

A Global Picture of the Gamma-Ricker Map: A Flexible Discrete-Time Model with Factors of Positive and Negative Density Dependence

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Abstract The gamma-Ricker model is one of the more flexible and general discrete-time population models. It is defined on the basis of the Ricker model, introducing an additional parameter $\gamma > 0$. For some values of this parameter ($\gamma \leq 1$), population is overcompensatory, and the introduction of an additional parameter gives more flexibility to fit the stock–recruitment curve to field data. For other parameter values ($\gamma > 1$), the gamma-Ricker model represents populations whose per-capita growth rate combines both negative density dependence and positive density dependence. The former can lead to overcompensation and dynamic instability, and the latter can lead to a strong Allee effect. We study the impact of the cooperation factor in the dynamics and provide rigorous conditions under which increasing the Allee effect strength stabilizes or destabilizes population dynamics, promotes or prevents population extinction, and increases or decreases population size. Our theoretical results also include new global stability criteria and a description of the possible bifurcations.

Keywords Discrete-time population model · Gamma model · Extinction · Density dependence · Stability · Allee effect · Stock and recruitment

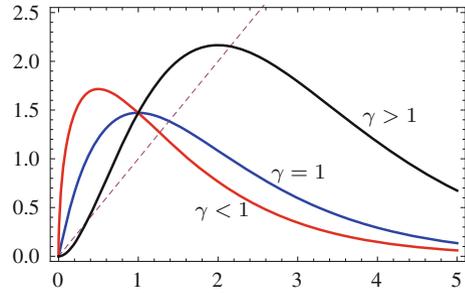
1 Introduction

Discrete-time population models are widely used to describe the life histories of many organisms, including fish, birds, insects, mammals and plants (Kot 2001). One important purpose of population models consists of helping to predict the long-term behavior of population abundance and to understand the influence of the involved parameters.

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Fig. 1 Graphs of the map f for $\delta = 1$, $\beta = 4$, and different values of γ : $\gamma = 1$ (Ricker map) in blue, $\gamma = 0.5 < 1$ in red and $\gamma = 2 > 1$ in black. The dashed line is the graph of $y = x$ (Color figure online)



Stock–recruitment models play a central role in theoretical ecology, especially in the context of fish populations (Quinn and Deriso 1999; Clark 2010). The so-called *stock–recruitment* or *spawner–recruit* relationship $R = f(S)$ establishes the recruits R that are produced by the spawning stock S in each time cycle (typically, annual), so that the discrete-time population model $x_{n+1} = f(x_n)$ governs the between-year dynamics. Here, x_n represents the population size after n generations, $n = 1, 2, \dots$. Function f involves a number of parameters that usually have (at least at a phenomenological level) a biological meaning: growth rate, carrying capacity, survival probability of juveniles, etc.

An important function of the involved parameters is that they offer some flexibility to find a suitable model that fits well the available population data. Perhaps the most typical stock–recruitment models are the compensatory Beverton–Holt model $x_{n+1} = \alpha x_n / (1 + \beta x_n)$, $\alpha > 0$, $\beta > 0$ (Beverton and Holt 1957) and the overcompensatory Ricker model $x_{n+1} = \beta x_n e^{-\delta x_n}$, $\beta > 0$, $\delta > 0$ (Ricker 1954). In both cases, function f has only two parameters, and it has been argued (e.g., Iles 1994) that these models are relatively inflexible. More flexible models involving three parameters have been suggested in the literature (see Quinn and Deriso 1999); among them, perhaps the best known is the Shepherd model $x_{n+1} = \alpha x_n / (1 + \beta x_n^\gamma)$, which gives the Beverton–Holt model for $\gamma = 1$, and it is overcompensatory for $\gamma > 1$, so that its dynamics for these parameter values are closer to those of the Ricker model.

We devote this paper to investigate the rich dynamics of another stock–recruitment model with three parameters, to which we will refer as the *gamma-Ricker* model:

$$x_{n+1} = \beta x_n^\gamma e^{-\delta x_n} = f(x_n), \quad (1)$$

where β , γ , δ are positive parameters. Model (1) is included in the list of spawner–recruit models in Chapter 3 from Quinn and Deriso (1999), where it is called the *gamma model*. A particular case of (1) is the Ricker model ($\gamma = 1$), and the Cushing model (Cushing 1971) is a limit case ($\delta = 0$). Equation (1) is defined as a flexible and general overcompensatory model, which exhibits a strong Allee effect for $\gamma > 1$ (see Fig. 1).

Model (1) has been employed in different scenarios and with different names; without trying to be exhaustive, we mention some of them: Reish et al. (1985) used (1) to fit spawner–recruitment data for the Atlantic menhaden, and they called it *unnormalized gamma model*. In his review of stock–recruitment relationships, Iles (1994) also

emphasizes the flexibility of (1) and refers to it as to the *Saila–Lorda equation*. Zheng et al. (1995) and Zheng and Kruse (2003) found that (1) fits well the stock–recruitment data for three Alaskan crab stocks, and they refer to (1) as to a *general Ricker equation*. Interestingly, they estimated stock–recruitment relationships using (1) with values of $\gamma < 1$ (overcompensatory growth) and $\gamma > 1$ (depensatory growth); see, e.g., Figure 7 in page 115 of Zheng and Kruse (2003). Avilés (1999) used model (1) with $1 < \gamma \leq 2$ in the context of cooperative interaction in a group of individuals, and she refers to (1) as to a *Ricker-type difference equation with a positive density-dependent factor*. Accordingly, the parameter γ is called *cooperation parameter*. We notice that depensation models are commonly known as models with Allee effects (Courchamp et al. 2008); in this context, Eq. (1) with $\gamma = 2$ has been already introduced by Asmussen (1979). A mechanistic derivation of particular cases of (1) can be found in Eskola and Geritz (2007) (the Ricker model, $\gamma = 1$) and Eskola and Parvinen (2007) (the Asmussen model, $\gamma = 2$). In the latter reference, the authors refer to (1) as to a *Ricker-type model with Allee effect*.

Following the approach in previous papers (Avilés 1999; Scheuring 1999; Schreiber 2003), we can rewrite model (1) in the following form:

$$x_{n+1} = \beta x_n I(x_n) G(x_n), \quad (2)$$

where $G(x) = e^{-\delta x}$ and

$$I(x) = \left(\frac{x}{\alpha}\right)^{\tilde{\gamma}}, \quad \tilde{\gamma} \in \mathbb{R}, \quad \alpha > 0. \quad (3)$$

In the above factorization, each factor represents an ecological mechanism or effect. Namely, βx_n is the spawning stock, $G(x)$ describes the intraspecific competition, and $I(x)$ is a cooperation or interference factor, depending on $\tilde{\gamma}$. Parameter α in (3) is used to scale x , avoiding dimensional problems when raising powers. Clearly, Eq. (2) can be rescaled so that α effectively drops out, and we can restrict our analysis to the three-parameter model (1).

We can distinguish three cases in formulation (2), depending on $\tilde{\gamma}$:

- if $\tilde{\gamma} = 0$, then the term $I(x)$ drops out, and we get the Ricker model;
- if $\tilde{\gamma} > 0$, then $I(x)$ is a cooperation or “self-facilitation” factor;
- if $\tilde{\gamma} < 0$, then $I(x)$ is an interference or “self-inhibition” factor.

The case $\tilde{\gamma} > 0$ combines both negative density dependence and positive density dependence, so it allows to study the impact of cooperation in different dynamical regimes, especially on the persistence of a population and on its equilibrium population size.

In the case $\tilde{\gamma} < 0$, model (2) contains two factors of negative density dependence. We notice that $I(x)$ tends to infinity as x tends to zero, which is biologically problematic. This effect is hidden in model (2) if $-1 < \tilde{\gamma} < 0$ [which corresponds to $0 < \gamma < 1$ in (1)] by interaction with some other effects. Thus, although this case has been used as an admissible (phenomenological) population model (Quinn and Deriso 1999; Zheng and Kruse 2003), it is important to keep in mind that the per-capita

production of stock goes to infinity if population size becomes too small, which is questionable from a mechanistic point of view. Actually, if $\tilde{\gamma} \leq -1$, Eq. (1) does not correspond to a valid spawner–recruitment model because $f(0) \neq 0$ (Quinn and Deriso 1999, p. 97). In this case, the odd behavior of $I(x)$ near the origin is translated to $f(x)$, and it is not hidden anymore by interaction with other factors. We will not address this case in the paper, but it is worth mentioning that, in contrast to the case $\tilde{\gamma} > -1$, (2) has unbounded solutions for any $\tilde{\gamma} < -1$; this odd behavior in an equation with two interference factors can be explained by the fact that population reaches very low values, which at the next generation become arbitrarily big because $f(x)$ tends to infinity as x tends to zero.

Given the history of the gamma-Ricker model, and considering that the case $0 < \gamma < 1$ has also been employed in the ecological literature, and it has not been analyzed in detail, we give a thorough picture of the dynamics of (1) for all $\gamma > 0$. We obtain new results, which include sharp stability conditions, establishing the exact basins of attraction (Theorem 1), as well as a precise statement for the stabilizing/destabilizing effects of γ (Proposition 3), and for the transitions between extinction and persistence (Proposition 4). We are particularly interested in the effects of the cooperation/interference term $I(x)$ on population size, and we are able to determine the exact conditions, depending on the other parameter values β and δ , for which population size at equilibrium increases as γ is increased (Theorem 2).

For convenience of the reader, we will give a “phenomenological” name to the involved parameters for later use in the paper. We call β the productivity parameter, δ the competition parameter, and, following Avilés (1999), we refer to γ as the cooperation parameter (although the corresponding term can actually represent interference, namely if $\gamma < 1$).

2 Dynamical Analysis

In this section, we study the dynamics of (1), with $\beta, \gamma, \delta > 0$. In our first result, we list several basic properties of the map $f : [0, \infty) \rightarrow [0, \infty)$ that defines the right-hand side of (1). We omit the elementary proof.

Proposition 1 *The map $f(x) = \beta x^\gamma e^{-\delta x}$ ($\beta, \gamma, \delta > 0$) satisfies the following properties:*

- (a) $f(0) = 0$ and $\lim_{x \rightarrow \infty} f(x) = 0$.
- (b) $f'(0) = 0$ if $\gamma > 1$, $f'(0) = \beta$ if $\gamma = 1$, and $\lim_{x \rightarrow 0^+} f'(x) = \infty$ if $0 < \gamma < 1$.
- (c) f is a C^∞ -unimodal map in $(0, \infty)$, with a unique critical point at $c = \gamma/\delta$, and $f(c)$ is the global maximum of f . In consequence, all solutions $\{x_n\}_{n \geq 0}$ of (1) are bounded by $f(c)$ for all $n \geq 1$.
- (d) If $\gamma < 1$, then (1) is persistent and f has a unique positive fixed point p . Moreover, $f(x) > x$ if $0 < x < p$, and $f(x) < x$ if $x > p$.
- (e) If $\gamma = 1$, then f has a unique positive fixed point if $\beta > 1$ and no positive fixed points if $\beta \leq 1$.
- (f) If $\gamma > 1$, then f can have two positive fixed points, one positive fixed point or no positive fixed points.

When $\gamma > 1$ and f has two positive fixed points, the smallest one is unstable and it is usually referred to as the Allee threshold (Courchamp et al. 2008). If population abundance falls below the Allee threshold, then extinction occurs.

In our discussion about the dynamics of (1), an important question is the sign of the Schwarzian derivative of f . We recall that the Schwarzian derivative of f is defined for every $x > 0, x \neq c = \gamma/\delta$, by the expression

$$(Sf)(x) = \left(\frac{f'''(x)}{f'(x)} \right) - \frac{3}{2} \left(\frac{f''(x)}{f'(x)} \right)^2.$$

The next proposition establishes the sign of $(Sf)(x)$. The proof of this proposition and the subsequent results in the paper are given in ‘‘Appendix’’.

Proposition 2 Consider the map $f(x) = \beta x^\gamma e^{-\delta x}$, with $\beta > 0, \delta > 0$.

- (i) If $\gamma \geq 1$, then $(Sf)(x) < 0$ for all $x \in (0, \infty), x \neq \gamma/\delta$.
- (ii) If $0 < \gamma < 1$, then $(Sf)(x) < 0$ for all $x \in (\gamma/\delta, \infty)$.

Proposition 2 is crucial to find sharp estimates for the basins of attraction of the equilibria in (1) and also to apply previous results for one-dimensional population models with Allee effects. For example, the results of Schreiber (2003) ensure that (1) is not persistent for all initial conditions if $\gamma > 1$; actually, the dynamics falls in one of the following generic categories: *total extinction* if the unique fixed point is 0; *bistability* if f has two positive fixed points (the Allee threshold A and $p > A$) and $f(f(c)) > A$; *essential extinction* if $f(f(c)) < A$ (here, $c = \gamma/\delta$ is the critical point of f). In case of bistability, population persists for intermediate values of initial population densities, while essential extinction means that extinction occurs with probability one for a randomly chosen initial condition.

2.1 Bifurcations

A description of the possible bifurcations in (1) helps to understand the possible dynamics and the role played by the parameters. We identify the bifurcations observed in the model, which are important in the discussion about stability, extinction and population abundance. We do not aim to give a rigorous bifurcation analysis; we refer the reader to Wiggins (1990) for a systematic study of bifurcations in discrete dynamical systems.

- Generic bifurcations of fixed points.

Taking β as the bifurcation parameter, we observe two important bifurcations of fixed points.

- Tangent (saddle-node) bifurcations: A tangent bifurcation occurs for $\gamma > 1$. For fixed values of $\gamma > 1$ and $\delta > 0$, there is a critical value $\beta^* = \beta^*(\gamma, \delta)$ such that f has two positive fixed points if $\beta > \beta^*$, one positive fixed point if $\beta = \beta^*$ and no positive fixed points if $\beta < \beta^*$. The value of β^* has already been identified by Avilés (1999), and is given by

$$\beta^* = e^{\gamma-1} \left(\frac{\gamma-1}{\delta} \right)^{1-\gamma}. \quad (4)$$

The smallest fixed point that is born after the tangent bifurcation is always unstable, and the largest one is stable for values of β close enough to β^* . Interestingly, if we look at tangent bifurcations taking γ as the bifurcation parameter, extinction windows can appear in the bifurcation diagram; see Proposition 4 and Fig. 3.

- Period-doubling (flip) bifurcations: Let p be the unique positive fixed point of the difference Eq. (1) if either $\gamma < 1$ or $\gamma = 1$ and $\beta > 1$, or the largest fixed point if $\gamma > 1$ and $\beta > \beta^*$. The equilibrium p loses its asymptotic stability after a supercritical period-doubling bifurcation occurs when $f'(p) = -1$. The analytic expression for the bifurcation curve can also be found in Avilés (1999) and is defined by

$$\beta = e^{\gamma+1} \left(\frac{\gamma+1}{\delta} \right)^{1-\gamma}. \quad (5)$$

Analogously to the previous case, considering γ as the bifurcation parameter, flip bifurcations can give rise to stability windows between two stability switches; see Proposition 3 and Fig. 4.

Using β as the bifurcation parameter, these are the only bifurcations of fixed points that (1) can undergo, with the exception of the case $\gamma = 1$, for which a transcritical bifurcation occurs at $\beta = 1$ (switching the system from extinction to persistence). Since we are also interested in changes in the dynamics of (1) as γ is varied, we look below at other possible bifurcations of fixed points.

- Bifurcations at $\gamma = 1$, $x = 0$: When the parameter γ crosses the critical value 1, the dynamics of (1) near zero changes because the behavior of the multiplier $f'(0)$ changes abruptly (see Proposition 1 (b)). We observe the following bifurcations:
 - Transcritical bifurcation: If $\beta \leq 1$, then a transcritical bifurcation occurs at the bifurcation point $(x, \gamma) = (0, 1)$. For $\gamma < 1$, the positive fixed point is stable and 0 is unstable. For $\gamma > 1$, 0 becomes asymptotically stable and the branch of positive fixed points disappears. See, e.g., Fig. 3a.
 - Pitchfork bifurcation: If $\beta > 1$, then a curve of positive fixed points passes through the bifurcation point $(x, \gamma) = (0, 1)$, and is defined for $\gamma \in (1, 1 + \varepsilon)$, $\varepsilon > 0$. For $\gamma \leq 1$, 0 is unstable, and, for $\gamma > 1$, 0 becomes asymptotically stable, and the new positive equilibrium is unstable. This bifurcation can be identified as a subcritical pitchfork bifurcation. See Figs. 3b and 4.
- Transcritical bifurcation for $\beta = e^\delta$: This is a special case for which $x = 1$ is an equilibrium of (1) for all $\gamma > 0$. If $\gamma \leq 1$, then 1 is the unique positive equilibrium; if $\gamma > 1$, then there is another positive equilibrium p . At the critical value $\gamma = 1 + \delta$, a transcritical bifurcation occurs, in such a way that 1 is asymptotically stable for $\gamma < 1 + \delta$, and unstable for $\gamma > 1 + \delta$, and the opposite occurs for p . See Fig. 4a.
- Other bifurcations

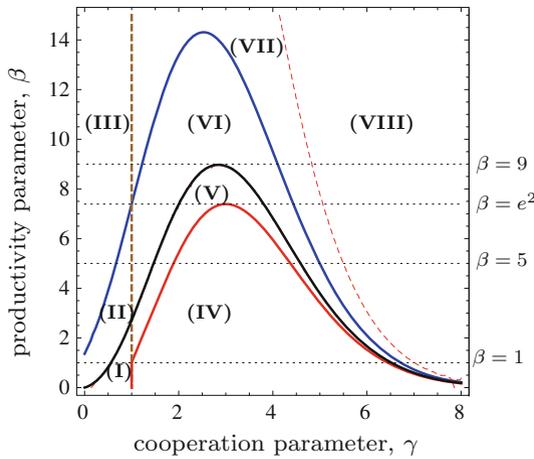


Fig. 2 Main bifurcation boundaries for Eq. (1) with $\delta = 2$, and regions with different dynamical behavior (see the text). From below, solid lines: extinction boundary (red color); monotone/oscillatory convergence (black color); stability boundary (blue color). The red dashed curve represents the border between bistability and essential extinction. Finally, the brown dashed line ($\gamma = 1, \beta > 1$) is the boundary between persistence and bistability. The horizontal dotted lines correspond to the case studies chosen for the bifurcation diagrams in Figs. 3 and 4 (Color figure online)

- Route of period-doubling bifurcations to chaos: After the period-doubling bifurcation occurs, further increasing of the parameter β results in a cascade of period-doubling bifurcations leading to chaos. This phenomenon is observed both for the persistent case ($\gamma \leq 1$) and for the case with Allee effects ($\gamma > 1$).
- Boundary collision (crisis) leading to essential extinction. If $\gamma > 1$, then a crisis bifurcation occurs when the basin of attraction of the chaotic attractor collides with the basin of attraction of zero. This situation happens when the second iteration of the critical value $c = \gamma/\delta$ is the Allee threshold A . At the parameter values for which this boundary collision occurs, Eq. (1) is chaotic; for more details, see, e.g., Schreiber (2001, 2003) and Liz (2010). Boundary collisions leading to essential extinction are shown in Figs. 3 and 4.

In Fig. 2, we show the main bifurcation boundaries for Eq. (1) with $\delta = 2$, which allows to divide the plane of parameters (γ, δ) in eight regions with different dynamics.

The behavior of the solutions in each region is as follows (we give precise explanations later in the paper):

- Regions (I), (II), and (III) correspond to $\gamma < 1$, or $\gamma = 1, \beta > 1$, so all nonzero solutions of (1) are bounded away from zero (**persistence**). In the first region, all nonzero solutions converge to the positive equilibrium, and the convergence is eventually monotone; in the second one, the convergence is oscillatory; finally, in region (III) the positive equilibrium is unstable and all positive solutions converge to a periodic solution or they exhibit chaos.
- In region (IV), the unique equilibrium is 0, and it is a global attractor (**total extinction**).

- In regions (V), (VI) and (VII) the equilibrium 0 is asymptotically stable, and it coexists with other attractor (**bistability**); the nonzero attractor is an equilibrium in regions (V) (monotone convergence) and (VI) (oscillatory convergence), and it is a periodic or chaotic attractor in region (VII).
- Finally, in region (VIII) almost every initial condition converges to zero (**essential extinction**).

2.2 Global Stability

Our next result states that the positive equilibrium p is globally asymptotically stable whenever it is asymptotically stable in the persistent case. In case of bistability, Theorem 1 shows that the largest positive equilibrium p attracts all initial conditions that do not converge to 0 if p is asymptotically stable (excluding the Allee threshold A and its preimage $f^{-1}(A)$, which obviously are driven to A and remain there).

Theorem 1(A) *Assume that $0 < \gamma < 1$, or $\gamma = 1$ and $\beta > 1$. Then the unique positive equilibrium p is globally asymptotically stable for the difference Eq. (1) if the following condition holds:*

$$\beta \leq e^{\gamma+1} \left(\frac{\gamma + 1}{\delta} \right)^{1-\gamma}. \tag{6}$$

If condition (6) does not hold, then p is unstable.

- (B) *Assume that $\gamma > 1$ and $\beta > \beta^*$ [defined in (4)], and let A, p ($A < p$) be the positive equilibria of (1). Then the largest equilibrium p is asymptotically stable if and only if (6) holds. Moreover, in this case, p attracts all initial conditions of (1) starting at the interval $J = (A, f^{-1}(A))$, while initial conditions $x_0 \notin [A, f^{-1}(A)]$ are driven to 0.*

In both cases, the convergence to the equilibrium is eventually monotone if and only if the following inequality holds:

$$\beta \leq e^{\gamma} \left(\frac{\gamma}{\delta} \right)^{1-\gamma}. \tag{7}$$

Remark Although the stability condition (6) has been found in previous papers (e.g., Avilés 1999), the global stability result for $\gamma < 1$ is new. For $\gamma = 1$, we recover the known global stability condition $\beta \leq e^2$ for the Ricker map.

Theorem 1 allows us to know the influence of the different parameters on the stability of the positive equilibrium of (1). First, it is clear from (6) that increasing β is destabilizing for fixed values of γ and δ . Solving (6) for δ , it can be easily seen that increasing δ for fixed values of β and γ is stabilizing if $\gamma > 1$, destabilizing if $\gamma < 1$, and does not have any influence if $\gamma = 1$. The influence of γ for fixed values of β and δ is more subtle. The stabilizing/destabilizing effects of the parameter γ are stated in the following result:

Proposition 3 *Let p be the unique positive equilibrium of the difference Eq. (1) if $\gamma \leq 1$, or the largest positive equilibrium if $\gamma > 1$ and $\beta > \beta^*$. Then:*

- (i) *Increasing γ is destabilizing if either $\delta \leq e^{-2}$ and $\beta < e/\delta$, or $\delta > e^{-2}$ and $\beta \leq e/\delta$.*
- (ii) *Increasing γ produces two stability switches (first stabilizes and then destabilizes) if $\delta > e^{-2}$ and $e/\delta < \beta < T_\delta(\bar{\gamma})$, where, for every fixed value of δ , $\bar{\gamma}$ can be calculated as the unique root of the equation $(1 + \gamma) \exp(-2/(1 + \gamma)) = \delta$, and*

$$T_\delta(x) := e^{x+1} ((x + 1)/\delta)^{1-x}.$$

- (iii) *If $\delta \leq e^{-2}$ and $\beta \geq e/\delta$, or $\delta > e^{-2}$ and $\beta > T_\delta(\bar{\gamma})$, then p is unstable for all $\gamma > 0$.*

A consequence of Proposition 3 is that, for some fixed values of δ and β , increasing γ may change the stability properties of a positive equilibrium of (1) either stabilizing an unstable equilibrium or inducing oscillations in a stable system.

2.3 Total Extinction

We say that there is total extinction in the population governed by (1) if 0 is a global attractor, that is, if $\lim_{n \rightarrow \infty} x_n = 0$ starting at any initial condition $x_0 > 0$. The boundaries for total extinction are defined by (4) if $\gamma > 1$, and by $0 < \beta \leq 1$ if $\gamma = 1$. Thus, it is clear that decreasing β or increasing δ leads to extinction if $\gamma > 1$. In our next result, we list the extinction/survival effects of the parameter γ for Eq. (1).

Proposition 4 *The following properties hold for Eq. (1):*

- (i) *If $\beta < e^\delta$, then increasing γ produces two extinction/survivorship switches (with an extinction window in between) at some critical values $\gamma_1 < \gamma_2$. Moreover, $\gamma_1 = 1$ if $\beta \leq 1$, and $\gamma_1 > 1$ if $1 < \beta < e^\delta$.*
- (ii) *If $\beta \geq e^\delta$, then the population governed by (1) does not exhibit total extinction for any value of γ .*

We emphasize that increasing β or decreasing δ can lead to essential extinction if $\gamma > 1$, which, from a biological point of view, is equivalent to total extinction. However, probably the parameter values necessary for essential extinction are less realistic from a population modeling perspective.

2.4 Population Abundance

In this subsection, we establish rigorously the range of values of γ for which population abundance at the largest positive equilibrium increases as γ is increased. Theorem 2 has to be considered together with Theorem 1, because the positive effects of γ on population size at equilibrium can be effectively observed if the equilibrium is asymptotically stable. As for the previous results, the proof of Theorem 2 is given in ‘‘Appendix’’.

Theorem 2 For fixed values of β and δ , let $p = p(\gamma)$ be the unique positive equilibrium of the difference Eq. (1) if $\gamma \leq 1$, or the largest positive equilibrium if $\gamma > 1$ and $\beta > \beta^*$. Then:

- (i) If $\beta > e^\delta$, then $p(\gamma)$ exists for all $\gamma \in (0, \infty)$, and it is an increasing function of γ .
- (ii) If $\beta = e^\delta$, then $p(\gamma)$ exists for all $\gamma \in (0, \infty)$, it is constant ($p(\gamma) = 1$) for $\gamma \leq 1 + \delta$, and it is an increasing function of γ for $\gamma > 1 + \delta$.
- (iii) If $\beta < e^\delta$, let γ_1, γ_2 be defined as in Proposition 4. Then, $p(\gamma)$ exists on $(0, \gamma_1] \cup [\gamma_2, \infty)$, $p(\gamma)$ is decreasing for $\gamma < \gamma_1$ and increasing for $\gamma > \gamma_2$.

2.5 Case Studies

We choose four different case studies to illustrate the main features of the gamma-Ricker model with respect to bifurcations, stability, extinction and population abundance. We fix $\delta = 2$ and produce a numerical bifurcation diagram with parameter γ for four different values of β .

We begin with $\beta = 1$ (see Fig. 3a). In the persistent regime ($\gamma < 1$), the positive equilibrium $p = p(\gamma)$ is a global attractor because $\beta < e/\delta$. Total extinction occurs for γ between $\gamma_1 = 1$ and $\gamma_2 \approx 6.436$. At $\gamma = 1$, there is a transcritical bifurcation, and, at $\gamma = \gamma_2$, there is a saddle-node bifurcation. Since $\beta < e^\delta$, the largest positive equilibrium $p = p(\gamma)$ decreases for $\gamma \in (0, 1)$ and increases for $\gamma > \gamma_2$. The positive effect of γ is observable until $p(\gamma)$ becomes unstable after a period-doubling bifurcation occurs at $\gamma \approx 6.715$. Then, a route of period-doubling bifurcations to chaos starts, and a chaotic attractor collides with the Allee threshold A at $\gamma \approx 7.008$. Thus, bistability occurs for $\gamma \in (6.436, 7.008)$, and there is essential extinction for $\gamma > 7.008$.

For $\beta = 5$ (Fig. 3b), the equilibrium $p(\gamma)$ is unstable for small values of γ because $e/\delta < \beta$. The equilibrium $p(\gamma)$ becomes (globally) asymptotically stable after a

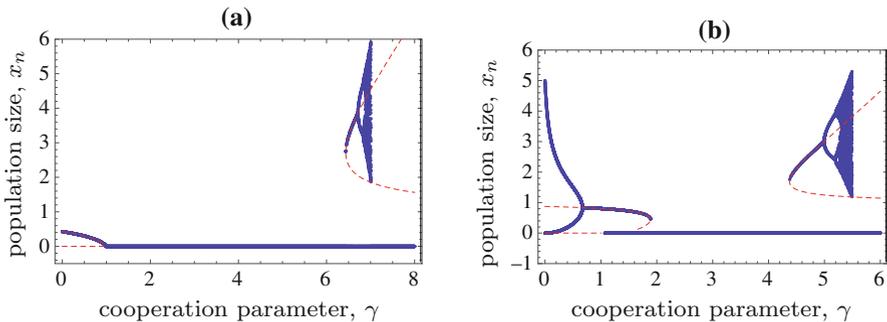


Fig. 3 Bifurcation diagrams for Eq. (1) with $\delta = 2$, using γ as the bifurcation parameter. Red dashed lines correspond to unstable equilibria, which, in case of bistability, establish the boundary between the immediate basins of attraction of the extinction equilibrium 0 and the nontrivial attractor p . **a** $\beta = 1$, **b** $\beta = 5$. In both cases, $\beta < e^\delta$, and therefore, there is an extinction window, as Proposition 4 states (Color figure online)

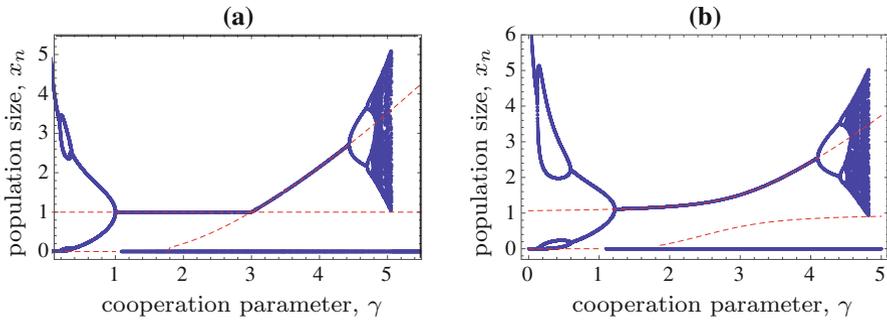


Fig. 4 Bifurcation diagrams for Eq. (1) with $\delta = 2$, using γ as the bifurcation parameter. Red dashed lines correspond to unstable equilibria. **a** $\beta = e^2$, **b** $\beta = 9$. In both cases, $\beta \geq e^\delta$, and therefore, total extinction does not occur for any value of $\gamma > 0$ (Color figure online)

period-halving bifurcation at $\gamma \approx 0.669$. Since $\beta > 1$, a pitchfork bifurcation occurs at $\gamma = 1$, so a branch of unstable positive fixed points is born and is continued until it collides with the branch of stable fixed points $p(\gamma)$ at a saddle-node bifurcation (at $\gamma = \gamma_1 \approx 1.888$). After γ_1 , there is an extinction window $[\gamma_1, \gamma_2]$, with $\gamma_2 \approx 4.374$. As in the previous example, the positive equilibrium $p(\gamma)$ becomes unstable at a period-doubling bifurcation at $\gamma \approx 4.994$, and there is essential extinction after a boundary collision at $\gamma \approx 5.496$. Since $\beta < e^\delta$, the largest positive equilibrium $p(\gamma)$ is decreasing for $\gamma < \gamma_1$ and increasing for $\gamma > \gamma_2$.

The case $\beta = e^2 = e^\delta$ (Fig. 4a) is special because $x = 1$ is an equilibrium of (1) for all $\gamma > 0$. Since $\beta > e/\delta$, this equilibrium is unstable for small values of γ . Actually, it remains unstable until a period-halving bifurcation occurs at $\gamma = 1$. At the same value of γ , a pitchfork bifurcation occurs at $x = 0$, and a branch of unstable positive fixed points is born. This branch is increasing and reaches the value 1 at $\gamma = 1 + \delta = 3$, where there is a transcritical bifurcation at which the equilibrium $x = 1$ loses again its stability, and the largest equilibrium $p(\gamma)$ becomes an increasing function of γ ; the positive effect is observable until $p(\gamma)$ becomes unstable at the second flip bifurcation ($\gamma \approx 4.436$). Since $\beta \geq e^\delta$, the population does not exhibit total extinction for any value of γ . However, essential extinction occurs for $\gamma > 5.061$.

The case $\beta = 9 > e^\delta$ (Fig. 4b) is similar to the previous one. The main difference is that the branch $p(\gamma)$ is asymptotically stable and increasing for all γ in the stability window $[\gamma_1, \gamma_2] \approx [1.220, 4.102]$. As before, total extinction does not occur, but population undergoes essential extinction for $\gamma > 4.826$.

3 Discussion

The gamma-Ricker equation (1) is a very interesting discrete-time population model. On the one hand, it has proved to give greater flexibility than other two-parameter models (Ricker, Cushing) to fit data in different animal populations, including Atlantic menhaden (Reish et al. 1985), flatfish (Iles 1994) and crabs (Zheng et al. 1995; Zheng and Kruse 2003). On the other hand, (1) with $\gamma > 1$ can represent the growth of a population subject to both positive and negative density dependence (Avilés 1999).

In regard to the first aspect, the dynamics of (1) for different parameter values allows flexibility to fit data for overcompensatory populations, which can exhibit Allee effects (for $\gamma > 1$). Of course, this flexibility comes at the cost of an additional parameter. The dynamics ranges from monotone convergence to an equilibrium (a typical dynamics for compensatory population models such as the Beverton–Holt), oscillatory convergence to an equilibrium, sustained periodic oscillations and chaos. The theoretical results given in this paper allow to get two-parameter bifurcation diagrams that help to understand the underlying dynamics (Fig. 2).

The role of the additional parameter γ introduced in the Ricker model is better understood with the formulation (2) given in “Introduction.” If $0 < \gamma < 1$, an interference factor $I(x) = (x/\alpha)^{\gamma-1}$ is introduced in the model; this case is questionable from a biological point of view, because the per-capita production tends to infinity as the population size tends to zero, which is not biologically admissible. Yet, this parameter range has been used in the ecological literature and is probably the consequence of using phenomenological fitting models without thinking about their mechanistic consistency.

The case $\gamma > 1$ corresponds to Eq. (2) with $\tilde{\gamma} = \gamma - 1 > 0$, that is, the term $I(x) = (x/\alpha)^{\gamma-1}$ is a factor of positive density dependence. In this case, the gamma-Ricker map $f(x) = \beta x^\gamma e^{-\delta x}$ meets the technical hypotheses given in “Appendix” of Schreiber (2003), so (1) displays typical dynamics of discrete-time population models with Allee effects and overcompensation. The dynamics include some effects already observed in previous published work, such as population disappearances preceded by chaotic transients, and transitions from extinction to bistability through a saddle-node bifurcation (Avilés 1999; Schreiber 2003). Our results show that sudden collapses preceded by a stable regime can also occur, leading to extinction windows between two stable regimes (see, e.g., Fig. 3b); this phenomenon seems to be new in the literature of discrete models with Allee effects when the cooperation factor is used as a bifurcation parameter. We notice that a similar effect has been shown for other discrete and continuous models with Allee effects, but for different bifurcation parameters (e.g., Hilker 2010; Cid et al. 2014).

Regarding stability, Scheuring (1999) shows that increasing the Allee effect strength in a discrete overcompensatory model increases the stability of the largest positive equilibrium, while Avilés (1999) and Schreiber (2003) show a transition from simple to complex dynamics. We prove rigorously that both stabilization and destabilization are possible outcomes of increasing the cooperation parameter; indeed, usually two consecutive flip bifurcations occur, being the first one stabilizing and the second one destabilizing, in such a way that a stability window between two periodic regimes shows up (see, e.g., Fig. 4). As far as we know, this is the first time in the literature of populations with Allee effect and overcompensation where this effect is reported.

Other dynamically interesting results are the variety of bifurcations that can be observed in Eq. (1). Though saddle-node, period-doubling and boundary collisions are typically observed in models with Allee effect (Schreiber 2003; Liz 2010), we show that transcritical and pitchfork bifurcations are also possible in bifurcation diagrams for the cooperation parameter γ (see, e.g., Fig. 4).

We hope our results shed some new light on the response of models with Allee effects to changes in the cooperation parameter. The Allee effect is defined as a causal

positive relationship between the number of individuals in a population and their fitness (“the more the better”) (Courchamp et al. 2008), but it is sometimes considered as a negative effect; for example, Scheuring (1999) calls it “the cost of rarity,” and Eskola and Parvinen (2007) define it as a reduction in individual fitness at low population densities. The reason is that the Allee effect makes the fixed point zero asymptotically stable, driving small enough initial population densities to extinction. Actually, Fig. 3b shows this negative effect of cooperation: When there is a low population density at the equilibrium in the absence of cooperation (because the production parameter β is small compared with the competition parameter δ), then the strong Allee effect induced by the cooperation factor $I(x) = x^\gamma$ with positive γ reduces both the population size at the stable positive equilibrium and the size of its basin of attraction. At some critical value of γ , this basin of attraction collapses, and population is doomed to extinction. This negative effect is not observed in Fig. 4, where cooperation prevails over intraspecific competition, so that an increasing value of γ results in an increase in population abundance.

However, even in case of strong intraspecific competition, cooperation can be beneficial for population persistence. This point has been emphasized by Hilker et al. (2017) in their study of predator–prey models with foraging facilitation among predators (see also Berec 2010; Alves and Hilker 2017). The analysis of a predator–prey model with hunting cooperation shows that cooperation-mediated persistence is a positive consequence of the Allee effect: hunting cooperation can ensure the persistence of the predator population when predators would go extinct in the absence of cooperation (Hilker et al. 2017). A similar effect is observed in the gamma-Ricker model; see, for example, Fig. 3a, where for $\gamma = 1$ (Ricker model), populations are leading to extinction, but for $\gamma \in (6.436, 7.008)$, populations can persist at intermediate population levels.

Another analogy between the gamma-Ricker model with $\gamma > 1$ and predator–prey models with hunting cooperation is that the interplay between overcompensation and a strong production increase due to high cooperation rates can lead to population cycles and their sudden disappearance.

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A Appendix

Proof of Proposition 2 Computing the Schwarzian derivative of f and simplifying, we get

$$(Sf)(x) = \frac{-q(x)}{2x^2(\gamma - \delta x)^2}, \quad \forall x \neq \gamma/\delta, \tag{8}$$

where

$$q(x) = \delta^4 x^4 - 4\gamma\delta^3 x^3 + 6\gamma^2\delta^2 x^2 - 4(\gamma^3 - \gamma)\delta x + \gamma^4 - \gamma^2.$$

Since $q''(x) = 12\delta^2(\gamma - \delta x)^2$, it follows that q is convex. On the other hand, equation $q'(x) = 0$ has a unique real root $x_0 = (\gamma - \gamma^{1/3})/\delta$, and

$$m = q(x_0) = 3\gamma \left(\gamma - \gamma^{1/3} \right)$$

is a global minimum of q .

It is clear that $m > 0$ if $\gamma > 1$, and therefore, $q(x) > 0$ for all $x \in \mathbb{R}$. If $\gamma = 1$, then $x_0 = m = 0$, and hence, $q(x) > 0$ for all $x > 0$. In both cases, it follows from (8) that $(Sf)(x) < 0$ for all $x \in (0, \infty)$, $x \neq \gamma/\delta$.

If $0 < \gamma < 1$, then $q(x)$ has two real roots x_1, x_2 , with $x_1 < 0 < x_2$. Moreover, $q(x) > 0$ for all $x > x_2$. Since $q(\gamma/\delta) = 3\gamma^2 > 0$, it follows that $\gamma/\delta > x_2$, and therefore, $q(x) > 0$ for all $x > \gamma/\delta$. Again (8) ensures that $(Sf)(x) < 0$ for all $x \in (\gamma/\delta, \infty)$. □

Proof of Theorem 1 We need two auxiliary results that we include here for completeness of the proof. The first one is a consequence of Corollary 2.10 in El-Morshedy and Jiménez-López (2008):

Proposition 5 *Let $f : (0, \infty) \rightarrow (0, \infty)$ be a C^3 map with a unique fixed point p and a unique critical point c , which is a local maximum. If $-1 \leq f'(p) < 1$ and $(Sf)(x) < 0$ for all $x \in (c, \infty)$, then p is globally asymptotically stable.*

The second one is taken from Proposition 1 in Liz and Ruiz-Herrera (2015):

Proposition 6 *Consider the difference equation*

$$x_{n+1} = f(x_n),$$

where f satisfies the following conditions:

- (H1) $f : [0, \infty) \rightarrow [0, \infty)$ is a C^1 -unimodal map, with a unique critical point $c > 0$, such that $f'(x) > 0$ for all $x \in (0, c)$ and $f'(x) < 0$ for all $x \in (c, \infty)$.
- (H2) $f(0) = f'(0) = 0$, and $\lim_{x \rightarrow \infty} f(x) = 0$.
- (H3) f has three fixed points $0 < x_1 < x_2$, so that $f(x) < x$ for all $x \in (0, x_1) \cup (x_2, \infty)$ and $f(x) > x$ for all $x \in (x_1, x_2)$.
- (H4) f is three times differentiable, and $(Sf)(x) < 0$ whenever $f'(x) \neq 0$.

If $f^2(c) > x_1$ and $f'(x_2) \geq -1$, then x_2 is asymptotically stable and its immediate basin of attraction is $(x_1, f^{-1}(x_1))$.

We proceed with the proof of Theorem 1 (A). First, we observe that condition (6) is equivalent to $f'(p) \geq -1$. Indeed,

$$f'(p) = \beta p^{\gamma-1} e^{-\delta p} (\gamma - \delta p) = \frac{f(p)}{p} (\gamma - \delta p) = \gamma - \delta p.$$

Hence,

$$f'(p) \geq -1 \iff p \leq \frac{\gamma + 1}{\delta} \iff f\left(\frac{\gamma + 1}{\delta}\right) \leq \frac{\gamma + 1}{\delta}.$$

It is clear that the last inequality is equivalent to (6).

Now, the result follows easily from Propositions 1, 2 and 5. Notice that the inequality $f'(p) < 1$ always holds because

$$f'(p) = \gamma - \delta p < 1 \iff \delta p > \gamma - 1.$$

The last inequality trivially holds because $\gamma - 1 \leq 0$.

If (6) does not hold, then $f'(p) < -1$, and therefore, p is unstable.

The proof of Theorem 1 (B) follows from Proposition 6. Propositions 1 and 2 ensure that assumptions (H1)–(H4) hold.

Finally, the convergence to the equilibrium p is eventually monotone if and only if $f'(p) \geq 0$, which is equivalent to say that $f(c) \leq c$ for the unique critical point $c = \gamma/\delta$ of f . It is clear that condition $f(\gamma/\delta) \leq \gamma/\delta$ is equivalent to (7). \square

Proof of Proposition 3 The equilibrium is asymptotically stable if $\beta \leq T_\delta(\gamma)$. It is easily seen that $T_\delta(0) = e/\delta$ and $\lim_{x \rightarrow \infty} T_\delta(x) = 0$. Moreover, $T'_\delta(x) = 0$ if and only if

$$(1 + x)e^{-2/(1+x)} = \delta. \tag{9}$$

It is clear that Eq. (9) has a unique positive solution $\bar{\gamma}$ if and only if $\delta > e^{-2}$.

Thus, if $\delta \leq e^{-2}$ then T_δ is decreasing on $(0, \infty)$, and therefore, increasing γ is destabilizing if $\beta < e/\delta$, and the fixed point p is unstable for all values of $\gamma > 0$ if $\beta \geq e/\delta$. See Fig. 5a.

If $\delta > e^{-2}$, then T_δ attains a local maximum at $\bar{\gamma} > 0$. Thus, there are three possibilities (see Fig. 5b):

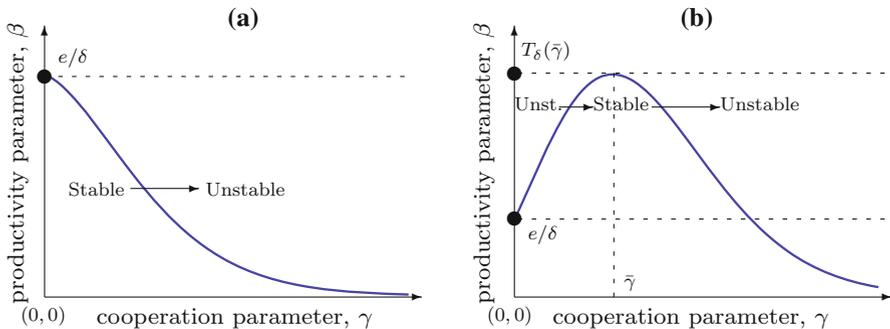
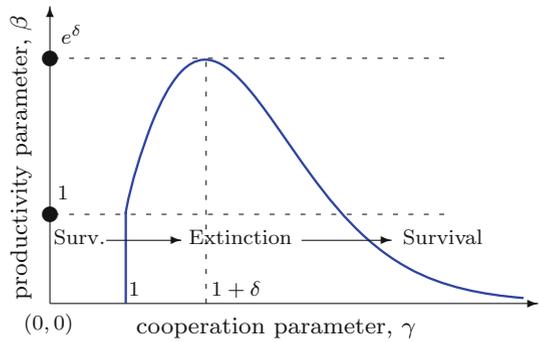


Fig. 5 (Color Figure Online) Graph of the map $\beta = T_\delta(\gamma)$ showing the stability switches for the largest positive equilibrium of (1). **a** T_δ is decreasing for $\delta = 0.1 < e^{-2}$, **b** T_δ is unimodal for $\delta = 1 > e^{-2}$

Fig. 6 (Color Figure Online) Graph of the map $\beta = G_\delta(\gamma)$ showing the survival/extinction switches for (1)



- If $\beta \leq e/\delta$, the increasing γ is destabilizing.
- If $e/\delta < \beta < T_\delta(\gamma)$, then there are two stability switches.
- If $\beta > T_\delta(\gamma)$, then p is unstable for all $\gamma > 0$.

A singular case is $\beta = T_\delta(\gamma)$, for which p is only asymptotically stable if $\gamma = \bar{\gamma}$.

Proof of Proposition 4 The proof of Proposition 4 is very similar to the proof of Proposition 3, using the map G_δ that defines the extinction boundary:

$$G_\delta(x) := e^{x-1} \left(\frac{x-1}{\delta} \right)^{1-x} = \left(\frac{\delta e}{x-1} \right)^{x-1}, \quad x > 1.$$

In this case, G_δ is unimodal, with a global maximum $G_\delta(1 + \delta) = e^\delta$. Moreover, $\lim_{x \rightarrow 1^+} G_\delta(x) = 1$, $\lim_{x \rightarrow \infty} G_\delta(x) = 0$. See Fig. 6. We leave the details to the reader.

Proof of Theorem 2 The equation that defines a positive equilibrium of (1) is $\beta p^{\gamma-1} e^{-\delta p} = 1$, or, equivalently, $p^{1-\gamma} e^{\delta p} - \beta = 0$. For a fixed value of $\beta > 0$, define the map

$$F(p, \gamma) := p^{1-\gamma} e^{\delta p} - \beta, \quad p > 0, \gamma > 0.$$

By the implicit function theorem, equation $F(p, \gamma) = 0$ defines a function $p = p(\gamma)$ if $\partial F/\partial p \neq 0$. By Proposition 4, we know that $p(\gamma)$ exists for $\gamma \in (0, \infty)$ if $\beta \geq e^\delta$, and otherwise, $p(\gamma)$ exists in two open intervals $(0, \gamma_1], [\gamma_2, \infty)$, with $0 < 1 \leq \gamma_1 < \gamma_2$.

Moreover, we can compute

$$\frac{\partial p}{\partial \gamma} = \frac{-\partial F/\partial \gamma}{\partial F/\partial p} = \frac{p \ln(p)}{1 - \gamma + \delta p}.$$

First we show that the denominator is always positive. Indeed, if $\gamma \leq 1$, then $1 - \gamma + \delta p \geq \delta p > 0$. If $\gamma > 1$, then it is clear that the largest equilibrium point p

satisfies $p > p^*$, where p^* is the fixed point at which $f'(p^*) = 1$. Now, it is easy to check that $p^* = (\gamma - 1)/\delta$, and therefore,

$$p > \frac{\gamma - 1}{\delta} \implies 1 - \gamma + \delta p > 0.$$

Thus, $\partial p/\partial \gamma > 0$ if $p > 1$, and $\partial p/\partial \gamma < 0$ if $p < 1$.

Now, if $\gamma \leq 1$, then it is clear that $p = 1$ if and only if $\beta = e^\delta$. Moreover, since $f(x) > x$ for $x < p$ and $f(x) < x$ for $x > p$, it follows that $p > 1$ if $\beta > e^\delta$, and $p < 1$ if $\beta < e^\delta$.

If $\gamma > 1$ and $\beta > e^\delta$, a simple graphical analysis also shows that $p > 1$. Hence, $p(\gamma)$ is an increasing function of γ for $\gamma \in (0, \infty)$ if $\beta > e^\delta$.

If $\gamma > 1$ and $\beta < e^\delta$, then two extinction switches occur at γ_1, γ_2 , with $1 \leq \gamma_1 < \gamma_2$. Moreover, since $\gamma_1 < 1 + \delta < \gamma_2$, we get that $p(\gamma_1) = (\gamma_1 - 1)/\delta < 1 < (\gamma_2 - 1)/\delta = p(\gamma_2)$. Thus, $p(\gamma)$ is a decreasing function of γ in $(0, \gamma_1)$ and an increasing function of γ in (γ_2, ∞) .

Finally, if $\beta = e^\delta$, then $x = 1$ is an equilibrium of (1) for all $\gamma > 0$. Moreover, $p = 1$ is the largest positive equilibrium if $\gamma \leq 1 + \delta$; for $\gamma > 1 + \delta$, $x = 1$ is unstable, and the largest positive equilibrium is $p > 1$. Thus, $p(\gamma)$ is an increasing function of γ in $(1 + \delta, \infty)$. \square

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