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Chaos and population disappearances in simple ecological models

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Abstract. A class of truncated unimodal discrete-time single species models for which low or high densities result in extinction in the following generation are considered. A classification of the dynamics of these maps into five types is proven: (i) extinction in finite time for all initial densities, (ii) semistability in which all orbits tend toward the origin or a semistable fixed point, (iii) bistability for which the origin and an interval bounded away from the origin are attracting, (iv) chaotic semistability in which there is an interval of chaotic dynamics whose compliment lies in the origin's basin of attraction and (v) essential extinction in which almost every (but not every) initial population density leads to extinction in finite time. Applying these results to the Logistic, Ricker and generalized Beverton-Holt maps with constant harvesting rates, two birfurcations are shown to lead to sudden population disappearances: a saddle node bifurcation corresponding to a transition from bistability to extinction and a chaotic blue sky catastrophe corresponding to a transition from bistability to essential extinction.

1. Introduction

Populations can exhibit abrupt changes in their abundance in response to changes in environmental factors. Dramatic examples include the precipitous drop of blue pike from annual catches of 10 million pounds to less than one thousand pounds in the mid 1950s [2], the unexpected collapse of the Peruvian anchovy population in 1973 [6], and the sudden reduction of Great Britain's grey partridge population in 1952 [22]. While it is natural to assume that these dramatic changes correspond to a discontinuous change in an environmental factor, ecologists have long realized that gradual changes can lead to dramatic changes in population abundance [14, 18]. For instance, Beeton [2] has attributed the collapse of the blue pike populations to the relatively gradual onset of eutrophication.

One explanation for these sudden changes is that ecological communities can exhibit a multiplicity of stable dynamical states and small environmental changes can push the system from one stable state to another [14, 18]. A simple continuous

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time model that exhibits this behavior involves a population experiencing a constant rate of depletion (e.g., constant rate of predation, harvesting for constant yield, constant emigration) [5]. If N denotes the population density, r the intrinsic rate of growth of the population, K the carrying capacity and D the rate of depletion, then this model is given by

$$\frac{dN}{dt} = rN(1 - N/K) - D.$$

Non-dimensionalizing the state variable N by setting $x = N/K$, we get

$$\frac{dx}{dt} = rx(1 - x) - d \tag{1}$$

where $d = D/K$. For this model to make biological sense, solutions $x(t)$ of (1) are truncated to $\max\{x(t), 0\}$. For the truncated flow, the origin is an attractor. The dynamics of this model are summarized in Fig. 1. When $d < r/4$, there is a bistability, and the populations experience either extinction in finite time or approach a stable non-zero fixed point depending on initial conditions. When $d > r/4$, extinction in finite time occurs for all initial conditions. The sudden population disappearance as d crosses over the value $r/4$ corresponds to a saddle node bifurcation. Since $d = D/K$ decreases as K increases, enriching this system (i.e., increasing the rate at which limiting nutrients enter the system) does not result in population disappearances.

For many species, population growth is a seasonal affair rather than a continuous affair. In which case, continuous changes should be replaced by discrete changes and differential equations should be replaced by difference equations. Surprisingly, even though May discussed the discrete time analogs of (1) in a 1977 review article [18], it was not until two decades later that the dynamics of these difference equations were looked at more closely. In 1996, Sinha & Parthasarathy [26] considered the Ricker map with depletion, $x_{n+1} = x_n \exp(r(1 - x_n)) - d$, while in 1999 Vandermeer & Yodzis [28] considered the discretized Logistic map with depletion $x_{n+1} = rx_n(1 - x_n) - d$. These authors numerically uncovered two remarkable behaviors that the continuous time model does not exhibit: (i) populations can persist under a high rate of depletion even when lower rates of depletion lead to extinction; (ii) populations undergoing constant depletion can persist chaotically with relatively high minimum population densities, thereby reducing the risk of extinction. Also in 1996, Gyllenberg, Osipov, and Söderbacka [10] analyzed a general class of maps that they called Allee functions: unimodal maps for which extinction is inevitable for too high or too low initial population densities. They proved that under certain conditions Allee functions exhibit chaotic dynamics on a repelling set.

In this article, we consider Allee functions that have a negative Schwarzian derivative. In section 2, we introduce this class of functions formally, and show that harvested Logistic, Ricker, and Beverton-Holt models lie within this class. Our main results categorize the dynamics of these maps into five types (extinction, semistability, bistability, chaotic semistability, essential extinction), three of which

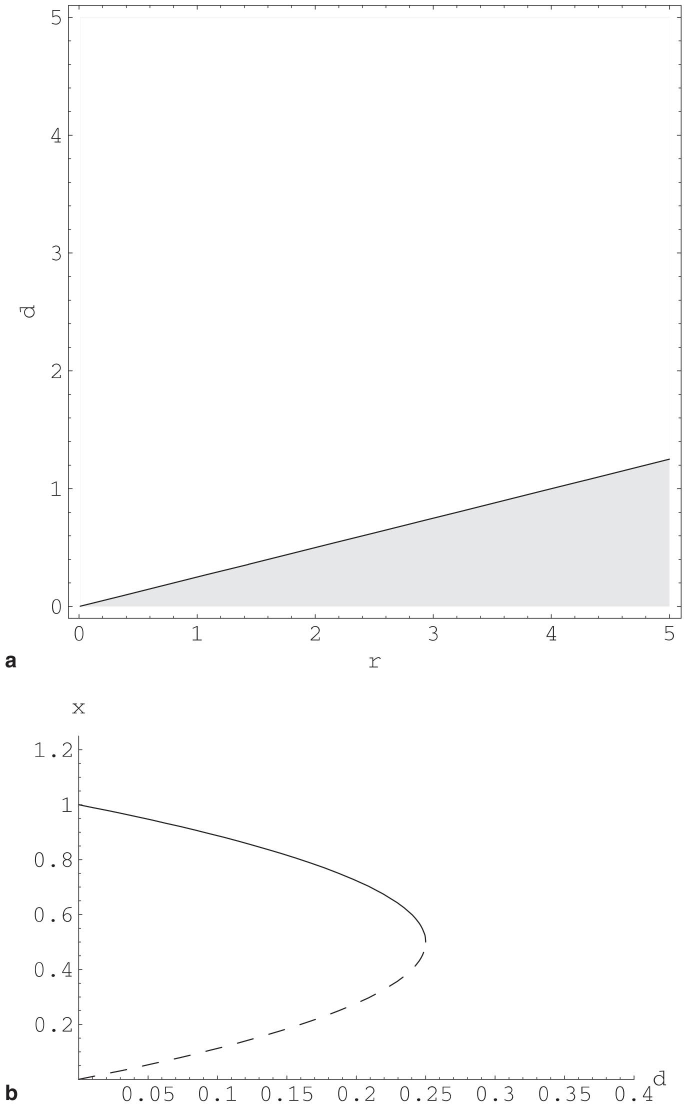

Fig. 1. Bifurcation diagrams for (1): In (a), the white region corresponds to extinction in finite time, and the shaded region corresponds to bistability. In (b), r is set to 1.0 and the equilibria of (1) are plotted as functions of d. The stable and unstable fixed points are drawn as solid and dashed lines, respectively.

(extinction, bistability, essential extinction) are generic. For one of these types (essential extinction), we discuss how our results in conjunction with the work of Gyllenberg, Osipov, and Söderbacka [10] imply the existence of chaotic transients prior to extinction. We also provide an example that illustrates the necessity of the negative Schwarzian derivative assumption. In section 3, we show how these results can be used to detect basin boundary collisions and population disappearances for the harvested Logistic, Ricker and generalized Beverton-Holt maps. In section 4, we discuss the biological implications these results. In section 5, we prove the main theorem.

2. Definitions, examples and main results

We consider a certain class of discrete time single species models of the form

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

where x_n denotes the population density in the n-th generation. The models we consider are such that high or low population densities in any given generation result in the extinction of the population in the following generation. Low densities resulting in extinction may occur when a population experiences a constant rate of depletion or when low densities prevent individuals from finding mates (i.e., the Allee effect). Alternatively, high densities resulting in extinction may occur when populations achieve sufficiently large numbers to exhaust their resources leaving nothing for the next generation.

Let $\mathbf{R}_+ = \{x \in \mathbf{R} : x \geq 0\}$. We consider $f : \mathbf{R}_+ \to \mathbf{R}_+$ that satisfy the following assumptions:

(A1) f is continuous.
(A2) There exists $[a, b] \subset (0, \infty)$ such that $f = 0$ on $[0, a] \cup [b, \infty)$.
(A3) f restricted to $[a, b]$ is C^3.
(A4) f restricted to $[a, b]$ has a unique critical point $c \in (a, b)$.
(A5) f restricted to $[a, b]$ has *negative Schwarzian derivative*:

$$Sf(x) = \frac{D^3 f(x)}{Df(x)} - \frac{3}{2}\left(\frac{D^2 f(x)}{Df(x)}\right)^2 < 0$$

for all $x \in [a, c) \cup (c, b]$.

The Schwarzian derivative Sf in (A5) was originally formulated by Herman A. Schwarz in his work on conformal mappings [13]. Its significance for conformal maps resides in the fact that $Sf(x) = 0$ for all x if and if f is a fractional linear transformation (i.e., $f(x) = (ax + b)/(cx + d)$). Singer [25] was the first to study the dynamics of one-dimensional maps with negative Schwarzian derivative. His motivation for studying these maps was two fold: maps with negative Schwarzian derivative give rise to a minimum principle which has strong dynamical implications, and many single species models have negative Schwarzian derivative.

Three classes of maps that satisfy these assumptions are the harvested Logistic, Ricker and generalized Beverton-Holt models.

2.1. The Logistic map with depletion

The Logistic map is given by $g(N) = rN(1 - N/K)$ where r is the intrinsic rate of growth of the population and K is the carrying capacity. Since g only maps the interval $[0, K]$ onto itself when $0 \leq r \leq 4$, most studies of this map have been confined to his range of r values. Following Vandermeer & Yodzis [28], we permit any positive value of r as we truncate the map. Non-dimensionalizing the state variable of the harvested Logistic map $g(N) - D$ by setting $x = N/K$ and $d = D/K$, we get $rx(1-x) - d$. The proof of the following proposition is left as an exercise for the reader.

Proposition 1. *Let* $f(x) = \max\{rx(1-x) - d, 0\}$ *with* $r > 0$ *and* $d > 0$.

1. *If* $r \leq 4d$, *then* $f(x) = 0$ *for all* $x \geq 0$.
2. *If* $r > 4d$, *then* f *satisfies (A1)–(A5).*

2.2. The Ricker map with depletion

The Ricker map $g(N) = N\exp(r(1 - N/K))$ has a long history of use in the study of single species population dynamics [23] and its harvested form was studied by Sinha & Parthasarathy [26]. Non-dimensionalizing the state variable of the harvested Ricker map $g(N) - D$ by setting $x = N/K$ and $d = D/K$, we get $x\exp(r(1-x)) - d$. We leave the proof of the following proposition as an exercise for the reader.

Proposition 2. *Let* $f(x) = \max\{x\exp(r(1-x)) - d, 0\}$ *with* $r > 0$ *and* $d > 0$.

1. *If* $d \geq \exp(r-1)/r$, *then* $f(x) = 0$ *for all* x.
2. *If* $d < \exp(r-1)/r$, *then* f *satisfies (A1)–(A5).*

2.3. The generalized Beverton–Holt map with depletion

The generalized Beverton–Holt map is given by

$$g(N) = \frac{rN}{1 + (N/K)^\gamma}$$

where $\gamma \geq 1$ measures the abruptness of the onset of density dependence [8]. When $\gamma = 1$, $g(N)$ is the well known Beverton–Holt model [4] and is an increasing, saturating, concave function. The generalized form with $\gamma > 1$ are humped shaped functions that have provided good fits to insect population census data [3]. For γ slightly larger than one, the per-capita growth rate $r/(1 + (N/K)^\gamma)$ declines relatively gradually as N increases. For large values of γ, the per-capita growth rate $r/(1 + (N/K)^\gamma)$ remains close to r for $N < K$, plunges abruptly through $r/2$ when $N = K$ and rapidly approaches zero for $N > K$. For $\gamma < 2$, Getz [8] has shown that the unique positive fixed point of this map is linearly stable. Non-dimensionalizing the state variable of the harvested generalized Beverton–Holt map $g(N) - D$ by setting $x = N/K$ and $d = D/K$, we get $\frac{rx}{1+x^\gamma} - d$.

Proposition 3. *Let* $f(x) = \max\{\frac{rx}{1+x^\gamma} - d, 0\}$ *with* $r > 0$, $d > 0$ *and* $\gamma > 1$. *Define* $c = (\gamma - 1)^{-\frac{1}{\gamma}}$.

1. *If* $f(c) = 0$, *then* $f = 0$ *for all* $x \in \mathbf{R}_+$.

2. *If $f(c) > 0$ and $\gamma \geq 2$, then f satisfies (A1)–(A5).*

We present the proof of the following proposition to clarify the need for the assumption that $\gamma \geq 2$ in its second assertion.

Proof. Let $g(x) = \frac{rx}{1+x^\gamma}$. Assume that $\gamma > 1$. g has a unique critical point at $c = (\gamma - 1)^{-1/\gamma}$ at which it attains its maximum $g(c)$. It follows that if $g(c) \leq d$, then $f(x) = 0$ for all $x \geq 0$. Assume that $g(c) > d$. Since $g(0) = 0$ and $\lim_{x\to\infty} g(x) = 0$, $g^{-1}(d)$ consists of exactly two points, a and b, that satisfy $0 < a < c < b$. Taking the Schwarzian derivative of g, we get

$$\frac{-\left(x^{-2+\gamma}\ (-1+\gamma)\,\gamma\left(2\,(1+\gamma) + x^\gamma\left(2 - 3\gamma + \gamma^2\right)\right)\right)}{2(-1 + x^\gamma\ (-1+\gamma))^2}.$$

Since $2 - 3\gamma + \gamma^2 \geq 0$ whenever $\gamma \geq 2$, the Schwarzian derivative of $g(x)$ is strictly negative for all x provided that $\gamma \geq 2$.

2.4. Main results

To understand the dynamics of a map $f : \mathbf{R}_+ \to \mathbf{R}_+$ satisfying (A1)–(A5), we consider five cases. In two of these cases, extinction is inevitable. In the other three cases, populations persist or go extinct depending upon initial densities. We begin with the simplest case that requires a minimal amount of machinery to prove. Let f^n denote f composed with itself n times. Recall that a point $x \in \mathbf{R}_+$ is a *fixed point* of f if $f(x) = x$.

Lemma 1. *Let $f : \mathbf{R}_+ \to \mathbf{R}_+$ be a map that satisfies (A1)–(A4). If the only fixed point of f is 0, then*

$$\lim_{n\to\infty} f^n(x) = 0 \qquad \textit{for all } x \in \mathbf{R}_+.$$

If f has more than one fixed point, then

$$\lim_{n\to\infty} f^n(x) = 0 \qquad \textit{for all } x \in \mathbf{R}_+\backslash[p, p^*]$$

where $p = \min\{x : x > 0, f(x) = x\}$ and $p^* = \max f^{-1}(p)$.

Proof. Suppose 0 is the only fixed point. Continuity of f implies that $f(x) < x$ for all $x \in (0, \infty)$. Let $x \in \mathbf{R}_+$ be given. Since $f^n(x)$ is a decreasing sequence that is bounded below by 0, $f^n(x)$ converges to some point x^* in $\mathbf{R}_+$. Continuity of f implies that x^* is a fixed point of f and, therefore, must equal 0.

Suppose f has more than one fixed point. Define $p = \min\{x : x > 0, f(x) = x\}$. Since $f = 0$ on $\mathbf{R}_+\backslash(a, b)$, $p \in (a, b)$. We claim that $p \in (a, c)$. Suppose to the contrary that $p \in [c, b)$. Since $Df \leq 0$ on $[c, b)$ and $f(p) = p \geq c$, there exists a $y \in (a, c)$ such that $f(y) > y$. Since $f(a) = 0$, the Intermediate Value Theorem applied to $f(x) - x$ implies that there exists $x \in (a, y)$ such that $f(x) = x$. This contradicts the definition of p. Therefore, p must lie in (a, c). Let $p^* = \max f^{-1}(p)$. Since $a < p = f(p) < \min\{c, f(c)\}$ and $f([a, c)) = [0, f(c)) = f((c, b])$, we get that $p^* > c$ and, consequently, $Df < 0$ on (p^*, b). From this observation, it follows that $f((p^*, \infty)) \subset [0, p)$. Since 0 is the only fixed point in $\mathbf{R}_+ \backslash [p, p^*]$ and $f(x) \leq x$ for $x \in \mathbf{R}_+ \backslash [p, p^*]$, $f^n(x)$ is a decreasing sequence that converges to 0 for any $x \in \mathbf{R}_+ \backslash [p, p^*]$.

We remark that continuity of f and the fact that $f = 0$ on $[0, a)$ implies that whenever $f^n(x)$ converges to the origin, it does so in a finite number of iterates.

The remaining four cases are captured by the following theorem whose proof makes extensive use of results from the theory of one-dimensional dynamics [7, 17, 21, 25]. The proof of this theorem is delayed until section 5. Recall that a set $A \subset \mathbf{R}_+$ is called *forward invariant* if $f(A) \subseteq A$ and *invariant* if $f(A) = A$. The *basin of attraction* of a compact forward invariant set A is the set of points $x \in \mathbf{R}_+$ such that $\lim_{n \to \infty} \text{dist}(f^n x, A) = 0$. A fixed point x is *linearly stable* if $|Df(x)| < 1$ and *linearly unstable* if $|Df(x)| > 1$.

Theorem 1. *Let $f : \mathbf{R}_+ \to \mathbf{R}_+$ be a map that satisfies (A1)–(A5). Assume f has at least two fixed points. Let*

$$p = \min\{x : x > 0, f(x) = x\} \text{ and } p^* = \max f^{-1}(p).$$

Then the dynamics of f falls into one of four categories:

1. (Semi-stability) *If f has exactly two fixed points,* 0 *and p, then the basin of attraction of p is* $[p, p^*]$.
2. (Bistability) *If f has at least three fixed points and $f^2(c) > p$, then either there is a linearly stable fixed point $q \in (p, p^*)$ whose basin of attraction is (p, p^*) or the interval $I = [f^2(c), f(c)]$ is forward invariant with basin of attraction* (p, p^*).
3. (Chaotic semi-stability) *If f has at least three fixed points and $f^2(c) = p$, then $[p, f(c)]$ is invariant and for Lebesgue almost every $x \in [p, f(c)]$, $\overline{\cup_{n \geq 0} f^n(x)} = [p, f(c)]$ and $\lim_{n \to \infty} \frac{1}{n} \ln |Df^n(x)| > 0$.*
4. (Essential extinction) *If f has at least three fixed points and $f^2(c) < p$, then $\lim_{n \to \infty} f^n(x) = 0$ for Lebesgue almost every $x \in \mathbf{R}_+$.*

We can interpret these results as follows. When the per-capita growth rate of the population is strictly less than one for all population densities, Lemma 1 implies that extinction in finite time occurs for all initial densities. If the per-capita growth rate of the population is strictly less than one except at one population density, the dynamics are semi-stable.

To interpret what happens when the per-capita growth rates are greater than one for an interval of population densities, we notice that comparisons between $f^2(c)$ and p can be translated into comparisons between the maximum size $f(c)$ of a growing population and the critical population density p^*. When the maximum size of a growing population is less than the critical density, the population can persist indefinitely with densities bounded away from zero provided that the initial population size is of intermediate size. When the maximum size of a growing population exceeds the critical density, populations are almost surely doomed to extinction. In the spirit of Melbourne's definition of an essential attractor [20], we call this occurrence *essential extinction* as a randomly chosen initial density leads to extinction with probability one. On the compliment Γ of the origin's basin, the proof of Theorem 1 implies that $\lim_{n\to\infty} \frac{1}{n} \ln |Df^n(x)| > 0$ for all $x \in \Gamma$ (i.e., Γ is repellor and nearby orbits on Γ tend to diverge). In addition, the following result of Gyllenberg, Osipov, and Söderbacka [10, Prop. 3.9] which we state using our notation provides further information.

Theorem 2 (Gyllenberg, Osipov, and Söderbacka 1996). *Let f be a function such that*

1. *(A1)–(A4) are satisfied,*
2. *$f(x)$ has at least three fixed points,*
3. *$f^2(c) < p$, and*
4. *the compliment Γ of the origin's basin of attraction has Lebesque measure zero.*

Then Γ contains a dense orbit and infinitely many periodic points.

Theorem 1 implies that assumption 4 of Theorem 2 can be replaced by the negative Schwarzian assumption (A5). These results imply that in the case of essential extinction, the set of orbits that do not head toward extinction form a "chaotic repellor."

The third assertion of Theorem 1 implies that the transition between bistability and essential extinction occurs when the maximum size of a growing population equals the critical density. In this case, the populations can persist at a semistable chaotic interval.

2.5. *On the necessity of the negative Schwarzian derivative*

Before proceeding to examples of maps that satisfy the assumptions of Theorem 1, we illustrate the necessity of the negative Schwarzian derivative assumption in Theorem 1. Define

$$g(x) = -150 + \frac{667}{2}x - \frac{806}{3}x^2 + \frac{308}{3}x^3 - \frac{113}{6}x^4 + \frac{4}{3}x^5.$$

The function $g(x)$ has the following properties:

- $g(1) = g(4) = 0$,
- $g(x) > 0$ for $x \in (1, 4)$,
- the only critical point for $g(x)$ in the interval $[1, 4]$ is at $x = 3/2$,
- g has exactly two fixed points, $x = 3$ and $x = p$ where $p \in (1, 2)$, in the interval $[1, 4]$,
- $g'(3) = -1/2$,
- $g(3/2) > 5$, and
- the Schwarzian derivative of g at $x = 11/4$ is positive.

Define

$$f(x) = \begin{cases} g(x) & \text{if } x \in (1,4) \\ 0 & \text{else.} \end{cases}$$

By construction $f(x)$ satisfies (A1)–(A4) with critical point $c = 3/2$. Since, $f^2(c) = 0 < p$, the function f would fall into the case of essential extinction in Theorem 1 if the negative Schwarzian derivative condition were satisfied. However, since $x = 3$ is a linearly stable fixed point for f, there is an interval of initial conditions that do not lead to extinction. Hence, the negative Schwarzian hypothesis is necessary in Theorem 1.

3. Population disappearances and basin boundary collisions

In this section, we revisit the Logistic, Ricker, and generalized Beverton–Holt maps with constant depletion. These maps are of the form

$$f(x) = \max\{g(x) - d, 0\}$$

where g is the Logistic, Ricker or generalized Beverton–Holt map. To illustrate how the conditions in our main results can be checked analytically, we first revisit the Logistic map. We follow this up with numerical explorations of the Ricker and generalized Beverton-Holt maps.

Before preceding we make an observation about the attracting interval $I = [f^2(c), f(c)]$ (see assertion 2 of Theorem 1) for these choices of f. Since $I = [g(g(c) - d) - d, g(c) - d]$, the length of I is $L(d) = g(c) - g(g(c) - d)$. The proof of Theorem 1 implies that $g(c) - d > c$ whenever I is an attracting interval. Hence, $L'(d) = g'(g(c) - d) < 0$ when I is an attracting interval. This observation suggests that increasing the carrying capacity of a population or decreasing the depletion rates may increase the variability of persisting populations.

3.1. *The Logistic map revisited*

Consider the map from $\mathbf{R}_+$ to $\mathbf{R}_+$ given by

$$f(x) = \max\{rx(1 - x) - d, 0\}$$

where $r > 0$ and $d > 0$. Recall, if $r < 4d$, then $f(x) = 0$ for all $x \in \mathbf{R}_+$ and the population always goes extinct after one generation. Assume that $r > 4d$. We need to determine when f has non-zero fixed points. Solving $rx(1 - x) - d = x$ for x, we get

$$x = \frac{r - 1 \pm \sqrt{(r - 1)^2 - 4dr}}{2r}.$$

Therefore, if $(r - 1)^2 < 4dr$ or $r \le 1$, there are no non-zero fixed points and Lemma 1 implies that all orbits are attracted to the origin. Assume that $r > 1$ and $(r - 1)^2 \ge 4dr$. The smallest non-zero fixed point p is given by

$$p = \frac{r - 1 - \sqrt{(r - 1)^2 - 4dr}}{2r}.$$

If $(r - 1)^2 = 4dr$, then p is the only additional fixed point and Theorem 1 implies that p is semi-stable. On the other hand, if $(r - 1)^2 > 4dr$, then there are three fixed points and we need to consider the second iterate of the critical point $c = 1/2$,

$$f^2(c) = \max\{-d + \left(1 + d - \frac{r}{4}\right)\left(-d + \frac{r}{4}\right) r, 0\}.$$

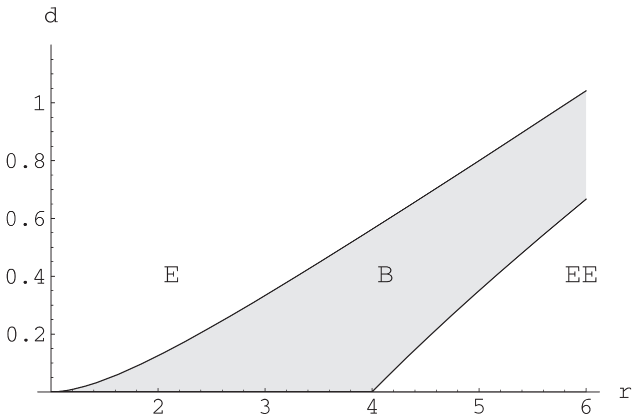

Fig. 2. Bifurcation diagram for $f(x) = \max\{rx(1-x) - d, 0\}$ where the region labeled E corresponds to extinction, the region labeled B corresponds to bistability, and the region labeled EE corresponds to essential extinction.

Solving for $f^2(c) = p$ for d, we get

$$d = \frac{-8 - 2r + r^2}{4r}.$$

If $d = \frac{-8-2r+r^2}{4r}$, then Theorem 1 implies that f restricted to $[p, r/4 - d]$ is chaotic. If $\frac{(r-1)^2}{4r} > d > \frac{-8-2r+r^2}{4r}$, then Theorem 1 implies that there is an attracting interval bounded away from zero. Therefore, the populations can persist at arbitrarily high depletion rates provided that their intrinsic rate of growth is sufficiently high. If $0 < d < \frac{-8-2r+r^2}{4r}$, then Theorem 1 implies essential extinction of the population. These results are summarized in Fig. 2.

To examine the effect of depletion rates and enrichment on population dynamics, we consider f when r is fixed and d is allowed to vary. Recall that $d = D/K$ where D is the depletion rate and K is the carrying capacity of the population. Suppose that $1 < r < 4$ as in Fig. 3a. When d is sufficiently small, f supports two attracting sets: the origin and an interval bounded away from the origin. As d increases, the attracting interval shrinks and collides with the fixed point p via a saddle node bifurcation. For larger d values, the population always goes to extinction in finite time. Hence, for this range of r values, the behavior of the harvested Logistic map is similar to its continuous counterpart. Now, suppose that $r > 4$ as in Fig. 3b. When d is sufficiently large, the populations are driven to extinction in finite time. As d decreases, the system undergoes a saddle node bifurcation and exhibits a period-doubling route to chaos. As d continues to decrease, the upper edge of the chaotic interval collides with the boundary of the origin's basin of attraction. This collision results in essential extinction. In this case, the compliment of the origin's basin of attraction is a chaotic repellor that can produce long-term chaotic transients as illustrated in Fig. 4.

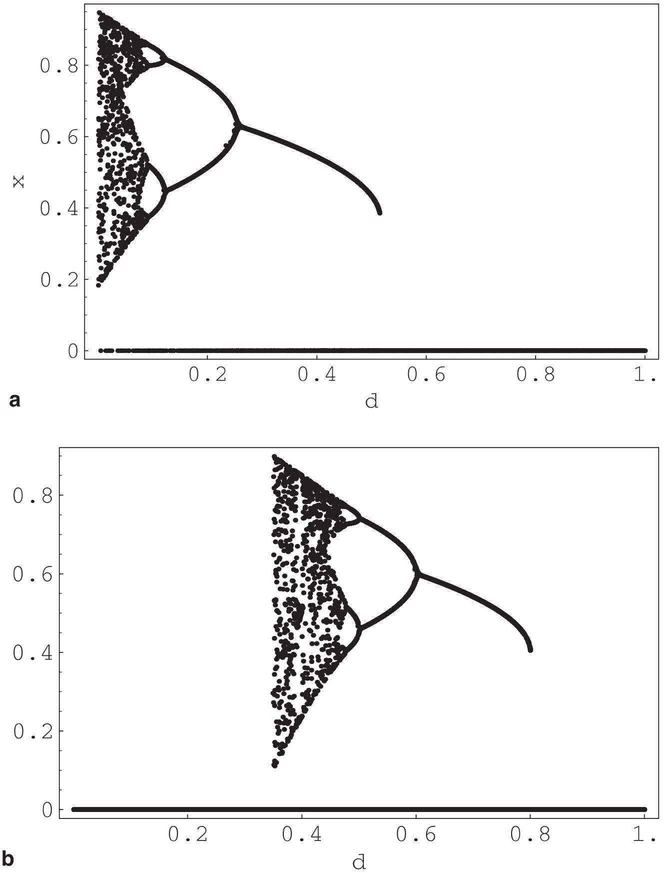

Fig. 3. Orbital bifurcation diagrams for $f(x) = \max\{rx(1-x) - d, 0\}$. For each d value a random initial condition $x \in [0, r/4 - d]$ is selected and $f^{100}(x)$ is plotted. In (a) $r = 3.8$, and in (b) $r = 5.0$.

3.2. The Ricker map revisited

Let $f : \mathbf{R}_+ \to \mathbf{R}_+$ be given by

$$f(x) = \max\{x \exp(r(1-x)) - d, 0\}.$$

Since it is not possible to solve explicitly for the non-zero fixed points, we numerically created a bifurcation diagram in Fig. 5a. When r is fixed at a value slightly larger than 2.55, this bifurcation diagram is qualitatively different from the corresponding bifurcation diagram in Fig. 2 for the Logistic equation. For these larger r values, populations can persist at an attracting interval at low as well as relatively high d values. We illustrate the orbital dynamics for $r = 2.6$ in Fig. 5b. At high depletion rates, the populations always experience extinction in a finite number of generations. As the depletion rate decreases or the system is enriched (i.e., K

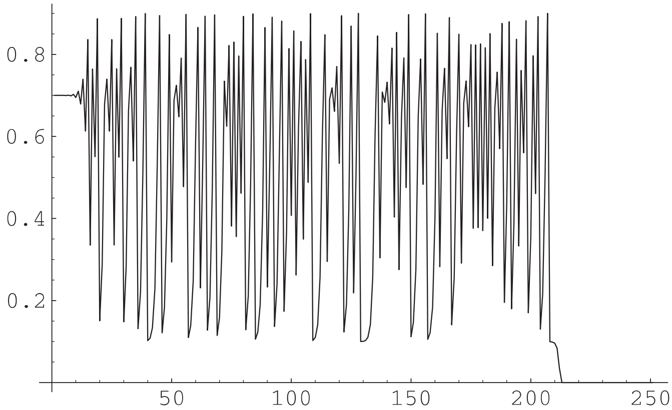

Fig. 4. Chaotic transients for $f(x) = \max\{rx(1-x) - d, 0\}$ with $r = 5.0$, $d = 0.3499$, and initial condition $x = \frac{r-1-\sqrt{(-1+r)^2-4mr}}{2r} + 0.00001$.

is increased), a linearly stable fixed point is created via a saddle-node bifurcation and period doubling cascade to chaos ensues. In this range of d values, the populations can exhibit chaotic dynamics bounded well above extinction. As the depletion rate continues to decrease or the system continues to be enriched, the size of the attracting interval increases until it collides with the boundary of the origin's basin of attraction. This collision results in an essential extinction. Alternatively, for low depletion rates or for highly enriched systems, the origin's immediate basin of attraction is sufficiently small to permit the persistence of highly variable populations.

3.3. The generalized Beverton–Holt map revisited

Let $f : \mathbf{R}_+ \to \mathbf{R}_+$ be given by

$$f(x) = \max\{\frac{rx}{1+x^\gamma} - d, 0\}$$

where $r > 1$, $d > 0$, and $\gamma \geq 1$. To apply our results, Proposition 3 requires that we assume that $\gamma \geq 2$. Since the behavior bifurcation behavior of this map with $\gamma > 2$ fixed while d and r vary is similar to the Ricker map, we fix r at 2 and examine the role of the abruptness parameter γ in Fig. 6. While sufficiently high intrinsic rates of growth permit population persistence at arbitrarily high depletion rates, Fig. 6 suggests that populations with abruptness in the onset of density dependence can not persist at arbitrarily high depletion rates.

4. Discussion

Our analysis implies populations that go extinct whenever achieving too high or too low densities will exhibit one of three types of "observable" dynamics. Extinction occurs for all initial population densities whenever the populations have per-capita

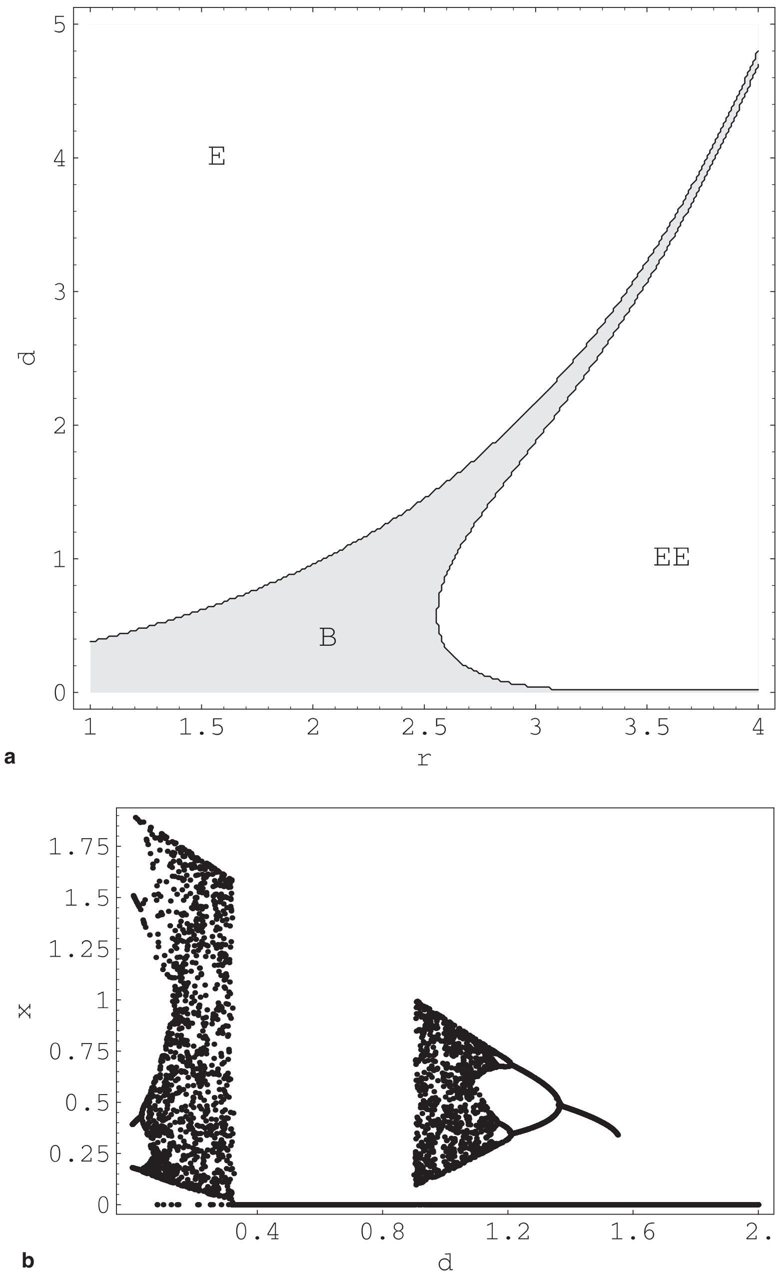

Fig. 5. Bifurcation diagrams for $f(x) = \max\{x \exp(r(1-x)) - d, 0\}$. In (a), the shading and labels are as in Fig. 2. In (b), $r = 2.6$ and for each d value a random initial condition is selected and $f^{100}(x)$ is plotted.

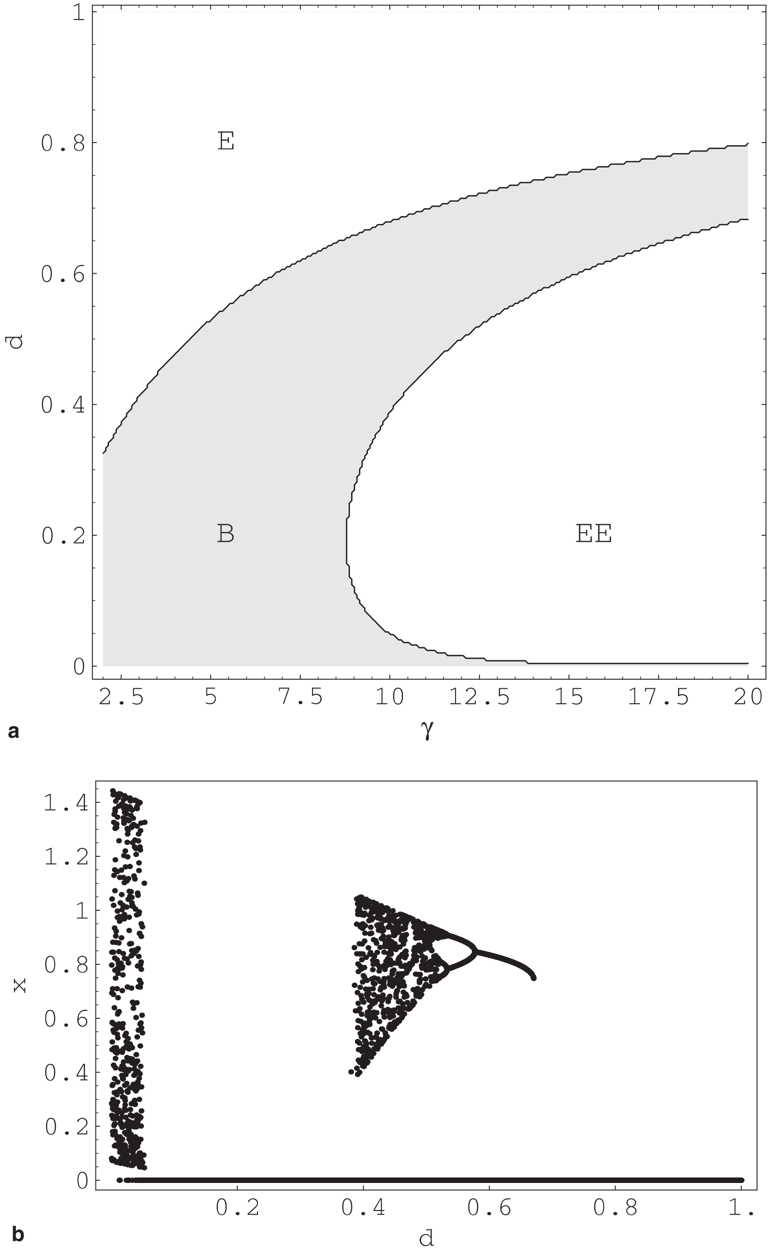

Fig. 6. Bifurcation diagrams for $f(x) = \max\{\frac{2x}{1+x^\gamma}\}$. In (a), the shading and labels are as in Fig. 2. In (b), $\gamma = 9$ and for each d value a random initial condition is selected and $f^{100}(x)$ is plotted.

growth rates that are strictly less than one for all densities. Bistability in which the populations either persist or go extinct depending on initial conditions occurs when the maximum size of a growing population lies below a critical threshold. Essential extinction in which populations go extinct for almost every initial density occurs when the maximum size of a growing population exceeds a critical threshold. Variation in environmental parameters such as depletion rates, carrying capacities, intrinsic rates of growth or abruptness of density dependence can result in transitions between these three types of dynamics. The transition between bistability and extinction corresponds to a saddle-node bifurcation, while the transition between bistability and essential extinction correspond to a basin boundary collision that Abraham & Stewart call a chaotic blue sky catastrophe [1,9].

Our results in conjunction with the work of Gyllenberg, Osipov, and Söderbacka [10] shows that when the maximum size of a population is too large, the population can exhibit long-term chaotic transients prior to extinction. As first noted by Hastings and Higgins [12], the importance of chaotic transients in ecological systems is two fold. First, the time scale of ecological interest is often relatively short, say tens or hundreds of years. Hence, predictions about the long-term behavior of the system may provide little or no information about the short-term behavior. Second, long-term transients can give the appearance of being the system's final behavior, and then, without warning, shift to an entirely different dynamical behavior. In our case, populations can persist for hundreds of generations, and then suddenly go extinct without any underlying change in the parameters.

Applying the analysis to the Logistic, Ricker and generalized Beverton–Holt maps with constant depletion, we confirm the observations of Sinha & Parthasarathy [26] and Vandermeer & Yodzis [28] that gradual changes in depletion rates as well as the rate at which limiting nutrients are supplied to an ecosystem can have unexpectedly dramatic consequences for population persistence. For slow growing populations that exhibit a relatively gradual onset of density dependence, the effect of enrichment or depletion is qualitatively similar to the continuous-time model. Namely, there is a critical depletion rate above which populations are driven to extinction for all initial densities and below which persistence is possible. Alternatively, there is a critical level of enrichment below which extinction is certain and above which persistence is possible. For fast growing populations or populations that exhibit an abruptness in the onset of density dependence, there exist two or more critical levels of depletion and enrichment. Consequently, populations are able to persist at relatively high levels of depletion even when lower rates of depletion result in extinction. Alternatively, if the depletion rate corresponds to the difference between the rates of immigration and emigration, then an increased flux of immigrants (i.e., a reduced depletion rate) can lead to extinction. These multiple critical levels also imply that populations persisting at relatively high levels of depletion can suddenly disappear if the system is enriched. Hence, fast growing populations or populations that exhibit an abruptness in the onset of density dependence give rise to an extreme form of the "paradox of enrichment" in which increasing the supply of limiting nutrients not only destabilizes the dynamics [24] but also leads to eventual extinction. An explanation for these counter-intuitive behaviors is that decreasing depletion rates or enriching the system increases population variability. This increased variability results in lower minimum population densities that coupled with constant depletion lead to extinction. This theoretical explanation is borne out in avifaunal field studies that have shown bird species with more variable densities on the main land are more prone to extinction on nearby land bridge islands [15].

Hastings [11] and Stone [27] have shown that passive dispersal and immigration, respectively, can stabilize chaotic dynamics. Alternatively, our study shows that increasing emigration or harvesting rates, or decreasing the rate at which limiting nutrients enter the system can also stabilize chaotic dynamics by shifting the dynamics from chaotic semistability to persisting at a linearly stable fixed point.

In conclusion, our analysis shows that gradual environmental changes can have consequences that are different from what conventional wisdom would indicate. Since most ecological communities involve several interacting species, reside in a spatially heterogeneous environment, and are influenced by many environmental factors, there is a need to further investigate how these additional complexities influence sudden population disappearances. For instance, McCann & Yodzis [19] have shown that in tritrophic systems the top predator species can exhibit sudden disappearances as the system is enriched. The mechanism behind this disappearance appears to be the collision of an attractor supporting all species with the basin of an attractor that only supports the two lower trophic species. Understanding other conditions for which these unforeseeable jumps occur between ecological configurations is likely to provide future challenges for ecologists and mathematicians.

5. Proof of Theorem 1

To prove Theorem 1, it will be necessary to adapt some basic tools for maps with negative Schwarzian derivative to our context. The text of de Melo and van Strien [7] provides a good survey of these methods. Singer [25] noted two important properties of functions with negative Schwarzian derivative. We state these properties as Lemmas, and refer the reader to the text of de Melo and van Strien [7] for a proof.

Lemma 2. *If I is a compact interval, $f : I \to \mathbf{R}$ is C^3 and $x, f(x), \ldots, f^{n-1}(x) \in I$, then*

$$Sf^n(x) = \sum_{i=0}^{n-1} Sf(f^i(x))|Df^i(x)|^2.$$

In particular, this composition formula for the Schwarzian derivative implies that if f has negative Schwarzian derivative along an orbit, then f^n has negative Schwarzian derivative along that orbit.

Lemma 3 (Minimum Principle). *If $I = [\alpha, \beta]$ is a compact interval and $f : I \to \mathbf{R}$ is a C^3 function that satisfies $Df(x) \neq 0$ for all $x \in I$ and $Sf(x) < 0$ for all $x \in I$, then*

$$|Df(x)| > \min\{|Df(\alpha)|, |Df(\beta)|\} \qquad \text{for all } x \in (\alpha, \beta).$$

Using these lemmas, we prove a modified version of Singer's Theorem [25]. To state this theorem, we recall a few definitions. The *orbit* of a point $x \in \mathbf{R}_+$ is given by $\mathcal{O}(x) = \cup_{n\geq 0} f^n(x)$. If $f^n(p) = p$ and $f^i(p) \neq p$ for all $1 \leq i \leq n-1$, then p is a *periodic point of period* n. The *basin of attraction* of a periodic point p is the set of points $x \in \mathbf{R}_+$ such that $\lim_{n\to\infty} \text{dist}(f^n(x), \mathcal{O}(p)) = 0$. The *immediate basin of attraction* of a periodic orbit is the union of the connected components of the basin of attraction that contain a point of the periodic orbit. We say that a periodic orbit is *attracting* provided the immediate basin of attraction contains an open interval. In particular, a semi-stable periodic point is attracting. A periodic point p of period n is a *neutral periodic point* provided that $|Df^n(x)| = 1$.

Theorem 3 (Modified Singer's Theorem). *If $f : \mathbf{R}_+ \to \mathbf{R}_+$ satisfies (A1)–(A5), then*

1. *The immediate basin of attraction of every attracting periodic orbit in $[a, b]$ contains the critical point c of f.*
2. *For each $n \geq 1$, f^n has a finite number of fixed points.*
3. *Each neutral periodic orbit is attracting.*

Proof. To prove the first assertion, suppose that $p > 0$ is an attracting periodic point of period n for f. Since p is attracting, $|Df^n(p)| \leq 1$. Let B be the immediate basin of attraction for $\mathcal{O}(p)$. Since $f = 0$ on $[0, a] \cup [b, \infty)$, it follows that $\overline{B} \subset (a, b)$. Since B is forward invariant, $f^i(B) \subset (a, b)$ for all $i \geq 0$. Suppose, to the contrary, $c \notin B$. Let B_p be the connected component of B that contains p. The chain rule implies that $Df^n(x) \neq 0$ for all $x \in B_p$. Hence, $Df^{2n}(x) > 0$ for all $x \in B_p$. Since B_p is a connected component of B and f^{2n} restricted to B_p is strictly increasing, $f^{2n}(B_p) = B_p$ and $f^{2n}(x) = x$ for $x \in \partial B_p$. Since all points in B_p are attracted to the orbit of p, it must be that $|Df^{2n}(x)| \geq 1$ for $x \in \partial B_p$. Since f has negative Schwarzian derivative on $[a, b]$ and $f^i(B) \subset (a, b)$ for all $i \geq 0$, Lemma 2 implies that f^{2n} restricted to B_p has negative Schwarzian derivative. The Minimum Principle applied to f^{2n} restricted to B_p implies that $|Df^{2n}(x)| > 1$ for all $x \in \text{int}B_p$. This contradicts the fact that $f^{2n}(B_p) = B_p$. Hence, the immediate basin of $\mathcal{O}(p)$ must contain c.

To prove the second assertion, assume to the contrary that there exists an n such that f^n has an infinite number of fixed points. Since the only fixed point of f^n restricted to $[0, a] \cup [b, \infty)$ is 0, we can find a sequence of distinct fixed points $x_k \in (a, b)$ for f^n that converge to a point $x \in (a, b)$. Continuity of f^n implies that x is a fixed point of f^n. For every k, let J_k denote the interval whose end points are given by x_k and x_{k+1}. The interiors of these intervals are non-empty as $x_{k+1} \neq x_k$. Since $x_{k+1} = f^n(x_{k+1})$ and $x_k = f^n(x_k)$, the Mean Value Theorem implies that there exists an x_k^* in J_k such that $Df^n(x_k^*) = 1$. Since x_k^* converges to x, continuity of Df^n implies that $Df^n(x) = 1$. By choosing k appropriately large, we can find an interval J^* whose endpoints are x and x_k^* such that there exists a x_m^* contained in the interior of J^*, $f^n(J^*) \subset [a, b]$ and $Df^n(x) \neq 0$ for all $x \in J^*$. By Lemma 2, f^n restricted to J^* has negative Schwarzian derivative. By the Minimum Principle, $1 = |Df^n(x_m^*)| > \min\{|Df^n(x)|, |Df^n(x_k^*)|\} = 1$ which is impossible. Hence, f^n must have only a finite number of fixed points.

To prove the final assertion, assume that $p > 0$ is a neutral periodic point of period n. Then $Df^{2n}(p) = 1$. Since there are only a finite number of periodic points of period $\leq 2n$, there is an interval $(\alpha, \beta) \subset (a, b)$ containing p such that $f^{2n}(x) \neq x$ for all $x \in (\alpha, p) \cup (p, \beta)$. If $f^{2n}(x) < x$ for all $x \in (p, \beta)$ or $f^{2n}(x) > x$ for all $x \in (\alpha, p)$, then the orbit of p is attracting (possibly semi-stable). Suppose to the contrary that $f^{2n}(x) > x$ for all $x \in (p, \beta)$ and $f^{2n}(x) < x$ for all $x \in (\alpha, p)$. Then there exists an interval $(\alpha', \beta') \subset (\alpha, \beta)$ containing the point p, satisfying $f^{2n}((\alpha', \beta')) \subset (a, b)$, $Df^{2n}(x) \neq 0$ for all $x \in (\alpha', \beta')$, $Df^{2n}(\alpha') > 1$ and $Df^{2n}(\beta') > 1$. Lemma 2 implies that f^{2n} restricted to (α', β') has negative Schwarzian derivative. The Minimum Principle applied to f^{2n} restricted to $[\alpha', \beta']$ implies that $|Df^{2n}(p)| > 1$. This contradicts our assumption that p is a neutral periodic point.

Now, we are ready to prove Theorem 1.

Proof (Theorem 1). Let $f : \mathbf{R}_+ \to \mathbf{R}_+$ be a map that satisfies (A1)–(A5). Assume that f has at least two fixed points. Define $p = \min\{x : x > 0, f(x) = x\}$ and $p^* = \max\{f^{-1}(p)\}$.

Suppose that f has exactly two fixed points, 0 and p. Since $f = 0$ on $[0, a]$, the definition of p implies that $f(x) < x$ for all $x \in (0, p)$. We claim that $f(x) \leq x$ for all $x \in (p, \infty)$. Suppose to the contrary that $f(x) > x$ for some $x \in (p, \infty)$. Since 0 and p are the only fixed points, it would follow that $f(x) > x$ for all $x \in (p, \infty)$. In particular, $f(b) > 0$ which violates assumption (A2). Therefore, $f(x) \leq x$ for all $x \in \mathbf{R}_+$. Since $x \geq f(x) \geq p$ for $x \in [p, p^*]$, $\lim_{n\to\infty} f^n(x) = p$ for $x \in [p, p^*]$.

For the remainder of the proof, assume that f has three or more fixed points. We begin by proving two useful facts:

$$Df(p) > 1 \tag{2}$$

and

$$\text{any fixed point in } (p, c] \text{ is linearly stable.} \tag{3}$$

To prove (2), suppose to the contrary that $Df(p) \leq 1$. If $Df(p) < 1$, then there exist $x \in (a, p)$ such that $f(x) > x$. Since $f(a) = 0$, the Intermediate Value Theorem implies that $f(x) = x$ for some $x \in (a, p)$ which contradicts our choice of p. If $Df(p) = 1$, then by the Modified Singer's Theorem p is an attracting fixed point and its immediate basin of attraction contains $[p, c]$. Consequently, $f(x) < x$ for all $x \in (p, c]$. Since $f(c)$ is the maximum value that f takes on, $f(x) < x$ for all $x \in (p, \infty)$. Hence, f has no fixed points in the interval (p, ∞) which contradicts our assumption that f has at least three fixed points. Therefore, $Df(p) > 1$. To prove (3), suppose that $q \in (p, c)$ is an fixed point for f. Since $f(p) = p$ and $f(q) = q$, the Mean Value Theorem implies there exists a point $y \in (p, q)$ such that $Df(y) = 1$. Since $|Df(p)| > 1$, the Minimum Principle applied to f restricted to $[p, q]$ implies that

$$|Df(q)| = \min\{|Df(p)|, |Df(q)|\} < |Df(y)| = 1.$$

Now, suppose that $f^2(c) > p$. We have two cases to consider. First, suppose that $q \in (p, p^*)$ is a linearly stable fixed point. By the Modified Singer's Theorem q is the only linearly stable fixed point in (p, p^*) and the immediate basin of attraction of q includes the orbit of c. Hence, $[\min\{c, q\}, \max\{c, f(c)\}]$ is contained in q's immediate basin of attraction. The assertion in (3) implies that $f(x) > x$ on $(p, \min\{q, c\})$ as q is the only linearly stable fixed point in (p, p^*). Therefore, $(p, \max\{c, f(c)\}]$ is contained in q's immediate basin of attraction. As f maps $[f(c), p^*)$ into $(p, f(c)]$, (p, p^*) lies in q's immediate basin of attraction. Second, suppose that (p, p^*) contains no linearly stable fixed point. The assertion in (3) implies that f has no fixed point in $(p, c]$. Hence, $f(x) > x$ for all $x \in (p, c]$. It follows that the orbit of every point $x \in (p, p^*)$ enters the interval $I = [f^2(c), f(c)]$. To show that $f(I) \subseteq I$, we note that f maps $[\max\{c, f^2(c)\}, f(c)]$ into I as $Df < 0$ on $(c, p^*]$. Since $f(x) > x$ on $(p, c]$, f maps $[\min\{c, f^2(c)\}, c]$ into I. Therefore, $f(I) \subseteq I$.

Suppose that $f^2(c) = p$. Since $Df > 0$ on $[p, c)$ and $f(p) = p$, f maps $[p, c]$ onto $[p, f(c)]$. Since $Df < 0$ on $(c, f(c)]$ and $f^2(c) = p$, f maps $[c, f(c)]$ onto $[p, f(c)]$. Hence, $f(I) = I$ where $I = [p, f(c)]$. To show that this interval admits complex dynamics, we recall a few definitions. A Borel probability measure μ on I is called f-*invariant* provided that $\mu(A) = \mu(f^{-1}A)$ for any Borel set $A \subset I$. We say an f-invariant measure μ is *ergodic* on I provided that $\mu(A)\mu(I \backslash A) = 0$ for any Borel set $A \subset I$. An f-invariant measure μ is called an *absolutely continuous invariant measure* on I provided that $\mu(A) > 0$ for a Borel set $A \subset I$ if only if the Lebesgue measure of A is positive. Using the following theorem [21], we show that f restricted to $[p, f(c)]$ admits an ergodic absolutely continuous invariant measure.

Theorem 4 (Misiurewicz 1981). *Let I be a compact interval and $f : I \to I$ a map satisfying the following conditions:*

1. *f is C^3,*
2. *f has a single critical point c,*
3. *f has negative Schwarzian derivative,*
4. *there exists no $n_i \uparrow \infty$ such that $\lim_{i\to\infty} f^{n_i}(c) = c$ and*
5. *f has no attracting periodic points,*

then f admits an ergodic absolutely continuous invariant probability measure μ and $\int \ln |Df| d\mu > 0$.

(A1)–(A5) imply that f restricted to $I = [p, f(c)]$ satisfies the first three conditions of Theorem 4. Since $f^2(c) = p$ and $f(p) = p$, it follows that $f^n(c) = p$ for all $n \geq 2$. Hence, the fourth condition of Theorem 4 is satisfied. Since p is linearly unstable and $f^2(c) = p$, the Modified Singer's Theorem implies that f restricted to $[p, f(c)]$ has no attracting periodic points. Theorem 4 implies that f restricted to $[p, f(c)]$ admits an ergodic absolutely continuous invariant measure μ. The Birkhoff Ergodic Theorem (see, e.g., [16]) implies that for Lebesgue almost every $x \in [p, f(c)]$,

$$\lim_{n\to\infty} \frac{1}{n} \ln |Df^n(x)| = \int \ln |Df| d\mu > 0.$$

Next, we show that the orbit of Lebesgue almost every $x \in [p, f(c)]$ is dense in $[p, f(c)]$. For every natural number k and $1 \le m \le k$, define $\Xi_{k,m}(x) = 1$ if $x \in [p + (f(c) - p)\frac{m-1}{k}, p + (f(c) - p)\frac{m}{k}]$ and 0 otherwise. The Birkhoff Ergodic Theorem implies that there exists a Borel set $U(k, m) \subset [p, f(c)]$ such that $\mu(U(k, m)) = 1$ and

$$\lim_{n\to\infty} \frac{1}{n} \sum_{i=0}^{n-1} \Xi_{k,m}(f^i(x)) = \int \Xi_{k,m} d\mu > 0 \qquad \text{for all } x \in U(k, m). \tag{4}$$

If $U = \cap_{k,m} U(k, m)$, then $\mu(U) = 1$ and U has full Lebesque measure in $[p, f(c)]$. Since (4) holds for $x \in U$, $k \ge 1$, and $1 \le m \le k$, the orbit of every $x \in U$ is dense in $[p, f(c)]$.

Suppose that $f^2(c) < p$. Let B be the basin of attraction of 0. Since $f(x) < x$ for all $x \in (0, p)$, $[0, p) \subset B$. Since $f^2(c) \in [0, p)$, it follows that $f((f(c), \infty)) \subset [0, p)$. Hence, $[0, p) \cup (f(c), \infty) \subset B$. Therefore, B is an open set in $\mathbf{R}_+$. Define $\Lambda = \mathbf{R}_+ \backslash B$. Λ is compact. Since $f^{-1}(B) \subset B$, it follows that $f(\Lambda) \subseteq \Lambda$. To show that Λ has Lebesgue measure zero, we make use of the following two results.

Theorem 5 (Mañé 1987). *Let I be a compact interval and $g : I \to I$ a C^2 map. If $\Lambda \subset I$ is a compact set satisfying*

1. *$g(\Lambda) \subseteq \Lambda$ and*
2. *Λ contains no critical points, neutrally stable periodic points or linearly stable periodic points,*

then Λ is a hyperbolic repelling set*: there exists $C > 0$ and $\lambda > 1$ such that $|Dg^n(x)| > C\lambda^n$ for all $n \ge 1$ and $x \in \Lambda$.*

The second result is proven in de Melo and van Strein [7, Theorem III.2.6]:

Theorem 6. *Let I be a compact interval and $g : I \to I$ a C^2 map. If $\Lambda \subset I$ is a compact hyperbolic repelling set for g, then Λ has Lebesgue measure zero.*

To use these theorems, choose $\epsilon > 0$ such that $\Lambda \subset (a + 2\epsilon, b - 2\epsilon)$. Let $\rho : \mathbf{R}_+ \to [0, 1]$ be a C^∞ function such that $\rho = 1$ on $(a + 2\epsilon, b - 2\epsilon)$ and $\rho = 0$ on $[0, a + \epsilon) \cup (b - \epsilon, \infty)$. Define $g : \mathbf{R}_+ \to \mathbf{R}$ by $g(x) = \rho(x) f(x)$. Since f restricted to $[a, b]$ is C^3, g is C^3. Since the critical point of f is attracted to the origin, the Modified Singer's Theorem implies that f restricted to Λ has no neutral periodic points or linearly stable periodic points. Since $f = g$ and $Dg = Df$ on Λ, g restricted to Λ contains no critical points, neutral periodic points or linearly stable periodic points. Mañé's Theorem implies that Λ is a hyperbolic repelling set for g. Applying Theorem 6 to g, we get that Λ has Lebesgue measure zero. Hence, the basin of attraction of the origin, $B = \mathbf{R}_+ \backslash \Lambda$, for f has full Lebesgue measure.

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