Effect of aggregating behavior on population recovery on a set of habitat islands

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Abstract

We consider a single-species model which is composed of several patches connected by linear migration rates and having logistic growth with a threshold. We show the existence of an aggregating mechanism that allows the survival of a species which is in danger of extinction due to its low population density. Numerical experiments illustrate these results. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

Many animals in nature enhance their chances of survival and reproduction by increasing their local density, or aggregating (cf. [1–3]). Perhaps the simplest theoretical example of a functional purpose of aggregation occurs when the net population change from birth and death exhibits the Allee effect ([4]). The Allee effect was originally proposed to model the reduction of reproductive opportunities at low population densities. A population may exhibit the Allee effect for a variety of reasons, see [5] and the literature therein.

The main feature of the Allee effect is that below a threshold value the death rate is higher than the birth rate because, on average, the individuals cannot reproduce successfully. This, in turn, imposes a threat to the survival of the species at low densities.

We will show in this paper that a set of habitat islands, interconnected by anisotropic and asymmetric density-independent dispersal rates, contains mechanisms for the survival of a
population menaced by extinction due to the Allee effect. In fact, we will give conditions for a population located in a neighborhood of low density, to cluster together in an attempt to raise their local population above the threshold at which the birth rate begins to exceed the death rate. We give the name of recovery, properly defined below, to this kind of behavior.

The concept of recovery, first used without this name by Grindrod [6], was introduced by Lizana and Padrón [7] to study this type of phenomenon and can also be seen as a measure of the capability of a model to produce aggregation.

In this paper, we study an island chain model for a single species described by a system of differential equations

\[ u_i'(t) = \sum_{j=1}^{n} [d_{ij}u_j(t) - d_{ji}u_i(t)] + f(u_i(t)), \quad i = 1, \ldots, n, \quad t \geq 0. \tag{1} \]

Here \( u_i(t) \) is the population in patch \( i \) at time \( t \). The coefficients \( d_{ij} \) are the rates at which the individuals migrate from patch \( j \) to patch \( i \), and satisfy the following conditions: (i) \( d_{ij} \geq 0 \), \( i, j = 1, \ldots, n \); (ii) \( \sum_{j=1}^{n} d_{ij} > 0 \) and \( \sum_{j=1}^{n} d_{ji} > 0 \), \( i = 1, \ldots, n \).

The function \( f(u) \) that describes the net population change from birth and death satisfies the following hypothesis:

**Hypotheses 1.**

1. \( f \) is continuously differentiable.
2. There exists \( 0 < a < b < \infty \) such that \( f \) is negative in \((0, a) \cup (b, +\infty)\) and positive in \((a, b)\).
3. \( f(0) = 0 \) and there exists a constant \( M > b \) such that \( -f(u) > \delta_1 u \), for all \( u \geq M \). Here \( \delta_1 \) is a positive constant such that \( \sum_{j=1}^{n} d_{ij} < \delta_1 \) and \( \sum_{j=1}^{n} d_{ji} < \delta_1 \), \( i = 1, \ldots, n \).

The second condition above states that the population is subject to an Allee effect. The first condition is technical and is needed together with the third condition to ensure, given initial data, the existence and uniqueness of solutions for (1) globally defined for \( t \geq 0 \) (see Proposition 1 below). The third condition assumes, as should be expected, that the migration mechanisms cannot override the carrying capacity of the environment, represented by the parameter \( b \), beyond a fixed value \( M > b \). That is, under this condition a population located below \( b \) can surpass this value at a later time but it can never go beyond the level \( M \) (see Proposition 1 below). The parameter \( M \) represents the relaxation of the carrying capacity \( b \) that is allowed by the migration mechanism.

**Definition 1.** We will say that problem (1) exhibits recovery, if there exists a relatively open subset \( \Omega \) of \( Q_a := \{ \xi \in \mathbb{R}^n : 0 \leq \xi_i < a, \ i = 1, \ldots, n \} \) with the property that for any solution \( u(t) \) of (1) with \( u(0) \in \Omega \) there exist \( t_0 > 0 \) and \( 1 \leq i_0 \leq n \) such that \( u_{i_0}(t_0) > a \). We will say that the recovery is permanent if \( u_{i_0}(t) > a \) for all \( t \geq t_0 \).

Note that if (1) exhibits permanent recovery, then (1) exhibits persistence in a local sense, i.e., there exists a relatively open subset \( A \) of \( \mathbb{R}^n \), the set of all \( n \)-tuples with non-negative coordinates, such that \( \liminf_{t \to \infty} u_i(t) > 0 \) for some \( i \). In general, the definition of recovery is a refinement of the concept of persistence. There has been considerable research in the role played by spatial factors.
in persistence and stability of populations, (cf. [8–10]). Nevertheless, these results are related to the concept of persistence defined globally, i.e., independent of positive initial data, and do not seem to be properly suited to address the more specific question of recovery. For example, neither the spectral conditions nor the irreducibility of the matrix of the coefficients of the system, imposed in [10] to obtain persistence, are necessary for system (1) to exhibit recovery as is shown by the example given at the end of Section 5.

In general, we are assuming that \( d_{ij} \neq d_{ji} \) for \( i \neq j \). Systems like (1) with \( d_{ij} = d_{ji} \) have been extensively studied in the literature (see [11] and the literature therein). Under this assumption the dispersal behavior is diffusive and no aggregation takes place. In particular, we show in Proposition 1(ii) that in this case the population cannot exhibit recovery. When the dispersal rates are asymmetric then \( \sum d_{ij} \neq \sum d_{ji} \) and some patches receive more immigrants than they lose causing the clumping of some of them. Godfrey and Pacala [12] studied the influence of this behavior on the stability of host–parasitoid and predator–prey interactions. That clumping enhances persistence of the population was already established by Adler and Nuernberger [13].

This paper explores the importance of clumping of patches in achieving recovery. We will show in Theorem 1 that a necessary and sufficient condition for problem (1) to exhibit recovery is the existence of at least a patch \( i_0 \) such that \( \sum_{j=1}^{n} d_{ij} > \sum_{j=1}^{n} d_{ji} \). This condition implies that there is a greater movement of the population from other patches into patch \( i_0 \) than out of patch \( i_0 \).

In the simplest case, when \( n = 2 \), we can already see some of the main features of the more complex situation described by (1). In this case, using the new variables \( x(t) \) and \( y(t) \), the system (1) is reduced to

\[
\begin{align*}
x' &= -cx + dy + f(x), \\
y' &= cx - dy + f(y).
\end{align*}
\]

Here \( d_{11} = c \) and \( d_{12} = d \). It follows from Theorem 1, that (2) exhibits recovery if and only if \( c \neq d \).

This is illustrated in Fig. 1(a), in which the threshold value \( a \) for the function \( f \) is equal to 1. This picture shows a number of trajectories starting in different locations on the line \( y = 1 \). We can see

![Phase portrait of the solutions of (2) with \( f(s) = s(s-1)(2-s) \). (a) \( c = 0.4, d = 0.5 \). The critical points shown are a node at \((0, 0)\) and a saddle at \((1.5355, 0.4645)\). There is another critical point at \((2.0623, 1.9231)\) not shown in the picture. (b) \( c = 0.3, d = 0.5 \). The critical points shown are two nodes at \((0, 0)\) and \((1.6976, 0.3024)\), respectively and a saddle at \((1.3321, 0.2083)\). There are other critical points at \((1.9131, 0.8446)\) and \((2.1160, 1.8151)\) not shown in the picture.](image)
a relatively small region of recovery in the upper right-hand side corner of the unit square. Nevertheless, the recovery exhibited here is not permanent.

In general, we need to impose further restrictions on the coefficients $d_{ij}$ to obtain permanent recovery. In the case of the particular system (2), this can be accomplished by choosing $c$ small enough. Fig. 1(b) illustrates permanent recovery. It is clear from this picture that there is a region of permanent recovery in the upper right-hand corner of the unit square.

In Theorem 2, we will show that a meta-population exhibits permanent recovery as long as at least one population can go from below the threshold $a$ to the ‘safe’ region described by Lemma 1. In both Theorems 1 and 2 we give simple algebraic conditions that guarantee the existence of the region $X$ of recovery and permanent recovery. These conditions can be tested and the parameters involved can be computed (see Remark 1). The experiments in Section 4 suggest a method, that can be applied in real situations, for a numerical estimation of $\Omega$.

This paper is organized as follows: In Section 2, we will show, for completeness, some results of existence and uniqueness of solutions to the initial value problem (1). In Section 3, we will show the main results of this paper: Theorems 1 and 2. These results are illustrated in Section 4 with the aid of some numerical simulations. In Section 5, we establish some results regarding the relationship between recovery and persistence.

2. Existence and uniqueness of solutions

Since the function $f$ is $C^1$, the existence and uniqueness of a locally defined solution to the initial value problem for the system (1) in $\mathbb{R}^n$, follows.

Before proving global existence, we describe some positive invariant regions for the solutions of (1).

A subset $S \subset \mathbb{R}$ is positive invariant for the problem (1) if $u_i(0) \in S$ for all $i = 1, \ldots, n$, implies $u_i(t) \in S$ for all $i = 1, \ldots, n$ and all $t \geq 0$.

**Proposition 1** (Positive invariant regions).

(i) If $N \geq M$, then the interval $S = [0, N)$ is positive invariant.

(ii) If $\sum_{j=1}^{n} d_{ij} \leq \sum_{j=1}^{n} d_{ji}$ for all $i = 1, \ldots, n$, then $S = [0, a]$ is positive invariant.

**Proof.** Let $u(t)$ be a solution of (1) defined in a maximal interval $(T_1, T_2)$ containing $t = 0$. Suppose that $u_i(0) \in S = [0, N)$ for all $i = 1, \ldots, n$. Standard arguments show that $u_i(t) \geq 0$ for all $i = 1, \ldots, n$ and all $0 \leq t < T_2$.

Suppose now by contradiction that there exist $t_0 > 0$ such that $u_i(t_0) = N$ and $u_i(t) < N$ for $0 \leq t < t_0$ and for all $i = 1, \ldots, n$. It is obvious that in this case $u_i'(t_0) \geq 0$. By Hypothesis 1(3) we obtain

$$u_i'(t_0) = \sum_{j=1}^{n} d_{ij} u_j(t_0) - \sum_{j=1}^{n} d_{ji} N + f(N) \leq \delta_i N + f(N) < 0.$$

This is a contradiction that proves (i).
To prove (ii) we first notice that $\sum_{j=1}^{n} d_{ij} \leq \sum_{j=1}^{n} d_{ji}$ for all $i = 1, \ldots, n$ implies that $\sum_{j=1}^{n} d_{ij} = \sum_{j=1}^{n} d_{ji}$ for all $i = 1, \ldots, n$. Certainly, suppose that there exists $i_0$ such that $\sum_{j=1}^{n} d_{i_0 j} < \sum_{j=1}^{n} d_{j i_0}$. In this case $\sum_{i=1}^{n} \sum_{j=1}^{n} d_{ij} < \sum_{i=1}^{n} \sum_{j=1}^{n} d_{ji}$, but this is a contradiction since both sides of this inequality are actually equal.

Suppose now that $u_i(0) \in S = [0, a]$ for all $i = 1, \ldots, n$. Assume by contradiction that there exist $t_1$ and $t_2$ such that $u_i(t_1) > a$. Let $t_0 := \inf \{ t < t_1 : u_i(t) > a \text{ for some } i \}$. By continuity there exists $i_0$ such that $u_{i_0}(t_0) = a$ and $u_i(t) < a$ for all $0 \leq t < t_0$. It is obvious that in this case $u_{i_0}'(t_0) \geq 0$. Since $v = (a, \ldots, a) \in \mathbb{R}^n$ is a steady solution of (1), then $u_i(t_0) = a$ for all $i$ implies that $u_i(t) = a$ for all $i$ and all $t \geq 0$. Hence, there exists at least one $i \neq i_0$ such that $u_i(t_0) < a$. In this case

$$u_{i_0}'(t_0) = \sum_{j=1}^{n} d_{i_0 j} u_j(t_0) - a \sum_{j=1}^{n} d_{j i_0} < a \sum_{j=1}^{n} d_{i_0 j} - a \sum_{j=1}^{n} d_{j i_0} = 0.$$ 

This is a contradiction that proves (ii). \qed

As an immediate consequence of Proposition 1, all solutions of system (1) are defined for all $t \geq 0$. Indeed, let $u(t)$ be a solution of (1) defined in a maximal interval $(T_1, T_2)$ containing $t = 0$, such that $u_i(0) \geq 0$ for all $i = 1, \ldots, n$. Then choosing $N \geq M$ such that $u_i(0) \leq N$ for all $i = 1, \ldots, n$ we obtain that $u_i(t) \leq N$ for all $i = 1, \ldots, n$ and all $0 < t < T_2$. This shows that $T_2 = +\infty$.

3. Recovery and permanent recovery

The first result of this section gives a necessary and sufficient condition for problem (1) to exhibit recovery.

**Theorem 1.** System (1) exhibits recovery if and only if there exists $0 \leq i_0 \leq n$ such that

$$\frac{\sum_{j=1}^{n} d_{i_0 j}}{\sum_{j=1}^{n} d_{j i_0}} > 1.$$ 

(3)

**Proof.** It follows from Proposition 1(ii) that (3) is a necessary condition for system (1) to exhibit recovery.

In order to prove sufficiency, let us assume that there exists $i_0$ such that inequality (3) holds. Hence, we can choose $0 < c < a$ such that

$$\frac{\sum_{j=1}^{n} d_{i_0 j}}{\sum_{j=1}^{n} d_{j i_0}} > \frac{a}{c}.$$ 

Let $\bar{u} \in \mathbb{R}^n$ be such that $\bar{u}_{i_0} = a$ and $c \leq \bar{u}_i < a$ for all $i \neq i_0$, and $u(t)$ be the solution of (1) such that $u(0) = \bar{u}$.
From (1) and (3) it follows that
\[ u'_{i_0}(0) = \sum_{j=1}^{n} [d_{i_0,j} \bar{u}_j - d_{j_i,j} a] \geq c \sum_{j=1}^{n} d_{i_0,j} - a \sum_{j=1}^{n} d_{j_i,j} > 0. \]

This relation implies that the set
\[ \Omega := \{ v \in \mathbb{R}^n : v = u(t; \bar{u}) \text{ for some } t < 0, \text{ and } 0 < v_j < a, j = 1, \ldots, n \} \]
is non-empty. Here \( u(t; \bar{u}) \) denotes the solution of (1) such that \( u(0; \bar{u}) = \bar{u} \). For a given \( v \in \Omega \), there exists \( \tilde{t} < 0 \) such that \( v = u(\tilde{t}; \bar{u}) \). From the uniqueness of the solutions of (1), \( u(t; v) = u(t; u(\tilde{t}; \bar{u})) = u(t + \tilde{t}; \bar{u}) \) satisfies the requirement of the definition of recovery. Indeed, \( u(0; v) = v, \ u(-\tilde{t}; v) = u(0, \bar{u}) = \bar{u} \text{ and } u'_{i_0}(-\tilde{t}; v) > 0 \). This certainly proves that there exists \( t_0 > -\tilde{t} > 0 \) such that \( u_{i_0}(t_0; v) > a \). Finally, by the continuous dependence of the solutions of (1) on the initial data, it follows that \( \Omega \) is open. This finishes the proof. \( \square \)

Next, we will give some conditions to assure that system (1) exhibits permanent recovery. For this we will need the following Lemma. For any \( d > 0 \) let
\[ \Delta(d) := \{ s \in \mathbb{R} : a < s < b \text{ and } f(s) - ds > 0 \}. \]

**Lemma 1.** Suppose that there exists \( 1 \leq i_0 \leq n \) such that \( \Delta(\sum_{j=1}^{n} d_{j_i,j}) \) is not empty. Let \( s \in \Delta(\sum_{j=1}^{n} d_{j_i,j}) \). Hence, if there exists \( t_0 \geq 0 \) such that \( u_{i_0}(t_0) = s \), then \( u_{i_0}(t) \geq s \) for all \( t \geq t_0 \).

**Proof.** Since \( f(s) - s \sum_{j=1}^{n} d_{j_i,j} > 0 \) we have that
\[ u'_{i_0}(t_0) = \sum_{j=1}^{n} d_{i_0,j} u_j(t_0) + f(s) - s \sum_{j=1}^{n} d_{j_i,j} > 0. \]

This certainly proves our assertion. \( \square \)

**Theorem 2.** Assume that there exists a partition of the set \( \{1, \ldots, n\} \) in two non-empty disjoint subsets \( I_1, I_2 \) such that
\[ \frac{\sum_{j=1}^{n} d_{i,j}}{\sum_{j=1}^{n} d_{j_i,j}} > 1, \]
for all \( i \in I_1 \), and
\[ \frac{\sum_{j=1}^{n} d_{i,j}}{\sum_{j=1}^{n} d_{j_i,j}} > 1, \]
for all \( i \in I_2 \). Then, there exists \( \delta > 0 \) such that if \( \sum_{j=1}^{n} d_{i,j} < \delta \) for all \( i \in I_1 \), then system (1) exhibits permanent recovery.

**Proof.** Since \( f \) is positive in the interval \( (a, b) \) it follows that there exists \( d_0 > 0 \) such that for any \( d < d_0 \), \( \Delta(d) \), defined by (4), is non-empty. Moreover, the continuity of \( f \) implies that \( s(d) := \inf \Delta(d) \) defines a function for \( 0 < d < d_0 \) with the following properties: (i) \( s(d) \) is strictly increasing; (ii) \( s(d) \to a \) as \( d \to 0 \); (iii) if \( 0 < d_1 < d_2 < d_0 \), then \( s(d_2) \in \Delta(d_1) \).
Choose $\epsilon > 0$ such that
\[
\sum_{j=1}^{n} d_{ji} > 1 + \epsilon,
\]
for all $i \in I_2$. Let $0 < c < e < a$, $\delta_2 := \inf_{i \in I_1} \sum_{j=1}^{n} d_{ij}$, and $\delta_3 := \inf_{i \in I_2} \sum_{j=1}^{n} d_{ij}$.

Without loss of generality we can assume that $d_0 < (c/s(d_0))\delta_2$. Choose $\delta > 0$ such that $\delta < d_0$, 
\[
f(s(\delta)) < a e \delta_3,
\]
and
\[
s(\delta) < a + \frac{e - c}{\eta(d_0)} \sigma(d_0).
\]
Here, $\sigma(d) := c \delta_2 - s(d) d$ and $\eta(d) := s(d) \delta_1 + \gamma$, where $\gamma := -\min_{0 \leq u \leq h} f(u)$ and $\delta_1$ as given in Hypothesis 1. Clearly, $\eta(d_0) > 0$ and since $d_0 < (c/s(d_0))\delta_2$ it follows that $\sigma(d_0) > 0$.

Suppose that $\sum_{j=1}^{n} d_{ji} < \delta,$
for all $i \in I_1$.

Let $v(t)$ be a solution of (1) such that $v_i(0) = a$ for $i \in I_1$, and $e \leq v_i(0) < a$ for $i \in I_2$. As in the proof of Theorem 1 we can show that this implies $v_i'(0) > 0$ for $i \in I_1$ and that there exists $\tau_0 < 0$ such that $c < v_j(\tau_0) < a$ for all $j = 1, \ldots, n$.

If we show that $v_{i_0}(t) > a$ for some $i_0 \in I_1$ and all $t > 0$, then it will follow that $u(t) := v(t + \tau_0)$ satisfies the requirement of the definition of permanent recovery.

To this end, choose $s := s(\delta)$. Notice that, since $\sum_{j=1}^{n} d_{ji} < \delta$, then $s \in \Delta(\sum_{j=1}^{n} d_{ji})$ for all $i \in I_1$.

Suppose that $c \leq v_j(t) \leq s$ for all $j = 1, \ldots, n$ and some $t \geq 0$. Then, if $i \in I_1$ and $v_i(t) > a$, then it follows that
\[
v_i'(t) \geq c \sum_{j=1}^{n} d_{ij} - s \sum_{j=1}^{n} d_{ji} \geq c \delta_2 - s(\delta) \delta = \sigma(\delta).
\]
Moreover, for all $i = 1, \ldots, n$
\[
v_i'(t) \geq -s(\delta) \delta_1 - \gamma \geq -\eta(\delta).
\]
Note that (11) implies that if $c \leq v_j(t) \leq s$ for all $j = 1, \ldots, n$, and all $0 \leq t \leq \tau$, then $v_i(t) > a$ for all $i \in I_1$ and all $0 < t \leq \tau$.

Now, suppose that there exist $\tau > 0$ and $i_0 \in I_2$ such that $v_{i_0}(\tau) = c$ and $c < v_j(t) < s$ for all $0 \leq t < \tau$ and for all $j = 1, \ldots, n$. Hence, it follows from (12) that there exists $0 < \xi_1 < \tau$ such that
\[
c - e \geq v_{i_0}(\tau) - v_{i_0}(0) = v_i'(\xi_1) \tau \geq -\eta(\delta) \tau.
\]
That is,
\[
\tau \geq (e - c)/\eta(\delta).
\]
Moreover, from (11) it follows that there exists $0 < \xi_2 < \tau$ such that $i \in I_1$
\[
v_i(\tau) - v_i(0) = v_i'(\xi_2) \tau \geq \sigma(\delta) \tau.
\]
Hence, from this inequality, (10), and since $\sigma(\delta) > \sigma(d_0)$ and $\eta(\delta) < \eta(d_0)$ it follows that

$$\tau \leq \frac{v_i(\tau) - v_i(0)}{\sigma(\delta)} \leq \frac{s(\delta) - a}{\sigma(\delta)} < \frac{e - c}{\eta(\delta)} \leq \tau.$$ 

This is a contradiction. Hence there are two alternatives

1. There exist $\tau < \infty$ and $1 \leq i_0 \leq n$ such that $v_{i_0}(\tau) = s$ and $c < v_j(t) < s$ for all $j = 1, \ldots, n$ and all $0 \leq t < \tau.$
2. $c < v_j(t) < s$ for all $j = 1, \ldots, n$ and all $t \geq 0.$

In the first case, if $i_0 \in I_1,$ then it follows from Lemma 1 that $v_{i_0}(t) \geq s$ for all $t \geq \tau.$

Suppose instead that $i_0 \in I_2.$ It is clear that in this case $v'_{i_0}(\tau) \geq 0.$ Nevertheless, by (6), (7) and (9) we have

$$v'_{i_0}(\tau) = \sum_{j=1}^{n} [d_{i_0j}v_j(\tau) - d_{ji_0}v_{i_0}(\tau)] + f(v_{i_0}(\tau)) \leq s \sum_{j=1}^{n} [d_{i_0j} - d_{ji_0}] + f(s)$$

$$\leq a \sum_{j=1}^{n} [d_{i_0j} - d_{ji_0}] + f(s(\delta)) < 0$$

and we reach a contradiction. Therefore $i_0 \in I_1.$

In the second case it follows from (11) that $v'_i(t) > 0$ for all $t > 0$ and all $i \in I_1.$

Hence, from both cases we obtain that there exists $i_0 \in I_1$ such that $v_{i_0}(t) > a$ for all $t > 0.$ This finishes the proof. □

Remark 1. Knowing the function $f,$ one can compute $s(d)$ to find $\delta > 0$ satisfying (8)–(10). This can certainly be done with the aid of a computer to obtain a numerical estimate of $\delta$ suitable for applications.

4. Numerical simulations

As an illustration of the results of Section 3 we will consider a habitat of 100 localities distributed into a square grid of points $(h, k)$ where $h = [(i - 1)/10] + 1$ and $k = (i - 1) \mod 10 + 1$ with $i = 1, \ldots, 100.$ Here $[p]$ denotes the greatest integer less than or equal to $p$ and $p \mod q$ is the remainder of $p$ divided by $q.$ The population density $v(h, k, t)$ at the point $(h, k)$ at time $t$ is given by $v(h, k, t) = u_{i0(h-1)+k}(t), h, k = 1, \ldots, 10,$ where $u$ is the solution of system (1).

We will assume that individuals move only to the four adjacent cells (three or two when they are located in the boundary), with dispersal rates $d_{ij} = d_j$ depending only on their present location $j.$ That is, the decision about moving is based only on the local conditions of the habitat (described here by the vector $d_i, i = 1, \ldots, 100$) and it is the same towards any of the adjacent locations. For instance, if $(h, k)$ is an interior point of the grid, then for $j = 10(h - 1) + k$ we have $d_{ij} = d_j$ for $i = j - 1, j + 1, j - 10, j + 10$ and $d_{ij} = 0$ otherwise.

Under these conditions, the matrix $A = (a_{ij})$ of system (1), with

$$a_{ij} = \begin{cases} d_{ij} & \text{for } i \neq j, \\ -\sum_{k=1, k\neq i}^{n} d_{ki} & \text{for } i = j, \end{cases}$$

has a sparse pattern as shown in Fig. 2, where the dots represent the non-zero elements.
Coming back to the square grid representation, since every locus is associated with a grid point \((h, k)\), we specify the migration rates \(d_i, i = 1, \ldots, 100\), by a matrix \(D = D(h, k)\). For our numerical experiments we choose \(D\) as

\[
D = \begin{bmatrix}
0.1943 & 0.1835 & 0.1718 & 0.1613 & 0.1549 & 0.1549 & 0.1613 & 0.1718 & 0.1835 & 0.1943 \\
0.1835 & 0.1669 & 0.1474 & 0.1284 & 0.1160 & 0.1160 & 0.1284 & 0.1474 & 0.1669 & 0.1835 \\
0.1718 & 0.1474 & 0.1160 & 0.0828 & 0.0607 & 0.0607 & 0.0828 & 0.1160 & 0.1474 & 0.1718 \\
0.1613 & 0.1284 & 0.0828 & 0.0356 & 0.0143 & 0.0143 & 0.0356 & 0.0828 & 0.1284 & 0.1613 \\
0.1549 & 0.1160 & 0.0607 & 0.0143 & 0.0100 & 0.0100 & 0.0143 & 0.0607 & 0.1160 & 0.1549 \\
0.1549 & 0.1160 & 0.0607 & 0.0143 & 0.0100 & 0.0100 & 0.0143 & 0.0607 & 0.1160 & 0.1549 \\
0.1613 & 0.1284 & 0.0828 & 0.0356 & 0.0143 & 0.0143 & 0.0356 & 0.0828 & 0.1284 & 0.1613 \\
0.1718 & 0.1474 & 0.1160 & 0.0828 & 0.0607 & 0.0607 & 0.0828 & 0.1160 & 0.1474 & 0.1718 \\
0.1835 & 0.1669 & 0.1474 & 0.1284 & 0.1160 & 0.1160 & 0.1284 & 0.1474 & 0.1669 & 0.1835 \\
0.1943 & 0.1835 & 0.1718 & 0.1613 & 0.1549 & 0.1549 & 0.1613 & 0.1718 & 0.1835 & 0.1943
\end{bmatrix}
\]

defined by the formula

\[
D(h, k) = 0.01 + 0.2 \exp \left( \frac{1}{6.05} \right) \exp \left( \frac{-1}{10((0.1h - 0.55)^2 + (0.1k - 0.55)^2)} \right)
\]  \( (14) \)

for \(h, k = 1, \ldots, 10\). The function \(f\) is taken as \(f(s) = 0.008s(s - 5)(10 - s)\) with a threshold level \(a = 5\).

Applying Theorem 1 to this particular case, we obtain that (1) exhibits recovery at a grid point \((h, k)\) if and only if \(D(h, k)\) is smaller than the average of its adjacent neighbors. This suggests the construction of the matrix \(M\), in which the entry \(M(h, k), (h, k = 1, \ldots, 10)\) is the difference between the average of the adjacent neighbors at point \((h, k)\) and \(D(h, k)\). For example, for any point \((h, k)\), not in the boundary, \(M(h, k)\) is given by

\[
M(h, k) = \frac{D(h, k - 1) + D(h, k + 1) + D(h - 10, k) + D(h + 10, k)}{4} - D(h, k).
\]  \( (15) \)
The entries of the matrix $M$ give a measure of the total migration (i.e., the difference between immigration and emigration) at a given location. In our particular example, the matrix $M$ is given by

$$
M = \begin{bmatrix}
-0.0109 & -0.0058 & -0.0077 & -0.0096 & -0.0108 & -0.0096 & -0.0077 & -0.0058 & -0.0109 \\
-0.0058 & -0.0014 & -0.0017 & -0.0015 & -0.0010 & -0.0015 & -0.0017 & -0.0014 & -0.0058 \\
-0.0077 & -0.0017 & -0.0009 & 0.0024 & 0.0078 & 0.0024 & -0.0009 & -0.0017 & -0.0077 \\
-0.0096 & -0.0015 & 0.0024 & 0.0130 & 0.0158 & 0.0158 & 0.0130 & 0.0024 & -0.0015 & -0.0096 \\
-0.0108 & -0.0010 & 0.0078 & 0.0158 & 0.0022 & 0.0022 & 0.0158 & 0.0078 & -0.0010 & -0.0108 \\
-0.0108 & -0.0010 & 0.0078 & 0.0158 & 0.0022 & 0.0022 & 0.0158 & 0.0078 & -0.0010 & -0.0108 \\
-0.0096 & -0.0015 & 0.0024 & 0.0130 & 0.0158 & 0.0158 & 0.0130 & 0.0024 & -0.0015 & -0.0096 \\
-0.0077 & -0.0017 & -0.0009 & 0.0024 & 0.0078 & 0.0024 & 0.0078 & 0.0024 & -0.0009 & -0.0017 & -0.0077 \\
-0.0058 & -0.0014 & -0.0017 & -0.0015 & -0.0010 & -0.0015 & -0.0017 & -0.0014 & -0.0058 \\
-0.0109 & -0.0058 & -0.0077 & -0.0096 & -0.0108 & -0.0096 & -0.0077 & -0.0058 & -0.0109
\end{bmatrix}
$$

The graphs of $D$ and $M$ as functions of $(x, y)$ in the square $S = [0, 10] \times [0, 10]$ are shown in Fig. 3(a) and (b), respectively. According to Theorem 2, we should expect permanent recovery to occur among the grid points of positive entries of the matrix $M$.

In Fig. 4, we show a sequence of graphs of the solutions $v(h,k,t)$ of (1), with initial data $v(h,k,0) = 4.55$, $h,k = 1, \ldots, 10$, below the threshold level $\alpha = 5$ at different times. We observe permanent recovery as the population aggregates at the points of minimum values of $D$. If we think of $D(h,k)$ as inversely proportional to the amount of resources available to the population in the location $(h,k)$, then this is telling us that the aggregation behavior that yields permanent recovery occurs at the points of higher resources (the smaller values of $D(h,k)$). The numerical values of the population density $v(h,k,t)$ at $t = 100$ are given in Table 1.

In the next example, we show that in general this is not the case. Comparing matrices $D$ and $M$ we notice that the points of more resources are not necessarily the ones with higher total migration rates. As a consequence, the aggregating behavior that yields permanent recovery may occur at points that are not necessarily the points of higher resources. This is illustrated in Fig. 5 where we show a sequence of graphs of the solutions $v(h,k,t)$ of (1), with initial data $v(h,k,0) = 4.25$, $h,k = 1, \ldots, 10$, at different times. Table 2 shows the numerical values for $v(h,k,t)$ at $t = 100$. Here, the individuals aggregate in a spatial pattern that surrounds, but does not include the points of higher resources available to the population.

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![Fig. 3. Graphs of functions: (a) $D(x,y)$; (b) $M(x,y)$, for $x, y \in S$.](image-url)
In both examples, permanent recovery also takes place in a region of $Q_\alpha$, where $Q_\alpha$ is given in Definition 1, bounded below by the given initial data $v(h, k, 0) = 4.55$, $h, k = 1, \ldots, 10$.

5. Recovery vs persistence

It is clear from Definition 1 that if (1) exhibits permanent recovery, then (1) exhibits persistence. The natural question of whether persistence implies permanent recovery arises. We already know,
by Theorem 1, that we will have to assume that (1) satisfies the inequality (3) for some $i_0$. We will show that, under this condition and with the added assumption that the matrix $A = (a_{ij})$ defined in (13) is irreducible, persistence implies that system (1) exhibits permanent recovery.

A matrix is said to be irreducible if it cannot be put into the form

$$\begin{bmatrix} B & C \\ 0 & D \end{bmatrix}$$
(where $B$ and $D$ are square matrices) by reordering the standard basis vectors. This condition implies that any $i$th patch can influence any $j$th patch. In fact, there is a simple test to see if an $n \times n$ matrix $A$ is irreducible. Write $n$ points $P_1, P_2, \ldots, P_n$ in the plane. If $a_{ij} \neq 0$, then draw a directed line segment $P_iP_j$ connecting $P_i$ to $P_j$. The resulting graph is said to be strongly connected if, for each pair $(P_i, P_j)$, there is a directed path $P_iP_{k_1}P_{k_2}P_{k_3} \ldots P_{k_l}P_j$. A square matrix is irreducible if and only if its directed graph is strongly connected, cf. [14, p. 529].

In the rest of this section, we will assume that the matrix $A$ is irreducible. The following Proposition gives a useful description about the distribution of the equilibria of system (1).

Proposition 2. Let $v \in \mathbb{R}^n_+$ be an equilibrium of system (1). If $v_j = 0$ for some $j$, then $v_i = 0$ for all $i = 1, \ldots, n$. Moreover, if $v_j > 0$ for some $j$, then either $v = (a, \ldots, a)$ or $v_i > a$ for some $i$.

Proof. Suppose that $v_j = 0$ for some $j$ and let $i \neq j$. We will show that $v_i = 0$.

Since $A$ is irreducible there exist distinct $k_1, \ldots, k_l$ such that $d_{jk_1} \neq 0, d_{k_1k_2} \neq 0, \ldots, d_{kl} \neq 0$.

Now, since $v_j = 0$, by (1) we have

$$d_{j1}v_1 + \cdots + d_{jj-1}v_{j-1} + d_{jj+1}v_{j+1} + \cdots + d_{jn}v_n = 0.$$ 

Thus, since $d_{jk_1} \neq 0$, $v_{k_1} = 0$ and by (1) we have that

$$d_{k_11}v_1 + \cdots + d_{k_1k_1}v_{k_1-1} + d_{k_1k_1+1}v_{k_1+1} + \cdots + d_{k_1n}v_n = 0.$$ 

Therefore, since $d_{k_1k_2} \neq 0$ it follows that $v_{k_2} = 0$.

We can continue this argument to show that $v_i = 0$.

The second part of the Proposition follows from the first part and the fact that $f(v_1) + \cdots + f(v_n) = 0$ and $f(s) < 0$ for $0 < s < a$. □

Next, we will recall some results of the theory of irreducible cooperative systems that will be used later. Consider the autonomous system of ordinary differential equations

$$x' = f(x),$$ 

(16)

where $f$ is continuously differentiable on an open and convex subset $E \subset \mathbb{R}^n$. The system (16) is said to be a cooperative system if

$$\frac{\partial f_i}{\partial x_j}(x) \geq 0, \quad i \neq j, \quad x \in E.$$ 

The system (16) is said to be cooperative and irreducible if it is a cooperative system and if the Jacobian matrix $(\partial f_i/\partial x)(x)$ is irreducible for any $x \in E$.

Since $d_{ij} \geq 0$ and the matrix $A$ is irreducible, (1) is a cooperative and irreducible system in $\mathbb{R}^n_+$. Moreover, the set $C := \{ \zeta \in \mathbb{R}^n_+ : \lim_{t \to -\infty} u(t; \zeta) \text{ exists} \}$ of convergent points of (1) contains an open and dense subset of $\mathbb{R}^n_+$, cf. [15, Theorem 4.1.2, p. 57]. Here, $u(t; \zeta)$ denotes the solution of (1) such that $u(0; \zeta) = \zeta$. 
Proposition 3. Suppose that the inequality (3) holds for some $i_0$. Assume that there exists a relatively open subset $A$ of $Q_a := \{ \xi \in \mathbb{R}^n : 0 \leq \xi_i < a, i = 1, \ldots, n \}$ such that if $\xi \in A$, then $\liminf_{t \to 0} u_i(t; \xi) > 0$ for some $i$. Hence, if $\xi \in A \cap C$, then $\liminf_{t \to 0} u_i(t; \xi) > 0$ for all $i = 1, \ldots, n$. Moreover, (1) exhibits permanent recovery.

Proof. If the inequality (3) holds, then the point $(a, \ldots, a) \in \mathbb{R}^n_+$ cannot be an equilibrium for (1). Therefore, if $\xi \in C$, by Proposition 2 if $\lim_{t \to \infty} u_j(t; \xi) > 0$ for some $j$, then $\lim_{t \to \infty} u_i(t; \xi) > 0$ for all $i = 1, \ldots, n$. Moreover, by the second part of Proposition 2 and since $(a, \ldots, a)$ is not an equilibrium, $\lim_{t \to \infty} u_j(t; \xi) > a$ for some $j$.

The proposition follows by choosing $\Omega = \text{int}(A \cap C)$ and noticing that, since $C$ contains an open and dense subset of $\mathbb{R}^n_+$, $\Omega$ is an open and non-empty subset of $Q_a$ satisfying the requirement of the definition of permanent recovery.  

The local concept of persistence that we have used in this paper seems to be better suited, in the light of the previous results, to the problem of recovery than the global concept, independent of positive initial data, considered by other authors in the literature. We would like to stress this point by showing, with the aid of an example, that the conditions imposed in [10] to obtain positive initial data, considered by other authors in the literature. We would like to stress the problem of recovery than the global concept, independent of the definition of permanent recovery.

The spectrum of a matrix $A$, written as $\delta(A)$, is the set of eigenvalues of $A$. Define the stability modulus of $A$, $s(A)$, as

$$s(A) := \max \{ \Re \lambda : \lambda \in \delta(A) \}.$$ 

Suppose that $f(u) = u \sigma(u)$, where $\sigma(u)$ is the net rate of population supply. Define the matrix $A_\sigma := A + \sigma(0)I$.

It is shown in [10, Theorem 1] that if $A$ is irreducible and $s(A_\sigma) > 0$, then $\liminf_{t \to 0} u_i(t) \geq \delta > 0$, for all $i = 1, \ldots, n$ and all positive initial data.

The following system does not satisfy these conditions. Let

$$u_i'(t) = d_{i-1}u_{i-1}(t) - 2d_iu_i(t) + d_{i+1}u_{i+1}(t) + f(u_i(t)), \quad i = 1, \ldots, n, \quad t \geq 0,$$

where $d_0 = d_1, u_0 = u_1, d_n = d_{n+1}$, and $u_n = u_{n+1}$. Then clearly, the matrix $A$ is not necessarily irreducible, and since $s(A) = 0$, it follows that $s(A_\sigma) < 0$. Nevertheless, under the hypothesis of Theorem 2, this system exhibits permanent recovery.

If we assume that $f'(0) < 0$, then the equilibrium $(0, \ldots, 0)$ is locally asymptotically stable. Therefore, this example also shows that the set $\Omega$ in the definition of recovery is not necessarily dense in $Q_a$, i.e., the concept of recovery is a local property.

6. Discussion

The main results of this paper, Theorems 1 and 2, although of theoretical nature, can be implemented, with the aid of a computer, in experimental situations. For species that can be adequately modeled by (1) they give criteria, well suited to numerical treatment, for the system to exhibit (permanent) recovery and to estimate the set $\Omega$ in Definition 1. This information can be
used by the applied scientist to induce a population that is in danger of extinction to find its natural way of survival.

The results presented here can be generalized to systems of the form

$$u_i(t) = \sum_{j \in I} [d_{ij} u_j(t) - d_{ji} u_i(t)] + f(u_i(t)), \quad i \in I, \quad t \geq 0$$

for any subset $I$ of natural numbers, not necessarily finite. We only need to assume, in addition to $d_{ij} \geq 0$, that there is a positive constant $\delta_1$ such that $0 < \sum_{j \in I} d_{ij} < \delta_1$ and $0 < \sum_{j \in I} d_{ji} < \delta_1$. The solutions to this equation, with initial values in $l^\infty(I)$, are globally defined for all $t \geq 0$. We obtain Theorem 1 for this case, and replacing (5) and (6) by

$$\frac{\sum_{j \in I} d_{ij}}{\sum_{j \in I} d_{ji}} > 1 + \epsilon$$

and

$$\frac{\sum_{j \in I} d_{ji}}{\sum_{j \in I} d_{ij}} > 1 + \epsilon,$$

respectively, for some $\epsilon > 0$, we also obtain Theorem 2.

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