Aggregation and heterogeneity from the nonlinear dynamic interaction of birth, maturation and spatial migration[☆]

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Abstract

We consider a single species structured population distributed in two identical patches connected by spatial dispersal. Assuming that the maturation time for each individual is a random variable with a gamma distribution and that the spatial dispersal rate is constant, we obtain from a hyperbolic differential equation a system of six ordinary differential equations for the matured populations and their moments. Our qualitative analysis and numerical simulations show that the nonlinear interaction of birth process, the maturation delay and the spatial dispersal can lead to a new mechanism for individual aggregation in the form of the existence of multiple stable heterogeneous equilibria, even though the spatial dispersal is assumed to be proportional to the population gradients with a *constant* rate.

1. Introduction

Aggregation and, more generally, heterogeneity have been important subjects in theoretical biology (see [2,5–7,11,12,16] and references therein). In models involving reaction differential equations or their discrete analogues where a diffusion term is used to model the spatial movement of the population, aggregation is described by stable heterogeneous solutions and this usually occurs when the diffusion coefficient is density

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dependent (see [1–4,8] and references therein). We should mention that in the work of Britton [2], it was observed that aggregation can occur in models of single species population when it was assumed that individuals can move to obtain resources so that intra-specific competition depends on a spatial average of the population in the whole space.

In this paper, we show that there is another mechanism for spatial heterogeneity, and in particular, for aggregation, due to the interplay of nonlinear birth functions, maturation period, and spatial migration, and that this type of aggregation occurs even though the migration rate is a constant.

Our starting point is a structured population model [10] described by a hyperbolic differential equation. Following the work of So et al. [14,15], we consider a single species population with two stages (mature and immature) and distributed over two identical patches connected by spatial dispersal. We assume, however, that the maturation times for individuals are not a fixed constant but rather a random variable with a gamma distribution. Following the work of Smith [13] and using the linear chain trick [9], we derive from this structured model a system of six ordinary differential equations describing the evolution and interaction of the matured population (and their statistical moments) in two patches. We show that homogeneous equilibria can be found by finding zeros of a scalar function, and their stability properties can be analyzed by describing the locations of zeros of two polynomials of degree three. We also show that stable spatially heterogeneous equilibria cannot take place through the mechanism of pitchfolk bifurcation, and we construct some concrete examples and provide numerical simulations to show that for certain classes of birth functions, when the delay (the maturation period) is large and when the spatial migration rate reaches a certain level, the system admits stable spatially heterogeneous equilibria.

This seems to suggest a new mechanism by which individuals in the population aggregate at particular patch or cluster in space. It would be interesting to further our investigation into the biological and even social consequences of this new mechanism in issues such as insect swarming, fish schooling and animal grouping.

The remaining part of this paper is organized as follows. In Section 2, we describe our model and reduction in details. In Section 3, we investigate the existence and stability of all possible spatially homogeneous equilibria. In Section 4, we provide more detailed computer simulation for aggregation using two different birth functions. And we exam these equilibria in more detail by computing the equilibria and the eigenvalues of the linearized system. In Section 5, we conclude with a brief discussion and some comments for future work.

2. Model derivation

We start with a stage-structured population model [10]. Assume

$U(t, a) =$ the population density at time t and age a,

$m(t) =$ the total mature population,

$d =$ the death rate,

$b(m) =$ the birth rate.

Then we have the conservation law

$$\frac{\partial U(t,a)}{\partial t} + \frac{\partial U(t,a)}{\partial a} = -dU(t,a), \quad t \geqslant 0, \ a \geqslant 0, \tag{2.1}$$

$$U(t,0) = b(m(t)). \tag{2.2}$$

Now we assume that the population has only two stages: mature and immature and, for the moment, we assume the maturation period is r. Then

$$m(t) = \int_r^\infty U(t,a)\,\mathrm{d}a, \tag{2.3}$$

and from (2.1) and (2.2), we obtain (see [13–15]).

$$\frac{\mathrm{d}m(t)}{\mathrm{d}t} = -\mathrm{d}m(t) + \mathrm{e}^{-\alpha r} b(m(t-r)), \tag{2.4}$$

which is a scalar delay differential equation.

Note that in the above derivation, we have assumed that the maturation period r is a constant. On the other hand, from biological point of view, species can reproduce at various age. Therefore, it is more realistic to treat r as a random variable. This leads to the following definition:

$$m(t) = \int_0^\infty U(t,a)P(a)\,\mathrm{d}a, \tag{2.5}$$

where $P(a)$ is the probability that an individual is matured at age a, and $f(a) = P'(a)$ is the probability density function. Throughout the remaining part of this paper, we will use

$$f(a) = \beta^2 a \mathrm{e}^{-\beta a}, \quad a \geqslant 0 \tag{2.6}$$

for a positive constant β. This function gives the mean (average) maturation time $1/\beta$ but allows randomness of the maturation process.

Using integration by parts and the linear chain trick [9], we obtain the following system of ordinary differential equations:

$$\frac{\mathrm{d}m(t)}{\mathrm{d}t} = -\mathrm{d}m(a) + m^{(2)}(t), \tag{2.7}$$

$$\frac{\mathrm{d}m^{(2)}(t)}{\mathrm{d}t} = -\mathrm{d}m^{(2)}(a) + \beta m^{(3)}(t) - \beta m^{(2)}(t), \tag{2.8}$$

$$\frac{\mathrm{d}m^{(3)}(t)}{\mathrm{d}t} = -\mathrm{d}m^{(3)}(a) + \beta b(m(t)) - \beta m^{(3)}(t), \tag{2.9}$$

where

$$m^{(2)}(t) = \beta^2 \int_0^\infty U(t,a)a\mathrm{e}^{-\beta a}\,\mathrm{d}a, \tag{2.10}$$

$$m^{(3)}(t) = \beta \int_0^\infty U(t,a) \mathrm{e}^{-\beta a}\, \mathrm{d}a. \tag{2.11}$$

Now, we add the factor of spatial heterogeneity by considering the case where the population is distributed in an environment containing n patches. Assuming that the rate of migration from patch j to patch i is given by constants $D_{ji} \geqslant 0$ and that $U_i(t,a)$ is the population density of patch i at time t and age a, we obtain

$$\frac{\partial U_i(t,a)}{\partial t} + \frac{\partial U_i(t,a)}{\partial a} = -\mathrm{d}U_i(t,a) + \sum_{j=1}^n D_{ji} U_j(t,a) - \sum_{j=1}^n D_{ij} U_i(t,a). \tag{2.12}$$

Therefore, for the mature populations

$$m_i(t) = \int_0^\infty U_i(t,a) P(a)\, \mathrm{d}a, \quad 1 \leqslant i \leqslant n, \tag{2.13}$$

we can apply integration by parts and the linear chain trick to obtain the following reduced system of ordinary differential equations:

$$\frac{\mathrm{d}m_i(t)}{\mathrm{d}t} = -\mathrm{d}m_i(a) + \sum D_{ji} m_j(t) - \sum D_{ij} m_i(t) + m_i^{(2)}(t), \tag{2.14}$$

$$\frac{\mathrm{d}m_i^{(2)}(t)}{\mathrm{d}t} = -\mathrm{d}m_i^{(2)}(a) + \sum D_{ji} m_j^{(2)}(t)$$
$$- \sum D_{ij} m_i^{(2)}(t) + \beta m_i^{(3)}(t) - \beta m_i^{(2)}(t), \tag{2.15}$$

$$\frac{\mathrm{d}m_i^{(3)}(t)}{\mathrm{d}t} = -\mathrm{d}m_i^{(3)}(a) + \sum D_{ji} m_j^{(3)}(t)$$
$$- \sum D_{ij} m_i^{(3)}(t) + \beta b(m_i(t)) - \beta m_i^{(3)}(t), \tag{2.16}$$

where

$$m_i^{(2)}(t) = \beta^2 \int_0^\infty U_i(t,a) a \mathrm{e}^{-\beta a}\, \mathrm{d}a, \tag{2.17}$$

$$m_i^{(3)}(t) = \beta \int_0^\infty U_i(t,a) \mathrm{e}^{-\beta a}\, \mathrm{d}a. \tag{2.18}$$

In what follows, we will consider the case of identical patches (that is, the migration rate D_{ji} is independent of the patches involved). We hope to address the mechanisms by which spatial heterogeneous stable patterns may form due to the dynamical interaction of the rates of death, birth, migration and maturation. It should be mentioned that a delay differential system was derived in So et al. [4,15] when the maturation period is assumed to be a constant. In their work, various bifurcations of stable synchronized (homogeneous) oscillations and unstable phase-locked oscillations were studied. Our focus here is the mechanism towards stable heterogeneous solutions.

3. Stability analysis of homogeneous equilibria

We shall concentrate on the special case where $n = 2$, $D_{12} = D_{21} = D$. In this case, equilibria are given by the following set of six equations

$$m_1 = \frac{1}{d + D} m_1^{(2)} + \frac{D}{d + D} m_2, \tag{3.1}$$

$$m_2 = \frac{1}{d + D} m_2^{(2)} + \frac{D}{d + D} m_1, \tag{3.2}$$

$$m_1^{(2)} = \frac{\beta}{d + D + \beta} m_1^{(3)} + \frac{D}{d + D + \beta} m_2^{(2)}, \tag{3.3}$$

$$m_2^{(2)} = \frac{\beta}{d + D + \beta} m_2^{(3)} + \frac{D}{d + D + \beta} m_1^{(2)}, \tag{3.4}$$

$$m_1^{(3)} = \frac{\beta}{d + D + \beta} b(m_1) + \frac{D}{d + D + \beta} m_2^{(3)}, \tag{3.5}$$

$$m_2^{(3)} = \frac{\beta}{d + D + \beta} b(m_2) + \frac{D}{d + D + \beta} m_1^{(3)}. \tag{3.6}$$

An equilibrium is homogeneous if $m_1 = m_2$, $m_1^{(2)} = m_2^{(2)}$ and $m_1^{(3)} = m_2^{(3)}$. Clearly, a homogeneous equilibrium is given by solving

$$m_1 = \frac{1}{d} m_1^{(2)}, \quad m_1^{(2)} = \frac{\beta}{d + \beta} m_1^{(3)}, \quad m_1^{(3)} = \frac{\beta}{d + \beta} b(m_1) \tag{3.7}$$

and this leads to

$$b(m_1) = \frac{d(d + \beta)^2}{\beta^2} m_1. \tag{3.8}$$

Obviously (and naturally), this equilibrium is independent of the migration rate D. Clearly, $m_1 = 0$ is a solution of (3.8) if $b(0) = 0$. Whether other solutions exist depends on the choice of birth functions.

We now consider the stability of a given homogeneous equilibrium $\vec{m}^* = (m_1^*, m_2^*, m_1^{*(2)}, m_2^{*(2)}, m_1^{*(3)}, m_2^{*(3)})^{\mathrm{T}}$. Assume that the linearized system at $\vec{m}^*$ is $\dot{\vec{m}} = A\vec{m}$ with $\vec{m} = (m_1, m_2, m_1^{(2)}, m_2^{(2)}, m_1^{(3)}, m_2^{(3)})^{\mathrm{T}}$. Then the eigenvalues of A are given by

$$- dx_1 + D(x_2 - x_1) + x_3 = \lambda x_1, \tag{3.9}$$

$$- dx_2 + D(x_1 - x_2) + x_4 = \lambda x_2, \tag{3.10}$$

$$- dx_3 + D(x_4 - x_3) + \beta(x_5 - x_3) = \lambda x_3, \tag{3.11}$$

$$- dx_4 + D(x_3 - x_4) + \beta(x_6 - x_4) = \lambda x_4, \tag{3.12}$$

$$- dx_5 + D(x_6 - x_5) + \beta(b^* x_1 - x_5) = \lambda x_5, \tag{3.13}$$

$$- dx_6 + D(x_5 - x_6) + \beta(b^* x_2 - x_6) = \lambda x_6, \tag{3.14}$$

where $b^* = b'(m_1^*)$.

Considering the differences of $(3.9) - (3.10)$, $(3.11) - (3.12)$ and $(3.13) - (3.14)$, we obtain

$$x_3 - x_4 = (\lambda + 2D + d)(x_1 - x_2), \tag{3.15}$$

$$\beta(x_5 - x_6) = (\lambda + 2D + d + \beta)(x_3 - x_4), \tag{3.16}$$

$$\beta b^*(x_1 - x_2) = (\lambda + 2D + d + \beta)(x_5 - x_6). \tag{3.17}$$

With a simple substitution, we have

$$(\lambda + 2D + d + \beta)^2(\lambda + 2D + d) = \beta^2 b^* \tag{3.18}$$

provided that $(x_1 - x_2)^2 + (x_3 - x_4)^2 + (x_5 - x_6)^2 \neq 0$.

Similarly, by considering the additions of $(3.9)+(3.10)$, $(3.11)+(3.12)$ and $(3.13)+(3.14)$, we obtain

$$x_3 + x_4 = (\lambda + d)(x_1 + x_2), \tag{3.19}$$

$$\beta(x_5 + x_6) = (\lambda + d + \beta)(x_3 + x_4), \tag{3.20}$$

$$\beta b^*(x_1 + x_2) = (\lambda + d + \beta)(x_5 + x_6). \tag{3.21}$$

This leads to

$$(\lambda + d + \beta)^2(\lambda + d) = \beta^2 b^* \tag{3.22}$$

provided that $(x_1 + x_2)^2 + (x_3 + x_4)^2 + (x_5 + x_6)^2 \neq 0$.

Thus, we can now state the following result about homogeneous equilibria:

Theorem 3.1. *Let* $\vec{m}^* = (m_1^*, m_2^*, m_1^{*(2)}, m_2^{*(2)}, m_1^{*(3)}, m_2^{*(3)})^T$ *be an equilibrium of* (2.14) *–*(2.16) *with* $n = 2$, $D_{12} = D_{21} = D > 0$. *Then*

(i) $\vec{m}^*$ *is homogeneous, if and only if* m_1^*, $m_1^{*(2)}$, *and* $m_1^{*(3)}$ *are given by* (3.7);
(ii) *If* $\vec{m}^*$ *is homogeneous and set* $b^* = b'(m_1^*)$, *then*

(a) λ *is an eigenvalue of the linearization of* $\vec{m}^*$, *if and only if* λ *satisfies either* (3.18) *or* (3.22);
(b) *If* λ *satisfies* (3.18) *but not* (3.22), *then the associated eigenvectors are heterogeneous and are constant multipliers of* $\vec{V}_d = (1, -1, \lambda + 2D + d, -(\lambda + 2D + d), \beta b^*(\lambda + 2D + d + \beta), -\beta b^*(\lambda + 2D + d + \beta))^T$; *if* λ *satisfies* (3.22) *but not* (3.18), *then the associated eigenvectors are homogeneous and are constant multipliers of* $\vec{V}_d = (1, 1, \lambda + d, \lambda + d, (\lambda + d + \beta)(\lambda + d)\beta^{-1}, -(\lambda + d + \beta)(\lambda + d)\beta^{-1})^T$;
(c) *Under the generic condition,* $(d + \beta)^2 d \neq \beta^2 b^*$, $\vec{m}^*$ *is asymptotically stable, if and only if* $(d + \beta)^2 d > \beta^2 b^*$.

Proof. (i) and (ii) (a), (b) have been verified above and (ii) (c) is a direct application of the Routh–Hurwitz Criteria. The Routh–Hurwitz Criteria states that all roots of a real polynomial $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ have negative real parts if and only if $a_1 > 0$, $a_3 > 0$ and $a_1a_2 > a_3$. On the other hand, (3.18) and (3.22) can be rewritten as

$$\lambda^3 + (3d^* + 2\beta)\lambda^2 + [(d^* + \beta)^2 + 2d^*(d^* + \beta)]\lambda + (d^* + \beta)^2 d^* - \beta^2 b^* = 0,$$

where $d^* = d$ for (3.22) and $d^* = d + 2D$ for (3.18). In this case, $a_1 = 3d^* + 2\beta > 0$, $a_1a_2 = (3d^* + 2\beta)(d^* + \beta)(3d^* + \beta) > (d^* + \beta)^2 d^* > a_3$. Therefore, the roots will have negative real parts if and only if $a_3 = (d^* + \beta)^2 d^* - \beta^2 b^* > 0$. Note that $(d + \beta)^2 d - \beta^2 b^* > 0$ implies $(d + 2D + \beta)^2(d + 2D) - \beta^2 b^* > 0$ and (ii) (c) follows.

As a final remark of this section, which serves as a motivation for the numerical simulation in the next section, we emphasize that a stable heterogeneous equilibrium cannot occur through the mechanism of pitchfolk bifurcation. To see this, we note that in order for a pitchfolk bifurcation of spatially heterogeneous equilibrium to occur, $\lambda = 0$ must be a zero of (3.18) for a certain value of D. However, if (3.22) holds for some $D > 0$ then $\beta^2 b^* > d(d + \beta)^2$ from which and Theorem 3.1 we conclude that $\vec{m}^*$ must be unstable even under spatially homogeneous perturbation. Therefore, even if a pitchfolk bifurcation of spatially heterogeneous equilibria may occur, these equilibria must be unstable. In summary, to obtain stable spatially heterogeneous equilibria, we must have a non-trivial birth function and the occurrence of heterogeneous equilibria can only take place though a non-pitchfolk bifurcation mechanism.

We conclude this section with several numerical simulation using a birth function $b_1(a) = ca^2 \exp(-ka)$. This function increases monotonically before reaching the peak, then decays almost exponentially to zero. Depending on the values of c and k, this birth function may intersect with the right-hand side of (3.8) $g(a) = d(d + \beta)^2 a/\beta^2$ once, twice, or three times, which corresponds to the cases of having one, two, and three homogeneous equilibria. In the following computations, we set $d = 0.1$, $\beta = 1/30$, $D = 1/300$, $k = 0.85$ and $c = 16$. These values are chosen so that three homogeneous equilibria exist, which can be computed numerically using (3.8) as $m_1 = m_2 = 0, 0.10978$, and 4.47076. In Fig. 1a, this birth function is plotted with $g(a) = d(d + \beta)^2 a/\beta^2$. Obviously, this birth function intersects with $g(a)$ at $a = 0$. From the figure, it is also clear that the function $b_1(a)$ intersects with $g(a)$ at $a \approx 4.5$.

We now solve the system of six equations (2.14)–(2.16) using Matlab and a built-in ODE solver `ode23` [1] for $0 \leqslant t \leqslant 2000$. Several different initial population distributions for the two patches are used, ranging from 0.001 to 10. Note that the total population is non-dimensionalized so that only the relative sizes of the two patches are of significance. The migration rate is set to be $D = 1/300$. In all the cases, the asymptotic steady state has been reached at $t = 2000$. Fig. 1b show the phase plots of m_1 and m_2 with squares indicating the initial states and circles for the final states. The numerical

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[1] Matlab built-in solver `ode23` uses the Runge–Kutta method of order 2 or 3. There is no particular reason for choosing this solver over others, such as `ode45`, Runge–Kutta method of order 4 or 5, or `ode15s`, a linear multi-step integrator. We have experimented with all the methods, but the results are not affected by the choice of methods.
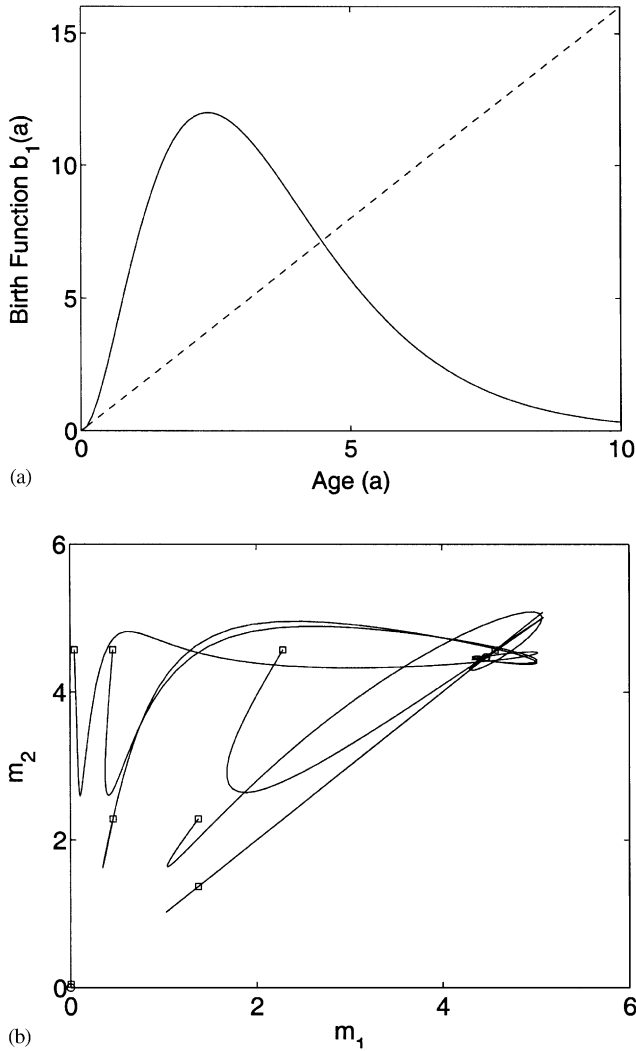
Fig. 1. Simulation of the two-patch population dynamics. (a). Birth function $b_1(a) = 16a^2 \exp(-0.85a)$ (solid-line) and $y = d(d+\beta)^2 a/\beta^2$ (broken-line); (b). Phase plots of m_1 and m_2 with initial total populations for the two patches varying from 0.001 to 10. The initial stages ($t = 0$) are indicated by the squares and the final stage ($t = 2000$) are denoted by the circles.

simulations indicate that there are two asymptotically stable equilibria: $m_1^* = m_2^* = 0$ and $m_1^* = m_2^* = 4.47076$.

It is straightforward to verify that the eigenvalues of the linearized system, given by (3.18) and (3.22), are $-d$, $-(d+2D)$, $-(d+\beta)$, and $-(d+2D+\beta)$ for $m_1^*=m_2^*=0$. The last two are repeated roots and all of the eigenvalues are negative, which indicates that this equilibrium is asymptotically stable. For the other two homogeneous equilibria, we

can compute the eigenvalues numerically and they are $\lambda = -0.204 \pm i0.129$, $-0.198 \pm i0.129$, 0.0222 and 0.0289 for $m_1^* = m_2^* = 0.10978$; and $\lambda = -0.0548 \pm i0.127$, $-0.0481 \pm i0.127$, -0.277 and -0.0548 for $m_1^* = m_2^* = 4.47076$. Clearly, the first equilibrium is unstable while the second one is asymptotically stable. This explains why the first equilibrium was not observed by the simulation. □

Finally, we remark that it is easy to observe that heterogeneous does not occur for this case. The questions that remain, then, are whether an example of a heterogeneous equilibrium can be observed for a different birth function, and whether there are any other ways by which such a desynchronization/aggregation phenomena may be realized.

4. Heterogeneous equilibria

We first present numerical simulations where stable heterogeneous and homogeneous equilibria co-exist. The first computation is similar to the one in the previous section, using the same birth function $b_1(a)$ with $c = 4$ while the values of the other parameters remain unchanged. The results are plotted in Fig. 2. It can be seen from Fig. 2a that there exist three homogeneous equilibria. However, only two of them are stable, cf. Fig. 2b. Furthermore, there appear to be a pair of heterogeneous equilibria, indicated by the phase plots of m_1 and m_2 in Fig. 2b. Note the problem is symmetric and only the results of $m_2(0) \geqslant m_1(0)$ are presented.

Similar to our discussion in the previous discussion, the values of the homogeneous equilibria, computed using (3.8), are $m_1^* = m_2^* = 0$, 0.76905, 1.70730. The eigenvalues of these equilibria can be computed using (3.18) and (3.22). All the eigenvalues have negative real parts except for $m_1^* = m_2^* = 0.76905$, which explains why this equilibrium was not observed by the simulation.

To compute the heterogeneous equilibria, the following equations can be derived from (3.1) to (3.6):

$$b(m_1) + b(m_2) = \frac{d(d + \beta)^2}{\beta^2} (m_1 + m_2), \tag{4.1}$$

$$b(m_1) - b(m_2) = \frac{(d + 2D)(d + 2D + \beta)^2}{\beta^2} (m_1 - m_2). \tag{4.2}$$

Obviously (3.7) is a special case of (4.1) and (4.2) with $m_1 = m_2$. Since the system is nonlinear, one normally seeks the solutions numerically. We will not attempt to find all the solutions here. Instead, we verify that $(m_1^*, m_2^*) = (0.14834, 1.2283)$, which is the heterogeneous equilibrium observed by the simulation, satisfies (4.1) and (4.2). We also note that it is not the only heterogeneous solution. For example, $(m_1^*, m_2^*) = (0.53400, 1.4568)$ is also a solution.[2]

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[2] The solutions are obtained using `fsolve` in Maple, which solves the system of nonlinear equations numerically. The user has the option to set the range where a particular solution belongs to. This solution was obtained when the default range is used.
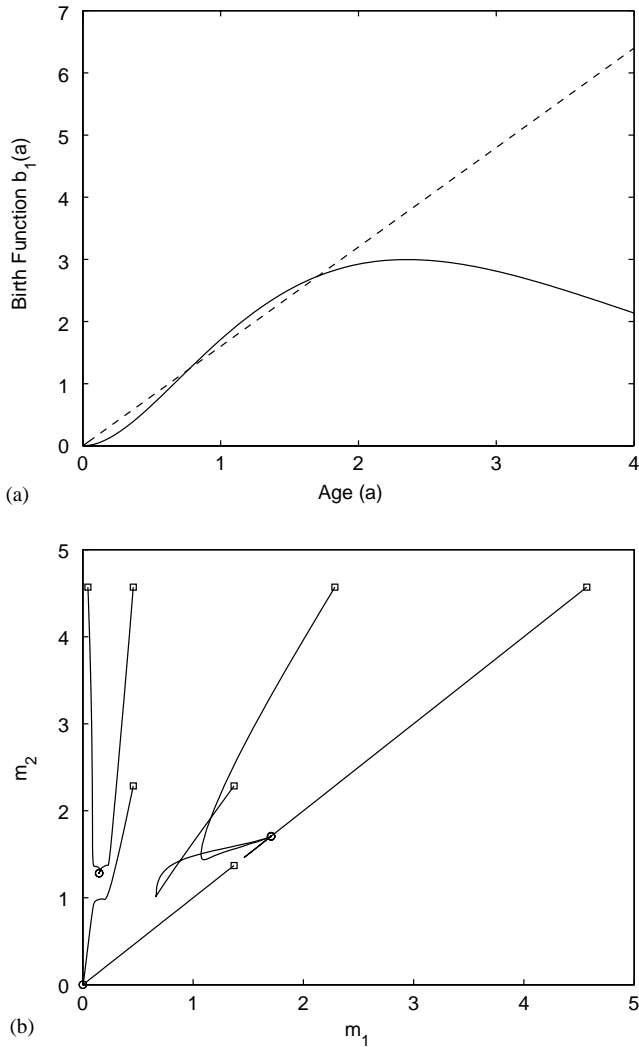
Fig. 2. Simulation of the two-patch population dynamics. (a). Birth function $b_1(a) = 4a^2 \exp(-0.85a)$ (solid-line) and $y = d(d + \beta)^2 a/\beta^2$ (broken-line); (b). Phase plots of m_1 and m_2 with initial total populations for the two patches varying from 0.1 to 10. The initial stages ($t = 0$) are indicated by the squares and the final stage ($t = 2000$) are denoted by the circles.

Next, we note that the linear stability of the heterogeneous equilibria $\vec{m}^*$ is determined by λ, which satisfies the following equations:

$$-dx_1 + D(x_2 - x_1) + x_3 = \lambda x_1, \tag{4.3}$$

$$-dx_2 + D(x_1 - x_2) + x_4 = \lambda x_2, \tag{4.4}$$

$$-dx_3 + D(x_4 - x_3) + \beta(x_5 - x_3) = \lambda x_3, \tag{4.5}$$

$$-dx_4 + D(x_3 - x_4) + \beta(x_6 - x_4) = \lambda x_4, \tag{4.6}$$

$$-dx_5 + D(x_6 - x_5) + \beta(b_1^* x_1 - x_5) = \lambda x_5, \tag{4.7}$$

$$-dx_6 + D(x_5 - x_6) + \beta(b_2^* x_2 - x_6) = \lambda x_6, \tag{4.8}$$

where $b_1^* = b'(m_1^*)$ and $b_2^* = b'(m_2^*)$. This leads to

$$[b_1^* - P_1(\lambda)][b_2^* - P_2(\lambda)] + [b_1^* - P_2(\lambda)][b_2^* - P_1(\lambda)] = 0, \tag{4.9}$$

where

$$P_1(\lambda) = \frac{1}{\beta^2}(\lambda + d + 2D)(\lambda + d + \beta + 2D)^2,$$

$$P_2(\lambda) = \frac{1}{\beta^2}(\lambda + d)(\lambda + d + \beta)^2.$$

We note that (3.18) and (3.22) are special cases of (4.9) when $b_1^* = b_2^*$.

Using (4.9), we can compute all six eigenvalues of the heterogeneous equilibrium $m_1^* = 0.14834$ and $m_2^* = 1.28295$. The values given by Maple are $\lambda = -0.18661 \pm \text{i}0.10282$, $-0.17730 \pm \text{i}0.088699$, -0.022016, -0.0034974. Clearly, the real parts of all the eigenvalues are negative. Thus, this heterogeneous equilibrium is asymptotically stable. The eigenvalues of the heterogeneous equilibrium $m_1^* = 0.53400$ and $m_2^* = 1.4568$ can be computed similarly as $\lambda = -0.19263 \pm \text{i}0.11357$, $-0.18217 \pm \text{i}0.097167$, -0.012292, 0.0085669. This equilibrium is unstable due to the existence of a positive real eigenvalue, which explains why it is not observed in the simulation.

Our second example is based on a more complicated birth function $b_2(a) = ca[(a - a_0)(a - a_1)(a - a_2) + a_3]\exp(-kx)$. Compared to the first birth function, this new function has more features. For example, $b_2(a)$ can intersect with $g(a)$ four times. Thus, there may exist four homogeneous equilibria, depending on the values of the parameters c and a_i.

The results of several simulations are presented in Fig. 3. The death rate d, migration rate D and delay parameter β are set to be the same as in the first example. The birth function $b_2(a)$ with $c = 2$, $a_0 = 0.1$, $a_1 = 0.5$, and $a_2 = a_3 = 1$ is plotted in Fig. 3a. Four homogeneous equilibria exist and their values are $m_1^* = m_2^* = 0$, 0.29521, 2.1743, 6.6572, obtained using (3.8). The number of heterogeneous equilibria is unknown and they can be obtained by solving (4.1) and (4.2) numerically. In Fig. 3b, the phase plots of m_1 and m_2 are presented for several initial populations of the two patches. It is easily observed that both stable homogeneous and heterogeneous equilibria exist, and the initial condition determines to which equilibrium a solution approaches. Note that the stability of the equilibria (both homogeneous and heterogeneous) can be determined by calculating the eigenvalues using (4.9). For homogeneous equilibria, all the eigenvalues have negative real parts except for $m_1^* = m_2^* = 2.1743$, which is not observed by the simulation. For heterogeneous equilibria, the eigenvalues for $m_1^* = 0.58525$ and $m_2^* = 2.2675$ are $\lambda = -0.20983 \pm \text{i}0.14443$, $-0.16633 \pm \text{i}0.068281$, -0.044012, 0.043004. Since the last eigenvalue has positive real part, this equilibrium is unstable and not observable by simulation. On the other hand, the eigenvalues for $m_1^* = 1.0188$ and $m_2^* = 6.4542$ are, $\lambda = -0.16864 \pm \text{i}0.072182$, $-0.058796 \pm \text{i}0.11382$, -0.039392, -0.25908. Clearly,
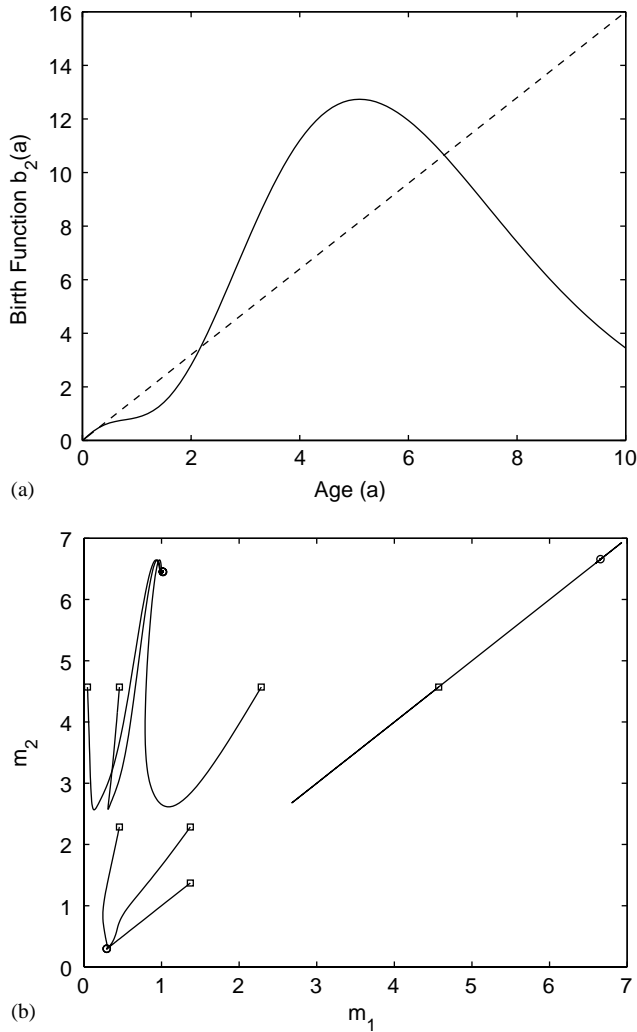
Fig. 3. Simulation of the two-patch population dynamics. (a). Birth function $b_2(a) = 2a[(a - 0.1)(a - 0.5)(a - 1) + 1]\exp(-0.85a)$ (solid-line) and $y = d(d + \beta)^2 a/\beta^2$ (broken-line); (b). Phase plots of m_1 and m_2 with initial total populations for the two patches varying from 0.1 to 10. The initial stages ($t = 0$) are indicated by the squares and the final stage ($t = 2000$) are denoted by the circles.

all the eigenvalues have negative real parts. Therefore, it is asymptotically stable and is observable by simulation.

Our final set of simulations is presented in Fig. 4. The main purpose is to explore the dynamic interaction of the death rate d, migration rate D, and delay rate β. Using birth function $b_2(a)$ with the same set of parameters, we compute the time history of mature populations of the two patches by changing β and D with all the other parameters
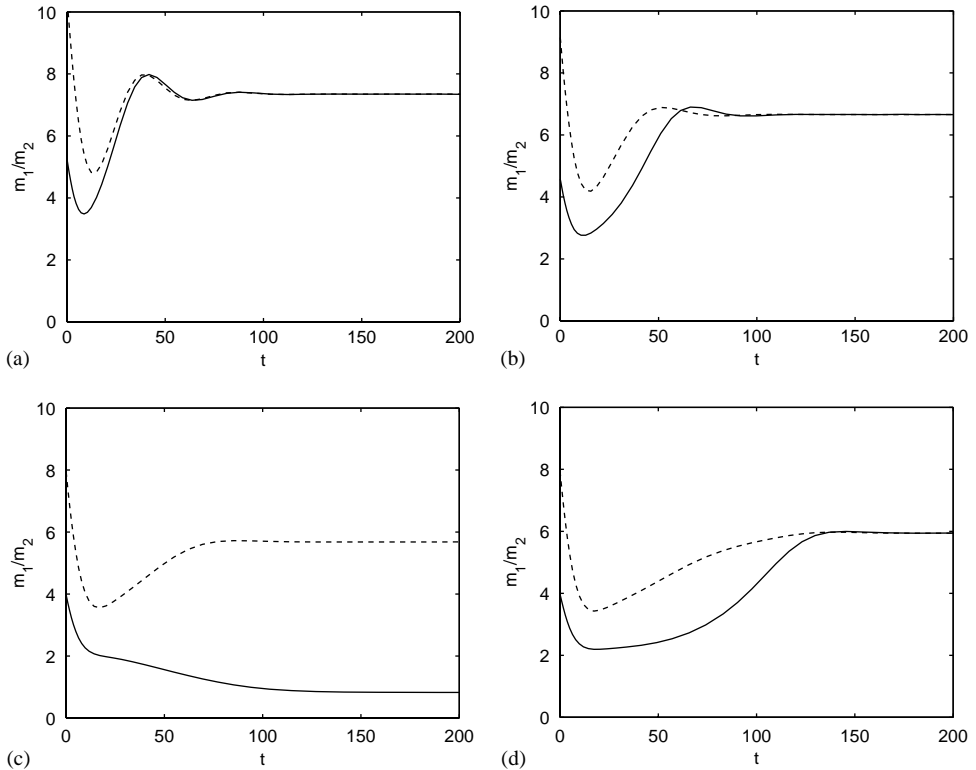
Fig. 4. Time history of mature populations m_1 (solid-lines) and m_2 (broken-lines), using birth function $b_2(a)$ with $d = 0.1$ and $m_2 = 2m_1$ initially: (a). $\beta = 1/25$ and $D = 1/300$; (b). $\beta = 1/30$ and $D = 1/300$; (c). $\beta = 1/35$ and $D = 1/300$; (d). $\beta = 1/35$ and $D = 1/100$.

unchanged. The effect of the delay rate and migration rate on the final (asymptotic) steady states is clear.

5. Conclusion

In this paper we have shown that a new mechanism exists for individual aggregation of population in a two-patch system. Using linear stability analysis and numerical simulation, we have shown that stable heterogeneous equilibria may exist through non-linear dynamic interaction of birth, death, maturation delay and spatial migration. Same principle should apply to an ecosystem consisting of a large number of patches and work is currently under way to generalize the results to multi-patch systems.

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