



## Global asymptotic stability of density dependent integral population projection models

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### ABSTRACT

Many stage-structured density dependent populations with a continuum of stages can be naturally modeled using nonlinear integral projection models. In this paper, we study a trichotomy of global stability result for a class of density dependent systems which include a Platte thistle model. Specifically, we identify those systems parameters for which zero is globally asymptotically stable, parameters for which there is a positive asymptotically stable equilibrium, and parameters for which there is no asymptotically stable equilibrium.

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### 1. Introduction

Stage structured populations are often described by discrete-time population projection models. We will describe a class of models which captures two essential biological processes – survival/growth and fecundity – that lead to a mathematical structure which can be exploited to prove global stability of the population modeled. To describe this model, we start with a general linear model

$$x_{t+1} = Px_t,$$

where  $x_t$  is the stage-structured population at time  $t \in \mathbb{N}$ , and  $P$  is a linear projection operator. The population vector  $x_t$  is in a vector space  $X$ . For instance, in a matrix projection model (see Caswell, 2001),  $X = \mathbb{R}^n$ . In order to analyze integral projection models (see Briggs et al., 2010; Childs et al., 2003; Easterling, 1998; Easterling et al., 2000; Ellner and Rees, 2006; Rees and Rose, 2002; Rose et al., 2005), we need to consider more general vector spaces; mathematical details are given later in this section. In this context, it is natural to then assume that  $P$  can be decomposed into a sum of a “survival operator”  $A$  and a “fecundity operator”  $F$ . In this paper, we will consider fecundity operators which can be written as  $bc^T$ , where  $b \in X$  and  $c^T$  is a functional on  $X$ . A functional on  $X$  is an operator from  $X$  into scalars; when  $X = \mathbb{R}^n$ , we think of vectors in  $X$  as column vectors, and functionals on

$X$  as row vectors. The fecundity structure  $F = bc^T$  is common in structured models of single-populations because  $c^T x_t$  can be interpreted as the number of offspring produced by the population  $x_t$ , and this offspring will be distributed into the stage classes with a distribution described by  $b$ . For instance, in the case of an integral projection model describing plant populations, this decomposition describes a situation where the number of seeds produced at time  $t$  is  $c^T x_t$ , and  $b$  describes the size distribution of the plants resulting from these seeds in the next time period.

In this plant population example, we can also include an average recruitment probability  $p_e$ , which represents the probability of a seed becoming a seedling in the following year. The resulting *density independent* (i.e. linear) system is then

$$x_{t+1} = Ax_t + p_e bc^T x_t. \quad (1.1)$$

Now consider a situation where the recruitment probability  $p_e$  is *density dependent*, i.e. it is a nonlinear function of the number of seeds. In particular, we expect that the recruitment probability will decrease with seed density. This type of density dependence has been seen in numerous plant species, see Tenhumberg et al. (in preparation), Rose et al. (2005) and Pardini et al. (2009) and the references therein. We write this density dependence as

$$(p_e)_t = g(c^T x_t),$$

where  $g$  is typically non-negative and decreasing. The resulting system becomes

$$x_{t+1} = Ax_t + bf(c^T x_t), \quad f(y) := yg(y). \quad (1.2)$$

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For natural choices of  $g$  motivated by ecological considerations, it has been observed in simulation studies that solutions of (1.2) converge to a limiting stable stage structure  $v$  as  $t$  goes to infinity, see for instance Rose et al. (2005). This apparently global asymptotic stability is in contrast with the linear model (1.1), where there is a limiting asymptotic growth rate, and hence no asymptotic population unless the asymptotic growth rate is 1.

Two papers that are closely related to our work are Hirsch and Smith (2005) and Krause and Ranft (1992). In Theorem 6.3 of Hirsch and Smith (2005), a trichotomy of stability results are given for general abstract monotone maps in a Banach space. These extend analogous results in Krause and Ranft (1992) for systems evolving on  $\mathbb{R}^n$ . However, for many ecological applications, the results in Hirsch and Smith (2005) and Krause and Ranft (1992) cannot be applied. This is because of the types of vector spaces and the types of vectors  $b$  and functionals  $c^T$  that are likely to appear in the applications we consider. This is explained at the end of Section 2. Our proofs are constructive, whereas the results in Hirsch and Smith (2005) and Krause and Ranft (1992) are existence proofs which do not show how to find the global asymptotic limit. By exploiting the specific structure in (1.2), we can characterize the trichotomy via computable formulas. Furthermore, our approach introduces nonlinear stability tools from control theory (Vidyasagar, 1993) to the modeling and analysis of density dependent population models. The formulas we obtain are easy to use, and can be readily adapted to other studies. For instance, in Eager et al. (in press), the asymptotic formula is used to make sure that two models have the same asymptotic population, so that we can accurately compare the transient dynamics.

The paper is organized as follows: In Section 2, we give the abstract formulation for this problem. In Section 3, we prove global asymptotic stability of a general class of systems of the form (1.2) in a Banach space  $X$ . In Section 4, we consider integral projection models (IPMs) which fit the abstract framework (1.2). A class of IPMs is introduced in Easterling (1998), Easterling et al. (2000) and Ellner and Rees (2006). Such models have been developed in Childs et al. (2003, 2004), Easterling (1998), Easterling et al. (2000), Ellner and Rees (2006, 2007), Rees and Rose (2002) and Rose et al. (2005). In Briggs et al. (2010), Easterling (1998) and Easterling et al. (2000) it is shown how to construct such an integral projection model, using continuous stage classes and discrete time. The types of density dependence we are considering can be found in Ellner and Rees (2006), Rose et al. (2005), Tenhumberg et al. (in preparation) and Zetlaoui et al. (2008) (the latter is a matrix model rather than an integral model). We discuss the integral projection model for the Platte thistle in Rose et al. (2005), which we will show to be of the form (1.2). By applying Corollary 4.1 (the IPM version of the more abstract Theorem 3.3), we prove that the global asymptotic stability seen (via simulation) in Rose et al. (2005) does indeed hold.

## 2. Abstract formulation

Let  $X$  be a Banach space with norm  $\|\cdot\|$ . The solutions will evolve in  $X$ , that is,  $x_t$  is in  $X$  for all  $t$ . In an integral projection model,  $X = L^1(\Omega)$  for some set of stages  $\Omega$ . We wish to work with nonnegative vectors in  $X$  and nonnegative operators on  $X$ . We will follow Krasnosel'skij et al. (1989) for this. Let  $K \subset X$  be a reproducing cone, see Krasnosel'skij et al. (1989, Section 1.5). For future reference, we note that  $K$  is reproducing if every element  $x \in X$  can be written as  $x = x^+ - x^-$  for  $x^+, x^- \in K$ . The cone  $K$  induces a partial order “ $\geq$ ” on  $X$ , where  $x \geq y$  means  $x - y \in K$ . If  $x \geq 0$ , i.e.  $x$  is in  $K$ , we say that  $x$  is a *non-negative* vector. An example of a reproducing cone in  $\mathbb{R}^n$  is  $K = \{[x_1, x_2, \dots, x_n]^T \mid x_j \geq 0 \text{ for } j = 1, \dots, n\}$ . An example of a reproducing cone in

$L^1[\alpha, \beta]$  is  $\{f \in L^1[\alpha, \beta] \mid f(x) \geq 0 \text{ a.e.}\}$ . In both these cases, the definition of a non-negative vector coincides with intuition. In Krasnosel'skij et al. (1989), such a vector is called “positive”, but this is not consistent with the cases where  $X = \mathbb{R}^n$  or  $X = L^1[\alpha, \beta]$ , so we say in this paper that such a vector is “non-negative”.

In Krasnosel'skij et al. (1989, Section 2.2), an operator on  $X$  is called a *positive operator* if it maps non-negative vectors to non-negative vectors. We will call such an operator *non-negative*; hence when  $X = \mathbb{R}^n$ , an  $n \times n$  matrix  $M$  represents a non-negative operator on  $\mathbb{R}^n$  if and only if all of its entries are non-negative.

We consider a system defined on  $X$  of the form

$$x_{t+1} = Ax_t + by_t g(y_t), \quad y_t = c^T x_t. \quad (2.1)$$

For our three main results, we need some hypotheses which are natural for applications to structured population dynamics. First, we state conditions on  $(A, b, c)$ .

- (A1)  $A \in \mathcal{L}(X)$  is a non-negative operator with spectral radius  $r(A) < 1$ ;
- (A2)  $b$  is a non-negative vector;
- (A3)  $c^T : X \rightarrow \mathbb{R}$  is a non-negative functional, i.e.

$$c^T x \geq 0, \quad \text{for all } x \geq 0.$$

Associated with (2.1) is the controlled, observed system:

$$x_{t+1} = Ax_t + bu_t, \quad y_t = c^T x_t, \quad (2.2)$$

with input  $u_t$  and output  $y_t$ . We note that by induction, if  $x_0$  is in the cone  $K$ , then  $x_t$  is in  $K$  and  $y_t \geq 0$  for all  $t \in \mathbb{N}$ . Central to our results is the concept of *stability radius* of  $(A, b, c)$ , see for example Hinrichsen and Pritchard (2005). Assume that  $r(A) < 1$ . The stability radius of (2.2), is the smallest positive number  $p_e^*$  such that if  $u_t = p_e^* y_t$ , then the resulting closed-loop system (2.2) is not asymptotically stable. As  $A$ ,  $b$  and  $c$  are non-negative,  $p_e^*$  is the smallest positive number such that  $r(A + p_e^* bc^T) = 1$ . It is proved in Hinrichsen and Pritchard (2005) that the stability radius is given by the formula

$$p_e^* = \frac{1}{c^T(I - A)^{-1}b}, \quad (2.3)$$

with the convention that  $p_e^* = \infty$  if  $c^T(I - A)^{-1}b = 0$ . In fact, it is easy to see that  $r(A + pbc^T)$  is nondecreasing in  $p$ , and that  $A + pbc^T$  has an eigenvalue 1 if, and only if,  $p = p_e^*$ . Hence  $r(A + pbc^T) > 1$  for  $p > p_e^*$  and  $r(A + pbc^T) < 1$  for  $p < p_e^*$ . Note that  $p_e^*$  is defined by the linear data  $A$ ,  $b$  and  $c$ .

In the Introduction, we mentioned that the papers Hirsch and Smith (2005) and Krause and Ranft (1992) contain very general global stability results, but that these results do not apply to many of the ecologically motivated systems we consider. We focus on Theorem 6.3 in Hirsch and Smith (2005), since that result is closely related to the results in this paper. The operators discussed in Theorem 6.3 are very general, and do not require the special structure that we consider in this paper. However, the nonnegative cone  $K$  in Theorem 6.3 is required to have a nonempty interior, which can be restrictive. In particular,  $L^1[\alpha, \beta]$  is a standard space for integral projection models (see Easterling, 1998; Easterling et al., 2000; Ellner and Rees, 2006; Rees and Rose, 2002), and the natural positive cone  $K = \{f \in L^1[\alpha, \beta] \mid f(x) \geq 0 \text{ a.e.}\}$  in  $L^1[\alpha, \beta]$  has an empty interior (since every element in  $K$  is arbitrarily close to an element in  $L^1[\alpha, \beta]$  not in  $K$ ). Furthermore, the type of operators we consider in this paper typically does not satisfy the conditions in Theorem 6.3 either, even in the finite dimensional case. Roughly speaking,  $b$  represents the stage distribution of newborns after one time step, and is likely to be zero for large stages. Hence  $b$  will not be a positive vector. Similarly, the number of offspring  $c^T x_t$  might be zero for some populations  $x_t$ . The results

in Theorem 6.3 in Hirsch and Smith (2005) (the result that is most related to this paper) require the nonlinear operator on the right side of (1.2) (which we will call  $T$ ) to be such that  $T^k$  is *strongly sublinear* for some positive integer  $k$ ; the finite dimensional results in Corollary 1 in Krause and Ranft (1992) require similar conditions. If  $k = 1$ , these conditions will require  $b$  to be positive. If  $k > 1$  in the matrix case, this will typically not happen when  $b$  is not positive and  $A$  is a survival (and hence typically reducible) matrix. If  $k > 1$  in the Banach space case, it will be very difficult to check conditions on the nonlinear operator  $T^k$ .

### 3. Global stability results

We present three global stability results for the density dependent system (2.1) which together form a trichotomy of stability (see Hirsch and Smith, 2005, Krause and Ranft, 1992 for a general approach to this problem): Theorem 3.1 shows that if  $p_e^*$  exceeds a certain threshold value determined by the nonlinear recruitment  $g$ , then the zero state is globally asymptotically stable, i.e. the population dies out. Theorem 3.2 shows that if  $p_e^*$  is below a lower threshold determined by  $g$ , then the population can grow without bound. In the case where  $p_e^*$  is between these two thresholds, Theorem 3.3 shows that the population model (2.1) has a globally asymptotically stable, strictly positive equilibrium vector. All convergence discussed in this paper is convergence in the Banach Space norm  $\|\cdot\|$ .

**Theorem 3.1.** Suppose that (A1), (A2) and (A3) hold, and  $g : [0, \infty) \rightarrow [0, \infty)$ . If  $p_e^* > \sup_{y>0} g(y)$ , then the zero vector is a globally stable equilibrium for (2.1) in the sense that for every  $x_0 \in K$ ,

$$\lim_{n \rightarrow \infty} x_n = 0. \quad (3.1)$$

Furthermore, for every  $\varepsilon > 0$ , there exists  $\delta > 0$  such that  $\|x_0\| \leq \delta$  implies  $\|x_n\| \leq \varepsilon$  for all  $n \in \mathbb{N}$ .

**Proof.** If  $p_e^* > \sup_{y>0} g(y)$ , then

$$x_{t+1} = Ax_t + bg(c^T x_t)c^T x_t \leq Ax_t + pbc^T x_t$$

for some  $p < p_e^*$ . By induction,

$$x_t \leq (A + pbc^T)^t x_0, \quad t \in \mathbb{N}. \quad (3.2)$$

Since  $p_e^*$  is the stability radius of  $(A, b, c^T)$ ,

$$r(A + pbc^T) < 1.$$

Combining this with (3.2),  $\lim_{n \rightarrow \infty} x_n = 0$ . The last statement in the result follows immediately from the boundedness of  $A + pbc^T$ .  $\square$

We next prove that if  $p_e^*$  is below a certain threshold, then solutions can grow without bound.

**Theorem 3.2.** Assume that (A1), (A2) and (A3) hold and  $g : \{x \geq 0\} \rightarrow \{x \geq 0\}$ . Let  $m_0 = \inf_{y>0} g(y)$ . If  $p_e^* < m_0$ , then there exists  $x_0 \in K$  such that  $\lim_{t \rightarrow \infty} \|x_t\| = \infty$ .

**Proof.** Since  $b \in K$  and  $A$  is non-negative, if  $x_0 \in K$ , then

$$x_{t+1} = A + bg(c^T x_t)c^T x_t \geq A + m_0 bc^T x_t. \quad (3.3)$$

Since  $m_0 > p_e^*$ , we have  $r(A + m_0 bc^T) > 1$ . We will show that this implies there exists  $x \in X$  such that  $\{(A + m_0 bc^T)^t x\}_{t \in \mathbb{N}}$  is unbounded. If not, the principle of uniform boundedness implies that  $\{\|(A + m_0 bc^T)^t\|\}_{t \in \mathbb{N}}$  is bounded. This would imply that

$$r(A + m_0 bc^T) = \lim_{t \rightarrow \infty} \|(A + m_0 bc^T)^t\|^{1/t} \leq 1,$$

which is a contraction. Since  $K$  is reproducing, there exists  $x^+$  and  $x^-$  in  $K$  such that  $x = x^+ - x^-$ . Then at least one of  $\{(A + mbc^T)^t x^+\}_{t \in \mathbb{N}}$  or  $\{(A + mbc^T)^t x^-\}_{t \in \mathbb{N}}$  is unbounded, so we can take  $x_0 = x^+$  or  $x_0 = x^-$ , and it follows from (3.3) that with this  $x_0$ ,  $\lim \|x_t\| = \infty$ .  $\square$

To study the case where  $p_e^*$  is between  $\inf_{y>0} g(y)$  and  $\sup_{y>0} g(y)$ , for our abstract result we need to replace the non-negativity condition (A3) on  $c^T$  by the stronger condition (A3'):

(A3')  $c^T : X \rightarrow \mathbb{R}$  is a strictly positive functional, i.e. there exists  $c_{\min} > 0$  so that

$$c^T x \geq c_{\min} \|x\|, \quad \text{for all } x \geq 0.$$

For integral projection models, we only need (A3) instead of (A3'), see Corollary 4.1. For finite dimensional systems, this condition can be restrictive; for instance, for a Leslie matrix, it requires all entries in the top row to be positive. For finite dimensional systems, (A3') can be replaced by primitivity of  $A + pbc^T$  for some  $p > 0$ , see Townley et al. (in press). Under the assumptions (A1), (A2) and (A3')

$$p_e^* = \frac{1}{c^T(I + A + A^2 + \dots)b} < \infty.$$

We also need an additional condition on density dependence. The sort of ecologically motivated recruitment functions  $g$  that we have in mind are typified by a power law of the form

$$g(y) = \beta y^\alpha \quad \text{with } \alpha \in (-1, 0) \text{ and } \beta > 0,$$

or by

$$g(y) = \frac{V}{K + y} \quad \text{with } V > 0 \text{ and } K > 0.$$

Note, in both cases, that if  $f(y) = yg(y)$ ,  $\lim_{y \searrow 0} f(y) = 0$  and that for  $y > 0$ , we have that  $f(y)$  is nonlinear, non-negative, non-decreasing, and possibly unbounded. More precisely, we assume that

(A4) Let  $f : [0, \infty) \rightarrow [0, \infty)$  be non-decreasing and convex down with  $f(0) = 0$ . Let  $g(y) = f(y)/y$  for  $y > 0$ . Assume that  $g \in C(0, \infty)$  and  $g_\infty := \lim_{y \rightarrow \infty} g(y) < \lim_{y \searrow 0} g(y) = 0$ .

Note that if (A4) is satisfied and

$$p_e^* \in (g_\infty, g_0) \quad (3.4)$$

then there exists  $y^* > 0$  such that

$$f(y^*) = p_e^* y^*. \quad (3.5)$$

This is illustrated in Fig. 3.1. We will see in the proof of Theorem 3.3 that  $y^*$  turns out to be the limiting value of the observation  $c^T x_t$ .

**Theorem 3.3.** Assume that (A1), (A2), (A3'), (A4) and (3.4) hold. The vector  $x^* \in X$  given by

$$x^* = (I - A)^{-1} p_e^* b y^* \quad (3.6)$$

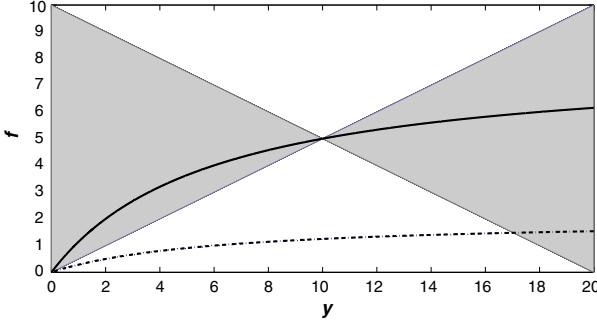
is a globally asymptotically stable equilibrium of (2.1) on  $K \setminus \{0\}$ , i.e.

$$\lim_{n \rightarrow \infty} x_n = x^*, \quad (3.7)$$

and for every  $\varepsilon > 0$ , there exists  $\delta > 0$  such that  $\|x_0 - x^*\| \leq \delta$  implies  $\|x_n - x^*\| \leq \varepsilon$  for all  $n \in \mathbb{N}$ .

**Proof.** The first step in the proof is to show that  $y_t = c^T x_t$  is bounded below. Define the functional

$$w^T = c^T (I - A)^{-1}.$$



**Fig. 3.1.** Typical nonlinearities (in black) and the line with slope  $p_e^*$ . With the solid black nonlinearity, there is a positive globally stable equilibrium. With the dotted black nonlinearities, zero is a globally stable equilibrium.

Since  $w^T b = 1/p_e^*$ , we see that  $w^T \geq 0$ . It is easy to verify that  $w^T(A + p_e^* b c^T) = w^T$ . Applying  $w^T$  to (2.1) we obtain

$$w^T x_{t+1} = w^T A x_t + w^T b f(y_t).$$

If  $y_t \leq y^*$ , then using (A4) we get  $f(y_t) \geq p_e^* y_t$ , so

$$w^T x_{t+1} \geq w^T A x_t + w^T b p_e^* y_t = w^T(A + p_e^* b c^T)x_t = w^T x_t. \quad (3.8)$$

If  $y_t > y^*$ , then (A4) implies that  $f(y_t) \geq p_e^* y^*$ , so

$$w^T x_{t+1} \geq w^T A x_t + w^T b p_e^* y^* \geq w^T b p_e^* y^*. \quad (3.9)$$

It follows that

$$w^T x_t \geq \min\{w^T x_0, y^*\} \quad \text{for all } t \in \mathbb{N}. \quad (3.10)$$

Recall that the norm of the functional  $w^T$  is

$$\|w^T\| = \sup_{\|x\|=1, x \in X} |w^T x|,$$

so

$$w^T x_t \leq \|w^T\| \|x_t\|, \quad \text{i.e. } \|x_t\| \geq \frac{1}{\|w^T\|} w^T x_t.$$

Using this, (3.10) and (A3'), it now follows that

$$y_t = c^T x_t \geq c_{\min} \|x_t\| \geq \frac{c_{\min}}{\|w^T\|} \min\{w^T x_0, y^*\}. \quad (3.11)$$

We note that since  $x_0 \in K$ ,

$$(I - A)^{-1} x_0 = x_0 + \sum_{k=1}^{\infty} A^k x_0 \geq x_0,$$

so, using (A3'),

$$w^T x_0 = c^T (I - A_0)^{-1} x_0 \geq c_{\min} \|x_0\|.$$

Similarly,  $w^T b p_e^* y^*$  is bounded below, so the right side of (3.11) is greater than zero.

Hence  $y_t$  is uniformly bounded away from zero from below for all  $t \geq 1$ . Therefore (see Fig. 3.1) the secant slope

$$\left| \frac{f(y_t) - f(y^*)}{y_t - y^*} \right| < p_e^*$$

for all  $t \geq 1$ . Hence there exists  $m < p_e^*$  so that

$$|f(y_t) - f(y^*)| \leq m |y_t - y^*|, \quad \text{for all } t \geq 1. \quad (3.12)$$

We see from (3.6) that  $x^* = Ax^* + p_e^* by^* = Ax^* + p_e^* bf(y^*)$ . Combining this with (2.1),

$$x_{t+1} - x^* = A(x_t - x^*) + p_e^* b(f(y_t) - f(y^*)).$$

From the variation of parameters formula, when  $t \geq 1$ ,

$$x_t - x^* = A^t(x_0 - x^*) + \sum_{j=0}^{t-1} A^{t-j-1} b(f(y_j) - f(y^*)). \quad (3.13)$$

Multiplying this on the left by  $c^T$  and using (3.12) gives

$$\begin{aligned} |y_t - y^*| &= \left| c^T A^t(x_0 - x^*) + \sum_{j=0}^{t-1} c^T A^{t-j-1} b(f(y_j) - f(y^*)) \right| \\ &\leq |c^T A^t(x_0 - x^*)| + m \sum_{j=0}^{t-1} c^T A^{t-j-1} b |y_j - y^*|. \end{aligned}$$

Hence, for an arbitrary  $N \in \mathbb{N}$ ,

$$\begin{aligned} \sum_{t=1}^N |y_t - y^*| &\leq \sum_{t=1}^N |c^T A^t(x_0 - x^*)| \\ &\quad + m \sum_{t=1}^N \sum_{j=0}^{t-1} c^T A^{t-j-1} b |y_j - y^*|. \end{aligned}$$

Switching the summation order and changing the summation variable in the last sum,

$$\begin{aligned} \sum_{t=1}^N |y_t - y^*| &\leq \sum_{t=0}^N |c^T A^t(x_0 - x^*)| + m \sum_{j=0}^{N-1} \sum_{k=0}^{N-j-1} c^T A^k b |y_j - y^*| \\ &\leq \sum_{t=0}^N |c^T A^t(x_0 - x^*)| + m \sum_{j=0}^{N-1} \sum_{k=0}^{\infty} c^T A^k b |y_j - y^*| \end{aligned}$$

Using  $\sum_{k=0}^{\infty} c^T A^k b = c^T (I - A)^{-1} b$ ,

$$\sum_{t=1}^N |y_t - y^*| \leq \sum_{t=0}^N |c^T A^t(x_0 - x^*)| + m c^T (I - A)^{-1} b \sum_{j=0}^N |y_j - y^*|.$$

Using (2.3) and the fact that  $m < p_e^*$ ,

$$\sum_{t=1}^N |y_t - y^*| \leq (1 - m/p_e^*)^{-1} \sum_{t=0}^{\infty} |c^T A^t(x_0 - x^*)|. \quad (3.14)$$

Since  $N$  is arbitrary and  $\rho(A) < 1$ , this shows that  $\lim_{t \rightarrow \infty} y_t = y^*$ . It follows from (3.12), the fact that  $r(A) < 1$  and (3.13) that (3.7) holds.

From (3.14) and the fact that  $r(A) < 1$ , there exists  $M > 0$  such that

$$|y_t - y^*| < M \|x_0 - x^*\|, \quad \text{for all } t \in \mathbb{N}.$$

The claimed stability of  $x^*$  then follows from (3.12) and (3.13).  $\square$

**Remark 3.4.** The limiting population vector  $x^*$  can be approximated by noting that it is the eigenvector of  $A + p_e^* b c^T$  associated with the eigenvalue 1. Furthermore, we note that  $p_e^*$  can be characterized as

$$p_e^* = \lim_{t \rightarrow \infty} f(y_t)/y_t = \lim_{t \rightarrow \infty} g(y_t).$$

**Remark 3.5.** We can summarize Theorems 3.1–3.3 (by taking the hypotheses from Theorem 3.3) to immediately get that if (A1), (A2), (A3') and (A4) hold, then a trichotomy of stability holds in the sense that:

1. If  $p_e^* < g_\infty$ , there is an  $x_0 \in K$  such that  $\lim_{t \rightarrow \infty} \|x_t\| = \infty$ .
2. If  $p_e^* \in (g_\infty, g_0)$ , then  $x^*$  is a globally stable equilibrium.
3. If  $p_e^* > g_0$ , then 0 is a globally stable equilibrium.

#### 4. Integral projection models

A class of *integral projection* models (2.1) was introduced by Easterling (1998) and Ellner et al. in Easterling et al. (2000) and Ellner and Rees (2006). We describe here a subclass of integral projection models, which are of the form (1.2). We will show that models in this subclass satisfy conditions (A1), (A2), (A3), and we prove a corollary to Theorem 3.3 to categorize the asymptotic stability properties of these models. We then describe the Platte thistle (*Cirsium canescens*) model found in Rose et al. (2005). We will give numerical simulations that are consistent with our results. Some of the discussion of the model below is adapted from Briggs et al. (2010), Easterling (1998), Easterling et al. (2000), Ellner and Rees (2006) and Rose et al. (2005).

Let  $n(\xi, t)$  be the population distribution as a function of stage  $\xi$  at time  $t$ . For example,  $\xi$  could be the size of the individual. We assume that  $\xi \in [m_s, M_s]$ , where  $m_s$  is the minimum size, and  $M_s$  is the maximum size. Assume that  $k$  is continuous on  $[m_s, M_s]^2$  and  $k(x, \xi) \geq 0$ , and consider the general linear integro-difference model

$$n(x, t+1) = \int_{m_s}^{M_s} k(x, \xi) n(\xi, t) d\xi. \quad (4.1)$$

The kernel  $k(x, \xi)$  determines how the stage-distribution of individuals at time  $t$  moves to the stage-distribution of individuals at time  $t+1$ . The kernel is determined by statistically derived functions for survival, growth and fecundity.

Let  $X = L^1(m_s, M_s)$  with the usual  $L^1$  norm. Let the positive reproducing cone be given by  $K = \{f \in L^1[\alpha, \beta] \mid f(x) \geq 0 \text{ a.e.}\}$ . For every  $t > 0$ , the population distribution  $\mathbf{n}(t) := n(t, \cdot)$  is in  $L^1(m_s, M_s)$ , and the total population is  $\|\mathbf{n}(t)\|$ . Define the operator  $P : L^1(m_s, M_s) \rightarrow L^1(m_s, M_s)$  by

$$(Pv)(\cdot) := \int_{m_s}^{M_s} k(\cdot, \xi) v(\xi) d\xi.$$

Then (4.1) is equivalent to

$$\mathbf{n}_{t+1} = P\mathbf{n}_t. \quad (4.2)$$

It follows immediately from the continuity and boundedness of  $k$  that  $P$  is a compact operator in  $L^1(m_s, M_s)$ .

We consider structured population models for which the kernel is the sum  $k(x, \xi) = p(x, \xi) + F(x, \xi)$ , where  $p$  is a growth and survival kernel and  $F$  is a fecundity kernel. The growth kernel  $p(x, \xi)$  is the probability that an individual of size  $\xi$  will survive and grow to be an individual of size  $y$  in one time step, so  $p(x, \xi) > 0$  for all  $x, \xi \in [m_s, M_s]$ . Therefore, we assume that

$$\sup_{x \in [m_s, M_s]} \int_{m_s}^{M_s} p(x, \xi) d\xi < 1, \quad (4.3)$$

that is, the probability that all individuals will survive is less than 1. Using this, it is easy to verify that the operator  $A : X \rightarrow X$  given by

$$(Av)(\cdot) := \int_{m_s}^{M_s} p(\cdot, \xi) v(\xi) d\xi$$

satisfies  $\|A\| < 1$ , which implies that  $r(A) < 1$ . Since it is clear that  $A$  is nonnegative if  $p(x, \xi) \geq 0$  for all  $x, \xi \in [m_s, M_s]$ ,  $A$  satisfies condition (A1).

The function  $F(x, \xi)$  is the number of offspring of size  $x$  that an individual of size  $\xi$  will produce in one time step. For details on the appropriate statistical models for obtaining the kernel, see Easterling et al. (2000), Ellner and Rees (2006), Rose et al. (2005) and Tenhumberg et al. (in preparation). We assume that  $F(x, \xi)$  can be decomposed as  $p_e b(x) c(\xi)$ , where  $b, c \in X$  are continuous on

$[m_s, M_s]$ ,  $b(x) \geq 0$  for  $x \in [m_s, M_s]$  and  $c(\xi) \geq 0$  for  $\xi \in [m_s, M_s]$ . The fecundity operator

$$A_1 : v \in X \rightarrow \int_{m_s}^{M_s} F(x, \xi) v(\xi) d\xi$$

can be decomposed into  $A_1 = p_e b c^T$ , where  $c^T$  is the functional on  $X$  given by

$$c^T v = \int_{m_s}^{M_s} c(\xi) v(\xi) d\xi.$$

Since  $b$  and  $c$  are both non-negative, it is clear that conditions (A2) and (A3) are satisfied. We now show that the conclusions of Theorem 3.3 hold for the density dependent system

$$\mathbf{n}_{t+1} = A\mathbf{n}_t + f(c^T \mathbf{n}_t) b. \quad (4.4)$$

**Corollary 4.1.** Suppose  $A, b$  and  $c$  are as in this section,  $f$  satisfies (A4), and  $p_e^*$  is given by (2.3) and satisfies (3.4). Then the vector  $x$  given in (3.6) is a globally asymptotically stable equilibrium of (4.4) as in Theorem 3.3.

**Proof.** The only part of the proof of Theorem 3.3 where the condition (A3') is used instead of (A3) is to establish that  $y_t$  is uniformly bounded above away from 0, i.e.

$$y_t > m \text{ for some } m > 0. \quad (4.5)$$

To prove this for the systems considered in this section, we introduce a new IPM system which is “close to” (4.4). For  $\varepsilon > 0$ , let

$$\begin{aligned} \Omega_\varepsilon &:= \{\xi \in [m_s, M_s] \mid c(\xi) > \varepsilon\}, & X_\varepsilon &:= L^1(\Omega_\varepsilon), \\ A_\varepsilon : X_\varepsilon &\rightarrow X_\varepsilon, & (A_\varepsilon v)(x) &= \int_{\Omega_\varepsilon} p(x, \xi) v(\xi) d\xi, \\ b_\varepsilon &= b|_{\Omega_\varepsilon}, & c_\varepsilon^T v &= \int_{\Omega_\varepsilon} c(\xi) v(\xi) d\xi. \end{aligned}$$

For  $v \in X$ , let  $v_\varepsilon$  be the restriction of  $v$  to  $\Omega_\varepsilon$ . From (4.3),

$$\sup_{x \in [m_s, M_s]} \int_{\Omega_\varepsilon} p(x, \xi) d\xi < 1,$$

so  $\rho(A_\varepsilon) \leq \rho(A) < 1$  and  $A_\varepsilon$  satisfies (A1). It is clear that  $b_\varepsilon$  satisfies (A2). Note that for  $v \geq 0$  and  $v \in X_\varepsilon$ ,  $c_\varepsilon^T v \geq \varepsilon \|v\|$ , so  $c_\varepsilon^T$  satisfies (A3') for all  $\varepsilon > 0$ . Let  $(p_e^*)(\varepsilon) = (c_\varepsilon^T(I - A_\varepsilon)^{-1} b_\varepsilon)^{-1}$ . It is easy to see that  $\lim_{\varepsilon \rightarrow 0} (p_e^*)(\varepsilon) = p_e^*$ . Since  $p_e^*$  satisfies (3.4), we can choose  $\varepsilon > 0$  such that  $(p_e^*)(\varepsilon)$  also satisfies (3.4). Let  $\mathbf{n}_t(\varepsilon)$  satisfy

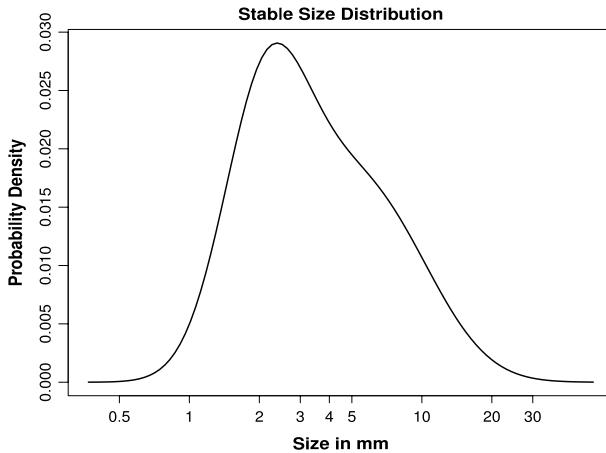
$$\mathbf{n}_{t+1}(\varepsilon) = A_\varepsilon \mathbf{n}_t(\varepsilon) + b_\varepsilon f(c_\varepsilon^T \mathbf{n}_t(\varepsilon))$$

and

$$y_t(\varepsilon) = c^T \mathbf{n}_t(\varepsilon).$$

Then by the proof of Theorem 3.3,  $y_t(\varepsilon)$  satisfies (4.5). Since  $\Omega_\varepsilon \subset [m_s, M_s]$ , it is easy to show that  $y_t \geq y_t(\varepsilon)$ , hence  $y_t$  satisfies (4.5). Hence we can apply the proof of Theorem 3.3 to (4.4), to get the desired conclusions.  $\square$

We now discuss the model for the Platte thistle found in Rose et al. (2005), modified to ignore effects of herbaceous predators. The Platte thistle is an indigenous perennial plant in the midgrass sand prairies of central North America. It is strictly monocarpic, meaning that plants die after reproducing, so the flowering probability will need to be incorporated into the kernel. In this model, we use the log root crown diameter  $\xi$  as the continuous stage variable. For the specific form of the survival kernel  $p$ , see Briggs et al. (2010) and Rose et al. (2005). For this model  $p$  satisfies (4.3). For the fecundity kernel  $F(x, \xi)$ , we note that in order to reproduce, a plant must survive, and it must also flower. Let  $s(\xi)$



**Fig. 4.2.** Asymptotic population density of the Platte thistle.

be the survival probability and  $f_p(\xi)$  be the flowering probability. Each plant will produce seeds, and these seeds must germinate and survive to the next population census for an offspring to be included in the next population census. Let  $S(\xi)$  be the number of seeds produced by a plant of size  $\xi$ , and the average germination probability be  $p_e$ . Finally, let the distribution of the offspring sizes be  $b(x)$  with  $b \in X$ . The  $b$  used here is the statistically derived distribution of offspring sizes. In general,  $b$  will be non-negative but not positive. Therefore the fecundity kernel can be written as

$$F(x, \xi) = b(x)c(\xi), \quad \text{where } c(\xi) = p_e S(\xi)f_p(\xi)S(\xi). \quad (4.6)$$

In Rose et al. (2005), it is assumed that the recruitment probability  $p_e$  is a function of  $S_T(t) = c^T \mathbf{n}_t$ , the total number of seeds produced; in particular, they chose the germination probability to be  $(p_e)_t = (S_T(t))^{-0.33}$ . This density dependent system can be written as

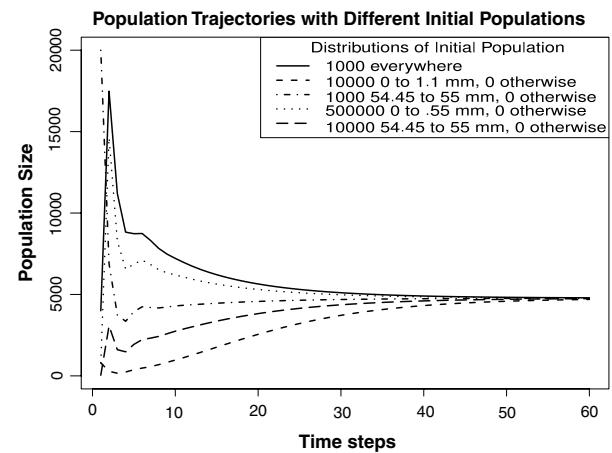
$$\begin{aligned} \mathbf{n}_{t+1} &= A\mathbf{n}_t + b(c^T \mathbf{n}_t)^{-0.33}c^T \mathbf{n}_t = A\mathbf{n}_t + bf(c^T \mathbf{n}_t), \\ f(y) &= y^{0.67}. \end{aligned}$$

This system clearly satisfies conditions (A1), (A2), (A3) and (A4). Since  $g(y) = f(y)/y = y^{-0.33}$ , we see that  $g_\infty = 0$  and  $g_0 = \infty$ , so (3.4) is satisfied. Therefore, Corollary 4.1 applies to this system. Using (2.3), we find that  $p_e^* = 0.067$ . The limiting number of seeds  $y^* = c^T x^* = \lim_{t \rightarrow \infty} S_T(t)$  satisfies (3.5), which becomes

$$y^* = p_e^{*-1/0.33} = 3609.$$

Therefore, the limiting population vector  $\mathbf{n}^*$  given by (3.6) is a globally stable equilibrium. The unit vector  $\mathbf{n}^*/\|\mathbf{n}^*\|$  is the limiting age distribution, which is shown in Fig. 4.2. It is found in Rose et al. (2005) that there is a good match between the model predictions and the observed size distributions—our simplified model has a similar size distribution to that in Rose et al. (2005).

It follows from the dominated convergence theorem that the total population  $N(t) = \|\mathbf{n}_t\|$  converges to  $\|x^*\|$  as  $t \rightarrow \infty$ , and that the limiting total population is independent of the initial population vector. This is illustrated in Fig. 4.3, where a numerical simulation of the total population as a function of time is shown for five different initial conditions. The continuity and boundedness of the integrand in the integral mapping implies that a Riemann approximation to the integral operator will approximate the operator to any desired accuracy. The total population size of the Platte thistle in the field decreases over a 12 year interval (Rose et al., 2005). We used a simplified version of the model in Rose et al. (2005) that did not include herbivores. Rose et al. (2005) showed that models including herbivory predicted decreasing population densities; simulations of models without herbivory predicted an asymptotic population size of 5000, which is consistent with Fig. 4.3.



**Fig. 4.3.** The trajectories of the total population. Each curve shows the trajectory with different initial states.

## 5. Concluding remarks

We proved the existence of globally asymptotically stable equilibria for a class of nonlinear discrete-time systems defined on Banach spaces. The conditions on the system are motivated by examples in population ecology, and these systems often do not satisfy the conditions in Hirsch and Smith (2005) and Krause and Ranft (1992). Conditions (A1), (A2), (A3) and (A4) are naturally satisfied for many plant and animal species, and are sufficient for a complete analysis of global asymptotic stability of a class of density dependent integral projection models, including the Platte thistle model we analyzed. These results are also applicable to matrix models, by taking  $X = \mathbb{R}^n$ ; however, the condition (A3') required in Theorem 3.3 is not typically satisfied by matrix models. In such matrix models, the functional  $c^T$  typically satisfies (A3) but not (A3'). In Townley et al. (in press), we restrict our attention to matrix models, and prove a result which is applicable to a wide range of density dependent matrix models. The proof is more involved, and uses matrix methods. In Townley et al. (in press), we also address asymptotic behavior when (A4) is not satisfied, and there is no asymptotically stable equilibrium. The techniques we use in this paper included “small gain” arguments and the use of the stability radius, which are common in engineering problems where nonlinear dynamical systems are often analyzed as feedback systems, see Vidyasagar (1993).

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