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Journal of Mathematical Biology

ISSN 0303-6812

J. Math. Biol.

DOI 10.1007/s00285-013-0689-z



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Global asymptotic stability of plant-seed bank models

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Received: 16 May 2012 / Revised: 8 May 2013
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Abstract Many plant populations have persistent seed banks, which consist of viable seeds that remain dormant in the soil for many years. Seed banks are important for plant population dynamics because they buffer against environmental perturbations and reduce the probability of extinction. Viability of the seeds in the seed bank can depend on the seed's age, hence it is important to keep track of the age distribution of seeds in the seed bank. In this paper we construct a general density-dependent plant-seed bank model where the seed bank is age-structured. We consider density dependence in both seedling establishment and seed production, since previous work has highlighted that overcrowding can suppress both of these processes. Under certain assumptions on the density dependence, we prove that there is a globally stable equilibrium population vector which is independent of the initial state. We derive an analytical formula for the equilibrium population using methods from feedback control theory. We apply these results to a model for the plant species *Cirsium palustre* and its seed bank.

Keywords Structured population model · Age-structured seed bank · Density dependence · Global asymptotic stability · Contest competition · Scramble competition

Mathematics Subject Classification (2000) 92D25 · 34D23 · 92D40

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1 Introduction

Many plant populations have persistent seed banks. Seed banks consist of viable seeds that have been produced in previous years. Instead of germinating, the seeds have undergone dormancy and can remain viable in the soil for more than one season. Seed banks buffer plant populations against environmental perturbations like fire or pest outbreaks. Hence, even if all above-ground plant material is destroyed, seeds germinate from the seed bank and, as a consequence, reduce the probability of population extinction. Furthermore, seed banks act as a reservoir for genes and/or gene complexes (Fenner and Thompson 2005; Venable 1989; MacDonald and Watkinson 1981; Kalisz and McPeck 1992, 1993; Kalisz 1991; Edelstein-Keshet 2005; Mohler 1993; Claessen et al. 2005; Brown and Venable 1991). The vital role of seed banks for population viability necessitates incorporating seed banks specifically into demographic models to avoid erroneous model predictions (Kalisz and McPeck 1992, 1993; Damgaard 2005).

Often the survival and/or germination probabilities decrease with seed age (Kalisz and McPeck 1992; Alexander and Schrag 2003; Charlesworth 1980), in which case it is important to keep track of the age distribution of seeds in the seed bank. In this paper we characterize the seed bank as an age-structured population (so that it is represented by a vector in \mathbb{R}^N), which is coupled with the dynamics of the associated plant population. Furthermore we assume that seed production depends on the total plant density and seedling establishment depends on the density of germinating seeds. These two density-dependent processes cannot simply be modeled with one nonlinear function, as density-dependent seed production only suppresses the density of newly created seeds, but density-dependent seedling recruitment affects the total density of germinating seeds in the population (which is the sum of new and old germinating seeds). We assume that the density dependence in seedling establishment is due to contest competition, and a derivation of this general relationship can be found in Eager (2012). We consider both contest and scramble competition assumptions for the density dependence in seed production, as per-capita seed production data in studies such as Jarry et al. (1995) suggests that either could be the case.

Seed banks have been modeled as structured populations (Kalisz and McPeck 1992; Brown and Venable 1991; Edelstein-Keshet 2005; Charlesworth 1980), but we are unaware of any studies of the global asymptotic stability of a density-dependent plant-seed bank model. We prove that, in the case where seed production is modeled with contest competition, there is a globally stable equilibrium vector which is independent of the initial population. In the case where seed production is modeled with scramble competition, we obtain weaker global stability results. We apply our analytical results to a plant-seed bank model for *Cirsium palustre* obtained from Ramula et al. (2009).

We show explicitly how the persistence of the population depends on the age-dependent survival and germination probabilities of the seeds in the seed bank. In agreement with Kalisz and McPeck (1992), Kalisz and McPeck (1993) and Damgaard (2005) our model illustrates that ignoring the seed bank stage (assuming that all non-germinating seeds die) leads to an overestimation of extinction risk: for some part of the parameter space our model can predict population extinction in the absence of the seed bank, but when including the seed bank an otherwise identical model predicted a non-zero equilibrium population.

2 Plant-seed bank model

2.1 Plant population

The plant population at time t is described by a vector n_t , which is assumed to be in the cone of non-negative vectors in a Banach space X_1 for $t = 0, 1, \dots$. In a population projection matrix (PPM) model (Caswell, 2001) X_1 is a finite dimensional space \mathbb{R}^m (so n_t is a population vector), and in an integral projection model (IPM) (Briggs et al. 2010; Childs et al. 2003, 2004; Ellner and Rees 2006; Rebarber et al. 2012; Ramula et al. 2009) X_1 is often the space $L^1[L, U]$ of integrable functions on the interval of stages $[L, U]$ (so $n_t(x)$ is a function of a continuous variable x). In the absence of a seed bank, and with the assumption that only newly created seedlings compete with each other for space to establish, the plant population is governed by the abstract nonlinear population projection model

$$n_{t+1} = An_t + bf(\alpha_1 h(c^T n_t)), \quad (2.1)$$

which is similar to the model studied in Rebarber et al. (2012) and Townley et al., 2012. The nonlinear functions f and h model density-dependent seedling recruitment and density dependent seed production, respectively.

The linear terms in (2.1) are as follows: the population projection operator A is in $\mathcal{L}(X_1)$, the space of bounded, linear operators from X_1 to itself. An example of such an A is an integral operator

$$An = \int_L^U k(x, y)n(y) dy,$$

from an IPM, where $n \in X_1 = L^1[L, U]$. The operator A models the two ecological processes of survival and movement from one stage to another. Since this process cannot create new members of the population, $r(A) < 1$ (where $r(A)$ is the spectral radius of A). The vector $b \in X_1$ models the stage distribution of juvenile plants, which is assumed to be independent of mother plant, (Ellner and Rees 2006), and c^T is a bounded linear functional on X_1 , where $c^T n_t$ gives the abundance of available seeds produced by the population at time t in a completely density-independent environment. The notation c^T is used instead of c in order to distinguish a functional on X_1 from a vector in X_1 , much like a row vector is distinguished from a column vector. An example of b is a continuous probability distribution $J(\cdot)$ in an IPM representing the stage distribution of juveniles. This is in contrast to the form that b commonly takes in a finite-dimensional space like \mathbb{R}^m , where the juvenile stage distribution is usually the vector $[1 \ 0 \ \dots \ 0]^T$. If $X_1 = L^1[L, U]$, there is no analogue for the vector $[1 \ 0 \ \dots \ 0]^T$ in \mathbb{R}^m , since a Dirac-Delta distribution centered at the smallest value for the stage variable, is not in X_1 . The size distribution of juvenile plants is not likely to be concentrated at a single value, as variations inevitably occur within populations, so a probability distribution is more appropriate in this setting.

An example of the functional c^T in an IPM is

$$c^T n = \int_L^U c(y)n(y) dy,$$

for $n \in L^1[L, U]$.

2.2 Density dependence

Consider the following feedback between plants, seeds and seedlings, which is assumed to occur in one time-step:

seed production: plants to seeds;
germination: seeds to seedlings;
establishment: seedlings to plants

We will assume that the seed production and establishment processes can be density dependent. The seed production density dependence will be modeled with the function h and the establishment density dependence with f .

Seed production: In many models the number of seeds produced by the plants in the population is assumed to be density independent (for example the model in [Rose et al. 2005](#)). In the model studied in Sect. 3.1 we assume such a density-independent relationship by letting $h(y) = y$, so the number of new seeds produced in the population during time t will simply be $c^T n_t$. However, some plant populations experience a density-dependent relationship between the abundance of plants and seeds produced (see, for example, [Jarry et al. \(1995\)](#)). Therefore, in Sects. 3.2 and 3.3 we will assume that the abundance of new seeds produced at time t is $h(c^T n_t)$, where h is a nonlinear function (which we'll assume has a maximum of $c^T n_t$, the seed production in the complete absence of density dependence).

Establishment: The density dependence in establishment will be modeled as follows: The scalar quantity $f(y)$ represents the density of juvenile plants generated by y available germinating seeds. We assume that y is the sum of newly created seeds that germinate at time t and the sum of all older seeds that germinate. We assume that seeds become seedlings (via germination) in a density-independent way. The diminishing amount of available microsites then causes a density-dependent relationship between the abundance of germinating seeds (seedlings) and the subsequent abundance of new plants in the population. Note that we are assuming that density-dependent feedbacks on seedling establishment are limited to feedbacks from other seedlings. This assumption was used in the IPM in [Rose et al. \(2005\)](#) for the monocarpic plant *Platte thistle* (*C. canescens*). It is certainly possible that adult conspecifics can demonstrate a negative density-dependent feedback on seedling establishment ([Silva Matos et al. 1999](#); [Picò and Retana 2008](#)), and therefore we will discuss the implications of weakening the assumption that feedbacks are limited to feedbacks from other seedlings in Sect. 3.4.

It is natural to view $f(y)$ as the product of the number of germinating seeds y available and the probability $g(y)$ that a germinating seed eventually becomes a new plant in that time-step. Thus

$$f(y) = g(y)y. \quad (2.2)$$

We will call the function g the *establishment probability* (which is sometimes known as the *recruitment* in the literature).

We consider the following conditions on f and g :

(D1) $g \in C(0, \infty)$, g is a decreasing function on $(0, \infty)$, $f(0) = 0$, and f is strictly increasing and concave down.

These are the same as the conditions on g and f assumed in [Rebarber et al. \(2012\)](#) and [Townley et al. \(2012\)](#). Some ecologically motivated functions that satisfy these assumptions are power functions of the form

$$f(y) = By^a \quad \text{with } a \in (0, 1) \quad \text{and } B > 0, \quad (2.3)$$

and Michaelis–Menten type functions of the form

$$f(y) = \frac{\alpha y}{\beta + y} \quad \text{with } \alpha > 0 \quad \text{and } \beta > 0. \quad (2.4)$$

See [Eager et al. \(2012\)](#) for a derivation of the Michaelis–Menten function for seed-to-plant density dependence in a general plant population at its equilibrium.

When seed production is density independent (so there is only one nonlinearity), the global asymptotic stability of the plant-seed bank population is a corollary of the work in [Rebarber et al. \(2012\)](#). When seed production is density dependent the two nonlinearities f and h are coupled. The analysis of global stability in Sects. 3.2 and 3.3 will therefore require a substantial modification of the results in [Rebarber et al. \(2012\)](#) and [Townley et al. \(2012\)](#), which is the main mathematical novelty in this paper.

General global stability results can be found in [Hirsch and Smith \(2005\)](#) and [Smith and Thieme \(2011\)](#). However, for many ecological applications, these results cannot be readily applied. This is because of the types of Banach spaces X_1 and the types of vectors b and functionals c^T that are likely to appear in the applications we consider. In particular, in order to apply [Hirsch and Smith \(2005\)](#), X_1 cannot be $L^1[L, U]$, a standard space for Integral Projection Models. since the positive cone in $L^1[L, U]$ has empty interior. Furthermore, since b represents the stage distribution of newborns after one time step, we expect it to have some entries which are zero, which makes it difficult to apply [Hirsch and Smith \(2005\)](#)—see Sect. 2 of [Rebarber et al. \(2012\)](#) for a discussion about this.

2.3 Age-structured seed bank model

We assume that the seed bank is structured with respect to the age of the seeds, in the sense that the survival and germination probabilities of the seeds in the seed bank are a function of age. There is evidence that this is true in general ([Alexander and Schrag 2003](#); [Kalisz and McPeck 1992](#); [MacDonald and Watkinson 1981](#)). We further assume that there is an age after which a dormant seed in the seed bank is either no longer viable or is placed in a final class of “old” seeds.

We will use the following notation: the seed bank at time t has N discrete *age* stages, $s_{1,t}, s_{2,t}, \dots, s_{N,t}$, where $s_{j,t}$ are seeds that are j time-steps old at time t . Then $s_t = [s_{1,t}, s_{2,t}, \dots, s_{N,t}]^T$ is the seed population vector at time t . As previously stated, the number of available germinating seeds \tilde{y}_t at time t is the sum of newly created seeds and available old seeds at time t . Written mathematically,

$$\tilde{y}_t := \alpha_1 h(c^T n_t) + \alpha_2 s_{1,t} + \alpha_3 s_{2,t} + \dots + \alpha_{N+1} s_{N,t},$$

where $\alpha_j \in (0, 1)$ is the probability that a $(j - 1)$ -year old seed germinates in one time-step.

We use $\gamma_j \in (0, 1)$ to denote the probability of not germinating and survival in one time step from the $(j - 1)$ th age class to the j th age class, for $j = 1, 2, \dots, N$. The number γ_{N+1} is the product of not germinating and survival in one time step from the N th age class to all later ages. Because old seeds cannot directly create new seeds we assume that $\alpha_j + \gamma_j < 1$ for all $j = 1, 2, \dots, N + 1$.

The seed population vector at time $t + 1$ is obtained from the seed population vector at time t by the following: $s_{1,t+1}$ consists of the number of seeds produced by plants which survive and do not germinate in the current year. Later seed classes $s_{j,t+1}$ consists of seeds that do not germinate and survive from seed class $s_{j-1,t}$, for $j = 2, \dots, N - 1$. The last seed class $s_{N,t}$ contains all ages N or higher, so $s_{N,t+1}$ also contains seeds that do not germinate and survive from $s_{N-1,t}$ and $s_{N,t}$.

Hence the seed bank population $\{s_t\}_{t=0}^\infty$ evolves in \mathbb{R}^N for some integer N which represents the oldest seed class. The resulting plant-seed bank model can be written as

$$\begin{aligned} n_{t+1} &= An_t + bf(\tilde{y}_t), \quad \tilde{y}_t = \alpha_1 h(c^T n_t) + \alpha_2 s_{1,t} + \dots + \alpha_{N+1} s_{N,t} \\ s_{1,t+1} &= \gamma_1 h(c^T n_t) \\ s_{2,t+1} &= \gamma_2 s_{1,t} \\ &\vdots \\ s_{N-1,t+1} &= \gamma_{N-1} s_{N-2,t} \\ s_{N,t+1} &= \gamma_N s_{N-1,t} + \gamma_{N+1} s_{N,t}. \end{aligned} \tag{2.5}$$

In applications $\{\alpha_j\}_{j=1}^{N+1}$ and $\{\gamma_j\}_{j=1}^{N+1}$ will be decreasing, but we do not insist upon this in our results.

2.4 Abstract formulation

We will write (2.5) as an abstract first-order system, in order to prove the desired global stability results. Let the norm on the Banach space X_1 be denoted by $\|\cdot\|_{X_1}$, and let X_2 be \mathbb{R}^N with associated 1-norm

$$\|[x_1, x_2, \dots, x_N]^T\|_1 = \sum_{j=1}^N |x_j|,$$

which measures total seed population. We wish to work with nonnegative vectors in, and nonnegative operators on, X_1 and X_2 . Let K_1 and K_2 be reproducing cones for X_1 and X_2 , respectively, with the partial ordering \geq (see Krasnosel'skij et al. (1989) for a general theory). We will call vectors in K_1 and K_2 non-negative vectors. An example of a reproducing cone in \mathbb{R}^N is $\{[x_1, x_2, \dots, x_N]^T | x_j \geq 0 \text{ for } j = 1, 2, \dots, N\}$. An example of a reproducing cone in $L^1[L, U]$ is $\{f \in L^1[L, U] | f(x) \geq 0 \text{ a.e.}\}$. In both of these examples the idea of a non-negative vector is consistent with intuition.

For $i = 1, 2$ we will call an operator on X_i that maps non-negative vectors to non-negative vectors a *non-negative operator*. An example of such an operator is an $N \times N$ matrix A with all non-negative entries, acting on \mathbb{R}^N .

The following hypotheses are natural in the study of plant-seed bank dynamics. First, we state the conditions on the data for the plant population, (A, b, c) .

- (E1) $A \in \mathcal{L}(X_1)$ is a non-negative operator with spectral radius $r(A) < 1$;
- (E2) b is a non-negative vector in $X_1 \setminus \{0\}$;
- (E3) $c^T : X_1 \rightarrow \mathbb{R}$ is a strictly positive, continuous, linear functional, i.e. there exists $c_{\min} > 0$ such that

$$c^T n \geq c_{\min} \|n\|, \quad \text{for all } n \geq 0; \quad (2.6)$$

- (E4) The coefficients $\alpha_j, \gamma_j \in (0, 1)$ for all $j = 1, 2, \dots, N+1$. Furthermore $\alpha_j + \gamma_j < 1$ for all $j = 1, 2, \dots, N+1$.

Conditions (E1) and (E2) are not restrictive for most plant population models. Condition (E3) is needed for us to prove the global stability of the nonzero equilibrium population for general X_1 , but can be weakened in the case where $X_1 = L^1[L, U]$ and A is an integral projection operator in an IPM. We discuss this case further after the proof of Theorem 3.3, and show via Corollary 3.1 that our global stability results hold under the weaker assumption that $c^T n \geq 0$ for all $n \in L^1[L, U]^+$.

We can describe the coupled system (2.5) by a single first order system. The state of this system is

$$\tilde{n}_t := [n_t \ s_t]^T \subset X := X_1 \otimes X_2.$$

All convergence discussed in this paper is in the Banach space norm defined on X by $\|\cdot\| = \|\cdot\|_{X_1} + \|\cdot\|_1$.

Let

$$\tilde{A} := \begin{bmatrix} A & \emptyset \\ \Gamma & S \end{bmatrix}, \quad \tilde{b} := \begin{bmatrix} b \\ 0 \\ \vdots \\ 0 \end{bmatrix}, \quad \tilde{c}^T := [\alpha_1 h(c^T \cdot) \ \alpha^T].$$

Here $\emptyset := [0 \ 0 \ \dots \ 0] \in \mathcal{L}(X_2, X_1)$ where 0 represents the zero vector in X_1 ;

$$\Gamma := [\gamma_1 h(c^T \cdot) \ 0^T \ \dots \ 0^T]^T \in \mathcal{L}(X_1, X_2)$$

where 0^T is the zero functional on X_1 ; and $S \in \mathcal{L}(X_2)$ is the $N \times N$ substochastic shift matrix

$$S = \begin{bmatrix} 0 & 0 & \cdots & 0 \\ \gamma_2 & 0 & \cdots & 0 \\ 0 & \gamma_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & \gamma_N & \gamma_{N+1} \end{bmatrix},$$

and $\alpha^T := [\alpha_2 \ \alpha_3 \ \cdots \ \alpha_{N+1}]$. We can write the coupled system (2.5) as

$$\tilde{n}_{t+1} = \tilde{A}\tilde{n}_t + \tilde{b}f(\tilde{y}_t), \quad \tilde{y}_t = \tilde{c}^T \tilde{n}_t. \quad (2.7)$$

Notice that, unless h is linear, Γ is a nonlinear operator, which makes \tilde{A} a nonlinear operator. The nonlinearity of h also implies that the functional \tilde{c}^T is nonlinear. These nonlinearities are the substantial difference between the model in this paper and that in [Rebarber et al. \(2012\)](#) and [Townley et al. \(2012\)](#).

3 Global stability results

3.1 Density independent seed production

In this section we consider density independent seed production, i.e. where $h(y) = y$ for all y . We will obtain global asymptotic stability results for (2.7), and hence for (2.5) by applying [Rebarber et al. \(2012\)](#). To do this we will need the concept of the stability radius of the linear system

$$\tilde{n}_{t+1} = \tilde{A}\tilde{n}_t + p\tilde{b}\tilde{c}^T \tilde{n}_t,$$

where p is a scalar and $f(y)$ is replaced with $f(y) = py$. The stability radius \tilde{p}_e is the smallest positive p such that $r(\tilde{A} + p\tilde{b}\tilde{c}^T) = 1$. See [Hinrichsen and Pritchard \(2005\)](#) for details, and for the fact that

$$\tilde{p}_e = (\tilde{c}^T (\tilde{I} - \tilde{A})^{-1} \tilde{b})^{-1}.$$

The asymptotic behavior of (2.7) depends upon the relationship between the function g (see (2.2)) and the stability radius \tilde{p}_e . Roughly speaking, the nonlinear establishment probability function g needs to be able to achieve the value \tilde{p}_e for there to be a non-zero equilibrium. In particular, if $g(y) < \tilde{p}_e$ for all $y \geq 0$, then the population dies out. Furthermore, g needs to be able to eventually fall below \tilde{p}_e for the population to settle down, i.e. if $g(y) > \tilde{p}_e$ for all $y \geq 0$ the population can grow without bound. If \tilde{p}_e is between these two thresholds the population has a globally asymptotically stable, strictly positive equilibrium vector. Let

$$g_\infty := \lim_{y \rightarrow \infty} g(y), \quad g_0 := \lim_{y \searrow 0} g(y). \quad (3.1)$$

Theorem 3.1 *Let $h(y) = y$ and suppose that (D1), (E1), (E2), (E3) and (E4) hold.*

- (1) *If $\tilde{p}_e > g_0$, then the zero vector is a globally stable equilibrium for (2.7) in the sense that for every non-negative \tilde{n}_0 ,*

$$\lim_{t \rightarrow \infty} \tilde{n}_t = 0.$$

Furthermore, for every $\epsilon > 0$, there exists $\delta > 0$ such that $\|\tilde{n}_t\| < \epsilon$ for all $t \in \mathbb{N}$ whenever $\|\tilde{n}_0\| < \delta$.

- (2) *If $\tilde{p}_e < g_\infty$, then there exists a non-negative initial vector \tilde{n}_0 such that*

$$\limsup_{t \rightarrow \infty} \|\tilde{n}_t\| = \infty.$$

- (3) *If $\tilde{p}_e \in (g_\infty, g_0)$ then there exists y^* such that $f(y^*) = \tilde{p}_e y^*$. The vector \tilde{n}^* given by*

$$\tilde{n}^* = \tilde{p}_e y^* (\tilde{I} - \tilde{A})^{-1} \tilde{b}$$

is a strictly positive globally asymptotically stable equilibrium of the system (2.7) in the sense that for every positive $\tilde{n}_0 \in X_1 \otimes X_2$

$$\lim_{t \rightarrow \infty} \tilde{n}_t = \tilde{n}^*.$$

Furthermore, for every $\epsilon > 0$, there exists $\delta > 0$ such that $\|\tilde{n}_t - \tilde{n}^\| < \epsilon$ for all $t \in \mathbb{N}$ whenever $\|\tilde{n}_0 - \tilde{n}^*\| < \delta$.*

Proof We need to show that when (E1), (E2), (E3) and (E4) are satisfied then (2.7) will satisfy conditions (A1), (A2) and (A3') in Rebarber et al. (2012), and we will be able to apply Theorems 3.1, 3.2 and 3.3 in that paper to obtain (1), (2) and (3) of Theorem 3.1, with p_e replaced by \tilde{p}_e . Since $b \geq 0$ in X_1 , it immediately follows that $\tilde{b} \geq 0$ in $X = X_1 \otimes X_2$, showing that (A2) is satisfied for \tilde{b} .

For every $\tilde{n} \in X_1 \otimes X_2$,

$$\tilde{c}^T \tilde{n} = \alpha_1 c^T n + \alpha^T s \geq \alpha_1 c_{\min} \|n\|_{X_1} + \alpha_{\min} \|s\|_1, \quad \alpha_{\min} := \min\{\alpha_j\} > 0.$$

Thus $\tilde{c}^T \tilde{n} \geq \tilde{c}_{\min} \|\tilde{n}\|$, where

$$\tilde{c}_{\min} := \min\{\alpha_1 c_{\min}, \alpha_{\min}\},$$

verifying (A3') for \tilde{c} . Since $r(A) < 1$ and $\gamma_{N+1} \in (0, 1)$,

$$r(\tilde{A}) = \max\{r(A), \gamma_{N+1}\} < 1,$$

verifying (A1) for \tilde{A} . □

It is important to note that, while Theorem 3.2 in Rebarber et al. (2012) suggests that (2) in Theorem 3.1 should state that $\lim_{t \rightarrow \infty} \|\tilde{n}_t\| = \infty$ we can only actually say that $\limsup_{t \rightarrow \infty} \|\tilde{n}_t\| = \infty$ in both Theorem 3.2 in Rebarber et al. (2012) and Theorem 3.1 in this paper.

While the proof of Theorem 3.1 is a simple corollary of Theorems 3.1, 3.2 and 3.3 in Rebarber et al. (2012), the above analysis reveals an interesting observation with regard to plant-only models and analogous plant-seed bank models. Notice that, by a simple calculation

$$\tilde{p}_e = \frac{p_e}{\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1}, \quad (3.2)$$

where $\Gamma_1 = [\gamma_1 \ 0 \ \dots \ 0]^T$ and $p_e = (c^T (I - A)^{-1} b)^{-1}$. Note that if one replaces the term

$$f(\alpha_1 h(c^T n_t))$$

in the plant-only model (2.1) with

$$p\alpha_1 c^T n_t,$$

one has

$$n_{t+1} = (A + p\alpha_1 b c^T) n_t,$$

from which it follows that the stability radius of the *plant-only* model (2.1) is $p = p_e/\alpha_1$.

By inspection it is clear that if a seed bank is present (i.e. $\gamma_1, \alpha_2 > 0$) the stability radius of the plant-seed bank model will be smaller than that of the plant-only model, i.e.

$$\tilde{p}_e = \frac{p_e}{\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1} < \frac{p_e}{\alpha_1},$$

as $(I - S)^{-1} \neq 0$ and ≥ 0 entry-wise. Therefore, since the conditions needed to have a positive globally stable equilibrium are $\tilde{p}_e < g_0$ (in the plant-seed bank case) and $p_e/\alpha_1 < g_0$ (in the plant-only case), if

$$\tilde{p}_e = \frac{p_e}{\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1} < g_0 < \frac{p_e}{\alpha_1}$$

then the plant-seed bank model will predict persistence while the plant-only model will predict extinction.

Furthermore, it follows from another simple calculation that

$$(I - \tilde{A})^{-1} \tilde{b} = \left[(I - A)^{-1} b \quad \frac{(I - S)^{-1} \Gamma_1}{p_e} \right]^T. \quad (3.3)$$

which implies that

$$\tilde{n}^* = (\tilde{p}_e y^*) \left[(I - A)^{-1} b \frac{(I - S)^{-1} \Gamma_1}{p_e} \right]^T. \quad (3.4)$$

Therefore, the long-term structure of the plant population $((I - A)^{-1} b)$ is the same in both the plant-seed bank and plant-only models. The only difference is that

$$\tilde{p}_e = \frac{p_e}{\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1} < \frac{p_e}{\alpha_1},$$

and therefore the solution y^* of the equation

$$f(y) = \tilde{p}_e y$$

is larger than the solution y^* of the equation

$$f(y) = \frac{p_e}{\alpha_1} y.$$

Since f is assumed to be increasing, the equilibrium recruitment $f(y^*) = \tilde{p}_e y^*$ in the plant-seed bank model will be larger than the equilibrium recruitment $f(y^*) = p_e/\alpha_1 y^*$ in the plant-only model (see Fig. 1a). Therefore having a seed bank increases the size of the equilibrium plant population, while keeping the equilibrium population structure $(I - A)^{-1} b$ the same.

If the equilibrium population in the plant-only model is already at or near saturation, the increase in equilibrium population achieved through having a viable seed bank

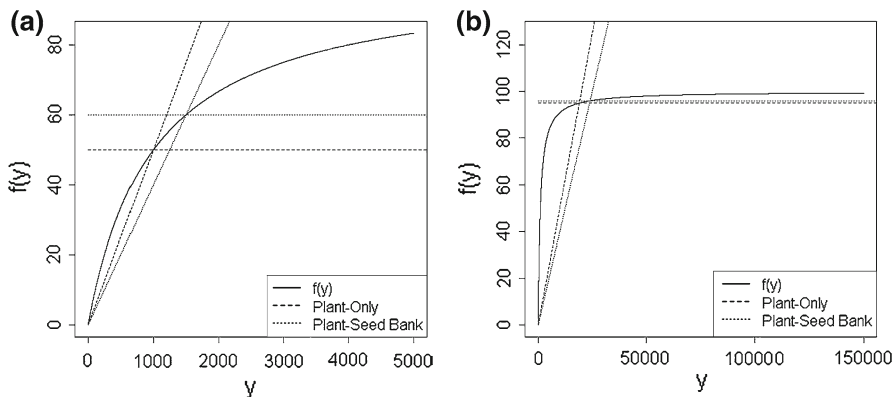


Fig. 1 An illustration of the differences between having and not having a viable seed bank through the calculation of the equilibrium recruitments $p_e y^*/\alpha_1$ (“plant-only”) and $\tilde{p}_e y^*$ (“plant-seed bank”) used in the calculation of n^* and \tilde{n}^* . **a** Illustrates the effect of having a seed bank when the equilibrium recruitment is not near saturation and **b** illustrates the effect of having a seed bank when the equilibrium recruitment is near saturation. The differences between the horizontal dashed lines indicates roughly the long-term effect of having a viable seed bank on the size of the equilibrium plant population

will be negligible. An example of this occurring can be seen in Fig. 1b. Therefore, while having a viable seed bank in the absence of environmental stochasticity (i.e. $\gamma_1, \alpha_2 > 0$) will always be advantageous for the plant population in the long-term (sometimes even elevating it from extinction), the degree to which the seed bank positively impacts the long-term plant population size is determined by how close the equilibrium population in the plant-only model is to its carrying capacity without help from the seed bank.

3.2 Density-dependent seed production: contest competition

We now assume that $h \in C[0, \infty)$ is increasing and concave down into $[0, \infty)$, with $h(0) = 0$. In this case the seed production nonlinearity models *contest competition* (Anazawa 2012), where it is assumed that when there are many competitors some competitors obtain all the resources they need for seed production, while the rest obtain insufficient resources. The mathematical assumptions on h are reflecting the idea that, as the number of potential seed production events increases, so does the number of successful seed productions, but at a decreasing rate. We also assume that $h(y) \leq y$ for every $y \geq 0$, so the maximum density-dependent seed production is no greater than the density-independent seed production. For the remainder of the paper we will assume that

$$g_\infty := \lim_{y \rightarrow \infty} g(y) = 0,$$

i.e. the establishment probability goes to zero as the number of seedlings goes to infinity.

We now motivate what we expect for the equilibrium vector. Since there are two nonlinearities f and h in this model, it is reasonable that our results should depend upon *two* stability radii, as \tilde{A} is a nonlinear operator. The presence of the second stability radius actually gives us an extra degree of freedom to identify a nonzero equilibrium vector. To see this, assume for the moment that $h(y) = p_2 y$ for some fixed $p_2 \in (0, 1)$. The number p_2 is what we envision as the equilibrium proportion of maximum seed production $c^T n_t$. This would indeed be a constant if y is an equilibrium population. Now consider the system (2.5), with $h(c^T n_t)$ replaced by $p_2 c^T n_t$. This modified system is equivalent to

$$\tilde{n}_{t+1} = \tilde{A}_{p_2} \tilde{n}_t + \tilde{b} f(\tilde{y}_t), \quad \tilde{y}_t = \tilde{c}_{p_2}^T \tilde{n}_t, \quad (3.5)$$

with

$$\tilde{A}_{p_2} := \begin{bmatrix} A & \emptyset \\ \Gamma_{p_2} & S \end{bmatrix}, \quad \tilde{c}_{p_2}^T := [p_2 \alpha_1 c^T \quad \alpha^T], \quad \Gamma_{p_2} := [p_2 \gamma_1 c^T \quad 0^T \quad \cdots \quad 0^T]^T.$$

Notice that \tilde{A}_{p_2} is now a linear operator. It follows from Theorem 3.1 that, if $g_0 > p_1$ the system has a globally stable equilibrium vector

$$\tilde{n}^* = p_1 y^* (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b},$$

with stability radius

$$p_1 = (\tilde{c}_{p_2}^T (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b})^{-1}$$

and y^* is the positive solution of

$$f(y^*) = p_1 y^*. \quad (3.6)$$

Since the linear data \tilde{A}_{p_2} , \tilde{b} and \tilde{c}_{p_2} are non-negative p_1 is the only positive number p such that $r(\tilde{A}_{p_2} + p\tilde{b}\tilde{c}_{p_2}^T) = 1$. Theorem 3.1 then implies that if $g_0 < p_1$ the equilibrium is the zero vector and if $g_0 > p_1$ the equilibrium is a non-zero vector. We will show in the upcoming theorem that this informal discussion actually coincides with the model predictions when we allow $h \in C[0, \infty)$ to be increasing and concave down into $[0, \infty)$, with $h(0) = 0$, instead of $h(y) = p_2 y$.

We can determine (p_1, p_2, y^*) at the equilibrium easily through a system of three equations and three unknowns, in terms of the original system data. Note that

$$(\tilde{I} - \tilde{A}_{p_2})^{-1} = \begin{bmatrix} (I - A)^{-1} & \emptyset \\ (I - S)^{-1} \Gamma_1 p_2 c^T (I - A)^{-1} & (I - S)^{-1} \end{bmatrix},$$

Hence, by a simple computation,

$$p_1^{-1} = \tilde{c}_{p_2}^T (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b} = \frac{p_2 (\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1)}{p_e}. \quad (3.7)$$

where $p_e := (c^T (I - A)^{-1} b)^{-1}$. Furthermore,

$$\tilde{n}^* = p_1 y^* (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b} = [n^* \ s^*]^T = p_1 y^* \left[(I - A)^{-1} b \ \frac{p_2 (I - S)^{-1} \Gamma_1}{p_e} \right]^T. \quad (3.8)$$

and, since $c^T n^* = \frac{p_1 y^*}{p_e}$,

$$h(c^T n^*) = p_2 c^T n^* = \frac{p_2 p_1 y^*}{p_e}. \quad (3.9)$$

We can think of Eqs. (3.6), (3.7) and (3.9) as the following three (slightly rewritten) equations in the three unknowns p_1 , p_2 and y^* :

$$\begin{aligned} g(y^*) &= p_1 \\ p_1 p_2 &= \frac{p_e}{(\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1)} \\ h\left(\frac{p_1 y^*}{p_e}\right) &= \frac{p_2 p_1 y^*}{p_e}. \end{aligned} \quad (3.10)$$

From the above discussion and component-wise calculation on (3.8) we see that if (p_1, p_2, y^*) satisfies (3.10), then \tilde{n}^* is a non-zero equilibrium for (3.5).

Since $p_1, p_2 > 0$ (by the second equation in (3.10)), either $y^* = 0$ or the point (p_1, p_2, y^*) is in $(0, g_0) \times (0, 1) \times (0, \infty)$. If $(p_1, p_2, y^*) \in (0, g_0) \times (0, 1) \times (0, \infty)$ one can obtain the triple (p_1, p_2, y^*) easily via (3.10) and compute the equilibrium $\tilde{n}^* = p_1 y^* (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b}$, whose global asymptotic stability is the subject of the next theorem.

Theorem 3.2 *Suppose that (E1), (E2), (E3), (E4) and (D1) hold, and that $h(y)$ is continuous, strictly increasing, and concave down on $[0, \infty)$ with $h(0) = 0$. Further assume that $h(y) \leq y$ on $[0, \infty)$.*

(1) *If*

$$\frac{p_e}{\alpha_1 + \alpha^T(I - S)^{-1}\Gamma_1} = (\tilde{c}_1^T(\tilde{I} - \tilde{A}_1)^{-1}\tilde{b})^{-1} > g_0,$$

then the zero vector is a globally stable equilibrium for the system (2.7) in the sense that for every non-negative \tilde{n}_0 ,

$$\lim_{t \rightarrow \infty} \tilde{n}_t = 0.$$

Furthermore, for every $\epsilon > 0$, there exists $\delta > 0$ such that $\|\tilde{n}_t\| < \epsilon$ for all $t \in \mathbb{N}$ whenever $\|\tilde{n}_0\| < \delta$.

(2) *If there exists a solution (p_1, p_2, y^*) of (3.10) in $(0, g_0) \times (0, 1) \times (0, \infty)$, then the vector \tilde{n}^* given by*

$$\tilde{n}^* = p_1 y^* (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b}$$

is a strictly positive globally asymptotically stable equilibrium of the system (2.7) in the sense that for every positive $\tilde{n}_0 \in X_1 \otimes X_2$

$$\lim_{t \rightarrow \infty} \tilde{n}_t = \tilde{n}^*.$$

Furthermore, for every $\epsilon > 0$, there exists $\delta > 0$ such that $\|\tilde{n}_t - \tilde{n}^\| < \epsilon$ for all $t \in \mathbb{N}$ whenever $\|\tilde{n}_0 - \tilde{n}^*\| < \delta$.*

The somewhat lengthy proof of this theorem has been put in Appendix A. The above result implies that the plant and seed bank populations converge to unique equilibrium populations, independent of non-zero initial populations, provided seedling establishment and seed production are limited by contest competition. Implicit in the statement of Theorem 3.2 is that if one writes the model (2.7) as

$$\tilde{n}_{t+1} = T\tilde{n}_t,$$

where $T : X^+ \rightarrow X^+$, and if g and h are assumed to be differentiable at 0, then T is Fréchet differentiable at the zero vector in X , with Fréchet derivative

$$T'(0) = \tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T.$$

A triple (p_1, p_2, y^*) in $(0, g_0) \times (0, 1) \times (0, \infty)$ solves (3.10) if and only if

$$1 \in \sigma(\tilde{A}_{p_2} + p_1 \tilde{b} \tilde{c}_{p_2}^T).$$

To show that $r(\tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T) > 1$ when (p_1, p_2, y^*) is in $(0, g_0) \times (0, 1) \times (0, \infty)$, we note that the stability radius

$$p_1 = (\tilde{c}_{p_2}^T (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{b})^{-1}$$

of the linear data $(\tilde{A}_{p_2}, \tilde{b}, \tilde{c}_{p_2}^T)$ is greater than the stability radius

$$p = (\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1}$$

of the linear data $(\tilde{A}_1, \tilde{b}, \tilde{c}_1^T)$, (expand $(\tilde{I} - \tilde{A}_{(\cdot)})^{-1}$ by its Neumann series and use the fact that $p_2 < 1$). Since $g_0 > p_1$, this implies that

$$r(\tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T) \geq 1.$$

We now rule out that $r(\tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T) = 1$. Suppose that it is. Then from Krasnosel'skij et al. (1989) (see also Theorem B.6 in Lubben et al. (2009), which places Krasnosel'skij et al.'s work into this $(\tilde{A}_{(\cdot)}, \tilde{b}, \tilde{c}_{(\cdot)})$ framework) there is an eigenvector \tilde{v} such that

$$(\tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T) \tilde{v} = \tilde{v}.$$

Using a standard manipulation we get that

$$g_0 = (\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1} = p < p_1$$

which contradicts that $g_0 > p_1$. Thus, $r(T'(0)) > 1$ implies that \tilde{n}^* is positive, as expected.

We've also shown in Theorem 3.2 (1) that

$$(\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1} > g_0$$

implies that $\tilde{n}^* = 0$. But $(\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1} > g_0$ if and only if

$$r(\tilde{A}_1 + g_0 \tilde{b} \tilde{c}_1^T) = r(T'(0)) < 1.$$

Thus, $r(T'(0)) < 1$ implies that $\tilde{n}^* = 0$, as expected.

3.3 Density-dependent seed production: scramble competition

In this section we consider the case where the function h models *scramble competition* (Anazawa 2012).

In scramble competition, when there are many competitors, the available resources are insufficient for any one competitor. This is often assumed to be the case for plant populations (Symonides et al. 1986). In this case we no longer require h to be increasing and concave down, since for large y it is possible that seed production eventually decreases to zero. However, a function h that describes scramble competition may, for small $y > 0$, look much like a function that describes contest competition (increasing, concave down, with $h(0) = 0$), only to eventually level off and decrease so that $\lim_{y \rightarrow \infty} h(y) = 0$.

A key to the proof of Theorem 3.1 is the fact that h is *sector bounded*, which means here that

$$|h(y) - h(y^*)| \leq p_2 |y - y^*| \quad (3.11)$$

for all $y > 0$.

It is clear that h does not need to be strictly increasing for this to occur. In this section we will consider the Ricker function proposed in Jarry et al. (1995) for seed production density dependence:

$$h_R(y) = y \exp(-y/c_m), \quad (3.12)$$

where $y = c_m$ elicits the maximum seed production $c_m \exp(-1)$. This function may or may not be sector bounded, see Fig. 2. We will show that some of Theorem 3.2 holds for $h = h_R$.

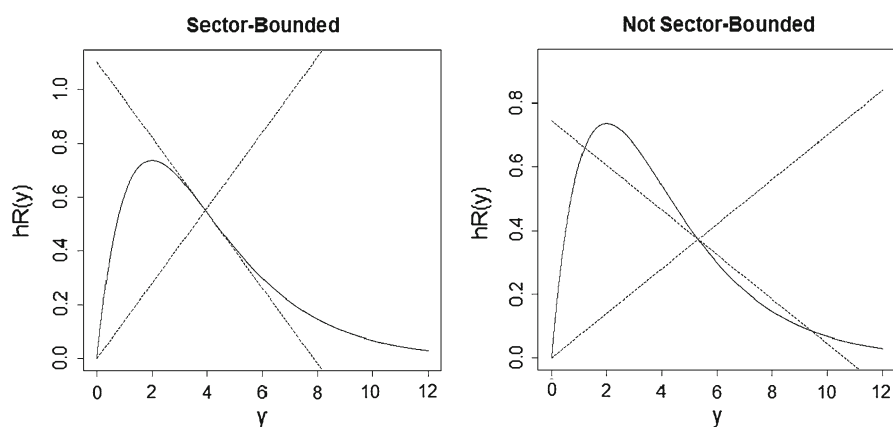


Fig. 2 An example of a Ricker function h_R (modeling scramble competition), with sectors defined by lines with slopes $\pm p_2$ (dotted). The figure on the left has $p_2 \in (\exp(-2), 1)$, which implies that h_R is sector bounded, while the figure on the right has $p_2 < \exp(-2)$, which implies that h_R is not sector bounded

Theorem 3.3 Suppose that (E1), (E2), (E3), (E4) and (D1) hold and $h = h_R$.

- (1) If $(\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1} > g_0$, then the conclusions in part 1) of Theorem 3.2 hold.
- (2) If there exists a solution (p_1, p_2, y^*) of (3.10) in $(0, g_0) \times (\exp(-2), 1) \times (0, \infty)$ then the conclusions in part (2) of Theorem 3.2 hold.
- (1) If there exists a solution (p_1, p_2, y^*) of (3.10) in $(0, g_0) \times (0, \exp(-2)) \times (0, \infty)$ and f is further assumed to be $C^1(0, \infty)$, with

$$r(\tilde{A}_{(1+\ln(p_2))p_2} + f'(y^*)\tilde{b}\tilde{c}_{(1+\ln(p_2))p_2}^T) < 1,$$

then \tilde{n}^* is asymptotically stable.

The proof of this theorem is in Appendix B. The assumptions and conclusions of Theorem 3.3 are very similar to that of Theorem 3.2, with the exception that the second stability radius p_2 cannot be so small that the decrease in seed production h , as the number of maximum seed production events increases, is too steep at equilibrium (see Fig. 2). Biologically this means that the equilibrium proportion of potential seed production events that actually produce seeds needs to be large enough to avoid the harsh consequences of scramble competition.

Now we consider specifically the case where $X_1 = L^1[L, U]$ and

$$X_1^+ = L^1[L, U]^+ = \{n \in L^1[L, U] | n(x) \geq 0 \text{ a.e.}\}. \quad (3.13)$$

Here, we assume the population projection operator $A \in \mathcal{L}(X_1)$ is an integral operator

$$An = \int_L^U k(x, y)n(y) dy, \quad (3.14)$$

from an IPM, and that the functional c^T is given by

$$c^T n = \int_L^U c(y)n(y) dy, \quad (3.15)$$

for $n \in L^1[L, U]^+$. If condition (E3) is changed to

$$c^T n = \int_L^U c(y)n(y) dy \geq 0 \quad (3.16)$$

for all $n \in L^1[L, U]^+$ (i.e. $c(x) \geq 0$ for all $x \in [L, U]$), we can obtain the results in Theorems 3.1, 3.2 and 3.3. Equation (3.16) is a weaker hypothesis than (E3), which insists upon the existence of a $c_{\min} > 0$ such that $c(x) \geq c_{\min}$ for all $x \in [L, U]$. $L^1[L, U]^+$ is a natural mathematical space for an IPM, and (3.16) is a reasonable assumption for an IPM to satisfy. Formally,

Corollary 3.1 Suppose that $X^1 = L^1[L, U]$ and X_1^+ , A and c^T are given by (3.13), (3.14) and (3.15), respectively. Assume further that (E1), (E2), (E4), (D1) and (3.16) hold.

- (1) If $h(y) = y$, then the conclusions of Theorem 3.1 hold.
- (1) If h is increasing, concave down, with $h(0) = 0$, then the conclusions of Theorem 3.2 hold.
- (1) If $h = h_R$, then the conclusions of Theorem 3.3 hold.

The proof of this corollary is in Appendix C.

3.4 Nonlinear feedbacks from adult plants

As alluded to in Sect. 2, in perennial plant populations adult conspecifics can elicit a negative density-dependent feedback on seedling establishment (Silva Matos et al. 1999; Picò and Retana 2008). To incorporate a negative feedback from adult conspecifics on seedling establishment we will assume that f is a function of \tilde{y}_t , and of some measurement of the amount of resources that are taken up by adult plants at time t , which we will call $\tilde{z}_t := d^T A n_t$. Here, d is a functional from X_1 to \mathbb{R}^+ modeling the amount of resources that a seedling would use for establishment that is taken up by the surviving plants in the plant population at time t . It is reasonable to assume, as before, that $f(\cdot, z)$ is increasing, concave down in y with $f(0, z) = 0$ for each fixed z . To model the negative feedback from adult plants we will then assume that $f(y, \cdot)$ is a decreasing function in z for each fixed y . Examples of functions that incorporate these assumptions are a modified power function of the form

$$f(y) = \frac{By}{(z + y)^{1-a}} \quad \text{with } a \in (0, 1) \quad \text{and } B > 0,$$

or a modified Michaelis-Menten-type function of the form

$$f(y) = \frac{\alpha y}{\beta + z + y} \quad \text{with } \alpha > 0 \quad \text{and } \beta > 0.$$

With these new assumptions, (2.7) becomes

$$\tilde{n}_{t+1} = \tilde{A}\tilde{n}_t + \tilde{b}f(\tilde{y}_t, \tilde{z}_t). \quad (3.17)$$

Because f no longer satisfies

$$|f(y_t, z_t) - f(y^*, z^*)| \leq p_1 |y_t - y^*|,$$

the methods used in Theorems 3.1, 3.2, 3.3 cannot be used to establish the global stability of the plant-seed bank population in (3.17) under these assumptions. However, if we assume that h is either linear or models contest competition, we can use the results from Theorems 3.1 and 3.2 to show that, in many cases, the plant-seed bank population is eventually bounded between two globally stable plant-seed bank populations. To see this, note that since f is decreasing in z and h is increasing, (3.17) is bounded from above by the model

$$\bar{n}_{t+1} = \tilde{A}\bar{n}_t + \tilde{b}f(\bar{y}_t, 0) \quad (3.18)$$

for all $t \geq 0$. Let

$$g_0(z) := \limsup_{y>0} \frac{f(y, z)}{y}.$$

Theorems 3.1 and 3.2 imply that, if $(\tilde{c}_1^T(\tilde{I} - \tilde{A}_1)^{-1}\tilde{b})^{-1} > g_0(0)$, then \bar{n}_t has a nonzero, globally stable equilibrium population \bar{n}^* . Since \tilde{n}_t is always less than \bar{n}_t , there exists an $M_0 \in \mathbb{N}$ such that, for all $t \geq M_0$,

$$\tilde{n}_t \leq \bar{n}^*. \quad (3.19)$$

Using this we find that, since f is decreasing in z , \tilde{n}_t is greater than \underline{n}_t for all $t \geq M_0$, where $\bar{z}^* := d^T A \bar{n}^*$ and

$$\underline{n}_{t+1} = \tilde{A}\underline{n}_t + \tilde{b}f(\underline{y}_t, \bar{z}^*). \quad (3.20)$$

By Theorems 3.1 and 3.2, if $(\tilde{c}_1^T(\tilde{I} - \tilde{A}_1)^{-1}\tilde{b})^{-1} > g_0(\bar{z}^*)$ then \underline{n}_t has a positive, globally stable equilibrium population \underline{n}^* and there exists a $M_1 \geq M_0$ such that, for all $t \geq M_1$,

$$\tilde{n}_t \geq \underline{n}^*. \quad (3.21)$$

The estimates (3.19) and (3.21) for large t provide an asymptotic estimate for n_t . As long as $\underline{n}^* \neq 0$ one could continue to in this way to construct a decreasing sequence $\{\bar{n}_j^*\}_{j=0}^\infty$ that overestimates the population in (3.17) and an increasing sequence $\{\underline{n}_j^*\}_{j=0}^\infty$ that underestimates the population in (3.17). The global stability of \tilde{n}_t would then follow if the limits of the two sequences are the same, which remains an open question.

4 Example

We now illustrate the utility of our results with a modified IPM model for the plant *C. palustre* L. (Asteraceae) and its seed bank (Ramula et al. 2009). *Cirsium palustre* is a tall, short-lived, monocarpic herb that is widely distributed throughout northern Europe and eastward to central Asia. Reproduction is usually fatal for *C. palustre*. In this model the plant's rosette diameter x is a continuous stage variable. We denote the plant population at each time t with the function $n(x)_t$, and the operator A is an integral operator, which takes the form

$$An := \int_L^U p(x, y)n(y)dy = \int_L^U s(y)(1 - f_p(y))g(x, y)n(y)dy,$$

for $n \in L^1[L, U]$, where $s(y)$ is probability of survival, $f_p(y)$ the probability of flowering, and $g(x, y)$ the probability of plants that were size y becoming plants of size x in one time-step. L and M are the minimum and maximum sizes for the plant population, respectively. The $(1 - f_p(\cdot))$ is present in $p(\cdot, \cdot)$ because flowering is fatal. The functional c^T takes the form

$$c^T n := \int_L^U F(y)n(y)dy = \int_L^U f_p(y)f_d(y)n(y)dy,$$

where $f_d(y)$ is the seed production of a plant of size y in each time-step. The vector b is assumed to be a (truncated) normal probability distribution $J(\cdot)$

In the model by [Ramula et al. \(2009\)](#) the seed bank was assumed to be one dimensional. We modify this assumption to allow for a two-dimensional seed bank, where seed survival in the seed bank is s_s for one-year old seeds and s_s^2 for seeds two years and older. Since the seed bank is two-dimensional we are assuming that all seeds two years and older have the same survival and germination probabilities as two-year old seeds. The germination rate for fresh seeds is s_e and the recruitment (germination) probability of older seeds is s_r . Thus, $\alpha_1 = s_e, \alpha_2 = \alpha_3 = s_r, \gamma_1 = (1 - s_e)$ and $\gamma_2 = (1 - s_r)s_s^2$. We will first assume that f and h are Holling functions of the form

$$f(y) = \frac{\alpha y}{\beta + y} \quad h(y) = \frac{c_m y}{c_m + y},$$

where α is the maximum density of established seedlings, c_m is the maximum possible seed production, and β is seedling establishment's half-saturation constant. In this scenario we are assuming that density dependence in seed production is subject to contest competition. With these assumptions, our model becomes

$$\begin{aligned} n(x)_{t+1} &= \int_L^U p(x, y)n(y)_t dy + J(x)f \left(s_e h \left(\int_L^U F(y)n(y)_t dy \right) + s_r(s_{1,t} + s_{2,t}) \right) \\ s_{1,t+1} &= (1 - s_e)h \left(\int_L^U F(y)n(y)_t dy \right) \\ s_{2,t+1} &= (1 - s_r)s_s s_{1,t} + (1 - s_r)s_s^2 s_{2,t}. \end{aligned} \quad (4.1)$$

Using the data in [Ramula et al. \(2009\)](#), with the assumption that $\alpha, \beta, c_m > 0$, (4.1) clearly satisfies the conditions (E1),(E2),(E4), (D1) and (3.16). Figure 3 shows trajectories of the solutions to (4.1) with two different (α, β, c_m) combinations and several initial populations, as well as the (p_1, p_2, y^*) combinations elicited by these parameter combinations. Notice that, while both parameter combinations elicit eventual convergence to the equilibrium vector, transient amplifications and attenuations can be very pronounced depending on the initial population structure.

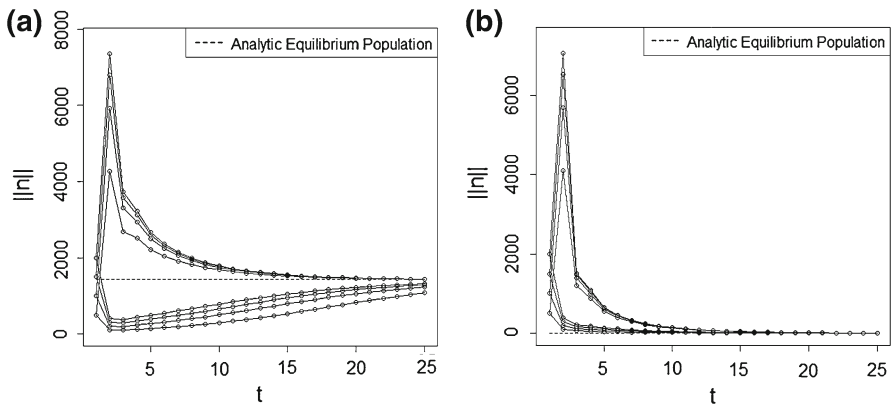


Fig. 3 Example population trajectories from the model (4.1) for the following (α, β, c_m) combinations: **a** (2,000, 2,500, 10,000) and **b** (200, 400, 10,000), with (p_1, p_2, y^*) combinations **(a)** $(0.509, 0.861, 1429) \in (0, g_0) \times (0, 1) \times (0, \infty) = (0, 0.8) \times (0, 1) \times (0, \infty)$ and **(b)** $(0.648, 1, 0) \notin (0, 0.500) \times (0, 1) \times (0, \infty)$. The model in **(a)** predicts global asymptotic stability of a non-zero population vector, while the model in **(b)** predicts the population will go extinct. The initial populations are $\|\tilde{n}_0\| = 500, 1, 000, 1, 500, 2, 000$ both distributed uniformly across plant sizes and skewed towards smaller plants

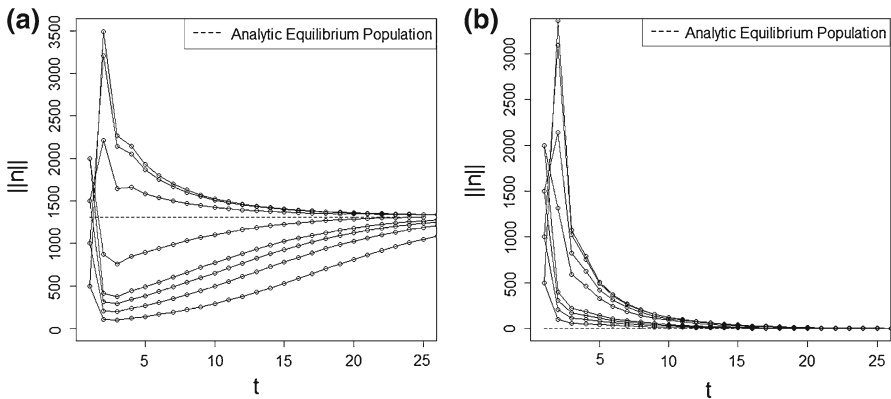


Fig. 4 Example population trajectories from the model (4.1) with the same (α, β, c_m) combinations as in Fig. 3, with (p_1, p_2, y^*) combinations **(a)** $(0.520, 0.858, 1349) \in (0, g_0) \times (e^{-2}, 1) \times (0, \infty) = (0, 0.8) \times (0, 1) \times (0, \infty)$ and **(b)** $(0.648, 1, 0) \notin (0, 0.500) \times (e^{-2}, 1) \times (0, \infty)$. The model in **(a)** predicts global asymptotic stability of a non-zero population vector, while the model in **(b)** predicts the population will go extinct. The initial populations are $\|\tilde{n}_0\| = 500, 1, 000, 1, 500, 2, 000$ both distributed uniformly across plant sizes and skewed towards smaller plants

We now assume that density dependence in seed production is subject to scramble competition. Figure 4 shows trajectories of the solutions to (4.1) with h equal to the Ricker function

$$h_R(y) = ye^{-y/cm},$$

where now c_m/e is the maximum possible seed production. These trajectories were for the same (α, β, c_m) combinations and initial populations as Fig. 3. Notice that, much

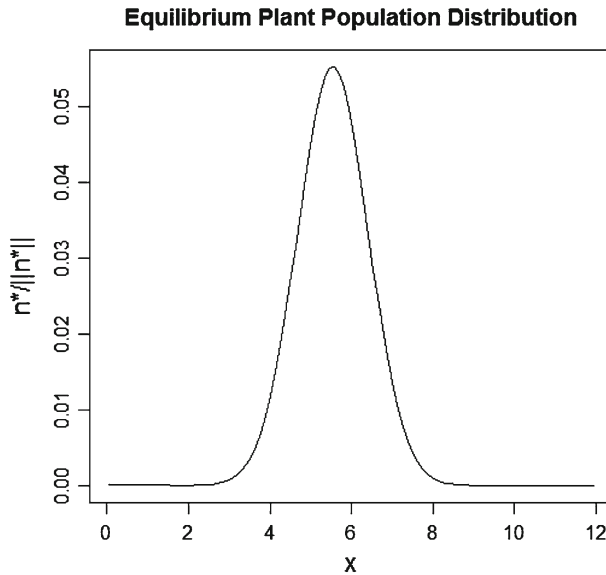


Fig. 5 The long-term distribution of the plant population from (4.1), which is proportional to $(I - A)^{-1}b$

like the model with contest competition, both parameter combinations elicit eventual convergence to the equilibrium vector, with transient amplifications and attenuations that can be very pronounced depending on the initial population structure. This global asymptotic stability was present for all biologically realistic (α, β, c_m) combinations. Thus, while Theorem 3.3 states that there are (p_1, p_2, y^*) combinations that do not elicit global asymptotic stability, in this example these combinations do not appear to occur.

Figure 5 shows the long-term size distribution of the plant population which, provided that the equilibrium is non-zero, will always be proportional to the vector $(I - A)^{-1}b$, regardless of what (α, β, c_m) and h are.

5 Discussion

We proved the existence and global stability of an equilibrium population for a class of density-dependent structured plant population models with an age-structured seed bank. We showed mathematically how a plant-only model can predict extinction, while the addition of a seed bank (i.e. assuming that seeds that don't germinate initially are still viable after one year) can cause the prediction of persistence of the same plant population as $t \rightarrow \infty$. We applied our theoretical results to a plant-seed bank model for *C. palustre*. The techniques we used include so-called “small gain” arguments and the use of different stability radii that are common in engineering problems involving feedback systems, which have been modified from Rebarber et al. (2012) and Townley et al. (2012). When the seed production is density independent, the modification is minor, see Sect. 3.1. However, if the seed production is density dependent (i.e. h is

nonlinear) there are two nonlinearities present in the model. In his case the global stability properties are determined by the relationship (3.10) between the two stability radii p_1 and p_2 (determined by the linear part of the system) and the nonlinearities g and h . These techniques point the way towards analysis of more complicated density dependence.

We provide an explicit formula for the equilibrium population, which can then be analyzed using sensitivity analysis to gain biological insight with regard to how different life-history traits influence the size and structure of the population at equilibrium. Also, one could use the results of this model to study the upper bound, lower bound, mean or moments of a stochastic population model with a deterministic signature similar to that of (2.7).

The results in this paper are applicable to different types of density-dependent plant-seed bank models in ecology due to the fact that we assumed very little about the mathematical object used to model the plant population. For example, many ecologists use integral projection models (IPMs) for plant populations (because fecundity and survival typically depend on plant size, which is a continuous stage variable (Childs et al. 2003, 2004; Rose et al. 2005; Ellner and Rees 2006; Ramula et al. 2009)). One limitation of the mathematical analysis in this paper is that we initially assume that density-dependent feedbacks only occur from seedlings to other seedlings and ignore density-dependent feedbacks from adult plants. While the ramifications of this oversimplification is dependent on the biological system of interest (whether the plant is an annual or perennial, for example), we showed that, in the case where h is linear or models contest competition, when one adds the assumption of negative density-dependent feedbacks from adult plants the resulting population is often eventually bounded between two positive, globally stable equilibrium populations. This suggests that, in many cases, our initial oversimplification is not an egregious one.

In addition to addressing feedback from adult plants, other future research related to the results in this paper include broadening the class of ecologically plausible functional forms for h , structuring the seed bank with respect to a variable other than age (e.g. how deep the seeds are buried in the soil), as well as incorporating stochasticity into the model.

Acknowledgments The authors would like to thank professors Glenn Ledder and Steve Dunbar for their helpful comments about the mathematical model during the final stages of this work. The authors would also like to thank Associate Editor Sebastian Schreiber and the two anonymous reviewers for their constructive suggestions that greatly improved the quality of the manuscript.

Appendix A

Proof of Theorem 3.2 Without loss of generality, we can assume that n_0 is in $K_1 \setminus \{0\}$. If it is not, then $s_i \neq 0$ for some $i = 1, 2, \dots, N$, which would imply that $n_1 \in K_1 \setminus \{0\}$.

To prove part (1) of Theorem 3.2, since $(\tilde{c}_1^T (\tilde{I} - \tilde{A}_1)^{-1} \tilde{b})^{-1} > g_0 = \sup_{y>0} g(y)$ and $h(y) \leq y$,

$$\tilde{n}_{t+1} \leq \tilde{A}_1 \tilde{n}_t + \tilde{b} g(\tilde{c}_1^T \tilde{n}_t) \tilde{c}_1^T \tilde{n}_t \leq \tilde{A}_1 \tilde{n}_t + m \tilde{b} \tilde{c}_1^T \tilde{n}_t,$$

for some $m < p_1$. By induction

$$\tilde{n}_t \leq (\tilde{A}_1 + m\tilde{b}\tilde{c}_1^T)^t \tilde{n}_0, \quad t \in \mathbb{N}.$$

Since $p_1 = (\tilde{c}_1^T(\tilde{I} - \tilde{A}_1)^{-1}\tilde{b})^{-1}$ is the stability radius of $(\tilde{A}_1, \tilde{b}, \tilde{c}_1^T)$, we have that $r(\tilde{A}_1 + m\tilde{b}\tilde{c}_1^T) < 1$. Thus

$$\lim_{t \rightarrow \infty} \tilde{n}_t = 0.$$

The (ϵ, δ) conclusion follows from the boundedness of $\tilde{A}_1 + m\tilde{b}\tilde{c}_1^T$.

For (2), with the triple $(p_1, p_2, y^*) \in (0, g_0) \times (0, 1) \times (0, \infty)$ satisfying (3.10) define the functional

$$\tilde{w}_{p_2}^T := \tilde{c}_{p_2}^T(\tilde{I} - \tilde{A}_{p_2})^{-1}. \quad (6.1)$$

It is straightforward to verify that

$$\tilde{w}_{p_2}^T(\tilde{A}_{p_2} + p_1\tilde{b}\tilde{c}_{p_2}^T) = \tilde{w}_{p_2}^T. \quad (6.2)$$

Applying $\tilde{w}_{p_2}^T$ to (2.7),

$$\tilde{w}_{p_2}^T \tilde{n}_{t+1} = \tilde{w}_{p_2}^T \tilde{A} \tilde{n}_t + \tilde{w}_{p_2}^T \tilde{b} f(\tilde{y}_t). \quad (6.3)$$

If $\tilde{y}_t \leq y^*$ and $c^T n_t \leq c^T n^*$, then, since both f and h are increasing, concave down with $f(0) = h(0) = 0$, we have that $f(\tilde{y}_t) \geq p_1 y_t$ and $h(c^T n_t) \geq p_2 c^T n_t$, so (6.3) implies that

$$\tilde{w}_{p_2}^T \tilde{n}_{t+1} \geq \tilde{w}_{p_2}^T (\tilde{A}_{p_2} + p_1 \tilde{b} \tilde{c}_{p_2}^T) \tilde{n}_t = \tilde{w}_{p_2}^T \tilde{n}_t. \quad (6.4)$$

If $\tilde{y}_t \leq y^*$ and $c^T n_t \geq c^T n^*$, then $f(\tilde{y}_t) \geq p_1 \tilde{y}_t$ and $h(c^T n_t) \geq p_2 c^T n^*$, so (6.3) implies that

$$\tilde{w}_{p_2}^T \tilde{n}_{t+1} \geq \tilde{w}_{p_2}^T \tilde{A} \tilde{n}_t + \tilde{w}_{p_2}^T p_1 \tilde{b} (\alpha_1 h(c^T n_t) + \alpha^T s_t) \geq p_2 p_1 \alpha_1 \tilde{w}_{p_2}^T \tilde{b} c^T n^*. \quad (6.5)$$

If $\tilde{y}_t \geq y^*$, then $f(\tilde{y}_t) \geq p_1 y^*$, so (6.3) implies that

$$\tilde{w}_{p_2}^T \tilde{n}_{t+1} \geq \tilde{w}_{p_2}^T \tilde{A} \tilde{n}_t + \tilde{w}_{p_2}^T p_1 \tilde{b} y^* \geq p_1 \tilde{w}_{p_2}^T \tilde{b} y^*. \quad (6.6)$$

Hence (6.4), (6.5) and (6.6) imply that

$$\tilde{w}_{p_2}^T \tilde{n}_t \geq \min\{\tilde{w}_{p_2}^T \tilde{n}_0, p_2 p_1 \alpha_1 \tilde{w}_{p_2}^T \tilde{b} c^T n^*, p_1 \tilde{w}_{p_2}^T \tilde{b} y^*\}. \quad (6.7)$$

By Holder's inequality

$$\tilde{w}_{p_2}^T \tilde{n}_t \leq \|\tilde{w}_{p_2}\| \|\tilde{n}_t\|, \quad \text{so} \quad \|\tilde{n}_t\| \geq \frac{1}{\|\tilde{w}_{p_2}\|} \tilde{w}_{p_2}^T \tilde{n}_t. \quad (6.8)$$

Using again that either $h(c^T n_t) \geq p_2 c^T n_t$ or $h(c^T n_t) \geq p_2 c^T n^* = \frac{p_1 p_2 y^*}{p_e}$, it follows from (6.8) that

$$\tilde{y}_t = \alpha_1 h(c^T n_t) + \alpha^T s_t \geq \min\left\{\frac{\min\{\alpha_1 p_2 c_{\min}, \alpha_{\min}\}}{\|\tilde{w}_{p_2}^T\|} \tilde{w}_{p_2}^T \tilde{n}_t, \frac{\alpha_1 p_1 p_2 y^*}{p_e}\right\}.$$

Finally, since \tilde{n}_0 is a positive vector in $X_1 \otimes X_2$,

$$(\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{n}_0 = \tilde{n}_0 + \sum_{j=1}^{\infty} \tilde{A}_{p_2}^j \tilde{n}_0 \geq \tilde{n}_0. \quad (6.9)$$

Thus,

$$\tilde{w}_{p_2}^T \tilde{n}_0 = \tilde{c}_{p_2}^T (\tilde{I} - \tilde{A}_{p_2})^{-1} \tilde{n}_0 > \min\{\alpha_1 p_2 c_{\min}, \alpha_{\min}\} \|\tilde{n}_0\| \quad (6.10)$$

Similarly, $p_2 p_1 \alpha_1 \tilde{w}_{p_2}^T \tilde{b} c^T n^*$, and $\tilde{w}_{p_2}^T \tilde{b} p_1 y^*$ are positive, so \tilde{y}_t is bounded away from zero for all $t > 0$. Also, using condition (E3) and the fact that $n_0 \in K_1 \setminus \{0\}$, $c^T n_t$ is bounded away from zero for all $t > 0$, by a similar argument. Thus, since f and h are increasing and concave down (see Fig. 6), from the secant slopes

$$\frac{|f(\tilde{y}_t) - f(y^*)|}{|\tilde{y}_t - y^*|} < p_1 \quad \frac{|h(c^T n_t) - h(c^T n^*)|}{|c^T n_t - c^T n^*|} < p_2, \quad (6.11)$$

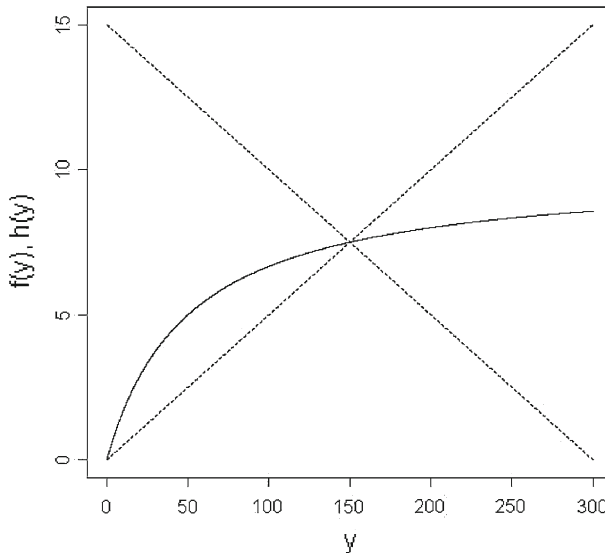


Fig. 6 Example nonlinearities f or h which satisfy (D1) with sectors defined by lines with slopes $\pm p_1$ or $\pm p_2$ (dotted), showing how (6.12) holds

we can find $m_1 < p_1$ and $m_2 < p_2$ such that for all $t \geq 0$,

$$|f(\tilde{y}_t) - f(y^*)| \leq m_1 |\tilde{y}_t - y^*| \quad |h(c^T n_t) - h(c^T n^*)| \leq m_2 |c^T n_t - c^T n^*|. \quad (6.12)$$

We can easily verify from (3.8) that $\tilde{n}^* = \tilde{A}_{p_2} \tilde{n}^* + p_1 \tilde{b} \tilde{c}_{p_2}^T \tilde{n}^* = \tilde{A} \tilde{n}^* + \tilde{b} f(y^*)$ by construction. Thus

$$\tilde{n}_{t+1} - \tilde{n}^* = \tilde{A} \tilde{n}_t - \tilde{A} \tilde{n}^* + \tilde{b} f(\tilde{y}_t) - \tilde{b} f(y^*). \quad (6.13)$$

Since \tilde{A} is nonlinear, the variation of parameters formula becomes

$$\begin{aligned} \tilde{n}_t - \tilde{n}^* &= \tilde{A}(\tilde{A}(\cdots \tilde{A}(\tilde{A} \tilde{n}_0 + \tilde{b} f(\tilde{y}_0)) + \tilde{b} f(\tilde{y}_1)) + \cdots) \\ &\quad + \tilde{b} f(\tilde{y}_{t-2})) + \tilde{b} f(\tilde{y}_{t-1}) - \tilde{A} \tilde{n}^* - \tilde{b} f(y^*) \end{aligned} \quad (6.14)$$

Since the $X_1 \rightarrow X_1$ and $X_2 \rightarrow X_1$ components of \tilde{A} ($[A \quad 0]$) are linear, and $\tilde{b} = [b \quad 0]^T$ we have that the X_1 component of $\tilde{n}_t - \tilde{n}^*$ satisfies

$$n_t - n^* = A^t(n_0 - n^*) + \sum_{j=0}^{t-1} A^{t-j-1} b(f(\tilde{y}_j) - f(y^*)). \quad (6.15)$$

Multiplying (6.15) on the left by $\tilde{c}_{p_2}^T$, we have

$$\begin{aligned} \alpha_1 p_2 c^T (n_t - n^*) &= \alpha_1 p_2 c^T A^t (n_0 - n^*) \\ &\quad + \alpha_1 p_2 \sum_{j=0}^{t-1} c^T A^{t-j-1} b(f(\tilde{y}_j) - f(y^*)), \end{aligned} \quad (6.16)$$

Taking absolute values and using positivity gives us that

$$\begin{aligned} |\alpha_1 p_2 c^T (n_t - n^*)| &\leq \alpha_1 p_2 |c^T A^t (n_0 - n^*)| \\ &\quad + \alpha_1 p_2 \sum_{j=0}^{t-1} c^T A^{t-j-1} b |f(\tilde{y}_j) - f(y^*)|. \end{aligned} \quad (6.17)$$

Using (6.12),

$$\begin{aligned} |\alpha_1 p_2 c^T (n_t - n^*)| &\leq \alpha_1 p_2 |c^T A^t (n_0 - n^*)| + \alpha_1 p_2 m_1 \sum_{j=0}^{t-1} c^T A^{t-j-1} b (\alpha_1 |h(c^T n_j) \\ &\quad - h(c^T n^*)| + |\alpha^T (s_j - s^*)|) \\ &\leq \alpha_1 p_2 |c^T A^t (n_0 - n^*)| + \alpha_1 p_2 m_1 \sum_{j=0}^{t-1} c^T A^{t-j-1} b \end{aligned}$$

$$\times (\alpha_1 m_2 |c^T n_j - c^T n^*| + |\alpha^T (s_j - s^*)|).$$

Summing from $t = 0$ to M , where M is large, we have

$$\begin{aligned} \sum_{t=0}^M |\alpha_1 p_2 c^T (n_t - n^*)| &\leq \sum_{t=0}^M \alpha_1 p_2 |c^T A^t (n_0 - n^*)| \\ &\quad + \alpha_1 p_2 m_1 \sum_{t=0}^M \sum_{j=0}^{t-1} c^T A^{t-j-1} b \\ &\quad \times \left(\alpha_1 m_2 |c^T n_j - c^T n^*| + |\alpha^T (s_j - s^*)| \right). \end{aligned} \quad (6.18)$$

Since $r(A) < 1$ the first term in (6.18) converges as $M \rightarrow \infty$. If we rearrange the second sum and use the fact that the system is positive, we have

$$\begin{aligned} \sum_{t=0}^M |\alpha_1 p_2 c^T (n_t - n^*)| &\leq \sum_{t=0}^{\infty} \alpha_1 p_2 |c^T A^t (n_0 - n^*)| \\ &\quad + \alpha_1 p_2 m_1 \sum_{j=0}^{M-1} (\alpha_1 m_2 |c^T n_j - c^T n^*| + |\alpha^T (s_j - s^*)|) \\ &\quad \times \sum_{t=j+1}^M c^T A^{t-j-1} b. \end{aligned}$$

Adding more terms and changing indices

$$\begin{aligned} \sum_{t=0}^M |\alpha_1 p_2 c^T (n_t - n^*)| &\leq \sum_{t=0}^{\infty} \alpha_1 p_2 |c^T A^t (n_0 - n^*)| \\ &\quad + \alpha_1 p_2 m_1 \sum_{t=0}^{M-1} (\alpha_1 m_2 |c^T n_t - c^T n^*| + |\alpha^T (s_t - s^*)|) \\ &\quad \times \sum_{k=0}^{\infty} c^T A^k b \leq \sum_{t=0}^{\infty} \alpha_1 p_2 |c^T A^t (n_0 - n^*)| \\ &\quad + \frac{\alpha_1 p_2 m_1}{p_e} \sum_{t=0}^M (\alpha_1 m_2 |c^T n_t - c^T n^*| + |\alpha^T (s_t - s^*)|). \end{aligned} \quad (6.19)$$

The X_2 component of \tilde{n}_t satisfies

$$s_t = \left(\sum_{j=0}^{t-1} S^{t-j-1} \Gamma_1 h(c^T A^j n_0 + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(\tilde{y}_k)) \right) + S^t s_0, \quad (6.20)$$

where $\Gamma_1 := [\gamma_1 \ 0 \ \dots \ 0]^T$. Since

$$c^T A^j n_0 + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(\tilde{y}_k) = c^T n_j$$

it follows that

$$s_t = \left(\sum_{j=0}^{t-1} S^{t-j-1} \Gamma_1 h(c^T n_j) \right) + S^t s_0. \quad (6.21)$$

Since \tilde{n}^* was a fixed point of our system, if we insert $[n^* \ s^*]^T$ for $[n_0 \ s_0]^T$ in (6.20) we obtain

$$\begin{aligned} s^* &= \left(\sum_{j=0}^{t-1} S^{t-j-1} \Gamma_1 h(c^T A^j n^* + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(y^*)) \right) + S^t s^* \\ &= \left(\sum_{j=0}^{t-1} S^{t-j-1} \Gamma_1 h(c^T n^*) \right) + S^t s^*. \end{aligned} \quad (6.22)$$

Thus, subtracting (6.22) from (6.21), and multiplying by α^T on the left gives us

$$\alpha^T (s_t - s^*) = \left(\sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 (h(c^T n_j) - h(c^T n^*)) \right) + \alpha^T S^t (s_0 - s^*), \quad (6.23)$$

Using (6.12), and the positivity of the system, we have that

$$|\alpha^T (s_t - s^*)| \leq \left(\sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 m_2 |c^T n_j - c^T n^*| \right) + |\alpha^T S^t (s_0 - s^*)|. \quad (6.24)$$

Putting

$$c^T n_j = c^T A^j n_0 + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(\tilde{y}_k)$$

and

$$c^T n^* = c^T A^j n^* + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(y^*)$$

back into (6.24) we obtain

$$\begin{aligned} |\alpha^T (s_t - s^*)| &\leq \left(\sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 m_2 |c^T A^j n_0 + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(\tilde{y}_k) - c^T A^j n^*| \right. \\ &\quad \left. + \sum_{k=0}^{j-1} c^T A^{j-k-1} b f(y^*) \right) + |\alpha^T S^t (s_0 - s^*)| \\ &\leq |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j (n_0 - n^*)| \\ &\quad + m_2 \sum_{j=0}^{t-1} \sum_{k=0}^{j-1} \alpha^T S^{t-j-1} \Gamma_1 c^T A^{j-k-1} b |f(\tilde{y}_k) - f(y^*)|. \end{aligned}$$

Summing from $t = 0$ to M , for M large, and rearranging we have

$$\begin{aligned} \sum_{t=0}^M |\alpha^T (s_t - s^*)| &\leq \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j n_0 - n^*| \\ &\quad + m_2 \sum_{k=0}^{M-2} |f(\tilde{y}_k) - f(y^*)| \sum_{t=k+2}^M \sum_{j=k+1}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 c^T A^{j-k-1} b \end{aligned}$$

Adding more terms and changing indices, we have

$$\begin{aligned} \sum_{t=0}^M |\alpha^T (s_t - s^*)| &\leq \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j n_0 - n^*| \\ &\quad + m_2 \sum_{t=0}^M |f(\tilde{y}_t) - f(y^*)| \sum_{j=0}^{\infty} \alpha^T S^j \Gamma_1 \sum_{k=0}^{\infty} c^T A^k b. \end{aligned}$$

Using (6.12) again,

$$\sum_{t=0}^M |\alpha^T (s_t - s^*)| \leq \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j (n_0 - n^*)|$$

$$\begin{aligned}
 & +m_1m_2 \sum_{t=0}^M |\tilde{y}_t - y^*| \sum_{j=0}^{\infty} \alpha^T S^j \Gamma_1 \sum_{k=0}^{\infty} c^T A^k b \\
 \leq & \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j (n_0 - n^*)| \\
 & +m_1m_2 \sum_{t=0}^M |\alpha_1 h(c^T n_t) + \alpha^T s_t - \alpha_1 h(c^T n^*) \\
 & -\alpha^T s^*| \sum_{j=0}^{\infty} \alpha^T S^j \Gamma_1 \sum_{k=0}^{\infty} c^T A^k b.
 \end{aligned}$$

Using the triangle inequality, as well as (6.12) again,

$$\begin{aligned}
 \sum_{t=0}^M |\alpha^T (s_t - s^*)| & \leq \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j (n_0 - n^*)| \\
 & +m_1m_2 \sum_{t=0}^M (\alpha_1 m_2 |c^T n_t - c^T n^*| + |\alpha^T (s_t - s^*)|) \\
 & \times \sum_{j=0}^{\infty} \alpha^T S^j \Gamma_1 \sum_{k=0}^{\infty} c^T A^k b.
 \end{aligned}$$

Since $\sum_{j=0}^{\infty} S^j = (I - S)^{-1}$ and $\sum_{k=0}^{\infty} A^k = (I - A)^{-1}$ we have

$$\begin{aligned}
 \sum_{t=0}^M |\alpha^T (s_t - s^*)| & \leq \sum_{t=0}^M |\alpha^T S^t (s_0 - s^*)| + m_2 \sum_{t=0}^M \sum_{j=0}^{t-1} \alpha^T S^{t-j-1} \Gamma_1 |c^T A^j (n_0 - n^*)| \\
 & + \frac{m_1m_2\alpha^T (I - S)^{-1} \Gamma_1}{p_e} \sum_{t=0}^M (\alpha_1 m_2 |c^T n_t - c^T n^*| \\
 & + |\alpha^T (s_t - s^*)|)
 \end{aligned} \tag{6.25}$$

The first two terms of (6.25) converge as $M \rightarrow \infty$, since $r(A) < 1$ and $\gamma_i < 1$ for all i . Define

$$\begin{aligned}
 L & := \sum_{t=0}^{\infty} \alpha_1 p_2 |c^T A^t (n_0 - n^*)| + \sum_{t=0}^{\infty} |\alpha^T S^t (s_0 - s^*)| \\
 & + m_2 \sum_{k=0}^{\infty} \sum_{j=0}^k S^j \Gamma_1 |c^T A^k (n_0 - n^*)| < \infty.
 \end{aligned}$$

Adding the (6.19) and (6.25) together, we obtain

$$\begin{aligned} \sum_{t=0}^M (|\alpha_1 p_2 c^T (n_t - n^*)| + |\alpha^T (s_t - s^*)|) &\leq L + \frac{\alpha_1 p_2 m_1 + m_2 m_1 \alpha^T (I - S)^{-1} \Gamma_1}{p_e} \\ &\quad \times \sum_{t=0}^M (\alpha_1 m_2 |c^T n_t - c^T n^*| + |\alpha^T (s_t - s^*)|). \end{aligned}$$

Since $m_1 < p_1$ and $m_2 < p_2$, and using (3.7) there exists an $m < 1$ such that

$$\frac{\alpha_1 p_2 m_1 + m_2 m_1 \alpha^T (I - S)^{-1} \Gamma_1}{p_e} \leq p_2 m_1 \frac{\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1}{p_e} \leq \frac{p_2 m_1}{p_1 p_2} \leq m < 1.$$

Hence

$$\begin{aligned} &\sum_{t=0}^M (|\alpha_1 p_2 c^T (n_t - n^*)| + |\alpha^T (s_t - s^*)|) \\ &\leq L + m \sum_{t=0}^M (\alpha_1 m_2 |c^T n_t - c^T n^*| + |\alpha^T (s_t - s^*)|), \end{aligned}$$

which implies that

$$\sum_{t=0}^M (|\alpha_1 (p_2 - m_2) c^T (n_t - n^*)| + |\alpha^T (s_t - s^*)|) \leq (1 - m)^{-1} L \quad (6.26)$$

This bound is independent of M . Therefore the sequence

$$\{\alpha_1 c^T (n_t - n^*) + |\alpha^T (s_t - s^*)|\}_{t=0}^{\infty} \in \ell_1(\mathbb{N}),$$

so

$$\lim_{t \rightarrow \infty} (|\alpha_1 c^T (n_t - n^*)| + |\alpha^T (s_t - s^*)|) = 0, \quad (6.27)$$

which, by the continuity of h , implies that

$$\lim_{t \rightarrow \infty} |\tilde{y}_t - y^*| = 0. \quad (6.28)$$

By (6.13), (6.28) and assumptions (E1) and (E4) we therefore have that

$$\lim_{t \rightarrow \infty} \tilde{n}_t = \tilde{n}^*, \quad (6.29)$$

as sought. The (ϵ, δ) conclusion follows from Holder's inequality and assumption (E1). \square

Appendix B

Proof of Theorem 3.3 The proof of (1) is identical to the proof of (1) in Theorem 3.2.

For (2) note that if there exists a solution (p_1, p_2, y^*) of (3.10) in $(0, g_0) \times (\exp(-2), 1) \times (0, \infty)$ and $m > 0$ such that $\tilde{y}_t > m$ and $c^T n_t \geq m$ for all $t \in \mathbb{N}$, then h_R is sector bounded as in (3.11) (Fig. 2). This follows from the fact that

$$h'_R(y) = (1 - \frac{y}{c_m})\exp(-y/c_m), \quad h''_R(y) = \frac{1}{c_m}(\frac{y}{c_m} - 2)\exp(-y/c_m).$$

Thus h_R has $\exp(-2)$ as its maximum negative slope. If \tilde{y}_t and $c^T n_t$ are uniformly bounded away from 0, h_R satisfies

$$|h_R(c^T n_t) - h_R(c^T n^*)| \leq m_2 |c^T n_t - c^T n^*|$$

for some $m_2 < p_2$. To see that there exists $m > 0$ such that $\tilde{y}_t \geq m$ and $c^T n_t \geq m$ for all $t \in \mathbb{N}$, we note that if $\tilde{y}_t \leq y^*$ and $c^T n_t \leq c^T n^*$ or $\tilde{y}_t \geq y^*$ the lower bound follows as in Theorem 3.2. If $\tilde{y}_t \leq y^*$ and $c^T n_t \geq c^T n^*$ we need to show that the solution $\{\tilde{n}_t\}_{t=0}^\infty$ is bounded above. Noting that $f(y) \leq f(y^*) + m_1 y$ for some $m_1 < p_1$ and $y \geq 0$ and $h_R(y) \leq c_m \exp(-1)$ for all $y \geq 0$, it follows that

$$\tilde{c}_1^T \tilde{n}_t \leq \tilde{c}_1^T \hat{A} \tilde{n}_{t-1} + c^T b f(y^*) + (m_1 c^T b + \gamma_1) c_m \exp(-1) := \tilde{c}_1^T \hat{A} \tilde{n}_{t-1} + K,$$

where

$$\hat{A} := \begin{bmatrix} A & B_{m_1} \\ \Gamma_0 & S \end{bmatrix}, \quad B_{m_1} := [m_1 b \ m_1 b \ \cdots \ m_1 b],$$

and $r(\hat{A}) < 1$. Thus $\tilde{c}_1^T \tilde{n}_t \leq M$ for some $M < \infty$, which implies that $c^T n_t \leq M/\alpha_1$ for all $t \geq 0$. Thus, if $\tilde{y}_t \leq y^*$ and $c^T n_t \geq c^T n^*$ we have that $f(\tilde{y}_t) \geq f(y^*)$ and $h_R(c^T n_t) > \min\{h_R(c^T n^*), h_R(M/\alpha_1)\} > 0$. Letting $\tilde{w}_{p_2}^T$ be defined as in Theorem 3.2,

$$\tilde{w}_{p_2}^T \tilde{n}_t \geq \min\{\tilde{w}_{p_2}^T \tilde{n}_0, p_2 p_1 \alpha_1 \tilde{w}_{p_2}^T \tilde{b} c^T n^*, \tilde{w}_{p_2}^T \tilde{b} p_1 h_R(M/\alpha_1)\}, \quad (7.1)$$

thus \tilde{y}_t , and similarly $c^T n_t$, are bounded from below as in Theorem 3.2. The remainder of the proof for (2) is the same as in Theorem 3.2.

For part (3) note that

$$h'_R(c^T n^*) = p_2(1 + \ln(p_2)) < -p_2, \quad (7.2)$$

so we cannot sector-bound h_R as we did in (2) of this theorem. The linearization about \tilde{n}^* yields

$$\tilde{n}_{t+1} \simeq (\tilde{A}_{(1+\ln(p_2))p_2} + f'(y^*)\tilde{b}\tilde{c}^T_{(1+\ln(p_2))p_2})\tilde{n}_t.$$

Thus if $r(\tilde{A}_{(1+\ln(p_2))p_2} + f'(y^*)\tilde{b}\tilde{c}^T_{(1+\ln(p_2))p_2}) < 1$ then \tilde{n}^* is asymptotically stable, as sought. \square

Appendix C

Proof of Corollary 3.1 To prove (1) we need to show that $(\tilde{A}, \tilde{b}, \tilde{c})$ satisfies hypotheses (A1), (A2) and (A3) in [Rebarber et al. \(2012\)](#). We verified that (A1) and (A2) are met by \tilde{A} and \tilde{b} in the proof of Theorem 3.1. To prove that (A3) is met by \tilde{c}^T , note that (3.16) implies that $c^T n \geq 0$ for all $n \in X_1$. This, coupled with (E4) implies that $\tilde{c}^T \tilde{n} \geq 0$ for all $\tilde{n} \in X_1 \otimes X_2$, proving (1).

To prove (2) and (3) note that (E3) is only used in the proof of Theorem 3.2 (2) and Theorem 3.3 (2), i.e. when \tilde{n}^* is positive and globally stable. Also, the only place where we needed to use (E3) in the proofs of Theorems 3.2 and 3.3 is where we assert that there exists an $m > 0$ such that $\tilde{y}_t, c^T n_t \geq m$ for all $t \geq 0$. To prove this in the case where h is continuous, increasing, concave down, with $h(0) = 0$, we introduce a new IPM system which is “close” to the original system (2.7). For $\epsilon > 0$, let $I_\epsilon := \{x \in [L, U] | c(x) > \epsilon\}$, $X_{1,\epsilon} := L^1(I_\epsilon)$ and $A_\epsilon : X_{1,\epsilon} \rightarrow X_{1,\epsilon}$ be such that

$$A_\epsilon n = \int_{I_\epsilon} k(x, y)n(y) dy,$$

with $b_\epsilon = b|_{I_\epsilon}$ and

$$c_\epsilon^T n = \int_{I_\epsilon} c(y)n(y) dy.$$

It follows that $r(A_\epsilon) \leq r(A) < 1$, so A_ϵ satisfies (E1). It's straightforward that, for sufficiently small ϵ , b_ϵ satisfies (E2) and that c_ϵ^T satisfies (E3) with $c_{\min} = \epsilon$. Let

$$p_e(\epsilon) = (c_\epsilon^T (I - A_\epsilon)^{-1} b_\epsilon)^{-1}.$$

It follows that $\lim_{\epsilon \rightarrow 0} p_e(\epsilon) = p_e$. Since in Theorem 3.2 (2) the system of Eqs. (3.10) has a solution $(p_1, p_2, y^*) \in (0, g_0) \times (0, 1) \times (0, \infty)$, we can choose $\epsilon > 0$ such that the system of equations

$$\begin{aligned} g(y^*(\epsilon)) &= p_1(\epsilon) \\ p_1(\epsilon)p_2(\epsilon) &= \frac{p_e(\epsilon)}{(\alpha_1 + \alpha^T(I - S)^{-1}\Gamma_1)} \end{aligned}$$

$$h\left(\frac{p_1(\epsilon)y^*(\epsilon)}{p_e(\epsilon)}\right) = \frac{p_2(\epsilon)p_1(\epsilon)y^*(\epsilon)}{p_e(\epsilon)}.$$

has a solution $(p_1(\epsilon), p_2(\epsilon), y^*(\epsilon)) \in (0, g_0) \times (0, 1) \times (0, \infty)$. Let $[n(\epsilon)_t \ s(\epsilon)_t]^T \subset X_\epsilon := X_{1,\epsilon} \otimes X_2$ solve

$$\begin{aligned} n(\epsilon)_{t+1} &= A_\epsilon n(\epsilon)_t + b_\epsilon f(\tilde{y}(\epsilon)_t), \\ \tilde{y}(\epsilon)_t &= \alpha_1 h(c_\epsilon^T n(\epsilon)_t) + \alpha_2 s(\epsilon)_{1,t} + \cdots + \alpha_{N+1} s(\epsilon)_{N,t} \\ s(\epsilon)_{1,t+1} &= \gamma_1 h(c_\epsilon^T n(\epsilon)_t) \\ s(\epsilon)_{2,t+1} &= \gamma_2 s(\epsilon)_{1,t} \\ &\vdots \\ s(\epsilon)_{N-1,t+1} &= \gamma_{N-1} s(\epsilon)_{N-2,t} \\ s(\epsilon)_{N,t+1} &= \gamma_N s(\epsilon)_{N-1,t} + \gamma_{N+1} s(\epsilon)_{N,t}. \end{aligned}$$

Since $(p_1(\epsilon), p_2(\epsilon), y^*(\epsilon)) \in (0, g_0) \times (0, 1) \times (0, \infty)$ we have, by the proof of Theorem 3.2, the existence of an $m > 0$ such that $\tilde{y}(\epsilon)_t, c_\epsilon^T n(\epsilon)_t \geq m$ for all $t \geq 0$. By the monotonicity of f and h and the positivity of (A, b, c) , $\{\alpha_j\}_{j=1}^{N+1}$ and $\{\gamma_j\}_{j=1}^{N+1}$ we have $\tilde{y}_t \geq \tilde{y}(\epsilon)_t$ and $c^T n_t \geq c_\epsilon^T n(\epsilon)_t$ for all $t \geq 0$. Thus there exists an $m > 0$ such that $\tilde{y}, c^T n_t \geq m$ for all $t \geq 0$ and (2) is proved.

For (3) $h(y)$ is equal to $h_R(y) = ye^{-y/c_m}$, which is not monotone once y becomes larger than c_m . Thus we cannot bound \tilde{y}_t and $c^T n_t$ from below by $\tilde{y}(\epsilon)_t$ and $c(\epsilon)^T n(\epsilon)_t$ for all $t \geq 0$, unless $c^T n_t$ does not exceed c_m for all $t \geq 0$.

In the proof of Theorem 3.3, we showed that there exists an $M > 0$ (which depends on \tilde{n}_0) such that $\tilde{c}_1^T \tilde{n}_t \leq M$ for all $t \geq 0$, which implies that $c^T n_t \leq M/\alpha_1$ for all $t \geq 0$. If $M/\alpha_1 \leq c_m$ we can use the same arguments as in (2), due to the monotonicity of $h_R(y)$ for $y \leq c_m$. If $M/\alpha_1 > c_m$ we will construct a seed production function \underline{h} that is continuous, increasing, concave down, with $\underline{h}(0) = 0$, $\underline{h}'(0) = 1$ such that $\underline{h}(y) \leq h_R(y)$ for all $y \in [0, M/\alpha_1]$. The population in a model with \underline{h} instead of h_R will be smaller than \tilde{n}_t for all $t \geq 0$. If this smaller population has a nonzero globally stable equilibrium population then we will have our desired lower bound.

Define the function

$$\underline{h}(y) = \frac{My}{M + \alpha_1 \left(e^{\frac{M}{\alpha_1 c_m}} - 1 \right) y},$$

which is continuous, increasing, concave down, with $\underline{h}(0) = h_R(0) = 0$, $\underline{h}'(0) = h'_R(0) = 1$ and $\underline{h}(M/\alpha_1) = h_R(M/\alpha_1) = M/\alpha_1 e^{-\frac{M}{\alpha_1 c_m}}$. Since $c_m < M/\alpha_1$ implies that

$$\underline{h}''(0) = \frac{2\alpha_1 \left(e^{\frac{M}{\alpha_1 c_m}} - 1 \right)}{M} < \frac{-2}{c_m} = h''_R(0),$$

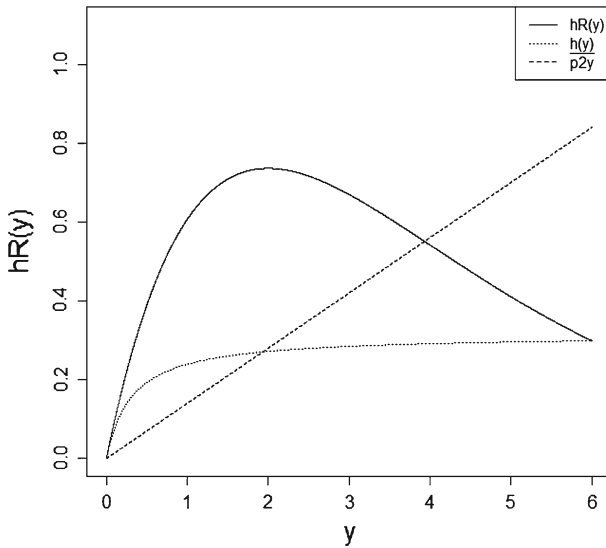


Fig. 7 An example of the comparison between h_R and the increasing, concave down h , with $M/\alpha_1 = 6$. Notice that if the equation $h_R(y) = p_2 y$ has a solution $(p_2, y) \in (e^{-2}, 1) \times (0, \infty)$, then the equation $\underline{h}(y) = p_2 y$ has a solution in $(0, 1) \times (0, \infty)$, as $h_R(0) = \underline{h}(0) = 0$ and $h'_R(0) = \underline{h}'(0) = 1$

we have that $\underline{h}(y) \leq h_R(y)$ for all $y \in [0, M/\alpha_1]$ (see Fig. 7). Let $\tilde{n}_t = [\underline{n}_t \ \underline{s}_t]^T \subset X$

$$\begin{aligned} \underline{n}_{t+1} &= A \underline{n}_t + b f(\underline{y}_t), \\ \underline{y}_t &= \alpha_1 \underline{h}(c^T \underline{n}_t) + \alpha_2 \underline{s}_{1,t} + \cdots + \alpha_{N+1} \underline{s}_{N,t} \\ \underline{s}_{1,t+1} &= \gamma_1 \underline{h}(c^T \underline{n}_t) \\ \underline{s}_{2,t+1} &= \gamma_2 \underline{s}_{1,t} \\ &\vdots \\ \underline{s}_{N-1,t+1} &= \gamma_{N-1} \underline{s}_{N-2,t} \\ \underline{s}_{N,t+1} &= \gamma_N \underline{s}_{N-1,t} + \gamma_{N+1} \underline{s}_{N,t}. \end{aligned}$$

It follows that, if $\tilde{n}_0 = \tilde{n}_0$, we have that $\tilde{n}_t \leq \tilde{n}_t$, and thus $c^T \underline{n}_t \leq c^T n_t$, for all $t \geq 0$. Since in Theorem 3.3 (2) the system of Eqs. (3.10) has a solution $(p_1, p_2, y^*) \in (0, g_0) \times (e^{-2}, 1) \times (0, \infty)$ it follows that the system of equations

$$\begin{aligned} g(\underline{y}^*) &= \underline{p}_1 \\ \underline{p}_1 \underline{p}_2 &= \frac{p_e}{(\alpha_1 + \alpha^T (I - S)^{-1} \Gamma_1)} \\ \underline{h}\left(\frac{\underline{p}_1 \underline{y}^*}{p_e}\right) &= \frac{\underline{p}_2 \underline{p}_1 \underline{y}^*}{p_e}. \end{aligned}$$

has a solution $(\underline{p}_1, \underline{p}_2, \underline{y}^*) \in (0, g_0) \times (0, 1) \times (0, \infty)$ (see Fig. 7). This implies, from the above proof of (2), that \tilde{n}_t converges to a positive, globally stable equilibrium population \tilde{n}^* . Since $\tilde{n}_t \geq \underline{n}_t$ for all $t \geq 0$ we have the desired positive lower bound m for \tilde{y}_t and $c^T n_t$, proving (3). \square

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