A NEW FLEXIBLE DISCRETE-TIME MODEL FOR STABLE POPULATIONS

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Abstract. We propose a new discrete dynamical system which provides a flexible model to fit population data. For different values of the three involved parameters, it can represent both globally persistent populations (compensatory or overcompensatory), and populations with Allee effects. In the most relevant cases of parameter values, there is a stable positive equilibrium, which is globally asymptotically stable in the persistent case. We study how population abundance depends on the parameters, and identify extinction windows between two saddle-node bifurcations.

1. **Introduction.** Discrete-time single-species models are the most appropriate mathematical description of life histories of organisms whose reproduction occurs only once a year during a very short season, and it is assumed that, in the rest of the year, the population is only subjected to mortality, but not to births (see, e.g., [17]). Thus, the between-year dynamics is governed by a first-order difference equation $x_{n+1} = f(x_n)$, where x_n denotes the population at the n-th generation, censused after reproduction. These models are widely used in fisheries, but are well-suited for many other organisms [10, Chapter 4].

The production function f is usually density-dependent (which means that $f(x)/x$ is not constant), and the strength of density dependence is determined by several parameters related to the growth rate (per capita number of offspring), the probability of surviving the reproductive season, the carrying capacity of the environment, and intraspecific cooperation or competition factors. In fisheries, discrete-time models have a long tradition, and the map f is usually referred to as the stock-recruitment relationship. Finding a good stock-recruitment curve for fitting the population dynamics of a particular species has been one of the major problems in theoretical studies of fisheries [3, 9, 12].

There are different forms of density-dependence, which correspond to different characteristics of the production function f. Density dependence is compensatory if survival decreases with increasing population abundance. In mathematical terms, it is described by conditions $f'(x) > 0$, $F'(x) < 0$, being $F(x) = f(x)/x$ the per capita production function. Perhaps the most well-known compensatory function is the

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Beverton-Holt map $f(x) = \beta x/(1+\delta x)$ [2]. Here, β is a productivity parameter, and δ controls the level of density dependence [12]. Another example of compensatory growth is provided by the Cushing model $f(x) = \beta x^{\gamma}$, $\gamma < 1$ [5].

Density dependence is overcompensatory if $F'(x) < 0$ but $f'(x) < 0$ after a critical value of population size. This means that not only per capita production, but also the net recruitment can decrease with increasing density. Well known examples of overcompensatory curves are given by the quadratic map $f(x) = rx(1 - x/K)$, and the Ricker map $f(x) = \beta x e^{-\delta x}$ [13], where the latter is more meaningful than the quadratic for population modeling, because it takes only positive values for $x > 0$.

Finally, density dependence is depensatory (or exhibits Allee effects [4]) if early survival (i.e., population production at small x) increases with increasing spawning abundance, which is represented by condition $F'(x) > 0$. A simple example is provided by the modified Beverton-Holt map $f(x) = \beta x^2/(1+\delta x)$ [6]. An important characteristic of models with Allee effects is that, at low spawning levels, recruitment is not sufficient to replace spawning stock, and, in consequence, population is driven to extinction [12].

A good population model should be flexible enough to use it for fitting field data. In this sense, it has been argued that models with two parameters, such as the Beverton-Holt, the Ricker, and the Cushing models, are relatively inflexible [9]. Looking for more flexibility, some models have been proposed adding a third parameter to a two-parameter model. Among them, we mention the Shepherd model $f(x) = \beta x/(1+\delta x^{\gamma})$ [15], which generalizes the Beverton-Holt map, and the gamma model $f(x) = \beta x^{\gamma} e^{-\delta x}$ [1, 8, 12], which generalizes the Ricker map. Both models represent different forms of density dependence for different parameter ranges. On the one hand, the Shepherd model exhibits overcompensation for $\gamma > 1$, and compensation for $\gamma \le 1$. On the other hand, the gamma model is overcompensatory for $\gamma \le 1$, and exhibits Allee effects for $\gamma > 1$.

In this paper, we introduce and study a new model, which is able to show the three different forms of density dependence, namely,

$$x_{n+1} = \frac{\beta x_n^{\gamma}}{1 + \delta x_n} := f(x_n), \tag{1.1}$$

where β, γ, δ are positive parameters. Clearly, equation (1.1) can be obtained as a generalization of the Beverton-Holt ($\gamma = 1$) and the Cushing ($\delta = 0$) models. As we show below, (1.1) represents a compensatory population if $\gamma = 1$ (actually, it is the Beverton-Holt model), overcompensatory if $\gamma < 1$, and depensatory if $\gamma > 1$. In the latter case, it usually has a stable positive equilibrium if $1 < \gamma < 2$, and no stable positive equilibria if $\gamma \ge 2$ (displaying a dynamics similar to the Cushing model with $\gamma > 1$). Thus, the new model is very flexible. However, it is worth emphasizing that it does not exhibit the complicated behavior typical of such overcompensatory models as the quadratic and the Ricker maps [11]. Equation (1.1) is suitable to model stable populations, that is, populations that tend to an equilibrium in the long-term.

For $\gamma > 1$, equation (1.1) can be introduced in a phenomenological way multiplying the classical Beverton-Holt model by a density-dependent factor $I(x) = x^{\gamma-1}$. Thus, it can be seen as a model with a factor of positive density dependence $I(x)$ and a factor of negative density-dependence $1/(1 + \delta x)$. A similar approach has been used by Avilés [1] to obtain the gamma model $x_{n+1} = \beta x_n^{\gamma} e^{-\delta x_n}$ from the

Ricker map; see [14] for related models with Allee effects, and [8] for a detailed study of the gamma model.

When positive and negative density-dependent factors interact in a population model, an interesting question is whether population abundance increases in response to an increment of parameter γ in the factor of positive density dependence (Avilés refers to γ as the cooperation parameter). We show that this is not always the case, and establish the exact conditions on the involved parameters that ensure that the positive equilibrium is an increasing function of γ.

2. **Preliminary results.** In our first result, we list several basic properties of the map $f : [0, \infty) \to [0, \infty)$ that defines the right-hand side of (1.1).

Proposition 1. *The map* $f(x) = \beta x^\gamma/(1 + \delta x)$ *($\beta, \gamma, \delta > 0$) is of class* $\mathcal{C}^\infty$ *in* $(0, \infty)$, *and the following properties hold:*

(i) *$f(0) = 0$, and $f(x) > 0$ for all $x > 0$.*
(ii) *If $\gamma < 1$, then f is unimodal, with a unique critical point at*

$$c = \frac{\gamma}{\delta(1 - \gamma)},$$

where f attains its global maximum, $\lim_{x \to \infty} f(x) = 0$, and $\lim_{x \to 0} f'(x) = \infty$.
(iii) *If $\gamma = 1$, then f is increasing and convex, $\lim_{x \to \infty} f(x) = \beta/\delta$, and $f'(0) = \beta$.*
(iv) *If $\gamma > 1$, then f is increasing, $\lim_{x \to \infty} f(x) = \infty$, and $f'(0) = 0$.*
(v) *If $\gamma \geq 2$, then f is convex in $(0, \infty)$.*
(vi) *If $\gamma < 2$ and $\gamma \neq 1$, then f has a unique inflexion point*

$$d = \frac{2\gamma - \gamma^2 \pm \sqrt{2\gamma - \gamma^2}}{\delta(\gamma^2 - 3\gamma + 2)},$$

where the sign $\pm$ is positive if $\gamma < 1$, and negative if $1 < \gamma < 2$.

Proof. The proof is elementary. We just state the simplified expressions for the first and the second derivatives of f for future reference:

$$f'(x) = \frac{\beta x^{\gamma-1}(\gamma + \delta x(\gamma - 1))}{(1 + \delta x)^2}; \tag{2.1}$$

$$f''(x) = \frac{\beta x^{\gamma-2}((\gamma^2 - 3\gamma + 2)\delta^2 x^2 - 2(2\gamma - \gamma^2)\delta x + \gamma^2 - \gamma)}{(1 + \delta x)^3}. \tag{2.2}$$

$\square$

In Figure 1, we plot different graphs of f, depending on the involved parameters.

The case $\gamma = 1$ is the so-called Beverton-Holt model [2]. The dynamics for this particular case are well known, and we just state them without proof in the following result:

Proposition 2. *If $\gamma = 1$, then equation (1.1) has a unique positive equilibrium p if $\beta > 1$, and no positive equilibria if $\beta \leq 1$. Moreover:*

- *If $\beta > 1$, then $\lim_{n \to \infty} f^n(x) = p$, for all $x > 0$.*
- *If $\beta \leq 1$, then $\lim_{n \to \infty} f^n(x) = 0$, for all $x > 0$.*

The case $\gamma \geq 2$ is also elementary because f is increasing and convex. In the next result, we state the dynamics for (1.1) in this case:
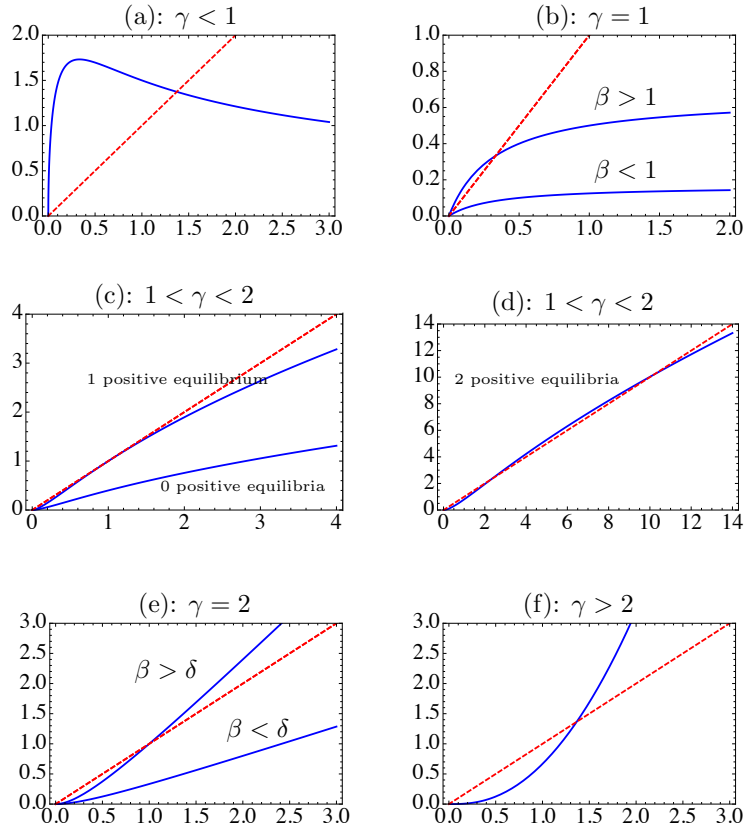
FIGURE 1. Different graphs of the map f defined in (1.1). (a): f is unimodal for $\gamma < 1$; (b): f is increasing for $\gamma = 1$, with a unique positive fixed point if $\beta > 1$; (c) and (d): f is increasing for $1 < \gamma < 2$, and can have 0, 1, or 2 positive fixed points; (e): f is increasing and convex for $\gamma = 2$, with linear growth at infinity; it has a unique positive fixed point if $\beta > \delta$ and no positive fixed points if $\beta \leq \delta$; (f): f is increasing and convex, with superlinear growth at infinity, if $\gamma > 2$. In all cases, the red dashed line represents the graph of $y = x$.

Proposition 3. *If $\gamma > 2$, or $\gamma = 2$ and $\beta > \delta$, then equation (1.1) has a unique positive equilibrium p, which is a repeller. Moreover,*

$$\lim_{n \to \infty} f^n(x) = 0 \,, \ \forall \, x < p, \quad and \quad \lim_{n \to \infty} f^n(x) = \infty \,, \ \forall \, x > p.$$

If $\gamma = 2$ and $\beta \leq \delta$, then the unique equilibrium of (1.1) is 0, and it is a global attractor.

Actually, the case $\gamma > 2$ seems of limited application in population modeling because $f(x)$ increases with superlinear growth as x tends to infinity. The same limitation has been pointed out for the Cushing model $x_{n+1} = \beta x_n^\gamma$, with $\gamma > 1$ (see [12, Section 3.1.3]). For $\gamma = 2$, f increases linearly at infinity; in this particular

case, model (1.1) has been derived in a mechanistic way in the context of Allee effects due to mate limitation [6].

In the following sections, we address the cases $\gamma < 1$ and $1 < \gamma < 2$. As we will see, equation (1.1) has a unique positive fixed point if $\gamma < 1$, and can have 0, 1, or 2 positive fixed points if $1 < \gamma < 2$ (see Figure 1). When f has two fixed points, the smallest one is unstable, and it is usually referred to as the Allee threshold [4]. If population abundance falls below the Allee threshold, then extinction occurs.

3. **The overcompensatory case** $\gamma < 1$. In this section, we prove that equation (1.1) has a globally attracting positive equilibrium if $0 < \gamma < 1$. For it, we shall use the following result from [17, Section 9.3]:

Proposition 4. *Assume that* $f : (0, \infty) \to (0, \infty)$ *is continuous, has a unique fixed point* p, *and is bounded on* $(0, p)$. *Moreover, assume there exist* x_1, x_2, $0 < x_1 < p < x_2$, *such that* $f(x_1) > x_1$ *and* $f(x_2) < x_2$. *Then* p *is a global attractor of (1.1) in* $(0, \infty)$ *if and only if there is no fixed point of* f^2 *different from* p.

It is clear from Proposition 1 that $f(x) = \beta x^\gamma / (1 + \delta x)$ is continuous and bounded if $\gamma < 1$. Next we prove that there is a unique positive equilibrium, and it is a global attractor in $(0, \infty)$.

Theorem 3.1. *For all* $\gamma \in (0, 1)$, *the difference equation (1.1) has a unique positive equilibrium, and it is globally asymptotically stable in* $(0, \infty)$.

Proof. A point $x > 0$ is an equilibrium of (1.1) if and only if it solves equation

$$f_1(x) := \beta x^{\gamma - 1} = 1 + \delta x =: f_2(x). \tag{3.1}$$

On the one hand, since $\gamma < 1$, $f_1(x)$ is decreasing, $\lim_{x \to 0^+} f_1(x) = \infty$, and $\lim_{x \to \infty} f_1(x) = 0$. On the other hand, $f_2(x)$ is increasing, $\lim_{x \to \infty} f_2(x) = \infty$, and $f_2(0) = 1$. Thus, by the intermediate value theorem, it is clear that there is a unique positive solution p of (3.1).

We prove that p is asymptotically stable. Indeed, using (2.1) and (3.1), we get

$$f'(p) = \gamma - \frac{\delta p}{1 + \delta p},$$

from where it is clear that $|f'(p)| < 1$, and therefore p is asymptotically stable.

To prove that p is a global attractor, we show that equation $f^2(x) = x$ has no positive solutions different from p (so Proposition 4 applies). We have:

$$f(f(x)) = x \iff \beta(f(x))^\gamma = x(1 + \delta f(x)) \iff f(x) = \left(\frac{x}{\beta}(1 + \delta f(x)) \right)^{1/\gamma} =: g(x).$$

We have to demonstrate that equation $f(x) = g(x)$ has a unique positive solution (which is clearly the fixed point p of f). First, we prove that f is concave in $(0, c)$, where $c = \gamma / (\delta(1 - \gamma))$ is the unique critical point of f. We know from Proposition 1 that f has a unique inflexion point

$$d = \frac{2\gamma - \gamma^2 + \sqrt{2\gamma - \gamma^2}}{\delta(\gamma^2 - 3\gamma + 2)}.$$

It is easy to prove that f is concave in the interval $(0, d)$, and $c < d$. Therefore, f is concave in $(0, c)$.

To conclude the proof, it is enough to show that g is increasing and convex in $(0, \infty)$. Assume this claim is true; then, since $f'(0^+) = \infty$ and $g'(0) = 0$, equation $f(x) = g(x)$ has at least one positive solution. Let p_1 be the first intersection point

of the graphs of f and g. Notice that $g'(p_1) > f'(p_1)$, g' is increasing and positive in (p_1, ∞), and f' is decreasing in (p_1, c) and negative in (c, ∞). Thus $g'(x) > f'(x)$ for all $x > p_1$, which ensures that additional intersections are not possible.

g is increasing: Indeed, we have:

$$g'(x) = \frac{1}{\gamma} \left(\frac{x}{\beta} (1 + \delta f(x)) \right)^{1/\gamma - 1} \frac{1 + \delta f(x) + \delta x f'(x)}{\beta}.$$

To prove that $g'(x) > 0$ for all $x > 0$, it is enough to prove that $x f'(x) + f(x) > 0$ for all $x > 0$. Indeed:

$$x f'(x) + f(x) = \frac{\beta x^\gamma}{(1 + \delta x)^2} (\gamma + \delta x (\gamma - 1)) + \frac{\beta x^\gamma}{1 + \delta x} = \frac{\beta x^\gamma}{(1 + \delta x)^2} (\gamma + \gamma \delta x + 1) > 0.$$

g is convex: Since

$$g(x) = \left(\frac{x}{\beta} (1 + \delta f(x)) \right)^{1/\gamma} = \left(\frac{1}{\beta} \right)^{1/\gamma} (x(1 + \delta f(x)))^{1/\gamma},$$

it is enough to prove that $g_1''(x) > 0$ for all $x > 0$, where $g_1(x) := (x(1 + \delta f(x)))^{1/\gamma}$. After some computations, we get the following expression:

$$g_1''(x) = x \left(1 + \frac{\delta x^\gamma}{1 + \delta x} \right)^{1/\gamma} [\gamma x (1 + \delta x)(1 + \delta(x + x^\gamma))]^{-2} q(x),$$

where

$$q(x) = (1 - \gamma)(1 + 4\delta x + 6\delta^2 x^2 + 4\delta^3 x^3 + \delta^4 x^4) + (2 - \gamma^2 + \gamma^3)\delta x^\gamma + (1 + \gamma)\delta^2 x^{2\gamma}$$

$$+ q_1(\gamma)\delta^2 x^{1+\gamma} + q_2(\gamma)\delta^3 x^{2+\gamma} + q_3(\gamma)\delta^4 x^{3+\gamma};$$

$$q_1(\gamma) = 4 - 5\gamma^2 + 3\gamma^3, \quad q_2(\gamma) = 2 + 2\gamma - 7\gamma^2 + 3\gamma^3, \quad q_3(\gamma) = 2\gamma - 3\gamma^2 + \gamma^3.$$

It is an elementary exercise to prove that $q_i(\gamma) > 0$ for all $\gamma \in (0, 1)$, and $i = 1, 2, 3$, so the proof is complete. $\square$

4. **The case with Allee effect** $1 < \gamma < 2$. For $\gamma > 1$, $f'(0) = 0$, so the extinction equilibrium $x = 0$ is asymptotically stable. This fact induces the so-called strong Allee effect: low population densities are driven to extinction. Our next result states the dynamics of (1.1) when $\gamma \in (1, 2)$.

Theorem 4.1. *For $\gamma \in (1, 2)$, let us define*

$$\beta^* = \left(\frac{1}{2 - \gamma} \right)^{2 - \gamma} \left(\frac{\delta}{\gamma - 1} \right)^{\gamma - 1}.$$

Then, equation (1.1) has three equilibria $x = 0, x = A, x = p$ ($0 < A < p$) if $\beta > \beta^*$, two equilibria $x = 0, x = p$ if $\beta = \beta^*$, and only one equilibrium $x = 0$ if $\beta < \beta^*$.

- *If $\beta > \beta^*$, then p and 0 are asymptotically stable, and A is unstable. Moreover, the basin of attraction of p is (A, ∞), and the basin of attraction of 0 is $(0, A)$.*
- *If $\beta = \beta^*$, then p is semistable, with basin of attraction $[p, \infty)$, and 0 is asymptotically stable, with basin of attraction $(0, p)$.*
- *If $\beta < \beta^*$, then all solutions of (1.1) converge to 0.*

Proof. We recall that a positive equilibrium of (1.1) is a solution of equation $f_1(x) = f_2(x)$, where $f_1(x) = \beta x^{\gamma-1}$, and $f_2(x) = 1 + \delta x$. Since $1 < \gamma < 2$, f_1 is increasing and concave, and therefore (3.1) can have 0, 1, or 2 positive solutions. It has exactly one positive solution when the graphs of f_1 and f_2 have a tangency at a point $p > 0$, that is, when the system of equations $f_1(x) = f_2(x)$, $f_1'(x) = f_2'(x)$ has a positive solution. This system leads to

$$\frac{\delta x}{\gamma - 1} = \beta x^{\gamma-1} = 1 + \delta x,$$

and therefore the values of x and β that solve the system are

$$x = \frac{\gamma - 1}{(2 - \gamma)\delta} =: p^* \quad , \quad \beta = \beta^* = \left(\frac{1}{2 - \gamma}\right)^{2-\gamma} \left(\frac{\delta}{\gamma - 1}\right)^{\gamma-1}. \qquad (4.1)$$

A simple graphical analysis shows that (3.1) has one solution for $\beta = \beta^*$, two solutions for $\beta > \beta^*$, and no solution for $\beta < \beta^*$.

Next we show that, for $\beta > \beta^*$ the smallest positive fixed point A is unstable and the largest one p is asymptotically stable.

Since $A < p^* < p$, where p^* is defined in (4.1), we get

$$f'(A) = \gamma - \frac{\delta A}{1 + \delta A} > \gamma - \frac{\delta p^*}{1 + \delta p^*} = 1 > \gamma - \frac{\delta p}{1 + \delta p} = f'(p) > 0,$$

where we have used that the map $x \mapsto x/(1 + \delta x)$ is increasing in $(0, \infty)$.

The basins of attraction are obtained as a simple consequence of the fact that f is increasing. $\qquad \square$

5. **The influence of γ on population abundance. Extinction windows.** In this section, we study the response of population abundance to a variation of $\gamma \in (0, 2)$. We are only interested in the stable positive equilibrium, which we denote $p(\gamma)$ to emphasize that we use γ as the bifurcation parameter.

Theorem 5.1. *For $\beta > 0$ and $\delta > 0$ fixed, denote by $p(\gamma)$ the stable fixed point of (1.1), whenever it exists, and define $\gamma^* := (1 + 2\delta)/(1 + \delta)$. Then we have the following cases:*

a) *If $\beta > 1 + \delta$, then $p(\gamma)$ exists for all $\gamma \in (0, 2)$, and $p(\gamma)$ is an increasing function of γ.*

b) *If $\beta = 1 + \delta$, then $p(\gamma)$ exists for all $\gamma \in (0, 2) \setminus \{\gamma^*\}$, $p(\gamma) = 1$ for $\gamma < \gamma^*$, and $p(\gamma)$ is an increasing function of γ for $\gamma > \gamma^*$. For $\gamma = \gamma^*$, the positive equilibrium is semistable.*

c) *If $\delta < \beta < 1 + \delta$, then $p(\gamma)$ exists for all $\gamma \in (0, \gamma_1) \cup (\gamma_2, 2)$, with $1 \le \gamma_1 < \gamma_2 < 2$, $p(\gamma)$ is decreasing in $(0, \gamma_1)$ and increasing in $(\gamma_2, 2)$.*

d) *If $\beta \le \delta$, then $p(\gamma)$ exists for all $\gamma \in (0, \gamma_1)$, with $1 \le \gamma_1 < 2$, and $p(\gamma)$ is decreasing.*

Before proving Theorem 5.1, we list some remarks:

- In cases a), b), c), $\lim_{\gamma \to 2^-} p(\gamma) = \infty$.
- In cases c), d), $\gamma_1 = 1$ if $\beta \le 1$, and $\gamma_1 > 1$ if $\beta > 1$.
- The values of γ_1 and γ_2 can be calculated using the equation that defines β^* in (4.1).

Proof. For each value of δ, we define the map $F_\delta : (1, 2) \to (0, \infty)$ by

$$F_\delta(\gamma) = \left(\frac{1}{2-\gamma}\right)^{2-\gamma} \left(\frac{\delta}{\gamma-1}\right)^{\gamma-1}.$$

We know from Proposition 2 and Theorems 3.1 and 4.1 that $p(\gamma)$ exists if either $\gamma < 1$, $\gamma = 1$ and $\beta > 1$, or $1 < \gamma < 2$ and $\beta > F_\delta(\gamma)$.

It is elementary to prove that F_δ is unimodal, with a global maximum $F_\delta(\gamma^*) = 1 + \delta$, $F(1^+) = 1$, $F(2^-) = \delta$. Existence of $p(\gamma)$ in the four cases of the statement of Theorem 5.1 follows easily from these properties; see Figure 2. Notice that if $\beta = 1+\delta$, then $x = 1$ is always a positive equilibrium of (1.1), but it is asymptotically stable only if $f'(1) < 1$, which is equivalent to $\gamma < \gamma^*$. For $\gamma > \gamma^*$, 1 is unstable, and the asymptotically stable equilibrium $p(\gamma)$ is greater than 1.
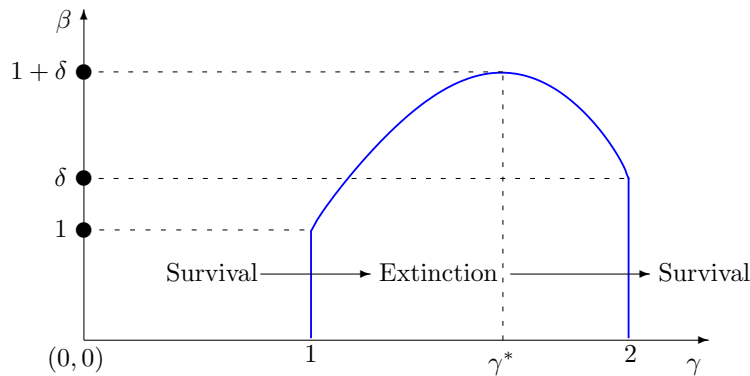

FIGURE 2. Graph of the map $\beta = F_\delta(\gamma)$ showing the survival/extinction switches for (1.1), which only occur if $\beta < 1 + \delta$.

To establish the increasing or decreasing character of the branch $p(\gamma)$ of positive stable equilibria of (1.1), we use implicit differentiation. Denoting by

$$G(p, \gamma) := \beta p^{\gamma-1} - 1 - \delta p,$$

equation $G(p, \gamma) = 0$ defines the positive equilibria of (1.1). We get

$$\frac{\partial p}{\partial \gamma} = \frac{-\partial G/\partial \gamma}{\partial G/\partial p} = \frac{\beta \ln(p) p^\gamma}{\delta p + (1-\gamma)\beta p^{\gamma-1}} = \frac{(1+\delta p)p \ln(p)}{1 - \gamma + p\delta(2-\gamma)}. \tag{5.1}$$

We first show that the denominator is always positive. Indeed, if $\gamma \leq 1$, then

$$1 - \gamma + p\delta(2-\gamma) \geq p\delta(2-\gamma) > 0.$$

If $\gamma > 1$, then $p > p^*$, where p^* is the point of tangency defined in (4.1). Hence,

$$1 - \gamma + p\delta(2-\gamma) > 1 - \gamma + p^*\delta(2-\gamma) = 0.$$

Thus, it follows from (5.1) that $\partial p/\partial \gamma > 0$ if $p > 1$, and $\partial p/\partial \gamma < 0$ if $p < 1$.

If $\gamma \leq 1$, then $f(x) > x$ if $x < p$, and $f(x) < x$ if $x > p$. Thus, $p > 1 \iff f(1) > 1 \iff \beta > 1 + \delta$, and $p < 1 \iff f(1) < 1 \iff \beta < 1 + \delta$.

If $1 < \gamma < 2$, then the relative positions of f_1 and f_2 also ensure that $p > 1$ if $\beta > 1 + \delta$. See Figure 3.
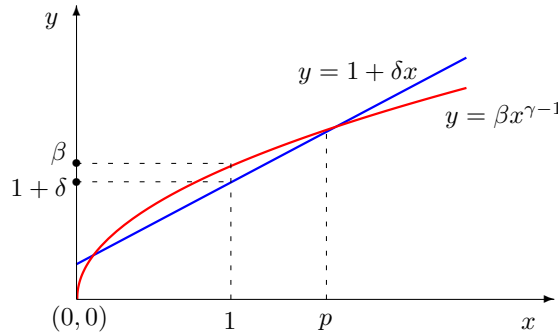
FIGURE 3. Relative position of the graphs of $f_1(x) = \beta x^{\gamma-1}$ (red color) and $f_2(x) = 1 + \delta x$ (blue color) when equation $f_1(x) = f_2(x)$ has two positive solutions.

If $\beta < 1 + \delta$ and $\beta > \max\{1, \delta\}$, then there are two extinction switches γ_1, γ_2, with $1 < \gamma_1 < \gamma_2 < 2$. Moreover, $p(\gamma_1) < 1 < p(\gamma_2)$. Indeed, using (4.1), we get

$$\gamma_i = \frac{1 + 2p(\gamma_i)\delta}{1 + p(\gamma_i)\delta}, \ i = 1, 2.$$

Since the map $x \mapsto (1 + 2x)/(1 + x)$ is increasing in $(0, \infty)$, we get

$$\gamma_1 = \frac{1 + 2p(\gamma_1)\delta}{1 + p(\gamma_1)\delta} < \frac{1 + 2\delta}{1 + \delta} < \frac{1 + 2p(\gamma_2)\delta}{1 + p(\gamma_2)\delta} = \gamma_2 \Longrightarrow p(\gamma_1) < 1 < p(\gamma_2).$$

Hence, $p(\gamma)$ is decreasing for $\gamma < \gamma_1$ and increasing for $\gamma > \gamma_2$.

Finally, if $1 < \beta \leq \delta$ (resp., $\delta < \beta < 1$), then a similar argument proves that $p(\gamma)$ is decreasing in $(0, \gamma_1)$ (resp., $p(\gamma)$ is increasing in $(\gamma_2, 2)$). $\square$

To illustrate the main results of the paper, we show in Figures 4 and 5 several bifurcation diagrams corresponding to the different cases in the statement of Theorem 5.1. Following [1], we use the name "cooperation parameter" for γ. In the four cases displayed in Figure 4, a subcritical pitchfork bifurcation occurs at $\gamma = 1$, $x = 0$. For $\gamma > 1$, the extinction equilibrium $x = 0$ becomes asymptotically stable, and a branch of unstable positive equilibria is born. This branch remains defined and unstable for all $\gamma > 1$ if $\beta > 1 + \delta$ (Figure 4 (a)); it becomes stable after a transcritical bifurcation occurs at $\gamma = (1 + 2\delta)/(1 + \delta)$ if $\beta = 1 + \delta$ (Figure 4 (b)); and it disappears after a saddle-node bifurcation occurs at $\gamma_1 \in (1, 2)$ if $1 < \beta < 1 + \delta$ (Figure 4 (c), (d)). If $\delta < \beta < 1 + \delta$, then another saddle-node bifurcation occurs at $\gamma_2 > \gamma_1$, so that there is an extinction window for $\gamma \in (\gamma_1, \gamma_2)$ (Figure 4 (c)).

In the four bifurcation diagrams displayed in Figure 4, we take $\beta > 1$. If $\beta \leq 1$, then the local bifurcation at $\gamma = 1$, $x = 0$ is a transcritical bifurcation, after which the extinction equilibrium $x = 0$ becomes globally asymptotically stable for $\gamma \in (1, \gamma_2)$, where $\gamma_2 = 2$ if $\beta \leq \delta$ (Figure 5 (a)), and $\gamma_2 < 2$ if $\delta < \beta$ (Figure 5 (b)). For a rigorous description of bifurcations of fixed points of maps, we refer to [18].

6. **Discussion.** We have introduced the discrete-time single-species model (1.1), which generalizes the Beverton-Holt and the Cushing models. The main feature of (1.1) is its flexibility, being capable of exhibiting compensatory, overcompensatory, and depensatory growth. For $\gamma < 1$, the stock-recruitment curve is unimodal, with
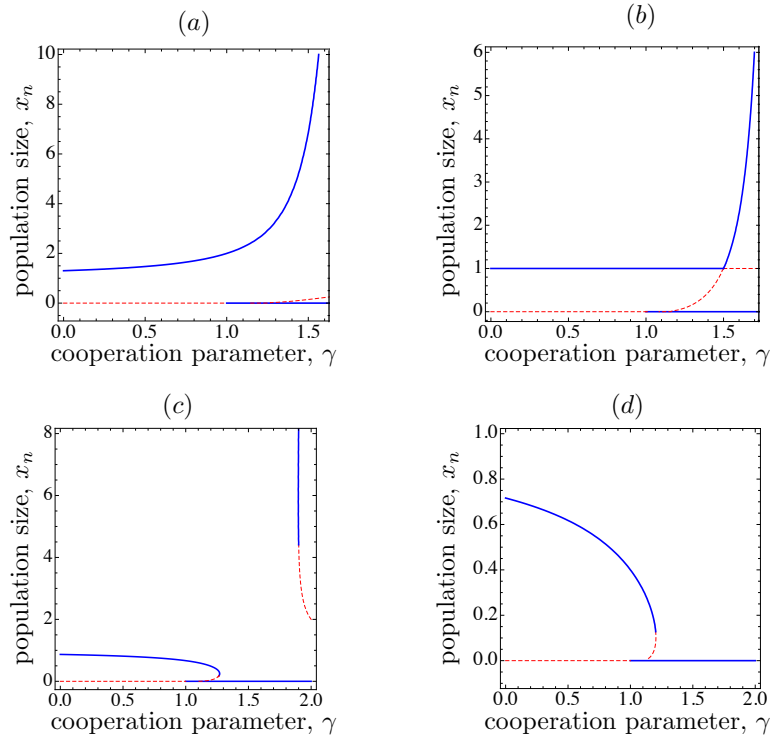
FIGURE 4. Bifurcation diagrams for equation (1.1), using γ as the bifurcation parameter. Red dashed lines correspond to unstable equilibria, which, in case of bistability, establish the boundary between the basins of attraction of the extinction equilibrium 0 and the nontrivial attractor p. (a): $\beta = 3, \delta = 1$; (b): $\beta = 2, \delta = 1$; (c): $\beta = 2, \delta = 1.5$; (b): $\beta = 2, \delta = 2.5$. Each case is an example of the corresponding case in Theorem 5.1.
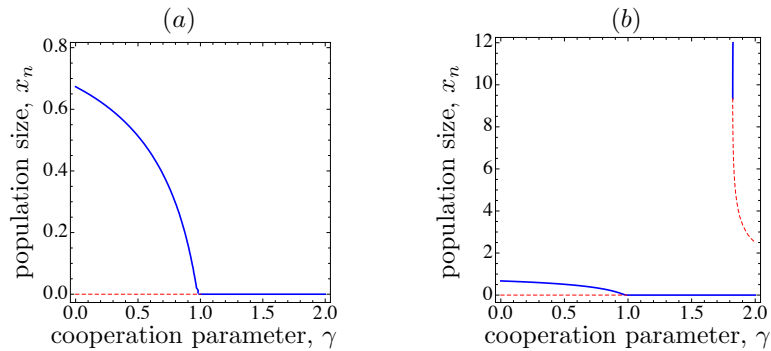

FIGURE 5. Bifurcation diagrams for equation (1.1), using γ as the bifurcation parameter. Red dashed lines correspond to unstable equilibria. (a): $\beta = 0.9, \delta = 1.5$; (b): $\beta = 0.9, \delta = 0.5$.

a unique positive fixed point p. We have proved that p is a global attractor, which excludes the possibility of periodic or chaotic behavior; however, convergence to the equilibrium can be oscillatory. If $\gamma = 1$, equation (1.1) is the Beverton-Holt model, characterized by a monotone convergence of all positive solutions either to a positive global attractor ($\beta > 1$), or to the extinction equilibrium ($\beta \leq 1$). If $\gamma > 1$, then the extinction equilibrium is asymptotically stable, inducing an Allee effect. For $\gamma \in (1, 2)$, the dynamics of (1.1) falls into one of two generic possibilities: extinction (if 0 is the unique equilibrium), or bistability, when the extinction equilibrium coexists with an asymptotically stable positive equilibrium. In the latter case, initial population densities below the Allee threshold A are doomed to extinction, but populations above A persist and converge to the largest positive equilibrium. If $\gamma \geq 2$, then populations above the positive equilibrium grow indefinitely, as in the Cushing model.

Although the dynamics of (1.1) is simple, it is still an interesting equation from a dynamical point of view, because it exhibits all types of generic bifurcations of fixed points with an eigenvalue of 1 (saddle-node, transcritical, pitchfork). An interesting feature of the bifurcation diagrams is the possibility of extinction windows when γ is used as the bifurcation parameter.

For $\gamma < 2$, the interplay between the three involved parameters determines in a subtle way when the cooperation parameter γ is beneficial for population abundance. While this is true for $\beta > 1 + \delta$, if $\beta < 1 + \delta$ then increasing γ can have negative effects, leading the population smoothly to extinction (Figure 5), or even to a sudden collapse (Figure 4 (c), (d)).

The ecological significance of our results about the influence of γ on population abundance is related to cooperation-mediated persistence, and there are some interesting analogies with predator-prey models where predators cooperate to exploit their preys [7, 16]. In the one-dimensional model considered here, the population cooperates and exploits resources, for which they compete intraspecifically. We showed that cooperation can help persistence; for example, Figures 4 (c) and 5 (b) show a "rescue" effect: populations that would go extinct in the absence of cooperation can survive for sufficiently large cooperation, provided initial population size is large enough. However, if productivity or competition are too large, cooperation cannot change the outcome (Figures 4 (a), 4 (b) and 5 (a)). This point has been made for predators subject to high disease mortality [7]. Figures 4 (c) and 4 (d) show a somehow counterintuitive effect: population abundance can decrease with increasing cooperation parameter values $\gamma > 1$. A possible explanation is that population tends to grow with γ but intraspecific competition for resources becomes stronger because of increasing population size. In these cases, the high value of δ results in a prevalence of competition over cooperation. A similar phenomenon has been observed in a predator-prey model with hunting cooperation [16].

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