Permanence and viability

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The history of Systems Analysis and its forerunners displays an interesting tension between dynamic and static viewpoints. In intention, the dynamical aspects were stressed again and again. In effect, the outcome was most often a static analysis of equilibria.

One reason for this shortcoming lies obviously in the mathematical intricacies of non-equilibrium situations, which for a long time led to their neglect. Even if Poincaré and other classical authors stressed the amazing complexity of some mechanical problems, the general trend, as reflected in many a textbook, ignored such 'subtleties' and concentrated on a handful of tractable equations and on localized stability analysis. It is only in the last decade that the prevalent and exciting nature of complicated asymptotic behaviour became generally recognized. This shift in perspective is due to the development of new mathematical techniques, to the spread of computing facilities and, possibly, to the growing recognition of the limits of human abilities of handle, predict or control complex situations.

Other reasons for the dominating influence of equilibrium concepts in the history of Systems Analysis are of a non-mathematical nature. In the most diverse fields of physics and chemistry, ecology and economy, steady states were recognized, or at least postulated, as prime objects of study. It may be the fact that we are living today in a less stable world which has caused a shift in the focus of our interests, "from being to becoming", to quote Prigogine's expression. Irreversibility, oscillations, synergetic phenomena, phase transitions, turbulence and chaos forced themselves in to the foreground of scientific investigation. Climacting ecosystems à la Clements or economic *optima sensu* Pareto appear in many instances now as too good to be true. The tremendous progress of equilibrium theories and optimization techniques forced the subject to level off, like a plane reaching thinner layers of the atmosphere. By their very precision, mathematical investigations restricted the domains where we are prepared to expect stable equilibria. Their existence is something which has to be proved and cannot be taken for granted.

The growing interest in nonequilibrium situations has led to the emergence of new notions whose meanings have not settled down yet to formal definitions, but which, partly because of this, prove to be highly stimulating. As an example, we mention here 'resilience', a concept introduced by Holling [5] in ecological context. Loosely speaking, it measures the ability of a system to maintain its structure in the face of disturbance, but stands in contrast to the concept of stability in the strict static sense. "Stability... emphasizes on equilibrium condition, low

variability, and resistence to and absorption of change. In sharp contrast, resilience emphasizes the boundary of a stability domain and events far from equilibrium, high variability and adaptation to change" [6]. Resilience is therefore a thoroughly dynamic notion. (The fact that it has also been defined as "how fast the variables return to equilibrium" [12] shows that the static viewpoint is extremely resilient, however).

It is quite clear that resilience has so many facets that it will eventually give rise to a whole family of mathematical descriptions. We shall not try to do so here, but rather discuss two concepts from nonequilibrium theory which, while certainly no substitutes for resilience, share with it the emphasis on behaviour near the boundary. One of these notions, 'permanence', belongs to the qualitative theory of differential equations. The other one, 'viability', plays a central role in the theory of differential inclusions.

To introduce permanence, we consider systems whose state space is either the positive orthant $\mathbb{R}^n_+$ or the unit simplex S_n. The system will be called permanent if the boundary (including, in the first case, infinity) is an unreachable repellor, or equivalently if there exists a compact subset in the interior of the state space where all orbits starting from the interior eventually end up. What happens in the inside of this compact set—whether the asymptotic behaviour leads to equilibria, cycles, strange attractors or what not—is irrelevant in this context.

Permanence is of particular interest for ecological equations of the type

$$\dot{x}_i = x_i f_i(x) \tag{1}$$

on $\mathbb{R}^n_+$, or replicator equations

$$\dot{x}_i = x_i \left(f_i(x) - \sum x_j f_j \right) \tag{2}$$

on the (invariant) space S_n. For such equations, the boundary of the state space—which consists of the states where one or several of the components are zero—is invariant.

Equations (1) and (2) play a prominent role in several fields of biomathematics. Even the special case where $f_i(x)$ is an affine linear function (leading to Lotka–Volterra equations in case (1) and first order replicator equations in case (2)) covers a wide variety of examples. They have been investigated independently in (1) population ecology (ii) population genetics (iii) the theory of prebiotic evolution of selfreplicating polymers and (iv) sociobiological studies of evolutionarily stable traits of animal behaviour. Within these contexts, the dynamics describe the effects of selection upon (i) densities of interacting species (ii) allele frequencies in a gene pool (iii) concentrations of polynucleotides in a dialysis reactor and (iv) distributions of behavioural phenotypes in a given species (see [16] and [17]). We mention in particular the 'game-dynamics' associated with (iv). Indeed, it has often been remarked that game theory is essentially static. However, the first order replicator equations offer dynamic models for normal form games. In fact, the dynamic extension is already implicit in the notion of evolutionarily stable state [11], which is a refinement of the concept of Nash equilibrium (cf. [15]). It turns out that Nash equilibria will represent in many cases not the limits of orbits, but the limits of their time averages.

Systems of type (1) or (2) are permanent if there is an $\epsilon > 0$ such that $x_i(t) \geq \epsilon$ (and, in case (1), $x_i(t) \leq 1/\epsilon$) for all i and for all sufficiently large t, provided $x_i(0) > 0$ for all i. Such systems, then, are robust in a sense which is obviously of great practical importance in ecology, genetics or chemical kinetics (cf. [17]). On the one hand, the state remains bounded away from the boundary even if it oscillates in some regular or irregular fashion: therefore a population (or

component) within this system cannot by wiped out by small fluctuations. On the other hand, if the system starts on the boundary, i.e. with one or more components missing, and if some exterior influence (a mutation, for example) introduces these components, even if only in tiny quantities, they will spread, with the result that the system will soon be safely cushioned away from the faces of the simplex.

We should make here a few remarks. Firstly, permanence is not a structurally stable property (in the same way that the asymptotic stability of a fixed point is not necessarily structurally stable).

Secondly, a non-permanent system does not always lead to the exclusion of some components. It can also happen that each interior orbit remains bounded away from the faces, but by a threshold which depends on the orbit; for permanence, the threshold must be uniform. As a consequence of Brouwer's fixed point theorem, there must be an equilibrium in the interior of the state space if the system (1) or (2) is permanent. But this equilibrium may be unstable and have no physical relevance at all.

The most useful sufficient condition for permanence is the existence of a function P defined on the state space, vanishing on the boundary and strictly positive in the interior, such that $\dot{P} = P\psi$ where ψ is a continuous function with the property that, for all x on the boundary, there is some $T > 0$ such that

$$\frac{1}{T}\int_0^T \psi(x(t)) \, dt > 0. \tag{3}$$

We shall describe P as an 'average Ljapunov function'. Near the boundary, P increases 'on average', so that the orbits move away from the boundary (see [4] and, for a refinement, [8]). There are many cases where one can display an average Ljapunov function but not a Ljapunov function in the strict sense.

Permanence has been analyzed in many different contexts. In the ecological sphere, for example, Hutson and Vickers [7] have characterized permanence for Volterra-Lotka equations modelling one predator and two preys, and Hutson [8] has investigated permanence for 'switching predators'. These papers furthermore describe examples showing that a limitation of the discussion to a local or global stability analysis can be quite misleading. Hutson and Law [10] characterize permanent 3-species systems for a very general class of ecological equations. Within the context of autocatalytic chemical systems, Schuster et al. [13] and Hofbauer [4] have proved permanence for the 'hypercycle', which is described by (2) with $f_i(x) = x_{i-1}F_i(x)$ (the indices being counted mod n) and $F_i(x) > 0$. Such catalytic feedback loops occur at a central place in the theory of Eigen and Schuster on macromolecular selforganization (cf. [2]). If the F_i are constants, such hypercycles exhibit a globally attracting equilibrium for $n \le 4$. For a larger number of components, however, the oscillations will not settle down. Permanence guarantees, however, that no molecular information stored in the feedback loop gets lost.

Other systems where the notion of permanence can be usefully applied are described by difference equations, differential equations with delays, functional differential equation etc. However, such deterministic systems seem too narrow to describe the evolution of large classes of macrosystems arising in economic and social sciences as well as in biological evolution. For really complex systems, indeed, we should take into account not only:

(1) our ignorance of the future environment of the system, but also:

(2) the absence of determinism (including the impossibility of a comprehensive description of the dynamics of the systems),

(3) our ignorance of the laws relating certain controls to the states of this system, and

(4) the variety of dynamics available to the system.

It is possible to translate these requirements into mathematics by means of differential inclusions which describe how the velocity depends in a multivalued way upon the current state of the system. This leads to equations of the type

$$\dot{x} = f(x, u) \tag{4}$$

where u is a control depending on the state x through a set valued mapping

$$u \in F(x) \quad (\text{see } [1]). \tag{5}$$

In many cases, biological, economical or other mechanisms will constrain the system to remain in a certain 'viability domain' K which we shall assume closed in $\mathbb{R}^n$. A trajectory $x(t)$ solving (4) and (5) is viable if

$$x(t) \in K \quad \text{for all } t. \tag{6}$$

This viability restriction involves naturally restrictions of the dynamical system at the boundary of K. It happens that the best way to describe these conditions is to use the contingent cone to K at x defined by

$$T_K(x) = \left\{ v \in \mathbb{R}^n : \liminf_{h \to 0^+} \frac{d_K(x + hv)}{h} = 0 \right\}$$

where $d_K(x + hv)$ is the distance from $x + hv$ to K. We then introduce the feedback regulation map R defined by

$$R(x) := \{ u \in F(x) \mid f(x, u) \in T_K(x) \}. \tag{7}$$

We observe that any viable trajectory of the controlled system is a solution to the 'feedback' differential inclusion

$$\dot{x} = f(x, u) \quad \text{with } u \in R(x) \tag{8}$$

(the initial set-valued map F is replaced by the feedback map R). The main viability theorem (see [3] and [1]) provides necessary and sufficient conditions for the existence of viable trajectories of (4)-(5). We assume that F is upper semicontinuous with nonempty convex compact images, and that f is continuous and affine with respect to the control. Then the tangential condition

$$\forall x \in K, \quad R(x) \neq \phi \tag{9}$$

is necessary and sufficient for the existence of a viable trajectory of the controlled system (8) for all initial values $x(0) \in K$. Furthermore, if we assume that K is convex and compact, there exists an equilibrium of the system, i.e. a solution of

$$\hat{x} \in K, \quad \hat{u} \in F(\hat{x}) \quad \text{and } f(\hat{x}, \hat{u}) = 0. \tag{10}$$

We can interpret equations (4) and (5) in several ways. In biological evolution, the control u can represent the genotype, the state x the phenotype, equation (4) the evolution of the phenotype controlled by the genotype, inclusion (5) biological feedbacks. The viability condition (6) describes environmental and ecological constraints, which react upon the evolution of the genotype through the regulation relation (9). This provides a mathematical metaphor of Darwinian evolution.

In economics, the control can represent the price system, summarizing enough informations for letting n consumers modify their consumptions x_i according to decentralized dynamical laws

$$\dot{x}_i = c_i(x_i, p). \tag{11}$$

Several economic agents constrain the price to obey a feedback relation of the type

$$p \in P(x). \tag{12}$$

Let M be the set of available commodities. The viability condition states that it is impossible to consume more physical commodities than available

$$x \in M. \tag{13}$$

The price evolves according to the rule

$$p \in R(x) \tag{14}$$

which provides a mathematical metaphor of Adam Smith's invisible hand. Observe that planning procedures amount to find closed loop controls $\pi(x) \in R(x)$ such that the planning bureau sets prices according to the rule $p = \pi(x)$.

Finally another feature shared by those macrosystems is the *high inertia* of the controls which change only when the viability of the system is at stake. Associated trajectories are called *heavy viable trajectories*: they minimize at each instant the norm of the velocity of the control. We can provide a formal definition of heavy viable trajectories, which requires an adequate concept of derivative of the set-valued feedback map. We show that as long as the state of the system lies in the interior of the viability domain, any regulating control will work. Therefore, along a heavy trajectory, the system can maintain the control inherited from the past. (The regulatory control remains constant even though the state may evolve quite rapidly).

What happens when the state reaches the boundary of the viability domain? If the chosen velocity is 'inward' in the sense that it pushes the trajectory back into the domain, then we can still keep the same regulatory control.

However, if the chosen velocity is 'outward', we are in a period of crisis and must find, as slowly as possible, another regulatory control such that the new associated velocity pushes the trajectory back into the viability domain.

When this strategy for 'structural change' fails, the trajectory 'dies' i.e., it is no longer viable (see Fig. 1).

The equations which govern the evolution of heavy viable trajectories also revealed a division of the viability domain into 'cells'; each cell is the subset of viable states which can be regulated by a given control. To pass from one cell to another requires the control to be changed. The boundaries of these cells signal the need for structural change. We mentioned biological evolution as a motivation for studying heavy viable trajectories. Paleontological concepts such as *punctuated equilibria* proposed by Elredge and Gould are consistent with the concept of heavy viable trajectories.

Indeed, for the first time, excavations at Kenya's Lake Turkana have provided clear fossil evidence of evolution from one species to another. The rock strata there contain a series of fossils that show every small step of an evolutionary journey that seems to have proceeded in fits and starts. Williamson examined 3300 fossils showing how thirteen species or molluscs changed over several million years. What the record indicated was that the animals stayed much the same for immensely long stretches of time. But twice, about 2 million years ago and then again 700 000
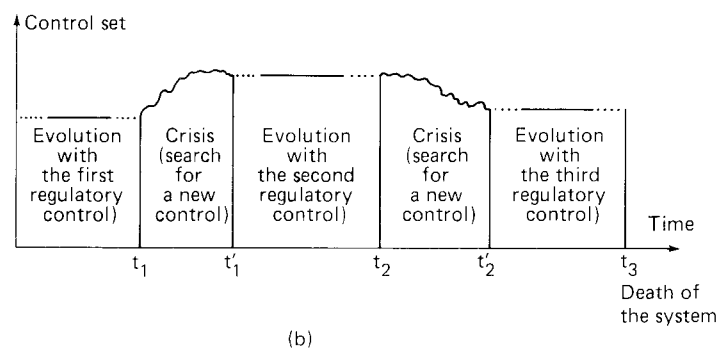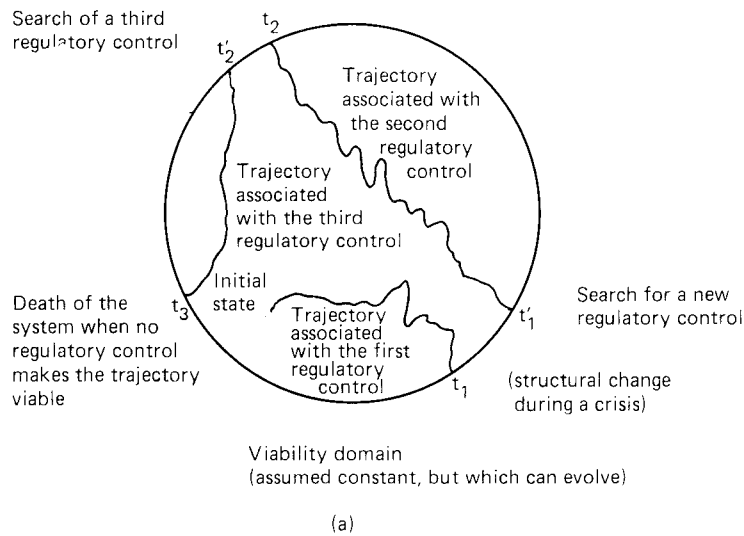
Fig. 1. (a) Evolution of the state (in the state space). (b) Evolution of the control.

years ago, the pool of life seemed to explode—set off, apparently, by a drop in the lake's water level. In an instant of geologic time, as the changing lake environment allowed new types of molluscs to win the race for survival, all of the species evolved into varieties sharply different from their ancestors. That immediate forms appeared so quickly, with new species suddenly evolving in 5000 to 50000 years after millions of years of constancy, challenges the traditional theories of Darwin's disciples since the fossils of Lake Turkana don't record any gradual change; rather, they seem to reflect eons of stasis interrupted by brief evolutionary 'revolutions'.

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