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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 non-linear 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.

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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 the 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, of firms, and of 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, to our knowledge, there exists no mathematical model describing this kind of evolution. It is the aim of the present paper 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 four following 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:

$$\frac{dN(t)}{dt} = rN(t) \left[1 - \frac{N(t)}{K} \right]. \quad (1)$$

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 equation

$$\frac{dN(t)}{dt} = rN(t) \left[1 - \frac{N(t - \tau)}{K} \right], \quad (2)$$

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 process 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 $N(t)$:

$$\frac{dN(t)}{dt} = \gamma N(t) - \frac{CN^2(t)}{K(t)}. \quad (3)$$

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

$$\gamma = \gamma_{birth} - \gamma_{death} = \gamma_{gain} - \gamma_{loss}. \quad (4)$$

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

$$C = C_{comp} - C_{coop} . \quad (5)$$

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 co-existence of both creative and destructive processes impacting the carrying capacity $K(t)$, we formulate it as the sum of two different contributions:

$$K(t) = A + BN(t - \tau) . \quad (6)$$

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 the sequel, 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 a series of stagnations interrupted by fast changes. The duration of these plateaus is controlled by the characteristic delay time scale τ , which can be arbitrarily long or short depending on the domain of application. We capture this remarkable phenomenon by using the term *punctuated evolution* in the title (in contrast with “punctuated equilibrium”).

2.2 Reduced variables and parameters

The quantity $N(t)$ is always measured in some units N_{eff} . For instance, this could be millions of persons when population is considered, or billions of currency units for economic systems, or thousands of tons of goods for firm production. Hence, it is reasonable to define the relative quantity

$$x(t) \equiv \frac{N(t)}{N_{eff}} . \quad (7)$$

For mathematical analysis, it is convenient to deal with dimensionless quantities. We thus define the dimensionless value of the pre-existing resources

$$a \equiv \frac{A}{N_{eff}} \left| \frac{\gamma}{C} \right| \quad (8)$$

and of the production (or destruction) factor

$$b \equiv B \left| \frac{\gamma}{C} \right| . \quad (9)$$

The dimensionless carrying capacity is defined as

$$y(t) \equiv \frac{K(t)}{N_{eff}} \left| \frac{\gamma}{C} \right| . \quad (10)$$

Using (8) and (9), expression (6) becomes

$$y(t) = a + bx(t - \tau) . \quad (11)$$

We also define the following notation for the signs of γ and of C :

$$\sigma_1 \equiv \frac{\gamma}{|\gamma|} , \quad \sigma_2 \equiv \frac{C}{|C|} . \quad (12)$$

Using a time measured in unit of $1/\gamma$, and keeping the same notation of time, Eq. (3) reduces to the evolution equation for $x = x(t)$,

$$\frac{dx}{dt} = \sigma_1 x - \sigma_2 \frac{x^2}{y} , \quad (13)$$

in which $y = y(t)$ is given by Eq. (11).

There are two time scales in this problem. The first time scale, $1/\gamma$ in the dimensional units of Eq. (3) and 1 in the dimensionless units of Eq. (13), corresponds to the characteristic exponential growth or decay of the population in the absence of interactions ($C = 0$). The second time scale is the delay parameter τ in (11), which is expressed in units of the first time scale in our following investigation.

This equation is complemented by an initial history condition

$$x(t) = x_0 \quad (t \leq 0) , \quad (14)$$

according to which

$$y(t) = y_0 = a + bx_0 \quad (t \leq 0) . \quad (15)$$

Equation (13) possesses two trivial solutions: $x(t) = 0$, under any initial conditions; and

$$x(t) = x_0 \quad (y_0 = \sigma_1 \sigma_2 x_0), \quad (16)$$

occurring under the special initial conditions, given in brackets. In the following, we will mainly focus our attention on nontrivial solutions.

We now discuss the range of variation of the different parameters.

- The coefficient a , characterizing the initial resources provided by Nature, is non-negative.
- The coefficient b , controlling the impact of past population on the present carrying capacity, can be either positive or negative, depending on whether production or destruction dominates. A known example for $b < 0$ is the destruction of habitat by humans, associated with deforestation, reduction of biodiversity, and climate changes [34–37]. The destruction of the global Earth ecosystem is caused by the rapid growth of the human population, which is sometimes compared with a pathological cancer process that could result in the eventual extinction of the human population [38]. Another example of destructive activity is firm mismanagement, and operational risks, which can result in firm bankruptcy and even in a global economic crisis, when many economic and financial institutions are mismanaged [39, 40]. One more illustration is the destruction of the economy of a country by a corrupted government. In contrast, a positive b corresponds to improved exploitation of resources and increased productivity.
- The initial value x_0 of the dimensionless population is positive.
- The initial value y_0 of the carrying capacity can be either positive or negative. The standard case is, of course, $y_0 > 0$. A negative value y_0 of the effective carrying capacity at $t = 0$ can be interpreted as describing a strongly destructive action of the agents that occurred in the preceding time interval $[-\tau, 0]$.

Summarizing,

$$a \geq 0, \quad -\infty < b < \infty, \quad x_0 > 0, \quad -\infty < y_0 < \infty. \quad (17)$$

We restrict our investigation to non-negative dimensionless population size $x(t) \geq 0$.

Finally, we need to discuss the signs σ_1 and σ_2 , that is, the signs of γ and C . If gain or birth (respectively, loss or death) prevails, γ is positive (respectively, negative). Similarly, C is positive (respectively, negative) if competition (respectively, cooperation) dominates. Competition describes the fight of individuals for scarce resources [1,2]. But in human, as well as in animal societies, cooperation is often active through feedback selection [41]. Summarizing, there are thus four possible types of societies, depending on the signs of σ_1 and σ_2 :

$$\begin{aligned} \sigma_1 > 0 \quad \& \quad \sigma_2 > 0 && \text{(gain + competition),} \\ \sigma_1 > 0 \quad \& \quad \sigma_2 < 0 && \text{(gain + cooperation),} \\ \sigma_1 < 0 \quad \& \quad \sigma_2 > 0 && \text{(loss + competition),} \\ \sigma_1 < 0 \quad \& \quad \sigma_2 < 0 && \text{(loss + cooperation).} \end{aligned} \quad (18)$$

We shall study each of these variants in turn in the following sections.

3 Scheme of stability analysis

Before studying the different variants of the evolution equation (13) with (11), it is necessary to explain the methodology that we have used to deal with such equations. The theory of linear delay equations and the stability of their solutions have been described in detail in several books [31–33] and many articles (see Refs. [42–45]). Mao theorem [46] proves that, for time lags close to zero, nonlinear delay equations inherit some properties of the nonlinear ordinary differential equations. Increasing the time lag can result in novel solutions, which are principally different from those obtained in the limit of small lags. One can even obtain multistability [47]. Thus, nonlinear delay equations are essentially more difficult to study than ordinary differential equations. The investigation of the solutions of nonlinear delay equations is usually accomplished by combining analytical methods to study the asymptotic stability of their stationary points, together with the direct numerical solution of these equations [31–33, 48].

The study of the asymptotic stability of the stationary fixed points of the nonlinear delay equation (13) with (11) is performed using the general Lyapunov stability analysis as follows. If stationary solutions x^* exist, they satisfy the equation

$$\sigma_1 x^* - \frac{\sigma_2 (x^*)^2}{a + bx^*} = 0 . \quad (19)$$

This gives two fixed points

$$x_1^* = 0 , \quad x_2^* = \frac{a\sigma_1}{\sigma_2 - b} \quad (20)$$

that are assumed to be non-negative. Considering a small deviation from these fixed points given by (20),

$$x_j(t) \simeq x_j^* + \delta x_j(t) \quad (j = 1, 2) , \quad (21)$$

the linearized version of Eq. (13) reads

$$\frac{d}{dt} \delta x_j(t) = C_j \delta x_j(t) + D_j \delta x_j(t - \tau) , \quad (22)$$

in which

$$C_j \equiv \sigma_1 - \frac{2\sigma_2 x_j^*}{a + bx_j^*} , \quad D_j \equiv b\sigma_2 \left(\frac{x_j^*}{a + bx_j^*} \right)^2 . \quad (23)$$

For the first fixed point, this yields

$$C_1 = \sigma_1 , \quad D_1 = 0 , \quad (24)$$

while for the second point, this gives

$$C_2 = \sigma_1 \frac{b(\sigma_1 - 1) - \sigma_2}{b(\sigma_1 - 1) + \sigma_2} , \quad D_2 = \frac{b\sigma_2}{[b(\sigma_1 - 1) + \sigma_2]^2} . \quad (25)$$

Looking for solutions of Eq. (21) in the form $\delta x_j(t) \propto e^{-\lambda_j t}$, we get the following equation for the characteristic exponent λ_j :

$$\lambda_j = C_j + D_j e^{-\lambda_j \tau} . \quad (26)$$

Introducing the variables

$$W \equiv (\lambda_j - C_j)\tau , \quad (27)$$

and

$$z \equiv \tau D_j e^{-C_j \tau} \quad (28)$$

transforms Eq. (26) into the equation

$$W e^W = z . \quad (29)$$

The solution to this equation, in terms of the variable W as a function of the variable z , defines the Lambert function $W(z)$. Denoting

$$\hat{W}(\tau) = W(z(\tau)) = W(\tau D_j e^{-C_j \tau}) , \quad (30)$$

allows us to obtain the solution of (26) as

$$\lambda_j = C_j + \frac{\hat{W}(\tau)}{\tau} . \quad (31)$$

A fixed point is stable when $\text{Re } \lambda_j < 0$; it is neutrally stable when $\text{Re } \lambda_j = 0$, which usually defines a center; and it is unstable if $\text{Re } \lambda_j > 0$.

It is necessary to keep in mind that the Lyapunov stability analysis for a nonlinear delay equation only gives sufficient conditions on the domain of parameters inside which the stationary solutions are stable. According to the Mao's theorem [46], a nonlinear delay equation possesses the same stable fixed points as the related nonlinear ordinary differential equation, but only in the vicinity of zero delay time. Increasing the delay time can result in new solutions, which are unrelated to those of the associated ordinary, non-delayed, equation. In addition, when there are no fixed points, there can arise different types of solutions under varying delay time. Therefore, for delay equations, the stability analysis has to be complemented by detailed numerical investigation. In the following sections, we will first apply the above stability analysis to the differential delay equation (13) with (11), for the four different regimes (18). We will then complement it with a thorough numerical investigation of the trajectories. In particular, our goal is to present an exhaustive classification of all qualitatively different types of solutions of Eq. (13) with (11) for the whole possible ranges of the parameters a , b , and τ .

4 Prevailing gain and competition ($\sigma_1 > 0, \sigma_2 > 0$)

4.1 General analysis

When gain (birth) prevails over loss (death) and competition prevails over cooperation, this corresponds to the first line in the classification (18). Then Eq. (13) translates into

$$\frac{dx(t)}{dt} = x(t) - \frac{x^2(t)}{a + bx(t - \tau)} . \quad (32)$$

At the initial stage for $t < \tau$, for which $x(t - \tau) = x_0$, Eq. (32), is explicitly solvable, giving

$$x(t) = \frac{x_0 y_0 e^t}{y_0 + x_0 (e^t - 1)} \quad (t < \tau) , \quad (33)$$

where y_0 is defined in Eq. (15). However, the following evolution of x for $t > \tau$ cannot be described analytically.

In the general case, there are two stationary solutions

$$x_1^* = 0, \quad x_2^* = \frac{a}{1-b}. \quad (34)$$

The first of them is unstable for any $a > 0$ and any b , and all $\tau > 0$. The second fixed point x_2^* is stable in one of the regions, when either

$$a > 0, \quad -1 < b < 1, \quad \tau \geq 0, \quad (35)$$

or

$$a = 0, \quad 0 < b < 1, \quad \tau \geq 0, \quad (36)$$

or

$$a > 0, \quad b < -1, \quad \tau < \tau_0, \quad (37)$$

where

$$\tau_0 \equiv \frac{1}{\sqrt{b^2 - 1}} \arccos\left(\frac{1}{b}\right). \quad (38)$$

The point x_2^* becomes a stable center (associated with a vanishing Lyapunov exponent λ_2) for

$$a > 0, \quad b < -1, \quad \tau = \tau_0. \quad (39)$$

The value τ_0 diverges, if $b \nearrow -1$, as

$$\tau_0 \simeq \frac{\pi}{\sqrt{2(|b| - 1)}} \quad (b \nearrow -1).$$

Varying the system parameters yields the different solutions, which we analyze successively.

4.2 Punctuated unlimited growth

When the carrying capacity increases, due to the intensive creative activity of the agents forming the system, which corresponds to the parameters

$$a \geq 0, \quad b \geq 1, \quad \tau \geq 0, \quad (40)$$

then $x_0 < y_0$ and the fixed point x_2^* does not exist. The function $x(t)$ grows by steps of duration $\simeq \tau$, tending to infinity as time increases to infinity. Figures 1, 2, and 3 demonstrate the behavior of $x = x(t)$ as a function of time for different values of the parameters a (Fig. 1), b (Fig. 2), and the delay time τ (Fig. 3). Different initial conditions of x_0 result in the shift of the curves, as is shown in Fig. 4. The evolution goes through a succession of stages where x is practically constant, which are interrupted by periods of fast growth. To show that, on average, the growth is exponential, we present in Fig. 5 the dependence of $\ln x(t)$ for a long time interval (long compared with τ).

4.3 Punctuated growth to a stationary level

For a lower creative activity (quantified by b) of the population affecting the effective carrying capacity, i.e., for

$$a > (1 - b)x_0, \quad 0 \leq b < 1, \quad \tau \geq 0, \quad (41)$$

which implies that

$$x_0 < y_0 < x_2^*,$$

the value of $x(t)$ monotonically grows to the stationary solution x_2^* , as is shown in Figs. 6, 7, and 8 for the varying parameters a (Fig. 6), b (Fig. 7), and x_0 (Fig. 8).

4.4 Punctuated decay to a stationary level

When the pre-existing carrying capacity a is smaller than in the previous cases and the creation coefficient b is not too high, so that

$$0 \leq a < (1 - b)x_0, \quad 0 \leq b < 1, \quad \tau \geq 0, \quad (42)$$

which means that

$$x_0 > x_2^* > y_0 > 0,$$

then $x(t)$ monotonically decays to the stationary solution x_2^* , as is shown in Fig. 9 for different parameters b .

4.5 Punctuated alternation to a stationary level

When the initial capacity a is large, but the agent activity is destructive, with the parameters

$$a > |b|x_0, \quad -1 \leq b < 0, \quad \tau \geq 0, \quad (43)$$

there are two subcases. If

$$a > (1 + |b|x_0),$$

so that

$$x_0 < x_2^* < y_0,$$

then $x(t)$ grows initially. And if

$$|b|x_0 < a < (1 + |b|x_0),$$

so that

$$x_0 > x_2^* > y_0 > 0,$$

then $x(t)$ decreases initially. However, the following behavior in both these subcases is similar: $x(t)$ tends to the stationary solution x_2^* through a sequence of up and down alternations, as shown in Fig. 10.

4.6 Oscillatory approach to a stationary level

If the capacity is large and the destructive activity is rather strong, such that

$$a > |b|x_0, \quad b < -1, \quad \tau < \tau_0, \quad (44)$$

where τ_0 is given by Eq. (38), there are again two subcases, when $x(t)$ either increases or decays initially. But the following behavior for both these subcases is again similar: $x(t)$ tends towards the focus x_2^* by oscillating around it. Contrary to the previous case 4.5, here the stagnation stages are practically absent, so that the overall evolution is purely oscillatory, with a decaying amplitude of oscillations, as shown in Fig. 11.

4.7 Everlasting nondecaying oscillations

With the parameters a and b as in the previous case, but with the time lag being exactly equal to τ_0 given by (38), that is, when

$$a > |b|x_0, \quad b < -1, \quad \tau = \tau_0, \quad (45)$$

then $x(t)$ oscillates around the center x_2^* without decaying, as shown in Fig. 12. At the initial time, x can either increase or decrease, as in the previous cases. But, it will rapidly set into a stationary oscillatory behavior without attenuation.

4.8 Punctuated alternation to finite-time death

The fact that the behavior of the system depends sensitively on the time lag τ is well exemplified by the regime in which the values of a and b are the same as in regime 4.7, but the lag becomes longer, so that

$$a > |b|x_0, \quad b < -1, \quad \tau > \tau_0. \quad (46)$$

In this regime, $x(t)$ alternates between upward and downward jumps, with increasing amplitude, until it hits the zero level at a finite death time t_d defined by the equation

$$a + bx(t_d - \tau) = 0, \quad (47)$$

at which time the rate of decay becomes minus infinity. As in the previous cases, depending on whether $x_0 < y_0$ or $x_0 > y_0$, the initial motion can be either up or down, respectively. But the following behavior follows a similar path, with $x(t)$ always going to zero in finite time, as shown in Fig. 13. The abrupt fall of the population $x(t)$ to zero can be interpreted as a *mass extinction*, as has occurred several times for species on the Earth [49-54]. Here, as in all previous cases, the considered parameters are such that the initial carrying capacity is positive, $y_0 > 0$. The effect of mass extinction in the present example is caused by the intensive destructive activity ($b < -1$) of the agents composing the system. This is an example of total collapse caused by *the destruction of habitat*.

4.9 Growth to a fixed finite-time singularity

Another example of catastrophic behavior happens when the initial carrying capacity is negative ($y_0 < 0$). This occurs when the habitat has been destroyed in the preceding time interval $[-\tau, 0]$ and the destruction goes on for $t > 0$. For the set of parameters

$$a < |b|x_0, \quad b < 0, \quad \tau \geq t_c, \quad (48)$$

with a sufficiently long time lag τ , the function $x(t)$, solution of Eq. (33), diverges at the singularity time t_c , given by the expression

$$t_c = \ln \left(1 - \frac{y_0}{x_0} \right). \quad (49)$$

The divergence is hyperbolic, i.e., in the vicinity of t_c ,

$$x(t) \simeq \frac{y_0}{t_c - t} \quad (t \rightarrow t_c - 0). \quad (50)$$

For the parameters (48), the singularity always occurs at the critical time (49) determined by the values of x_0 and y_0 , independently on the delay time τ as long as τ is larger than t_c .

4.10 Growth to a moving finite-time singularity

When the delay time τ is smaller than the singularity time t_c given by Eq. 49, with the following parameters

$$a < |b|x_0, \quad b < 0, \quad \tau_c < \tau \leq t_c, \quad (51)$$

then the critical lag τ_c , for the given parameters, can only be determined numerically. In this regime, $x(t)$ grows without bound and reaches infinity in finite time at a moving singularity time $t_c^* \geq t_c$ which is a function of τ . We find that t_c^* goes to infinity as τ decreases to τ_c . The dependence of the singularity time t_c^* as a function of τ is presented in Fig. 14.

While the model does not describe what happens beyond the singularity, the catastrophic divergence of $x(t)$ can be interpreted as a diagnostic of a transition to another state or to a different regime in which other mechanisms become dominant. In analogy with the divergences occurring at the critical points of phase transitions of many-body systems [55–57], it is natural to interpret the critical points as periods of transitions to new regimes. Ref. [58] has reviewed several examples of the application and interpretation of the occurrence of finite-time singularities in the dynamics of the world population, economics, and finance.

4.11 Exponential growth to infinity

As the delay time τ becomes smaller than the threshold value τ_c defined in the previous section, i.e., for the following parameters

$$a < |b|x_0, \quad b < 0, \quad 0 < \tau \leq \tau_c, \quad (52)$$

the finite-time singularity does not exist anymore. The function $x(t)$ exhibits a simple unbounded exponential growth to infinity, as time tends to infinity.

The exact limit of a zero time delay $\tau = 0$ is not included in this regime. When τ is exactly zero, the exponential growth regime is replaced abruptly into the regime of subsection 4.9, with a fixed-time singularity.

Figure 15 demonstrates the change of behavior of $\ln x(t)$ as a function of time for different values of the delay time τ , for fixed parameters a and b . In this regime, the variable $y(t)$ tends to minus infinity with increasing time, and it becomes difficult to interpret it as an effective carrying capacity. Rather, this regime with negative b expresses the existence of a positive feedback provided by the cooperation between agents of the system.

5 Prevailing gain and cooperation ($\sigma_1 > 0, \sigma_2 < 0$)

5.1 General analysis

When gain (birth) and cooperation prevail (second line of classification (18)), Eq. (13) becomes

$$\frac{dx(t)}{dt} = x(t) + \frac{x^2(t)}{a + bx(t - \tau)}. \quad (53)$$

The same history $x(t) = x_0$ for $t \leq 0$ as in (14) is assumed. For $t < \tau$, for which $x(t - \tau) = x_0$, the solution is

$$x(t) = \frac{x_0 y_0 e^t}{y_0 - x_0(e^t - 1)} \quad (t < \tau),$$

with y_0 given by Eq. (15).

Equation (53) possesses two fixed points

$$x_1^* = 0, \quad x_2^* = -\frac{a}{b + 1}. \quad (54)$$

The second fixed point x_2^* is positive for $b < -1$. The stability analysis, performed following the methodology explained in Section 3, shows that the first point x_1^* is always unstable. The second fixed point x_2^* can be stable, while non-negative, only for

$$a = 0, \quad -1 < b < 0, \quad \tau \geq 0. \quad (55)$$

For $a \rightarrow 0$, it merges with the first fixed point. The full analysis yields the following different types of solutions.

5.2 Growth to a fixed finite-time singularity

For the parameters

$$a > -bx_0, \quad \forall b, \quad \tau \geq t_c, \quad (56)$$

when $y_0 > 0$, the solution is monotonically increasing and becomes singular at the finite catastrophe time

$$t_c = \ln \left(1 + \frac{y_0}{x_0} \right), \quad (57)$$

which does not depend on the delay time τ , similarly to the behavior in Sec. 4.9. The occurrence of the singularity, in the presence of the positive initial carrying capacity and positive production

coefficient b , shows that the simultaneous gain and cooperation is not sustainable, since the system diverges in finite time. This paradox, that initial positive carrying capacity and ever increasing carrying capacity, intrinsically associated with a positive feedback, leads to a runaway, has been analyzed in detail in Ref. [58] in another context. To preserve stability, one would need that either the gain has to turn into loss or cooperation to be replaced by competition.

5.3 Growth to a moving finite-time singularity

For smaller delay time, when either

$$a \geq 0, \quad b > 0, \quad \tau_c < \tau < t_c, \quad (58)$$

or

$$a > |b|x_0, \quad b < 0, \quad 0 < \tau \leq t_c, \quad (59)$$

the time of the singularity becomes dependent on the lag. The singularity occurs at $t_c^* > t_c$, if $b > 0$ and at $t_c^* < t_c$, if $b < 0$. The divergence is hyperbolic as in expression (50). Keeping the parameters a and b fixed, but increasing the delay time τ , moves the singularity time t_c^* to the left towards t_c for $b > 0$, while t_c^* moves to the right again towards t_c for $b < 0$.

5.4 Exponential growth to infinity

Under the conditions

$$a \geq 0, \quad b > 0, \quad 0 < \tau \leq \tau_c, \quad (60)$$

the function $x(t)$ grows exponentially without bounds. The behavior of $x(t)$ is analogous to that of Sec. 4.11. The growth of $x(t)$ is continuous, following the increase of the effective carrying capacity associated with the positive production coefficient b . Contrary to the previous cases of Sections 5.2 and 5.3, there is no finite-time catastrophe as the shorter delay time allows for a better matching the carrying capacity and population size.

5.5 Punctuated unlimited growth

When the initial carrying capacity is negative, $y_0 < 0$, having been destroyed in the preceding time interval $[-\tau, 0]$, and the parameters are

$$a \geq 0, \quad b < -1 - \frac{a}{x_0}, \quad \tau \geq 0, \quad (61)$$

$x(t)$ follows a punctuated unlimited growth, as in Sec. 4.2. In this regime, $y(t)$ remains negative and goes to $-\infty$ at large times. Thus, $y(t) \rightarrow -\infty$ is difficult to interpret as an effective carrying capacity.

5.6 Punctuated decay to finite-time death

For the parameters

$$a > 0, \quad -1 - \frac{a}{x_0} < b < 0, \quad \tau \geq 0, \quad (62)$$

there exists a time t_d , defined by Eq. (47), when $x(t)$ sharply drops to zero, as shown in Fig. 16. This is the point of mass extinction. While the decay of $x(t)$ is a finite succession of plateaus and drops, contrary to the case of Sec. 4.8, there are no oscillations, but just a monotonic decay to death. The disappearance of $x(t)$ in this regime is due to the destructive activity ($b < 0$) aggravated by the prevailing birth (gain) and cooperation.

5.7 Punctuated decay to zero

For the parameters as in (55), that is,

$$a = 0, -1 < b < 0, \tau \geq 0, \quad (63)$$

$x(t)$ decays to zero as time tends to infinity in a punctuated fashion following a succession of plateaus followed by sharp drops. This behavior is illustrated in Fig. 17 for different values of the parameters. As in section 5.5, the decay of $x(t)$ is due to the destructive activity ($b < 0$) aggravated by the prevailing birth (gain) and cooperation.

6 Prevailing loss and competition ($\sigma_1 < 0, \sigma_2 > 0$)

6.1 General analysis

Let us now consider the regime corresponding to the third line of classification (18). In this case, Eq. (13) takes the form

$$\frac{dx(t)}{dt} = -x(t) - \frac{x^2(t)}{a + bx(t - \tau)}. \quad (64)$$

The initial history is the same as in Eq. (14). In the time interval $t < \tau$, the solution reads

$$x(t) = \frac{x_0 y_0 e^{-t}}{y_0 + x_0(1 - e^{-t})} \quad (t < \tau), \quad (65)$$

with y_0 given by Eq. (15).

There are two fixed points

$$x_1^* = 0, \quad x_2^* = -\frac{a}{1 + b}. \quad (66)$$

The second fixed point x_2^* is relevant only when it is non-negative.

The stability analysis, complemented by numerical investigations, shows the following properties. The first stationary solution $x_1^* = 0$ is stable for the parameters

$$a \neq 0, \quad \forall b, \quad \tau \geq 0. \quad (67)$$

The second stationary solution $x_2^* \neq 0$ is stable, while being positive, for

$$a > 0, \quad b < -1, \quad \tau < \tau_0, \quad (68)$$

where

$$\tau_0 \equiv \frac{1}{\sqrt{b^2 - 1}} \arccos\left(-\frac{1}{b}\right). \quad (69)$$

A distinct regime occurs for $a = 0$, for which the two fixed points merge together ($x_1^* = x_2^* = 0$). This double fixed point 0 is stable when either

$$a = 0, \quad b < -1, \quad \tau \geq 0 \quad (70)$$

or

$$a = 0, \quad b > 0, \quad \tau \geq 0. \quad (71)$$

The domains (67) and (68) overlap, indicating the existence of bistability, i.e., both stationary solutions (66) are stable simultaneously for $a > 0$ and $b < -1$. For these parameters, the solution $x(t)$ tends to one of these fixed points depending on whether the initial condition x_0 falls in the domain of attraction of the first or second fixed point. The basin of attraction of the fixed point x_1^* (respectively, x_2^*) is defined by the condition $x_0 < x_2^*$ (respectively, $x_0 > x_2^*$).

6.2 Monotonic decay to zero

For any positive starting carrying capacity $y_0 > 0$, when

$$a \geq 0, \quad b > -\frac{a}{x_0}, \quad \tau \geq 0, \quad (72)$$

the solutions to Eq. (64) always monotonically decay to zero, as is shown in Fig. 18. The case (71) is included here. The same behaviour occurs under conditions (70), though then y_0 is negative. The meaning of such a decay is evident: Prevailing loss and competition do not favor the system development.

6.3 Oscillatory approach to a stationary level

The situation is much more ramified, when $y_0 < 0$. If $y_0 < -x_0$, so that

$$a > 0, \quad b < -1 - \frac{a}{x_0}, \quad 0 < \tau < \tau_0, \quad (73)$$

where τ_0 is given by Eq. (69), then the solution $x(t)$ oscillates around the focus x_2^* , tending to it as time increases. This behaviour is illustrated by Fig. 19.

6.4 Everlasting nondecaying oscillations

In the region of the parameters

$$a > 0, \quad b < -1 - \frac{a}{x_0}, \quad \tau_0 \leq \tau < \tau_1, \quad (74)$$

where τ_1 depends on the values of a and b , the solution $x(t)$ oscillates without decay, as is presented in Fig. 20. The amplitude of the oscillations increases with increasing time lag τ . Note that the period of the oscillations is much longer than the time lag. Though this case looks similar to that studied in Sec. 4.6, there is a principal difference. Here, the oscillations persist not just for one particular lag τ_0 , but in the whole interval of lags, given in Eq. (74).

6.5 Punctuated growth to a moving finite-time singularity

With the same range of the parameters a and b , as in Eq. (74), but with the larger delay time in the interval

$$\tau_1 \leq \tau < \tau_2 , \quad (75)$$

when $y_0 < -x_0$, a finite-time singularity occurs at time t_c^* , defined by the equation

$$a + bx(t_c^* - \tau) = 0 , \quad (76)$$

where $x(t)$ diverges hyperbolically as in Eq. (50). The second characteristic delay time τ_2 depends also on the values of a and b . The difference from the divergences of Sec. 4.10, depicted in Fig. 15, is that in the present case the function $x(t)$ first decreases with time before accelerating towards the singularity. In Fig. 21, we observe that there can be several punctuated phases, the first decay followed by growth, followed by decay, followed by the final acceleration to infinity in finite time.

For $\tau > \tau_2$, the divergence is replaced by a monotonic decay to zero, as in Sec. 6.2.

The cases of Secs. 6.3, 6.4, and 6.5 illustrate how, being in the same range of the parameters a and b , but merely varying the time lag τ , can result in a principally different behaviour of the solution $x(t)$.

6.6 Up-down approach to a stationary level

The cases of Secs. 6.3, 6.4, and 6.5 correspond to $y_0 < -x_0$. We now consider the case

$$-x_0 < y_0 < 0 , \quad (77)$$

for which the behavior $x(t)$ depends on the relative value of τ compared with a characteristic τ_c , which can be defined only numerically, being such that

$$\tau_c < \tau_0 < t_c , \quad (78)$$

where τ_0 is given by Eq. 38 and

$$t_c \equiv -\ln \left(1 + \frac{y_0}{x_0} \right) . \quad (79)$$

With a good approximation, τ_c is close to τ_0 . For the parameters satisfying the conditions

$$a > 0 , \quad -1 - \frac{a}{x_0} < b < -1 , \quad 0 < \tau < \tau_c , \quad (80)$$

the solution $x(t)$ first increases sharply before decaying to the stationary point x_2^* , as shown in Fig. 22.

6.7 Growth to a finite-time singularity

There are several cases of infinite growth occurring in finite time, which are similar to one of the cases considered above, although they happen under quite different conditions. For the parameters

$$a \geq 0 , \quad -1 - \frac{a}{x_0} < b < -\frac{a}{x_0} , \quad \tau > t_c , \quad (81)$$

with t_c given by Eq. (79), the divergence occurs at time t_c , analogously to the behavior documented in Sec. 5.2.

When the delay time τ becomes smaller than t_c , in the region of the parameters

$$a \geq 0, \quad -1 - \frac{a}{x_0} < b < -\frac{a}{x_0}, \quad \tau_c < \tau \leq t_c, \quad (82)$$

there exists a critical time t_c^* which is a function of a, b and τ , at which $x(t)$ diverges hyperbolically as in Sections 5.3 or 6.5.

6.8 Exponential growth to infinity

For time delays τ smaller than τ_c and the parameters

$$a \geq 0, \quad -1 < b < -\frac{a}{x_0}, \quad 0 < \tau \leq \tau_c, \quad (83)$$

the point of singularity moves to infinity, and $x(t)$ exhibits an exponential growth with time, as in Secs. 4.11 or 5.4.

7 Prevailing loss and cooperation ($\sigma_1 < 0, \sigma_2 < 0$)

7.1 General analysis

If loss (death) and cooperation prevail, this corresponds to the fourth line of classification (18). Then, Eq. (13) becomes

$$\frac{dx(t)}{dt} = -x(t) + \frac{x^2(t)}{a + bx(t - \tau)}. \quad (84)$$

As everywhere above, the same history condition (14) is assumed. As above, there exists a first regime for $t < \tau$, for which the solution can be written explicitly as

$$x(t) = \frac{x_0 y_0 e^{-t}}{y_0 - x_0(1 - e^{-t})} \quad (t < \tau), \quad (85)$$

where y_0 is given by Eq. (15).

Equation (84) possesses two stationary points

$$x_1^* = 0, \quad x_2^* = \frac{a}{1 - b}. \quad (86)$$

The second fixed point x_2^* is non-negative for either $a > 0$ and $b < 1$ or $a \equiv 0$. The stability analysis of Sec. 3 shows that the first fixed point x_1^* is stable for all nonzero a , any b , and any τ , as in Eq. (67). In contrast, the second fixed point x_2^* is unstable for any $a > 0$ and $b < 1$ for which it is positive.

The special case $a \equiv 0$ is such that the two fixed points merge together: $x_1^* = x_2^* \equiv x^* = 0$. Then the Lyapunov stability analysis of Sec. 3 indicates that x^* is unstable for $0 < b < 1$. It is stable, when either

$$a = 0, \quad b < 0, \quad \tau \geq 0, \quad (87)$$

or

$$a = 0, \quad b > 3, \quad \tau \geq 0, \quad (88)$$

or

$$a = 0, \quad 1 < b < 3, \quad \tau < \tau_0, \quad (89)$$

where

$$\tau_0 \equiv \frac{b}{\sqrt{(b-1)(3-b)}} \arccos(2-b) \quad (1 < b < 3). \quad (90)$$

It is worth stressing that these results follow from the stability analysis of the linearized delay equation. As has been emphasized in Sec. 3, the Lyapunov analysis of the asymptotic stability for the delay equations gives only sufficient conditions of stability. The determination of the actual region of parameters, for which the stationary solutions of a delay equation are stable, requires to complement the Lyapunov analysis by detailed numerical checks. This has been done everywhere above.

To stress the necessity of accomplishing detailed numerical calculations for delay equations, let us consider the present case that provides a good illustration of such a necessity. The Lyapunov analysis for the fixed point $x^* = 0$, when $1 < b < 3$, indicates that this point is stable for $\tau < \tau_0$, as expressed by conditions (89). However, from numerical calculations, it follows that the actual region of stability is larger, and extends to all $\tau > 0$. In order to illustrate this difference, we present in Fig. 23, for the case of $a = 0$, the solutions to the exact delay equation (84), compared with its linearized variant. The linearized approximation exhibits an unstable behavior, while the solution to the full Eq. (84) is stable.

In this way, we have determined that the stationary solution $x^* = 0$ is stable for all non-negative a , any b , and all τ .

7.2 Monotonic decay to zero

When $x_0 < y_0$, and the parameters are

$$a \geq 0, \quad b > 1 - \frac{a}{x_0}, \quad \tau \geq 0, \quad (91)$$

the function $x(t)$ monotonically decays to zero. This behavior is similar to that of Sec. 6.2, with the difference that, for some parameters, the decaying solution does not have a constant convexity, as is demonstrated in Fig. 24. A similar decay to zero occurs for $y_0 < 0$, with the parameters

$$a = 0, \quad b < 0, \quad \tau \geq 0. \quad (92)$$

This decaying behavior is caused by the prevailing loss.

7.3 Growth to a fixed finite-time singularity

For $0 < y_0 < x_0$ and

$$a > 0, \quad -\frac{a}{x_0} < b < 1 - \frac{a}{x_0}, \quad \tau \geq t_c, \quad (93)$$

where

$$t_c \equiv -\ln\left(1 - \frac{y_0}{x_0}\right), \quad (94)$$

the solution $x(t)$ diverges hyperbolically at t_c . The finite singularity time t_c is independent of the delay time τ as long as the latter remains larger than t_c .

7.4 Growth to a moving finite-time singularity

For $\tau < t_c$, the catastrophic divergence occurs at a singularity time t_c^* , whose value depends on τ . For the parameters

$$a > 0, \quad -\frac{a}{x_0} < b \leq 0, \quad 0 < \tau < t_c, \quad (95)$$

the divergence occurs at $t_c^* < t_c$, which moves to the right towards t_c , as τ increases to t_c . In contrast, for the parameters

$$a > 0, \quad 0 < b < 1 - \frac{a}{x_0}, \quad \tau_c < \tau < t_c, \quad (96)$$

where τ_c depends on the parameters a and b , the divergence occurs at a point $t_c^* > t_c$, which moves to the left towards t_c , as τ increases. This behavior is analogous to that described in Sec. 5.3.

7.5 Exponential grows to infinity

For the parameters a and b as defined in Eq. (96), but for smaller time lags, such that

$$0 < \tau \leq \tau_c, \quad (97)$$

the solution $x(t)$ to Eq. (84) grows exponentially at large times, similarly to the regimes documented in Secs. 5.4 and 6.8.

7.6 Monotonic decay to finite-time death

For $y_0 < 0$, and for the parameters

$$a > 0, \quad b < -\frac{a}{x_0}, \quad \tau \geq 0, \quad (98)$$

the solution $x(t)$ decays monotonically to zero in finite time, reaching zero at time t_d , defined by the equation $a + bx(t_d - \tau) = 0$. When t tends to t_d from below, $x(t)$ sharply drops to zero, as shown in Fig. 25. This behavior differs from the finite-time death regime described in Sec. 4.8 by the absence of punctuated alternations. And it also differs from the finite-time death regime of Sec. 5.6 by the absence of punctuated steps. Here, death in the present regime is due to the destructive activity of agents under the prevailing loss term in Eq. (84).

8 Conclusion

We have suggested a new variant of the logistic-type equation, in which the carrying capacity consists of two terms. One of them corresponds to a fixed carrying capacity, provided by Nature. And another term is the carrying capacity created (or destroyed) by the activity of the agents

composing the considered society. The created (or destroyed) capacity is naturally delayed, as far as any creation/destruction requires some time. We take into account both the creative but also destructive impact of the agents on the carrying capacity. This is quantified by a coefficient b of activity which is positive for creation and negative for destruction.

Four different situations have been analyzed, depending on the signs of the two terms entering our delay logistic equation. We have taken into account that the growth rate is positive, when gain (birth) prevails and it is negative if loss (death) is prevailing. The sign of the second term in the equation is negative if the competition between agents is stronger than the effects resulting from their cooperation. The sign of the second term turns positive when their cooperation is dominant.

We have carefully investigated all the possible emergent regimes, using both analytical and numerical methods. This has led to a complete classification of the possible types of different solutions. It turns out that there exists a large variety of solution types. In particular, we find a rich and rather sensitive dependence of the structural properties of the solutions on the value of the delay time τ . For instance, in the regime where loss and competition are dominant, depending on the value of the initial carrying capacity and of τ , we find monotonic decay to zero, oscillatory approach to a stationary level, sustainable oscillations and moving finite-time singularities. This should not be of too much surprise, since delay equations are known to enjoy much richer properties than ordinary differential equations. In this spirit, Kolmanovskii and Myshkis [32] provide an example of a delay-differential equation, whose properties are as rich as those of a system of ten coupled ordinary differential equations. We have illustrated in different figures the main qualitative properties of the different solutions, not repeating the presentations of solutions with similar behavior.

The rich variety of all possible regimes is summarized in Figs. 26 to 29. The solution types, occurring in the most realistic and the most complicated case of Sec.4, when gain and competition prevail, is presented in the scheme of Fig. 26. Respectively, Fig. 27 illustrates the admissible regimes of Sec. 5, when gain prevails over loss and cooperation is stronger than competition. Figure 28 summarizes the qualitatively different regimes of Sec. 6, when loss prevails over gain and competition is stronger than cooperation. Finally, Fig. 29 demonstrates the variety of solution types described in Sec. 7, when loss is larger than gain and competition prevails over collaboration.

The main goal of the present paper has been the formulation of the novel model of evolution and the study of the mathematical and structural properties of its solutions. In the introduction, we have briefly mentioned some possible interpretations. To keep the paper within reasonable size limits, we defer the detailed discussions of possible applications to future publications. However, in order to connect the particular solutions, and the related figures, to real-life situations, we can mention several concrete cases, where experimental observations are summarized in explicit graphs.

The experimental data for the dynamics of the world urban population growth, presented in Ref. [3] (Fig. 7) is very close to the punctuated evolution of our Figs. 1 and 2. The total world population growth, considered back to 10^6 years before present (see Figs. 1 and 2 in Ref.[59]) is also reminiscent of our Fig. 2. The data on the energy production and consumption, listed in several tables and figures of the BP Statistical Review of World Energy [60], are again very similar to our Figs. 1, 2, and 6. Percentage of women in economics [61] (Figs. 1, 2, and 3) follow the ladder-type dynamics as in our Figs. 1 and 2. The same type of ladder evolution is documented for the growth of some cells in humans [62] (Fig. 1) and in insects [63] (Fig. 3).

The decay of human cells [64] (Fig. 6) is analogous to that of our Figs 9 or 16. The diminishing woman fertility rate in European countries [65] (Figs. 6 and 7) corresponds to our Fig. 9. There are many other experimental data whose dynamics correspond to some of the solutions we have described and whose more quantitative investigation is left for the future.

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Figure Captions

Fig. 1. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $a = 2$ (solid line) and $a = 5$ (dashed-dotted line). Other parameters are: $x_0 = 1$, $b = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow +\infty$.

Fig. 2. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = 2$ (solid line) and $b = 3$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

Fig. 3. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $\tau = 10$ (solid line) and $\tau = 20$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $b = 1$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

Fig. 4. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $x_0 = 1$ (solid line) and $x_0 = 3$ (dashed-dotted line). Other parameters are: $a = 2$, $b = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

Fig. 5. Logarithm of the solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = 2$ (solid line) and $b = 5$ (dashed-dotted line) exemplifying their average long-term exponential growth. Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 10$.

Fig. 6. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $a = 2$ (solid line), $a = 3$ (dashed line), and $a = 4$ (dashed-dotted line). Other parameters are: $x_0 = 1$, $b = 0.5$, and $\tau = 20$. The solutions $x(t)$ monotonically grow by steps to their stationary points $x_2^* = a/(1-b)$ as $t \rightarrow \infty$. Stationary points are: $x_2^* = 4$ (for solid line), $x_2^* = 6$ (for dashed line), and $x_2^* = 8$ (for dashed-dotted line).

Fig. 7. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = 0.25$ (solid line), $b = 0.5$ (dashed line), and $b = 0.75$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 20$. The solutions $x(t)$ monotonically grow by steps to their stationary points $x_2^* = a/(1-b)$ as $t \rightarrow \infty$. Stationary points are: $x_2^* = 8/3 \approx 2.67$ (for solid line), $x_2^* = 4$ (for dashed line), and $x_2^* = 8$ (for dashed-dotted line).

Fig. 8. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $x_0 = 0.5$ (solid line), $x_0 = 2$ (dashed line), and $x_0 = 3.5$ (dashed-dotted line). Other parameters are: $a = 2$, $b = 0.5$, and $\tau = 20$. The solutions $x(t)$ monotonically grow by steps to their stationary point $x_2^* = a/(1-b) = 4$ as $t \rightarrow \infty$.

Fig. 9. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = 0.1$ (solid line), $b = 0.4$ (dashed line), and $b = 0.7$ (dashed-dotted line). Other parameters are: $a = 0.25$, $x_0 = 3$, and $\tau = 20$. The solutions $x(t)$ monotonically decrease by steps to their stationary points $x_2^* = a/(1-b)$ as $t \rightarrow \infty$. Stationary points are: $x_2^* = 5/18 \approx 0.278$ (for solid line), $x_2^* = 5/12 \approx 0.417$ (for dashed line), and $x_2^* = 5/6 \approx 0.833$ (for dashed-dotted line).

Fig. 10. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = -0.66$ (solid line) and $b = -0.33$ (dashed-dotted line). Other parameters are: $a = 3$, $x_0 = 1$, and $\tau = 20$.

The solutions $x(t)$ non-monotonically grow by steps to their stationary points $x_2^* = a/(1 - b)$ as $t \rightarrow \infty$. The stationary points are: $x_2^* = 1.80723$ (for solid line) and $x_2^* = 2.25564$ (for dashed-dotted line).

Fig. 11. Solution $x(t)$ to Eq. (32) as a function of time for the parameter $\tau = 5 < \tau_0 = 5.91784$. Other parameters are: $a = 3$, $x_0 = 1$, and $b = -1.1$. The solution $x(t)$ tends in an oscillatory manner to its stationary point $x_2^* = a/(1 - b) = 1.42857$ as $t \rightarrow \infty$.

Fig. 12. Solution $x(t)$ to Eq. (32) as a function of time for the parameter $\tau = \tau_0 = 5.91784$. Other parameters are: $a = 2$, $x_0 = 1$, and $b = -1.1$. The solution $x(t)$ oscillates around its stationary point $x_2^* = a/(1 - b) = 0.952381$ as $t \rightarrow \infty$.

Fig. 13. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = -1.25$ (solid line) and $b = -1.75$ (dashed-dotted line). Other parameters are: $a = 3$, $x_0 = 1$, and $\tau = 20$. The solutions $x(t)$ oscillate with increasing amplitude until time $t_d = 149.932$ (for solid line) and $t_d = 105.972$ (for dashed-dotted line) defined by the equation $a + bx(t_d - \tau) = 0$, at which $\dot{x}(t)|_{t \rightarrow t_d - 0} = -\infty$.

Fig. 14. Dependence of the critical time $t_c^*(\tau)$, where the function $x(t)$ exhibits a singularity, as a function of the lag τ . Here the parameters are: $a = 0$, $x_0 = 1$, and $b = -1.5$. At time $t = t_c^*$, the solution has a singularity: $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. The instant t_c^* is defined by $a + bx(t_c^* - \tau) = 0$. The time $t_c = \ln(1 - y_0/x_0) = 0.916291$ is the point of singularity.

Fig. 15. Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $\tau = 0.1$ (dashed-dotted line), $\tau = 0.2$ (dotted line), $\tau = 0.3$ (dashed line), and $\tau = 0.4$ (solid line). The other parameters are: $a = 2$, $x_0 = 2$, and $b = -1.5$. For all $\tau > t_c = \ln(1 - y_0/x_0) = 0.405465$, we have $t_c^* = t_c$. If $\tau \leq t_c$, there exists $\tau_c \approx 0.27217$ such that if $0 < \tau \leq \tau_c$, then $x(t)$ grows exponentially to $+\infty$. If $\tau_c < \tau \leq t_c$, then there exists a point of singularity $t_c^* > t_c$, defined by $a + bx(t_c^* - \tau) = 0$, such that $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. When $\tau \rightarrow t_c - 0$, then $t_c^* \rightarrow t_c + 0$. The values of t_c^* are respectively $t_c^* = 0.40560$ (for solid line, $\tau = 0.4$) and $t_c^* = 0.50993$ (for dashed line, $\tau = 0.3$).

Fig. 16. Solutions $x(t)$ to Eq. (53) as functions of time for the parameters $b = -1.5$ (solid line) and $b = -1.8$ (dashed-dotted line). Other parameters are: $a = 1$, $x_0 = 1$, and $\tau = 10$. The solutions $x(t)$ decrease by steps until time $t_d = 10.6932$ (for solid line) and $t_d = 22.0171$ (for dashed-dotted line) defined by the equation $a + bx(t_d - \tau) = 0$. At these times, $\dot{x}(t)|_{t \rightarrow t_d - 0} = -\infty$.

Fig. 17. Solutions $x(t)$ to Eq. (53) as functions of time for the parameters $b = -0.25$ (solid line), $b = -0.5$ (dashed line), and $b = -0.75$ (dashed-dotted line). Other parameters are: $a = 0$, $x_0 = 1$, and $\tau = 20$. The solutions $x(t)$ monotonically decrease by steps to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

Fig. 18. Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $b = -2$ (solid line) and $b = 8$ (dashed-dotted line). Other parameters are: $a = 3$, $x_0 = 1$, and $\tau = 10$. The solutions $x(t)$ monotonically decrease to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

Fig. 19. Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.4$ (solid line) and $\tau = 0.5$ (dashed-dotted line), where $\tau < \tau_0 = 0.505951$. Other parameters are: $a = 1$, $x_0 = 1$, and $b = -2.5$. The solutions $x(t)$ converge by oscillating to their stationary point $x_2^* = -a/(b+1) = 2/3$ as $t \rightarrow \infty$.

Fig. 20. Solution $x(t)$ to Eq. (64) as a function of time for the parameter $\tau = 0.605 > \tau_0$, where $\tau_0 = 0.505951$. Other parameters are the same as for Fig. 19. The solution $x(t)$ exhibits sustained oscillations with an amplitude which is an increasing function of the delay time τ and a period much larger than τ .

Fig. 21. Logarithmic behavior of solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.626$ (solid line), $\tau = 1.126$ (dashed line), $\tau = 1.626$ (dotted line), and $\tau = 2.126$ (dashed-dotted line), where $\tau_1 < \tau < \tau_2$. Other parameters are the same as for Fig. 19. There exist points of singularity t_c^* , defined by $a + bx(t_c^* - \tau) = 0$, where $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. These points are: $t_c^* = 11.4328$ (for solid line), $t_c^* = 2.87170$ (for dashed line), $t_c^* = 3.33026$ (for dotted line), and $t_c^* = 3.83074$ (for dashed-dotted line).

Fig. 22. Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.48$ (solid line) and $\tau = 0.485$ (dashed-dotted line), where $\tau < \tau_0 = 0.495125$. Other parameters are: $a = 2$, $x_0 = 1$, and $b = -2.5$. The solutions $x(t)$ tend non-monotonically to their stationary point $x_2^* = -a/(b+1) = 4/3$ as $t \rightarrow \infty$.

Fig. 23. Solutions $x(t)$ to Eq. (84) (solid line) and to the corresponding equation obtained by linearizing Eq. (84) around the fixed point $x^* = 0$ (dashed-dotted line). Parameters for the equations are: $a = 0$, $b = 2$, and $\tau = 4$ (note that $\tau > \tau_0 = \pi$). The figure shows that the solution to the linearized equation is unstable for $\tau > \tau_0$, as the stability analysis prescribes, whereas the solution to the nonlinear equation is stable for $\tau > \tau_0$, tending to its stationary point $x^* = 0$ as $t \rightarrow \infty$.

Fig. 24. Solutions $x(t)$ to Eq. (84) as functions of time for the parameters $b = 0.55$ (solid line) and $b = 5$ (dashed-dotted line). Other parameters are: $a = 1$, $x_0 = 2$, and $\tau = 20$. The solutions $x(t)$ decrease monotonically to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

Fig. 25. Solutions $x(t)$ to Eq. (84) as functions of time for the parameters $b = -5$ (solid line), $b = -7.5$ (dashed line), and $b = -10$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 0.5$. The solutions $x(t)$ decrease monotonically with a sharp but continuous drop ending at 0 at time $t_d = 1.24290$ (for solid line), $t_d = 1.66635$ (for dashed line), and $t_d = 1.97114$ (for dashed-dotted line) defined by the equation $a + bx(t_d - \tau) = 0$. At these moments, of time $\dot{x}(t)|_{t \rightarrow t_d - 0} = -\infty$.

Fig. 26. Scheme of the variety of qualitatively different solution types for the most complicated and the most realistic regime of Sec. 4, when gain (birth) prevails over loss (death) and competition is stronger than cooperation.

Fig. 27. Scheme of qualitatively different solution types for the case of Sec. 5, when gain prevails over loss and cooperation prevails over competition.

Fig. 28. Summarizing scheme of qualitatively different solution types for the case of Sec. 6, when loss prevails over gain and competition prevails over cooperation.

Fig. 29. Summarizing scheme of qualitatively different solution types for the case of Sec. 7, when loss prevails over gain and cooperation prevails over competition.

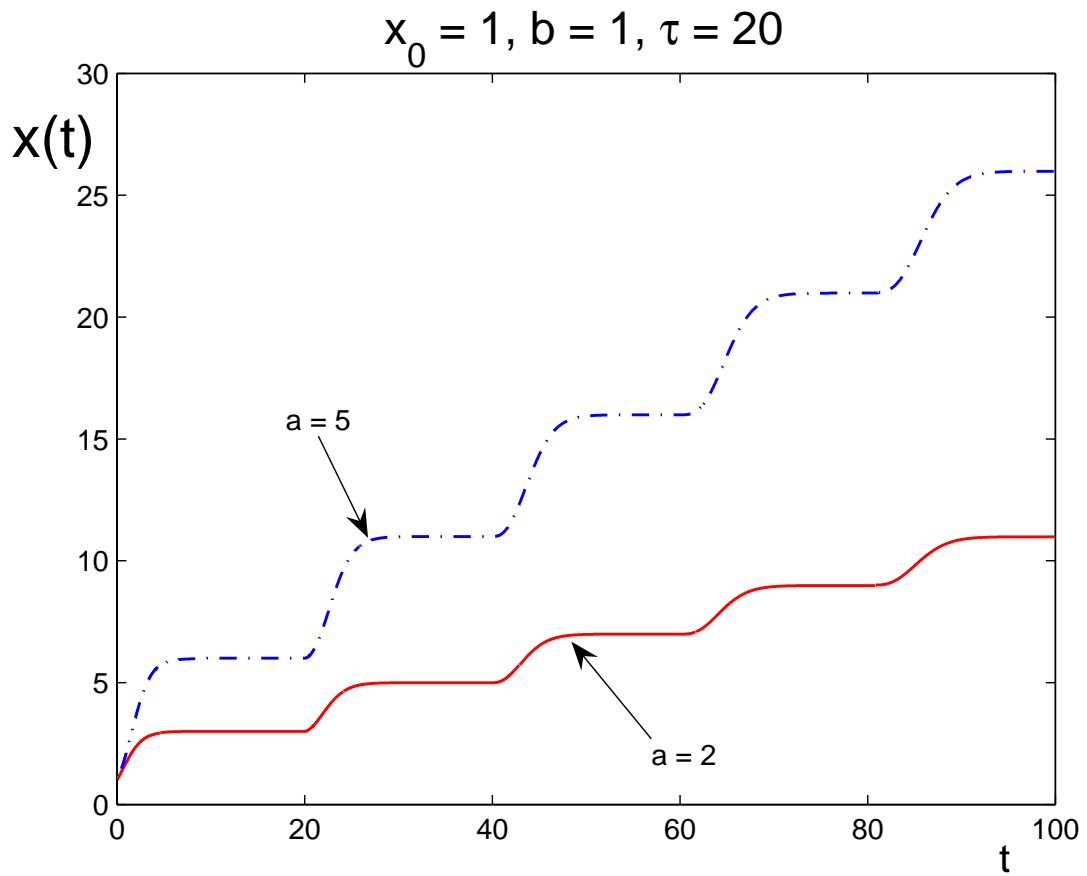


Figure 1: Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $a = 2$ (solid line) and $a = 5$ (dashed-dotted line). Other parameters are: $x_0 = 1$, $b = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow +\infty$.

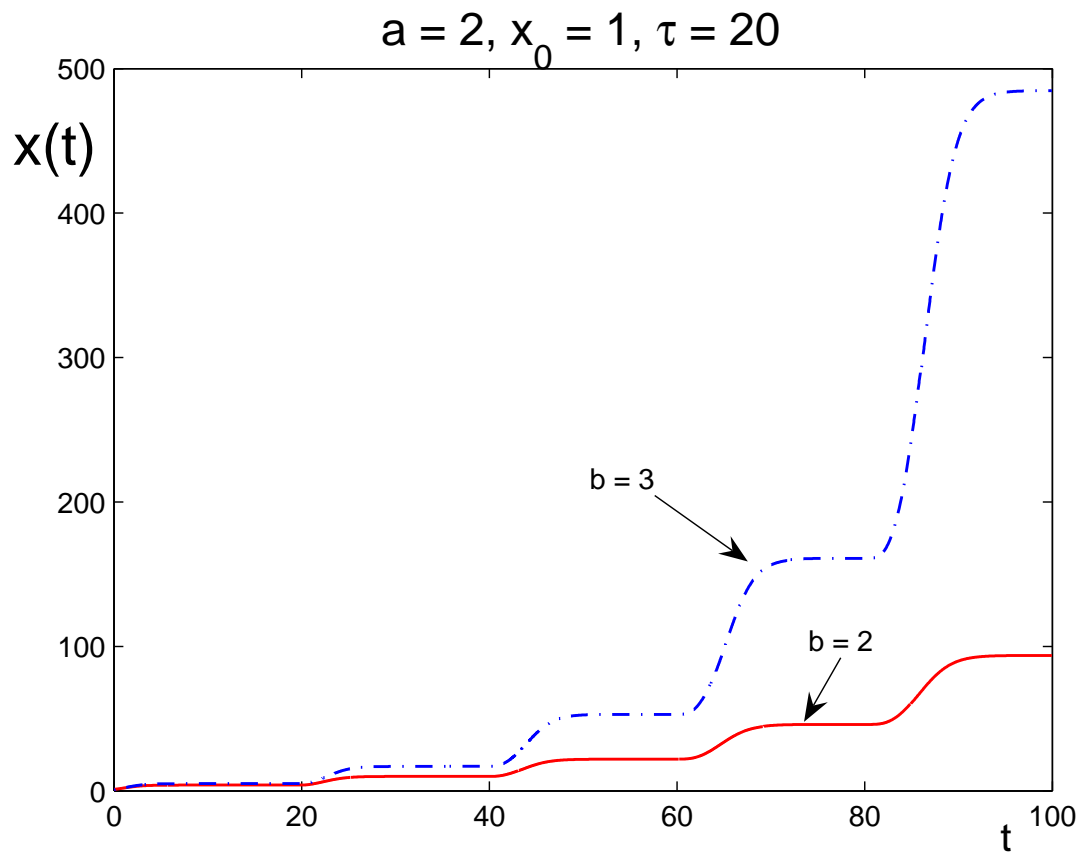


Figure 2: Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $b = 2$ (solid line) and $b = 3$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

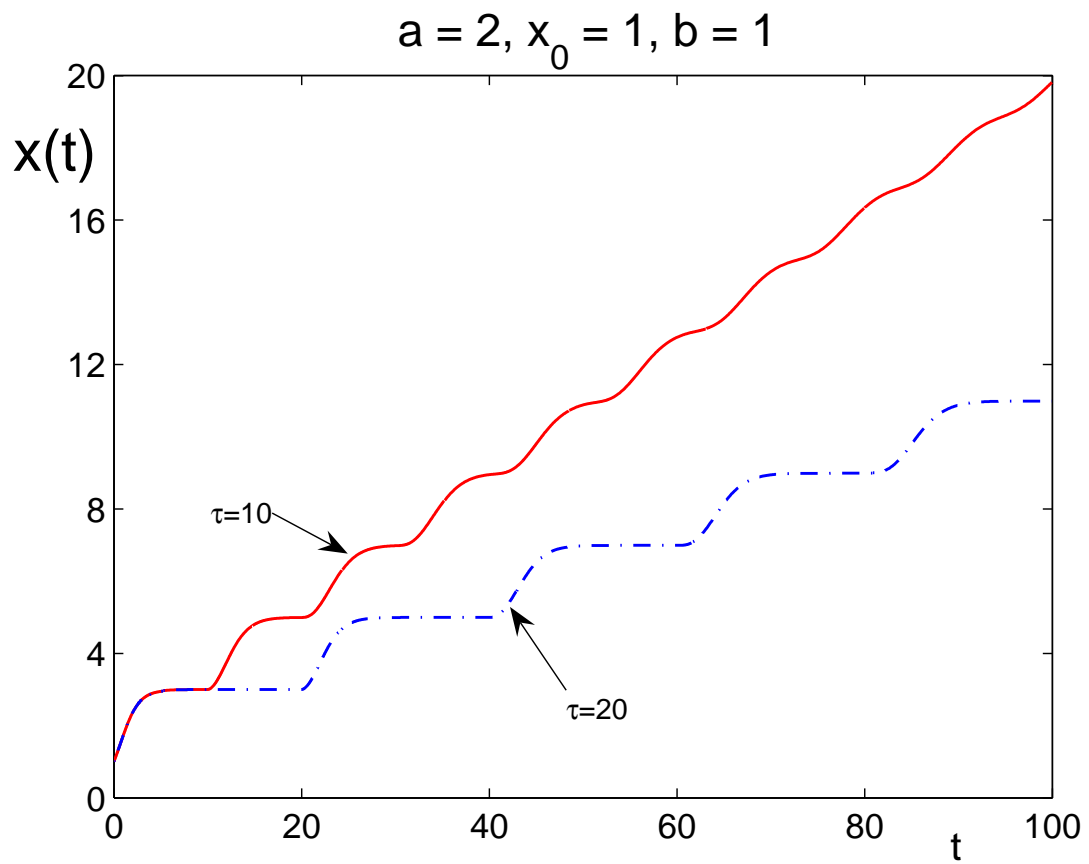


Figure 3: Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $\tau = 10$ (solid line) and $\tau = 20$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $b = 1$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

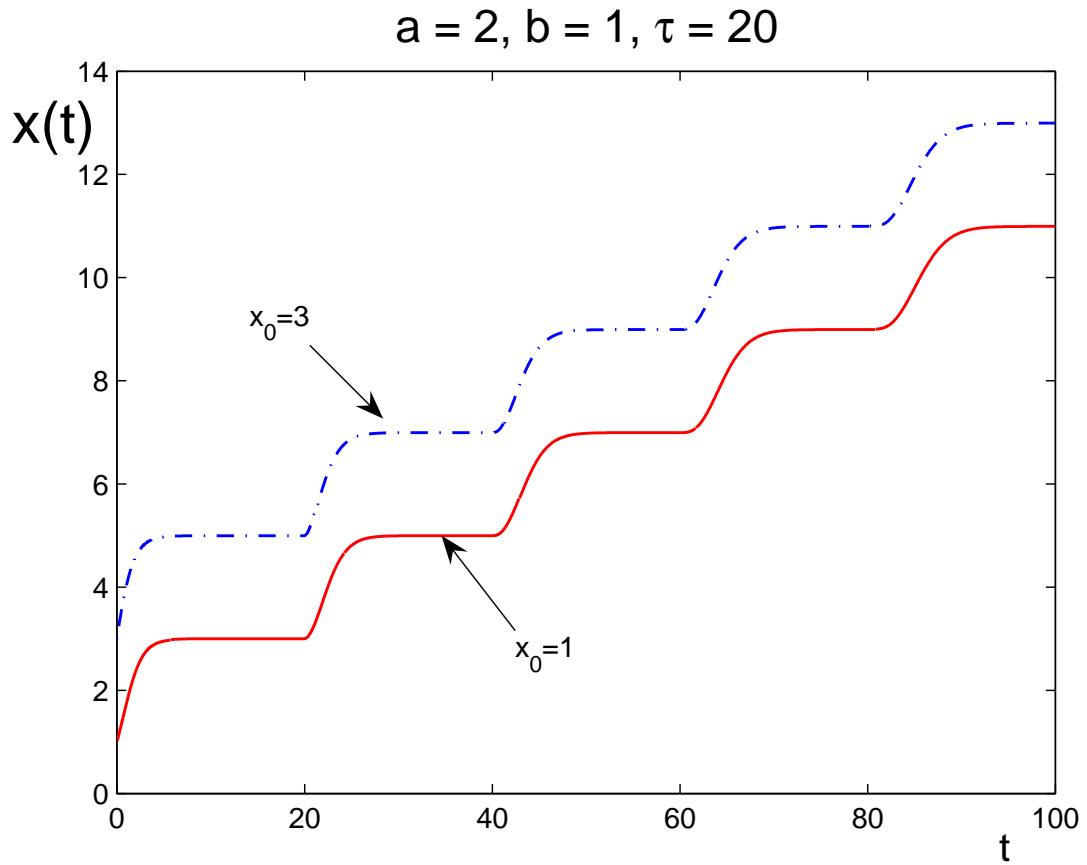


Figure 4: Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $x_0 = 1$ (solid line) and $x_0 = 3$ (dashed-dotted line). Other parameters are: $a = 2$, $b = 1$, and $\tau = 20$. Solutions grow monotonically by steps of duration $\simeq \tau$, and $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$.

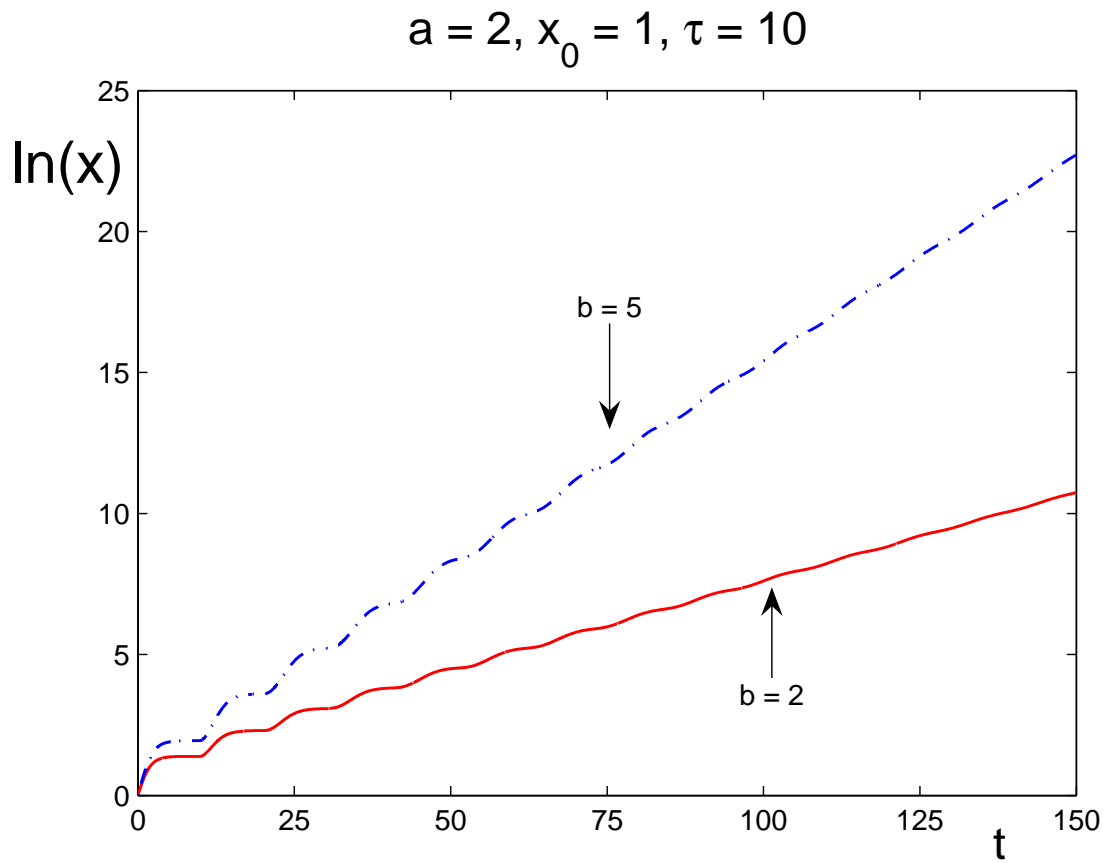


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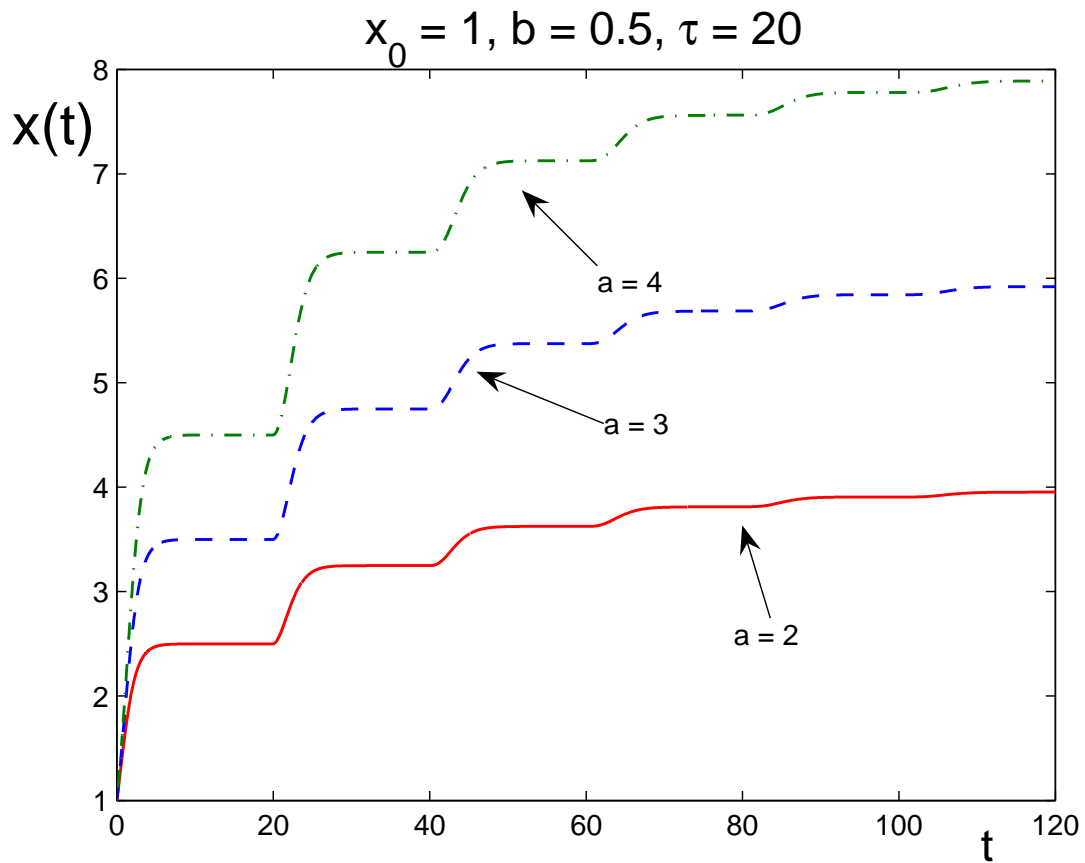


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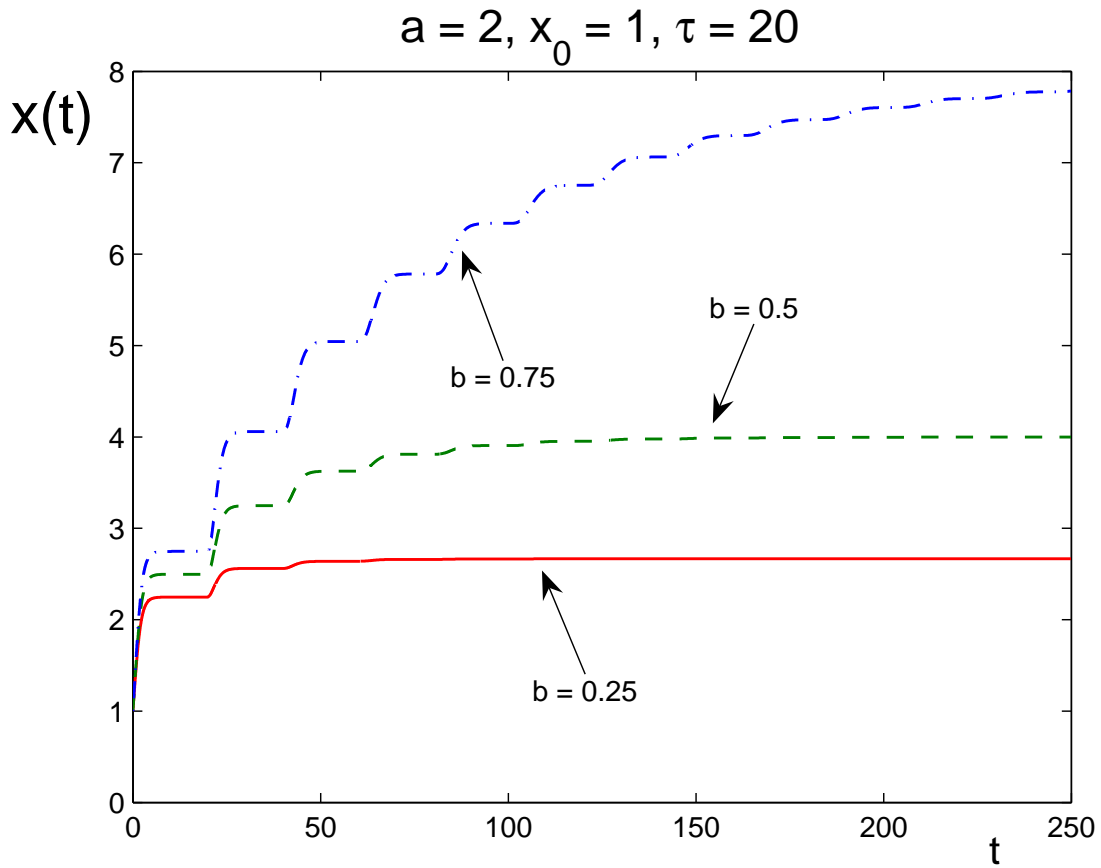


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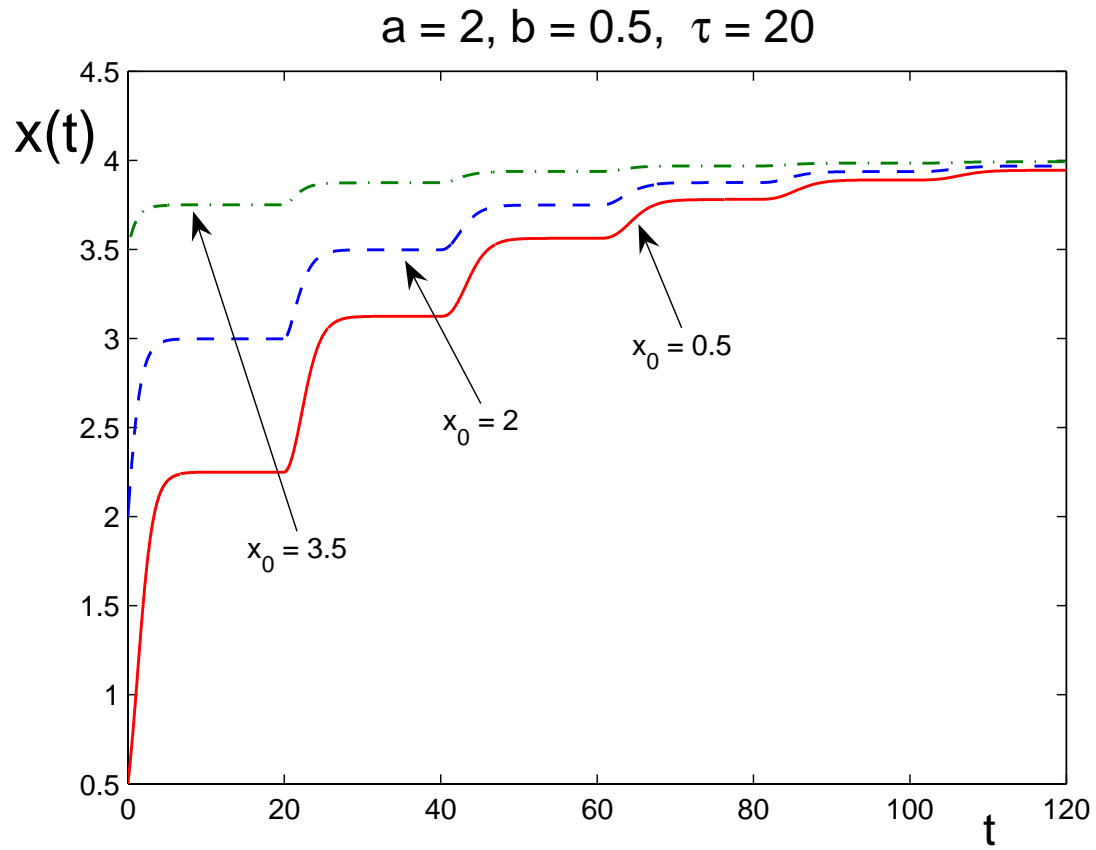


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$$a = 0.25, x_0 = 3, \tau = 20$$

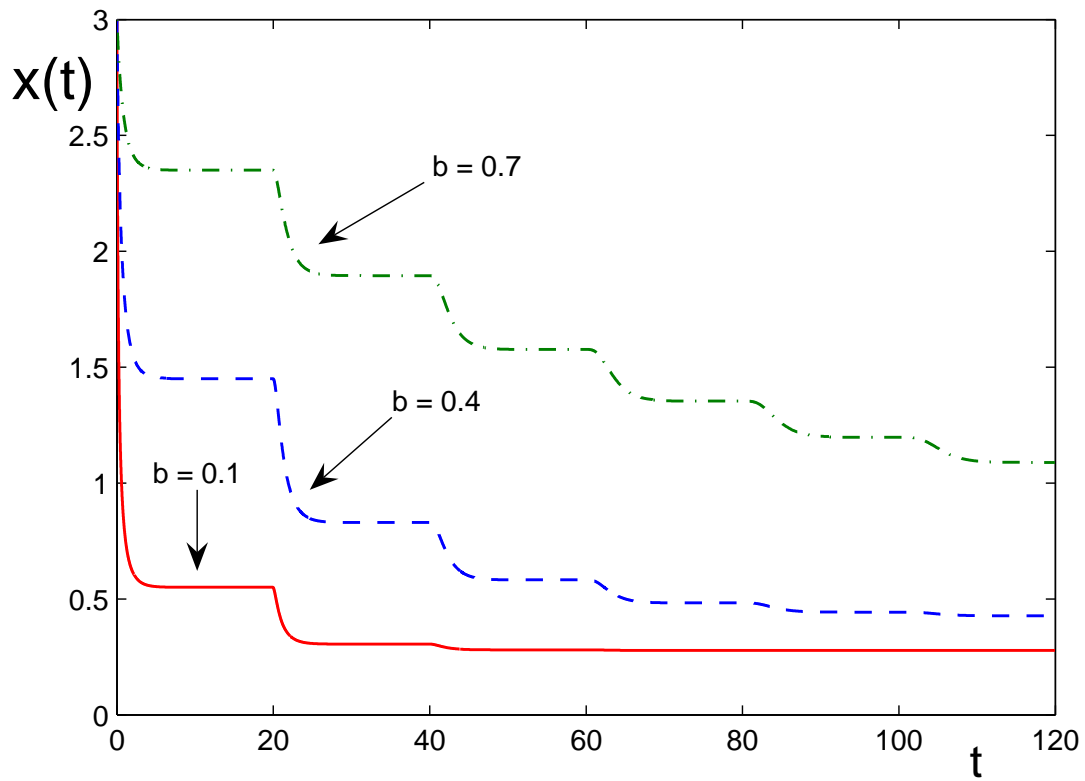


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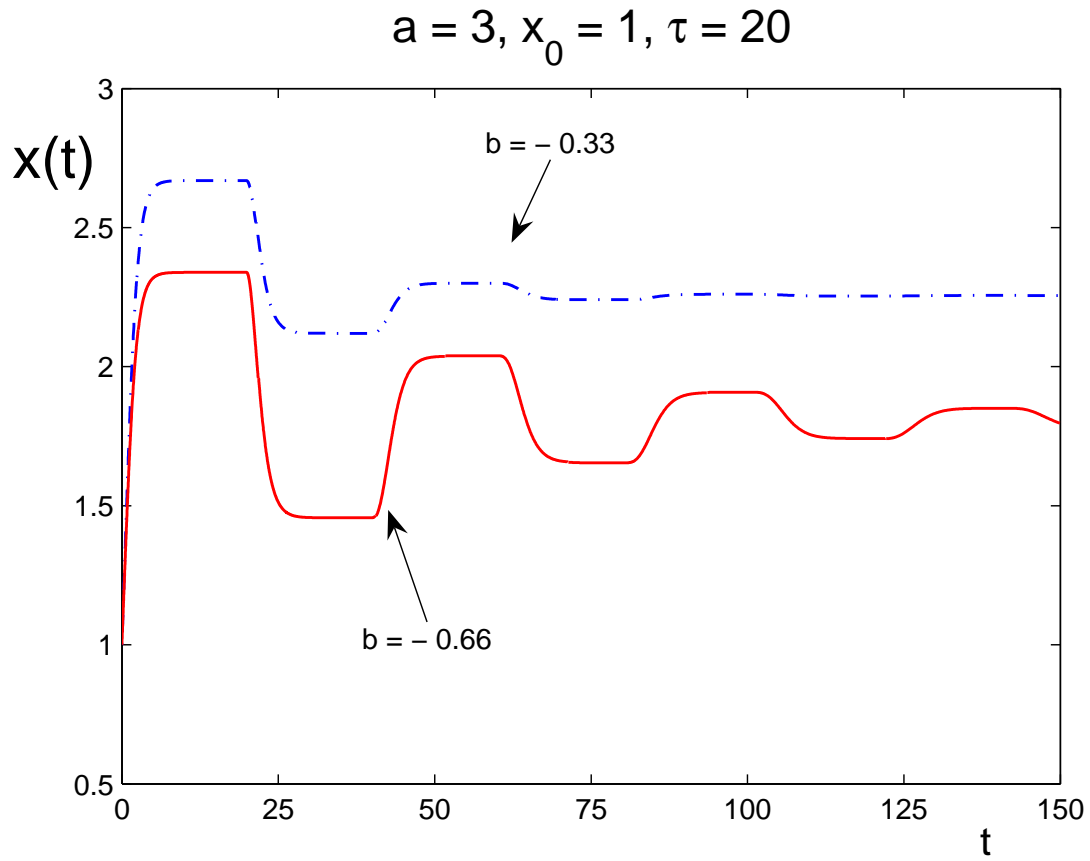


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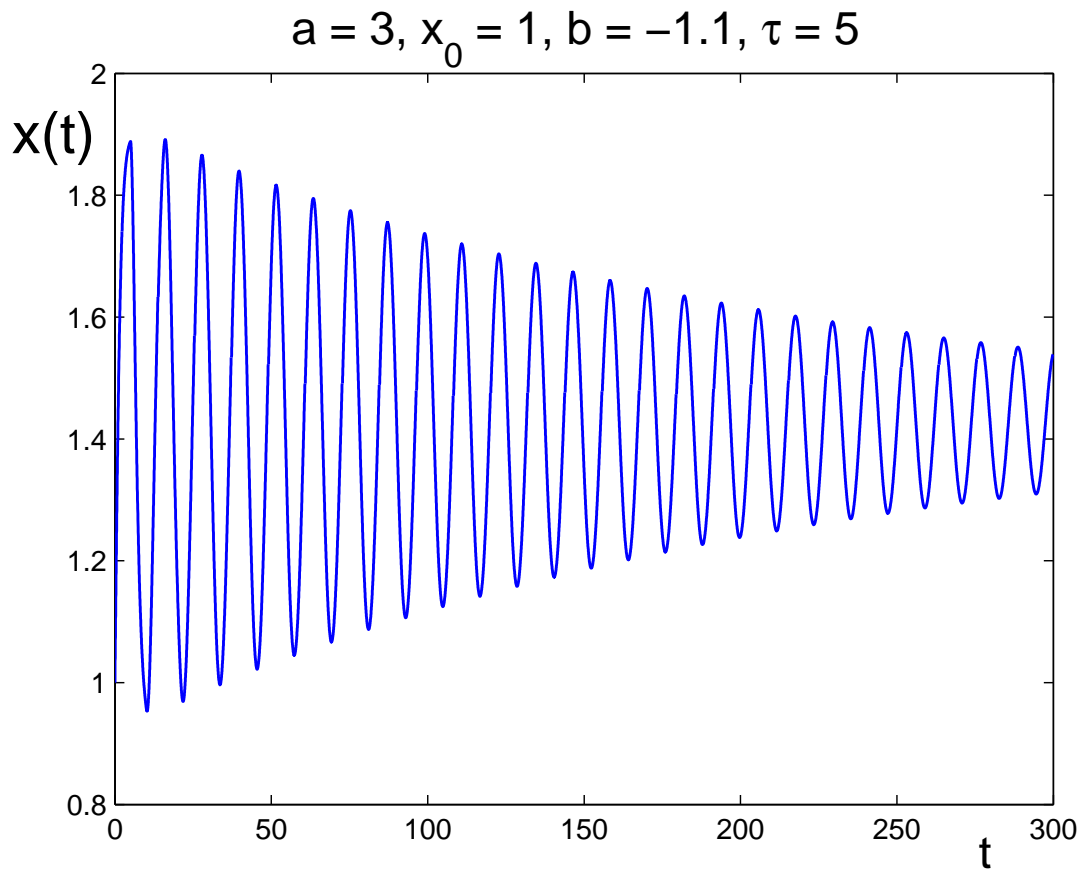


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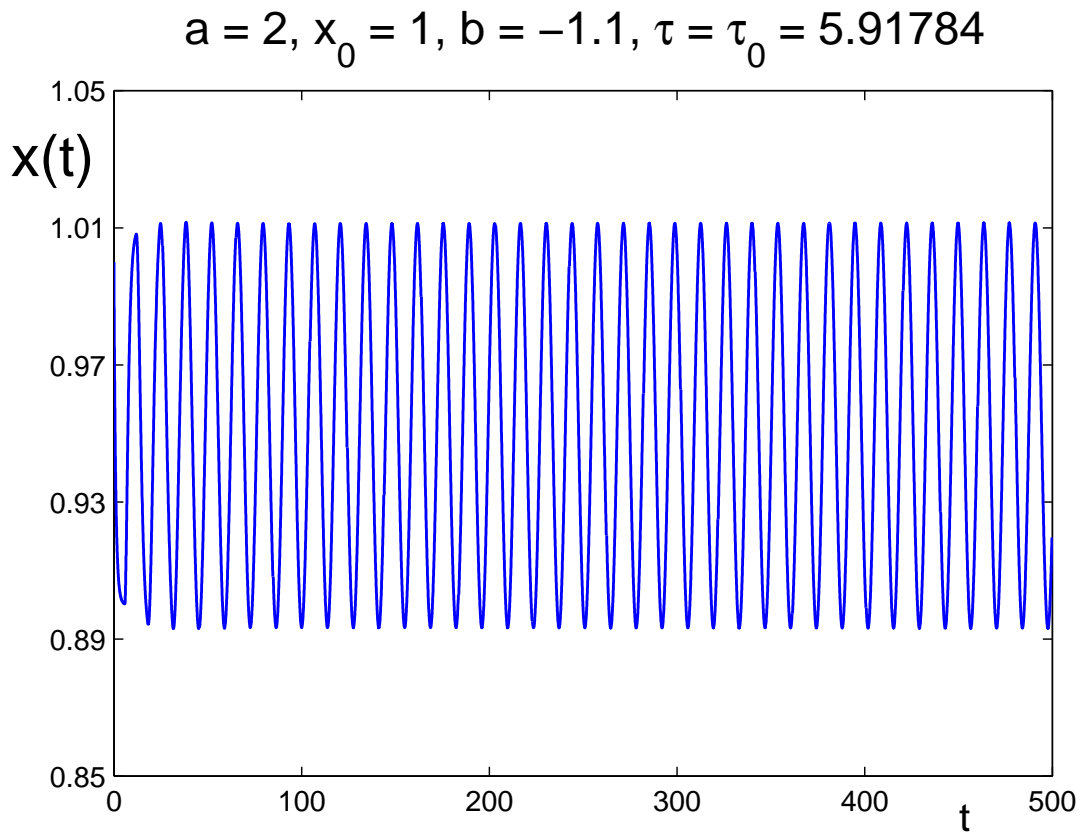


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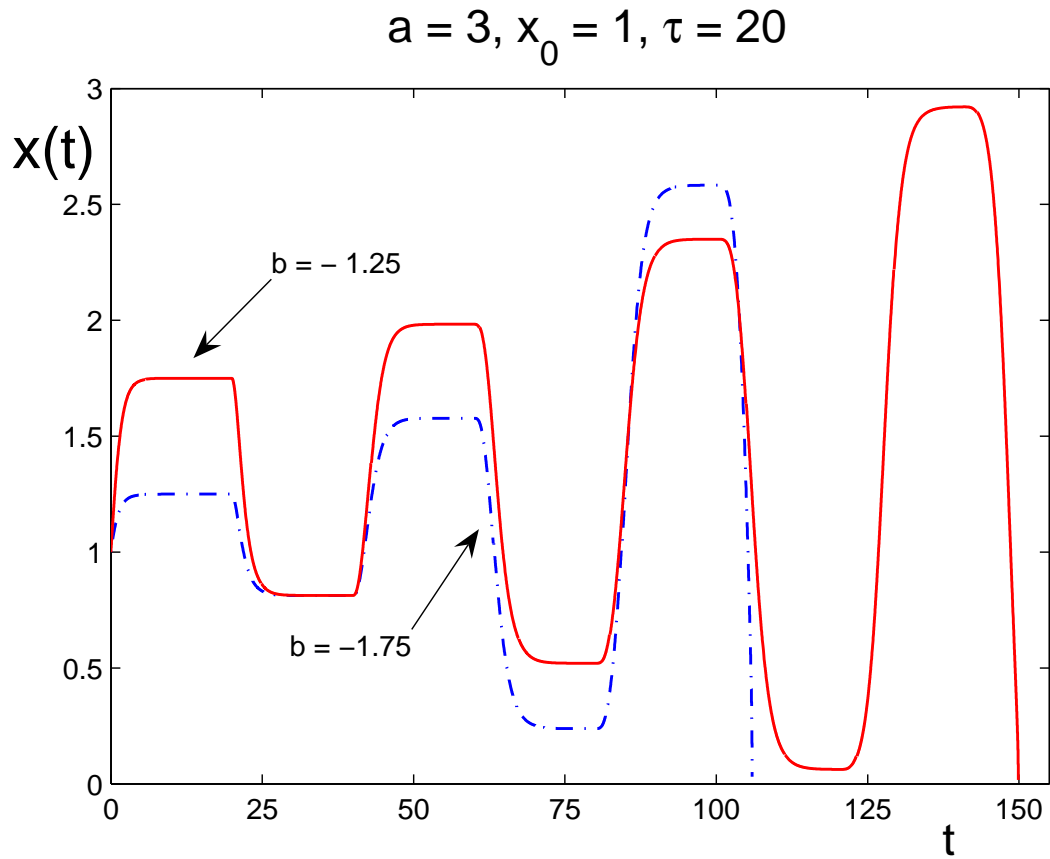


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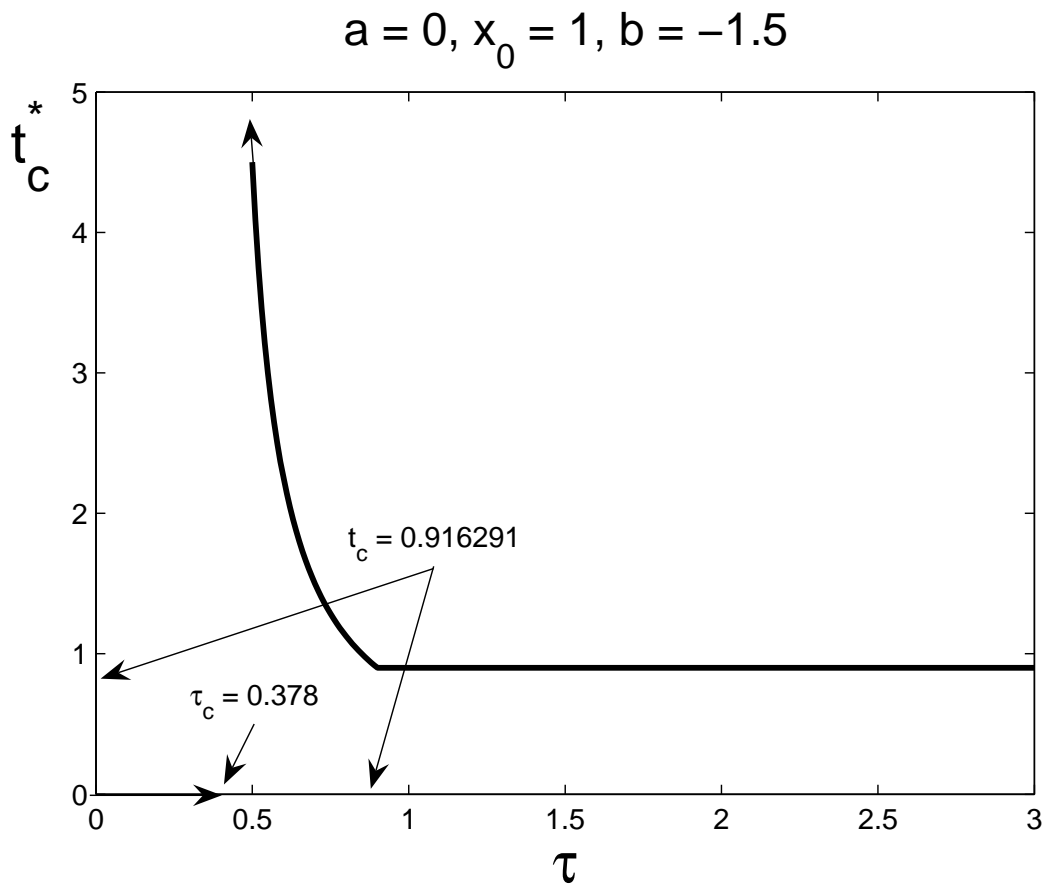


Figure 14: Dependence of the critical time $t_c^*(\tau)$, where the function $x(t)$ exhibits a singularity, as a function of the lag τ . Here the parameters are: $a = 0$, $x_0 = 1$, and $b = -1.5$. At time $t = t_c^*$, the solution has a singularity: $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. The instant t_c^* is defined by $a + bx(t_c^* - \tau) = 0$. The time $t_c = \ln(1 - y_0/x_0) = 0.916291$ is the point of singularity.

$$a = 2, x_0 = 2, b = -1.5$$

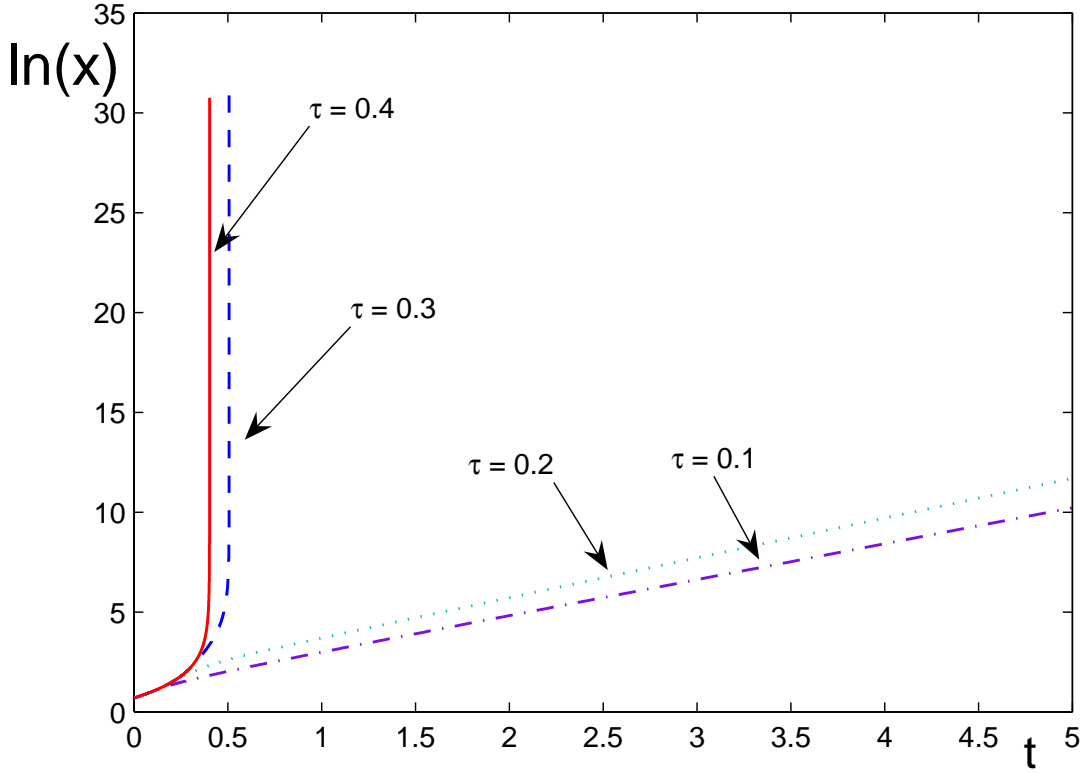


Figure 15: Solutions $x(t)$ to Eq. (32) as functions of time for the parameters $\tau = 0.1$ (dashed-dotted line), $\tau = 0.2$ (dotted line), $\tau = 0.3$ (dashed line), and $\tau = 0.4$ (solid line). The other parameters are: $a = 2$, $x_0 = 2$, and $b = -1.5$. For all $\tau > t_c = \ln(1 - y_0/x_0) = 0.405465$, we have $t_c^* = t_c$. If $\tau \leq t_c$, there exists $\tau_c \approx 0.27217$ such that if $0 < \tau \leq \tau_c$, then $x(t)$ grows exponentially to $+\infty$. If $\tau_c < \tau \leq t_c$, then there exists a point of singularity $t_c^* > t_c$, defined by $a + bx(t_c^* - \tau) = 0$, such that $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. When $\tau \rightarrow t_c - 0$, then $t_c^* \rightarrow t_c + 0$. The values of t_c^* are respectively $t_c^* = 0.40560$ (for solid line, $\tau = 0.4$) and $t_c^* = 0.50993$ (for dashed line, $\tau = 0.3$).

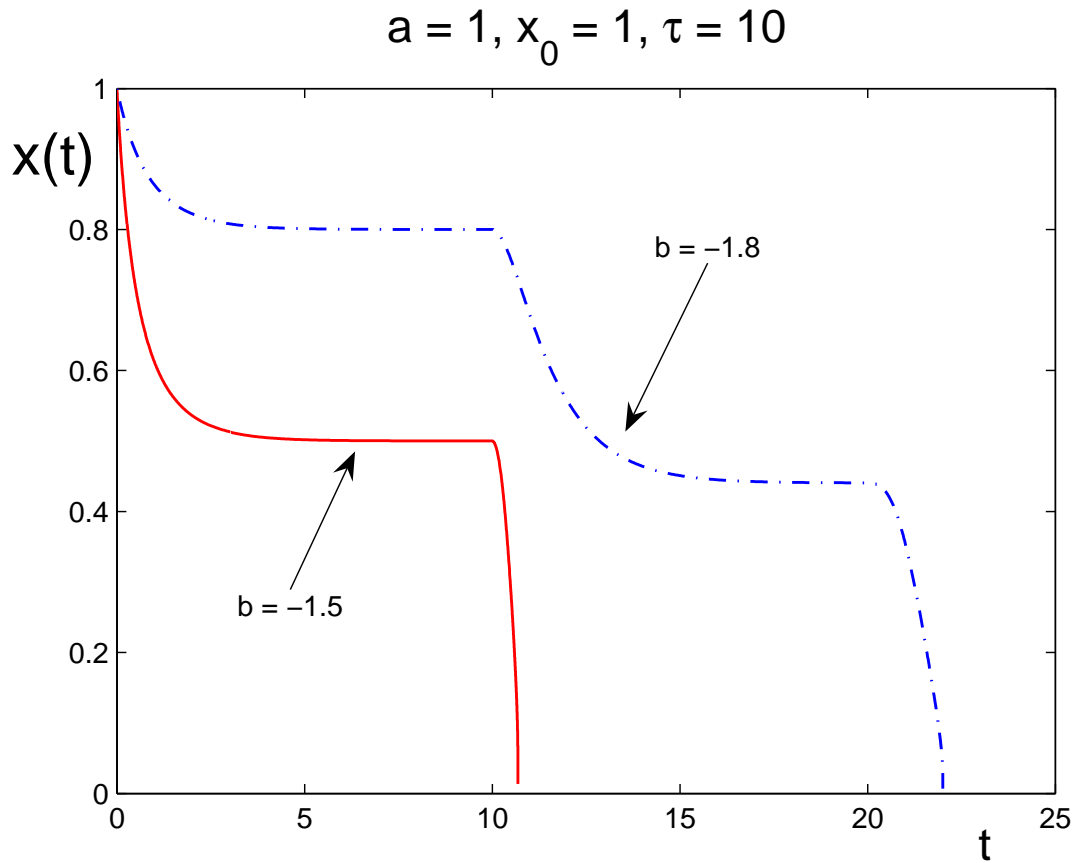


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$$a = 0, x_0 = 1, \tau = 20$$

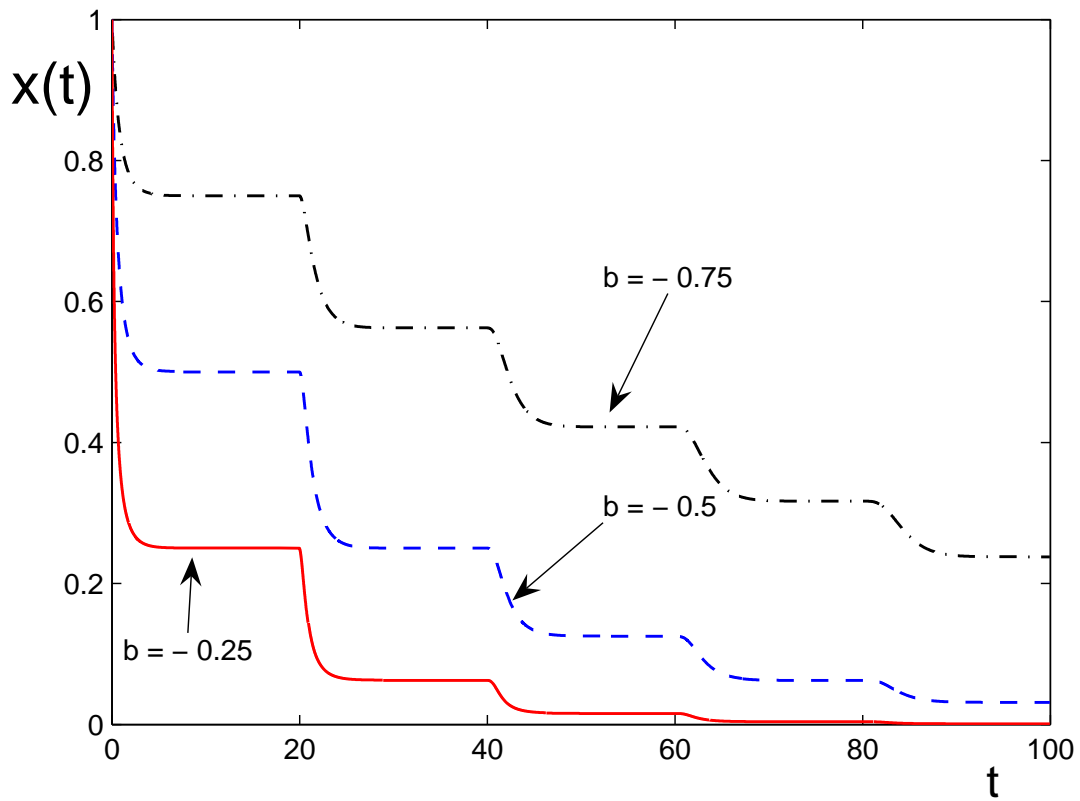


Figure 17: Solutions $x(t)$ to Eq. (53) as functions of time for the parameters $b = -0.25$ (solid line), $b = -0.5$ (dashed line), and $b = -0.75$ (dashed-dotted line). Other parameters are: $a = 0$, $x_0 = 1$, and $\tau = 20$. The solutions $x(t)$ monotonically decrease by steps to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

$$a = 3, x_0 = 1, \tau = 10$$

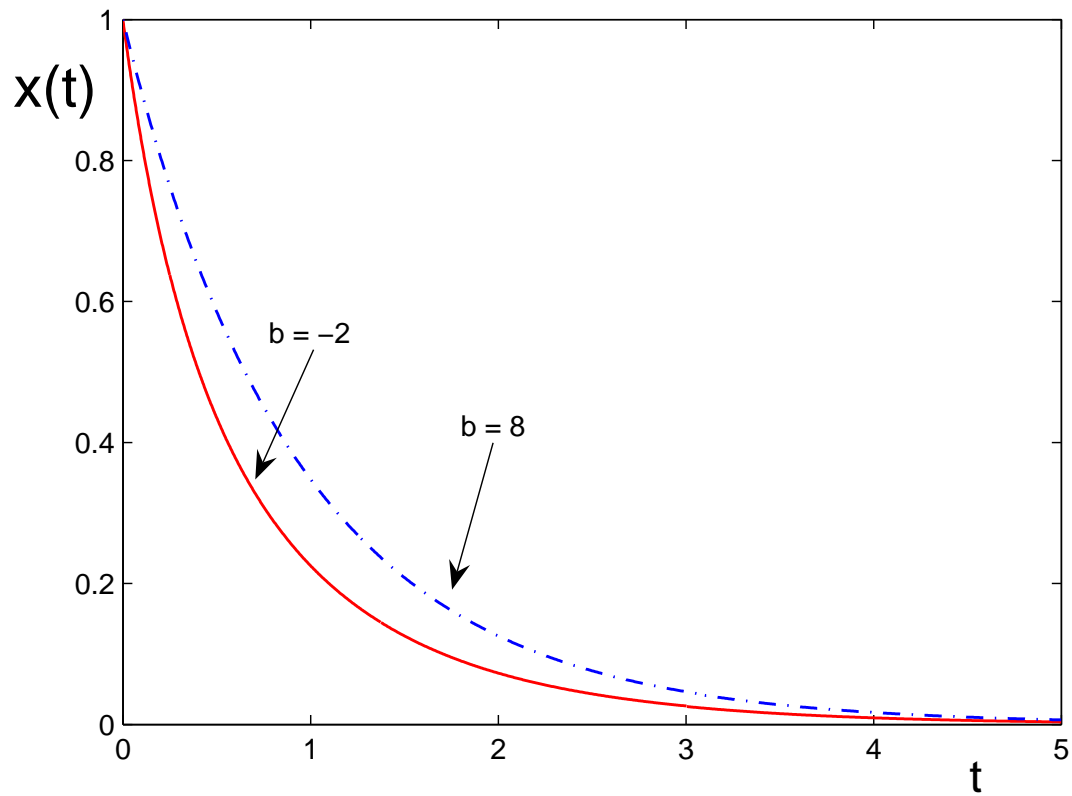


Figure 18: Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $b = -2$ (solid line) and $b = 8$ (dashed-dotted line). Other parameters are: $a = 3$, $x_0 = 1$, and $\tau = 10$. The solutions $x(t)$ monotonically decrease to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

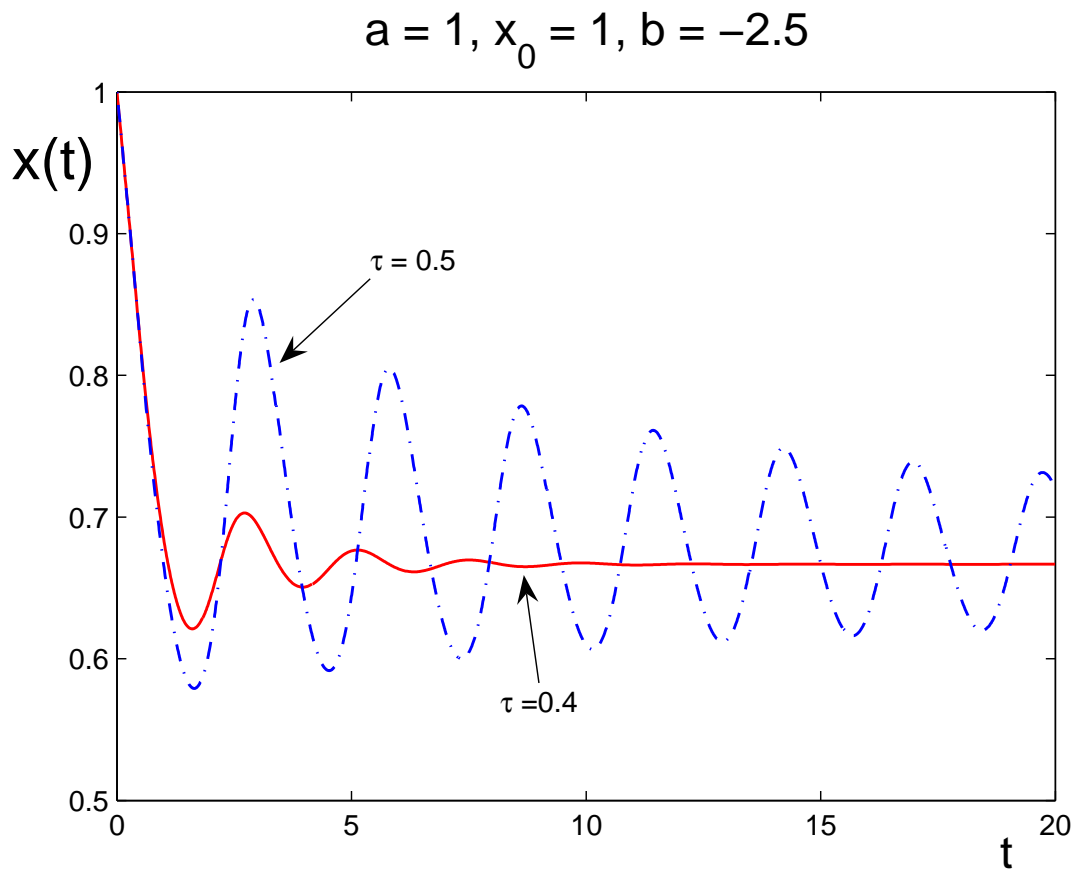


Figure 19: Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.4$ (solid line) and $\tau = 0.5$ (dashed-dotted line), where $\tau < \tau_0 = 0.505951$. Other parameters are: $a = 1$, $x_0 = 1$, and $b = -2.5$. The solutions $x(t)$ converge by oscillating to their stationary point $x_2^* = -a/(b + 1) = 2/3$ as $t \rightarrow \infty$.

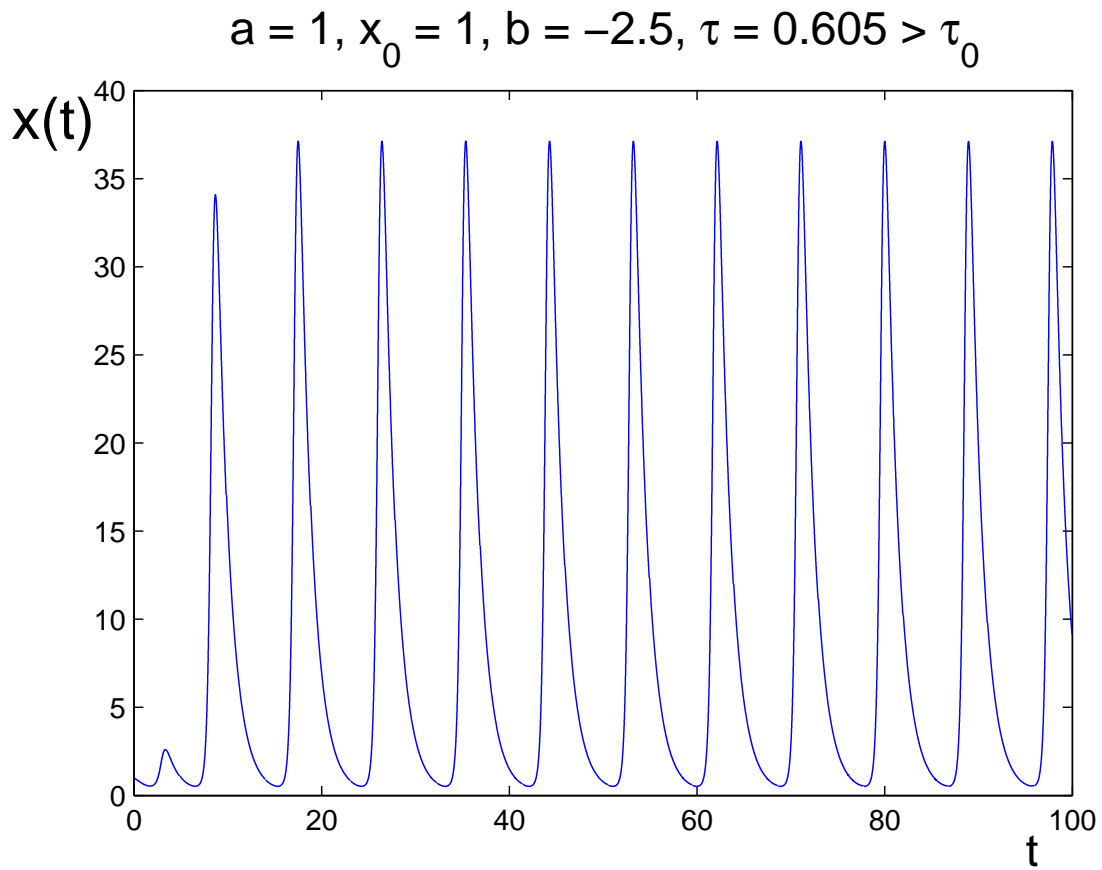


Figure 20: Solution $x(t)$ to Eq. (64) as a function of time for the parameter $\tau = 0.605 > \tau_0$, where $\tau_0 = 0.505951$. Other parameters are the same as for Fig. 19. The solution $x(t)$ exhibits sustained oscillations with an amplitude which is an increasing function of the delay time τ and a period much larger than τ .

$$a = 1, x_0 = 1, b = -2.5$$

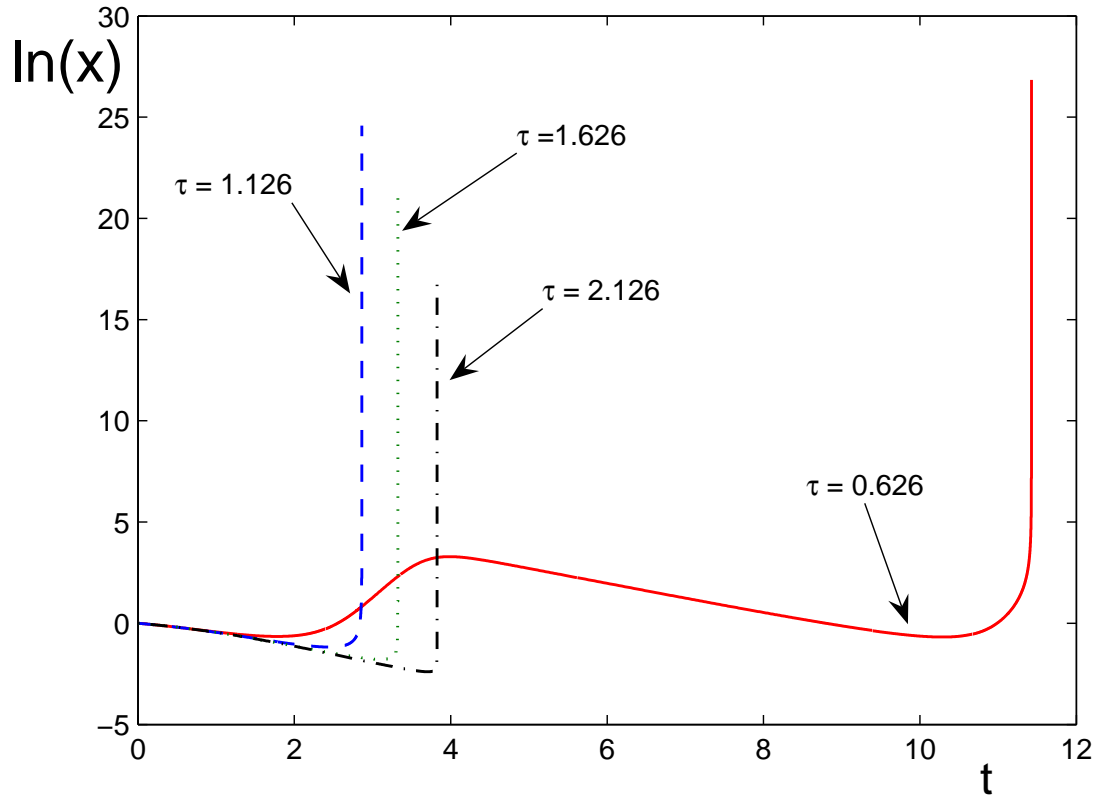


Figure 21: Logarithmic behavior of solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.626$ (solid line), $\tau = 1.126$ (dashed line), $\tau = 1.626$ (dotted line), and $\tau = 2.126$ (dashed-dotted line), where $\tau_1 < \tau < \tau_2$. Other parameters are the same as for Fig. 19. There exist points of singularity t_c^* , defined by $a + bx(t_c^* - \tau) = 0$, where $x(t)|_{t \rightarrow t_c^* - 0} = +\infty$. These points are: $t_c^* = 11.4328$ (for solid line), $t_c^* = 2.87170$ (for dashed line), $t_c^* = 3.33026$ (for dotted line), and $t_c^* = 3.83074$ (for dashed-dotted line).

$$a = 2, x_0 = 1, b = -2.5$$

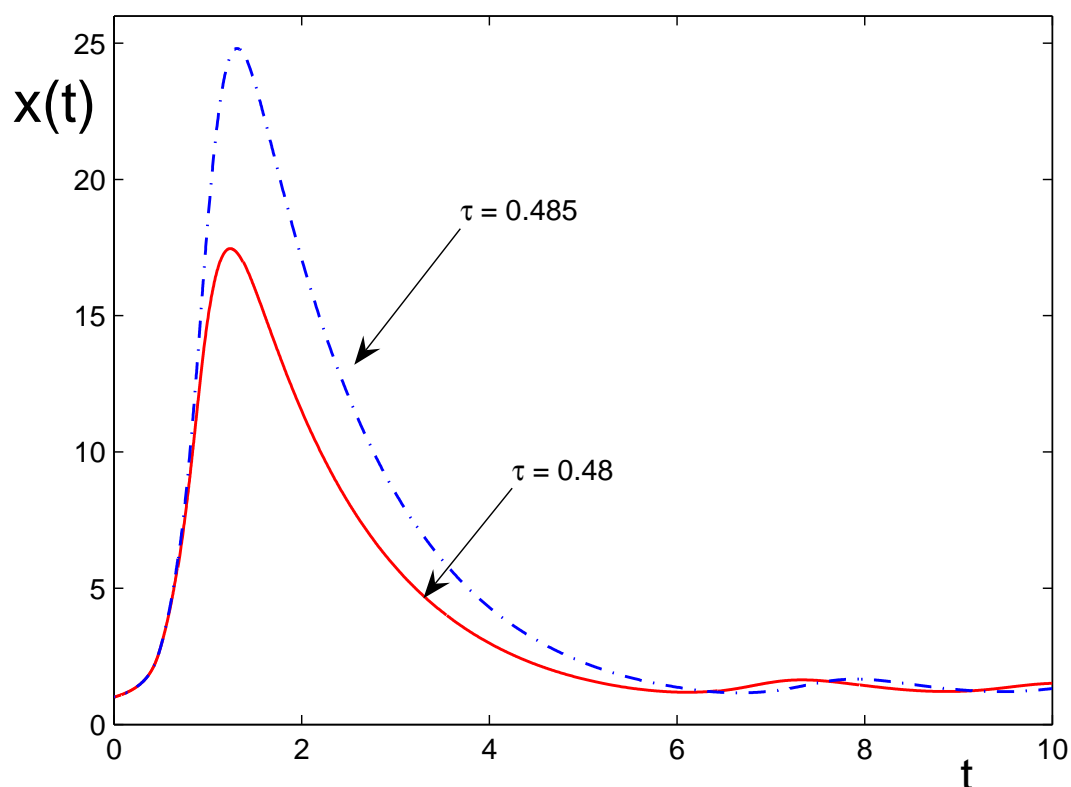


Figure 22: Solutions $x(t)$ to Eq. (64) as functions of time for the parameters $\tau = 0.48$ (solid line) and $\tau = 0.485$ (dashed-dotted line), where $\tau < \tau_0 = 0.495125$. Other parameters are: $a = 2$, $x_0 = 1$, and $b = -2.5$. The solutions $x(t)$ tend non-monotonically to their stationary point $x_2^* = -a/(b + 1) = 4/3$ as $t \rightarrow \infty$.

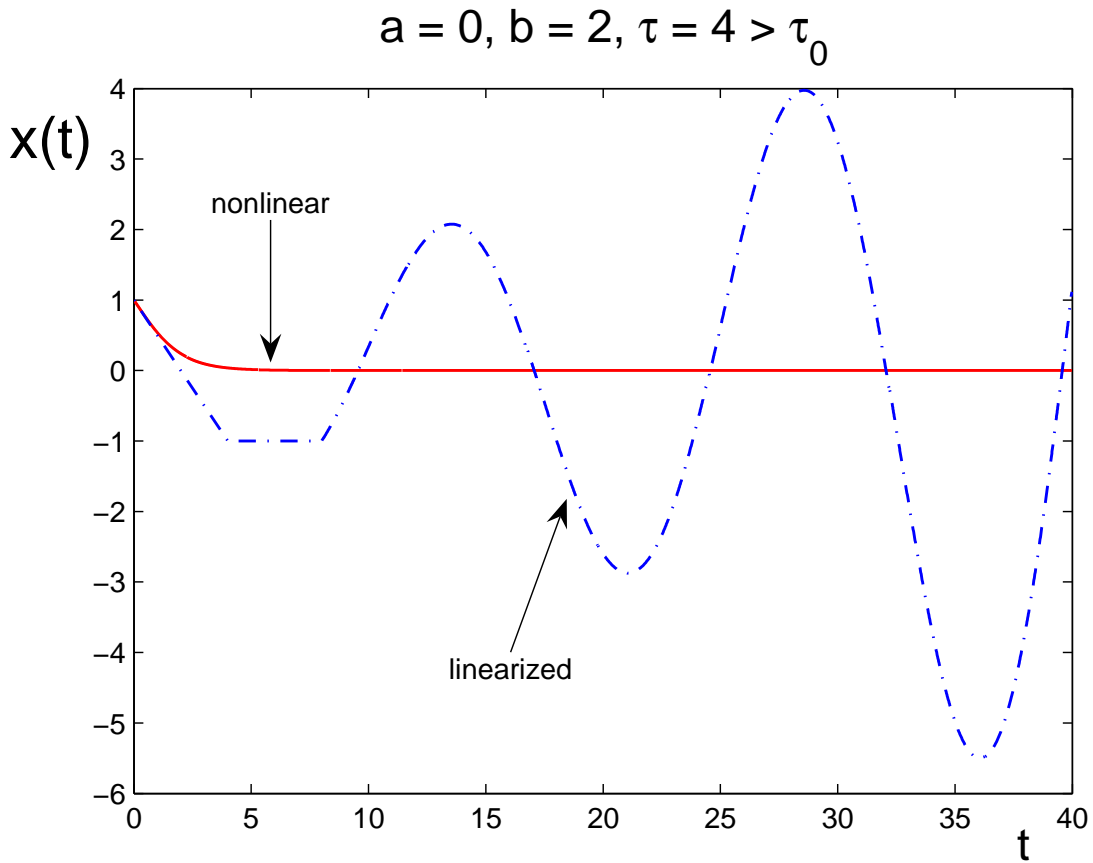


Figure 23: Solutions $x(t)$ to Eq. (84) (solid line) and to the corresponding equation obtained by linearizing Eq. (84) around the fixed point $x^* = 0$ (dashed-dotted line). Parameters for the equations are: $a = 0, b = 2$, and $\tau = 4$ (note that $\tau > \tau_0 = \pi$). The figure shows that the solution to the linearized equation is unstable for $\tau > \tau_0$, as the stability analysis prescribes, whereas the solution to the nonlinear equation is stable for $\tau > \tau_0$, tending to its stationary point $x^* = 0$ as $t \rightarrow \infty$.

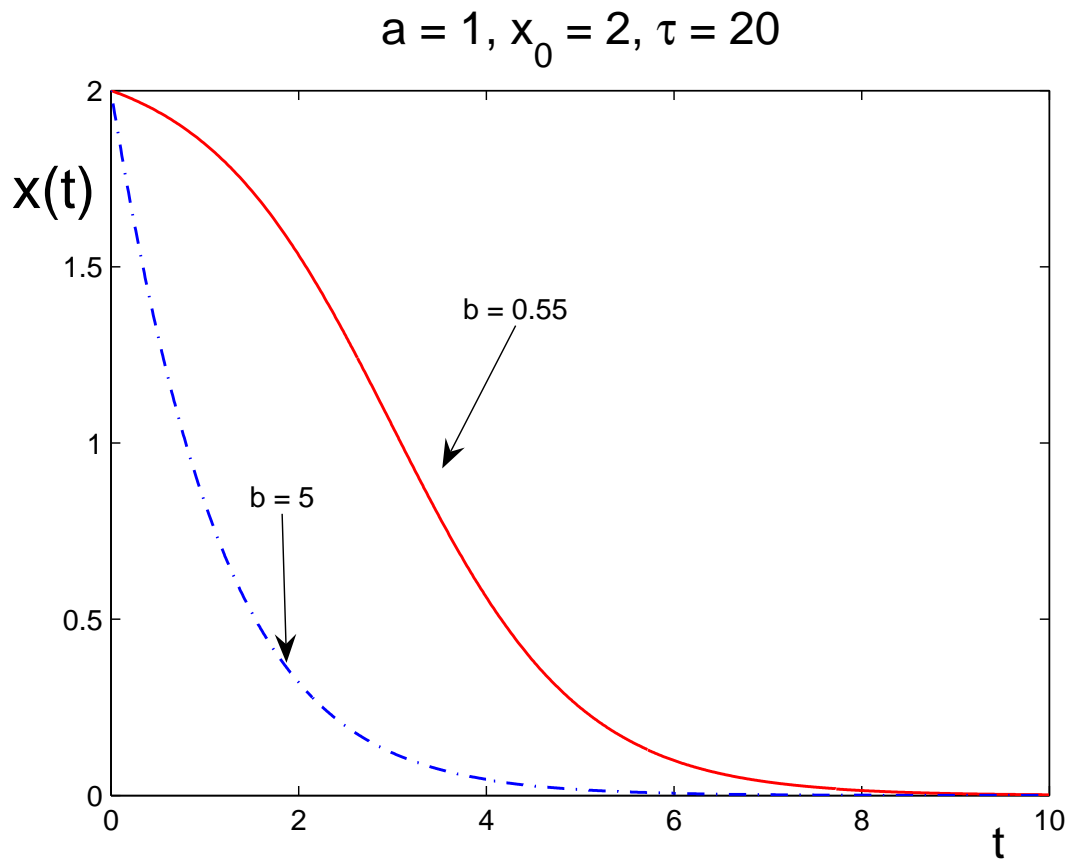


Figure 24: Solutions $x(t)$ to Eq. (84) as functions of time for the parameters $b = 0.55$ (solid line) and $b = 5$ (dashed-dotted line). Other parameters are: $a = 1$, $x_0 = 2$, and $\tau = 20$. The solutions $x(t)$ decrease monotonically to their stationary point $x^* = 0$ as $t \rightarrow \infty$.

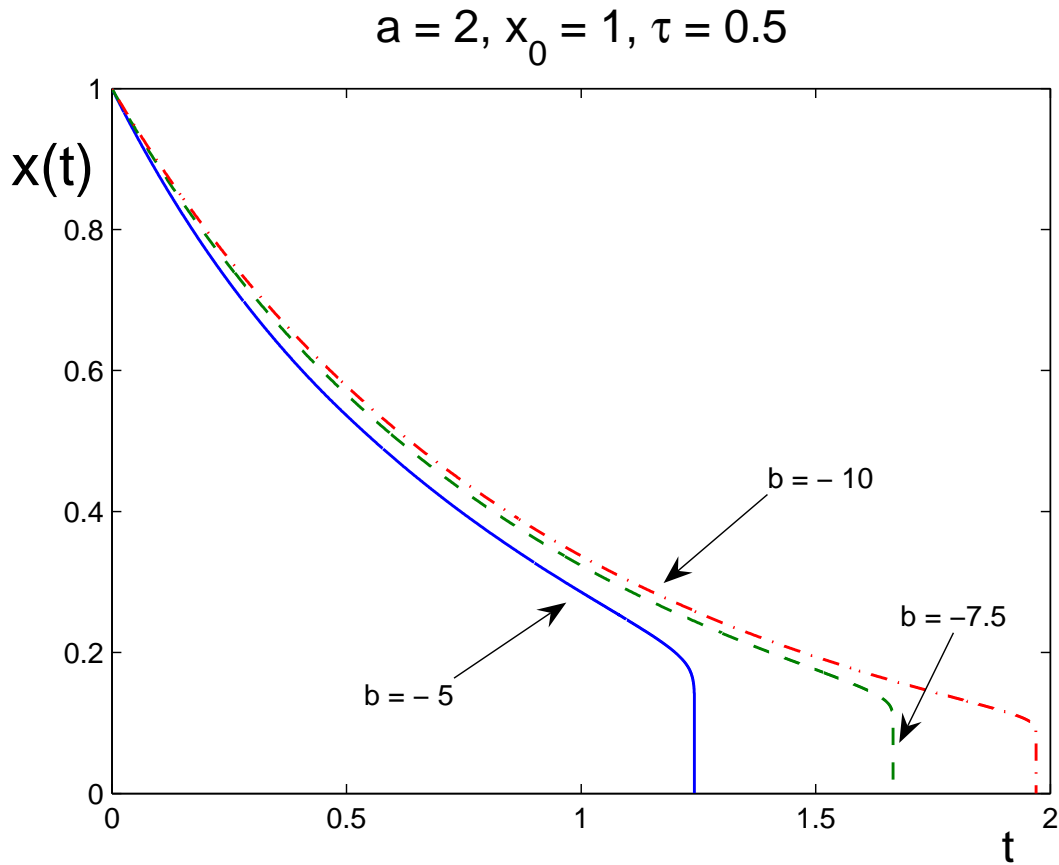


Figure 25: Solutions $x(t)$ to Eq. (84) as functions of time for the parameters $b = -5$ (solid line), $b = -7.5$ (dashed line), and $b = -10$ (dashed-dotted line). Other parameters are: $a = 2$, $x_0 = 1$, and $\tau = 0.5$. The solutions $x(t)$ decrease monotonically with a sharp but continuous drop ending at 0 at time $t_d = 1.24290$ (for solid line), $t_d = 1.66635$ (for dashed line), and $t_d = 1.97114$ (for dashed-dotted line) defined by the equation $a + bx(t_d - \tau) = 0$. At these moments, of time $\dot{x}(t)|_{t \rightarrow t_d-0} = -\infty$.

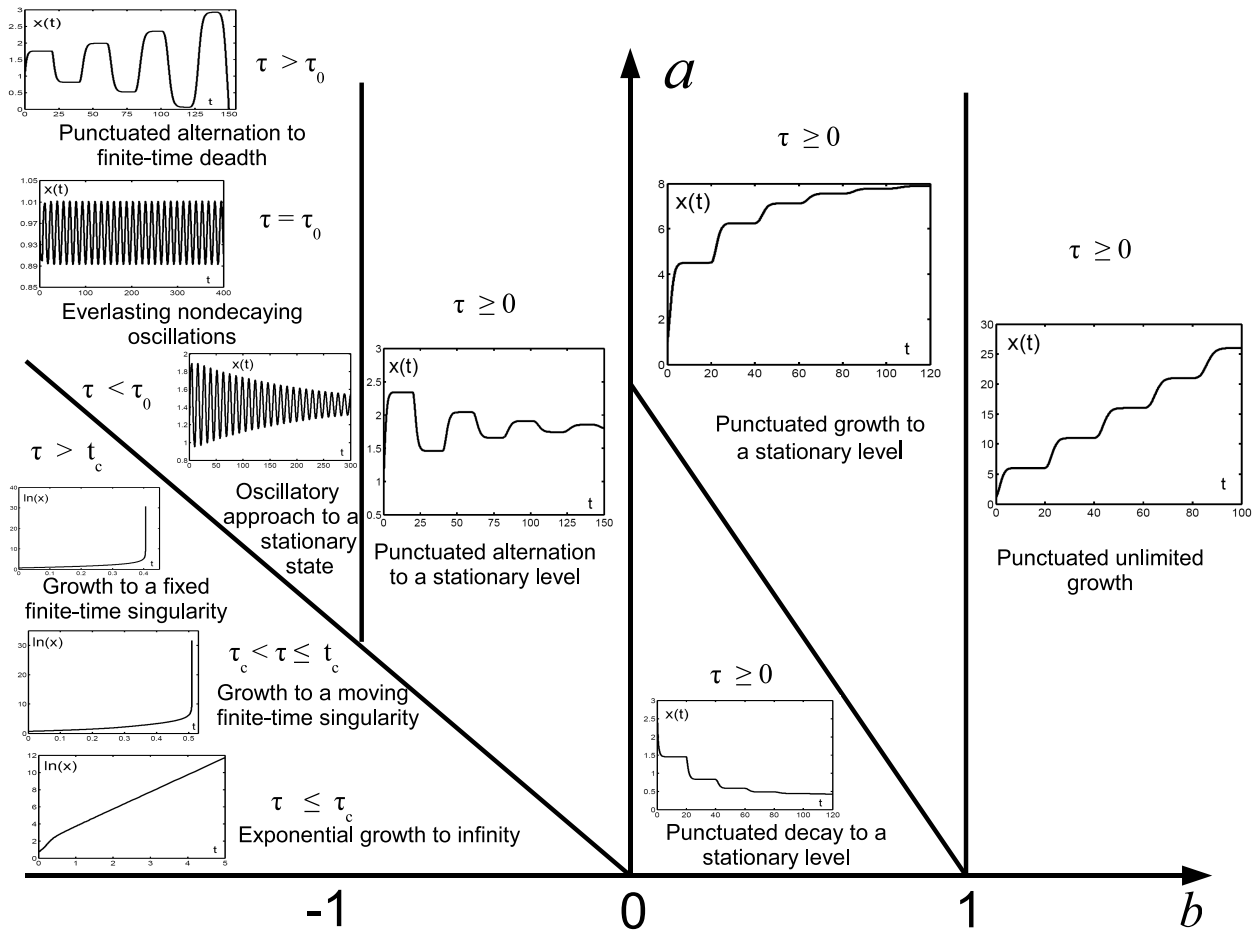


Figure 26: Scheme of the variety of qualitatively different solution types for the most complicated and the most realistic regime of Sec. 4, when gain (birth) prevails over loss (death) and competition is stronger than cooperation.

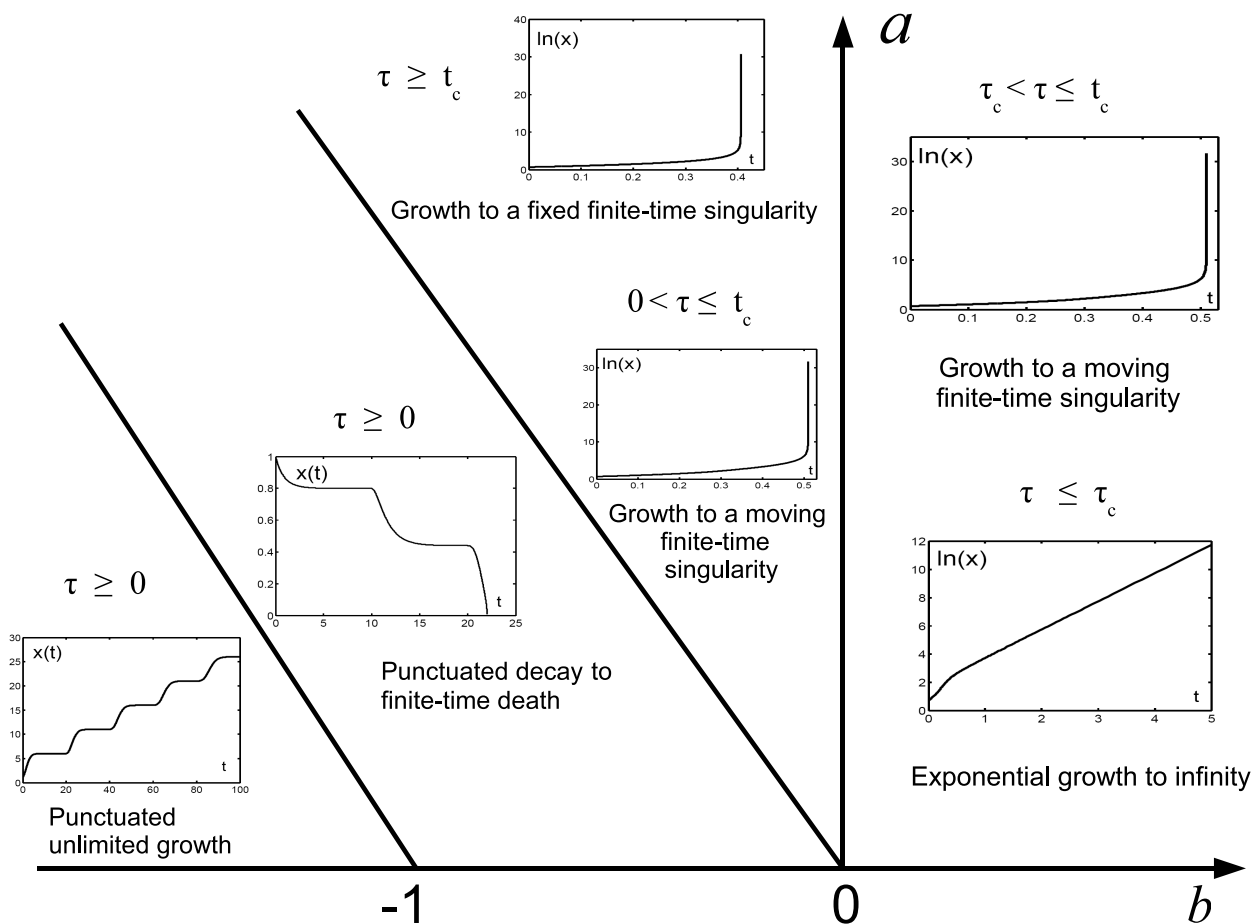


Figure 27: Scheme of qualitatively different solution types for the case of Sec. 5, when gain prevails over loss and cooperation prevails over competition.

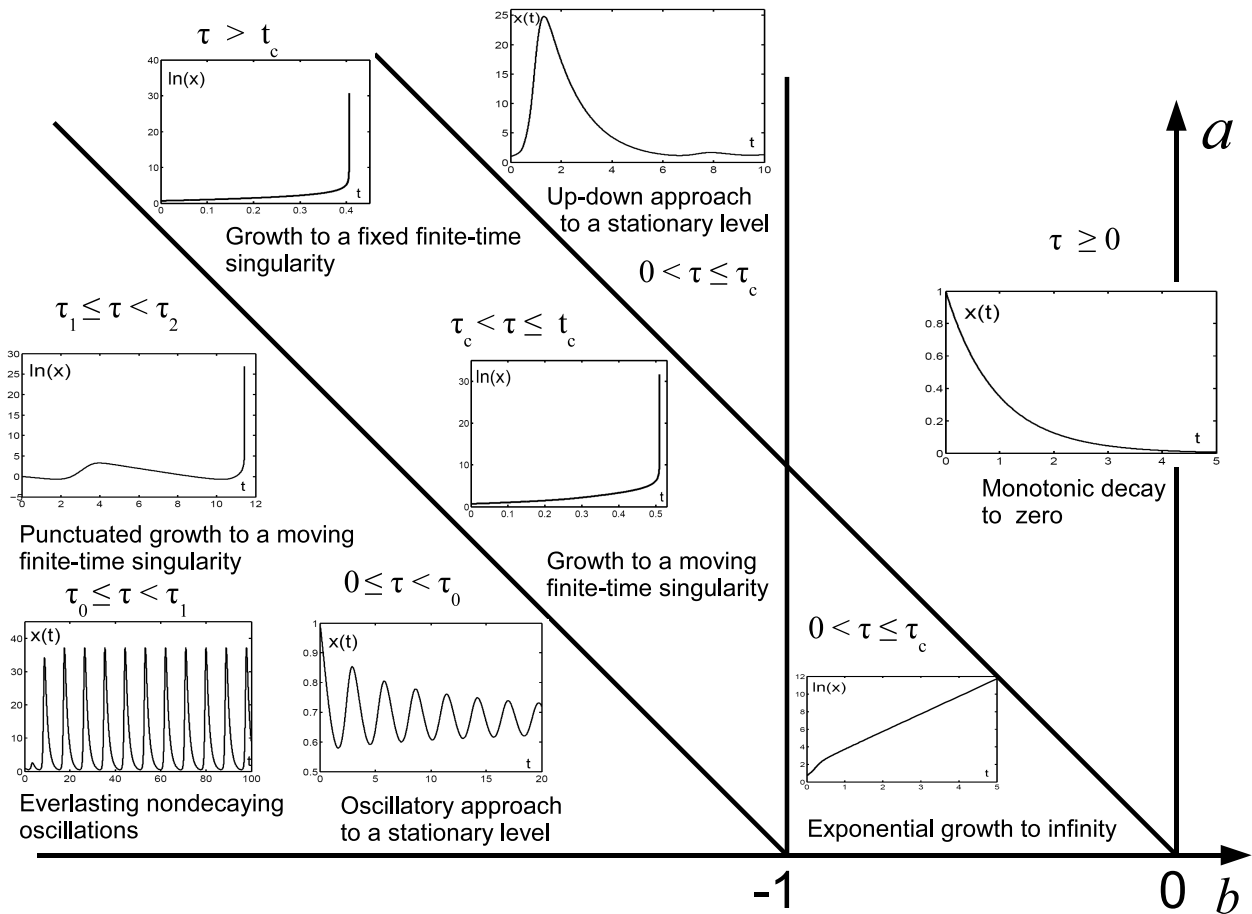


Figure 28: Summarizing scheme of qualitatively different solution types for the case of Sec. 6, when loss prevails over gain and competition prevails over cooperation.

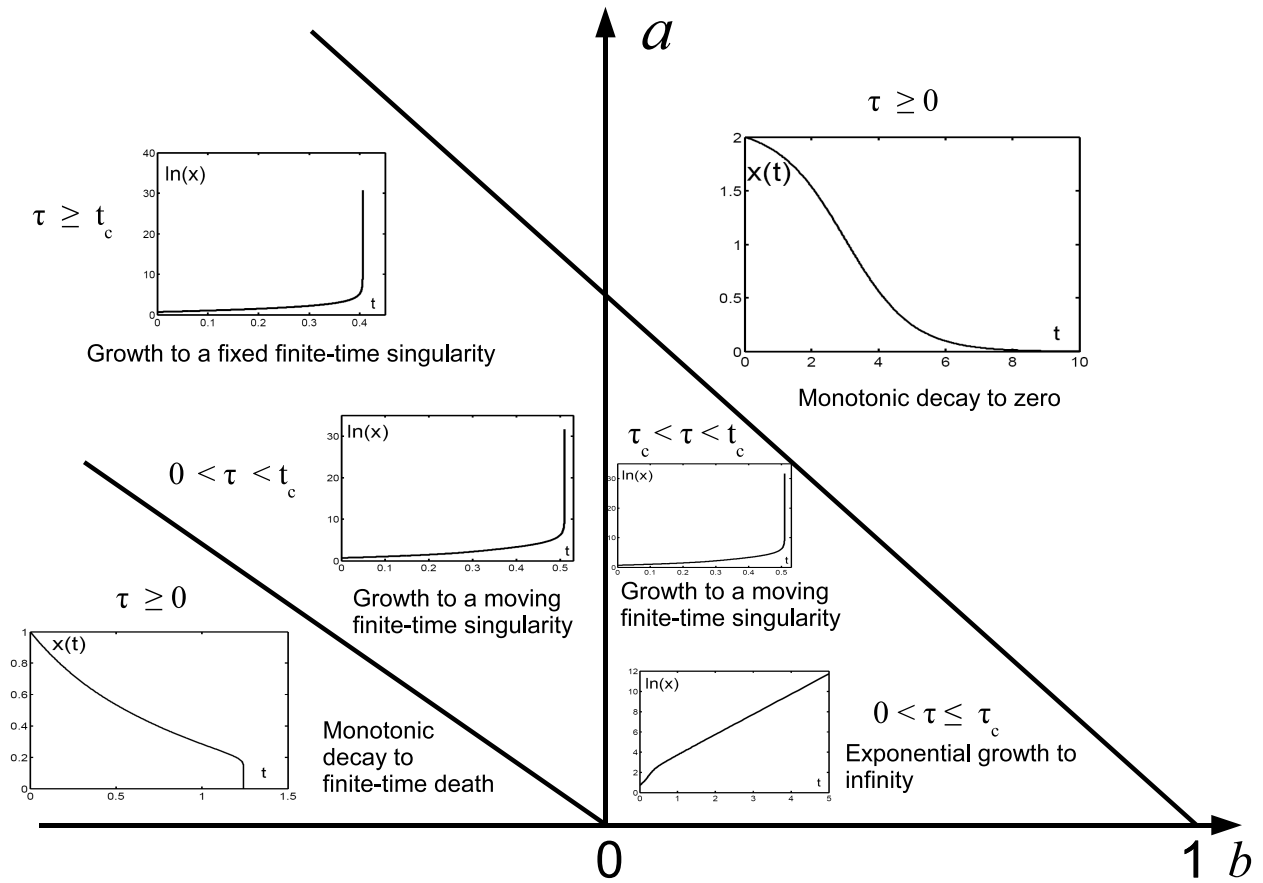


Figure 29: Summarizing scheme of qualitatively different solution types for the case of Sec. 7, when loss prevails over gain and cooperation prevails over competition.