

Impact of Dispersion on Dynamics of a Discrete Metapopulation Model

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Abstract. We propose and analyze a discrete time model for metapopulation on two patches with local logistic dynamics. The model carries a delay in the dispersion terms, and our results on this model show that the impact of the dispersion on the global dynamics of the metapopulation is complicated and interesting: it can affect the existence of a positive equilibrium; it can either drive the metapopulation to global extinction, or prevent the metapopulation from going to global extinction and stabilize a positive equilibrium; it can also destabilize a positive equilibrium or a periodic orbit.

1. Introduction

The ecological importance of spatial structure to the maintenance of population was pointed out by Andrewartha and Birch [1] based on the studies of insect populations. They observed that although local populations frequently become extinct, their patches become subsequently recolonized by migrants from other patches occupied by the same species, thus allowing the population to persist globally over the patch environment. The concept of metapopulation (R. Levine [11]) provides a theoretical framework for studying spatially structured populations. A metapopulation is a collection of subpopulations, each of which occupies a patch. Subpopulations of different patches are linked via migration or dispersal of individuals between the patches. Therefore, the global population is affected by the local environments as well as by the forms and strengths of dispersals.

The impact of spatial dispersion on each subpopulation and on the metapopulation has long been one of the main issues in studying populations over patch environments. There have been many studies on meta-populations using *continuous time* models, and it has been found that the dispersals in such models can interplay with the local dynamics to cause very rich and complicated global

dynamics. See, for examples, [6, 8, 9, 10, 13, 14, 19, 20, 22, 21, 24] and the references therein. However, under certain circumstances, discrete time models are more appropriate to describe population growth (e.g., for insects and fish). Yet in the context of both discrete time and discrete spatial environments, there are relatively fewer examples in the literature. Recently, Gyllenberg [7] considered the model

$$\begin{cases} x_{n+1} &= r_1(1 - \theta/2)x_n(1 - x_n) + r_2(\theta/2)y_n(1 - y_n), \\ y_{n+1} &= r_2(\theta/2)x_n(1 - x_n) + r_2(1 - \theta/2)y_n(1 - y_n), \end{cases} \tag{1.1}$$

where $0 \leq \theta < 1$, r_1 and r_2 are positive numbers and x_n and y_n are population sizes of the same species in two different patches at time n , and gave a characterization of the fixed point and 2-periodic orbits of the model. More recently, Yakubu and Castillo-Chavez [25] studied a generalization of (1.1) to a metapopulation over N patches,

$$x_i(t+1) = \left(1 - \sum_{j=1, j \neq i}^N d_{ij}\right) f_i(x_i(t)) + \sum_{j=1, j \neq i}^N d_{ji} f_j(x_j(t)), \quad i = 1, 2, \dots, N. \tag{1.2}$$

Here, $x_i(n)$ is the population size of the i -th patch at time n , and for each $i \in \{1, 2, \dots, N\}$, $f_i(x_i) = x_i g_i(x_i)$, $0 < d_{ij} < 1$ with $0 < \sum_{j=1, j \neq i}^N d_{ij} < 1$ and $d_{ii} = 0$. Instead of logistic nonlinearity, both general compensatory and over-compensatory local dynamics are considered in [25].

We will consider a different dispersion mechanism which is motivated by Levin [10] where continuous models over patches are proposed. Take one species and two patches as an example, and denote by $x_i(t)$ the population of a species in patch i , $i = 1, 2$. Then, in the simplest case, the net exchange from patch i to patch j is proportional to $x_i(t) - x_j(t)$ with a nonnegative proportion constant D_{ij} for $i \neq j$. Corresponding to this simple case, the ordinary differential equation model proposed in Levin [10] takes the form

$$\begin{cases} \frac{dx_1(t)}{dt} &= f_1(x_1(t)) + D_{21}[x_2(t) - x_1(t)] \\ \frac{dx_2(t)}{dt} &= f_2(x_2(t)) + D_{12}[x_1(t) - x_2(t)]. \end{cases} \tag{1.3}$$

Since the terms $x_2(t) - x_1(t)$ ($x_1(t) - x_2(t)$ resp.) accounts for the gradient of the population in patch 1 (patch 2 resp.) to patch 2 (patch 1 resp.), such a dispersion mechanism indeed corresponds to the Fickian type diffusion.

However, when the patches are far away from one another, *long distance dispersal* has to be considered, which means that the dispersion terms should carry delays to account for the time it takes for individuals to migrate between patches. In the mean time, for species with good memory (human beings, for instance), an individual intention/decision of migration to a patch may be a result of comparison of the *previous* experience in that patch and the currently residing patch. Such

considerations suggest a modification of (1.3) to the following

$$\begin{cases} \frac{dx_1(t)}{dt} = f_1(x_1(t)) + D_{21}[x_2(t - \tau) - x_1(t - \tau)] \\ \frac{dx_2(t)}{dt} = f_2(x_2(t)) + D_{12}[x_1(t - \tau) - x_2(t - \tau)]. \end{cases} \quad (1.4)$$

We point out that in the context of patch environment and continuous time, Wu and Krawcewicz [24] incorporated delay into the dispersion in an ODE model over more than two patches with ring structure, and found very rich dynamics in the model; Azer and van den Driessche [2] proposed and studied a two-patch ODE model but with distributed time delays in the dispersal term; both of these two models are similar to (1.4) and demonstrate very rich dynamics. In the case of spatially continuous case and continuous time, Olmstead *et al.* [18] and Duffy *et al.* [5] also considered similar models but in the form of reaction-diffusion equation with delay in the diffusion term accounting for memory. There are numerous models for population dynamics which incorporate time delays in the *reaction terms* to reflect maturation time, and for such models and their justifications, we refer interested readers to Cushing [4], MacDonanld [12] and May [15, 16], Murray [17], Brauer and C. Castillo-Chávez [3] and the references therein.

Motivated by these continuous time models with delays in the dispersion/diffusion, and considering the importance of discrete time models in population dynamics, it seems reasonable to propose the following model system

$$\begin{cases} x(n+1) = f(x(n)) + d_1[y(n-k) - x(n-k)], \\ y(n+1) = g(y(n)) + d_2[x(n-k) - y(n-k)]. \end{cases} \quad (1.5)$$

which is obviously the discrete analogue of (1.4). Obviously, the incorporation of delay increases the dimension of the discrete model system. In order to avoid the important biological features from being hidden behind the complexity caused by high dimensions, in this paper, we only consider a special case of (1.5): $k = 1$ and $d_1 = d_2 =: b$ (meaning symmetric dispersal). Also, as far as local dynamics are concerned, logistic nonlinearity is representative. Thus, in the rest of the paper, we will follow [7] and [25] to adopt the logistic local dynamics by choosing $f(x) = \mu_1 x[1-x]$ and $g(y) = \mu_2 y[1-y]$. That is, we will consider the the following model system

$$\begin{cases} x(n+1) = \mu_1 x(n)(1-x(n)) + b[y(n-1) - x(n-1)], \\ y(n+1) = \mu_2 y(n)(1-y(n)) + b[x(n-1) - y(n-1)]. \end{cases} \quad (1.6)$$

Our focus is on how the interaction of dispersion rate and the local dynamics will affect the dynamics of the metapopulation model (1.6).

Note that when $b = 0$, there is no coupling and each subpopulation in (1.6) is governed by the well known discrete logistic equation of the form

$$u_{n+1} = \mu u_n(1 - u_n). \quad (1.7)$$

This one dimensional dynamical system has been studied extensively and its dynamics, such as period doubling process from a stable 2^{m-1} orbit to a stable 2^m

orbit and a route to chaos as the parameter μ increase in [3, 4], is well understood. Comparing our results for (1.6) with that for (1.7), we find that the impact of dispersion on the global dynamics could be complicated and interesting: it can affect the existence of positive equilibrium (Theorem 2.1); it can either drive the metapopulation to global extinction (Theorem 3.2-A-2), or prevent the metapopulation from global extinction (Theorem 3.3-B-2) and stabilize a positive equilibrium; it can also destabilize a positive equilibrium or a periodic orbit (Theorem 4.1). Although very simple, the model (1.6) does give some insight into the joint impact of the local dynamics and the dispersion strength on the dynamics of the metapopulation. Also even for this simple model, there are still some interesting yet challenging mathematical problems (see, e.g., Remark 4.2), let alone various possibilities of modifying the model.

2. Existence of Positive Equilibrium of (1.6)

As is well known, equilibria of a system play a crucial role in determining the dynamics of a system. Thus, we will naturally start with an investigation to the structure of equilibria of (1.6). Obviously, $(0, 0)$ is an equilibrium. For biological reason, we are mainly interested in positive equilibria. We will also determine the dependence of the positive equilibria on the dispersion rate b and estimate their locations. Such information will be useful in Sect. 3 in determining the stability of these equilibria.

Throughout this section, we will assume

$$0 < \mu_1 < 1 < \mu_2 < 4. \tag{2.1}$$

When $b = 0$, under condition (2.1), we know that (1.6) has no positive equilibrium. However, the presence of dispersion will bring one positive equilibrium into existence, as will be shown in the sequel.

THEOREM 2.1 *Assume that (2.1) holds.*

(i) *If $\mu_1 + \mu_2 < 2$, then (1.6) has an unique positive fixed point for $0 < b < b_1$, where*

$$b_1 = \frac{(\mu_2 - 1)(1 - \mu_1)}{2 - \mu_1 - \mu_2}. \tag{2.2}$$

(ii) *If $\mu_1 + \mu_2 \geq 2$, then for any $b > 0$, (1.6) has an unique positive fixed point.*

Proof. A fixed point of (1.6) satisfies the following equations

$$\begin{cases} \mu_1 x(1 - x) + b(y - x) = x, \\ \mu_2 y(1 - y) + b(x - y) = y, \end{cases} \tag{2.3}$$

that is

$$\begin{cases} y = \frac{1}{b}[\alpha_1 x + \mu_1 x^2] \triangleq h_1(x), \\ x = \frac{1}{b}[\alpha_2 y + \mu_2 y^2] \triangleq h_2(y), \end{cases} \tag{2.4}$$

where

$$\alpha_1 = 1 + b - \mu_1, \quad \alpha_2 = 1 + b - \mu_2. \tag{2.5}$$

Thus, (x^*, y^*) is a positive fixed point of (1.6) if and only if it is an intercept of the two parabolas $y = h_1(x)$ and $x = h_2(y)$ in $\mathbb{R}^+ \times \mathbb{R}^+$.

If $\mu_1 + \mu_2 < 2$, then $b_1 > 0$. Since $\alpha_1 > 0$ for any $b > 0$, the two parabolas have a unique positive intercept if and only if either $\alpha_2 < 0$, or

$$\alpha_2 > 0 \quad \text{and} \quad h'_1(0) < \frac{1}{h'_2(0)}. \tag{2.6}$$

See Fig. 1 for an illustration. Observe that $\alpha_2 < 0$ is equivalent to $b < \mu_2 - 1$ which is implied by $b < b_1$, since

$$\frac{1 - \mu_1}{2 - \mu_1 - \mu_2} = \frac{1 - \mu_1}{(1 - \mu_1) - (\mu_2 - 1)} > 1$$

when $\mu_2 - 1 < 1 - \mu_1$. Noting that $h'_1(0) = \alpha_1/b$ and $h'_2(0) = \alpha_2/b$, (2.6) holds provided that

$$(2 - \mu_1 - \mu_2)b < (\mu_2 - 1)(1 - \mu_1),$$

which also holds when $b < b_1$. Hence, for $0 < b < b_1$, there is an unique positive equilibrium for (1.6), where b_1 is given by (2.2).

Part (ii) can be proved in a similar way, and the details are omitted here. \square

Next, we estimate the location of the positive equilibrium. This is not trivial at all, and we proceed as bellow.

Consider the positive equilibrium of (1.6) as a function of the parameter b , and denote it by

$$x^* = \varphi(b), \quad y^* = \psi(b). \tag{2.7}$$

Then, by Theorem 2.1, we know that $\varphi(b)$ and $\psi(b)$ are both positive maps from \mathbb{R}^+ to \mathbb{R}^+ in the case $\mu_1 + \mu_2 \geq 2$, and from $(0, b_1]$ to \mathbb{R}^+ in the case $\mu_1 + \mu_2 < 2$.

THEOREM 2.2 *Assume that (2.1) holds and let functions $\varphi(\cdot)$ and $\psi(\cdot)$ be defined by (2.7). Then the ranges $R(\varphi)$ and $R(\psi)$ of φ and ψ satisfy*

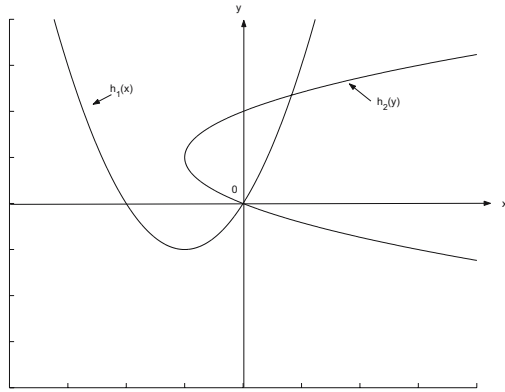
$$R(\varphi) \subset (0, 1), \quad R(\psi) = (0, 1 - 1/\mu_2). \tag{2.8}$$

Proof. If (x^*, y^*) is the unique positive fixed point of (1.6), then, by (2.4), x^* and y^* satisfy the following cubic equations, respectively.

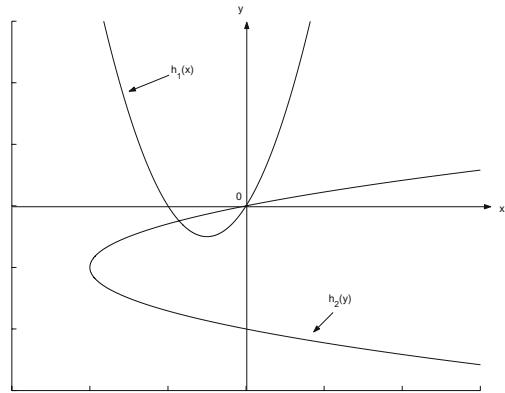
$$b^2 = (\alpha_1 + \mu_1 x) \left[\alpha_2 + \frac{\mu_2}{b} (\alpha_1 + \mu_1 x) \right] \triangleq h(x), \tag{2.9}$$

$$b^2 = (\alpha_2 + \mu_2 y) \left[\alpha_1 + \frac{\mu_1}{b} (\alpha_2 + \mu_2 y) \right] \triangleq g(y). \tag{2.10}$$

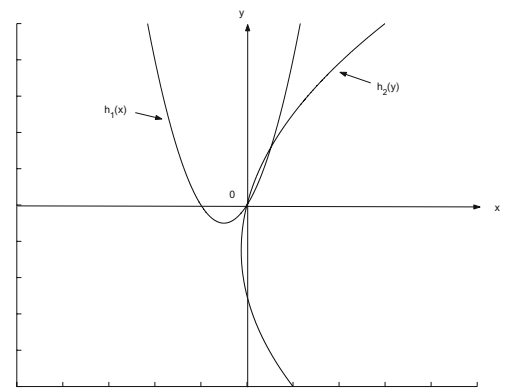
Direct but tedious calculation shows that $h(0) < b^2$ and $h(1) > b^2$. By the existence and uniqueness of positive equilibrium established in Theorem 2.1 and



(a)



(b)



(c)

Fig. 1: The graphs of $y = h_1(x)$ and $x = h_2(y)$: (a) $\alpha_2 < 0$; (b) $\alpha_2 > 0$, $h'_2(0) > 1/h'_1(0)$; (c) $\alpha_2 > 0$, $h'_2(0) < 1/h'_1(0)$.

the Intermediate Value Theorem for continuous functions, we conclude that $x^* \in (0, 1)$, proving the first part of (2.8).

Similarly, by showing $g(0) = h(0) < b^2$ and $g(1 - 1/\mu_2) = b^2 + b(1 - \mu_1/\mu_2) > b^2$, we prove that $y^* \in (0, 1 - 1/\mu_2)$, implying $R(\psi) \subset (0, 1 - \mu_1/\mu_2)$. It remains to prove $(0, 1 - 1/\mu_2) \subset R(\psi)$. From (2.10), a direct calculation shows that

$$\begin{aligned} g(y) &= (1 + b - (1 - y)\mu_2) \left(1 + b - \mu_1 + \frac{y\mu_1}{b}(1 + b - (1 - y)\mu_2) \right) \\ &= (1 + b - (1 - y)\mu_2) \left[(1 + b - (1 - y)\mu_1) + \frac{y\mu_1}{b}(1 - (1 - y)\mu_2) \right] \\ &= b^2 + (2 - (1 - y)(\mu_1 + \mu_2))b + (1 - (1 - 2y)\mu_1)(1 - (1 - y)\mu_2) \\ &\quad + \frac{y\mu_1}{b}(1 - (1 - y)\mu_2)^2. \end{aligned}$$

Thus

$$b(g(y) - b^2) = A(y)b^2 + B(y)b + C(y), \tag{2.11}$$

where

$$\begin{aligned} A(y) &= 2 - (1 - y)(\mu_1 + \mu_2) \\ B(y) &= (1 - (1 - 2y)\mu_1)(1 - (1 - y)\mu_2) \\ C(y) &= y\mu_1(1 - (1 - y)\mu_2)^2. \end{aligned}$$

For every $y \in (0, 1 - 1/\mu_2)$, we can compute

$$\begin{aligned} B^2(y) - 4A(y)C(y) &= \\ &= (1 - (1 - y)\mu_2)^2 [(1 - (1 - 2y)\mu_1)^2 - 4y\mu_1(2 - (1 - y)(\mu_1 + \mu_2))] \\ &= (1 - (1 - y)\mu_2)^2 [1 - 2\mu_1 - 4y\mu_1 + \mu_1^2 + 4y\mu_1\mu_2(1 - y)] \\ &= (1 - (1 - y)\mu_2)^2 [(1 - \mu_1)^2 + 4\mu_1(\mu_2 - 1)y - 4\mu_1\mu_2y^2]. \end{aligned} \tag{2.12}$$

Now by the property of the quadratic function $q(y) = (1 - \mu_1)^2 + 4\mu_1(\mu_2 - 1)y - 4\mu_1\mu_2y^2$, we know that it is positive for all $y \in (0, r_2)$ where

$$r_2 = \frac{1}{2\mu_1\mu_2} \left[\mu_1(\mu_2 - 1) + \sqrt{\mu_1^2(\mu_2 - 1)^2 + \mu_1\mu_2(\mu_1 - 1)^2} \right].$$

It is easily verified that $1 - 1/\mu_2 < r_2$. Therefore $q(y) > 0$ for $y \in (0, 1 - 1/\mu_2)$, and so is $B^2(y) - 4A(y)C(y)$. Hence, for every $y \in (0, 1 - 1/\mu_2)$, $A(y)b^2 + B(y)b + C(y) = 0$ has a positive solution b , and so does (2.10). This, together with Theorem 2.1, establishes $(0, 1 - 1/\mu_2) \subset R(\psi)$, and hence, completes the proof. \square

Remark 1 For each $y \in (0, 1/\mu_2)$, there may be two positive values $b_1 < b_2$ for b at which y is a solution of (2.10). In such a case, take the larger value b_2 , then $(x, y) = (\phi(b_2), y)$ gives the unique positive equilibrium of (1.6).

Remark 2 Similarly, if $1 < \mu_1 < \mu_2 < 4$, we have

$$R(\psi) = (0, 1 - 1/\mu_1). \tag{2.13}$$

3. Driven to and Prevented from Global Distinction by Dispersion

In this section, we discuss the stability of the trivial equilibrium and the positive equilibrium. To this end, we set

$$w_1(n) = x(n - 1) - y(n - 1), \quad w_2(n) = x(n), \quad w_3(n) = y(n).$$

Then (1.6) can be rewritten as the following discrete three-dimensional system

$$\begin{pmatrix} w_1(n + 1) \\ w_2(n + 1) \\ w_3(n + 1) \end{pmatrix} = \begin{pmatrix} w_2(n) - w_3(n) \\ \mu_1 w_2(n)(1 - w_2(n)) - b w_1(n) \\ \mu_2 w_3(n)(1 - w_3(n)) + b w_1(n) \end{pmatrix} \triangleq F \begin{pmatrix} w_1(n) \\ w_2(n) \\ w_3(n) \end{pmatrix}. \tag{3.1}$$

The trivial equilibrium $(0, 0)$ of (1.6) corresponds to the equilibrium $W_0 = (0, 0, 0)$ for the system (3.1), while the positive equilibrium (x^*, y^*) is transformed to $W^* = (x^* - y^*, x^*, y^*)$.

The derivative matrix of F is

$$DF(W) = \begin{pmatrix} 0 & 1 & -1 \\ -b & \beta_1 & 0 \\ b & 0 & \beta_2 \end{pmatrix}, \tag{3.2}$$

where

$$\beta_1 \triangleq \mu_1(1 - 2w_2), \quad \beta_2 \triangleq \mu_2(1 - 2w_3). \tag{3.3}$$

The stability of an equilibrium of (3.1) is then determined by the characteristic equation of matrix (3.2):

$$\lambda(\lambda - \beta_1)(\lambda - \beta_2) = b(-2\lambda + \beta_1 + \beta_2), \tag{3.4}$$

where β_1 and β_2 are given by (3.3) and are evaluated at the corresponding equilibrium.

We first obtain some general information about the roots of (3.4). Without loss of generality, we assume that

$$0 < \beta_1 < \beta_2, \tag{3.5}$$

and denote

$$h(\lambda) = \lambda(\lambda - \beta_1)(\lambda - \beta_2), \tag{3.6}$$

$$g_b(\lambda) = b(-2\lambda + \beta_1 + \beta_2). \tag{3.7}$$

THEOREM 3.1 *Assume that (3.5) holds.*

(i) *For any $b > 0$, (3.4) has a real root $\lambda_3(b)$ in $(\frac{\beta_1 + \beta_2}{2}, \beta_2)$. Moreover, $\lambda_3(b)$ is strictly decreasing in b and*

$$\lim_{b \rightarrow 0^+} \lambda_3(b) = \beta_2, \quad \lim_{b \rightarrow +\infty} \lambda_3(b) = \frac{\beta_1 + \beta_2}{2}. \tag{3.8}$$

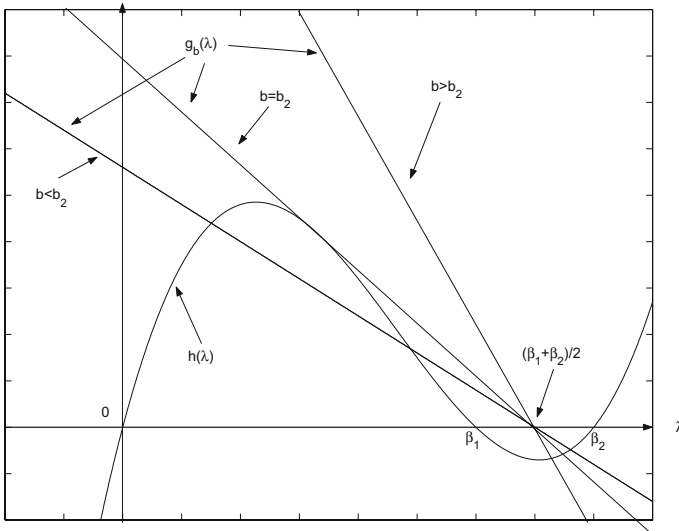


Fig. 2: The graphs of $y = h(\lambda)$ and $y = g_b(\lambda)$, with $b < b_2$, $b = b_2$ and $b > b_2$, respectively.

(ii) There exists a (critical) value $b_2 > 0$ such that for $0 < b \leq b_2$, (3.4) has three real roots $\lambda_i(b)$, $i = 1, 2, 3$ with $\lambda_1(b), \lambda_2(b) \in (0, \beta_1)$.

(iii) Let b_2 be given by (ii). Then when $b > b_2$ (3.4) has a pair of complex roots $\lambda_1(b)$ and $\lambda_2(b) = \bar{\lambda}_1(b)$ and their norm $|\lambda_1(b)|$ is strict increasing with respect to b satisfying

$$\lim_{b \rightarrow +\infty} |\lambda_1(b)| = +\infty. \tag{3.9}$$

Proof. (i) and (ii) are obvious (see the graphs of $h(\lambda)$ and $g_b(\lambda)$ in Fig. 2). Thus, we only need to prove (iii). Let $\lambda_3(b)$ be the real eigenvalue in $((\beta_1 + \beta_2)/2, \beta_2)$. The characteristic equation (3.4) can be rewritten as

$$\lambda^3 - (\beta_1 + \beta_2)\lambda^2 + (2b + \beta_1\beta_2)\lambda - b(\beta_1 + \beta_2) = 0. \tag{3.10}$$

Hence, if $b > b_2$,

$$|\lambda_1|^2 \lambda_3 = \lambda_1 \lambda_2 \lambda_3 = b(\beta_1 + \beta_2),$$

from which we obtain

$$|\lambda_1(b)|^2 = \frac{b(\beta_1 + \beta_2)}{\lambda_3(b)}. \tag{3.11}$$

Now, (iii) follows from (3.11) and (ii). □

Similar to Theorem 3.1, we can prove the following result.

THEOREM 3.2 Assume $\beta_1 < \beta_2$ with $|\beta_1| \leq 1$ and $|\beta_2| \leq 1$. If $0 < b < 1/2$. Then the roots of equation (3.4) satisfy $|\lambda| < 1$.

When $b = 0$, by the existing results on the logistic maps, we know there is no positive equilibrium for (1.7), and that W_0 is unstable (saddle) since $x(n) \rightarrow 0$ and $y(n) \rightarrow 1 - 1/\mu_2$ as $n \rightarrow \infty$. When $b > 0$, under the assumptions of Theorem 2.1, both W_0 and the positive equilibrium W^* exist. In the rest of this section, we will investigate the impact of the dispersion rate $b > 0$ on the stability of W_0 and W^* .

We begin with W_0 , for which $\beta_1 = \mu_1$ and $\beta_2 = \mu_2$. Although W_0 exist regardless of values μ_1 and μ_2 , we confine ourselves to the restriction $0 < \mu_1 \leq 1 < \mu_2$ for consistency. We have the following two cases: Case (i) $\mu_1 + \mu_2 \geq 2$; Case (ii) $\mu_1 + \mu_2 < 2$.

In case (i), for any $b > 0$, by Theorem 3.1-(i), (3.2) always a real eigenvalue $\lambda_3 > 1$. From (ii) and (iii) of Theorem 3.1, there exists a constant $b_3 > 0$ such that

- (i-1) if $0 < b < b_3$, the other two eigenvalues λ_1, λ_2 of (3.2) are also real with $\lambda_1 < \lambda_2 < 1$. Hence the equilibrium W_0 is a saddle;
- (i-2) if $b > b_3$, then the other two eigenvalues λ_1, λ_2 of (3.2) are complex with $|\lambda_1| = |\lambda_2| > 1$. In this case, W_0 is an expanding fixed point.
- (i-3) if $b = b_3$, then the other two eigenvalues λ_1, λ_2 of (3.2) are complex with $|\lambda_1| = |\lambda_2| = 1$.

Case (ii) seems to be more interesting, as is described by the following theorem.

THEOREM 3.3 *Assume $0 < \mu_1 \leq 1 < \mu_2, \mu_1 + \mu_2 < 2$ and let b_1 be given by (2.2).*

(A) *If*

$$(\mu_1 + \mu_2)(\mu_1 + \mu_2 - \mu_1\mu_2) < 2, \tag{3.12}$$

then there exists a positive number $b_4 > b_1$ such that

- (A-1) *If $0 < b \leq b_1$, then $|\lambda_1| < 1, |\lambda_2| < 1$ and $\lambda_3 \geq 1$, and hence W_0 is a saddle;*
- (A-2) *If $b_1 < b < b_4$, then the norms of all three eigenvalues are less than 1, and hence, W_0 is a stable fixed point;*
- (A-3) *If $b > b_4$, then λ_1 and λ_2 are complex with the norm larger than 1 and $\lambda_3 < 1$, and again, W_0 is a saddle.*

(B) *If*

$$(\mu_1 + \mu_2)(\mu_1 + \mu_2 - \mu_1\mu_2) > 2, \tag{3.13}$$

then there exists a constant $0 < b_5 < b_1$ such that

- (B-1) *If $0 < b < b_5$, then $|\lambda_1| < 1, |\lambda_2| < 1$ and $\lambda_3 > 1$, that is, W_0 is a saddle;*
- (B-2) *If $b_5 < b < b_1$, then λ_1 and λ_2 are complex with their norm larger than 1 and $\lambda_3 > 1$, that is, W_0 is an expanding fixed point;*
- (B-3) *If $b_1 < b$, then λ_1 and λ_2 are complex with their norm larger than 1 but $\lambda_3 < 1$, that is, W_0 is again a saddle.*

Remark 3 (A-2) shows that for some ranges of μ_1 and μ_2 , larger dispersion can drive both subpopulations to extinction, although the second subpopulation would survive in the absence of dispersion, while (B-2) implies that an appropriate dispersion strength can prevent the metapopulation from global extinction.

Proof. When $b = b_1$, it is easy to see that $\lambda_3 = 1$. The other two eigenvalues are the roots of the equation

$$\lambda^2 + (1 - \mu_1 - \mu_2)\lambda + 1 - (\mu_1 + \mu_2) + \mu_1\mu_2 + 2b_1 = 0. \tag{3.14}$$

By the Jury criterion (see, e.g., [3] or [17]), The two roots of the quadratic equation (3.14) have norms less than 1 if and only if

$$1 - (\mu_1 + \mu_2) + \mu_1\mu_2 + 2b_1 < 1, \tag{3.15}$$

$$1 - (\mu_1 + \mu_2) + \mu_1\mu_2 + 2b_1 + 1 > \mu_1 + \mu_2 - 1. \tag{3.16}$$

From (2.2), (3.15) is equivalent to

$$\begin{aligned} 2\frac{(1 - \mu_1)(\mu_2 - 1)}{2 - \mu_1 - \mu_2} &< (1 - \mu_1)(\mu_2 - 1) + 1, \\ \iff (1 - \mu_1)(\mu_2 - 1)(\mu_1 + \mu_2) &< 2 - \mu_1 - \mu_2, \\ \iff (\mu_1 + \mu_2)(\mu_1 + \mu_2 - \mu_1\mu_2) &< 2. \end{aligned}$$

The last inequality holds by condition (3.12).

On the other hand, (3.16) holds provided that

$$\begin{aligned} 2(\mu_1 + \mu_2) - 3 - \mu_1\mu_2 &< 2b_1 \\ \iff 2(1 - \mu_1)(\mu_2 - 1) + \mu_1\mu_2 - 1 &< 2\frac{(1 - \mu_1)(\mu_2 - 1)}{2 - \mu_1 - \mu_2} \\ \iff 2(1 - \mu_1)(\mu_2 - 1) &< 2\frac{(1 - \mu_1)(\mu_2 - 1)}{2 - \mu_1 - \mu_2} \\ \iff 1 &< \mu_1 + \mu_2 \end{aligned}$$

since $\mu_1\mu_2 - 1 < 0$ (otherwise $\mu_1 + \mu_2 \geq 2$). The last inequality holds. Thus the two roots of (3.14) have their norms less than 1. It follows from Theorem 3.1 that there exists a constant $b_4 > b_1$ such that Part A of the theorem holds.

For Part B, if (3.13) holds, from the proof of Part A, we know that at least one of the roots of (3.14) has norm larger than 1. Thus, the two roots λ_1 and λ_2 of (3.14) are indeed both complex with $|\lambda_1| = |\lambda_2| > 1$. Hence the results follows from Theorem 3.1. \square

Now, we consider the stability of the positive equilibrium point W^* of (3.1), which corresponds to the stability of the positive equilibrium (x^*, y^*) of (1.6). Here we are only concerned with the conditions under which W^* is stable.

THEOREM 3.4 *Assume $0 < \mu_1 < 1 < \mu_2 < 3$. Then there exists a constant $0 < b_6 < 1/2$ such that for $0 < b < b_6$, the positive equilibrium W^* is stable.*

Proof. From (3.2)–(3.4), it suffices to prove that the roots of the equation

$$\lambda(\lambda - \beta_1)(\lambda - \beta_2) = b(-2\lambda + \beta_1 + \beta_2) \tag{3.17}$$

satisfy $|\lambda| < 1$, where by (3.3)

$$\beta_1 = \mu_1(1 - 2x^*), \quad \beta_2 = \mu_1(1 - 2y^*).$$

From Theorem 3.2, we need to verify that $|\beta_1| < 1$ and $|\beta_2| < 1$ since $b < 1/2$. But the first condition $|\beta_1| < 1$ is a direct result of (2.8). Hence we only need to find a constant b_6 with $0 < b_6 < 1/2$ such that for any $b \in (0, b_6)$, the corresponding $y^* > 0$ satisfies

$$|\beta_2| = |\mu_2(1 - 2y^*)| < 1. \tag{3.18}$$

From the proof of Theorem 2.2, we know that b and $y = y^*$ satisfy the following equation

$$A(y^*)b^2 + B(y^*)b + C(y^*) = 0, \tag{3.19}$$

where $A(y)$, $B(y)$ and $C(y)$ are given in Sect. 2. If $\mu_1 + \mu_2 < 2$, then $A > 0$, $B < 0$ and $C > 0$ for any $y \in (0, 1 - 1/\mu_2)$. Calculation shows that $B^2 - 4AC = [1 - (1 - y)\mu_2]^2(\mu_2 - 1 - \mu_2y) > 0$ for all $y \in (0, 1 - 1/\mu_2) = R(\psi)$. This together with the signs of A , B and C implies that (3.19) has two real roots for b for every $y \in R(\psi) = (0, 1 - 1/\mu_2)$. Again by the Jury criterion, these two roots satisfy $0 < b < 1/2$ if and only if

$$r_1(y) \triangleq A + 2B + 4C > 0, \tag{3.20}$$

$$r_2(y) \triangleq A - 4C > 0. \tag{3.21}$$

Since

$$r_1\left(1 - \frac{1}{\mu_2}\right) = r_2\left(1 - \frac{1}{\mu_2}\right) = 1 - \frac{\mu_1}{\mu_2} > 0,$$

and by the continuity of r_1 and r_2 , there exists a left neighborhood of $1 - 1/\mu_2$, on which (3.20) and (3.21) hold. Let $(y_1, 1 - 1/\mu_2)$ be the largest such interval. On the other hand, the condition

$$|\beta_2| = |\mu_2(1 - 2y)| < 1$$

holds if and only if

$$\frac{1}{2}\left(1 - \frac{1}{\mu_2}\right) < y < \frac{1}{2}\left(1 + \frac{1}{\mu_2}\right).$$

Let

$$y_2 = \max\left\{y_1, \frac{1}{2}\left(1 - \frac{1}{\mu_2}\right)\right\}.$$

Then, we obtain the conclusion of the theorem by choosing

$$b_6 = \max\left\{b : b = \varphi(y), \text{ for } y \in (y_2, 1 - 1/\mu_2)\right\},$$

where ψ is as in (2.7).

Finally, if $\mu_1 + \mu_2 > 2$, then for any $y \in (1 - 2/(\mu_1 + \mu_2), 1 - 1/\mu_2)$, we have $A > 0$, $B < 0$ and $C > 0$. The rest of the proof is the same as the first part. \square

Remark 4 Theorem 3.4 shows that in some ranges of μ_1 and μ_2 , *smaller* dispersion can play a role of saviour, since it can make both subpopulations survive and approach the positive equilibrium, while the second subpopulation would go to extinction in the absence of dispersion. This is in contrast to Theorem 3.3-(A-2) (see Remark 3.1), and is also related to Theorem 3.3-(B-2).

4. Dispersion Driven Instability

In Sect. 3, we have studied the impact of dispersion on the dynamics of the metapopulation, under the assumption that in the absence of dispersion, one subpopulation goes to extinction ($0 < \mu_1 < 1$) and the other survives ($1 < \mu_2 < 4$). In this section, we consider a different combination of local dynamics for the two subpopulation:

$$1 < \mu_1 < \mu_2 < 4. \tag{4.1}$$

Under condition (4.1) and in the absence of dispersion ($b = 0$), system (1.6) has the positive equilibrium $(1 - 1/\mu_1, 1 - 1/\mu_2)$, and both subpopulations would survive but not necessarily converge to this equilibrium. We will study the impact of dispersion on the dynamics of the metapopulation under (4.1).

It is well known that in the case of reaction diffusion equations (spatially continuous environment), diffusion can drive an otherwise stable equation to unstable one. Such instability has been referred to as Turing instability or diffusion-driven instability (see Turing [23]). In the rest of this section, we will show that similar instability can occur to the spatially discrete model (1.6).

To formulate the problem simply, we only consider the symmetric case

$$\begin{cases} x(n+1) = \mu x(n)(1 - x(n)) + b(y(n-1) - x(n-1)), \\ y(n+1) = \mu y(n)(1 - y(n)) + b(x(n-1) - y(n-1)), \end{cases} \tag{4.2}$$

meaning that the two patches are environmentally identical. When $b = 0$, the dynamics of (4.2) is determined by the one-dimensional dynamical (logistic) system (1.7). It is well known that this logistic equation undergoes from stable to period doubling and finally to chaotic as μ increases. More precisely, there exists a sequence $\mu_0 = 1 < \mu_1 = 3 < \mu_2 = 1 + \sqrt{6} < \mu_3 < \dots < \mu_m < \dots < \mu_\infty \approx 3.59$ such that when $\mu \in (\mu_m, \mu_{m+1})$, $m = 0, 1, 2, \dots$, (1.7) has an unique stable 2^m -period orbit.

Now, for $\mu \in (\mu_m, \mu_{m+1})$, let $\{u_i, i = 1, 2, \dots, 2^m\}$ be the corresponding stable 2^m -periodic orbit of the logistic equation (1.7). Then $\{(u_i, u_i), i = 1, 2, \dots, 2^m\}$ is an 2^m -periodic orbit (which is called “in phase” 2^m -cycle in some references) of (4.2) for any $b > 0$. We now investigate the impact of $b > 0$ on the the stability of this “in phase” 2^m -cycle.

Let

$$s(n) = \frac{x(n) + y(n)}{2}, \quad d(n) = \frac{x(n) - y(n)}{2}, \tag{4.3}$$

in terms of which, (4.2) becomes

$$\begin{cases} s(n+1) &= \mu(s(n) - s(n)^2 - d(n)^2), \\ d(n+1) &= \mu(d(n) - 2s(n)d(n)) - 2bd(n-1). \end{cases} \tag{4.4}$$

Denoting

$$w_1(n) = s(n), \quad w_2(n) = d(n-1), \quad w_3(n) = d(n),$$

we can rewrite the difference system (4.4) as the three dimensional discrete dynamical system

$$\begin{pmatrix} w_1(n+1) \\ w_2(n+1) \\ w_3(n+1) \end{pmatrix} = \begin{pmatrix} \mu(w_1(n) - w_1(n)^2 - w_3(n)^2) \\ w_3(n) \\ \mu(w_3(n) - 2w_1(n)w_3(n)) - 2bw_2(n) \end{pmatrix} \triangleq G \begin{pmatrix} w_1(n) \\ w_2(n) \\ w_3(n) \end{pmatrix}. \tag{4.5}$$

By the above transformation, the “in phase” 2^m -cycle $\{(u_i, u_i), i = 1, 2, \dots, 2^m\}$ of the difference system (4.2) is transformed to the 2^m -periodic orbit $\{W^i, i = 1, 2, \dots, 2^m\}$ of the dynamical system (4.5), where $W^i = (u_i, 0, 0)^T$.

THEOREM 4.1 *Let $1 < \mu \leq 4$ and $b > 1/2$. Then every in phase p -cycle $W^i = (u_i, 0, 0)^T$ of (4.5), $i = 1, 2, \dots, p$, is unstable.*

Proof. From (4.5), the Jacobian of G at a point $W = (u, 0, 0)$ is

$$J(W) = \begin{pmatrix} \mu(1 - 2u) & 0 & 0 \\ 0 & 0 & 1 \\ 0 & -2b & \mu(1 - 2u) \end{pmatrix}. \tag{4.6}$$

For $i = 1, 2, \dots, p$, let $a_i = \mu(1 - 2u_i)$ and

$$N_i = \begin{pmatrix} 0 & 1 \\ -2b & \mu(1 - 2u_i) \end{pmatrix}.$$

Then the stability of the in-phase cycle $\{W^i = (u_i, 0, 0)^T, i = 1, 2, \dots, p\}$ is determined by the eigenvalues of the matrix

$$M_p := J(W^1) \cdot J(W^2) \cdots J(W^p).$$

Note that

$$J(W^i) = \begin{pmatrix} a_i & 0_{1 \times 2} \\ 0_{2 \times 1} & N_i \end{pmatrix},$$

where $0_{1 \times 2} = (0, 0)$ and $0_{2 \times 1} = (0, 0)^T$. By multiplication of block matrices, we can express M_p as

$$M_p = \begin{pmatrix} a & 0_{1 \times 2} \\ 0_{2 \times 1} & R_p \end{pmatrix}, \tag{4.7}$$

where $a = a_1 a_2 \cdots a_p$ and $R_p = N_1 \cdot N_2 \cdots N_p$. It is easily seen that

$$\lambda_1 = a = \prod_{i=1}^p \mu(1 - 2u_i)$$

is one eigenvalue of M_p , the other two λ_2, λ_3 are precisely the eigenvalues of the matrix N and hence, satisfy

$$\lambda_2 \lambda_3 = \det(R_p) = \prod_{i=1}^p \det(N_i) = (2b)^p. \tag{4.8}$$

By (4.8), if $b > 1/2$,

$$\max\{|\lambda_2|, |\lambda_3|\} > 1, \tag{4.9}$$

therefore, the in-phase p -cycle is unstable. □

Clearly, λ_1 given above is precisely the number that determines the stability of the p -period cycle $\{u_i, i = 1, 2, \dots, p\}$ of the scalar system (1.7). In particular, when $\mu \in (\mu_m, \mu_{m+1})$, the scalar system (1.7) has a stable 2^m -periodic orbit $\{u_i, i = 1, 2, \dots, 2^m\}$. It is natural to expect that when the dispersal rate b is small, the corresponding in-phase 2^m -cycle $\{u_i, u_i, i = 1, 2, \dots, 2^m\}$ of (4.2) remains stable. Now, Theorem 4.1 shows that larger b (i.e., $b > 1/2$) would destabilize this 2^m -periodic orbit. Corresponding to $m = 0$, we see that larger dispersion destabilize the positive equilibrium $(1 - 1/\mu, 1 - 1/\mu)$ of system (4.2), giving a discrete version of Turing instability. A natural question arises:

- (Q) Is $b = 1/2$ the critical value in the sense that when $\mu \in (\mu_m, \mu_{m+1})$, the corresponding in-phase 2^m -periodic orbit remains stable provided $0 < b < 1/2$?

In the remainder of this section, we answer this question for the cases $m = 0$ (corresponding to the positive equilibrium) and $m = 1$ (corresponding to the 2-periodic orbit).

THEOREM 4.2 *Let $\mu_0 = 1 < \mu < 3 = \mu_1$. Then the positive equilibrium $W_1 = (1 - 1/\mu, 0, 0)$ of (4.5) is stable $0 \leq b < 1/2$.*

Proof. Since $1 < \mu < 3$, from the proof of Theorem 4.1 with $p = 2^0 = 1$, the first eigenvalue λ_1 of M_1 satisfies $|\lambda_1| = |\mu(1 - 2(1 - 1/\mu))| = |2 - \mu| < 1$, and the other two eigenvalue λ_2, λ_3 of M_1 are the roots of the quadratic equation

$$\lambda^2 + \lambda_1 \lambda + 2b = 0.$$

Now the Jury criterion implies that $|\lambda_i| < 1, i = 2, 3$ if and only if $b < 1/2$. □

From Theorem 4.2, we see that when $1 < \mu < 3$, the number $\frac{1}{2}$ is the critical value of the dispersion parameter b at which the in-phase positive fixed point of (4.2) loses its stability.

Next, we consider $\mu_1 = 3 < \mu < 1 + \sqrt{6} = \mu_2$. In this case, the in-phase 2-period cycle $\{(u_i, u_i), i = 1, 2\}$ of (4.2) corresponds to the 2-period cycle $\{W^i = (u_i, 0, 0), i = 1, 2\}$ of (4.5), where

$$u_1 = \frac{(\mu + 1) - \sqrt{(\mu + 1)(\mu - 3)}}{2\mu}, \quad u_2 = \frac{(\mu + 1) + \sqrt{(\mu + 1)(\mu - 3)}}{2\mu}. \quad (4.10)$$

THEOREM 4.3 *Let $3 < \mu < 1 + \sqrt{6}$. We have the following two cases*

(i) *If $3 < \mu \leq 1 + \sqrt{5}$, then the 2-cycle $\{W^i = (u_i, 0, 0), i = 1, 2\}$ of (4.5) is stable for $0 \leq b < 1/2$;*

(ii) *If $1 + \sqrt{5} < \mu < 1 + \sqrt{6}$, then the 2-cycle $\{W^i = (u_i, 0, 0), i = 1, 2\}$ of (4.5) is stable if and only if*

$$0 \leq b < b(\mu),$$

where

$$b(\mu) \triangleq \frac{1 - \sqrt{\mu^2 - 2\mu - 4}}{2} \in (0, 1/2).$$

Proof. Let

$$\alpha_i = \mu(1 - 2u_i), \quad i = 1, 2.$$

From the proof of Theorem 4.1 with $p = 2^1 = 2$, we know that the first eigenvalue λ_1 of the matrix M_2 satisfies

$$\lambda_1 = \alpha_1\alpha_2 = -(\mu^2 - 2\mu - 4) = -(\mu - (1 - \sqrt{5}))(\mu - (1 + \sqrt{5})), \quad (4.11)$$

and hence $|\lambda_1| < 1$ (see, e.g., p.42 in Murray [17]). The other two eigenvalues λ_2, λ_3 of M_2 are precisely the two eigenvalues of the 2×2 matrix R_2 which is now given by

$$R_2 = \begin{pmatrix} 0 & 1 \\ -2b & \alpha_1 \end{pmatrix} \begin{pmatrix} 0 & 1 \\ -2b & \alpha_2 \end{pmatrix} = \begin{pmatrix} -2b & \alpha_2 \\ -2b\alpha_1 & \alpha_1\alpha_2 - 2b \end{pmatrix}.$$

Thus, λ_2 and λ_3 are roots of

$$\lambda^2 + (4b - \alpha_1\alpha_2)\lambda + 4b^2 = 0. \quad (4.12)$$

If $0 \leq b < 1/2$, by the Jury criterion, the norms of the two roots of (4.12) are less than 1 if and only if

$$|4b - \alpha_1\alpha_2| < 1 + 4b^2.$$

That is,

$$-(2b - 1)^2 < \alpha_1\alpha_2 < (2b + 1)^2. \quad (4.13)$$

It follows from (4.11) that if $3 < \mu \leq 1 + \sqrt{5}$ then $\alpha_1\alpha_2 > 0$. In this case, (4.13) holds automatically, and this proves (i).

For (ii), Let $1 + \sqrt{5} < \mu < 1 + \sqrt{6}$. If $0 < b < 1/2$, then (4.13) holds if and only if

$$b^2 - b + \frac{1 - (\mu^2 - 2\mu - 4)}{4} > 0.$$

The last inequality is equivalent to

$$0 < b < \frac{1 - \sqrt{\mu^2 - 2\mu - 4}}{2} \triangleq b(\mu).$$

The proof is completed. \square

Remark 5 It is easily seen that

$$\lim_{\mu \rightarrow (1+\sqrt{6})^-} b(\mu) = 0, \quad \lim_{\mu \rightarrow (1+\sqrt{5})^-} b(\mu) = \frac{1}{2}. \quad (4.14)$$

Remark 6 Comparing Theorem 4.3 with Theorem 4.2, we feel that the answers to the question (Q) for $m > 2$ would be more complicated and thus, we have to leave it as a future project.

5. Conclusions

In this paper, we propose a system of two difference equations with time delay to describe the population dynamics of a single species over two patches. We assume that each subpopulation is governed by the discrete logistic equation with an intrinsic growth rate μ_i , $i = 1, 2$, and the interaction of the two subpopulations is reflected by the dispersal parameter b . The main concern is how the local dynamics (represented by μ_i , $i = 1, 2$) and the dispersal jointly affect the dynamics of the metapopulation. The presence of a delay in the dispersion term raises the dimension of the system, and thus, makes the analysis of the model more challenging. Our results show that the interplay of μ_i , $i = 1, 2$ and b may lead to very rich dynamics: depending on the ranges of μ_i , $i = 1, 2$ and b , the interplay can affect the existence of a positive equilibrium; can either drive the metapopulation to global extinction, or prevent the metapopulation from going to global extinction and stabilize a positive equilibrium; it can also destabilize a positive equilibrium or a periodic orbit. Such rich dynamics is a reflection of the biological diversity in nature.

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