while in soils these rates may depend on the quality of the organic matter or its association with mineral surfaces (Ågren and Bosatta, 1996; Sierra et al., 2011; Gleixner, 2013).

4.1.4 Transfers and transformations of organic material: \mathbf{A}

In vegetation, carbon may be transferred among different pools or transformed into different organic compounds. For example, carbohydrates in the leaves

may be transferred to stems and roots, or they can be transformed into more complex polymers such as lignin and cellulose that constitute structural growth. Similarly, carbon is also continuously transformed in the soils, from plant derived compounds to microbial-derived organic acids (Ågren and Bosatta, 1996; Gleixner, 2013). These transfers and transformations imply that carbon gets transferred from one ecosystem pool to another; or in other words, it moves from one element to another of the vector $\mathbf{x}(t)$.

The rates at which these transfers and transformation occur are represented as elements of the matrix \mathbf{A} of the general model. This matrix contains only the value of -1 in the diagonal, and in the off-diagonals the proportions at which carbon moves from one ecosystem pool to another.

4.1.5 Environmental effects on cycling rates: $\xi(t)$

Cycling rates in ecosystems change at seasonal, annual and decadal time scales due to changes in the environment, mostly by climatic fluctuations. Increases in temperature for example, usually increases the rates of cycling in vegetation and soils (Ryan, 1991; Davidson and Janssens, 2006). Water deficits negatively affect plant and microbial growth, while excess water may create anoxic conditions in soils negatively affecting plant and microbial physiology (Skopp et al., 1990).

Ecosystem models usually include functions that modify cycling rates (elements of the matrix \mathbf{C}) based on changes in abiotic variables such as air temperature, soil moisture, vapor pressure deficit, etc. In general, these functions are multiplicative and are expressed by the scalar

$$\xi(t) = \prod_i^n f_i(X_i(t)), \quad (10)$$

where each $f_i(X_i(t))$ represents a function that takes as independent variable a time dependent environmental variable $X_i(t)$. Each function produces a factor that indicates the proportion by which the environmental variable increases ($f_i(X_i(t)) > 1$) or decreases ($f_i(X_i(t)) < 1$) the cycling rates of the ecosystem components.

4.2 Examples of linear ecosystem carbon models

4.2.1 Simple vegetation-soil model

We can represent the model in Figure (1) using the general framework provided by equation (9). First, we need to define the dimension of the system, i.e. how many entries are allowed in the vectors and matrices. In this particular case, the dimension of the system is 2, because we are only dealing with two carbon pools represented by two equations (eq. 3 and 4). This means then that our vectors will be of length 2 and our matrices will be of dimension 2×2 .

Second, we define the vector $\mathbf{x}(t)$ as

$$\mathbf{x}(t) = \begin{pmatrix} V(t) \\ S(t) \end{pmatrix} \quad (11)$$

therefore,

$$\frac{d\mathbf{x}(t)}{dt} = \begin{pmatrix} \frac{dV(t)}{dt} \\ \frac{dS(t)}{dt} \end{pmatrix} \quad (12)$$

Third, we will define the first term of the right-hand side of equation (9), $U(t) \cdot \mathbf{b}$. In this case we are assuming that photosynthetic inputs are constant over time, so $U(t) = P$, and the carbon allocation vector is defined as

$$\mathbf{b} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad (13)$$

because the products of photosynthesis only enter directly to the vegetation pool.

Now let's look at the second term of the right-hand side of equation (9). The proportion of transfer of carbon from vegetation to soil is given by the parameter α , so the matrix of transfer coefficients is given by

$$\mathbf{A} = \begin{pmatrix} -1 & 0 \\ \alpha & -1 \end{pmatrix} \quad (14)$$

The coefficients determining the proportion of carbon leaving each pool determine the diagonal of the matrix

$$\mathbf{C} = \begin{pmatrix} c_1 & 0 \\ 0 & c_2 \end{pmatrix} \quad (15)$$

therefore, the multiplication between these two matrices results in

$$\mathbf{A} \cdot \mathbf{C} = \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix} \quad (16)$$

In this case, we are not assuming climatic effects on the rates of carbon cycling, therefore $\xi(t) = 1$. Putting all together, our two-pool ecosystem model expressed in matrix form is given by

$$\frac{d\mathbf{x}(t)}{dt} = \begin{pmatrix} \frac{dV(t)}{dt} \\ \frac{dS(t)}{dt} \end{pmatrix} = P \begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix} \begin{pmatrix} V(t) \\ S(t) \end{pmatrix} \quad (17)$$

It is possible to recover the initial model in equations (3) and (4) by performing the multiplication and addition of matrices and vectors.

4.2.2 The eight-pool model of Luo & Weng

Luo and Weng (2011) proposed an eight-pool model to simulate the observed C dynamics at a temperate forest in North Carolina, USA (Figure 3). The authors used data on carbon fluxes and stocks measured at this forest to parameterize the model. They found that the daily amount of photosynthetically fixed carbon

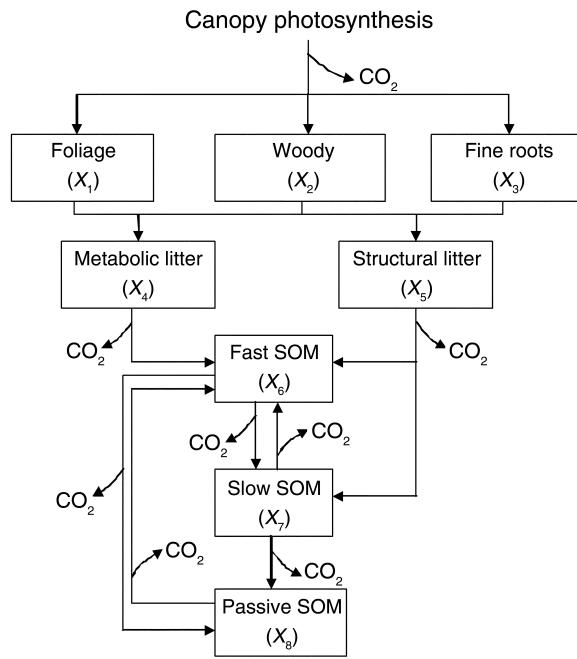


Figure 3: Structure of the Terrestrial Ecosystem Carbon Model (TECO) representing flows through various pathways and partitioning to eight pools. The fraction to plant pools is determined by partitioning the coefficient in vector \mathbf{b} in Eq. 9. The fraction to litter and soil pools via each pathway is determined by the transfer coefficient matrix \mathbf{A} . The values of vector \mathbf{b} and matrix \mathbf{A} are estimated from data collected in Duke Forest via data assimilation approach (Weng and Luo, 2011). The fraction of carbon from photosynthesis is large to plant pools and small to soil pools, particularly to the passive soil carbon pool.

in this forest (GPP) is $U = 3.37 \text{ g C m}^{-2} \text{ day}^{-1}$. The vector of carbon allocation in this model is given by

$$\mathbf{b} = \begin{pmatrix} 0.14 \\ 0.26 \\ 0.14 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

which shows that from all photosynthetically fixed carbon, 14% is allocated to foliage, 26% to woody biomass, and 14% to roots. Net primary production (NPP) in this case is the proportion of GPP that stays in the system, i.e. NPP = $U(0.14 + 0.26 + 0.14) = 1.82 \text{ g C m}^{-2} \text{ day}^{-1}$.

Each pool in the model cycles at daily rates given by the matrix

$$\mathbf{C} = \begin{pmatrix} 0.00258 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0000586 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.00239 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0109 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.00095 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.0105 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.0000995 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.0000115 \end{pmatrix},$$

which shows the faster cycling rates in the metabolic litter ($1.09 \times 10^{-2} \text{ day}^{-1}$) and the fast soil organic matter pools ($1.05 \times 10^{-2} \text{ day}^{-1}$), and the slowest cycling rates in the passive soil organic matter pool ($1.15 \times 10^{-5} \text{ day}^{-1}$).

The coefficients of the transfer and transformation matrix are

$$\mathbf{A} = \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 \\ 0.9 & 0 & 0.2 & -1 & 0 & 0 & 0 & 0 \\ 0.1 & 1 & 0.8 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.45 & 0.275 & -1 & 0.42 & 0.45 \\ 0 & 0 & 0 & 0 & 0.275 & 0.296 & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.004 & 0.01 & -1 \end{pmatrix},$$

and shows, for example, that 90% of the outputs from the foliage are transferred to the metabolic litter pool and 10% to the structural litter pool (4th and 5th entries of the 1st column, respectively). Similarly, 45% of the outputs from the passive soil organic matter (SOM) pool are transferred to the fast SOM pool, while the slow SOM pool transfers 42% to the same fast SOM pool (6th entries of the 7th and 8th column, respectively).

The behavior of each pool over time can be obtained by solving the model numerically, i.e. using some initial values of carbon storage in each pool and using the differential equation $d\mathbf{x}/dt$ to update the values of each pool at very small time-steps. There are many methods to compute numerical solutions, but a very accurate method is the 4th order Runge-Kutta method (Soetaert and Herman, 2009), which we use here to compute the time dependent behavior of the pools assuming there is no carbon stored at the beginning of the simulation

(Figure 4). With this particular parameterization, the model predicts accumulation of carbon up to a steady-state value for all pools, with larger storage in the woody biomass and the slow SOM pool and lower accumulation in the metabolic litter and the fast SOM pool.

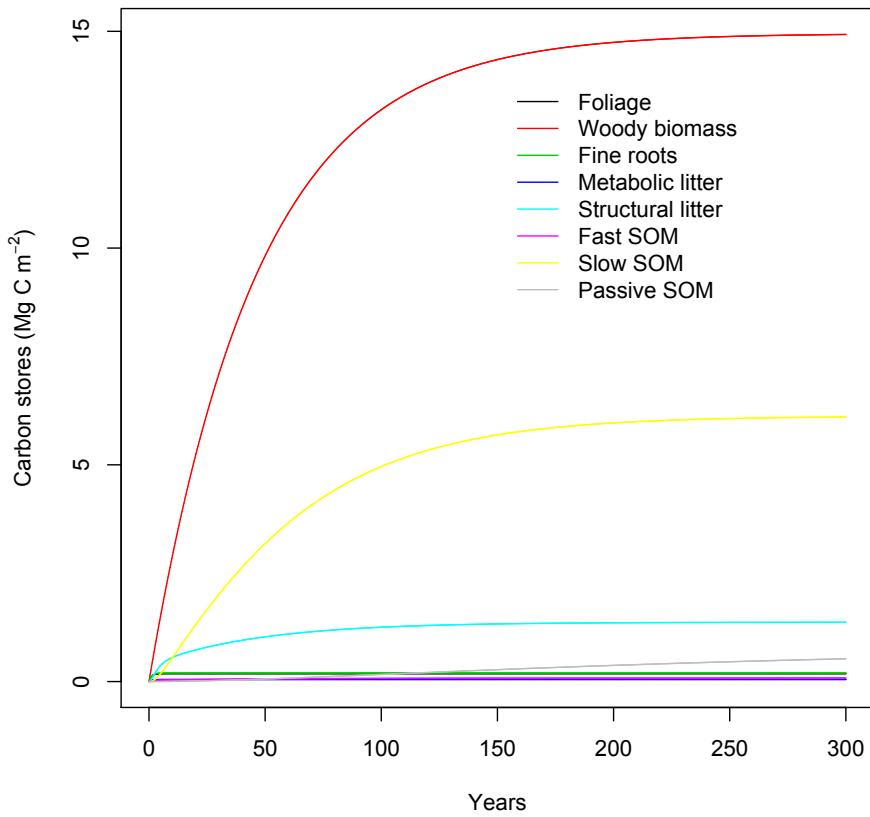


Figure 4: Carbon accumulation in all ecosystem pools of the 8-pool model proposed by Luo and Weng (2011). The model is given by equation (9), with the parameterization proposed by the authors (see section 4.2.2).

As we will see in the next section, all linear models, and therefore most ecosystem models, always reach a steady-state carbon storage where the amount of inputs to each pool are equal to the outputs from them. Changes in the environment can either increase or decrease the steady-state carbon storage value depending on whether the environment increases or decreases the internal cycling rates.

To explore the effects of the environment, we run two more simulations in which we double or decrease by half the values of the elements in the matrix \mathbf{C} . In other words, we will look at the effect of either doubling or reducing by half the rates of carbon flow out of the pools. For example, changes in climate by 10°C can double these rates, so this is a way to explore the effects of climate change on carbon storage and CO_2 exchanges with the atmosphere. We can achieve this by modifying the value of $\xi(t)$ in equation (9) (Figure 5).

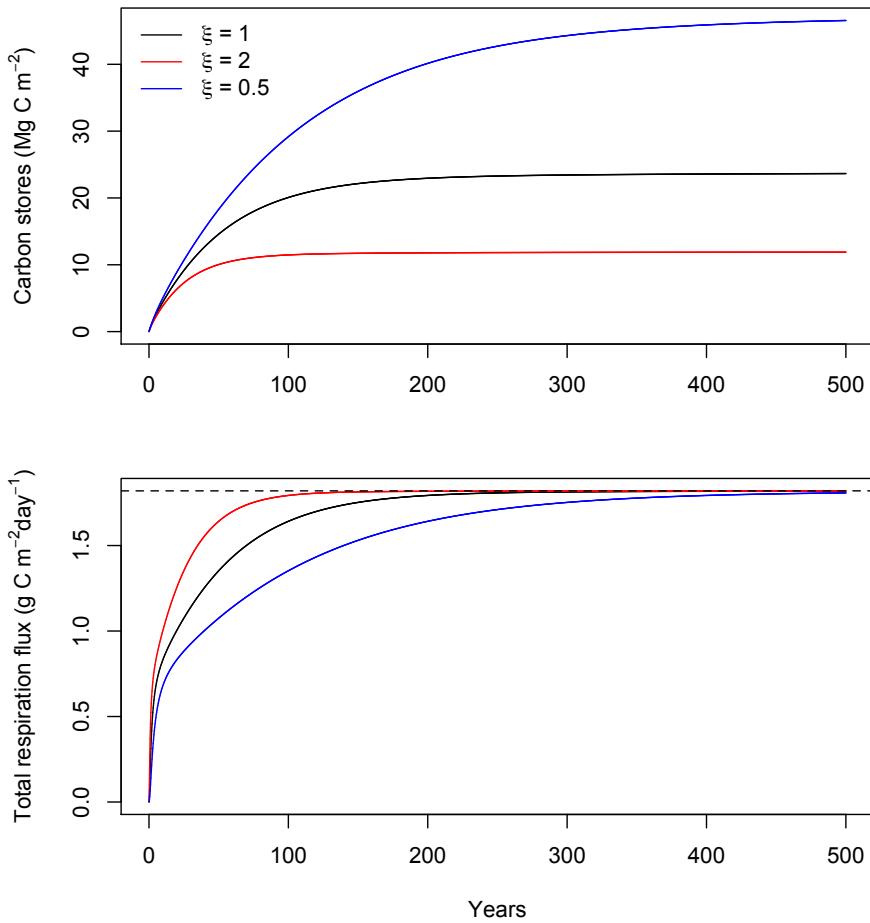


Figure 5: Effect of doubling ($\xi = 2$) or reducing cycling rates by half ($\xi = 0.5$) in the 8-pool ecosystem model proposed by Luo and Weng (2011). The upper panel shows the effect on carbon stores and the lower panel the effect on the total respiration flux.

There are two important aspects to look at in Figure (5). 1) decreasing cycling rates increases the amount of carbon storage while increasing cycling

rates decreases the amount of carbon storage. In other words, carbon storage and cycling rates are inversely related. 2) As the cycling rates decrease the amount of time required to reach equilibrium increases.

We can also gain important insights by studying the fluxes of respired carbon. Figure (5) shows that 1) All simulations converge to a constant respiration flux independent on the value of the cycling rates. Remember that at steady-state the outputs are equal to the inputs and because in all cases the inputs are the same ($U \cdot b$), then the three simulations converge to a common value of 1.82 g C m⁻² day⁻¹. 2) The time required to reach equilibrium depends on the value of the cycling rates. The lower the cycling rates the longer it takes to reach equilibrium.

4.3 General model

Although the model of equation (9) generalizes many models of the terrestrial carbon cycle, there are some special cases that are not covered by it, and therefore a broader generalization is required. For instance, the fact that the amount of foliage determines the amount of photosynthesis that can be performed by the system is not explicitly included in equation (9). Dependences of the rates of one compartment on the amounts stored in other compartments are also cases not covered by the model, which are expressed as nonlinear terms among the state variables of the dynamical model.

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

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{u}(\mathbf{x}, t) + \mathbf{B}(\mathbf{x}, t) \cdot \mathbf{x}(t), \quad (18)$$

where $\mathbf{u}(\mathbf{x}, t)$ is a vector of external inputs to the system, and \mathbf{B} a matrix of cycling and transfer rates, where both can depend on the vector of states \mathbf{x} and can also change over time t .

This general representation reveals an important classification of models according to mathematical properties (Table 3), i.e. according to model dependence on the vector of states (linearity), and time (autonomy). We call a model linear when the vector of inputs and the matrix of cycling rates are not dependent on the vector of states, and non-linear otherwise. Similarly, we call a model autonomous when inputs and cycling rates are not time dependent, and non-autonomous otherwise.

The model proposed by Luo and Weng (2011) and studied in previous sections can be classified as linear non-autonomous because there are no dependencies on the vector of states, but rates and inputs are time dependent. We will see in subsequent sections that this classification is of fundamental importance to study the mathematical properties of ecosystem models.

Table 3: Classification of carbon cycle models according to their dependence on time (autonomy), and on the vector of states (linearity). Table cells are expressions for the differential equation $\dot{\mathbf{x}}$ that captures the change of carbon contents with respect to time.

		<i>t</i> -dependence	
<i>x</i> -dependence			
		Autonomous	
		Non-autonomous	
Linear		$\mathbf{u} + \mathbf{B} \cdot \mathbf{x}(t)$	$\mathbf{u}(t) + \mathbf{B}(t) \cdot \mathbf{x}(t)$
Nonlinear		$\mathbf{u}(\mathbf{x}) + \mathbf{B}(\mathbf{x}) \cdot \mathbf{x}(t)$	$\mathbf{u}(\mathbf{x}, t) + \mathbf{B}(\mathbf{x}, t) \cdot \mathbf{x}(t)$

5 Properties of ecosystem carbon models

The properties we observed in the 8-pool model can be generalized to most ecosystem models that conform to the structure of equation (9). We will use some simple mathematical concepts below to explore these general properties of ecosystem models.

5.1 The role of inputs and cycling rates on ecosystem carbon storage

Assuming constant environmental conditions ($\xi(t) = 1$) and constant photosynthetic rates ($U(t) = U$), we can expect ecosystem models to reach a steady-state in which the amount of inputs are equal to the outputs. This assumption implies that the rate of change of carbon in each reservoir is zero, so from equation (9) we obtain

$$\mathbf{u} = -\mathbf{B} \cdot \mathbf{x}, \quad (19)$$

where $\mathbf{B} = \mathbf{A} \cdot \mathbf{C}$, and $\mathbf{u} = U \cdot \mathbf{b}$. The carbon stocks for each ecosystem pool at steady-state (\mathbf{x}_{ss}) can then be calculated by solving this equation as

$$\mathbf{x}_{ss} = -\mathbf{B}^{-1} \cdot \mathbf{u}. \quad (20)$$

This simple equation shows that as the amount of photosynthetic inputs increases the total amount of carbon that can be stored in steady-state increases as well, and as the cycling and transfer rates become faster the capacity of carbon storage decreases. The effects of environmental change on carbon storage would depend then on how much the environment can modify photosynthetic rates $U(t)$ versus cycling rates $\xi(t)$.

The current generation of ecosystem models are focusing on identifying how changes in atmospheric CO₂, nitrogen deposition, air temperatures, and soil water status, among other factors, affect the rates of photosynthetic inputs, the allocation to different vegetation and soil pools, and the cycling rates in each compartment. In other words, they evaluate how the environment modifies the elements of equation (9), and how they affect carbon storage capacity (equation 20).

5.2 Time-scales of element cycling

Ecosystem models integrate information about the rates of element input, processing, transformation, and release of elements for the entire system, and it is difficult to combine all this information into useful diagnostics of element cycling. However, useful diagnostics are commonly expressed as time-scales, metrics that capture all system dynamics and serve to compare different models with different structure, or different parameterizations of the same model. There are many approaches used to calculate these time-scales, mostly dependent on the mathematical classification presented in section 4.3.

Two main concepts help as diagnostics of ecosystem processes and ecosystem models of the C cycle, the age of the mass of carbon in a system at a given time, which is defined here as system age; and the age of the mass in the output flux at a given time, which we define here are transit time (Eriksson, 1971; Bolin and Rodhe, 1973; Thompson and Randerson, 1999; Manzoni et al., 2009). Different formulas can be used to obtain these two diagnostics, but they depend on the classification presented in Table (3).

Formulas to calculate ages and transit time are relatively simple to use for linear systems at steady-state, and we present here two different approaches for their calculation: the impulse response function, and the inverse-matrix approach.

5.2.1 Impulse response function

Transit times are computed only under the assumption of constant environmental conditions and steady-state (equation 20). For these linear autonomous models, the output flux $O(t)$ can be calculated as

$$O(t) = \int_0^\infty \psi(T) I(t - T) dT \quad (21)$$

where $\psi(T)$ is the transit time distribution. Under the assumption of an impulsive input, the transit time distribution is equal to the time evolution of the output flux, i.e. $\psi(T) = O(t)$ (Thompson and Randerson, 1999; Manzoni et al., 2009). Intuitively, this means that the transit time distribution is equal to the time required to empty a system that is under steady-state and no external perturbations. The mean residence time therefore can be calculated as

$$\overline{\psi(t)} = \int_0^\infty t \cdot O(t) dt. \quad (22)$$

In practice, it is possible to calculate the transit time distribution by solving a model numerically with initial conditions at steady-state and an impulsive input. The model must be run for a period of time at least as long as the inverse of the smallest non-zero eigenvalue of the matrix \mathbf{B} .

Eigenvalues of the matrix \mathbf{B} provide in fact very interesting information about the rates of cycling and recovery of ecosystems after a perturbation in autonomous systems. The *response time*, also called the *adjustment time*, of

a system is defined as the time required for a system to attain steady-state conditions after a perturbation. Mathematically, it is defined as

$$\tau_{cycle} = \frac{1}{\min(|\lambda_i|)} \quad (23)$$

where λ_i are the i eigenvalues of the matrix \mathbf{B} .

For example, the inverse of the eigenvalues of the matrix \mathbf{B} in the 8-pool model studied previously are given by

$$\frac{1}{|\lambda|} = \begin{pmatrix} 91.7 \\ 95.1 \\ 387.6 \\ 418.4 \\ 1052.6 \\ 11487.6 \\ 17064.8 \\ 87292.6 \end{pmatrix}, \quad (24)$$

in units of days. Therefore, the response time of the 8-pool model is 87292.6 days, or 239 years.

5.2.2 Inverse matrix approach

The transit time and the system age distribution can also be computed using a simpler method that does not require to run simulations. This method takes advantage of the matrix representation of the general model in its linear autonomous form. For this method, it is essential to be able to calculate the inverse matrix \mathbf{B}^{-1} (Table 4). Details about the derivation of formulas and examples can be found in Metzler and Sierra (2017).

If we applied the formulas in Table (4) to the model of Luo and Weng (2011), we can obtain the distribution of ages and transit times (Figure 6), as well as the age distribution for each pool (Figure 7). Notice that the age of carbon stored in the system is generally older than the age of the carbon released from the system. Pools with slow cycling rates such as the woody biomass and the slow and passive soil pools have very wide age distributions, with significant amounts of very old carbon.

5.3 Disturbance effects

Disturbances such as fires, wind-throws, or massive herbivory remove a significant part of the carbon stored in the ecosystem. During these events, most but not all carbon is removed from the vegetation component. A portion of the remaining carbon is left in situ where it decomposes and may get transferred to the soil (Janisch and Harmon, 2002). If the ecosystem does not suffer a major change in nutrient stocks or vegetation composition, it may return to the same equilibrium point if left to recover for a sufficient amount of time. In

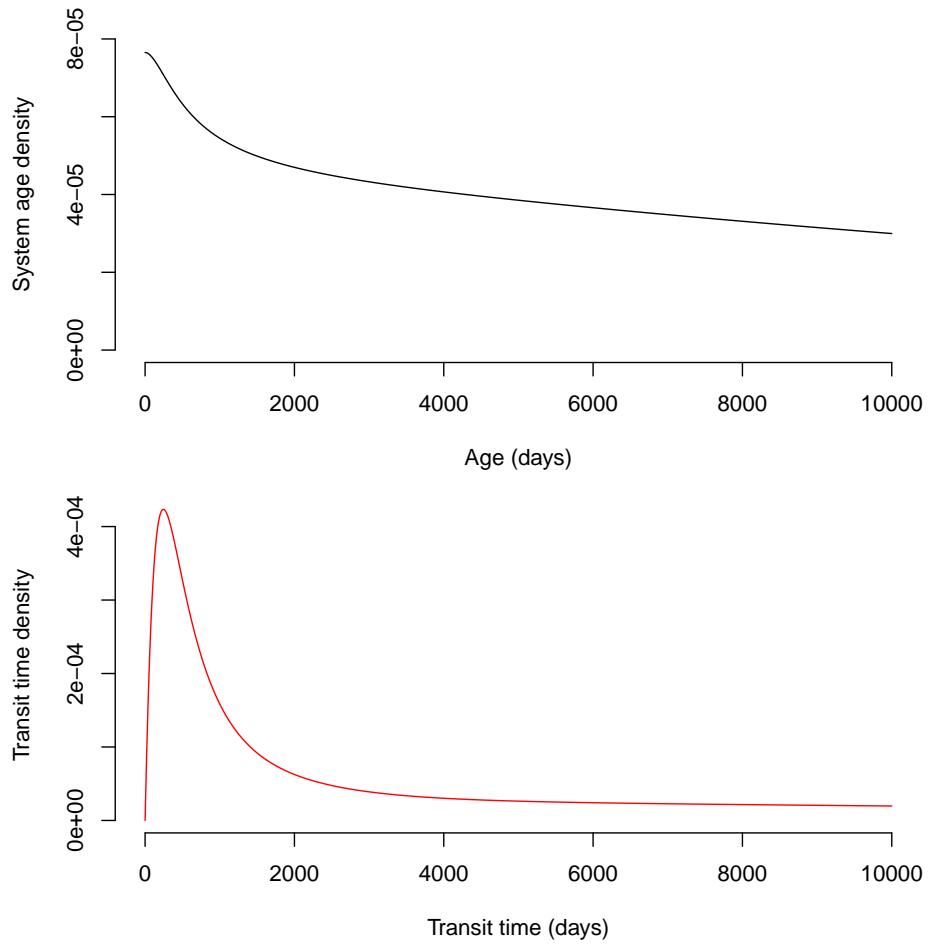


Figure 6: Density distribution function for the system age (top) and transit time (below) calculated using the formulas from Table 4. Mean system age for this distribution is 21088 days (57.8 years) and the mean transit time is 13070 days (35.8 years).

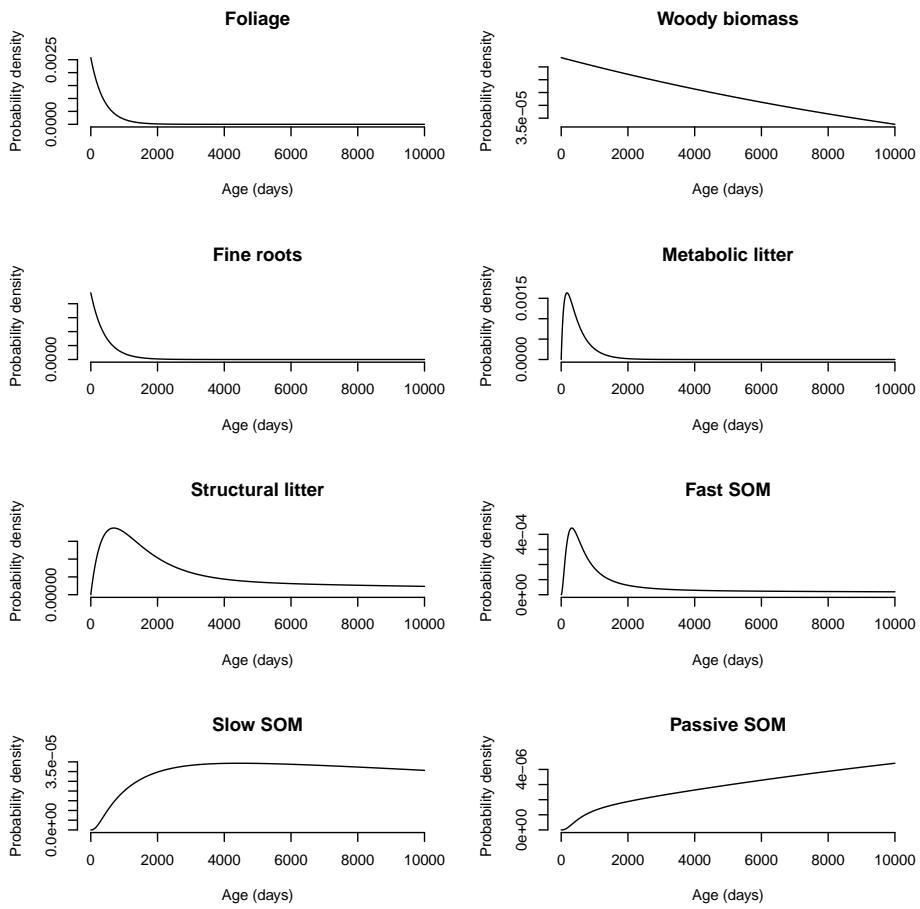


Figure 7: Density distribution functions for the age of different pools calculated using the formulas from Table 4.

Table 4: Formulas for the density distribution, moments of the distribution of transit times and ages in open linear autonomous compartmental systems of the form $\frac{d}{dt} \mathbf{x}(t) = \mathbf{B} \mathbf{x}(t) + \mathbf{u}$. Original formulas are presented in Metzler and Sierra (2017).

Metric	Density	n th moment	First moment
Transit time	$\mathbf{z}^T e^{t\mathbf{B}} \frac{\mathbf{u}}{\ \mathbf{u}\ }$	$(-1)^n n! \mathbf{1}^T \mathbf{B}^{-n} \frac{\mathbf{u}}{\ \mathbf{u}\ }$	$-\mathbf{1}^T \mathbf{B}^{-1} \frac{\mathbf{u}}{\ \mathbf{u}\ },$ $\frac{\ \mathbf{x}^*\ }{\ \mathbf{u}\ }$
System age	$\mathbf{z}^T e^{y\mathbf{B}} \frac{\mathbf{x}^*}{\ \mathbf{x}^*\ }$	$(-1)^n n! \mathbf{1}^T \mathbf{B}^{-n} \frac{\mathbf{x}^*}{\ \mathbf{x}^*\ }$	$-\mathbf{1}^T \mathbf{B}^{-1} \frac{\mathbf{x}^*}{\ \mathbf{x}^*\ },$ $\frac{\ \mathbf{B}^{-1} \mathbf{x}^*\ }{\ \mathbf{x}^*\ }$
Age vector	$(\mathbf{X}^*)^{-1} e^{y\mathbf{B}} \mathbf{u}$	$(-1)^n n! (\mathbf{X}^*)^{-1} \mathbf{B}^{-n} \mathbf{x}^*$	$-(\mathbf{X}^*)^{-1} \mathbf{B}^{-1} \mathbf{x}^*$

$\mathbf{z}^T = -\mathbf{1}^T \mathbf{B}$ is the row vector of release rates

$\mathbf{x}^* = -\mathbf{B}^{-1} \mathbf{u}$ is the steady-state vector

$\mathbf{X}^* = \text{diag}(x_1^*, x_2^*, \dots, x_d^*)$ is the diagonal matrix comprising the components of the steady-state vector

other words, if the elements of the vector \mathbf{u} or the matrix \mathbf{B} do not change, the ecosystem will reach the same steady-state \mathbf{x}_{ss} after a disturbance event (see equation 20).

Long-term carbon storage however, can be affected dramatically even when \mathbf{u} or \mathbf{B} do not change, but the frequency of disturbance events change. Under frequent disturbances that do not allow enough time for the ecosystem to recover, long-term carbon storage would be reduced proportionally to the time between disturbances (Harmon et al., 1990; Harmon, 2001; Luo and Weng, 2011).

As an example, lets consider the 8-pool model studied previously. The ecosystem can recover after a disturbance in about 239 years, so if disturbance events occur at 250 year intervals the ecosystem has enough time to recover its total stock of carbon and reach the same steady-state value as the undisturbed system (Figure 8). However, if the disturbance events occur more frequently the ecosystem cannot reach the steady-state value of the undisturbed condition and therefore would store, on average, less carbon on the long-term (Figure 8).

Although in real ecosystems the recovery patterns may differ substantially from the regular patterns shown in Figure 8, this mathematical analysis helps in understanding the possible set of behaviors to be expected from an ecosystem model. Furthermore, the model can help in understanding possible changes in ecosystem carbon stores due to changes in disturbance regimes, and how disturbances shape the structure of natural landscapes.

Disturbances related to natural processes such as wind, fire, and pests as well as human related disturbances, introduce a large degree of heterogeneity in forest landscapes. Each patch of forest that is subject to a disturbance event will recover by processes of natural regeneration and will accumulate biomass until the next disturbance event. The forest landscape therefore, can be thought

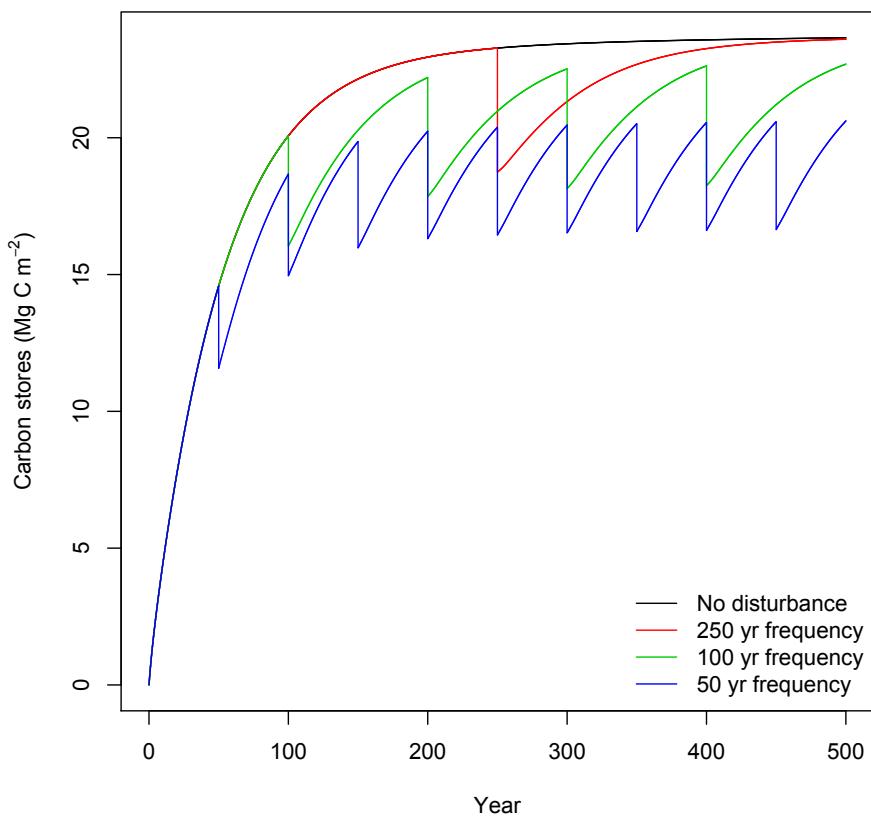


Figure 8: Simple example on how frequent disturbance events affect long-term carbon storage in ecosystems. As the frequency of the disturbance increases the long-term average carbon stock decreases. In each simulation, the disturbance event removes 70% of the carbon stored in the foliage, woody biomass, and metabolic litter pools.

of as a collection of patches of different sizes that are recovering from previous disturbances. Each patch may have different ages after the previous disturbance event and the frequency of these different events may vary dramatically over space and time. This idea of a heterogenous landscape has been introduced previously in the concept of the Shifting Mosaic Steady-State proposed by Bormann and Likens (1979). This concept helps to understand the spatial and temporal heterogeneity of ecosystem structure and function as shaped by disturbances.

In tropical forests for example, large heterogeneity in forest growth is usually observed in field surveys and it is challenging to attribute long-term patterns of ecosystem function to particular predictors. Using an ecosystem model, Chambers et al. (2013) were able to attribute variability in tree growth and mortality to different sources of disturbance events for the Amazon region. Their analysis used a similar approach as the multiple simulations in Figure 6, but repeated thousands of times over a 100-ha area. Their results showed how patterns of growth and mortality studied under the framework of the Shifting Mosaic Steady-State gives better insights on ecosystem responses to climate change than previous analyses that did not consider disturbance-related heterogeneity.

Analyses of the effects of disturbances on ecosystem processes with models also provide important insights for policy analyses. For instance, in the Pacific Northwest region of the United States, changes in forest management policies in the early 1990s led to a significant change in amounts of timber harvest and rotation lengths (times between successive harvests). Using an ecosystem carbon model, Krankina et al. (2012) were able to predict net changes in carbon stores for the entire region (4.3 million hectares) due to the implementation of the new forest protection policy. Furthermore, the authors were able to predict possible changes in carbon storage for the region in the scenario of changes in forest management proposed by new legislation. This example shows how an ecosystem model not only helps to understand the dynamics of the system over time, but also the effects of human actions and their nature protection policies on ecosystem properties.

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