GLOBAL ASYMPTOTIC BEHAVIOR AND DISPERSION IN AGE-STRUCTURED, DISCRETE COMPETITIVE SYSTEMS

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ABSTRACT. The model for this study is a two-species discrete competitive system with two age classes, juveniles and adults. As the juveniles of one of the species mature, they disperse between two patches. We provide sufficient conditions that guarantee global convergence to the extinction states of each of the two competing species. With an example, we illustrate that providing a safe refuge for an endangered species in an age-structured model could lead to the stable coexistence of all the competing species where there is extinction without the refuge. This shows that dispersal between patches could represent a powerful strategy for the long-run stable coexistence of competing species.

Irrespective of initial population densities, we prove that an individual species with a sufficiently large carrying capacity persists in the age-structured model with patches.

1. Introduction. In most natural ecosystems, the total population of species is more or less the sum of subpopulations of the species distributed over many patches. Thus, in an age-structured ecological system with competing juvenile and adult populations, the most probable strategy for the juveniles of species to adopt for their survival and reproduction may not necessarily consist of remaining in the same patch, but may rather consist of dispersing to a safe refuge from competition. Franke and Yakubu, in recent papers, studied the population dynamics of discrete age-structured systems with no dispersion [8, 10]. The model for this study, system (1), is a two-species discrete ecological system that includes the modeling of competition between two age classes, juveniles and adults. In contrast to the models of Franke and Yakubu [8, 10], in system (1) we capture more biological "realism" by allowing the juveniles of one of the two competing species to disperse between two patches, patches A and B.
System (1) consists of the following nonlinear difference equations:

\[
\begin{align*}
    x_{1A}(t+1) &= y_{1A}(t)g_1\left(\sum_{j=1}^{2}\{\alpha_{1j}x_{jA}(t) + \beta_{1j}y_{jA}(t)\}\right) \\
    x_{2A}(t+1) &= y_{2A}(t)g_2\left(\sum_{j=1}^{2}\{\alpha_{2j}x_{jA}(t) + \beta_{2j}y_{jA}(t)\}\right) \\
    x_{2B}(t+1) &= y_{2B}(t)g_3(\alpha_{33}x_{2B}(t) + \beta_{33}y_{2B}(t)) \\
    y_{1A}(t+1) &= s_1x_{1A}(t) \\
    y_{2A}(t+1) &= s_2x_{2A}(t) - d(s_2x_{2A}(t) - s_3x_{2B}(t)) \\
    y_{2B}(t+1) &= s_3x_{2B}(t) + d(s_2x_{2A}(t) - s_3x_{2B}(t))
\end{align*}
\]  

(1)

where each \(\alpha_{ij}, \beta_{ij}, s_i\) and \(d\) is a nonnegative constant with \(\beta_{ii} > 0\), the survival rates \(s_i \in (0, 1]\) and the diffusion coefficient \(d \in (0, 1/2]\).

For each species \(i \in \{1, 2\}\), in patch \(A\), \(x_{iA}(t)\) and \(y_{iA}(t)\) respectively denote the population densities of its juveniles and adults at generation \(t\). In patch \(B\), \(x_{2B}(t)\) and \(y_{2B}(t)\) denote the population densities of the juveniles and adults of species 2 at generation \(t\), respectively. The constants \(s_i\) are the survival rates of the juveniles as they mature to adulthood. In system (1), for each \(i \in \{1, 2, 3\}\), the growth function \(g_i : [0, \infty) \to (0, \infty)\) is a strictly decreasing, positive continuous function. This makes system (1) a competitive system.

In system (1), species 1 and 2 compete in patch \(A\) with species 1 being sedentary in patch \(A\). However, as the juveniles of species 2 mature to adulthood, population pressure causes them to disperse between patches \(A\) and \(B\). The diffusion term is a fraction of the difference between the juvenile populations of species 2 in patches \(A\) and \(B\). Consequently, patch \(B\) is a safe refuge from competition for the juveniles of species 2. Franke and Yakubu [9] have studied discrete competitive models with a refuge for one of the competitors but with no age-structure, see [17, 19, 20] for similar examples of continuous models.

We now simplify system (1) with a change of variables. Let \(\bar{x}_{iA} = \beta_{ii}s_ix_{iA}\), \(\bar{y}_{iA} = \beta_{ii}y_{iA}\), \(\bar{\alpha}_{ij} = \alpha_{ij}/s_j\beta_{jj}\), \(\bar{\beta}_{ij} = \beta_{ij}/\beta_{jj}\), \(\bar{g}_i = s_ig_i\) for \(i, j \in \{1, 2\}\) and \(\bar{x}_{2B} = \beta_{33}s_3x_{2B}\), \(\bar{y}_{2B} = \beta_{33}y_{2B}\), \(\bar{\alpha}_{33} = \alpha_{33}/s_3\beta_{33}\).
\[ \bar{\beta}_{33} = \beta_{33}/\beta_{33} = 1, \quad \bar{g}_3 = s_3g_3. \] Then

\[
\bar{x}_{iA}(t + 1) = \beta_{ii}s_iy_{iA}(t)g_i\left( \sum_{j=1}^{2} \frac{\alpha_{ij}s_j\beta_{jj}}{s_j\beta_{jj}} x_{jA}(t) + (\beta_{ij}\beta_{jj}/\beta_{jj})y_{jA}(t) \right) = \bar{y}_{iA}(t)\bar{g}_i\left( \sum_{j=1}^{2} \bar{\alpha}_{ij}x_{jA}(t) + \bar{\beta}_{ij}\bar{y}_{jA}(t) \right)
\]

\[
\bar{x}_{2B}(t + 1) = \bar{y}_{2B}(t)\bar{g}_3\left( \sum_{j=1}^{2} \bar{\alpha}_{33}\bar{x}_{2B}(t) + \bar{\beta}_{33}\bar{y}_{2B}(t) \right)
\]

\[
\bar{y}_{1A}(t + 1) = \beta_{11}y_{1A}(t + 1) = \beta_{11}s_1x_{1A}(t) = \bar{x}_{1A}(t)
\]

\[
\bar{y}_{2A}(t + 1) = \beta_{22}(s_2x_{2A}(t) - d(s_2x_{2A}(t) - s_3x_{2B}(t)))
= \beta_{22}s_2x_{2A}(t) - d(s_2\beta_{22}x_{2A}(t) - s_3\beta_{22}x_{2B}(t))
\]

\[
\bar{y}_{2B}(t + 1) = \beta_{33}s_3x_{2B}(t) + d(s_2\beta_{33}x_{2A}(t) - s_3\beta_{33}x_{2B}(t)).
\]

Now if \( \beta_{22} = \beta_{33} \), then

\[
\bar{y}_{2A}(t + 1) = \bar{x}_{2A}(t) - d(\bar{x}_{2A}(t) - \bar{x}_{2B}(t))
\]

\[
\bar{y}_{2B}(t + 1) = \bar{x}_{2B}(t) + d(\bar{x}_{2A}(t) - \bar{x}_{2B}(t)).
\]

Consequently, all the barred quantities have similar asymptotic properties as the corresponding quantities in system (1). Notice that \( \bar{\beta}_{ii} \) and the new survival rates are 1. Biologically, the condition \( \beta_{22} = \beta_{33} \) is reasonable. It states that the effect of the adult populations of species 2 in patches A and B on the reproductive rates of their juveniles is the same. Thus, in system (1) we assume that \( \beta_{ii} = 1 \) and \( s_i = 1 \) for each \( i \in \{1, 2, 3\} \). The model we shall analyze is:

\[
x_{1A}(t + 1) = y_{1A}(t)g_1\left( \sum_{j=1}^{2} \{\alpha_{1j}x_{jA}(t) + \beta_{1j}y_{jA}(t)\} \right)
\]

\[
x_{2A}(t + 1) = y_{2A}(t)g_2\left( \sum_{j=1}^{2} \{\alpha_{2j}x_{jA}(t) + \beta_{2j}y_{jA}(t)\} \right)
\]

\[
x_{2B}(t + 1) = y_{2B}(t)g_3(\alpha_{33}x_{2B}(t) + y_{2B}(t))
\]

\[
y_{1A}(t + 1) = x_{1A}(t)
\]

\[
y_{2A}(t + 1) = x_{2A}(t) - d(x_{2A}(t) - x_{2B}(t))
\]

\[
y_{2B}(t + 1) = x_{2B}(t) + d(x_{2A}(t) - x_{2B}(t)).
\]
In system (2) we will assume that, for each $i \in \{1, 2, 3\}$, the growth function $g_i : [0, \infty) \to (0, \infty)$ strictly decreases from values greater than 1 to values less than 1. This allows populations to grow at low population densities and at the same time prevents population explosions, Lemma 2.

It is well known that system (2) is capable of generating complex dynamics such as period doubling bifurcation route to chaos, Hopf bifurcations and strange attractors [3–13, 16]. If species 1 dominates 2 in patch $A$ and patch $B$, the safe refuge, is not suitable for growth and reproduction of its juveniles, then it drives species 2 to extinction. On the other hand, if species 2 dominates 1 in patch $A$ and the safe refuge is a suitable habitat for its survival, then it dominates species 1 in system (2). We provide sufficient conditions that guarantee global convergence to the extinction state of each of the two competitors, Theorems 1 and 2. Due to biological populations’ natural propensity for exponential growth, we apply the extinction results to system (2) with all growth functions being exponential, Examples 1 and 2.

Example 3 illustrates that providing a safe refuge for an endangered species in an age-structured model could lead to stable coexistence of the competing species where there is extinction without the refuge. This example shows that dispersal between patches could represent a powerful strategy for the long-run stable coexistence of competing species.

Persistence captures the idea of nonextinction of species. Irrespective of initial conditions, we prove that an individual species with a sufficiently large carrying capacity persists in system (2) whenever each growth function is a function of the total population.

2. Notation and preliminaries. To write system (2) as a map, we denote the vector of population densities $x(t) = (x_{1A}(t), x_{2A}(t), x_{2B}(t))$ by $x = (x_1, x_2, x_3)$ and $y(t) = (y_{1A}(t), y_{2A}(t), y_{2B}(t))$ by $y = (y_1, y_2, y_3)$. Now define the map $F : \mathbb{R}_+^3 \times \mathbb{R}_+^3 \to \mathbb{R}_+^3 \times \mathbb{R}_+^3$ by $F(x(t), y(t)) = (x(t + 1), y(t + 1))$. Thus, for each $i \in \{1, 2\}$, $F_i(x, y) = y_i g_i(\sum_{j=1}^{\infty} \{\alpha_{ij} x_j + \beta_{ij} y_j\})$, $F_3(x, y) = y_3 g_3(x_3 + y_3)$, $F_4(x, y) = x_1$, $F_5(x, y) = x_2 - d (x_2 - x_3)$ and $F_6(x, y) = x_3 + d (x_2 - x_3)$. The iterates of the map $F$ are equivalent to the density sequence generated by system (2). $F^t$ is the map $F$ composed with itself $t$ times,
and $F^t_j(x, y)$ is the $j$th component of $F^t$ evaluated at the point $(x, y)$ in $\mathbb{R}_+^3 \times \mathbb{R}_+^3$. Therefore, $F^t$ gives the population densities in generation $t$.

For each $i \in \{1, 2, 3\}$, define the map $f_i : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ by $f_i(x_i, y_i) = (y_i g_i(x_i x_i + y_i), x_i)$. If all species are missing except species $i$ in either patch $A$ or $B$ and there is no diffusion between patches, $d = 0$, then the iterates of the map $f_i$ are equivalent to the density sequence generated by system (2). Now define the map $h_i : \mathbb{R}_+ \to \mathbb{R}_+$ by $h_i(y_i) = y_i g_i(y_i)$. Observe that $f_i(f_i(0, y_i)) = (0, h_i(y_i))$. Therefore, if an initial population density consists solely of adults of species $i$ in either patch $A$ or $B$, then the dynamics of the single species ecological model $f_i$ is intimately related to that of the map $h_i$. Note that if $g_i(y_i) = \exp(r - y_i)$, then $h_i$ is the classical single species population model of May [18].

The map $F$ sends the $x_2, x_3$ plane to the $y_2, y_3$ plane and back. Thus $F^2$ maps the $x_2, x_3$ plane into itself. When $g_i(y_i) = \exp(r - y_i)$, $F^2$ restricted to the $x_2, x_3$ plane is the one species diffusion model studied by Hastings [14].

The map $F$ sends the $x_1, y_1$ plane to itself. This restricted system is the following system of two equations:

\[
x_1(t + 1) = y_1(t) g_1(\alpha_{11} x_1(t) + y_1(t)) \]
\[
y_1(t + 1) = x_1(t).
\]


System (2) also contains a Kolmogorov type, two-species competitive system. To see this subsystem, let $d = 0$. Now $F$ maps the $x_1, x_2$ plane to the $y_1, y_2$ plane and back. $F^2$ restricted to the $x_1, x_2$ plane gives the desired system:

\[
x_1(t + 1) = x_1(t) g_1(x_1(t) + \beta_{12} x_2(t))
\]
\[
x_2(t + 1) = x_2(t) g_2(\beta_{21} x_1(t) + x_2(t)).
\]

Continuing to let $d = 0$, $F$ maps the $x_1, x_2, y_1, y_2$ plane into itself. The restriction of $F$ to this four-dimensional plane gives the two species,
two age class model studied by Franke and Yakubu [10].

\[
x_1(t + 1) = y_1(t)g_1 \left( \sum_{j=1}^{2} (\alpha_{1j} x_j(t) + \beta_{1j} y_j(t)) \right)
\]

\[
x_2(t + 1) = y_2(t)g_2 \left( \sum_{j=1}^{2} (\alpha_{2j} x_j(t) + \beta_{2j} y_j(t)) \right)
\]

(3)

\[
y_1(t + 1) = x_1(t)
y_2(t + 1) = x_2(t).
\]

In Section 5, we use system (3) with exponential growth functions to show that providing a safe refuge for a threatened species can save it from the brink of extinction.

Franke and Yakubu [9] also studied a two-species model with a safe refuge for one of the species. To obtain this three-dimensional system from system (2), note that \(F\) sends the \(x_1, x_2, x_3\) plane to the \(y_1, y_2, y_3\) plane and back. The required system, the restriction of \(F^2\) to the \(y_1, y_2, y_3\) plane, is the following system of three equations:

\[
y_1(t + 1) = y_1(t)g_1(y_1(t) + \beta_{12} y_2(t))
\]

\[
y_2(t + 1) = y_2(t)g_2(\beta_{21} y_1(t) + y_2(t)) - d \{y_2(t)g_2(\beta_{21} y_1(t) + y_2(t)) - y_3(t)g_3(y_3(t))\}
\]

\[
y_3(t + 1) = y_3(t)g_3(y_3(t)) + d \{y_2(t)g_2(\beta_{21} y_1(t) + y_2(t)) - y_3(t)g_3(y_3(t))\}.
\]

One of the relevant properties of system (2) is that it contains so many important biologically significant subsystems.

Recall that, for each \(i \in \{1, 2, 3\}\), the growth function \(g_i : [0, \infty) \to (0, \infty)\) is a strictly decreasing continuous function that takes on positive values bigger than 1 and less than 1. As a result, the equation \(g_i(y_i) = 1\) has a unique positive solution, denoted by \(Y_i\) in \((0, \infty)\). Notice that \(Y_i\) is the unique positive fixed point of the map \(h_i\).

Since \(g_i\) is a strictly decreasing continuous function, if \(0 < y_i < Y_i\), then \(h_i(y_i) > y_i\) and if \(y_i > Y_i\), then \(h_i(y_i) < y_i\). Consequently, under \(h_i\) iterations, every point is attracted to the compact invariant set \(T_i \equiv h_i([0, Y_i])\). We will use the following results in constructing invariant sets for \(F\) and \(F^2\).
Lemma 1. (i) Let \( i \in \{1, 2, 3\} \). If \( y_i \in [0, \max T_i] \), then \( F_i(x, y) \in [0, \max T_i] \).

(ii) If \( y_1 \in [0, \max T_1] \), then \( F_1^2(x, y) \in [0, \max T_1] \).

(iii) \( F_5(x, y) \leq \max\{x_2, x_3\} \) and \( F_6(x, y) \leq \max\{x_2, x_3\} \).

Proof. (i) By the decreasing nature of \( g_i \) and the fact that each \( \beta_{ii} = 1 \), one sees that, for \( i \in \{1, 2, 3\} \), \( F_i(x, y) \leq h_i(y_i) = y_i g_i(y_i) \). As a result, if \( y_i \in [0, \max T_i] \), then \( h_i(y_i) \in [0, \max T_i] \) and hence \( F_i(x, y) \in [0, \max T_i] \).

(ii) Since \( F_4^2(x, y) = F_1(x, y) \) and \( y_1 \in [0, \max T_1] \) implies that \( F_4^2(x, y) \in [0, \max T_1] \).

(iii) Notice that \( F_5(x, y) = (1-d)x_2 + dx_3 \) and \( F_6(x, y) = dx_2 + (1-d)x_3 \). Thus, if \( x_2 \leq x_3 \), then \( F_5(x, y) \leq x_3 \) and \( F_6(x, y) \leq x_3 \). Also, if \( x_2 \geq x_3 \), then \( F_5(x, y) \leq x_2 \) and \( F_6(x, y) \leq x_2 \) and the result is established.

Let \( T = [0, \max T_1] \times [0, \max\{\max T_2, \max T_3\}] \times [0, \max\{\max T_2, \max T_3\}] \). Recall that, for each \( i \in \{1, 2, 3\} \), if \( y_i > \max T_i \), then \( F_i(x, y) < y_i \). On using Lemma 1 and the fact that \( F_4(x, y) = x_1 \), we obtain that \( T \times T \) is a compact \( F \) invariant set, Corollary 1.

Corollary 1. \( F(T \times T) \subset T \times T \).

Lemma 2. Every point in system (2) has a bounded orbit.

Proof. By Corollary 1, the set \( T \times T \) is a compact \( F \) invariant set. Thus, if some iterate of a point gets in \( T \times T \), it must remain there under all iterations. Consequently, such an orbit is bounded.

By Lemma 1 if \( y_1 \in [0, \max T_1] \), then \( F_4^2(x, y) \in [0, \max T_1] \). Thus, for initial adult populations that are not bigger than \( \max T_1 \), the adults of species 1 in patch A are bounded by \( \max T_1 \) at least in every other generation. If \( y_1 > \max T_1 \geq Y_1 \), then \( F_4^2(x, y) = F_1(x, y) = y_1 g_1(\sum_{j=1}^{2}(\alpha_{1j} x_j + \beta_{1j} y_j)) \leq h_1(y_1) = y_1 g_1(y_1) \) by the decreasing nature of \( g_i \) and the fact that \( \beta_{ii} = 1 \). Recall that \( g_i(y_i) < 1 \) whenever \( y_i > Y_i \). Thus, \( F_4^2(x, y) \leq y_1 g_1(y_1) < y_1 \). This shows that
the adult population of species 1 decreases in every other generation unless it gets less than \( \max T_1 \). Notice that the adult population of species 1 in patch \( A \) either decreases to \( \max T_1 \) or, for some generations, it is less than or equal to \( \max T_1 \) under \( F^2 \). To find the adult population of species 1 in patch \( A \) for the odd generations, use the fact that \( F_4(x, y) = x_1 \) and repeat the above argument with \( x_1 \). Thus, \( \max \{x_1, y_1, \max T_1\} \) is an upper bound for the adult population of species 1 in patch \( A \).

If \( y_2 > \max T_2 \geq Y_2 \), then \( F_2(x, y) = y_2g_2(\sum_{j=1}^{2} \{\alpha_{2j}x_j + \beta_{2j}y_j\}) \leq h_2(y_2) = y_2g_2(y_2) \) by the decreasing nature of \( g_2 \) and the fact that \( \beta_{22} = 1 \). Recall that \( g_i(y_i) < 1 \) whenever \( y_i > Y_i \). Thus \( F_2(x, y) \leq y_2g_2(y_2) < y_2 \). If \( y_3 > \max T_3 \geq Y_3 \), then \( F_3(x, y) = y_3g_3(\alpha_{33}x_3 + y_3) \leq h_3(y_3) = y_3g_3(y_3) \) by the decreasing nature of \( g_3 \). Thus, \( F_3(x, y) \leq y_3g_3(y_3) < y_3 \). Hence, \( \max \{F_2(x, y), F_3(x, y)\} \leq \max \{y_2, y_3, \max T_2, \max T_3\} \). By Lemma 1, we have \( \max \{F_5(x, y), F_6(x, y)\} \leq \max \{x_2, x_3\} \). Thus,

\[
\max \{F_5^2(x, y), F_6^2(x, y)\} \leq \max \{x_2, x_3, y_2, y_3, \max T_2, \max T_3\}.
\]

This shows that \( \max \{x_2, x_3, y_2, y_3, \max T_2, \max T_3\} \) is an upper bound for the adults of species 2 in both patches \( A \) and \( B \). Note that, in every other generation, the maximum of the adult populations of species 2 in patches \( A \) and \( B \) decreases, whenever it is larger than \( \max \{\max T_2, \max T_3\} \). Thus, the maximum of the adult populations of species 2 in patches \( A \) and \( B \) either decreases to \( \max \{\max T_2, \max T_3\} \) or becomes less than or equal to it under some iterate of \( F^2 \).

Since the adult population is bounded, the juvenile population is bounded by the product of the maximum \( g_i(0) \) and the maximum adult population. Consequently, no point in system (2) has an unbounded orbit.

The following result is a consequence of the proof of Lemma 2.

**Corollary 2.** In system (2), the \( \omega \)-limit set of every point in \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \) is a nonempty subset of the compact invariant set \( T \times T \).

In the following result of Franke and Yakubu [10], \( f \) is a continuous map of a metric space into itself, and \( \omega(v, f^2) \) is the \( \omega \)-limit set of \( v \) under \( f^2 \) iterations.
Lemma 3. (i) If $z \in \omega(v, f^2)$, then $f(z) \in \omega(f(v), f^2)$.
(ii) If $z \in \omega(f(v), f^2)$, then $f(z) \in \omega(v, f^2)$.
(iii) If $z \in \omega(v, f)$, then $z \in \omega(v, f^2) \cup \omega(f(v), f^2)$.

The following result, Corollary 3, is an immediate consequence of Lemma 3.

**Corollary 3.** In system (2), $\omega((x, y), F) = \omega((x, y), F^2) \cup \omega(F(x, y), F^2)$ with $\omega((x, y), F^2)$ and $\omega(F(x, y), F^2)$ each mapped to the other by $F$.

Now we obtain a simple but important inequality that will be used in establishing Lyapunov functions for system (2).

**Lemma 4.** If $a_i, b_i \geq 0$ and each $b_i \neq 0$, then

$$\frac{\sum_{i=1}^{n} a_i}{\sum_{i=1}^{n} b_i} \leq \max_{j \in \{1, 2, \ldots, n\}} \left\{ \frac{a_j}{b_j} \right\}.$$

To prove Lemma 4, observe that for each $i \in \{1, 2, \ldots, n\}$, $a_i \leq b_i \max_j \{a_j/b_j\}$. Thus,

$$\frac{\sum_{i=1}^{n} a_i}{\sum_{i=1}^{n} b_i} \leq \frac{\left( \max_{j \in \{1, 2, \ldots, n\}} \{a_j/b_j\} \right) \sum_{i=1}^{n} b_i}{\sum_{i=1}^{n} b_i} \leq \max_{j \in \{1, 2, \ldots, n\}} \left\{ \frac{a_j}{b_j} \right\}.$$

3. **Species 1 dominance.** In system (2), species 1 is the sedentary species in patch $A$ and species 2 diffuses between patches $A$ and $B$. Consequently, if species 1 is the dominant species in patch $A$ and patch $B$ is not suitable for the growth and reproduction of the juveniles of species 2, then species 1 drives species 2 to the brink of extinction. Here we provide a sufficient condition that is shown to guarantee the dominance of species 1 in system (2).

**Definition 1.** In system (2), species 1 *dominates* 2 if there exists a
positive constant $c$ such that
\[
\left( g_1 \left( \sum_{j=1}^{2} \{ \alpha_{1j} x_j + \beta_{1j} y_j \} \right) \right)^c 
> \max \left\{ d g_2 \left( \sum_{j=1}^{2} \{ \alpha_{2j} x_j + \beta_{2j} y_j \} \right) + (1 - d) g_3 (\alpha_{33} x_3 + y_3), \right. \\
\left. (1 - d) g_2 \left( \sum_{j=1}^{2} \{ \alpha_{2j} x_j + \beta_{2j} y_j \} \right) + d g_3 (\alpha_{33} x_3 + y_3) \right\},
\]
for all points $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in T \times T$.

If species 1 dominates 2, then the growth rate of species 1 in patch $A$ raised to a positive power on a compact set always exceeds linear combinations of the growth rates of species 2 in patches $A$ and $B$. Every positive population density leads to the extinction of species 2 whenever species 1 dominates 2, Theorem 1.

**Theorem 1.** In system (2), if species 1 dominates 2, then $x_1 > 0$ and $y_1 > 0$ at the point $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3)$ in $\mathbb{R}^3_+ \times \mathbb{R}^3_+$ imply that $\omega((x, y), F) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}^3_+ \times \mathbb{R}^3_+ | x_2 = x_3 = y_2 = y_3 = 0 \}$. Hence species 1 drives species 2 to extinction.

**Proof.** The $\omega$-limit set of every point in $\mathbb{R}^3_+ \times \mathbb{R}^3_+$ is a nonempty subset of the compact invariant set $T \times T$, Corollary 2. Hence, under $F$ iterations, every point eventually enters and remains inside small neighborhoods of $T \times T$.

We first prove the result for points $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3)$ in $T \times T$ with $x_1 > 0$ and $y_1 > 0$. By Corollary 2, $\omega((x, y), F^2) \neq \emptyset$. Let $(p, q) = (p_1, p_2, p_3, q_1, q_2, q_3) \in \omega((x, y), F^2)$. Then there exists $t_i \to +\infty$ such that $F^{2t_i}(x, y) \to (p, q)$. We need to show that, for each $j \in \{1, 2, 3, 4, 5, 6\}$, if $j \neq 1$ or 4, then $F^{2t_i}(x, y) \to 0$ as $t_i \to +\infty$.

Define $V : T \times T \to \mathbb{R}_+$ by $V(x, y) = \max \{ y_2/y_1^c, y_3/y_1^c \}$ where $y_1 > 0$ and where $c > 0$ is given by the dominance condition. Next we show that $V$ is a Lyapunov function under $F^2$ iteration. The monotonic decreasing nature of $V$ is used to show that each $\omega$-limit point $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3)$ must have $x_2 = x_3 = y_2 = y_3 = 0$. Notice
that $V(F^2(x, y)) = \max\{F_6^2(x, y)/(F_4^2(x, y))^c, F_6^2(x, y)/(F_4^2(x, y))^c\}$. Moreover,

$$
\frac{F_6^2(x, y)}{(F_4^2(x, y))^c} = \frac{(1-d)g_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}) + dy_3g_3(\alpha_{33}x_3 + y_3)}{(y_1g_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\}))^c} < \frac{(1-d)g_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}) + dy_3g_3(\alpha_{33}x_3 + y_3)}{y_1^cg_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}) + dg_3(\alpha_{33}x_3 + y_3)}
$$

by the fact that species $i$ dominates 2. On applying Lemma 4 to the last inequality, we obtain that $F_6^2(x, y)/(F_4^2(x, y))^c < \max\{y_2/y_1^c, y_3/y_1^c\}$. Also,

$$
\frac{F_6^2(x, y)}{(F_4^2(x, y))^c} = \frac{dy_3g_3(\alpha_{33}x_3 + y_3)}{(y_1g_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\}))^c} < \frac{dy_3g_3(\alpha_{33}x_3 + y_3)}{y_1^c\{dg_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}) + (1-d)g_3(\alpha_{33}x_3 + y_3)\}}
$$

by species 1 dominates 2. Again, by Lemma 4, we obtain $F_6^2(x, y)/(F_4^2(x, y))^c < \max\{y_2/y_1^c, y_3/y_1^c\}$. Thus, for all points $(x, y) \in T \times T$ satisfying $y_1 > 0$ and $y_2$ or $y_3 > 0$, we have that $V(F^2(x, y)) < V(x, y)$.

If $q_1 > 0$ and $q_2$ or $q_3 > 0$, then $V(F^2(p, q)) < V(p, q)$. This, however, is impossible for an $\omega$-limit point. Therefore, $q_2 = q_3 = 0$ if $q_1 > 0$. If $q_2$ or $q_3 > 0$ and $q_1 = 0$, then the sequence $\{V(F^{2^n}(x, y))\}$ is unbounded, a contradiction. Thus, $\omega((x, y), F^2) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3; x_2 = x_3 = y_2 = y_3 = 0\}$.

By Lemma 3, $(p, q) \in \omega((x, y), F^2)$ implies $F(p, q) \in \omega(F(x, y), F^2)$. If $F_4(p, q) > 0$ and $F_5(p, q) = 0$, then $V(F^2(F(p, q))) < V(F(p, q))$ is a contradiction. Therefore, $F_5(p, q) = F_6(p, q) = 0$ if $F_4(p, q) > 0$. If $F_5(p, q) > 0$ but $F_4(p, q) = 0$, then $\{V(F^{2^n}(x, y))\}$ is an unbounded sequence, a contradiction. Hence, $(p, q) \in \omega((x, y), F^2)$ implies $F(p, q) \in \omega(F(x, y), F^2)$ with $F_5(p, q) = F_6(p, q) = 0$. However, $F_5(p, q) = (1-d)p_2 + dp_3 = 0$ or $F_6(p, q) = dp_2 + (1-d)p_3 = 0$ imply that $p_2 = p_3 = 0$. Consequently $\omega(F(x, y), F^2) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3; x_2 = x_3 = y_2 = y_3 = 0\}$. By Corollary 3, $\omega(x, y) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3; x_2 = x_3 = y_2 = y_3 = 0\}$, and the result is established for points in $T \times T$. 
Next we consider points that do not enter the compact invariant set \( T \times T \). By continuity, there exists a neighborhood of \( T \times T \) in \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \) on which species 1 dominates 2. By Corollary 2 every point eventually enters and remains in this neighborhood. Recall that the Lyapunov function \( V \) is eventually decreasing on the orbit of every point \( (x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3 \) with \( x_1 > 0 \) and \( y_1 > 0 \). Consequently, as in the first situation, \( \omega(x, y) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3 \mid x_2 = x_3 = y_2 = y_3 = 0 \} \), and this completes the proof. \( \square \)

Now we use a specific example to illustrate an application of Theorem 1. In this example we consider two species with juvenile and adult age classes, and with a safe refuge from competition,

\[
\begin{align*}
  x_1(t+1) &= y_1(t) \exp\left( p_1 - \left( q_1 \sum_{j=1}^{2} \{ \alpha_{1j}x_j(t) + \beta_{1j}y_j(t) \} \right) \right) \\
  x_2(t+1) &= y_2(t) \exp\left( p_2 - \left( q_2 \sum_{j=1}^{2} \{ \alpha_{2j}x_j(t) + \beta_{2j}y_j(t) \} \right) \right) \\
  x_3(t+1) &= y_3(t) \exp(p_3 - \{ q_3 \{ \alpha_{33}x_3(t) + \beta_{33}y_3(t) \} \}) \\
  y_1(t+1) &= x_1(t) \\
  y_2(t+1) &= x_2(t) - d(x_2(t) - x_3(t)) \\
  y_3(t+1) &= x_3(t) + d(x_2(t) - x_3(t)).
\end{align*}
\]

(4)

Notice that system (4) is system (2) with all growth functions being decreasing exponential functions.

**Example 1.** Set the following parameter values in system (4). For each \( i, j \in \{1, 2\} \), \( \alpha_{ij} = \beta_{ij} = 1 \), \( d = 1/2 \), \( p_1 = p_2 \), \( q_1 = q_2 \) and \( \min_{(x, y) \in T \times T} e^{p_2 - q_2 \{ \sum_{j=1}^{2} \{ \alpha_{2j}x_j + \beta_{2j}y_j \} \}} > e^{p_3} \).

By our choice of parameters, for each point \( (x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \)
$\in T \times T$ we have
\[
\left\{ e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\})} + e^{p_3-q_3(\alpha_{33}x_3+y_3)} \right\}/2 \\
\leq \left\{ e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\})} + e^{p_3} \right\}/2 \\
\leq e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\})} \\
e^{p_1-q_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j+\beta_{1j}y_j\})}.
\]

Hence species 1 dominates 2.

In Example 1, if for each $i \in \{1, 2, 3\}$, $p_i \in (0, 1]$, then $Y_i = p_i = \max T_i$. If, in addition, $q_1 = q_2 = 0.01$, $p_1 = p_2 = 1$ and $p_3 < 0.96$, then
\[
e^{p_3} < e^{0.96} = \min_{(x,y) \in T \times T} e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\})},
\]
and hence species 1 drives species 2 to extinction, Theorem 1.

4. **Species 2 dominance.** If the growth rate of species 2 in patch $A$ always exceeds that of species 1, then species 2 dominates 1 in patch $A$. In addition, if patch $B$ is suitable for the growth and reproduction of the mobile juveniles of species 2, then species 2 drives species 1 to extinction.

We now develop a criterion that will be useful in obtaining global convergence to the extinction state of species 1, $\{0\} \times \mathbb{R}_+^2 \times \{0\} \times \mathbb{R}_+^2$.

**Definition 2.** In system (2), species 2 dominates 1 if there exists a positive constant $c$ such that
\[
\left(g_1\left(\sum_{j=1}^{2}\{\alpha_{1j}x_j+\beta_{1j}y_j\}\right)\right)^c < \min \left\{ d g_2\left(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\}\right) + (1-d) g_3(\alpha_{33}x_3+y_3), \right. \\
\left. (1-d) g_2\left(\sum_{j=1}^{2}\{\alpha_{2j}x_j+\beta_{2j}y_j\}\right) + d g_3(\alpha_{33}x_3+y_3) \right\}
\]
for all points \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in T \times T\).

By Definition 2, linear combinations of the growth rates of species 2 in patches \(A\) and \(B\) always exceed the growth rate of species 1 in patch \(A\) raised to a positive power on a compact set whenever species 2 dominates 1. The next result, Theorem 2, states that a dominant species 2 drives species 1 to extinction.

**Theorem 2.** In system (2), if species 2 dominates 1, then \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3)\) is an interior point of \(\mathbb{R}^3_+ \times \mathbb{R}^3_+\) implies that \(\omega((x, y), F) \subset \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}^3_+ \times \mathbb{R}^3_+ | x_1 = y_1 = 0\}\). Hence, species 2 drives species 1 to extinction.

The proof of Theorem 2 is similar to that of Theorem 1. In the proof of Theorem 2, define the Lyapunov function \(V : T \times T \rightarrow \mathbb{R}_+\) by \(V(x, y) = \max\{y_1^c/y_2, y_2^c/y_3\}\) where \(y_2, y_3 > 0\) and \(c > 0\) is given by the dominance condition. Then

\[
V(F^2(x, y)) = \max \left\{ \left( \frac{(F_4^2(x, y))^c}{F_5^2(x, y)} \right), \left( \frac{(F_4^2(x, y))^c}{F_6^2(x, y)} \right) \right\}.
\]

By direct computation and using the fact that species 2 dominates 1, we obtain

\[
\left( \frac{(F_4^2(x, y))^c}{F_5^2(x, y)} \right) = \frac{(y_1g_1(\sum_{j=1}^2(\alpha_{1j}x_j + \beta_{1j}y_j)))^c}{(1-d)y_2g_2(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + dy_3g_3(\alpha_{33}x_3 + y_3)} < \frac{y_1^c((1-d)g_2(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + g_3(\alpha_{33}x_3 + y_3))}{(1-d)y_2g_2(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + dy_3g_3(\alpha_{33}x_3 + y_3)}.
\]

On applying Lemma 4 to the last inequality, we obtain that \((F_4^2(x, y))^c/F_5^2(x, y) < \max\{y_1^c/y_2, y_2^c/y_3\}\). Also,

\[
\left( \frac{(F_4^2(x, y))^c}{F_6^2(x, y)} \right) = \frac{(y_1g_1(\sum_{j=1}^2(\alpha_{1j}x_j + \beta_{1j}y_j)))^c}{dy_2g_2(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + (1-d)y_3g_3(\alpha_{33}x_3 + y_3)} < \frac{y_1^c(dy_3g_3(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + (1-d)y_3g_3(\alpha_{33}x_3 + y_3))}{dy_2g_2(\sum_{j=1}^2(\alpha_{2j}x_j + \beta_{2j}y_j)) + (1-d)y_3g_3(\alpha_{33}x_3 + y_3)}.
\]
by the dominance condition. Again, on applying Lemma 4, we obtain
\((F^2(x, y))^c/F^2_c(x, y) < \max\{y^c_1/y_2, y^c_2/y_3\}\). As a result, \(V(F^2(x, y)) < V(x, y)\). Now proceed exactly as in the proof of Theorem 1 to establish Theorem 2.

For an application of Theorem 2, we set the following parameter values in system (4).

**Example 2.** For each \(i, j \in \{1, 2\}\), let \(\alpha_{ij} = \beta_{ij} = 1\), \(\alpha_{33} = \beta_{33} = 1\), \(d = 1/2\), \(q_1 = q_2 = q_3 = 0.1\) and \(e^{p_1} < (1/2)e^{p_2-0.04}\) where \(p_i \in (0, 1]\) for each \(i \in \{1, 2, 3\}\).

With our choice of constants, \(Y_i = p_i = \max T_i\) for each \(i \in \{1, 2, 3\}\). Thus, for each point \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in T \times T\) we have
\[
e^{p_1-q_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\})} \leq e^{p_1} < \frac{1}{2}e^{p_2-0.04} \\
= \min_{(x, y) \in T \times T} \frac{1}{2}e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\})} \\
\leq \frac{1}{2}\left\{e^{p_2-q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\})} \\
+ e^{p_3-q_3(\alpha_{33}x_3 + y_3)}\right\}.
\]

Hence, species 2 dominates 1 and Theorem 2 gives global convergence to the extinction state of species 1.

5. **Coexistence.** For Kolmogorov systems of difference equations with no age-structure, Franke and Yakubu [9] proved that a dominant species drives all the dominated species to extinction. In such systems, Franke and Yakubu used a safe refuge for the endangered species to save it from the brink of extinction [9]. In this section we use system (4) to illustrate stable coexistence of species with dispersion where there is extinction of species without dispersion.

When there is no dispersion between patches, \(d = 0\), and the density of species 2 in patch \(B\) is zero, \(x_3 = y_3 = 0\), then system (2) becomes system (3). Franke and Yakubu have studied the dynamics of system (3), the two species, two age-structured model of Ebenmann [4–7, 10].
We will use the following result of Franke and Yakubu on system (3) [10].

**Theorem 3** [10]. In system (3), if there exists a positive number $c$ such that for all points $(x, y) = (x_1, x_2, y_1, y_2)$ in $\mathbb{R}_+^2 \times \mathbb{R}_+^2$, 
\[
(g_2(\sum_{j=1}^{2} \{\alpha_{2j}x_j + \beta_{2j}y_j\}))^c < g_1(\sum_{j=1}^{2} \{\alpha_{1j}x_j + \beta_{1j}y_j\}),
\]
then $p_1 > 0$ and $q_1 > 0$ at the point $(p, q) = (p_1, p_2, q_1, q_2)$ in $\mathbb{R}_+^2 \times \mathbb{R}_+^2$ imply that
\[
\omega((p, q), F) \subset \{(x, y) = (x_1, x_2, y_1, y_2) \in \mathbb{R}_+^2 \times \mathbb{R}_+^2 | x_2 = y_2 = 0\}.
\]
Hence, species 2 goes extinct.

**Example 3.** In system (4) set the following parameter values: For each $i, j \in \{1, 2\}$, $\alpha_{ij} = \beta_{ij} = 1$, $\alpha_{33} = \beta_{33} = 1$, $q_1 = q_2 = q_3 = 1$, $p_1 = 1.1$, $p_2 = 1$ and $p_3 = 2$. For all points $(x, y) = (x_1, x_2, y_1, y_2)$ in $\mathbb{R}_+^2 \times \mathbb{R}_+^2$, 
\[
g_2(\sum_{j=1}^{2} \{\alpha_{2j}x_j + \beta_{2j}y_j\}) = \exp(p_2 - q_2(\sum_{j=1}^{2} \{\alpha_{2j}x_j + \beta_{2j}y_j\})) < g_1(\sum_{j=1}^{2} \{\alpha_{1j}x_j + \beta_{1j}y_j\}) = \exp(p_1 - q_1(\sum_{j=1}^{2} \{\alpha_{1j}x_j + \beta_{1j}y_j\})).
\]
By Theorem 3, if there is no diffusion between patches and the population of species 2 in the safe refuge is zero, that is, $d = x_3 = y_3 = 0$, then species 2 goes extinct. However, our numerical experiments seem to suggest that with any amount of diffusion, a stable coexistence of the two competing species occurs. In particular, if the diffusion coefficient $d = 0.1$, then our numerical calculations show the existence of a period 2 orbit that attracts positive population densities. The points in the period 2 orbit are $(0, 0.46517, 1.53472, 0.63483, 0, 0) \rightarrow (0.63483, 0, 0, 0, 0.57212, 1.42776)$.

The period 2 orbit illustrates a stable coexistence of the adults of species 1 with the juveniles of species 2 in patch A. This alternatives with the stable coexistence of the juveniles of species 1 with the adults of species 2 in patch A.

In Example 3 we obtained the stable coexistence of the two competing species by providing a safe refuge for the endangered species, Theorem 3. Next we illustrate the stable coexistence of the two competing species by providing a safe refuge for the dominant species, Example 4.

**Example 4.** In system (2), set the following parameter values: For each $i, j \in \{1, 2\}$, $\alpha_{ij} = \beta_{ij} = 1$, $\alpha_{33} = \beta_{33} = 1$, $q_1 = q_2 = q_3 = 1$, $p_1 = 1$, $p_2 = 1.1$ and $p_3 = 0.1$. For all points
\((x, y) = (x_1, x_2, y_1, y_2)\) in \(\mathbb{R}^2_+ \times \mathbb{R}^2_+\), \(g_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\}) = \exp(p_1 - q_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\})) < g_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}) \equiv \exp(p_2 - q_2(\sum_{j=1}^{2}\{\alpha_{2j}x_j + \beta_{2j}y_j\}))\). Species 2 is the dominant species provided there is no diffusion, Theorem 3.

With the introduction of diffusion between patches, a dramatic bifurcation occurs. With our choice of constants, as the diffusion coefficient \(d\) increases past 0.13, the system changes from the extinction of species 1 to the stable coexistence of the two competing species. In particular, at \(d = 0.3\) the system has a period 2 orbit that attracts positive population densities. The points in the period 2 orbit are

\[
(0.73193, 0.29626, 0.20228, 0, 0, 0) \\
\rightarrow (0, 0, 0, 0.73193, 0.26807, 0.23048).
\]

The period 2 orbit illustrates a stable coexistence of the juveniles of the two competitors. This alternates with the stable coexistence of their adults.

6. Persistence. Persistence or the nonextinction of species is an important ecological concept. In this section, we obtain that an individual species with a sufficiently large carrying capacity persists in system (2). We make the following additional assumptions throughout this section.

(a) \((X, d)\) is a locally compact metric space with metric \(d\),

(b) \(f : X \rightarrow X\) is a continuous map,

(c) \(C\) and \(D\) are subsets of the metric space \(X\),

(d) \(D\) is compact and positively invariant, \(f(D) \subset D\),

(e) \(C\) is closed with \(C\) and \(X \backslash C\) being positively invariant,

(f) \(E = C \cap D\).

Definition 3. The map \(f : X \rightarrow X\) is uniformly persistent (with respect to \(C\)) if there exists \(k > 0\) such that for all \(x \in X \backslash C\),

\[
\liminf_{n \to \infty} d(f^n(x), C) > k \ [1, 2, 9, 15].
\]

To prove the persistence results for system (2), we need the following result of Franke and Yakubu [9].
Proposition 1 [9]. Let $\omega(x) \subset D$ for all $x \in X$. Then, for all $x \in X \setminus C$, $\omega(x) \cap C = \emptyset$ if there exists a continuous function $p : X \to [0, \infty)$ such that the following two conditions are satisfied:

(a) $p(x) = 0$ for all $x \in E$, and

(b) there exists a closed neighborhood $U$ of $E$ such that, for all $x \in U \setminus C$, there exists $n = n(x) > 0$ satisfying $p(f^n(x)) > p(x)$.

Moreover, $f$ is uniformly persistent with respect to $C$.

The persistence result, Theorem 4, states that if the carrying capacities of species 2 in patches $A$ and $B$ are sufficiently large, then it continues to persist in system (2) with each growth function being a function of the total population in the patch.

Theorem 4. In system (2), $F$ is uniformly persistent with respect to $\mathbb{R}_+ \times \{0\} \times \{0\} \times \mathbb{R}_+ \times \{0\} \times \{0\}$ whenever $\alpha_{ij} = \beta_{ij} = 1$ for each $i, j$ and $\min \{Y_2, Y_3\} > 2 \max T_1$. Hence, for each point $(x, y)$ in the interior of $\mathbb{R}_+^3 \times \mathbb{R}_+^3$, $\omega(x, y) \cap \mathbb{R}_+ \times \{0\} \times \{0\} \times \mathbb{R}_+ \times \{0\} \times \{0\} = \emptyset$, and species 2 persists.

Proof. By the result of Franke and Yakubu, Proposition 1 [9], it is sufficient to show that all the hypotheses of Proposition 1 are satisfied.

Recall that $D = T \times T$ is a nonempty compact, positively $F$ invariant set, and $\omega(x, y) \subset D$ for all $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3$.

Corollary 2. Let $C = \mathbb{R}_+ \times \{0\} \times \{0\} \times \mathbb{R}_+ \times \{0\} \times \{0\}$. Then the set $C$ is a closed, positively $F$ invariant subset of $\mathbb{R}_+^3 \times \mathbb{R}_+^3$, and $\mathbb{R}_+^3 \times \mathbb{R}_+^3 \setminus C$ is also $F$ invariant.

Let $E = C \cap D$. Now we construct a neighborhood $U$ of $E$ in $\mathbb{R}_+^3 \times \mathbb{R}_+^3$. Choose $\epsilon > 0$ satisfying $0 < \epsilon < (1/2)||\min \{Y_2, Y_3\} - 2 \max T_1||$. Let $U$ be the closed region in $\mathbb{R}_+^3 \times \mathbb{R}_+^3$ bounded by the six coordinate planes and the hyperplane $\{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3 | \sum_{j=1}^3 (x_j + y_j) = 2 \max T_1 + \epsilon\}$.

Note that $U$ is a closed neighborhood of the set $E$ in $\mathbb{R}_+^3 \times \mathbb{R}_+^3$. Since each $\alpha_{ij} = \beta_{ij} = 1$, we have that, for all points $(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in U \setminus C$, $\sum_{j=1}^3 (\alpha_{ij} x_j + \beta_{ij} y_j) = \sum_{j=1}^3 (x_j + y_j) \leq 2 \max T_1 + \epsilon < \min \{Y_2, Y_3\}$. Consequently, $g_2(\sum_{j=1}^3 (\alpha_{2j} x_j + \beta_{2j} y_j)) >$
1 and \( g_2(\alpha_{33}x_3 + y_3) > 1 \) for all points \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in U \setminus C \). Define the continuous function \( p : \mathbb{R}_+^3 \times \mathbb{R}_+^3 \to \mathbb{R}_+ \) by \( p(x, y) = y_2 + y_3 \). It is easy to see that \( p(x, y) = 0 \) for all points \((x, y) \in E \). Furthermore, for all points \((x, y) \in U \setminus C \), \( p(F^2(x, y)) = F_2(x, y) + F_3(x, y) = y_2g_2(\sum_{j=1}^2 (\alpha_{2j}x_j + \beta_{2j}y_j)) + y_3g_3(\alpha_{33}x_3 + y_3) > y_2 + y_3 \), since \( y_2 \) and \( y_3 \) are not simultaneously equal to zero. All the conditions of Proposition 1 are satisfied. Hence \( F \) is uniformly persistent with respect to the repelling set \( C = \mathbb{R}_+ \times \{0\} \times \{0\} \times \mathbb{R}_+ \times \{0\} \times \{0\} \). \( \Box \)

Independent of the ability of the juveniles of species 2 to diffuse between patches \( A \) and \( B \), if the carrying capacity of species 1 is sufficiently large and each growth function is a function of the total population of species in the patch, then species 1 persists in system (2), Theorem 5.

**Theorem 5.** In system (2), \( F \) is uniformly persistent with respect to \( \{0\} \times \mathbb{R}_+^2 \times \{0\} \times \mathbb{R}_+^2 \) whenever \( \alpha_{ij} = \beta_{ij} = 1 \) for each \( i, j \) and \( Y_1 > 4 \max\{\max T_2, \max T_3\} \). Hence, for each point \((x, y) \) in the interior of \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \), \( \omega(x, y) \cap \{0\} \times \mathbb{R}_+^2 \times \{0\} \times \mathbb{R}_+^2 = \emptyset \), and species 1 persists.

**Proof.** The proof of Theorem 5 is similar to that of Theorem 4. As in the proof of Theorem 4, we will show that all the hypotheses of Proposition 1 are satisfied. The result then follows by a similar application of Proposition 1.

\( D = T \times T \) is a nonempty compact, positively \( F \) invariant set, and \( \omega(x, y) \subset D \) for all \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3 \), Corollary 2. Now let \( C = \{0\} \times \mathbb{R}_+^2 \times \{0\} \times \mathbb{R}_+^2 \). \( C \) is a closed positively invariant subset of \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \) and \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \setminus C \) is also \( F \) invariant.

Let \( E = C \cap D \). Choose \( \varepsilon > 0 \) satisfying \( 0 < \varepsilon < (1/2)|Y_1 - 4 \max\{\max T_2, \max T_3\}| \). Let \( U \) be the closed region in \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \) bounded by the six coordinate planes and the hyperplane \( \{(x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in \mathbb{R}_+^3 \times \mathbb{R}_+^3 | \sum_{j=1}^3 (x_j + y_j) = 4 \max\{\max T_2, \max T_3\} + \varepsilon \} \). Then \( U \) is a closed neighborhood of the set \( E \) in \( \mathbb{R}_+^3 \times \mathbb{R}_+^3 \). For all points \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in U \), \( \sum_{j=1}^2 (\alpha_{1j}x_j + \beta_{1j}y_j) = \sum_{j=1}^2 (x_j + y_j) \leq 4 \max\{\max T_2, \max T_3\} + \varepsilon < Y_1 \). By the
decreasing nature of \( g_1 \), we have \( g_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\}) > g_1(Y_1) = 1 \) for all points \((x, y) = (x_1, x_2, x_3, y_1, y_2, y_3) \in U\). Now define the continuous function \( p : \mathbb{R}^3_+ \times \mathbb{R}^3_+ \rightarrow \mathbb{R}_+ \) by \( p(x, y) = y_1 \). For all points \((x, y) \in E\), \( p(x, y) = 0 \). However, for all points \((x, y) \in U \setminus C\), \( p(F^2(x, y)) = F_1(x, y) = y_1 g_1(\sum_{j=1}^{2}\{\alpha_{1j}x_j + \beta_{1j}y_j\}) > y_1 \) if \( y_1 > 0 \). If \( y_1 = 0 \), then \( x_1 \neq 0 \), \( p(x, y) = 0 \) and \( p(F(x, y)) = x_1 \). Hence all the conditions of Proposition 1 are satisfied. Thus, \( F \) is uniformly persistent with respect to the repelling set \( C \).

REFERENCES


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