Dynamical Results of Discrete Pioneer and Climax Species Models

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Abstract

Two types of species, pioneer and climax species, are modeled. When the functions describing the dynamics of these species satisfy certain assumptions, we show limitations of the dynamics within these species, both as independent and as competing species.

1 Introduction

The use of mathematics to describe biology has been on the rise for years. Among the biological phenomenon described by mathematics is the dynamics of both pioneer and climax species. Pioneer species are species that thrive at very small population densities; pine trees in forest ecosystems as well as bobwhite quails are examples of pioneer species. These species are characterized by large growth rates at small densities. Climax species are species that require a minimum threshold for survival. Oak trees are an example of a climax species. In the present project we use difference equations to model populations with non-overlapping generations. We first model a single pioneer species, a single climax species, and then address the dynamics of an interaction of both types of species.

In this paper we show that there are limits to the behavior of the dynamics of both the pioneer species' growth and the growth of the climax species. Formally, we show that there is an upper bound for the number of attracting periodic cycles of population sizes in each model. Informally, one could describe this by stating that the equilibrium population will either be a fixed point or establish an oscillation of populations. We then investigate the dynamics of a special case of the interaction between competing pioneer and climax species.

2 Background

There exist biological populations in which growth takes place at discrete intervals of time, and where the generations of these species are non-overlapping. These species can be modeled using nonlinear difference equations. These discrete models have been used to describe the dynamics of a single species [3], two competing species [5, 4], and predator-prey interactions [6], among a host of other applications. Previous models have included both deterministic and stochastic elements; analytical results have been presented as well as results from computer simulations. The possible dynamics include stable population equilibria, unstable population equilibria, population cycles, and even chaotic behavior.

Different stages of development can be distinguished in the process of biological colonization of a natural environment. The first species to appear in an environment is called a pioneer species. This species is characterized by high reproduction in low population densities, with the reproduction eventually decreasing as population density increases. Examples of pioneer species include alder, big leaf maple, poplar, birch and some pine trees [4].

These species later give way to climax species, which thrive in higher population densities once some minimum density for survival is achieved. An example of a climax species is oak trees.

In this paper we model both pioneer and climax species with Kolmogorov type difference equations, which are equations of the form $x(n+1) = f(x(n)) = x(n) \cdot g(x(n))$, where $g(x)$ is the per-capita growth function.

3 Model Derivation

- A *discrete model* used to describe the population growth of a discretely reproducing species is a difference equation

$$x_{n+1} = x_n \cdot g(x_n).$$

The pioneer species is a species with per-capita growth function $g(x)$, where $g : [0, \infty) \rightarrow [0, \infty)$ and satisfies the following conditions:

1. g a C^3 function;
2. $g(0) > 1$;
3. $\lim_{x \to \infty} g(x) = 0$.

The climax species is a species with per-capita growth function $g(x)$, where $g : [0, \infty) \rightarrow [0, \infty)$ and satisfies the following conditions:

1. g a C^3 function;
2. $g(0) < 1$;
3. $\lim_{x \to \infty} g(x) = 0$;
4. $\exists$ 2 non-trivial fixed points.

- A *fixed point* ψ of a function f satisfies the condition

$$f(\psi) = \psi.$$

A *stable fixed point* satisfies $|f'(\psi)| < 1$. If ψ exists but is not unique, we define Ψ to be the maximum fixed point.

- A *critical point* c of a function f satisfies the condition

$$f'(c) = 0.$$

- A *Schwarzian derivative* of a function f denoted by $Sf(x)$ is defined as

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

- An *orbit* of a point x is the set

$$\{x, f(x), f^2(x), f^2(x), \dots\}$$

- A *periodic point with periodic* n is a point which satisfies $f^n(x) = x$ and $f^i(x) \neq f^j(x)$ for $i, j < n$ and $i \neq j$.

- A *periodic orbit* is the set $\{x, f(x), f^2(x), \ldots, f^{n-1}(x)\}$ with all different elements and $f^n(x) = x$.

- Let $E = \{x, f(x), f^2(x), \ldots, f^{n-1}(x)\}$. Then an *attracting periodic orbit* is a periodic orbit such that for all x in the domain

$$\lim_{m\to\infty} f^m(x) \to E.$$

- A set I is *invariant* under a function f if $f(I) \subset I$.

- $W(p)$ is defined as the maximal interval about an attracting periodic point p in which $\lim\limits_{m\to\infty} f^m(x) = p$ for all points $x \in W(p)$.

4 The Pioneer Species

We begin with the analysis of the pioneer species (see Figure 1 for an example); the climax species will follow. We present Singer's Theorem without proof (proof shown in Devaney [1]); it is this theorem upon which we will rely heavily for the present project.

Singer's Theorem. *Suppose $Sf < 0$ ($Sf(x) = -\infty$ is allowed). Suppose f has n critical points. Then f has at most $n + 2$ attracting periodic points.*

Singer's Theorem asserts that any function with n critical points will have at most $n + 2$ attracting periodic orbits, with n possible attracting periodic points resulting from the existence of the n critical points, and the 2 remaining possible attracting periodic points resulting from the endpoints of W in the case that either or both of the endpoints of the invariant set $W(p)$ are infinite. What remains to be shown to eliminate these 2 possibilities is that the endpoints of $W(p)$ are finite.

We are presently focusing on pioneer functions. Because of the conditions they satisfy, the theorem will further limit the existence of attracting periodic orbits to at most n, instead of $n + 2$.

In order to clarify the proof, we begin with the case $n = 1$ with the simplification that $g(x)$ is strictly decreasing, as shown below.

Theorem 1. *Any pioneer growth function $f(x)$ with $Sf(x) < 0$ with one critical point c has at most one attracting periodic orbit.*

Proof. We first present the following lemmas:

Lemma 1. *In the model $f(x) = x \cdot g(x)$ with $g(x)$ satisfying the conditions $g(0) > 1$ and $\lim\limits_{x\to\infty} g(x) = 0$, 0 and ∞ are repelling.*

Remark. This prevents the detrimental effects of population explosion.

Proof. Recalling the definition for the stability of a fixed point, we need to prove that $|f'(0)| > 1$ for zero to be repelling. Since $f'(x) = g(x) + x \cdot g'(x)$, then $f'(0) = g(0) > 1$; hence 0 is repelling. We have that $\lim_{x \to \infty} g(x) = 0$ so $\forall \epsilon > 0$, $\exists M$ such that if $x > M$, then $g(x) < \epsilon$. Let $\epsilon < 1$, we get that $g(x) < 1$ and multiplying by x both sides $f(x) < x$. This implies that the sequence $\{f(x), f^2(x), \dots\}$ is strictly decreasing after M, so infinity cannot be an attracting point. QED

Lemma 2. *The pioneer map $f(x) = x \cdot g(x)$ (with $g(x)$ strictly decreasing) has a unique positive fixed point ψ. In addition, if $0 < x < \psi$, then $f(x) > x$. If $x > \psi$, then $f(x) < x$.*

Proof. To find the fixed points, we find all points which satisfy $x \cdot g(x) = x$. We see that zero is a fixed point; to find the positive fixed points it remains to solve $g(x) = 1$.

As $\lim_{x \to \infty} g(x) = 0$, we have that for all $\epsilon > 0$, there exists M such that for $x > M$ implies $|g(x)| < \epsilon$. Then choose $\epsilon = \frac{1}{2}$. As $g(x)$ is continuous with $g(0) > 1$, we see that there must exists ψ in $(0, M)$ such that $g(\psi) = 1$ by the Intermediate Value Theorem. As $g(x)$ is decreasing, we see that ψ is unique.

We have show $g(\psi) = 1$. As g is decreasing, we see that for $0 < x < \psi$, $g(x) > g(\psi) = 1$. Multiplying by x, we see that $x \cdot g(x) > x$, and therefore $f(x) > x$. A similar approach yields $f(x) < x$ for $x > \psi$. QED

Lemma 3. *$I \equiv f([0, \psi])$ is a compact invariant set for the pioneer map $f(x) = x \cdot g(x)$, with $g(x)$ a strictly decreasing function, into which every point enters and stays forever, or at least limits on it.*

Proof. As f is continuous and $[0, \psi]$ is compact, we see that $f([0, \psi])$ is compact. We will prove that I is an invariant set. If there exists $q \in [0, \psi]$ such that $f(q) > \psi$, we first see that $f(q) \in f([0, \psi])$. We then see by Lemma 2 that $f^2(q) < f(q)$, and hence $f^2(q) \in I$. For $r \in I$, with $f(r) < \psi$, we see that $f(r) \in I$.

To see that every point enters I or limits on it, we see that for any $x > \psi$, $f(x) < x$ by Lemma 1. If the orbit does not contain a point in I, then the orbit is strictly decreasing and by assumption is bounded below by the fixed point ψ, hence converging to ψ. If the orbit contains a point in I, then as I is an invariant set, we are done. QED

Corollary 1. *There is no population explosion in the pioneer species.*

Proof. For populations inside I, the population remains in I forever under iteration. And as Lemma 2 shows, populations greater than I tend to the invariant set I; hence the population is always bounded. QED

Lemma 4. *Let p be an attracting periodic point of period m. Then there is an open interval U about p such that if $x \in U$, then $\lim_{n \to \infty} f^n(x) = p$.*

Proof. As p is attracting, we have that $|f'(p)| < 1$. As f is continuously differentiable, we see that $\exists\, \epsilon > 0$ such that $|f'(x)| < A < 1$ for $x \in [p - \epsilon, p + \epsilon]$. Applying the Mean Value Theorem shows that $|f(x) - p| = |f(x) - f(p)| \leq A|x - p|$ where $|x - p| \leq \epsilon$.

We then conclude that $f(x)$ is contained in $[p - \epsilon, p + \epsilon]$ and is closer to p than x. Similarly we get that $|f^n(x) - p| \leq A^n|x - p|$ so that $\lim_{n\to\infty} f^n(x) = p$. QED

Lemma 5. *If $Sf(x) < 0$ then f' cannot have a positive local minimum or a negative local maximum.*

Proof. Let c be a critical point of $f'(x)$, then $f''(c) = 0$. It follows from $Sf(x) < 0$ that $f'''(c)/f'(c) < 0$. So the signs of $f'(c)$ and $f'''(c)$ are opposite. QED

Lemma 6. *If $f(x)$ has finitely many critical points, then so does $f^m(x)$.*

Proof. The proof is shown in [1]. QED

Proof of Theorem 1. We now proceed with the proof of Theorem 1. Assume $\exists$ attracting periodic point p of period m in the pioneer map f. If we define $W(p)$ as the maximum interval containing p such that it contains all points that tend asymptotically to p under f^m, clearly $W(p) \subset I(\psi)$. By Lemma 4 we get that $W(p)$ is an open interval, and $f^m(W(p)) \subset W(p)$. First we will prove the case where p is a fixed point. Recall that $W(p)$ is the maximal set, and that $f(W(p)) \subset W(p)$. Then, if $W(p) = (l, r)$, as f is continuous it preserves its endpoints. Since $W(p) \subset I(p)$, which is finite, then $W(p)$ is also finite. We then have three cases:

1. $f(l) = l$ and $f(r) = r$.

2. $f(l) = r$ and $f(r) = l$.

3. $f(r) = f(l)$.

For the first case, applying the Mean Value Theorem for f shows that there exist a and b inside (l, r) such that $p \in (a, b)$ and $f'(a) = f'(b) = 1$. Since p is attracting $f'(p) < 1$ and by Lemma 5 f' cannot have a positive local minimum; thus there should exist a critical point in the interval (a, b). For the second case, the same result follows if we instead consider f^2. For the last case, there must exist a minimum or maximum for f in (l, r), hence there also exists a critical point in $W(p)$.

If p is periodic of period m, we define $g = f^m$. Then, by Lemma 5, the above argument establishes a critical point in $W(p)$. WE conclude that for every periodic orbit there has to be at least one critical point. QED

We now present an analogous theorem for f with any finite number of fixed points, based on the proof for the special case, where f contained a unique fixed point.

Theorem 2. *Any pioneer species model $f(x)$ with $Sf(x) < 0$ with n critical points has at most n attracting periodic orbits.*

The proof of Theorem 2 relies on the following lemma:

Lemma 7. *If $\lim_{x \to \infty} g(x) = 0$, then $f(x) < x \; \forall x > \Psi$.*

Proof. Ψ is, be definition, the largest x such that $f(x) = x$; thus $g(\Psi) = 1$. Then as $\lim_{x \to \infty} g(x) = 0$, $\forall x > \Psi \; g(x) < 1$. Then if we multiply both sides by x, we see that $f(x) < x$. QED

Theorem 2 generalizes to include any number of fixed points. Since $f(x)$ is bounded then Ψ, defined as the maximum of the fixed points, will be a finite number. We proceed in a manner similar to the proof of Theorem 1 but develop the invariant set as below:

Lemma 8. *$I \equiv f([0, \Psi])$ is invariant under the pioneer map $f(x)$, to which all points enter or limit on under iteration of $f(x)$.*

Proof. We first need to establish that I is invariant. Choosing any point $\gamma \in I$, we see that $f(\gamma) \in f(I_n)$. If $f(\gamma) < \Psi$, then $f(\gamma)$ is clearly in I. If $f(\gamma) > \Psi$, then as Lemma 7 establishes, $f^2(x) < f(x)$ and $f^2(x) \in I$.

It remains to show that all points enter or limit upon I under iteration of $f(x)$. As Lemma 7 establishes, for all $x > \Psi$, $f(x) < x$. There are then two cases. The first case is that the orbit of x never enters I. In this case, as the orbit is strictly decreasing and bounded below by I, we see that the orbit converges to I. In the case that x enters I for some iteration of $f(x)$, we are done. QED

We are now in a position to prove Theorem 2.

Proof of Theorem 2. Recalling Singer's theorem, it asserts the existence of at most $n + 2$ attracting periodic orbits. We have shown in the special case $n = 1$ that the number of periodic orbits reduces to n by constructing a finite interval $W(p)$. If we define $\wp \equiv \{p_1, p_2, \ldots, p_n\}$, where p_i are fixed points of $f(x)$, then $W(\wp)$ is the maximal interval containing $p \in \wp$ such that it contains all points that tend asymptotically to $p \in \wp$ under f^m. We now establish $W(\wp) = f([0, \Psi])$. Recalling that the crux of establishing $W(p)$ in the $n = 1$ case was showing that for $x > p$, $f(x) < x$, we see that Lemma 7 establishes the required condition; thus $W(\wp)$ is finite. QED

4.1 Application of Theorem 2

Example 1 (Pioneer Example). *Ricker's Model* is defined as

$$f(x) = x \cdot e^{r-kx}$$

with $r > 0$, $k > 0$ (see Figure 1 for an example). To show it satisfies our definition of pioneer, there are two requirements. The first is satisfied as follows: There exists a unique critical point at $x = \frac{1}{k}$. In this case $g(x) = e^{r-kx}$, so $g(0) = e^r > 1$.

The second criterion is satisfied as we see that $\lim_{x\to\infty} g(x) = 0$. We further note that $g(x)$ is strictly decreasing.

We see that the Schwarzian derivative of this function is $-\frac{k^2((k\cdot x-2)^2+2)}{2(1-k\cdot x)^2} < 0$. Hence, by the theorem it should only have one attracting periodic orbit.

5 The Climax Species

We now discuss the climax species (examples shown in Figure 2). Recall that the climax species are characterized as species that require some minimum population to insure survival, but which are more likely to survive at high densities than the pioneer species.

There are some subtle points associated with the climax species. Note the propositions below:

Proposition 1. *For the climax species with $Sf(y) < 0$ zero is repelling.*

Proof. As $g(0) < 1$, there exists some finite interval $(0, \epsilon)$ such that $f(y) < y$ for all $y \in (0, \epsilon)$. Thus, for $f(y) = y$ as required for the existence of a non zero fixed point ψ^1, and as $f(y)$ is continuous, we require that $f'(\psi^1) \geq 1$. Hence ψ^1 is not attracting. The negativeness of the Schwarzian precludes the possibility of an open interval J containing ψ^1 such that $f'(y) = 1$ for all $y \in J$; thus, since f is continuous, there must exist some $\epsilon > 0$ such that $f(y) > y$ for any y in the interval $(\psi^1, \psi^1 + \epsilon)$.

It is easy to see that $f(y) > y$ for all $y \in (\psi, \psi^1 + \epsilon) \Rightarrow g(x) > 1 \; \forall y \in (\psi, \psi^1 + \epsilon)$. Now as $\lim_{y\to\infty} g(y) = 0$, for all $\alpha > 0$, there must exist M such that if $y > M$, then $g(x) < \alpha$. Choosing $\alpha < 1$ and using the Intermediate Value Theorem asserts the existence of a second fixed point ψ^2, where $g(\psi^2) = 1$. QED

Proposition 2. *For all points $y \in (0, \psi^1)$ in the climax map $f(y)$, $\lim_{m\to\infty} f^m(x) = 0$.*

Proof. As $f(y) < y$ for all points $y \in (0, \psi^1)$, we see that $\{f^m(y)\}$ is strictly decreasing. And, as $\{f^m(y)\}$ is bounded below by zero, we see that $\{f^m(y)\}$ converges to zero as required. QED

Having establised some familiarity with the climax species, we are then ready to establish the following theorem:

Theorem 3. *Any climax growth function $f(y)$ with $Sf(y) < 0$ with $m \geq 2$ fixed points and n critical points has at most n attracting periodic orbits.*

Proof. This proof will follow nearly directly from the proof for the pioneer case, but some details require attention. We will present the following lemmas without proof (proofs similar to proofs for pioneer species and are easily seen):

Lemma 9. *For the climax species model $y(n+1) = y(n) \cdot g(y(n))$ with m fixed points, $f(y) < y$ for all points $y > \Psi$.*

Lemma 10. *$I \equiv f([0, \Psi])$ is a compact invariant set for the climax map $f(y(n)) = y(n) \cdot g(y(n))$, with $g(y(n)) < y(n)\ \forall y(n) > \Psi$ into which every point enters and stays forever, or at least limits on it.*

Corollary 2. *There is no population explosion in the climax species.*

We now proceed with the proof for Theorem 3. We again recall that Singer's Theorem asserts that the model will have at most $n+2$ attracting periodic points. The crux of proving that it is further limited to having at most $n+2$ attracting periodic points for Theorem 2 was establishing a finite invariant set $I(\wp)$ about the set of fixed points $\wp \equiv \{\psi_1, \psi_2, \ldots, \psi_m\}$, which every point in our domain will enter or at least limit on it under iteration of f. This $I(\wp) \equiv W(p)$ for Theorem 2. The case is the same for the present theorem; this is shown in Lemma 10. Having constructed our finite $I(p)$, we know that there exists at most n attracting periodic points for our climax species function f by Singer's Theorem. QED

5.1 Application of Theorem 3

Example 2 (Climax Example). Consider the climax model

$$y(n) = f(y(n)) = (y(n))^2 \cdot e^{p-x}$$

with $p > 0$. We see that $g(0) = 0 \cdot e^p < 1$, and that $\lim_{y \to \infty} g(y) = 0$ as required by our definition of a climax species function. We note that there are two non-zero fixed points for the case $p = 1.5$ (see Figure 2).

The Schwarzian derivative $Sf(y) = -\frac{12+(x^2-2x)(x^2-fx+12)}{2x^2(x-2)^2}$ is a bit elusive when we try to assert negativeness analytically. We turn to plotting the Schwarzian for all values $p > 0$ and for all values $x > 0$. We show typical plots of the Schwarzian in Figure 3; it is indeed negative. Thus, Theorem 3 asserts that this model will have at most 2 attracting periodic points.

6 A Pioneer-Climax Interaction

If we consider the interaction of a pioneer species and a climax species, each reproducing in non-overlapping generations, we may obtain a system of difference equations:

$$x(n+1) = x(n) \cdot g_1(x(n) + y(n));$$
$$y(n+1) = y(n) \cdot g_2(x(n) + y(n))$$

where the pioneer species is governed by $x(n)$ and the climax species is governed by $y(n)$.

If we assume that $y(n)$ has only two fixed points, we can see that Figures 1 and 2 are illustrations of our $x(n)$ and our $y(n)$. We are then able to assert the following theorem:

Theorem 4. *Consider the pioneer-climax model*

$$x(n+1) = f_1(x(n)) = x(n) \cdot g_1(x(n) + y(n))$$
$$y(n+1) = f_2(y(n)) = y(n) \cdot g_2(x(n) + y(n))$$

with $Sf_1(x) < 0$, $Sf_2(y) < 0$, *one non-zero fixed point* ψ_x *for the pioneer map* $f_1(x)$ *and two non-zero fixed points* ψ_y^1 *and* ψ_y^2 *of our climax map* $f_2(y)$, *and the invariant set* I_x *of* $f_1(x)$ *is defined as* $[0, \beta_x]$. *For the special case* $\beta_x < \psi_y^1 < \psi_y^2$, *the set* $I_{xy} \equiv \{(x, y) \mid x + y < \psi_y^1\}$ *is invariant, and* $\lim_{m \to \infty} f^m(y) = 0$ *(see Figure 4).*

Proof. We first need to show that any point $(x, y) \in I_{xy}$ remains in I_{xy} under iteration of the model. We can investigate the dynamics of each equation independently for each time step.

For $(x, y) \in I_{xy}$, we see that $x + y < \psi_x < \psi_y^1$, so that the change in the species $y(n)$ matches that of the independent climax model for $y < \psi_y^1$. As this is decreasing by Proposition 2, we see that $y(n+1) < y(n) \; \forall \, (x, y) \in I_{xy}$, hence $y(n+1)$ remains in I_{xy}.

We see that for any $(x, y) \in I_{xy}$, $x(n)$ changes like the independent pioneer model where $x < \psi_x$. As this is an invariant set by Lemma 3, $x(n+1)$ remains in I_{xy}. Hence we have shown invariance in both the pioneer and the climax species, and the set is invariant.

Now $\{f_2^m(y)\}$ is strictly decreasing (Proposition 2). As this set is bounded below by $y = 0$, we see that $y(n)$ converges to $y = 0$ under iteration. QED

We are now prepared to present our final theorem.

Theorem 5. *Consider the pioneer-climax model*

$$x(n+1) = f_1(x(n)) = x(n) \cdot g_1(x(n) + y(n))$$
$$y(n+1) = f_2(y(n)) = y(n) \cdot g_2(x(n) + y(n))$$

where $Sf_1(x) < 0$, $Sf_2(y) < 0$, *with* β_x *defined as the endpoint of the invariant set* I_x, ψ_y^1 *and* ψ_y^2 *the non-zero fixed points of* $f_2(y)$ *satisfying* $\beta_x < \psi_y^1 < \psi_y^2$. *For any initial condition* $(x, y) \in (0, \infty) \times (0, \infty)$, *there will be one of two results:*

1. $\lim_{n\to\infty} f_1^n(x) = 0$; *or*

2. $\lim_{n\to\infty} f_2^n(y) = 0$.

Proof. Theorem 4 asserts that for any $(x, y) \in I_{xy}$, $\lim_{n\to\infty} f_2^n(y) = 0$; thus we need only concern ourselves with $(x, y) \notin I_{xy}$.

We need only address the pioneer species to see this result. We see that for any $(x, y) \in I_{xy}$, i.e. $x + y > \beta_x$, $x(n)$ changes like the independent pioneer model for $x > \beta_x$. As Lemma 7 establishes, for all $x > \Psi$, $g(x) < x$, which implies that $f(x)$ is strictly decreasing. We address two possibilities: either (x, y) enters the invariant set I_{xy} due to the decreasing iterations of $f_1(x)$ or it does not enter the invariant set I_{xy}. If (x, y) enters the invariant set under iteration, we see that $\lim_{n\to\infty} f_2^n(y) = 0$. If (x, y) does not enter I_{xy} under iteration of $f_1(x)$, then as $f_1(x)$ is strictly decreasing and bounded below be zero, we see that $\lim_{n\to\infty} f_1^n(x) = 0$. QED

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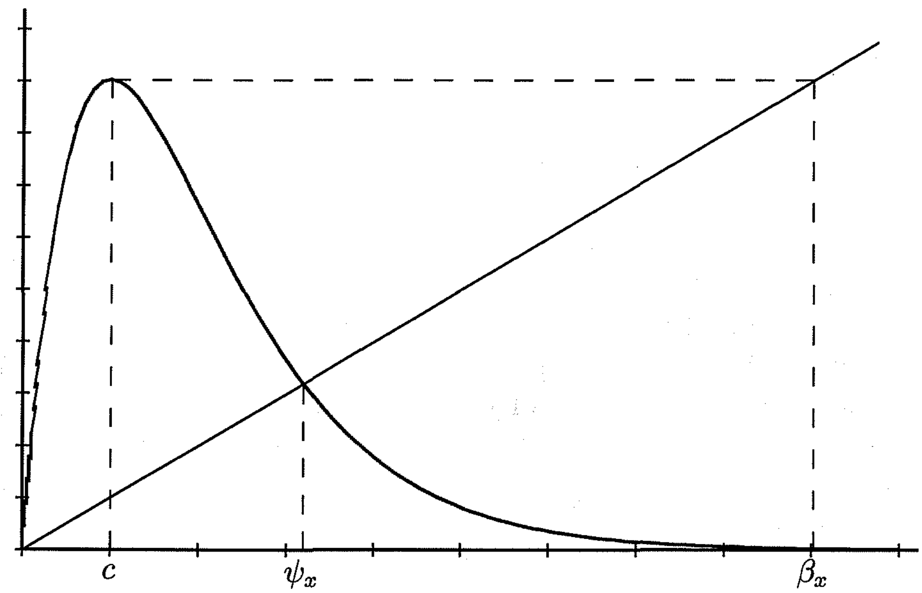

Figure 1: An illustration of the pioneer species model $f(x) = x \cdot e^{r-kx}$. Known as Ricker's Model. we see that in this choice of parameters, the endpoint β_x of the invariant set I_x happens to be $f(c)$, where c is the critical point.

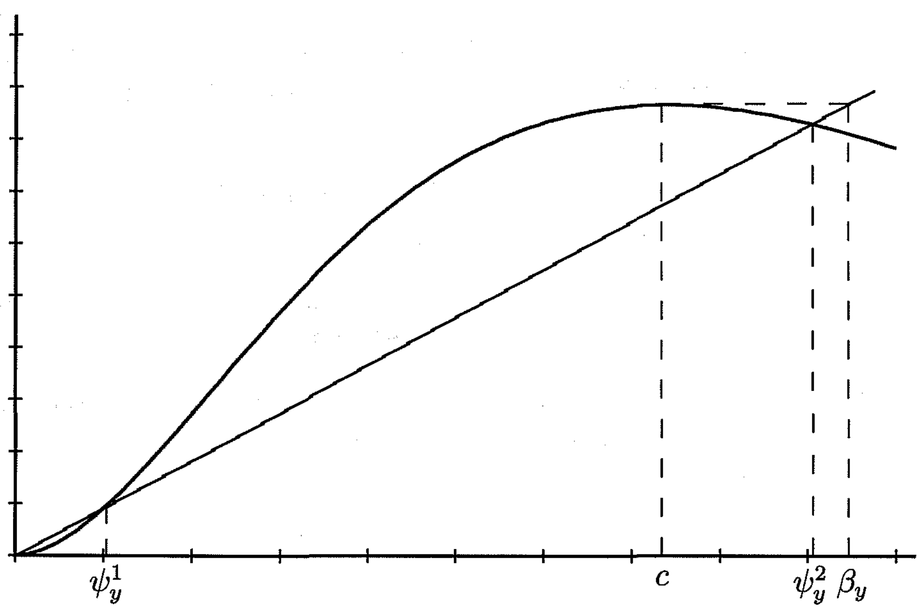

Figure 2: An illustration of the climax species model $f(y) = y^2 \cdot e^{r-ky}$. We see again that the endpoint β_y of the invariant set in this case ($r = 1.5$, $k = 1$) is $f(c)$.

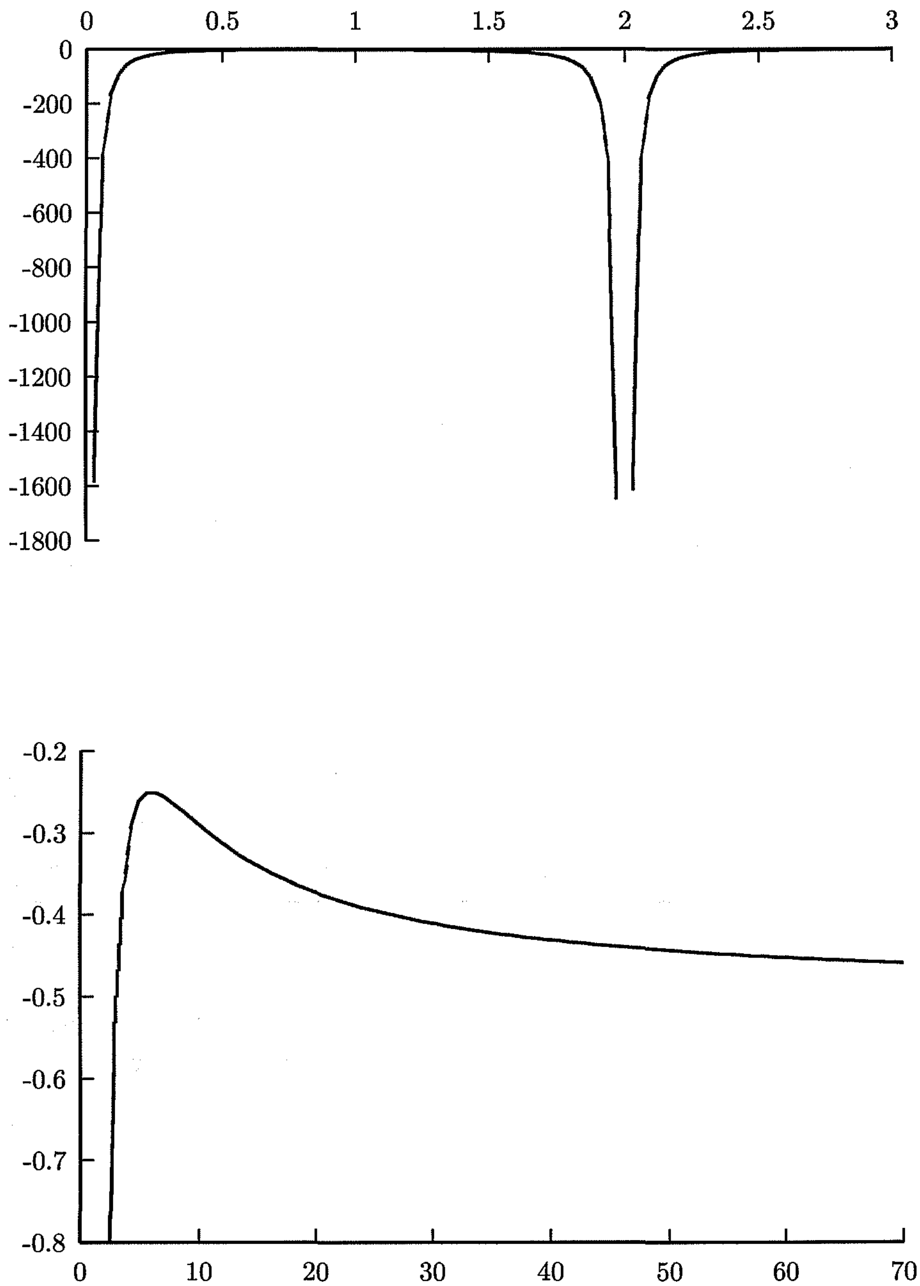

Figure 3: A typical plot of the Schwarzian derivative of the climax species function $f(y) = y^2 \cdot e^{p-qx}$. The Schwarzian was found to be negative for all values $p > 0$, $q > 0$ and for all values x.

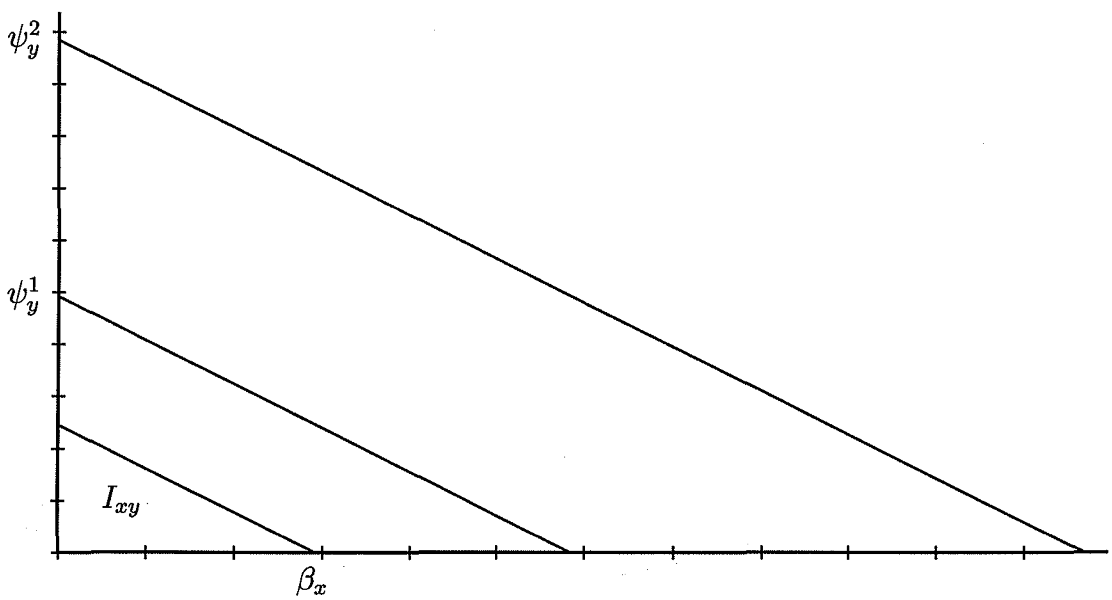

Figure 4: The xy-plane, where x is the pioneer species with negative Schwarzian and y is the climax species. The region labeled $I_{xy} = \{(x, y) \mid x + y < \beta_x\}$ (where β_x is the endpoint of the invariant set I_x) is shown to be invariant.