

The notion of stability in mathematics, biology, ecology and environmental sustainability

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Abstract: The term “stability” has many different meanings and its interpretation and application in various sciences is not absolutely identical. Historically, stability has been first formally defined in mathematical form by Lyapunov to describe equilibrium behaviour of the solar system. Lyapunov stability considers the behaviour of a system solution if its initial state is in the neighbourhood of an equilibrium point. Conceptually, it states that the equilibrium point is stable if all solutions originating in its neighbourhood forever remain “close enough” to equilibrium. Due to its precise definition and well-established mathematical technique, Lyapunov stability has found a widespread application outside its original context, particularly to analyse solutions of mathematical models of biological communities in order to determine conditions they must satisfy to be stable. Research of this kind has been a dominating trend and, in words of Justus (2006), set much of the agenda of twentieth century mathematical ecology.

There are, however, intrinsic features of the ecological systems that distinguish them from physical systems and limit a mechanical application of mathematical technique of stability study. An ecosystem is comprised of living (biotic) components and their non-living (abiotic) factors. A biotic part of an ecosystem (i.e., plants, animals and micro-organisms) is organized in hierarchical structures according to their role in the energetic and metabolic processes called trophic levels.

The ecosystem processes (like production, destruction, respiration, transformation, *etc.*) as well as intro- and interspecific interactions (e.g., competition, predation, parasitism, mutualisms, and so on) are characterized by the quantitative values of the corresponding parameters.

An adequate description of an ecosystem (E) is a three-compartment tuple, which includes a set $\{C\}$ of biotic components and abiotic factors (i.e., ecosystem constituents), a set $\{S\}$ of their particular assemblages and interrelationships (i.e., ecosystem structure) and a set $\{P\}$ of ecosystem parameters designating quantitative values of the ecological processes involving components, factors and interactions between them.

Intuitively, ecosystem stability is understood as an ability to persist in the course of a sufficiently long time in spite of exogenous perturbations. But, unlike systems studied in physics, parameter values and system structure of an ecosystem are not fixed, and exogenous perturbations may affect and change different aspects of the real-world ecosystem, including: (1) initial conditions (C-stress); (2) environmental abiotic factors (A-stress); (3) biological populations in biotic assemblages (B-stress); (3) parameter values (P-stress); and (4) ecosystem structure (S-stress).

An ecosystem affected by S-type of stress can cross a critical point and shift to a new structural quality. From this perspective, the perturbed dynamics of an ecosystem is a sequence of critical time instants, at which structural transformations occur. An ecosystem passing over a critical point must be modelled as a new system, though a new model can, to a different extent, inherit certain features of the old one (Pusachenko, 1989). Consequently, ecological stability can be studied only within a structural domain, and a new model has to be built and analysed once the ecosystem has crossed a critical point. Any judgement about ecosystem stability or instability is also valid only for a given structural domain.

Groups of dominant species, primary plant-based functions of productivity / respiration / decomposition as well as nutrient cycling and energy transfer / loss can be used as indicators of critical transitions leading the ecosystem to a new structural domain.

Keywords: *Lyapunov stability, biological communities, ecosystem parameters, exogenous perturbations, structural domain*

1. INTRODUCTION

The concept of stability is widely used for a long time in various sciences. According to Magnus (1959), the origin of stability studies can be found in the works of Aristotle and Archimedes. At the same time, there is no universal definition of stability which has always been adjusted to the specific requirements and needs of a particular science or problem at hand. As a result, stability is, perhaps, one of the most multi-meaning scientific terms.

In a broad sense, stability is understood as the ability of a system to maintain its functioning without changing the internal structure inspite of external perturbations.

The concept of “stability” has been first defined in the mathematical form by Lyapunov (1892) in his thesis titled “The general problem of the stability of motion”, in which he described equilibrium behaviour of the solar system. Lyapunov stability considers the behaviour of a system solution if its initial state is in the neighbourhood of an equilibrium point. Due to its precise definition and well-established mathematical technique, Lyapunov stability has found a widespread application outside its original context, particularly to analyse solutions of mathematical models of biological communities (Logofet, 1993; Svirezhev and Logofet, 1978). From these studies, a further generalization has been made whereby the concept was interpreted as ecological stability.

It is important to note that, apparently, there exists no acceptable qualitative definition of ecological stability (in the meaning of ecosystem stability) to be relied upon in quantitative studies, and the authors often employ the rule of contraries to argue what is not a proper or satisfactory usage of the notion (Justus, 2006; Odenbaugh, 2001).

In this paper, the application of stability in natural sciences (biology, ecology, environmental modelling) is analysed. An attempt has been made to present the main features of ecological stability and to discuss an extent, to which mathematical modelling and mathematical technique can be used in the studies of ecosystem stability.

2. BASIC CONCEPTS

Let's consider a non-autonomous nonlinear model of a dynamical system:

$$\frac{d\bar{\mathbf{x}}}{dt} = \mathbf{F}(t, \bar{\mathbf{x}}(t)), \bar{\mathbf{x}}(t_0) = \bar{\mathbf{x}}_0, \quad (1)$$

where $\bar{\mathbf{x}}(t) \in \Omega \subseteq \mathfrak{R}^n$ denotes the system state vector; Ω is an open set containing the origin, $I = [\tau; \infty]$, $\tau \in \mathfrak{R}^1$, vector-function \mathbf{F} is sufficiently smooth (e.g., is locally Lipschitz with respect to $\bar{\mathbf{x}}$ and piecewise continues in t) to ensure the existance and uniqueness of the solutions. Without loss of generality, we may assume that the origin is the equilibrium state for (1), i.e., $\mathbf{F}(t, \mathbf{0}) = \mathbf{0} \quad \forall t \geq 0$ attained by a translation of the coordinates if necessary. A point $\bar{\mathbf{x}}^* \in \Omega$ is an *equilibrium point* of (1) if $\mathbf{F}(t, \bar{\mathbf{x}}^*) \equiv \mathbf{0}$.

Definition. The equilibrium point $\bar{\mathbf{x}}^* = \mathbf{0}$ is said to be *Lyapunov stable* if for $\forall t_0 \in I$ and $\forall \varepsilon > 0$ there is $\delta(t_0, \varepsilon) > 0$ such that for any initial point $\bar{\mathbf{x}}_0$ from the δ -neighbourhood of $\bar{\mathbf{x}}^*$ the corresponding solution of (1) $\bar{\mathbf{x}}(t, t_0, \bar{\mathbf{x}}_0)$ will remain within the ε -neighbourhood for $\forall t \geq t_0$, i.e.:

$$(\forall \varepsilon > 0)(\forall t_0 \in I)(\exists \delta(t_0, \varepsilon) > 0)(\forall \bar{\mathbf{x}}_0 \in B_{\delta(t_0, \varepsilon)})(\forall t \geq t_0) \Rightarrow (\|\bar{\mathbf{x}}(t, t_0, \bar{\mathbf{x}}_0)\| < \varepsilon), \quad (2)$$

where $\|\cdot\|$ designates an Euclidian metric on \mathfrak{R}^n .

It is said that $\bar{\mathbf{x}}^*$ is *asymptotically Lyapunov stable* in Ω if, in addition to (2),

$$\lim_{t \rightarrow \infty} \bar{\mathbf{x}}(t) = \mathbf{0}, \quad (3)$$

The subspace Ω of \mathfrak{R}^n within which the system is (asymptotically) Lyapunov stable is called the

(attraction) stability domain of $\bar{\mathbf{x}}^*$. If the (attraction) stability domain is all of \mathfrak{R}^n , $\bar{\mathbf{x}}^*$ is said to be (asymptotically and) globally Lyapunov stable.

Conceptually, Lyapunov stability means that an equilibrium point is stable if all solutions originating in its neighbourhood forever remain "close enough" to equilibrium.

3. STABILITY OF BIOLOGICAL COMMUNITIES

Communities of biological organisms are usually modelled by differential equations, similar to those used in physics and other sciences. The only difference is that components of the state vector represent biological variables, usually population sizes of species in a community, instead of typical physical variables.

Lotka-Volterra model is one of the first models to incorporate interactions between the species at two trophic levels, and it included interacting populations of one predator and one prey. The model was independently proposed by Lotka (1925) and Volterra (1926) who argued that consumer and resource populations could be treated like particles interacting in a homogeneously mixed gas or liquid and represented in the following form:

$$\begin{aligned} \frac{dx_y(t)}{dt} &= ax_y(t) - \alpha x_y(t)x_d(t); \\ \frac{dx_d(t)}{dt} &= -bx_d(t) + \beta x_d(t)x_y(t), \end{aligned} \tag{4}$$

where x_d and x_y designate predator and prey population sizes; a represents prey birth rate; b represents predator death rate; and $\alpha, \beta > 0$ represent the effect of prey on predator and *vice versa*.

Different variations and a generalized form of model (4) to include populations of n species have been suggested:

$$\frac{dx_i}{dt} = x_i \left(r_i - \sum_{j=1}^n \gamma_{ij} x_j \right), \tag{5}$$

where r_i is the intrinsic growth rate of species i ; γ_{ij} is the effect of species j on species i which can represent any type of interspecific interactions.

Mathematical technique of Lyapunov stability has been successfully applied to models like (4) or (5) to determine conditions biological communities must satisfy to be stable. It is even possible to state that research of this kind was a dominating trend and, as noted by Justus (2006), set much of the agenda of twentieth century mathematical ecology.

It should, however, be noted that a mathematical model of biological communities in the form of (4) or (5) does not represent an ecosystem as a single whole. Further, exogenous perturbations affect ecosystems differently from physical systems and the perturbed ecosystem behaviour based on homeostatic mechanisms is also and substantially different from that observed in the physical systems. From these perspectives, a conclusion of an ecosystem stability or instability, derived from an analysis of the equilibrium properties of a mathematical model of biological communities, is a mathematical artefact rather than a real characteristic of ecosystem behaviour and, thus, is a matter of mathematical convenience rather than ecological usefulness (Straškraba, 1995). These fundamental reasons rooted in the specific nature of ecosystems and their responses to perturbations will be briefly reviewed in the subsequent sections.

4. WHAT IS AN ECOSYSTEM?

A natural ecosystem can be defined as an independent spatiotemporal unit of interrelated living (biotic) components interacting with non-living (abiotic) factors and the processes governing functioning and structure of the ecosystem components (Muller, 1997; Odum, 1953; Tansley, 1935).

Abiotic factors are broadly classified under three categories: (1) climatic factors which include the climatic regime and physical factors of the environment like solar radiation, humidity, atmospheric temperature, wind speed and direction, precipitation, current, salinity, *etc.*; (2) inorganic substances like water, carbon, sulphur,

nitrogen, phosphorus, potassium, calcium and so on; and (3) organic substances like proteins, lipids, carbohydrates, humic substances, *etc.*

A biotic part of an ecosystem (plants, animals and micro-organisms) is organized in hierarchical structures according to their role in the energetic and metabolic processes called trophic levels. Since 80 to 90% of potential energy is lost as heat at each trophic level, there are usually no more than 4 or 5 trophic levels in an ecosystem. The basis of any trophic structure is formed by the autotrophs, i.e. plants producing high-energy complex organic compounds from inorganic raw materials by means the process of photosynthesis. The upper trophic levels are called heterotrophs (or consumers), i.e. generally animals which feed directly on the autotrophic plants or prey upon other organisms at the lower heterotrophic levels. Saprotrophs (or decomposers), i.e. generally micro-organisms (bacteria and fungi) represent a special kind of heterotrophs which break down the complex organic compounds of dead or decaying matter converting them to a form of nutrients usable to autotrophs.

Biologically, biotic components of an ecosystem are assembled into populations of a particular species whereas two or more populations occupying the same geographical area form a community.

The ecosystem processes (like production, destruction, respiration, transformation, *etc.*) as well as intro- and interspecific interactions (e.g., competition, predation, parasitism, mutualisms and so on) are characterized by the quantitative values of the corresponding parameters.

Therefore, an adequate description of an ecosystem (E) is a three-compartment tuple, which includes a set $\{C\}$ of biotic components and abiotic factors (i.e., ecosystem constituents), a set $\{S\}$ of their particular assemblages and interrelationships (i.e., ecosystem structure), and a set $\{P\}$ of ecosystem parameters designating quantitative values of the ecological processes involving components, factors, and interactions between them:

$$E = \langle \{C\}, \{S\}, \{P\} \rangle. \quad (6)$$

5. GENERALIZED MODEL OF AN ECOSYSTEM

Suppose that at any given moment in time t the components (or sub-systems) of an ecological system can be represented by a non-negative n -dimensional state vector $\mathbf{x}(t) = [x_1(t), \dots, x_n(t)] \in \Omega \subseteq \mathfrak{R}^n$. The coordinates of vector $\mathbf{x}(t)$ quantitatively designate elements of the set $\{S\}$, i.e. both biotic and abiotic constituents of the ecosystem and their properties, such as richness and density of species or their assemblages, concentrations of organic and inorganic matters and polluting substances, *etc.* The system is influenced by exogenous perturbations denoted as an r -dimensional vector $\mathbf{u}(t) = [u_1(t), \dots, u_r(t)] \in U \subseteq \mathfrak{R}^r$. Parameters of the ecosystem, i.e., elements of the set $\{P\}$, are represented by an m -dimensional vector $\mathbf{p}(t) = [p_1(t), \dots, p_m(t)] \in P \subseteq \mathfrak{R}^m$. In general case, each coordinate of $\mathbf{x}(t)$ will depend on all coordinates, inputs \mathbf{u} and parameters \mathbf{p} ; each parameter $p_j(t)$ also depends on external disturbances. Then, a model for the evolution of the ecosystem is governed by an equation:

$$M[t, \mathbf{x}(t), \mathbf{u}(t), \mathbf{p}(t)] = 0 \quad (7)$$

with the initial conditions $\mathbf{x}(t_0) = \mathbf{x}_0$. Here M is the model dynamics operator. Admissible states of the model $(\mathbf{x}, \mathbf{u}, \mathbf{p}) \in \Omega \times U \times P \subseteq \mathfrak{R}^{n+r+m}$. Depending on the aim of the research, a particular ecosystem being modelled and observation data available, the operator M may be in the form of an algebraic expression, difference, differential or integral operator. Often in ecological applications, M characterizes ecosystem dynamics in terms of ordinary differential equations, in which case (7) can be rewritten as:

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(t, \mathbf{x}(t), \mathbf{u}(t), \mathbf{p}(t, \mathbf{u}(t))). \quad (8)$$

The structure of the modelled real-world ecosystem $\{S\}$ is expressed through the values of state variables and parameters and a particular structure of model (8), i.e., mathematical form of functions f_i ($i = \overline{1, n}$) in \mathbf{F} .

6. TYPES OF ECOSYSTEM PERTURBATIONS

There are several perspectives in the consideration of real-world perturbations within the problem of ecological stability. Firstly, in accord with the two major constituents of an ecosystem, it has been suggested (Khaiter and Erechtkhoukova, 2007) to distinguish between two kinds of stress: (1) a direct impact on abiotic environment (A-stress) and (2) that on biotic assemblages (B-stress). For example, acidic deposition, nutrient or toxic loading to a lake ecosystem will directly influence aquatic chemistry (A-stress) eventually producing distressed conditions for biotic components of the ecosystem. In contrast to that, such kinds of disturbances as hunting, forest cutting, fishing or grazing will directly affect biotic assemblages of the relevant ecosystems (B-stress).

Secondly, perturbations assume different forms in terms of their duration, shape and/or intensity. They can appear, for example, as: (1) instantaneous impulse (I-stress); (2) periodic signals (P-stress); (3) monotonous impact (M-stress); or (4) stepwise impulse (W-stress).

Thirdly, perturbations may affect and change different components of the real-world ecosystem as represented by its mathematical models like (7) or (8), including: (1) initial conditions (C-

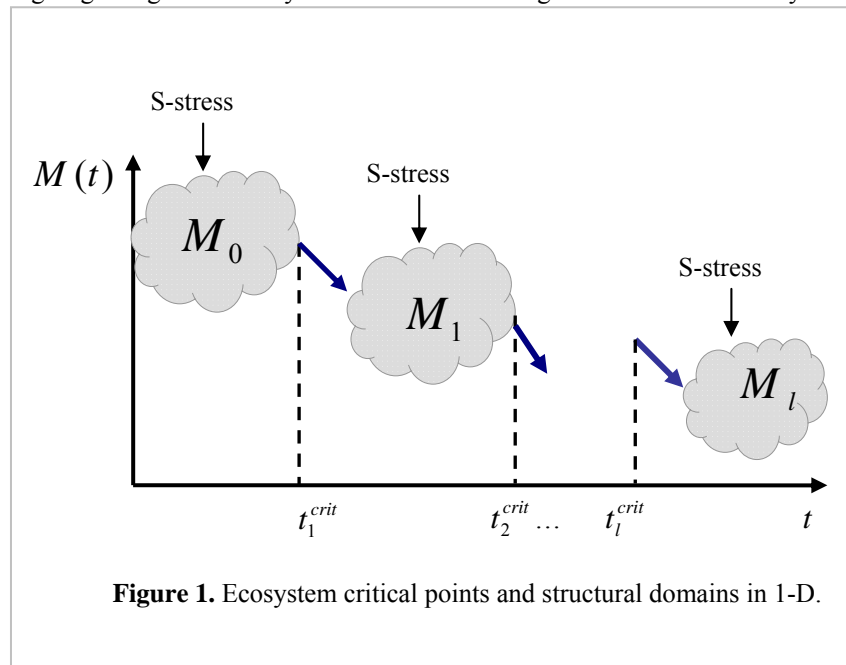


Figure 1. Ecosystem critical points and structural domains in 1-D.

stress); (2) environmental abiotic factors (A-stress); (3) biological populations in biotic assemblages and the corresponding values of the model variables (B-stress); (3) parameter values (P-stress); and (4) ecosystem structure (S-stress). S-stress or P-stress may alter the strength and qualitative nature of inter- and intraspecific community interactions whereby, for example, initially non-interacting species may begin competing or exhibiting other non-neutral interactions, and *vice versa* (Justus, 2006).

7. ECOLOGICAL DYNAMICS AND STABILITY

Intuitively, ecosystem stability is understood as an ability to persist in the course of a sufficiently long time in spite of perturbations coming from the environment. Many researchers noted that, though intuitively clear, the notion of ecosystem stability can scarcely be defined in a formal and unambiguous way.

It is undisputable that mathematical models and stability investigation exercise on their basis have to adequately represent ecosystem behaviour in response to each type of stress. It has been demonstrated (Khaiter and Erechtkhoukova, 2007) that there are common patterns in the behaviour of ecosystems as they respond to anthropogenically caused perturbations and, following classical papers by Holling (1973) and Odum (1983), five scenarios in ecosystem dynamics have been determined: (1) resistance; (2) deformation; (3) resilience; (4) degradation; and (5) shift.

In addition, ecological stability has to capture all possible changes exogenous perturbations may cause to an ecosystem (and its model), i.e., with regard to the state variables, parameters and the structure of the ecosystem. In particular, a system affected by S-type of stress can cross a critical point, shift to a new structural quality and get from one basis of homeostasis to another one. In this case, the perturbed dynamics of an ecosystem is a sequence of critical time instants $t_1^{crit}, t_2^{crit}, \dots, t_l^{crit}$ at which structural transformations occur. An ecosystem passing over a critical point must be studied and modelled as a new system, though a new model can, to a different extent, inherit certain features of the old one (Pusachenko, 1989). In terms of a generalized ecosystem model (7), critical transformations appear as a sequence of models, each suitable only for a certain domain where the ecosystem maintains its structure (see Fig. 1):

$$M_0 \xrightarrow[t_1^{crit}]{\text{S-stress}} M_1 \xrightarrow[t_2^{crit}]{\text{S-stress}} \dots \xrightarrow[t_l^{crit}]{\text{S-stress}} M_l. \quad (9)$$

Consequently, ecological stability can be studied only within a structural domain, and a new model has to be built and analysed once the ecosystem has crossed a critical point. Several important questions require answers:

- what change in the ecosystem should be considered as a critical transformation leading to a new structural domain?
- will one species extinction mark a critical transformation?
- is the critical transformation reversible or irreversible?

An ecosystem can be viewed in terms of its dominant species (e.g., Mueller-Dombois, 1988). A switch from one group of dominant species to another one is an example of structural transformation. Myster (2001) suggested that ecosystem structural pattern must be tied to the functions that are critical for the continued operation of the ecosystem. Primary plant-based functions of productivity / respiration / decomposition (Watt, 1947) as well as nutrient cycling and energy transfer / loss are the most important ecosystem functions. These characteristics can be used as indicators of critical transitions leading the ecosystem to a new structural domain.

8. CRITERION OF ENVIRONMENTAL SUSTAINABILITY

In application to environmental issues, *sustainability* is understood as maintaining natural capital and resources (Goodland, 1995) and most commonly defined as “development that meets the needs of present generations without compromising the ability of future generations to meet their needs” (Our Common Future, 1987). The breadth and vagueness of the definition, however, provides no criterion and makes it of little use in practice. Ecological stability and primary ecosystem functions can play a role in the building of a criterion of environmental sustainability. Let w denote a critical ecosystem function of interest. At each time instant, the value of w depends on exogenous perturbations and components of the state vector, i.e. $w = w(t, \mathbf{x}(t), \mathbf{u}(t))$. The process extends to some future time, $t_1 = T$. Assume there is a minimal level of critical function, w_{\min} , an ecosystem is required to maintain. Then, the problem of environmental sustainability can be formulated as finding permissible exogenous perturbations $\mathbf{u}^*(t)$ such that subject to model (7) or (8)

$$w(t, \mathbf{x}(t), \mathbf{u}(t)) \geq w_{\min} \quad \forall t \in [t_o, t_1] \quad (10)$$

The values of $\mathbf{u}^*(t)$ found as the solutions of problem (10) restrict anthropogenic impact onto the ecosystem in study so that its rehabilitation abilities were not exceeded and the ecosystem can operate within a certain structural domain, thus, preventing the ecosystem from critical transitions leading to ecosystem deterioration or destruction.

9. DISCUSSION AND CONCLUSIONS

An ecosystem is described by its biotic components, abiotic factors, parameters and structural organization. None of these characteristics remains fixed in the course of ecosystem perturbed dynamics. As suggested in the paper, exogenous perturbations affect and change different aspects of a real-world ecosystem, including: (1) initial conditions of the state variable (C-stress); (2) environmental abiotic factors (A-stress); (3) biological populations in biotic assemblages (B-stress); (3) parameter values (P-stress); and (4) ecosystem structure (S-stress).

A mathematical articulation of ecological stability and sustainability is expected to improve environmental decision making through employing the mathematical techniques for the investigation of anthropogenic impact onto ecosystems and prediction of their perturbed dynamics (Vincent, 1996). In many cases, the concept of ecological stability is derived from mathematical theory of stability under unspoken assumptions that there is a model which describes an investigated ecosystem realistically. However, mathematical stability is defined over the infinite time intervals and with model parameters and structure remaining invariable. The latter assumptions are inconsistent with the real ecosystem behaviour, and it is most likely that the original model would hardly describe it.

In particular, an ecosystem affected by S-type of stress can cross a critical point and shift to a new structural quality domain. Once structural transformation has occurred, an ecosystem must be modelled as a new system, though a new model can inherit certain features of the old one. Consequently, ecological stability can be studied only within a structural domain, and a new model has to be built and analysed once the ecosystem has crossed a critical point. Any judgement about ecosystem stability or instability is also valid only for a given structural domain and there should be a sequence of models reflecting structural transformations of the real world systems.

These remarks warn against a simplified interpretation of the stability analysis results in environmental modelling and decision making. At the same time, it is important to elaborate on the issues bridging theoretical ecology and mathematical stability within the scope of environmental sustainability including such questions as quantitative estimates of permissible anthropogenic loads, critical points of structural transformations in ecosystem dynamics, understanding the structural integrity and conditions causing structural shifts to take place. Answers to these and other related questions would make interpretation of the notion of ecological stability scientifically justifiable.

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