CHAPTER SEVEN

Compartmental Dynamical Systems and Carbon Cycle Models

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CONTENTS

Models of the terrestrial carbon cycle are particular cases of compartmental dynamical systems, which are systems of differential equations that must conserve mass. This chapter introduces the main mathematical properties of compartmental dynamical systems and proposes a classification scheme that is useful for the analysis of carbon cycle models. This classification scheme distinguishes between models where carbon inputs and rates change over time or remain constant (nonautonomous versus autonomous models), and between models in which the amount of mass in compartments interact with mass in other compartments (nonlinearity). We show that simple concepts such as steady state may not be well defined for some groups of models, and present alternative concepts such as the pullback attractor for the analysis of models with no steady state. In addition, this chapter introduces the theoretical basis for the mathematical analysis of models written in matrix form.

INTRODUCTION

The matrix representation of models has emerged as a very general representation of ecosystem models, particularly models that track the movement of carbon, nitrogen, and other elements inside vegetation and soil pools (Mulholland and Keener 1974; Matis et al. 1979; Bolin 1981; Luo and Weng 2011; Xia et al. 2013; Luo et al. 2017). For soil organic matter models, some of the first representations in matrix form were the models of Bolker et al. (1998), Baisden and Amundson (2003), and Tuomi et al. (2009). For these authors, the matrix representation helped them organize the set of differential equations that resulted in their model

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in a more manageable and compact form. This is also the case in other fields of science such as biology or chemistry, where large sets of differential equations can be organized using this compact representation.

In fact, any model that represents the mass balance of a quantity such as atoms or molecules, can be represented in this form. Compared to other systems of differential equations, mass-balanced systems are special in the sense that all quantities are generally non-negative; i.e., the information that is fed into the model, and the predictions it produces can only exist inside the domain of the positive real numbers. Furthermore, the mass balance constraint leads to a special type of dynamical system known as a compartmental system.

We will now introduce the mathematical concept of compartmental systems, and will show that models written in compartmental form have a specific set of mathematical properties. These properties however, depend on the specific structure analyzed, mostly on the time dependence of the elements of the model and intrinsic nonlinearities.

DEFINITION OF COMPARTMENTAL SYSTEMS

We start by the defining a *compartment* as an amount of material that is kinetically homogeneous and that follows the law of mass balance. The meaning of 'mass balance' is elaborated below. A compartmental system therefore, is a set of compartments that exchange mass with each other and with the external environment. This implies that a compartmental system is an open system with an observer defined boundary (Anderson 1983; Jacquez and Simon 1993).

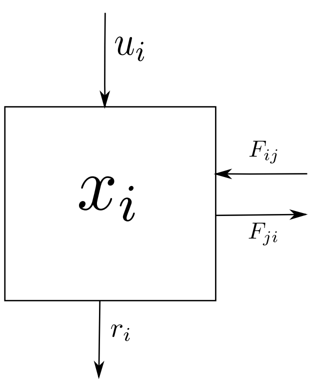

Figure 7.1. The mass balance of a single compartment.

Let's consider the mass stored in the compartment i, denoted by x_i, as the balance between (Figure 7.1):

- $u_i \geq 0$ inflow (uptake) from outside the system,
- $r_i \geq 0$ outflow (release) to outside the system,
- $F_{ji} \geq 0$ flow transfers from compartment i to compartment j,
- $F_{ij} \geq 0$ flow transfers from compartment j to compartment i.

The change in mass over time of this compartment, $\frac{dx_i}{dt} = \dot{x}_i$, must be balanced according to the equation:

$$\dot{x}_i = \sum_{j \neq i} \left(-F_{ji} + F_{ij}\right) + u_i - r_i,$$

where the constraints $F_{ij} \geq 0$, $u_i \geq 0$, and $r_i \geq 0$ must be met for all i, j, and t. The time dependence is omitted in the notation for simplicity, but all masses and flows may change over time.

An additional constraint for the system is that if the compartment is empty, no mass can flow out of it; i.e., if $x_i = 0$, then $r_i = 0$ and $F_{ji} = 0$ for all j, so that $\dot{x}_i \geq 0$.

If the flows F are continuously differentiable, i.e., they change smoothly over time without sudden jumps, we can define the flows as (Jacquez and Simon 1993):

$$F_{ji}(\mathbf{x}) \equiv b_{ji}(\mathbf{x}) \cdot x_i.$$

Therefore, we can write the mass balance equation for compartment i as:

$$\dot{x}_i = -\left(b_{0i} + \sum_{j \neq i} b_{ji}\right) x_i + \sum_{j \neq i} b_{ij} x_j + u_i.$$

The total outputs from compartment *i* can be expressed as $b_{ii} \equiv -\left(b_{0i} + \sum_{j \neq i} b_{ji}\right)$, then a general expression for each compartment satisfies the expression:

$$\dot{x}_i = \sum_j b_{ij} x_j + u_i.$$

A general expression for the entire system can be written as:

$$\dot{\mathbf{x}} = \mathbf{B}\mathbf{x} + \mathbf{u}, \tag{7.1}$$

where the elements may be time-dependent and the matrix **B** and vector **u** depend on the vector of states **x**. Notice that in contrast to other chapters, we follow here a different notation and use **B** to denote a matrix. The system of Equation 7.1 is a *compartmental or reservoir system*, and the matrix **B** is called the compartmental matrix.

For any compartmental system, the compartmental matrix **B** has three properties:

- $b_{ii} \leq 0$ for all i, $t \geq 0$,
- $b_{ij} \geq 0$ for all $i \neq j$, $t \geq 0$,
- $\sum_{i=1}^{n} b_{ij} = \sum_{i \neq j} b_{ij} + b_{jj} = -z_j \leq 0$ for all j, $t \geq 0$.

In words, the compartmental matrix **B** must always meet the requirement that all its diagonal entries are non-positive, its off-diagonal entries non-negative, and the sum of all elements inside each column must be non-positive. This column sum represents the fraction of matter that is released from the system, and it is called the *fractional release coefficient* z_j because it can be used to compute the amount of material that is released to the external environment from each pool j. The total release from the system can be obtained with the expression:

$$\mathbf{r} = \mathbf{z} \circ \mathbf{x},$$

where **z** is the vector of fractional release coefficients and ∘ is the entry-wise product between the two vectors.

The property $-z_j \leq 0$ implies that **B** is a diagonally dominant matrix, which means that each element in the diagonal is greater than or equal to the column sum for this entry. Mathematically, **B** is diagonally dominant if $|b_{ii}| \geq \sum_{j \neq i} |b_{ij}|$, and strictly diagonally dominant if $|b_{ii}| \geq \sum_{j \neq i} |b_{ij}|$.

One important property of strictly diagonally dominant matrices is that they are invertible (Taussky 1949); i.e., there exists an inverse matrix $\mathbf{B}^{-1}$ such that $\mathbf{B} \cdot \mathbf{B}^{-1} = \mathbf{I}$, where **I** is the identity matrix. Compartmental systems that meet this property contain no traps (Jacquez and Simon 1993); i.e., all mass that enters the system eventually leaves from any of the output flows.

CLASSIFICATION OF COMPARTMENTAL SYSTEMS

In the derivation of the compartmental system (Equation 7.1), the explicit representation of time dependencies and nonlinearities was omitted. We will now introduce a classification scheme for compartmental systems based on these two properties, time dependencies (autonomy), and interaction among state variables (linearity). We call a model linear when the vector of inputs and the compartmental matrix are not dependent on the vector of states, and nonlinear otherwise. Similarly, we call a model autonomous when the mass inputs and the compartmental matrix are not explicitly time dependent, and nonautonomous otherwise (Table 7.1).

This classification scheme leads to four distinct groups of compartmental systems, each with specific mathematical properties that we will explore in the following sections.

Autonomous Versus Nonautonomous Systems

In the autonomous case (Table 7.1), mass inputs and process rates in the system are constant. This implies that the external environment (e.g., solar radiation, air temperature, water content) are assumed constant. Although ecosystems are far from being

TABLE 7.1

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

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

surrounded by a constant environment, this assumption is sometimes useful to study basic properties of a system such as its long-term behavior.

However, it is important not to mix up concepts that belong to autonomous systems with concepts that do not apply for nonautonomous systems. For instance, an autonomous compartmental system generally converges to a steady state in the long term where the mass of each compartment does not change with time. In contrast, a nonautonomous system does not reach such a steady state because, by definition, the system is changing all the time. Therefore, it is wrong to talk about the steady state of a nonautonomous system (for additional details see Sierra et al. 2018).

Linear Versus Nonlinear Systems

In the linear case, the contents of compartments do not influence the rates at which mass flows into the system from the external environment, and do not influence the rates at which mass flows out of the compartments (Table 7.1). In other words, there are no feedbacks among compartment contents. However, nonlinear behavior can occur in ecosystems, for instance, when the amount of photosynthesis in the leaves depends on the amount of nonstructural carbohydrates or in fine roots.

Nonlinear compartmental systems can show a very rich set of qualitative behaviors (Jacquez and Simon 1993; Anderson and Roller 1991), which for nonlinear autonomous systems range from sustained oscillations to catastrophic shifts to alternate states (Wang et al. 2014). In the nonlinear nonautonomous case, the time-dependent signals that affect the system introduce an even larger degree of complexity, which complicates the behavior of these systems further (Müller and Sierra 2017).

PROPERTIES AND LONG-TERM BEHAVIOR OF AUTONOMOUS COMPARTMENTAL SYSTEMS

Even though the assumption of a constant environment is unrealistic, autonomous models can be very useful in illustrating potential behavior of compartmental systems. In the following, we will present a few properties of autonomous systems that are useful for many applications, which include: long-term behavior of stocks and fluxes, behavior in the neighborhood of the steady state after a perturbation, the age structure of the compartments and the release flux, and the behavior of an impulsive tracer.

Linear Systems

We will consider first linear autonomous compartmental systems of the form

$$\dot{\mathbf{x}}(t) = \mathbf{u} + \mathbf{B} \cdot \mathbf{x}(t), \qquad (7.2)$$

with $\mathbf{B}$ invertible and some initial conditions at $t = 0$

$$\mathbf{x}(0) = \mathbf{x}_0.$$

One advantage of systems of the form of Equation 7.2 compared to the other systems in Table 7.1, is that it is possible to compute their analytical solution. The general solution of this model is given by:

$$\mathbf{x}(t) = e^{\mathbf{B}\cdot t}\mathbf{x}_0 + \left(\int_0^t e^{\mathbf{B}\cdot(t-\tau)} d\tau \right) \mathbf{u}, \qquad (7.3)$$

where $e^{\mathbf{B}}$ is the matrix exponential.

Equation 7.3 shows that the solution of the system is composed of two terms. The first term accounts for the decomposition of the mass initially stored in the system at time zero. The second term accounts for decomposition of the inputs that entered the system until time t. At any given time, the mass stored in the system is the sum of both the remaining of the initial mass present at time $t = 0$ and all the un-decomposed mass that entered until time t.

The release of mass from the system is computed by multiplying the fractional release coefficients z_j by the amount of carbon stored in each pool as:

$$\mathbf{r}(t) = \left(z_j \cdot x_j(t) \right)_{j=1\ldots n}, \\ = \mathbf{z} \circ \mathbf{x}(t)$$

If the system runs for a very long time, it eventually reaches a point called the *steady state* where all inputs are equal to the outputs, and there are no changes in mass within the system. Technically, as $t \to +\infty$, $\mathbf{x}(t) \to \mathbf{x}^*$, where:

$$\mathbf{x}^* = -\mathbf{B}^{-1} \cdot \mathbf{u}, \tag{7.4}$$

and

$$\begin{aligned}\mathbf{r}^* &= \left(z_j \cdot x_j^*\right)_{j\ldots n}, \\ &= \mathbf{z} \circ \mathbf{x}^*\end{aligned}$$

Notice that the steady state does not depend on the initial conditions. It only depends on the compartmental matrix and the vector of external inputs, and represents the equilibrium point where the total amount of matter in the system and in the individual pools do not change, i.e., $\sum \dot{\mathbf{x}} = 0$, and $\dot{\mathbf{x}} = 0$, respectively.

Nonlinear Systems

In contrast to linear systems, nonlinear compartmental systems have no general explicit analytical solution. However, it is always possible to obtain a numerical solution of the system using any suitable numerical method (LeVeque 2007).

In most applications, we are interested in observing how the system evolves over time and eventually reaches a steady state. Therefore, it is of interest to find an equilibrium solution for the system:

$$\dot{\mathbf{x}} = \mathbf{u}\left(\mathbf{x}\right) + \mathbf{B}\left(\mathbf{x}\right) \cdot \mathbf{x}, \tag{7.5}$$

such that:

$$\mathbf{0} = \mathbf{u}\left(\mathbf{x}\right) + \mathbf{B}\left(\mathbf{x}\right) \cdot \mathbf{x}. \tag{7.6}$$

However, it is not certain that a specific nonlinear system has an equilibrium solution, or in case there is one, that this equilibrium is unique. Anderson and Roller (1991) show special cases of nonlinear compartmental systems with constant inputs that have unique solutions, but these cases are too specific for our purposes here.

Certain combinations of parameter values and pool sizes may lead to the situation in which the matrix $\mathbf{B}(\mathbf{x})$ is not compartmental, and therefore the system may not be mass balanced. For this reason, it is useful to define a space in which a nonlinear system is well defined. Following Anderson and Roller (1991), we define $\mathbb{R}_+^n := \left\{\mathbf{x} \in \mathbb{R}^n : \mathbf{x} \geq \mathbf{0}\right\}$ as the set of all non-negative real numbers in an n-dimensional space. Since the mass in all compartments is always non-negative, the solutions of the system can only occupy this space. Now we define the space within $\mathbb{R}_+^n$ where all solutions of the system obey mass balance constraints as:

$$\Omega := \left\{\mathbf{x} \in \mathbb{R}_+^n : \mathbf{B}\left(\mathbf{x}\right) \text{is a compartmental matrix}\right\}.$$

The space Ω is the set of all possible states the system can take without violating mass balance. One important use of Ω is that it can be used to test whether a particular nonlinear model does not violate mass balance for any value of $\mathbf{x}$ and t.

For the case of constant inputs, i.e., $\mathbf{u}$, Anderson and Roller (1991) propose an iteration strategy to find a steady-state solution for a nonlinear autonomous system. It consists of applying the formula:

$$\mathbf{x}^{p+1} = -\mathbf{B}\left(\mathbf{x}^p\right)^{-1} \cdot \mathbf{u}, \quad p = 0, 1, 2, \ldots,$$

until $\mathbf{x}^{p+1} \approx \mathbf{x}^p$. Notice that for this method to work, the compartmental matrix must be invertible. Also, the existence of one equilibrium point is not a guarantee that it is unique: other equilibria may exist as well. The choice of the starting $\mathbf{x}^{p=0}$ may determine what equilibrium point the method will find.

Stability Analysis Near Equilibria

In many applications, it is of interest to study the behavior of a system as it approaches an equilibrium point, or the behavior of the system when it is slightly perturbed from this equilibrium. The study of these behaviors usually falls under the label *stability analysis*. Again, the stability analysis would differ depending on whether the autonomous system is linear or nonlinear.

Linear Systems

For linear autonomous compartmental systems (Equation 7.2), their long-term behavior can be studied by analyzing the eigenvalues and eigenvectors of the compartmental matrix $\mathbf{B}$. It is well established that a compartmental matrix with constant coefficients has no eigenvalues with positive real part, which means that the mass inside the compartments never grows exponentially as long as inputs and rates are kept constant. This is ensured by the diagonally dominant property of the compartmental matrix.

In most applications, the eigenvalues of the linear autonomous compartmental matrix have a negative real part. In these cases, it is said that the compartmental system is asymptotically stable because all solutions converge in the long-term to the steady state of Equation 7.4. If the eigenvalues also contain a complex part, then the solution will approach the steady state through oscillations. If the eigenvalues contain no complex part, then the system approaches the steady state in the direction given by the eigenvector of the eigenvalue with the smallest absolute value of the real part.

A third possibility is that the compartmental matrix contains at least m eigenvalues with a real part equal to zero. In this case, it is said that the compartmental system contains m traps (Jacquez and Simon 1993). A trap is a compartment, or a set of connected compartments, where mass may flow in but cannot flow out. In this case, the system contains no equilibrium since $\mathbf{B}$ is not invertible and Equation 7.4 cannot be solved. The system therefore, will grow proportionally to the amount of mass entering the m traps.

Nonlinear Systems

For nonlinear systems, it is common to study the behavior of the system in the neighborhood of one or multiple equilibrium points. For compartmental systems, we are only interested in equilibria that reside in the space Ω, since they are the only ones that have a physical and biological interpretation.

We assume that the nonlinear autonomous system of Equation 7.5 has at least one equilibrium point in Ω, then we are interested in calculating the Jacobian matrix, defined as:

$$\mathbf{J}(\mathbf{x}) = \frac{\partial\left(\mathbf{B}(\mathbf{x}) \cdot \mathbf{x}\right)}{\partial \mathbf{x}},$$

at an equilibrium point $\mathbf{x} = \mathbf{x}^* \in \Omega$. This Jacobian matrix tells us about the behavior of trajectories that are close to the steady state, which is a point in the phase plane. Then, the properties of the Jacobian matrix, particularly its eigenvalues, tell us about the stability of the system in the neighborhood of the equilibrium (Guckenheimer and Holmes 1983). It is possible to treat the nonlinear system as a linear system in the neighborhood of the equilibrium, and for this reason one can perform the same analysis of eigenvalues as in the linear case (Guckenheimer and Holmes 1983).

If there are eigenvalues with positive real part, trajectories are repelled away from the equilibrium point, which is considered *unstable* (Strogatz 1994). The existence of unstable equilibria is an indication of possible tipping points and alternative states for the system (Scheffer et al. 2001). However, it is often the case that the Jacobian matrix of a compartmental system is also a compartmental matrix, in which case the existence of unstable equilibria is excluded.

When this Jacobian matrix has a compartmental structure, the system is said to be *cooperative*, which means that if the mass of one compartment increases, the fluxes to other compartments also increase (Jacquez and Simon 1993). In this case, trajectories close to the equilibrium point are attracted to it, and in some particular cases this equilibrium may be unique (Jacquez and Simon 1993; Bastin and Guffens 2006). This particular case of a unique equilibrium point means that the system is *global asymptotically stable* or GAS (Müller and Sierra 2017).

PROPERTIES AND LONG-TERM BEHAVIOR OF NONAUTONOMOUS SYSTEMS

Nonautonomous compartmental systems behave in a completely different way to autonomous systems. Since the mass inputs and the rates change with time, it is not possible for them to converge to a fixed point in the state space. Also, the stability analysis tools for autonomous systems are of little use for nonautonomous systems. Methods to analyze nonautonomous systems are relatively new, and they are currently an active branch of mathematical research (Rasmussen 2007; Kloeden and Rasmussen 2011). Concepts from control engineering can also be very useful to study nonautonomous systems, particularly nonlinear ones (Sontag 1998). Again, we will split the concepts for linear versus nonlinear nonautonomous systems in the sections below.

Linear Systems

We will consider two cases for linear autonomous compartmental systems: (1) the case of time-dependent inputs and constant rates, and (2) the case of time-dependent inputs and rates.

The first case is given by a system of the form:

$$\dot{\mathbf{x}}(t) = \mathbf{u}(t) + \mathbf{B} \cdot \mathbf{x}(t),$$

with initial condition $\mathbf{x}(0) = \mathbf{x}_0$. If the vector-valued function $\mathbf{u}(t)$ is known, an analytical solution can be obtained as:

$$\mathbf{x}(t) = e^{\mathbf{B}\cdot t}\mathbf{x}_0 + \int_0^t e^{\mathbf{B}\cdot(t-\tau)} \cdot \mathbf{u}(\tau) d\tau,$$

which is a general form for the linear autonomous solution of Equation 7.3. This analytical solution is only possible to compute because the rates in the compartmental matrix **B** are constant for all times, and therefore one can take advantage of the analytical properties of the matrix exponential.

For the second case, when both mass inputs and rates are time dependent, the system is expressed as:

$$\dot{\mathbf{x}}(t) = \mathbf{u}(t) + \mathbf{B}(t) \cdot \mathbf{x}(t), \qquad (7.7)$$

for which an analytical solution cannot be computed. However, a semi-explicit solution for Equation 7.7 can be expressed in terms of the *state transition operator* $\Phi(t, t_0)$, which is a matrix whose product with the state vector at an initial time t_0 gives $\mathbf{x}(t)$ at a later time t. In other words, $\Phi(t, t_0) \cdot \mathbf{x}_0$ is the solution to the homogeneous equation $\dot{\mathbf{x}} = \mathbf{B}(t) \cdot \mathbf{x}$.

The semi-explicit solution of the linear nonautonomous system of Equation 7.7 can be expressed as:

$$\mathbf{x}(t, t_0, \mathbf{x}_0) = \Phi(t, t_0) \cdot \mathbf{x}_0 + \int_{t_0}^t \Phi(t, \tau) \cdot \mathbf{u}(\tau) d\tau. \quad (7.8)$$

This solution explicitly depends on the initial conditions since for a nonautonomous system, where mass inputs and rates constantly change with time, the exact time and state when the system starts is of fundamental importance to compute a unique solution. In the autonomous case, solutions only depend on the time elapsed $t - t_0$, while in the nonautonomous case the solutions depend separately on the actual time t and the starting time t_0 (Kloeden and Rasmussen 2011).

Rasmussen et al. (2016) presents a sufficient condition for the global exponential stability of the nonautonomous linear compartmental system. If the compartmental matrix **B** of the homogeneous system $\dot{\mathbf{x}} = \mathbf{B}(t) \cdot \mathbf{x}$ is strictly diagonally dominant for all t, then this system is exponentially stable. This means that there is a minimal rate at which the initial mass in the system decays. Now, for the inhomogeneous case (Equation 7.7), we can think of two solutions $s_1(t, t_1, \mathbf{x}_1)$ and $s_2(t, t_2, \mathbf{x}_2)$ that have different initial conditions. As a consequence of the exponential stability property, the two solutions are said to be *forward attracting*, i.e. they get close to each other as $t \to +\infty$.

Rasmussen et al. (2016) also showed that for linear nonautonomous compartmental systems that meet the sufficient condition for exponential stability, there exists a unique *pullback attracting solution* or *pullback attractor* which all solutions are attracted to. It is defined as:

$$\mathbf{v}(t) := \int_{-\infty}^t \Phi(t, \tau) \cdot \mathbf{u}(\tau) d\tau,$$

and can be interpreted as the solution that has no influence whatsoever from the initial conditions (Kloeden and Rasmussen 2011). Therefore, the pullback attractor is the nonautonomous equivalent of the steady-state concept for autonomous systems (Carvalho et al. 2013).

A particular case is the linear nonautonomous system in which the mass inputs and the process rates are periodic. For example, this is the case of seasonal systems without noise in which the same periodic pattern for the mass inputs and for the process rates is repeated every year. More precisely, a periodic linear compartmental system is one in which $\mathbf{u}(t + T) = \mathbf{u}(t)$ and $\mathbf{B}(t + T) = \mathbf{B}(t)$ for a fixed period T and for all t. Mulholland and Keener (1974) showed that these types of systems have periodic solutions for which $\mathbf{x}(t + T) = \mathbf{x}(t)$. This periodic solution can be interpreted as a pullback attractor because it has no influence on the initial conditions.

Nonlinear Systems

Nonlinear nonautonomous compartmental systems are the most complex cases for their study and analysis. It is not possible in general to obtain analytical solutions, and, contrary to the autonomous case, it is not possible to study an equilibrium point for these systems because, by definition, compartment contents are always changing and they never reach a constant value.

As mass inputs, and process rates change in a nonlinear nonautonomous compartmental system, it is possible that specific combinations of parameter values and compartment sizes lead the system outside the space Ω where mass balance consideration must be met. Therefore, it is always important to check that solutions for these systems are always inside this space; i.e. $\mathbf{x}(t, t_0, \mathbf{x}_0) \in \Omega$ for all t, where $\mathbf{x}(t, t_0, \mathbf{x}_0)$ is a solution trajectory of the nonlinear nonautonomous compartmental system of the form:

$$\dot{\mathbf{x}}(t) = \mathbf{u}\big(\mathbf{x}(t), t\big) + \mathbf{B}\big(\mathbf{x}(t), t\big) \cdot \mathbf{x}(t). \qquad (7.9)$$

Concepts from control theory could be used to ensure that solutions are well behaved and inside Ω, and more importantly, within certain 'regions of stability' that solutions are attracted to (Müller and Sierra 2017; Kloeden and Rasmussen 2011).

Input-to-state stability (ISS) is a concept from the field of control theory that can be used to determine whether a nonlinear nonautonomous compartmental system meets stability properties. We say that a dynamical system is ISS if it is globally asymptotically stable in the absence of time-dependent perturbations, and if its trajectories are bounded by a function of the size of the input for all sufficiently large times (Sontag 1998; Müller and Sierra 2017). Therefore, we can expect the trajectories of an ISS system to remain within a certain region as long as the initial mass decays over time, and the mass inputs stay bounded within a certain limit.

We expect that for most applications, nonlinear nonautonomous compartmental systems meet the properties of ISS systems. However, mathematically showing that a system is ISS is not trivial, and this should be studied on a case-by-case basis (Sierra and Müller 2015; Müller and Sierra 2017).

FINAL REMARKS

The theory of compartmental dynamical systems offers a formal theoretical framework to express and analyze models of the carbon cycle and other biogeochemical elements that meet mass balance requirements. Using a matrix representation of carbon storage in ecosystem pools, it is possible to use the theory of compartmental dynamical systems to study important characteristics of models such as their long-term behavior, the presence of traps that retain carbon indefinitely in a model, and the response of ecosystem compartments to disturbances.

The representation of ecosystem models as compartmental systems is also useful to study system level properties of ecosystems (see Chapter 15). It is a useful mathematical representation that can relate ecosystem concepts to formal mathematical properties of dynamical systems.

SUGGESTED READING

General introductions to compartmental systems can be found in the monograph by Anderson (1983), and the comprehensive review of Jacquez and Simon (1993). More specific results about the application of compartmental systems to model the terrestrial carbon cycle can be found in the reference list and other chapters of this book.

QUIZZES

1. According to the general classification of models with respect to their dynamical properties, what type of compartmental systems have a fixed-point steady-state?
2. Can linear compartmental systems show transitions through tipping points?
3. What is the analogue of a steady state for nonautonomous systems? Why?