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Punctuated evolution due to delayed carrying capacity

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ABSTRACT

A new delay equation is introduced to describe the punctuated evolution of complex nonlinear systems. A detailed analytical and numerical investigation provides the classification of all possible types of solutions for the dynamics of a population in the four main regimes dominated respectively by: (i) gain and competition, (ii) gain and cooperation, (iii) loss and competition and (iv) loss and cooperation. Our delay equation may exhibit bistability in some parameter range, as well as a rich set of regimes, including monotonic decay to zero, smooth exponential growth, punctuated unlimited growth, punctuated growth or alternation to a stationary level, oscillatory approach to a stationary level, sustainable oscillations, finite-time singularities as well as finite-time death.

1. Introduction

Most natural and social systems evolve according to multistep processes. We refer to this kind of dynamics as *punctuated evolution*, because it describes the behavior of nonequilibrium systems that evolve in time, not according to a smooth or gradual fashion, but by going through periods of stagnation interrupted by fast changes. These include the growth of urban population [1,2], the increase of life complexity and the development of technology of human civilizations [3], and, more prosaically, the natural growth of human bodies [4].

According to the theory of punctuated equilibrium [5–9], the evolution of the majority of sexually reproducing biological species on Earth also goes through a series of sequential growth-stagnation stages. For most of their geological history, species experience little morphological change. However, when phenotypic variation does occur, it is temporally localized in rare, rapid events of branching speciation, called cladogenesis; these rapid events originate from genetic revolutions by allopatric and peripatric speciations [10–12]. The resulting punctuated-equilibrium concept of the evolution of biological species is well documented from paleontological fossil records [5–9,13,14]. It does not contradict Darwin's theory of evolution [15], but rather emphasizes that evolution processes do not unfold continuously and regularly. The change rates vary with time, being almost zero for extended geological periods, and strongly increasing for short time intervals. This supports Darwin's remark [15] that "each form remains for long periods unaltered, and then again undergoes modification". Here "long" and "short" are to be understood in terms of geological time scale, with "long" meaning hundreds of millions of years and "short" corresponding to thousands or hundreds of thousands of years.

The development of human societies provides many other examples of punctuated evolution. For instance, governmental policies, as a result of bounded rationality of decision makers [16], evolve incrementally [17]. The growth of organizations, firms, and scientific fields also demonstrates nonuniform developments, in which relatively long periods of stasis are followed by intense periods of radical changes [18–20]. During the training life of an athlete, sport achievements rise also in a stepwise fashion [21].

Despite these ubiquitous empirical examples of punctuated evolution occurring in the development of many evolving systems,

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to our knowledge, there exists no mathematical model describing this kind of evolution. The aim of the present paper is to propose such a mathematical model, which is very simple in its structure and its conceptual foundation. Nevertheless, it is surprisingly rich in the variety of regimes that it describes, depending on the system parameters. In addition to the process of punctuated increase, it demonstrates punctuated decay, punctuated up–down motion, effects of mass extinction, and finite-time catastrophes.

The paper is organized as follows. Section 2 presents the derivation of the novel logistic delay equation that we study in the rest of the paper. Section 3 describes the methodology used to study the logistic delay equation, both analytically and numerically. The next four Sections 4–7 present the classification of all possible types of solutions for the dynamics of a population obeying our logistic delay equations, analyzing successively the four possible situations dominated respectively by: (i) gain and competition, (ii) gain and cooperation, (iii) loss and competition, and (iv) loss and cooperation. Section 8 concludes by providing figures, which summarize all possible regimes.

2. Model formulation

2.1. Derivation of the general model

The logistic equation, advanced by Verhulst [22], has been the workhorse model for describing the evolution of various social, biological, and economic systems:

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\left[1 - \frac{N(t)}{K}\right]. \tag{1}$$

Here $N(t)$ is a measure characterizing the system development, e.g., the population size, the penetration of new commercial products or the available quantity of assets. The coefficient r is a reproduction rate and K is the carrying capacity. The expression $r(1 - N/K)$ is interpreted as an effective reproduction rate which, in expression (1), adjusts instantaneously to $N(t)$. It is possible to assume that this effective reproduction rate lags with a delay time τ, leading to the suggestion by Hutchinson [23] to consider the following equation

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\left[1 - \frac{N(t-\tau)}{K}\right], \tag{2}$$

termed the delayed logistic equation. Many other variants of the logistic equation have been proposed [24–30], uniform or nonuniform, with continuous or discrete time, and with one or several delays. An extensive literature on such equations can be found in the books [31–33].

All known variants of the logistic equation describe either a single-step evolution, called the S-curve, or an oscillatory behavior around a constant level. However, as summarized in the introduction, the development of many complex systems consists not just of a single step, where a period of fast growth is followed by a lasting period of stagnation or saturation. Instead, many systems exhibit a succession of S-curves, or multistep growth phases, one fast growth regime followed by a consolidation, which is itself followed by another fast growth regime, and so on. This multistep precess can be likened to a staircase with approximately planar plateaus interrupted by rising steps.

Motivated by the ubiquity of the multistep punctuated evolution dynamics on the one hand and the simplicity of the logistic equation on the other hand, we now propose what, we think, is the simplest generalization of the logistic equation that allows us to capture the previously described phenomenology and much more.

Our starting point is to take into account the main two causes of development, (i) the evolution of separate individuals composing the system and (ii) their mutual collective interactions, leading to the consideration of two terms contributing to the rate of change of $N(t)$:

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = \gamma N(t) - \frac{CN^2(t)}{K(t)}. \tag{3}$$

The first term $\gamma N(t)$ embodies the individual balance between birth and death, or gain and loss (depending on whether a population size or economic characteristics are considered), i.e., the growth rate can be written as follows

$$\gamma = \gamma_{birth} - \gamma_{death} = \gamma_{gain} - \gamma_{loss}. \tag{4}$$

The second term $CN^2(t)/K(t)$ describes collective effects, with the coefficient C defining the balance between competition and cooperation,

$$C = C_{comp} - C_{coop}. \tag{5}$$

The denominator in the second term of Eq. (3) can be interpreted as a generalized carrying capacity.

The principal difference between Eq. (3) and the logistic equation is the assumption that the carrying capacity is a function of time. We assume that the carrying capacity is not a simple constant describing the available resources, but that these resources are subjected to the change due to the activity of the system individuals, who can either increase the carrying capacity by creative work or decrease it by destructive actions. Given the coexistence of both creative and destructive processes impacting the carrying capacity $K(t)$, we formulate it as the sum of two different contributions:

$$K(t) = A + BN(t-\tau). \tag{6}$$

The first term A is the pre-existing carrying capacity, e.g., provided by Nature. In contrast, the second term is the capacity created (or destroyed) by the system. To fix ideas, let us illustrate by using this model the evolution of human population of the planet Earth. Then, the second term $BN(t-\tau)$ is meant to embody the delayed impact of past human activities in the present services provided by the planet. There are many complex feedback loops controlling how human activities interact with the planet regeneration processes and it is generally understood that these feedback loops are not instantaneous but act with delays. A full description of these phenomena is beyond the scope of this paper. For our purpose, we encapsulate the complex delayed processes by a single time lag τ, which will be one of the key parameters of our model. We stress that the delay time τ is introduced to describe the impact of past human activity on the present value of the carrying capacity. This is crucially different from the description (2) by Hutchinson [23] and others, in which $\tau > 0$ represents delayed interactions between individuals. In our model (3) with (6), the cooperation and competition between individuals are controlled by instantaneous interactions $N(t) \times N(t)$, while the present carrying capacity $K(t)$ reflects the impact of the population in the past at time $t - \tau$. The lag time τ is thought of as embodying a typical time scale for regeneration or decay of the renewable resources provided by the planet. If positive (respectively, negative), the parameter B describes a productive (respectively, destructive) feedback of the population on the carrying capacity.

Although Eq. (3) with (6) is reminiscent of the logistic equation (1), it is qualitatively different from it by the existence of the time-dependent delayed carrying capacity. As we show in what follows, this difference turns out to be mathematically extremely important, leading to a variety of evolution regimes that do not exist in the logistic equation, neither in the standard version nor in the delayed one of Hutchinson [23] and others.

In particular, the delayed response of the carrying capacity to the population dynamics is found to be responsible for the occurrences of regimes in which growth or decay unfold jerkily in