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Global Attracting Equilibria for Coupled Systems with Ceiling Density Dependence

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Abstract

In this paper, we present a system of two difference equations modeling the dynamics of a coupled population with two patches. Each patch can only house a

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limited number of individuals (called a carrying capacity), because resources like food and breeding sites are limited in each patch. We assume that the population in each patch is governed by a linear model until reaching a carrying capacity in each patch, resulting in map which is nonlinear and not sublinear. We analyze the global attractors of this model.

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1 Introduction

Many populations consist of subpopulations that are spatially separated in patches, often due to natural variation in the landscape (e.g. hills, ponds and islands), social grouping, geographic distance or the destruction and fragmentation of larger habitable areas caused by anthropogenic factors (Lande, et. al. [5], Münkemüller and Johnst [7], Vandermeer and Goldberg [8]). We call a collection of subpopulations a *metapopulation* when the patches are not completely isolated from each other and there is migration between subpopulations from one breeding season to another. Each patch can only house a limited number of individuals (carrying capacity) because resources like food and breeding sites are limited in each patch. As a consequence, birth and survival rates in each patch are decreasing functions of population size. However, often we have insufficient knowledge about the details of this density dependence to determine a functional form for this nonlinearity, in which case it is sensible to make the assumption that population size in each patch increases like a linear model until reaching a carrying capacity in each patch; this is sometimes known as a *ceiling density dependence*. For instance, this type of density dependence is incorporated in the widely used, simulation–based population viability software RAMAS/METAPOP (Akcakaya [1]).

In this paper, we explore the effect of this type of density dependence on a system of two linear difference equations modeling the dynamics of a coupled population with two patches. The ceiling density dependence is then applied to each patch, and we analyze the attractivity of model's equilibria. Mathematical models subject to monotone density dependence can often be handled with established fixed-point global attractivity theory (e.g. Hirsch and Smith [3] or Krause and Ranft [4]), utilizing sublinearity in a monotone map. However, the simple ceiling density dependence we consider is not sublinear, which presents some mathematical challenges.

Notation 1.1. For $x = [x_1, x_2]^T, y = [y_1, y_2]^T$, we write $x > y$ ($x \geq y$) if $x_1 > y_1$ ($x_1 \geq y_1$) and $x_2 > y_2$ ($x_2 \geq y_2$). If $x \geq [0, 0]^T$, we say that x is nonnegative. The set of all nonnegative vectors in $\mathbb{R}^2$ is the nonnegative cone $\mathbb{R}^2_+$ of $\mathbb{R}^2$. The spectrum of a matrix A is denoted by $\sigma(A)$ and the spectral radius of A is denoted by $\rho(A)$.

2 The Model

We denote the number (or density) of female members in patch i at time $t \in \mathbb{N}$ by $N_{i,t}$, and the vector of populations by $N_t = [N_{1,t}, N_{2,t}]^T$. We only count females in this model, with the implicit assumption that there is a sufficient number of males available for mating. We will assume that the population of patch i cannot exceed the carrying capacity $K_i > 0$. Let $K = [K_1, K_2]^T$. If the population in patch i is below the cap then the population dynamics in patch i are determined by a linear combination of members who were created or stayed in patch i from the previous time-step and members who migrated to patch i in the previous time-step. Let b_i be the probability that a given female in patch i gives birth at any time-step, and f_i be the (independent) probability that the newborn is a female. Let μ_i and m_i be the probabilities of death and migration in patch i, respectively. We finally assume that once a member of either patch begins to migrate, there is a probability α that the migration will be successful. With these assumptions, the difference equation model with the cap can be written as

$$\begin{aligned} N_{1,t+1} &= \min\{r_{11}N_{1,t} + r_{12}N_{2,t}, K_1\} \\ N_{2,t+1} &= \min\{r_{21}N_{1,t} + r_{22}N_{2,t}, K_2\}, \end{aligned} \tag{2.1}$$

where

$$\begin{aligned} r_{11} &= (1-\mu_1)(1+b_1f_1)(1-m_1) \\ r_{12} &= (1+b_2f_2)m_2\alpha \\ r_{21} &= (1+b_1f_1)m_1\alpha \\ r_{22} &= (1-\mu_2)(1+b_2f_2)(1-m_2). \end{aligned}$$

We will assume that $r_{ij} \geq 0$ for all $i, j \in \{1, 2\}$, and that $r_{12} > 0$ and $r_{21} > 0$, so that both of the patches in the metapopulation are connected through migration. The case where r_{12} and/or r_{21} are zero are not as interesting mathematically, since one population essentially decouples from the other and one can use the analytical solution to determine the global attractivity of the population.

Definition 2.1. Let $N_t = [N_{1,t}, N_{2,t}]^T$. A fixed point $N^* = [N_1^*, N_2^*]^T$ for (2.1) is *globally attracting* if

$$\lim_{t\to\infty} N_t = N^*,$$

for every $N_0 \in \mathbb{R}_+^2 \setminus \{[0,0]^T\}$.

Remark 2.2. In some of the literature on global attractivity, $\mathbb{R}_+^2 \setminus \{[0,0]^T\}$ is replaced by the interior of $\mathbb{R}_+^2$, but here we want to be able to consider initial populations which start with the population in only one patch. This is not a mathematical issue for this system, since if $N_{1,0} = 0$ or $N_{2,0} = 0$ (but not both), then at the next time step $N_{1,1} > 0$ and $N_{2,1} > 0$.

For $i = 1, 2$, let

$$G_i(N_{1,t}, N_{2,t}) = \min\{r_{i1}N_{1,t} + r_{i2}N_{2,t}, K_i\}.$$

Define the operator $G : \mathbb{R}^2 \to \mathbb{R}^2$ by

$$G(N_{1,t}, N_{2,t}) = \begin{bmatrix} G_1(N_{1,t}, N_{2,t}) \\ G_2(N_{1,t}, N_{2,t}) \end{bmatrix},$$

so model (2.1) can be written as

$$N_{t+1} = G(N_t). \tag{2.2}$$

We will first identify all of the fixed points of G. Let

$$J = \begin{bmatrix} r_{11} & r_{12} \\ r_{21} & r_{22} \end{bmatrix}.$$

Since J has all nonnegative entries with $r_{12} > 0$ and $r_{21} > 0$, it follows from the Perron–Frobenius theorem that its spectral radius $\rho(J)$ is given by a real, positive leading eigenvalue.

Theorem 2.3. *1. Suppose that $\rho(J) < 1$. Then $[0, 0]^T$ is a globally attracting equilibrium of G. Case 1 includes*

$$\begin{aligned} K_1 &\geq r_{11}K_1 + r_{12}K_2 \\ K_2 &\geq r_{21}K_1 + r_{22}K_2, \end{aligned} \tag{2.3}$$

where at least one of the inequalities is strict.

2. Suppose that

$$\begin{aligned} K_1 &\leq r_{11}K_1 + r_{12}K_2 \\ K_2 &\leq r_{21}K_1 + r_{22}K_2, \end{aligned} \tag{2.4}$$

where at least one of the inequalities is strict. Then $\rho(J) > 1$, $1 \notin \sigma(J)$ and the only fixed points of G in $\mathbb{R}^2_+$ are $[0, 0]^T$ and $[K_1, K_2]^T$.

3. Suppose $\rho(J) > 1$, $1 \notin \sigma(J)$ and

$$\begin{aligned} K_1 &\leq r_{11}K_1 + r_{12}K_2 \\ K_2 &> r_{21}K_1 + r_{22}K_2. \end{aligned} \tag{2.5}$$

Then $r_{22} < 1$ and the only fixed points of G in $\mathbb{R}^2_+$ are $[0, 0]^T$ and

$$[K_1, K_1 r_{21}/(1 - r_{22})]^T.$$

4. *Suppose* $\rho(J) > 1$, $1 \notin \sigma(J)$ *and*

$$\begin{aligned} K_1 &> r_{11}K_1 + r_{12}K_2 \\ K_2 &\leq r_{21}K_1 + r_{22}K_2. \end{aligned}$$

Then $r_{11} < 1$ *and the only fixed points of* G *in* $\mathbb{R}^2_+$ *are* $[0,0]^T$ *and*

$$[K_2 r_{12}/(1 - r_{11}), K_2]^T.$$

5. *Suppose* $\rho(J) \geq 1$, $1 \in \sigma(J)$ *and*

$$\begin{aligned} K_1 &\leq r_{11}K_1 + r_{12}K_2 \\ K_2 &\geq r_{21}K_1 + r_{22}K_2. \end{aligned}$$

Then $r_{22} < 1$, *and the fixed points of* G *in* $\mathbb{R}^2_+$ *are*

$$\{[N_1, N_1 r_{21}/(1 - r_{22})]^T \mid 0 \leq N_1 \leq K_1\}. \tag{2.6}$$

6. *Suppose* $\rho(J) \geq 1$, $1 \in \sigma(J)$ *and*

$$\begin{aligned} K_1 &\geq r_{11}K_1 + r_{12}K_2 \\ K_2 &\leq r_{21}K_1 + r_{22}K_2. \end{aligned}$$

Then $r_{11} < 1$, *and the fixed points of* G *in* $\mathbb{R}^2_+$ *are*

$$\{[N_2 r_{12}/(1 - r_{11}), N_2]^T \mid 0 \leq N_2 \leq K_2\}.$$

Remark 2.4. Note that if

$$\begin{aligned} K_1 &= r_{11}K_1 + r_{12}K_2 \\ K_2 &= r_{21}K_1 + r_{22}K_2, \end{aligned}$$

then $J[K_1, K_2]^T = [K_1, K_2]^T$, so $1 \in \sigma(J)$. Therefore the six cases above include all possibilities.

Proof of Theorem 2.3. It is clear that $[0,0]^T$ is a fixed point of G in all cases. Positive equilibria $[N_1^*, N_2^*]^T$ satisfy

$$\begin{aligned} N_1^* &= \min\{r_{11}N_1^* + r_{12}N_2^*, K_1\} \\ N_2^* &= \min\{r_{21}N_1^* + r_{22}N_2^*, K_2\}. \end{aligned} \tag{2.7}$$

Note that if $r_{ii} \geq 1$ for $i = 1, 2$, then (2.7) implies that $N_i^* = K_i$. From (2.7) it follows that

$$(N_1^* < K_1 \text{ and } N_2^* < K_2) \text{ if and only if } 1 \in \rho(J). \tag{2.8}$$

Proof of (1). We first show that if (2.3) holds, then $\rho(J) < 1$. We will assume that the first inequality in (2.3) is strict; the other case is similar. From the first inequality in (2.3),

$$\frac{(1 - r_{11})K_1}{r_{12}} > K_2.$$

From the second inequality in (2.3),

$$K_2 \geq \frac{r_{21}K_1}{1 - r_{22}}.$$

Combining these inequalities, we obtain

$$1 + \det(J) > \operatorname{tr}(J). \tag{2.9}$$

Since all parameters in the inequalities in (2.3) are positive, we see that $r_{11} \leq 1$ and $r_{22} \leq 1$. Hence

$$\det(J) = r_{11}r_{22} - r_{21}r_{12} \leq 1 - r_{21}r_{12} < 1. \tag{2.10}$$

Conditions (2.9) and (2.10) are the Jury conditions for $\rho(J) < 1$. If $\rho(J) < 1$, then $[0, 0]^T$ is an asymptotically stable equilibrium (and thus a global attractor) for the *linear* system of difference equations

$$\hat{N}_{t+1} = J\hat{N}_t.$$

If N_t satisfies (2.1) and $\hat{N}_0 = N_0$, then $N_t \leq \hat{N}_t$. Hence $\lim_{t\to\infty} N_t = [0, 0]^T$.

Proof of (2). It is easy to see that (2.4) holds if and only if

$$K_i = \min\{r_{i1}K_1 + r_{i2}K_2, K_i\}, \quad i = 1 \text{ and } 2.$$

Therefore, $[0, 0]^T$ and $[K_1, K_2]^T$ are equilibria of (2.1). Reversing the inequalities in the proof of part (1), we see (2.4) implies that

$$1 + \det(J) < \operatorname{tr}(J). \tag{2.11}$$

Thus the Jury conditions for $\rho(J) < 1$ are not satisfied. As noted above, J has a positive real leading eigenvalue, and (2.11) rules out $\lambda = 1$ being an eigenvalue, since the eigenvalues satisfy $\lambda^2 - \lambda \operatorname{tr}(J) + \det(J) = 0$. Hence $\rho(J) > 1$. To show that $[0, 0]^T$ and $[K_1, K_2]^T$ are the only equilibria of (2.1) note that since $1 \notin \sigma(J)$, (2.8) implies that $N_1^* = K_1$ and/or $N_2^* = K_2$. Assume without loss of generality that $N_2^* = K_2$. If $r_{11} \geq 1$, from above we see that $N_1^* = K_1$. If $r_{11} < 1$, from the first inequality in (2.4),

$$K_1 \leq \frac{r_{12}K_2}{1 - r_{11}}. \tag{2.12}$$

If $N_1^* \neq K_1$, from (2.7),

$$N_1^* = r_{11}N_1^* + r_{12}K_2,$$

so

$$N_1^* = \frac{r_{12}K_2}{1 - r_{11}}.$$

Combining this with (2.12), $N_1^* \geq K_1$. Since $N_1^* \leq K_1$, it follows that $N_1^* = K_1$. Hence $[0, 0]^T$ and $[K_1, K_2]^T$ are the only equilibria of (2.1).

Proof of (3). We first show that $[K_1, r_{21}K_1/(1 - r_{22})]$ is an equilibrium of G. The second condition in (2.5) implies that $r_{22} < 1$. Since $\rho(J) > 1$,

$$1 + \det(J) \leq \mathrm{tr}(J) \tag{2.13}$$

and/or

$$1 + \det(J) \geq 2. \tag{2.14}$$

If $r_{11} \geq 1$, then K_1 clearly solves the first equality in (2.7). The second inequality in (2.5) implies that $r_{21}K_1/(1-r_{22})$ solves the second equality of (2.7). If $r_{11} < 1$, (2.14) cannot hold, so (2.13) holds. This can be rearranged into

$$r_{11} + r_{12}r_{21}/(1 - r_{22}) \geq 1.$$

Multiplying this by K_1, we get

$$r_{11}K_1 + r_{12}r_{21}K_1/(1 - r_{22}) \geq K_1.$$

so $[K_1, r_{21}K_1/(1 - r_{22})]$ satisfies the first equality in (2.7). From the second inequality of (2.5), we see that

$$r_{21}K_1/(1 - r_{22}) < K_2.$$

This implies that

$$r_{21}K_1 + r_{22}r_{21}K_1/(1 - r_{22}) < K_2,$$

so $[K_1, r_{21}K_1/(1 - r_{22})]$ satisfies the second equality in (2.7). Hence

$$[K_1, r_{21}K_1/(1 - r_{22})]$$

is an equilibrium of G. Now suppose that $N^* = [N_1^*, N_2^*]^T$ is an equilibrium of G. Since $1 \notin \sigma(J)$, we see from (2.8) that at least one of $N_i^* = K_i$. Suppose $N_2^* = K_2$, but $N_1^* < K_2$. Then from (2.7), $r_{21}K_1 + r_{22}K_2 \geq K_2$, which contradicts the second inequality in (2.5). Suppose $N_1^* = K_1$ but $N_2^* < K_2$. Then from (2.7), $N_2^* = r_{21}K_1 + r_{22}N_2^*$, leading to the equilibrium we have already identified.

Proof of (4). This proof is analogous to the proof of part (3).

Proof of (5). As in the proof of part (3), we can show that $[K_1, r_{21}K_1/(1-r_{22})]^T$ is a fixed point of G. If $N_1^* < K_1$, then (as in the proof of part (3)),

$$[N_1^*, N_2^*]^T = J[N_1^*, N_2^*]^T.$$

Since $1 \in \sigma(J)$ by hypothesis, it is routine to show that this is solved by

$$\{[N_1, N_1 r_{21}/(1-r_{22})]^T \mid N_1 \in \mathbb{R}\}.$$

The second inequality in the hypotheses show that $r_{22} < 1$, so this line is in the first and third quadrants of $\mathbb{R}^2$. Therefore the fixed points of G in $\mathbb{R}^2_+$ are given by (2.6).

Proof of (6). This proof is analogous to the proof of part (5).

This completes the proof. □

Remark 2.5. In cases (5) and (6), the line of equilibria makes it impossible for any equilibrium to be globally attractive.

3 Approximating Maps

For some systems of the form

$$N_{t+1} = F(N_t), \tag{3.1}$$

global attractivity is guaranteed if some fairly easy-to-check conditions on the map F are satisfied.

Definition 3.1. A map $F : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ is sublinear if, for all $0 < \lambda < 1$ and $x \in \mathbb{R}^n_+$ such that $x > [0,0]^T$, it follows that $\lambda F(x) < F(\lambda x)$. F is a monotone map if for all $x, y \in \mathbb{R}^n_+$ such that $x \le y$, it follows that $Fx \le Fy$.

The following theorem sums up the long-term dynamics of difference equations determined by monotone, sublinear maps. We will only state the theorem in the case where the $\mathbb{R}^n_+ = \mathbb{R}^2_+$ (see [4] for the general finite dimensional result and [3] for the general infinite dimensional result).

Theorem 3.2 (Krause and Ranft, [4])**.** *Let $F : \mathbb{R}^2_+ \to \mathbb{R}^2_+$ be a monotone, sublinear and continuous operator over $\mathbb{R}^2_+$. Let $P = \operatorname{int} \mathbb{R}^2_+ = \{[x_1, x_2]^T \in \mathbb{R} \mid x_1 > 0, x_2 > 0\}$. Precisely one of the following three cases holds:*

1. *each nonzero orbit of* (3.1) *in P is unbounded;*

2. *each orbit of* (3.1) *in P is bounded with at least one limit point not contained in P.*

3. *each nonzero orbit of* (3.1) *in* P *converges to a unique fixed point of* P.

Recall from Remark 2.2 that we can replace P with $\mathbb{R}^2_+ \setminus \{[0,0]^T\}$ without loss of generality.

The operator G is not sublinear, so we cannot apply this theorem to system (2.2) to obtain global attractivity. Therefore, we construct a sequence of monotone sublinear maps $\{G_n\}$ that converge to G from below, and use the global attractivity properties of the approximating system to help derive the global attractivity of the nonnegative equilibrium of (2.2).

Theorem 3.3. *There exists maps* $G_n : \mathbb{R}^2_+ \to \mathbb{R}^2_+$, $n \in \mathbb{N}$, *such that* G_n *is monotone and sublinear and* $G_n \to G$ *uniformly on* R^2_+. *Furthermore,* G_n *is increasing in the sense that for every* $x \in \mathbb{R}^2_+$ *and* $n > m$, $G_n(x) > G_m(x)$.

Proof. For $z, K \in \mathbb{R}_+$, let

$$g(z, K) = \max\{z, K\}.$$

Fix $\epsilon > 0$ and let

$$g(z,\epsilon,K) = \begin{cases} g_1(z,\epsilon,K), & 0 \le z \le K - \dfrac{\epsilon}{2} \\ g_2(z,\epsilon,K), & z \ge K + \dfrac{\epsilon}{2} \\ g_3(z,\epsilon,K), & K - \dfrac{\epsilon}{2} < z < K + \dfrac{\epsilon}{2}, \end{cases}$$

where

$$\begin{aligned} g_1(z,\epsilon,K) &= \frac{\alpha z}{\alpha + z} \\ g_2(z,\epsilon,K) &= \frac{Kz}{\beta + z} \\ g_3(z,\epsilon,K) &= \frac{\gamma z}{\delta + z}. \end{aligned}$$

To ensure that g is continuous we choose $\alpha, \beta, \gamma, \delta \in \mathbb{R}_+$ so that

$$g_1(K - \frac{\epsilon}{2}, \epsilon, K) = g_3(K - \frac{\epsilon}{2}, \epsilon, K) = K - \epsilon$$
$$g_2(K + \frac{\epsilon}{2}, \epsilon, K) = g_3(K + \frac{\epsilon}{2}, \epsilon, K) = K - \frac{\epsilon}{2}.$$

Solving these equations,

$$\alpha = \frac{(2K-\epsilon)(K-\epsilon)}{\epsilon}, \quad \beta = \frac{2K\epsilon + \epsilon^2}{4K - 2\epsilon},$$

$$\gamma = \frac{(K-\epsilon)(2K+\epsilon)}{2K - \epsilon/2} + K - \epsilon, \quad \delta = \frac{4K^2 - \epsilon^2)}{4K - 3\epsilon}.$$

We see that $g_1(z, \epsilon, K)$ converges uniformly to $I(z) = z$ for $z \in [0, K]$ as $\epsilon \to 0$, and that $g_2(z, \epsilon, K)$ converges uniformly to K for $z \geq K$ as $\epsilon \to 0$. Furthermore, $g_3(K)$ converges to K as $\epsilon \to 0$, so $g(z, \epsilon, K)$ converges uniformly to $g(z, K)$ in $\mathbb{R}_+$ as $\epsilon \to 0$. It is a straightforward calculation that $\lambda g(z, \epsilon, K) < g(\lambda z, \epsilon, K)$, for all $0 < \lambda < 1, z > 0$, i.e. each $g(\cdot, \epsilon, K)$ is sublinear on $\mathbb{R}^+$.

Choose $(\epsilon_n)_{n=1}^{\infty} \subset (0, K/4)$ such that $\epsilon_n \searrow 0$, and define $g_n(z, K) := g(z, \epsilon_n, K)$. It is clear that if $n > m$, then $g_n(z, K) > g_m(z, K)$ for all $z \in \mathbb{R}^+$, so $(g_n(\cdot, K))_{n=1}^{\infty}$ is an increasing sequence of sublinear functions which converge uniformly to $g(\cdot, K)$ on $\mathbb{R}_+$.

Let $x = [x_1, x_2]^T$, and

$$G_n(x) = \begin{bmatrix} g_n(r_{11}x_1 + r_{12}x_2, K_1) \\ g_n(r_{21}x_1 + r_{22}x_2, K_2) \end{bmatrix} \tag{3.2}$$

All of the properties of G_n claimed in the theorem follow from the properties of g_n, and the fact that $r_{ij} \geq 0$, $r_{12} > 0$ and $r_{21} > 0$. □

4 Global Attractivity

In this section we will prove global attractivity results for (2.1). We will refer to the case numbers in Theorem 2.3. Note that in Case 1, $[0, 0]^T$ is a globally attractive equilibrium, while in Cases 5 and 6 the existence of a line of equilibria guarantees that none of the equilibria is globally attractive. In Cases 2, 3, and 4 there is a unique nonzero equilibrium $N^* = [N_1^*, N_2^*]^T$ in $\mathbb{R}_+^2$.

Theorem 4.1. *In the Cases 3, 4 and 5 from Theorem 2.3, the nonzero equilibrium is globally attractive.*

Proof. We approximate G in (2.1) with G_n:

$$\hat{N}_{t+1} = G_n(\hat{N}_t). \tag{4.1}$$

Note that

$$\frac{d}{dz} g_n(z, K) \mid_{z=0} = 1$$

for any $K > 0$ and $n \in \mathbb{N}$, so the Jacobian of G_n at $[0, 0]^T$ is J. In the cases we are considering $\rho(J) > 1$, so $[0, 0]$ cannot be globally attractive. Since $G_n(x) \leq [K_1, K_2]^T$ for all $x \in \mathbb{R}_+^2$, the trajectories of (4.1) are bounded by $K := [K_1, K_2]^T$. By Theorem 3.2, (4.1) has a unique globally attractive equilibrium in P, which we denote by $x_n = [x_n^1, x_n^2]^T$.

We will now show that $(x_n)_{n=1}^{\infty}$ is a nondecreasing sequence in $\mathbb{R}_+^2$. Pick an arbitrary $\hat{x} \in P$ and let $n, m \in \mathbb{N}$ be such that $n > m$. Then

$$x_n = \lim_{j \to \infty} x_n^j, \text{ where } x_n^{j+1} = G_n(x_n^j) \text{ and } x_n^0 = \hat{x},$$

$$x_m = \lim_{j\to\infty} x_m^j, \text{ where } x_m^{j+1} = G_m(x_n^j) \text{ and } x_m^0 = \hat{x}.$$

Since $G_n(x) > G_m(x)$ for all $x \in \mathbb{R}_+^2$, we see by induction that

$$x_n^j \geq x_m^j \text{ for all } j \in \mathbb{N}.$$

This shows that $x_n \geq x_m$.

Since $(x_n)_{n=1}^{\infty}$ is a nondecreasing bounded sequence, it has a limit $\tilde{x} \in \mathbb{R}_+^2$. Fix $\epsilon > 0$. There exists $N \in \mathbb{N}$ such that

$$\|G(x) - G_n(x)\| < \epsilon \text{ for all } n > N \text{ and } x \in \mathbb{R}_+^2.$$

Then, since $G_n(x_n) = x_n$,

$$\|G(x_n) - x_n\| = \|G(x_n) - G_n(x_n)\| < \epsilon \text{ for all } n > N.$$

Let $n \to \infty$, and using the fact that G is continuous, we get that

$$G(\tilde{x}) = \tilde{x}.$$

Since in the cases considered in Theorem 4.1 the only fixed points of G are $[0,0]^T$ and N^*, and since (x_n) is increasing, we get that $\tilde{x} = N^*$. In particular,

$$\lim_{n\to\infty} x_n = N^*. \tag{4.2}$$

Now consider the cases where $N_1^* = K_1$ (that is, Cases 2 and 3). Fix $\epsilon > 0$. From (4.2), there exists $N > 0$ such that

$$0 < K_1 - x_n^1 < \epsilon/2 \text{ for all } n > N. \tag{4.3}$$

Fix $n_0 > N$ and $\hat{x} \in P$. Consider the systems

$$N_{t+1} = G(N_t), \quad N_0 = \hat{x}$$

where $N_t = [N_{1,t}, N_{2,t}]^T$, and

$$x_{n_0,t+1} = G_{n_0}(x_{n_0,t}), \quad x_{n_0,0} = \hat{x}. \tag{4.4}$$

where $x_{n_0,t} = [x_{n_0,t}^1, x_{n_0,t}^2]^T$. Since $G_{n_0}(x) \leq G(x)$ for all $x \in \mathbb{R}_+^2$, we see that

$$x_{n_0,t}^1 \leq N_{1,t} \quad \text{for all } t \in \mathbb{N}. \tag{4.5}$$

Since (4.4) has an equilibrium $[x_{n_0}^1, x_{n_0}^2]^T$, there exists $T > 0$ such that

$$|x_{n_0,t}^1 - x_{n_0}^1| < \epsilon/2 \text{ for t} > T. \tag{4.6}$$

Combining (4.3), (4.5) and (4.6), we get that

$$|N_{1,t} - K_1| < \epsilon \ \text{ for } t > T.$$

This proves that

$$\lim_{t\to\infty} N_{1,t} = K_1. \tag{4.7}$$

Similarly, in the cases where $N_2^* = K_2$ (that is, Cases 2 and 4),

$$\lim_{t\to\infty} N_{2,t} = K_2. \tag{4.8}$$

Hence, in Case 2, we see from (4.7) and (4.8) that

$$\lim_{t\to\infty} N_t = K.$$

In Case 3, $N_1^* = K_1$ and $N_2^* < K_2$. Note that, in this case

$$r_{22}N_{2,t} + r_{21}N_{1,t} \le r_{21}K_1 + r_{22}K_2 < K_2.$$

In particular, the second equation in (2.1) becomes

$$N_{2,t+1} = r_{22}N_{2,t} + r_{21}N_{1,t}.$$

Since $r_{22} \in [0,1)$ and $\lim_{t\to\infty} r_{21}N_{1,t} = r_{21}K_1$, the variation of parameters formula shows that $N_{2,t}$ converges, and it follows that the limit is $N_2^* = r_{21}K_1/(1 - r_{22})$. The limits in Case 4 are proved similarly, proving Theorem 4.1. $\square$

5 Examples

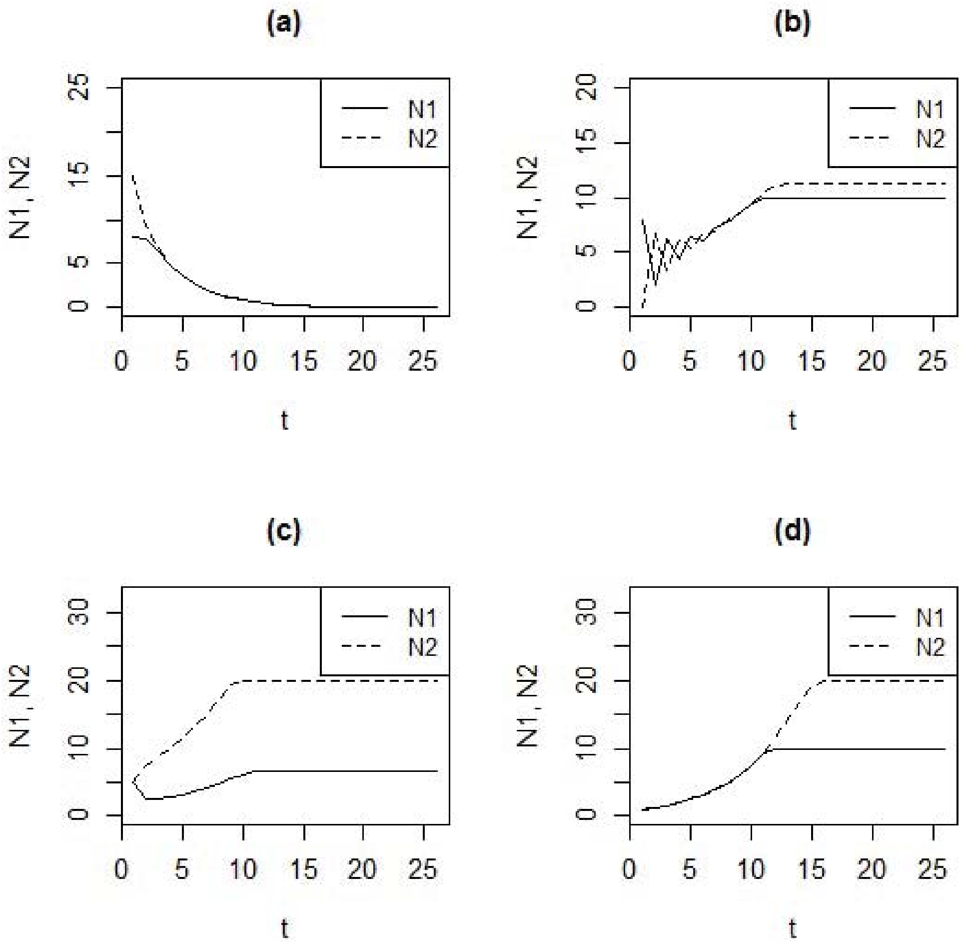

Figure 5.1: Example metapopulation trajectories for the model (2.1) with the parameter values (a) $r_{11} = r_{22} = 0.5, r_{12} = r_{21} = 0.25, K_1 = 10, K_2 = 20, N_{1,0} = 8, N_{2,0} = 15, \rho(J) = 0.75$ (b) $r_{11} = r_{22} = 0.25, r_{12} = r_{21} = 0.85, K_1 = 10, K_2 = 20, N_{1,0} = 8, N_{2,0} = 0, \rho(J) = 1.1$ (c) $r_{11} = 0.25, r_{22} = 1, r_{12} = 0.25, r_{21} = 0.5, K_1 = 10, K_2 = 20, N_{1,0} = N_{2,0} = 5, \rho(J) = 1.14$ and (d) $r_{11} = r_{22} = 1, r_{12} = r_{21} = 0.25, K_1 = 10, K_2 = 20, N_{1,0} = 1, N_{2,0} = 1, \rho(J) = 1.25$.

Figure 5.1 shows some metapopulation trajectories for the four different cases in Theorem 4.1.

- Figure 5.1(a) illustrates an example of a population where $\rho(J) < 1$, and thus the populations in both patches die out (Theorem 2.2 (1)), which can occur if the birth rates are lower than death rates in both patches.

- Figure 5.1(b) illustrates an example where the off-diagonal terms of the Jacobian J (r_{12} and r_{21}) are larger than the diagonal terms (r_{11} and r_{22}), while $\rho(J) > 1$. This situation can occur if the death rate in both patches is higher than the death rate during migration. This can be the case if the predation rate in patches is very high, and the habitat between patches is unsuitable for predators. Members of the population escape predation by migrating, but still need to go to a patch at some point to reproduce. We see a lack of monotonicity in the trajectories in 1(b) (even though the map G itself is monotone). When patch populations are low it is intuitively true that, because $\rho(J) > 1$, the populations would tend to increase until one hits its cap, where then the other population starts to settle into its equilibrium dynamics. However, if patch sizes and/or initial populations differ too drastically between the two patches, it may take a very long time before the dynamics of the metapopulation exhibits monotone dynamics.

- Figure 5.1(c) and (d) both illustrate roughly monotone population dynamics toward an equilibrium caused by high r_{22} (both (c) and (d)) and high r_{11} (d) rates, which can reflect high birth rates and/or low death rates within each patch. In 1(c) fewer individuals from the good patch arrive at the poor patch than vice versa. This could happen if the migration rate in the good patch is much smaller than that of the poor patch, because migration probability decreases with habitat quality. In 1(d) the habitat quality of both patches is identical, except one of them has a lower ceiling.

6 Conclusions and Future Directions

This model can be interpreted as an approximation to the dynamics of a two-patch metapopulation with density-dependence when the exact form of the density dependence is unknown. In the absence of explicit data about the functional form of the density-dependence in birth, death or migration processes, ceiling density dependence is the most parsimonious form of density dependence and has been used in ecological applications and software, [1]. The dynamics with ceiling density dependence are determined only by low density dynamics (which determine the linear part J), and the carrying capacities K_1 and K_2. We prove the expected global attractivity of the nonzero equilibrium when there is a single nonzero equilibrium. Due to the lack of sublinearity in the density dependence, in cases where the linear system has a line of equilibria, the nonlinear system also has a line segment of equilibria. This is not the case with the type of sublinear nonlinearities that often are used in population modeling (see, for example, Vandermeer and Goldberg [8, Chapter 1]), where the uniqueness of the equilibrium follows from Krause and Ranft [4] or Hirsch and Smith [3]. We have seen in Section 4 that when there is a unique attractor in the Ceiling Density Dependence Model, it is the limit of the equilibria of models with sublinear density dependence.

Future work includes studying cases where the density dependence is overcompensatory (see [7]) in one or more of the birth, death or migration processes, causing non-monotonicity in the model. In this case there may be instances where the global attractivity of the fixed point no longer holds, or perhaps there would be more than one fixed point, a cycle or even chaos (see [2]). We can also consider more than two patches. In this case the role of $\rho(J)$ will again be central to the analysis, but the details of the different cases (analogous to Theorem 2.3) will be messier.

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