

COMPARISON BETWEEN STOCHASTIC AND DETERMINISTIC SELECTION-MUTATION MODELS

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ABSTRACT. We present a deterministic selection-mutation model with a discrete trait variable. We show that for an irreducible selection-mutation matrix in the birth term the deterministic model has a unique interior equilibrium which is globally stable. Thus all subpopulations coexist. In the pure selection case, the outcome is known to be that of competitive exclusion, where the subpopulation with the largest growth-to-mortality ratio will survive and the remaining subpopulations will go extinct. We show that if the selection-mutation matrix is reducible, then competitive exclusion or coexistence are possible outcomes. We then develop a stochastic population model based on the deterministic one. We show numerically that the mean behavior of the stochastic model in general agrees with the deterministic one. However, unlike the deterministic one, if the differences in the growth-to-mortality ratios are small in the pure selection case, it cannot be determined a priori which subpopulation will have the highest probability of surviving and winning the competition.

1. Introduction. Deterministic selection-mutation models, also referred to as distributed rate population models with closed-open reproduction, have been studied by many researchers [1, 2, 3, 4, 9, 11, 12, 22]. These are models for the density of individuals with respect to some evolutionary discrete or continuous trait. In [4], a pure selection model (closed reproduction) with logistic type nonlinearity and a continuous 2-dimensional trait variable (growth and mortality) was studied. Therein, the authors proved that competitive exclusion occurs and the surviving subpopulation is the one with the largest growth-to-mortality ratio. In [3], these results were extended to a more general population model constructed on the (natural) space of measures. In this case, the limiting measure (a Dirac delta measure) is an element of the state space. In [1, 2], a nonlinear size-structured population model with a discrete trait variable (a finite number of subpopulations each having its own growth, mortality, and reproduction functions) was studied. It was shown that in the case of closed reproduction, competitive exclusion occurs and the winning subpopulation is the one with the highest ratio of reproduction to mortality. In the

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case of open reproduction, the authors showed that survival of all subpopulations is possible.

In [10] a simple population model with two groups of age (juveniles and adults) for the mean age at maturity was studied. The authors showed the existence and uniqueness of a globally attractive stationary solution. This simple model was then used in [11] to build a system of equations for the density of individuals with respect to age at maturity. In this model, there are two birth terms one for selection (closed reproduction) with a probability (in the form of a coefficient) $1 - \epsilon$ and another for pure mutation (open reproduction) with a probability ϵ . Therein, the authors proved the existence of L^1 stationary solutions, which tend to concentrate around the evolutionary stable value of the trait when the open reproduction term coefficient $\epsilon \rightarrow 0$. In [12] a pure mutation model was considered. The authors proved the existence of stationary solutions, and they investigated the behavior of these stationary solutions when the mutation is small.

It is well known that the deterministic and stochastic models may behave differently. Hence, the goal of this paper is to present a deterministic selection-mutation model, formulate a stochastic differential equation model based on it, and then compare the dynamics of these two models. The derivation of the stochastic differential equation model is based on the method developed in [6, 7, 18], where the variability inherent in the system is due only to demographic variability.

This paper is organized as follows: in Section 2 we present a selection-mutation model with a two-dimensional discrete trait variable. We recall that in the case of a pure selection birth term, competitive exclusion between the different traits occurs and the winner trait is the one with highest growth-to-mortality ratio. In Section 3 we establish stability results for the model when the selection-mutation matrix is either reducible or irreducible. In Section 4 we develop an Itô stochastic differential equation model which is based on the deterministic model. In Section 5 we consider two numerical examples, one for a pure selection case and another for a selection-mutation case. We show that in both cases the stochastic model behaves like the deterministic model. However, the main difference is that in the pure selection case, if the ratio of growth to mortality of the first subpopulation is not much larger than the other subpopulations, then unlike the deterministic model the subpopulation with the larger ratio may go extinct. Section 6 is devoted to concluding remarks.

2. Deterministic model. The selection-mutation deterministic model that we consider is given as follows:

$$\begin{aligned} \dot{x}_i &= a_i \sum_{j=1}^n p_{ij} x_j - b_i x_i \sum_{j=1}^n x_j, & i = 1, 2, \dots, n \\ x_i(0) &= x_i^0, & i = 1, 2, \dots, n. \end{aligned} \quad (1)$$

Here the total population $\mathbb{X} = \sum_{j=1}^n x_j$, and the i th subpopulation is identified by the two-dimensional discrete trait $(a_i, b_i) \in \mathbb{R}_+^2$, where a_i is a scaled per-capita growth rate and b_i is a scaled per-capita mortality rate. The parameter p_{ij} denotes the fraction of offspring of an individual in the j th subpopulation which belongs to the i th subpopulation, $0 \leq p_{ij} \leq 1$ and $\sum_{i=1}^n p_{ij} = 1$. For convenience, we will denote

by $P = (p_{ij})_{n,n}$ the selection-mutation matrix whose (i, j) entry is given by p_{ij} . Clearly P is a column stochastic matrix since each of the column sums of P is equal to one.

REMARK 1. For the special case where P is the identity matrix (i.e., $p_{ii} = 1$ and $p_{ij} = 0$ for $i \neq j$), (1) reduces to the following pure selection model:

$$\begin{aligned} \dot{x}_i &= x_i(a_i - b_i \sum_{j=1}^n x_j), & i &= 1, 2, \dots, n \\ x_i(0) &= x_i^0, & i &= 1, 2, \dots, n. \end{aligned} \quad (2)$$

Here the quotient $\frac{a_i}{b_i}$ can be thought of as a scaled reproductive ratio; i.e., it is a measure of the average amount of offspring an individual of trait (a_i, b_i) produces during its lifetime. The actual reproductive ratio at population density \mathbb{X} is given by $\frac{a_i}{b_i \mathbb{X}}$. It is well known that if $a_1/b_1 > a_i/b_i$ for $i = 2, \dots, n$, then solutions to (2) satisfy $x_i(t) \rightarrow 0$ for $i = 2, \dots, n$ and $x_1(t) \rightarrow a_1/b_1$ as $t \rightarrow \infty$. That is, competitive exclusion occurs and the surviving subpopulation is the one with the highest growth-to-mortality ratio a_1/b_1 . In fact, this is true for a more general selection model which includes this one as a special case [3].

For easy exposition, we will use the following notations throughout the paper. Let $B = \text{diag}(b_1, b_2, \dots, b_n)$ (i.e., the diagonal matrix with b_1, b_2, \dots, b_n as its main diagonal entries), and $A = \text{diag}(a_1, a_2, \dots, a_n)$. Let $e = [1, 1, \dots, 1]^T \in \mathbb{R}^n$; then the system of (1) can be written in the following vector form:

$$\begin{aligned} \dot{x} &= APx - (e^T x)Bx, \\ x(0) &= x^0, \end{aligned} \quad (3)$$

where $x = [x_1, x_2, \dots, x_n]^T$ and $x^0 = [x_1^0, x_2^0, \dots, x_n^0]^T$.

To establish stability results for the selection-mutation model presented in (3), we first recall the following two definitions and theorem concerning nonnegative matrices (e.g., see [5, 8, 13, 14, 15, 24]).

DEFINITION 2.1. A square nonnegative matrix H is called reducible if there is a permutation matrix Q for which QHQ^T has the form

$$QHQ^T = \begin{bmatrix} H_{11} & H_{12} \\ 0 & H_{22} \end{bmatrix},$$

where H_{11} and H_{22} are square matrices. A square nonnegative matrix is called irreducible if it is not reducible.

DEFINITION 2.2. A square nonnegative matrix H is called completely reducible if it is the direct sum of square nonnegative irreducible matrices. That is, H is completely reducible if there is a permutation matrix Q such that

$$QHQ^T = \begin{bmatrix} H_1 & 0 & \dots & 0 \\ 0 & H_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & H_m \end{bmatrix},$$

where H_1, \dots, H_m are square nonnegative irreducible matrices.

THEOREM 2.1. (*Perron-Frobenius*). *Let H be a square nonnegative irreducible matrix and $\rho(H)$ be its spectral radius. Then $\rho(H)$ is a positive (algebraically) simple eigenvalue of H , and to this eigenvalue there correspond positive right and left eigenvectors. Moreover, there cannot exist two independent nonnegative right (or left) eigenvectors.*

Next, we recall the following definition and theorem concerning M-matrices (see [21]).

DEFINITION 2.3. *A square matrix G that can be expressed in the form $G = sI - F$, where F is a nonnegative matrix, and $s \geq \rho(F)$ the spectral radius of F , is called an M-matrix.*

THEOREM 2.2. *The following are equivalent:*

- (1) G is a nonsingular M-matrix.
- (2) G is inverse-positive (i.e., G^{-1} is a nonnegative matrix).

3. Stability analysis of deterministic model. In this section, we will establish results concerning the existence and stability of equilibrium solutions of system (3). Our arguments are in the spirit of those used in [5]. Two cases are studied: the case where P is an irreducible matrix, and the case where P is reducible. The case where P is an irreducible matrix can be biologically interpreted as follows: all the subpopulations are connected with each other; i.e., any subpopulation contributes, either directly or indirectly, individuals to all the other subpopulations. Thus, survival of one subpopulation implies survival of all the other subpopulations. Indeed, this is confirmed in Section 3.1. Similarly by Definition 2.1, the biological interpretation of P as a reducible matrix is that the total population (i.e., all the subpopulations) can be separated into (at least) two classes, where each class is composed of several subpopulations. Furthermore, one of the two classes does not contribute individuals to the other class. Thus in this case, if the surviving class is the one that contributes individuals to the other class, then it is possible that the other class also survives. Again this is confirmed in Section 3.3.

3.1. Irreducible case. In this section, stability results will be established for the irreducible case. We first show that there exists a unique positive equilibrium for system (3), and then we show that this unique equilibrium is globally stable provided that the scaled per-capita mortality rates of all the subpopulations are equal.

THEOREM 3.1. *Suppose that P is an irreducible matrix; then there exists a unique positive equilibrium for system (3).*

Proof. Let $y = R^{-1}x$, where $y = [y_1, y_2, \dots, y_n]^T$ and $R = \text{diag} \left(\frac{a_1}{b_1}, \frac{a_2}{b_2}, \dots, \frac{a_n}{b_n} \right)$ be the diagonal matrix with $a_1/b_1, a_2/b_2, \dots, a_n/b_n$ as its main diagonal entries. Then by (3) we have

$$\begin{aligned} R\dot{y} &= APRy - (e^T Ry)BRy \\ Ry(0) &= x^0. \end{aligned}$$

Note that since $BR = A$ and $R^{-1}A = B$, we see that

$$\begin{aligned} \dot{y} &= B[PRy - (r^T y)y], \\ y(0) &= R^{-1}x^0, \end{aligned} \tag{4}$$

where $r = Re$. To show that there exists a unique positive equilibrium for (3), we need to show only that it is true for (4). Note that since $a_i/b_i > 0$ for $i = 1, 2, \dots, n$ and P is a column stochastic irreducible matrix, PR is a nonnegative irreducible matrix. By the Perron-Frobenius Theorem, we know that there exists a unique positive normalized right eigenvector \bar{y} (i.e., $e^T \bar{y} = 1$) corresponding to the spectral radius ρ^y of the matrix PR such that

$$PR\bar{y} = \rho^y \bar{y}. \quad (5)$$

Clearly $e^T \bar{y} = 1$, $e^T P = e^T$ and $e^T R = r^T$. Therefore, we find that

$$\rho^y = \rho^y(e^T \bar{y}) = e^T(\rho^y \bar{y}) = e^T PR\bar{y} = e^T R\bar{y} = r^T \bar{y}.$$

By substituting $\rho^y = r^T \bar{y}$ into (5), we have

$$PR\bar{y} = (r^T \bar{y})\bar{y}. \quad (6)$$

Hence, \bar{y} is an equilibrium of system (4). Suppose that there exists another positive equilibrium \bar{u} for (4), then \bar{u} is a positive (right) eigenvector of PR corresponding to the positive eigenvalue $r^T \bar{u}$. By the Perron-Frobenius Theorem, we have $\rho^y = r^T \bar{u}$. Since P is column stochastic, we get

$$\bar{u}^T e = \frac{(PR\bar{u})^T e}{r^T \bar{u}} = \frac{\bar{u}^T Re}{r^T \bar{u}} = \frac{r^T \bar{u}}{r^T \bar{u}} = 1. \quad (7)$$

This implies that \bar{u} is a positive normalized right eigenvector corresponding to ρ^y . Hence, $\bar{u} = \bar{y}$. Thus, there exists a unique positive equilibrium \bar{y} for the system (4), which implies that $R\bar{y}$ is the unique positive equilibrium for the system (3). \square

Next we show that the interior equilibrium is globally stable under some conditions on the model parameters.

THEOREM 3.2. *Assume that P is an irreducible matrix, and $b_i = \beta$ for $i = 1, 2, \dots, n$, where β is a positive constant. Then the unique positive equilibrium is globally asymptotically stable.*

Proof. Since P is an irreducible matrix, AP is irreducible. Let ρ be the spectral radius of the matrix AP . By the Perron-Frobenius Theorem, ρ is a simple eigenvalue of AP , and there exist a unique positive normalized right eigenvector \bar{x} such that $AP\bar{x} = \rho\bar{x}$ and a unique positive normalized left eigenvector \bar{x}^* such that $(\bar{x}^*)^T AP = \rho(\bar{x}^*)^T$. Let I be the identity matrix. It is known that

$\lim_{t \rightarrow \infty} \exp[(AP - \rho I)t]x^0 = \alpha\bar{x}$, where $\alpha = \frac{(x^0)^T \bar{x}^*}{\bar{x}^T \bar{x}^*} > 0$ (e.g., Theorem A.45 in [24] or [5]). However, for the convenience of the reader, we provide an argument to show this.

Since ρ is a simple eigenvalue of AP , we have $\mathbb{C}^n = \{\bar{x}\} \oplus \mathbb{V}$, where $\{\bar{x}\}$ is the (right) eigenspace corresponding to ρ , and \mathbb{V} is the generalized (right) eigenspace corresponding to all eigenvalues of AP except ρ . Hence, there exists a constant α and a vector $v \in \mathbb{V}$ such that $x^0 = \alpha\bar{x} + v$. It is well known that $v^T \bar{x}^* = 0$ for any $v \in \mathbb{V}$ (e.g., see [20] page 367). Thus, we have $(x^0)^T \bar{x}^* = \alpha\bar{x}^T \bar{x}^*$, which implies

$\alpha = \frac{(x^0)^T \bar{x}^*}{\bar{x}^T \bar{x}^*}$. Since \bar{x} and \bar{x}^* are both positive and x^0 is a nonzero nonnegative vector, we have $\alpha > 0$. Notice that $\exp[(AP - \rho I)t] = \exp(-\rho t)\exp(APt)$. Thus,

$$\begin{aligned} \exp[(AP - \rho I)t]x^0 &= \exp(-\rho t)[\alpha \exp(APt)\bar{x} + \exp(APt)v] \\ &= \exp(-\rho t)[\alpha \exp(\rho t)\bar{x} + \exp(APt)v] \\ &= \alpha\bar{x} + \exp[(AP - \rho I)t]v. \end{aligned}$$

Since V is invariant under AP and the spectrum of $(AP - \rho I)|_V$ lies strictly in the left half plane, it follows that $\lim_{t \rightarrow \infty} \exp[(AP - \rho I)t]v = 0$. Hence, $\lim_{t \rightarrow \infty} \exp[(AP - \rho I)t]x^0 = \alpha \bar{x}$.

Substituting $x(t) = g(t) \exp[(AP - \rho I)t]x^0$ into (3) with g being a scalar function of t , we find that

$$\begin{aligned} \dot{g} &= g[\rho - \beta(e^T \exp[(AP - \rho I)t]x^0)g] \\ g(0) &= 1. \end{aligned} \quad (8)$$

Hence, the limiting equation of (8) is given by the following logistic model,

$$\begin{aligned} \dot{g}_\infty &= g_\infty[\rho - \beta \alpha g_\infty] \\ g_\infty(0) &= 1, \end{aligned}$$

which has a unique positive equilibrium $\bar{g}_\infty = \frac{\rho}{\beta \alpha}$ and it is globally asymptotically stable. Furthermore, it is easy to see from (8) that g is bounded. Therefore, it follows from the theory on asymptotically autonomous systems that $\lim_{t \rightarrow \infty} g(t) = \bar{g}_\infty$ (e.g., [23]), which implies the theorem. \square

REMARK 2. *By a similar process, we can show that Theorem 3.2 still holds for the more general system $\dot{x} = APx - \beta f(e^T x)x$, where f is a Lipschitz continuous strictly increasing function with $f(0) = 0$ and $\lim_{q \rightarrow \infty} f(q) = \infty$.*

3.2. Completely reducible case. In this section, we establish stability results for the case P being a completely reducible matrix. By Definition 2.2, there exists a permutation matrix Q such that

$$QPQ^T = \begin{bmatrix} P_1 & 0 & \dots & 0 \\ 0 & P_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & P_m \end{bmatrix},$$

where $P_i \in \mathbb{R}^{n_i \times n_i}$ is an irreducible matrix, $i = 1, 2, \dots, m$, and $\sum_{i=1}^m n_i = n$. Hence,

in this case we have m population classes (each class is composed of n_i subpopulations) which are totally disconnected from each other. Since P is column-stochastic, then P_i is column-stochastic, $i = 1, 2, \dots, m$. Let $z = Qx$; then z satisfies the following differential equation:

$$\begin{aligned} \dot{z} &= QAPx - (e^T x)QBx \\ z(0) &= Qx^0. \end{aligned} \quad (9)$$

Let $\mathcal{A} = QAQ^T$ and $\mathcal{P} = QPQ^T$. Notice that $Q^T Q = I$ and $e^T x = e^T Qx$. Thus, equation (9) can be rewritten as follows:

$$\begin{aligned} \dot{z} &= \mathcal{A}Pz - (e^T z)QBQ^T z \\ z(0) &= Qx^0. \end{aligned} \quad (10)$$

Since A is a diagonal matrix, \mathcal{A} is also a diagonal matrix. We rewrite \mathcal{A} in the same block form as the matrix \mathcal{P} ; i.e.,

$$\mathcal{A} = \begin{bmatrix} A_1 & 0 & \dots & 0 \\ 0 & A_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & A_m \end{bmatrix},$$

where $A_i \in \mathbb{R}^{n_i \times n_i}$, $i = 1, 2, \dots, m$. Since P_i is irreducible and A_i is a diagonal matrix whose diagonal entries are positive, $A_i P_i$ is a nonnegative irreducible matrix, $i = 1, 2, \dots, m$. Let ρ_i be the spectral radius of the matrix $A_i P_i$, $i = 1, 2, \dots, m$. By the Perron-Frobenius Theorem, ρ_i is a simple eigenvalue of $A_i P_i$, and there exist a unique positive normalized right eigenvector $\bar{h}_i \in \mathbb{R}^{n_i}$ such that $A_i P_i \bar{h}_i = \rho_i \bar{h}_i$ and a unique positive normalized left eigenvector $\bar{h}_i^* \in \mathbb{R}^{n_i}$ such that $(\bar{h}_i^*)^T A_i P_i = \rho_i (\bar{h}_i^*)^T$, $i = 1, 2, \dots, m$. Let $\bar{z}_i \in \mathbb{R}^n$, $i = 1, 2, \dots, m$, be defined by

$$\bar{z}_1 = \begin{bmatrix} \bar{h}_1 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \bar{z}_2 = \begin{bmatrix} 0 \\ \bar{h}_2 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \bar{z}_3 = \begin{bmatrix} 0 \\ 0 \\ \bar{h}_3 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \dots, \bar{z}_m = \begin{bmatrix} 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ \bar{h}_m \end{bmatrix}, \quad (11)$$

and $\bar{z}_i^* \in \mathbb{R}^n$, $i = 1, 2, \dots, m$, be defined by

$$\bar{z}_1^* = \begin{bmatrix} \bar{h}_1^* \\ 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \bar{z}_2^* = \begin{bmatrix} 0 \\ \bar{h}_2^* \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \bar{z}_3^* = \begin{bmatrix} 0 \\ 0 \\ \bar{h}_3^* \\ \vdots \\ 0 \\ 0 \end{bmatrix}, \dots, \bar{z}_m^* = \begin{bmatrix} 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ \bar{h}_m^* \end{bmatrix}. \quad (12)$$

Then we have $\mathcal{A}\mathcal{P}\bar{z}_i = \rho_i \bar{z}_i$, and $(\bar{z}_i^*)^T \mathcal{A}\mathcal{P} = \rho_i (\bar{z}_i^*)^T$, $i = 1, 2, \dots, m$.

To establish stability results for (10), we assume that $x(0)$ is positive (which implies $z(0)$ is positive) and that $b_i = \beta$, $i = 1, 2, \dots, n$, where β is a positive constant. Let $z(t) = g(t) \exp[(\mathcal{A}\mathcal{P} - \rho_l I)t]z(0)$, where $\rho_l = \max_{i=1,2,\dots,m} \rho_i$. If $\rho_l > \rho_i$, $i = 1, 2, \dots, l-1, l+1, \dots, m$, then ρ_l is a simple eigenvalue of $\mathcal{A}\mathcal{P}$, \bar{z}_l is the unique normalized nonnegative (right) eigenvector of $\mathcal{A}\mathcal{P}$ that corresponds to ρ_l , and \bar{z}_l^* is the unique normalized nonnegative (left) eigenvector of $\mathcal{A}\mathcal{P}$ that corresponds to ρ_l . Using an argument similar to that in the proof of Theorem 3.2, it follows that there exists a positive constant $\alpha_l = \frac{z(0)^T \bar{z}_l^*}{\bar{z}_l^T \bar{z}_l^*}$ such that

$$\lim_{t \rightarrow \infty} \exp[(\mathcal{A}\mathcal{P} - \rho_l I)t]z(0) = \alpha_l \bar{z}_l, \text{ and } \lim_{t \rightarrow \infty} g(t) = \frac{\rho_l}{\beta \alpha_l}.$$

This implies that

$$\lim_{t \rightarrow \infty} z(t) = \frac{\rho_l}{\beta} \bar{z}_l.$$

Hence, under this case we have a nonnegative equilibrium (independent of the initial condition $z(0)$) which is globally stable.

If ρ_l is not unique, then there exist indices $i_j \in \{1, 2, \dots, l-1, l+1, \dots, m\}$ such that $\rho_{i_j} = \rho_l$, $j = 1, 2, \dots, k$, where k is a positive integer ($1 \leq k \leq m-1$). For easy exposition, we use i_{k+1} to denote l . By (11), we know that \bar{z}_{i_j} , $j = 1, 2, \dots, k+1$ are the disjoint (right) eigenvectors of \mathcal{AP} corresponding to ρ_l , $\bar{z}_{i_j}^*$, $j = 1, 2, \dots, k+1$ are the disjoint (left) eigenvectors of \mathcal{AP} corresponding to ρ_l , and $\bar{z}_{i_\iota}^T \bar{z}_{i_\tau}^* = 0$ if $\iota \neq \tau$ while $\bar{z}_{i_\iota}^T \bar{z}_{i_\iota}^* > 0$. Using an argument similar to that of proof of Theorem 3.2, we can show that there exist positive constants $\alpha_j = \frac{z(0)^T \bar{z}_{i_j}^*}{\bar{z}_{i_j}^T \bar{z}_{i_j}^*}$, $j = 1, 2, \dots, k+1$, such that

$$\lim_{t \rightarrow \infty} \exp[(\mathcal{AP} - \rho_l I)t]z(0) = \sum_{j=1}^{k+1} \alpha_j \bar{z}_{i_j},$$

and

$$\lim_{t \rightarrow \infty} g(t) = \frac{\rho_l}{\beta(\sum_{j=1}^{k+1} \alpha_j)}.$$

This implies that

$$\lim_{t \rightarrow \infty} z(t) = \frac{\rho_l}{\beta(\sum_{j=1}^{k+1} \alpha_j)} \sum_{j=1}^{k+1} \alpha_j \bar{z}_{i_j},$$

which indicates that the nonnegative equilibrium obtained here depends on the initial condition $z(0)$. Hence, in this case the nonnegative equilibrium is not stable.

We summarize the above discussion in the following theorem:

THEOREM 3.3. *Assume that x^0 is positive, P is completely reducible, and $b_i = \beta$ for $i = 1, 2, \dots, n$, where β is a positive constant.*

- (1) *If $\rho_l > \rho_i$, $i = 1, 2, \dots, l-1, l+1, \dots, m$, then we have*

$$\lim_{t \rightarrow \infty} x(t) = \frac{\rho_l}{\beta} Q^T \bar{z}_l.$$

- (2) *If there exist indices $i_j \in \{1, 2, \dots, l-1, l+1, \dots, m\}$ such that $\rho_{i_j} = \rho_l$, $j = 1, 2, \dots, k$ ($1 \leq k \leq m-1$), then we have*

$$\lim_{t \rightarrow \infty} x(t) = \frac{\rho_l}{\beta(\sum_{j=1}^{k+1} \alpha_j)} \sum_{j=1}^{k+1} \alpha_j Q^T \bar{z}_{i_j},$$

where $l = i_{k+1}$, and α_j , $j = 1, 2, \dots, k+1$, depends on the initial condition x^0 .

REMARK 3. *From case (1) in Theorem 3.3, we see that each subpopulation in class l survives but the subpopulations in all the other classes become extinct. This is competitive exclusion, and the surviving population class is the one with the largest spectral radius. If $\rho_1 = \rho_2 = \dots = \rho_m$, then from case (2) in Theorem 3.3 there exist positive constants α_j , $j = 1, 2, \dots, m$ such that*

$$\lim_{t \rightarrow \infty} x(t) = \frac{\rho_l}{\beta(\sum_{j=1}^m \alpha_j)} \sum_{j=1}^m \alpha_j Q^T \bar{z}_j.$$

Using (11), we see that $\lim_{t \rightarrow \infty} x(t)$ is positive. Hence, under this case we have a positive equilibrium but it is not stable.

3.3. Reducible but not completely reducible case. In this section we will consider the following case for P which is reducible but not completely reducible: Suppose that there exists a permutation matrix Q such that

$$QPQ^T = \begin{bmatrix} P_{11} & P_{12} \\ 0 & P_{22} \end{bmatrix}, \quad (13)$$

where $P_{11} \in \mathbb{R}^{n_1 \times n_1}$ and $P_{22} \in \mathbb{R}^{(n-n_1) \times (n-n_1)}$ are irreducible, and $P_{12} \in \mathbb{R}^{n_1 \times (n-n_1)}$ is a non-zero matrix. Thus, for such matrices P , the population is divided into two classes with subpopulations in class 2 able to contribute individuals to class 1, but not vice versa. We refer to class 1 as the *receiver class* and to class 2 as the *donor class*. Let $\mathcal{A} = QAQ^T$, $\mathcal{P} = QPQ^T$ and $z = Qx$, then z satisfies the following equation:

$$\begin{aligned} \dot{z} &= \mathcal{A}Pz - (e^T z)QBQ^T z \\ z(0) &= Qx^0. \end{aligned} \quad (14)$$

Rewriting \mathcal{A} in the same block form as \mathcal{P} , we get

$$\mathcal{A}\mathcal{P} = \begin{bmatrix} A_{11}P_{11} & A_{11}P_{12} \\ 0 & A_{22}P_{22} \end{bmatrix}, \quad \text{where } \mathcal{A} = \begin{bmatrix} A_{11} & 0 \\ 0 & A_{22} \end{bmatrix}.$$

Since P_{11} and P_{22} are irreducible, A_{11} and A_{22} are diagonal matrices with positive diagonal entries, we see that $A_{11}P_{11}$ and $A_{22}P_{22}$ are both irreducible. Let ρ_i be the spectral radius of $A_{ii}P_{ii}$, $i = 1, 2$. By the Perron-Frobenius Theorem, ρ_i is a simple eigenvalue of $A_{ii}P_{ii}$, and there exist a unique positive normalized right eigenvector \bar{h}_i such that $A_{ii}P_{ii}\bar{h}_i = \rho_i\bar{h}_i$ and a unique positive normalized left eigenvector \bar{h}_i^* such that $(\bar{h}_i^*)^T A_{ii}P_{ii} = \rho_i(\bar{h}_i^*)^T$, $i = 1, 2$. To establish stability results for (14), we use the same assumptions as in the completely reducible case. In particular, we let $x(0)$ be positive (which implies $z(0)$ is positive) and we assume that $b_i = \beta$, $i = 1, 2, \dots, n$, where β is a positive constant.

Suppose that $\rho_1 > \rho_2$. Let $I_{n-n_1} \in \mathbb{R}^{(n-n_1) \times (n-n_1)}$ be the identity matrix. Note that $\rho_1 I_{n-n_1} - (A_{22}P_{22})^T$ is a nonsingular M-matrix. Thus, from Theorem 2.2 $(\rho_1 I_{n-n_1} - (A_{22}P_{22})^T)^{-1}$ is a nonnegative matrix. Let $\bar{z}_1 \in \mathbb{R}^n$ and $\bar{z}_1^* \in \mathbb{R}^n$ be defined by

$$\bar{z}_1 = \begin{bmatrix} \bar{h}_1 \\ 0 \end{bmatrix}, \quad \bar{z}_1^* = \begin{bmatrix} \bar{h}_1^* \\ [\rho_1 I_{n-n_1} - (A_{22}P_{22})^T]^{-1} (A_{11}P_{12})^T \bar{h}_1^* \end{bmatrix}, \quad (15)$$

respectively, then we have $\mathcal{A}\mathcal{P}\bar{z}_1 = \rho_1\bar{z}_1$ and $(\bar{z}_1^*)^T \mathcal{A}\mathcal{P} = \rho_1(\bar{z}_1^*)^T$. Hence, \bar{z}_1 is the unique nonnegative normalized (right) eigenvector which corresponds to the spectral radius ρ_1 of the matrix $\mathcal{A}\mathcal{P}$. Let $z(t) = g(t) \exp[(\mathcal{A}\mathcal{P} - \rho_1 I)t]z(0)$. Following a similar argument as in the proof of Theorem 3.2, we can show that there exists a positive constant $\alpha_1 = \frac{z(0)^T \bar{z}_1^*}{\bar{z}_1^T \bar{z}_1^*}$ such that

$$\lim_{t \rightarrow \infty} \exp[(\mathcal{A}\mathcal{P} - \rho_1 I)t]z(0) = \alpha_1 \bar{z}_1, \quad \text{and} \quad \lim_{t \rightarrow \infty} g(t) = \frac{\rho_1}{\beta \alpha_1}.$$

This implies that

$$\lim_{t \rightarrow \infty} z(t) = \frac{\rho_1}{\beta} \bar{z}_1.$$

Hence, we have a nonnegative equilibrium (independent of the initial condition $z(0)$) which is globally asymptotically stable.

Now, suppose that $\rho_1 < \rho_2$. Let $I_{n_1} \in \mathbb{R}^{n_1 \times n_1}$ be the identity matrix. Note that $\rho_2 I_{n_1} - A_{11} P_{11}$ is a nonsingular M-matrix. Thus, from Theorem 2.2, $(\rho_2 I_{n_1} - A_{11} P_{11})^{-1}$ is a nonnegative matrix. Let $\bar{z}_2 \in \mathbb{R}^n$ and $\bar{z}_2^* \in \mathbb{R}^n$ be defined by

$$\bar{z}_2 = \begin{bmatrix} (\rho_2 I_{n_1} - A_{11} P_{11})^{-1} A_{11} P_{12} \bar{h}_2 \\ \bar{h}_2 \end{bmatrix}, \quad \bar{z}_2^* = \begin{bmatrix} 0 \\ \bar{h}_2^* \end{bmatrix}, \quad (16)$$

respectively; then we have $\mathcal{A}\mathcal{P}\bar{z}_2 = \rho_2 \bar{z}_2$, and $(\bar{z}_2^*)^T \mathcal{A}\mathcal{P} = \rho_2 (\bar{z}_2^*)^T$. Hence, \bar{z}_2 is unique in the sense that its last $n - n_1$ elements constitute a vector which is a normalized positive right eigenvector of $A_{22} P_{22}$ corresponding to its spectral radius ρ_2 . Let $z(t) = g(t) \exp[(\mathcal{A}\mathcal{P} - \rho_2 I)t] z(0)$. Following an argument similar to the proof of Theorem 3.2, we can show that there exists a positive constant $\alpha_2 = \frac{z(0)^T \bar{z}_2^*}{\bar{z}_2^T \bar{z}_2^*}$ such that

$$\lim_{t \rightarrow \infty} \exp[(\mathcal{A}\mathcal{P} - \rho_2 I)t] z(0) = \alpha_2 \bar{z}_2, \quad \text{and} \quad \lim_{t \rightarrow \infty} g(t) = \frac{\rho_2}{\beta \alpha_2 (e^T \bar{z}_2)},$$

which implies that

$$\lim_{t \rightarrow \infty} z(t) = \frac{\rho_2}{\beta (e^T \bar{z}_2)} \bar{z}_2.$$

Hence, in this case we again have a nonnegative equilibrium (independent of initial condition $z(0)$) which is globally stable.

We summarize the above discussion with the following stability result for system (3):

THEOREM 3.4. *Assume that x^0 is positive, P is a reducible matrix satisfying (13), and $b_i = \beta$ for $i = 1, 2, \dots, n$, where β is a positive constant.*

(1) *If $\rho_1 > \rho_2$, then we have*

$$\lim_{t \rightarrow \infty} x(t) = \frac{\rho_1}{\beta} Q^T \bar{z}_1.$$

(2) *If $\rho_1 < \rho_2$, then we have*

$$\lim_{t \rightarrow \infty} x(t) = \frac{\rho_2}{\beta (e^T \bar{z}_2)} Q^T \bar{z}_2.$$

REMARK 4. *The above theorem states that if the spectral radius of the receiver class is larger than that of the donor class, then we have a competitive exclusion case with all the subpopulations in the receiver class surviving and all the subpopulations in the donor class becoming extinct. However, if the spectral radius of the donor class is larger than that of the receiver class, then we have a coexistence case in the sense of classes; that is, all the subpopulations in the donor class survive and at least one subpopulation in the receiver class survives. Furthermore, if we also assume that each row of matrix P_{12} has at least one element that is positive, then from (16) we see that \bar{z}_2 is a vector with each element being positive. Hence, from case (2) in Theorem 3.4 we have a positive equilibrium which is globally stable. Thus all subpopulations coexist.*

We illustrate the results in Theorem 3.4 using the following example. Let

$$P = \begin{bmatrix} 0.3 & 0.2 & 0.1 & 0.1 \\ 0.7 & 0.8 & 0.3 & 0.4 \\ 0 & 0 & 0.4 & 0.4 \\ 0 & 0 & 0.2 & 0.1 \end{bmatrix},$$

$A = \text{diag}(0.4, 0.5, 2, 3)$ and $B = \text{diag}(0.1, 0.1, 0.1, 0.1)$. Under this case, we have two population classes: class 1 is composed of subpopulations 1 and 2, and class 2 is composed of subpopulations 3 and 4. The values of matrix P indicate that an individual in class 2 can reproduce an individual in class 1, but not vice versa. Using Matlab, we solve symbolically for the unique positive equilibrium to get

$$\bar{x} = [0.4976 \quad 2.1443 \quad 6.3572 \quad 3.8663]^T.$$

Furthermore, we find that the real part of each eigenvalue of the linearized system is less than zero. Thus the equilibrium is locally asymptotically stable. Note that the spectral radius of class 1, $\rho_1 = 0.4782$ and the spectral radius of class 2, $\rho_2 = 1.2865$. Thus from Theorem 3.4 it follows that this interior equilibrium is globally asymptotically stable. Under this case, we have coexistence of all the subpopulations (for a reducible matrix P).

However, if we set the values for A and B such that the spectral radius of class 1 is bigger than that of class 2, then no positive equilibrium exists anymore. For example, let $A = \text{diag}(0.4, 0.5, 0.8, 0.3)$ and keep the values for P and B the same as above. This results in class 1 having spectral radius $\rho_1 = 0.4782$ and population class 2 having spectral radius $\rho_2 = 0.3756$, and we obtain the following boundary equilibrium

$$\bar{x} = [0.8730 \quad 3.9087 \quad 0 \quad 0].$$

As above, using linearization techniques, one can show that this equilibrium is locally asymptotically stable and by Theorem 3.4 it is globally asymptotically stable. Hence, subpopulations 1 and 2 survive, but subpopulations 3 and 4 go to extinction. Therefore, we have a competitive exclusion result between the two classes.

4. Stochastic differential equation model. Since the deterministic model (1) defined in Section 2 is continuous in both time and state space, the objective of this section is to create a stochastic model based on the deterministic one which is continuous in both time and state space. Thus we use the method developed in [6, 7, 18] to derive an Ito stochastic differential equation model. In the derivation, it is assumed that the random variability is due to births and deaths, i.e., demographic variability.

Let $X_i(t)$ be a random variable for the total number of individuals in the i th population at time t , $i = 1, 2, \dots, n$, and $X(t) = (X_1(t), X_2(t), \dots, X_n(t))^T$ be a random vector of the n subpopulations. Let $\Delta X_i(t) = X_i(t + \Delta t) - X_i(t)$, $i = 1, 2, \dots, n$ be the incremental change in the i th population during the time interval Δt . Assume that Δt is chosen sufficiently small that the probabilities of a birth or a death in subpopulation i are given by

$$q_{2i-1} = \text{Prob}\{\Delta X_i(t) = 1 | X_i(t)\} = a_i \sum_{j=1}^n p_{ij} X_j \Delta t + o(\Delta t), \quad i = 1, 2, \dots, n,$$

$$q_{2i} = \text{Prob}\{\Delta X_i(t) = -1 | X_i(t)\} = b_i X_i \sum_{j=1}^n X_j \Delta t + o(\Delta t), \quad i = 1, 2, \dots, n,$$

Then the probability that no change occurs is given by

$$q_{2n+1} = \text{Prob}\{\Delta X_1(t) = 0, \Delta X_2(t) = 0, \dots, \Delta X_n(t) = 0 | (X_1(t), X_2(t), \dots, X_n(t))\}$$

$$= 1 - \left(\sum_{i=1}^n a_i \sum_{j=1}^n p_{ij} X_j + \sum_{i=1}^n b_i X_i \sum_{j=1}^n X_j \right) \Delta t + o(\Delta t).$$

Let $\eta = (\Delta X_1, \Delta X_2, \dots, \Delta X_n)^T$ be the vector representing the change in the n subpopulations over the time interval Δt . It is necessary to find the mean and covariance matrix for the change η . Neglecting multiple births or deaths in the time interval Δt which have probabilities of order $o(\Delta t)$, we have the following $2n + 1$ possibilities for the vector η in Δt :

$$\eta_{2i-1} = \nu_i, \quad i = 1, 2, \dots, n, \quad \eta_{2i} = -\nu_i, \quad i = 1, 2, \dots, n, \quad \eta_{2n+1} = \mathbf{0},$$

where $\nu_i = [0, \dots, 0, 1, 0, \dots, 0]^T$ is the standard unit vector in \mathbb{R}^{2n+1} with the i th component equal 1 and all the other components are equal to 0, and $\mathbf{0} = [0, 0, \dots, 0]^T$ is the zero vector in \mathbb{R}^{2n+1} . In the above expression η_{2i-1} represents the event that a single birth occurs in the i th subpopulation, η_{2i} represents the event that a single death occurs in the i th subpopulation, and η_{2n+1} represents the event that no change occurs in all the subpopulations.

Therefore, if terms of order $o(\Delta t)$ are neglected, the infinitesimal mean of η is approximated as follows:

$$E(\eta) = \sum_{i=1}^{2n+1} q_i \eta_i \approx \begin{bmatrix} a_1 \sum_{j=1}^n p_{1j} X_j - b_1 X_1 \sum_{j=1}^n X_j \\ a_2 \sum_{j=1}^n p_{2j} X_j - b_2 X_2 \sum_{j=1}^n X_j \\ \vdots \\ a_n \sum_{j=1}^n p_{nj} X_j - b_n X_n \sum_{j=1}^n X_j \end{bmatrix} \Delta t = \mu \Delta t. \quad (17)$$

The covariance matrix for η is

$$V(\eta) = E(\eta \eta^T) - E(\eta)E(\eta)^T.$$

Notice that $E(\eta)E(\eta)^T$ is of order $(\Delta t)^2$, and $E(\eta \eta^T) = \sum_{i=1}^{2n+1} q_i \eta_i \eta_i^T$. Therefore, we approximate the covariance matrix V as follows:

$$V(\eta) \approx \sum_{i=1}^{2n+1} q_i \eta_i \eta_i^T \approx \begin{bmatrix} \phi_{11} & 0 & \dots & 0 \\ 0 & \phi_{22} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \phi_{nn} \end{bmatrix} \Delta t = \Phi \Delta t, \quad (18)$$

where the diagonal elements

$$\phi_{ii} = \left(a_i \sum_{j=1}^n p_{ij} X_j + b_i X_i \sum_{j=1}^n X_j \right), \quad i = 1, 2, \dots, n.$$

Clearly ϕ_{ii} is positive. Thus

$$C = \sqrt{\Phi} = \begin{bmatrix} \sqrt{\phi_{11}} & 0 & \dots & 0 \\ 0 & \sqrt{\phi_{22}} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \sqrt{\phi_{nn}} \end{bmatrix}. \quad (19)$$

When $X(t)$ is sufficiently large and Δt is sufficiently small, we can assume that η has an approximate normal distribution with mean vector $\mu\Delta t$ and covariance $C^2\Delta t = \Phi\Delta t$, i.e., $\eta \sim N(\mu\Delta t, \Phi\Delta t)$, due to the Central Limit Theorem.

The random vector $\eta \sim N(\mu\Delta t, \Phi\Delta t)$ can be transformed into a simpler form using a random vector from the standard normal distribution $N(0, I)$. In particular, let $\xi = (\xi_1, \xi_2, \dots, \xi_n)^T \sim N(0, I)$. Then, the random vector $C\sqrt{\Delta t}\xi \sim N(0, \Phi\Delta t)$. Hence, $\eta - \mu\Delta t \sim N(0, \Phi\Delta t)$ and

$$\eta = \mu\Delta t + C\sqrt{\Delta t}\xi \sim N(\mu\Delta t, \Phi\Delta t).$$

Thus we have that

$$X(t + \Delta t) = X(t) + \mu\Delta t + C\sqrt{\Delta t}\xi \tag{20}$$

has an approximate normal distribution $N(X(t) + \mu\Delta t, \Phi\Delta t)$. The above equation is just an Euler approximation of an Itô stochastic differential equation for $X_i(t)$ with time step Δt ([16, 19]). Therefore, if μ and C satisfy certain conditions, then $X(t)$ converges in the mean square sense to the following Itô stochastic differential equation:

$$dX = \mu(X)dt + C(X)dW, \quad X(0) = X^0 \tag{21}$$

where μ and C are defined in (17) and (19), respectively, and $W = (W_1, W_2, \dots, W_n)^T$ is an n dimensional Wiener process. In particular, the following theorem states the conditions for existence and uniqueness of solutions to (21) and for convergence of Euler's approximation to the solution of (21) (see [18, 19]).

THEOREM 4.1. *Suppose $\mu(X)$ and $C(X)$ satisfy uniform growth and Lipschitz conditions; that is, there exists a constant $K_1 > 0$ and $K_2 > 0$ such that*

$$\|\mu(Y) - \mu(Z)\| + \|C(Y) - C(Z)\| \leq K_1\|Y - Z\|,$$

and

$$\|\mu(Y)\| + \|C(Y)\| < K_2(1 + \|Y\|)$$

for $Y, Z \in \mathbb{R}^n$, where $\|\bullet\|$ denotes the Euclidean norm. Then there exists a pathwise unique, t -continuous solution $X(t)$ of the Itô stochastic differential equation (21) with the property

$$\sup_{t \in [0, T]} E\|X(t)\|^2 < \infty,$$

where E denotes the expectation. In addition, there exists a constant K_3 such that

$$E\|X(t) - \tilde{X}(t)\|^2 \leq K_3\Delta t$$

where $X(t)$ is the solution to stochastic differential equation (21) and $\tilde{X}(t)$ is Euler's solution; i.e.,

$$\tilde{X}(t + \Delta t) = \tilde{X}(t) + \mu(\tilde{X}(t))\Delta t + C(\tilde{X}(t))\sqrt{\Delta t}\xi,$$

for $t \in \{0, \Delta t, 2\Delta t, \dots, T\}$.

If, for example, we add a boundedness restriction on the the random variables $X_i, i = 1, \dots, n$ (i.e., we assume that $X_i(t) \in [0, M]$ for a sufficiently large constant M), then it is straightforward to see that the existence and uniqueness conditions in Theorem 4.1 are satisfied with $\mu(X)$ and $C(X)$ as defined in (17) and (19), respectively. Hence, it follows that as $\Delta t \rightarrow 0$, $X(t)$ converges in the mean square sense to the solution of the Itô stochastic differential equation.

5. Numerical results. In this section, two cases will be studied. In Section 5.1 we study a selection birth term where for the deterministic model the subpopulation with the highest ratio, $\max_{i=1,2,\dots,n} \{a_i/b_i\}$, will survive and all the other subpopulations will die out. In Section 5.2 we study a selection-mutation case with P being an irreducible matrix (where all subpopulations survive in the deterministic model).

We use Euler's method to numerically approximate the sample paths for the stochastic model (21). In all the simulations for the stochastic model, we choose the time mesh size $\Delta t = 0.001$. The mesh points are given by: $t_k = k\Delta t$, $k = 0, 1, \dots, m$. Denote by X_i^k the numerical solution of $X_i(t_k)$. Then we have the following numerical scheme:

$$\begin{aligned} X_i^{k+1} = & X_i^k + \left(a_i \sum_{j=1}^n p_{ij} X_j^k - b_i X_i^k \sum_{j=1}^n X_j^k \right) \Delta t \\ & + \xi_i^k \sqrt{\left(a_i \sum_{j=1}^n p_{ij} X_j^k + b_i X_i^k \sum_{j=1}^n X_j^k \right) \Delta t}, \end{aligned} \quad (22)$$

where $\xi_1^k, \xi_2^k, \dots, \xi_n^k$ are independent random variables following a normal distribution with mean 0 and variance 1. In the simulation, if $X_i^{k+1} \leq 0$, then we set $X_i^{k+1} = 0$. The numerical method (22) constructed from Euler's approximation to the continuous Itô model is computationally simpler and faster than the numerical method for a continuous-time Markov chain model. This was another motivation for us to consider an Itô stochastic differential equation model.

In all of the examples below, we simulated N sample paths $X_{i,l}(t)$ with $l = 1, 2, \dots, N$ and $i = 1, 2, \dots, n$ for the corresponding stochastic model. The mean conditioned on nonextinction for the i th subpopulation $\mu_i(t)$ is calculated by averaging all the sample paths conditioned on nonextinction of the total population

$\mathcal{X}(t) = \sum_{j=1}^n X_j(t)$ at time t . The sample standard deviation for the i th subpopulation is represented by $\sigma_i(t)$. We use $\pi_i(0, t) = \text{Prob}\{X_i(t) = 0\}$, $i = 1, 2, \dots, n$

to denote the probability of extinction for the i th subpopulation at time t , and $\pi(0, 0, \dots, 0, t) = \text{Prob}\{X_1(t) = 0, X_2(t) = 0, \dots, X_n(t) = 0\}$ to denote the probability that all the subpopulation are driven to extinction at time t . We denote by $\pi_c(t) = \text{Prob}\{X_1(t) > 0, X_2(t) > 0, \dots, X_n(t) > 0\}$ the probability of coexistence at time t . These probabilities will be calculated based on the N sample Monte Carlo data set for all the following simulations.

5.1. Pure selection case. In this section, we consider a pure selection case, that is, $P = I$, which means that individuals in the i th subpopulation can only reproduce individuals in the i th subpopulation. In what follows, we choose $n = 3$, $T = 10$, and we use *ode23* in Matlab to solve numerically the deterministic model (1).

In the first example, we simulated 7000 ($N = 7000$) sample paths for the corresponding stochastic model. The initial population size is chosen to be $(10, 10, 10)$. The values for all the other parameters are chosen to be $a_1 = 3$, $a_2 = 1$, $a_3 = 1$, $b_1 = 0.1$, $b_2 = 0.2$ and $b_3 = 0.1$. Notice that since $a_1/b_1 > a_i/b_i$ for $i = 2, 3$, the solution of the deterministic model (1) satisfies

$$\lim_{t \rightarrow \infty} x_1(t) = 30, \quad \lim_{t \rightarrow \infty} x_2(t) = 0, \quad \lim_{t \rightarrow \infty} x_3(t) = 0.$$

Three randomly chosen stochastic realizations (out of 7000) and the solution to the deterministic model (1) for each subpopulation are plotted in Figure 1 (left column). The results show that both subpopulations 2 and 3 are driven to extinction after $t = 5$ and subpopulation 1 survives for all these three realizations. The mean conditioned on nonextinction $(\mu_1(t), \mu_2(t), \mu_3(t))$ and the solution to the deterministic model are plotted in Figure 1 (right column), which suggests that the mean conditioned on nonextinction is close to the deterministic equilibrium $(30, 0, 0)$.

The sample standard deviation $(\sigma_1(10), \sigma_2(10), \sigma_3(10))$ is approximately equal to $(5.6174, 0, 0.3094)$. The probabilities of extinction $\pi_i(0, t)$ and $\pi(0, 0, 0, t)$ are plotted in Figure 2 (left). From this figure it is clear that subpopulation 2 becomes extinct at approximately $t = 3$ while subpopulation 3 becomes almost extinct around $t = 5$. The numerical approximations at time $t = 10$ of these probabilities and their corresponding Wilson score confidence interval (see [17] for details) with significance level 0.05 are given in Table 1. The probability of coexistence $\pi_c(t)$

TABLE 1. Probability of extinction at time $t = 10$ and its corresponding confidence interval.

| | estimated value | confidence interval |
|--------------------|-----------------|---------------------|
| $\pi_1(0, 10)$ | 0.001 | [0.0005, 0.0021] |
| $\pi_2(0, 10)$ | 1 | [0.9995, 1] |
| $\pi_3(0, 10)$ | 0.999 | [0.9979, 0.9995] |
| $\pi(0, 0, 0, 10)$ | 0 | [0, 0.0005] |

is plotted in Figure 2 (right), which indicates that the subpopulations no longer coexist after $t = 3.5$. Hence, for this example the stochastic model behavior is similar to that of the deterministic model.

We point out that when the highest ratio a_1/b_1 is significantly larger than the ratios a_2/b_2 and a_3/b_3 , as in the above example, the stochastic (in the mean sense) and deterministic model behave similarly. To test whether the same outcome occurs when the highest ratio is close to the other ratios, we give the following example: the initial population size is chosen to be $(20, 20, 20)$. The values for all the other parameters are chosen to be $a_1 = 3\lambda$, $a_2 = 6\lambda$, $a_3 = 12\lambda$, $b_1 = 1$, $b_2 = 2.01$ and $b_3 = 4.01$, where λ is some positive constant. Since $a_1/b_1 > a_i/b_i$ for $i = 2, 3$, the solution of the deterministic model satisfies

$$\lim_{t \rightarrow \infty} x_1(t) = 3\lambda, \quad \lim_{t \rightarrow \infty} x_2(t) = 0, \quad \lim_{t \rightarrow \infty} x_3(t) = 0.$$

Figures 3 and 4 are obtained with $\lambda = 90$. We simulate 7000 ($N = 7000$) sample paths for the corresponding stochastic model. Three randomly chosen stochastic realizations and the solution to the deterministic model for each subpopulation are plotted in Figure 3 (left column). The results show that subpopulations 1 and 3 die out after $t = 1$ for these three realizations but subpopulation 2 survives. The mean conditioned on nonextinction $(\mu_1(t), \mu_2(t), \mu_3(t))$ and the solution to the deterministic model are plotted in Figure 3 (right column). The results suggest that the mean conditioned on nonextinction is far away from the deterministic equilibrium $(270, 0, 0)$.

The sample standard deviation $(\sigma_1(10), \sigma_2(10), \sigma_3(10))$ is approximately equal to $(124.3057, 112.9720, 134.2170)$. The probabilities of extinction $\pi_i(0, t)$ and $\pi(0, 0, 0, t)$ are plotted in Figure 4 (left), from which we can see that these probabilities are

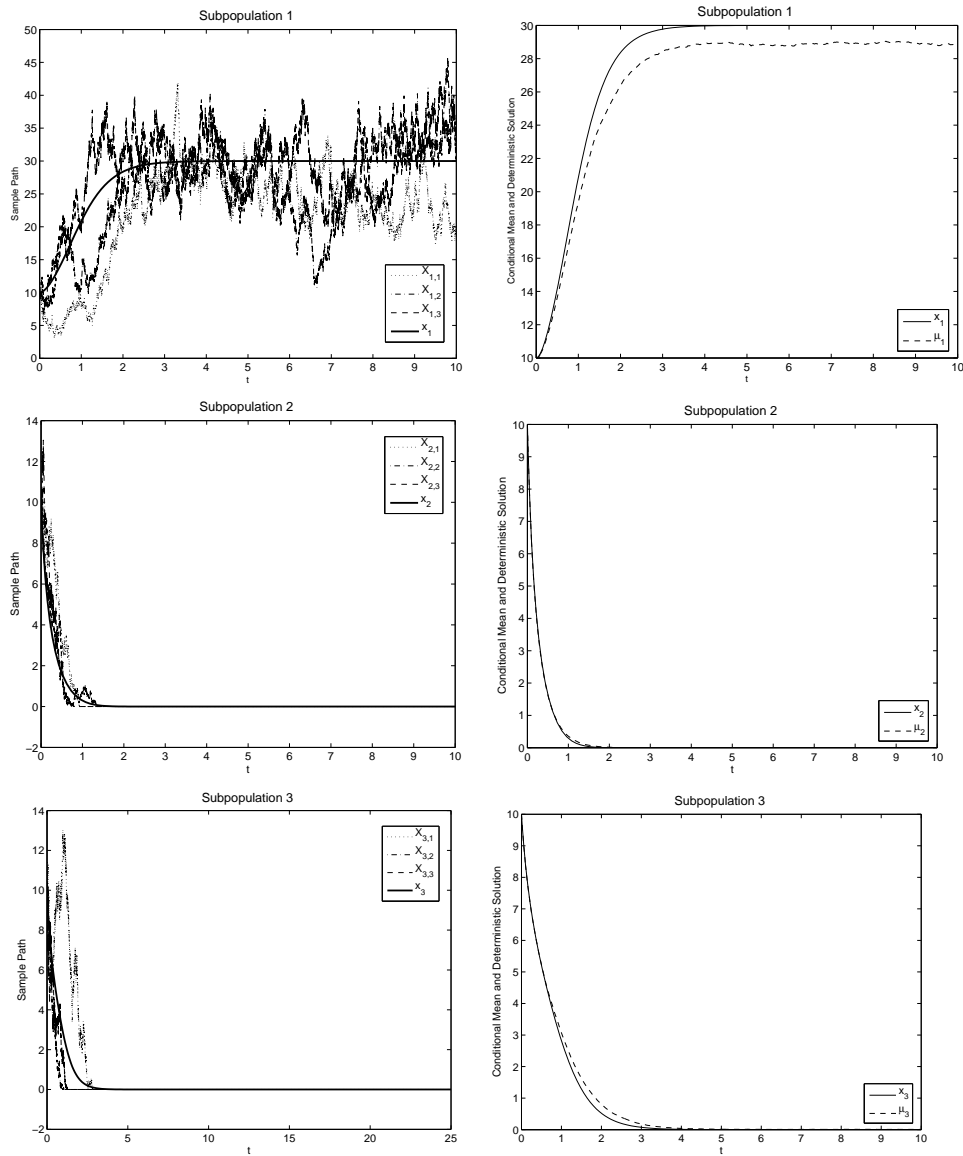


FIGURE 1. (left column) Three randomly chosen stochastic realizations and the solution to the deterministic model with $(a_1, a_2, a_3) = (3, 1, 1)$, $(b_1, b_2, b_3) = (0.1, 0.2, 0.1)$ and $P = I$. The initial population size for both the stochastic model and the deterministic model is $(10, 10, 10)$. (right column) The solution to the model (1) and the mean conditioned on nonextinction.

approximately constant for a large range of times. Their numerical approximations at time $t = 10$ and their corresponding Wilson score confidence interval with significance level 0.05 are illustrated in Table 2. The probability of coexistence $\pi_c(t)$ is plotted in Figure 4 (right), which indicates that the subpopulations no longer coexist after $t = 1$.

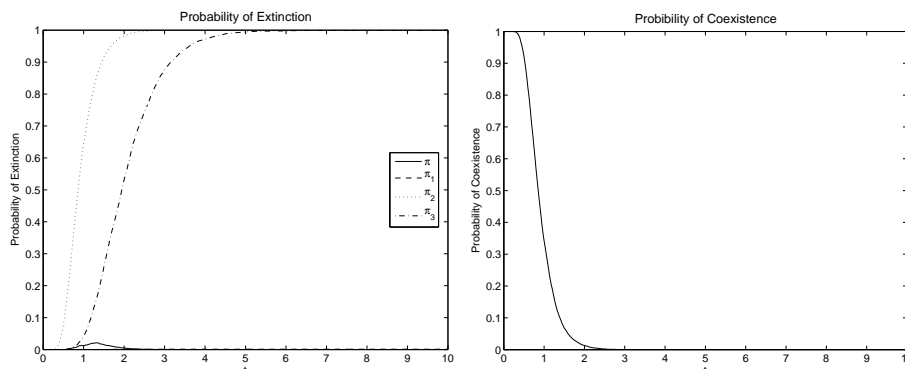


FIGURE 2. (left) The probability of extinction for each subpopulation and the probability that all subpopulations are driven to extinction. (right) The probability of coexistence.

TABLE 2. Probability of extinction at time $t = 10$ and its corresponding confidence interval.

| | estimated value | confidence interval |
|--------------------|-----------------|---------------------|
| $\pi_1(0, 10)$ | 0.6937 | [0.6828, 0.7044] |
| $\pi_2(0, 10)$ | 0.7691 | [0.7591, 0.7789] |
| $\pi_3(0, 10)$ | 0.5371 | [0.5254, 0.5488] |
| $\pi(0, 0, 0, 10)$ | 0 | [0, 0.0005] |

We performed many other numerical simulations with different λ values. In these simulations, we obtain many cases where the stochastic model differs from the deterministic one in picking the winning trait or subpopulation. The results in Table 3 and Figure 5 are obtained by simulating 1000 ($N = 1000$) sample paths. The probability of extinction $\pi_1(0, 10)$, $\pi_2(0, 10)$ and $\pi_3(0, 10)$ for some λ values less than 10 and bigger than 200 with initial condition $(20, 20, 20)$ are tabulated in Table 3. We can see that if λ is chosen very small or very big, then all the subpopulations are driven to extinction, which is expected for the stochastic model because of the variance.

TABLE 3. Probability of extinction $\pi_1(0, 10)$, $\pi_2(0, 10)$ and $\pi_3(0, 10)$ for λ values less than 10 and bigger than 200 with initial condition $(20, 20, 20)$.

| λ | 1 | 2 | 5 | 250 | 300 | 400 | 800 | 1000 |
|----------------|-------|-------|-------|-------|-------|-------|-------|------|
| $\pi_1(0, 10)$ | 0.999 | 0.882 | 0.268 | 0.311 | 0.219 | 0.013 | 0.707 | 1 |
| $\pi_2(0, 10)$ | 1 | 0.998 | 0.788 | 0.689 | 0.781 | 1 | 1 | 1 |
| $\pi_3(0, 10)$ | 1 | 1 | 0.958 | 1 | 1 | 1 | 1 | 1 |

The probabilities of extinction $\pi_1(0, 10)$, $\pi_2(0, 10)$ and $\pi_3(0, 10)$ with λ values between 10 and 200 are plotted in Figure 5, where the left part is the plot for results with initial condition $(20, 20, 20)$, and the right one is the plot for results with initial condition $(20, 40, 80)$. We can see from Figure 5 that the results remain similar even if we choose the initial condition to be $(20, 40, 80)$, scaled according to

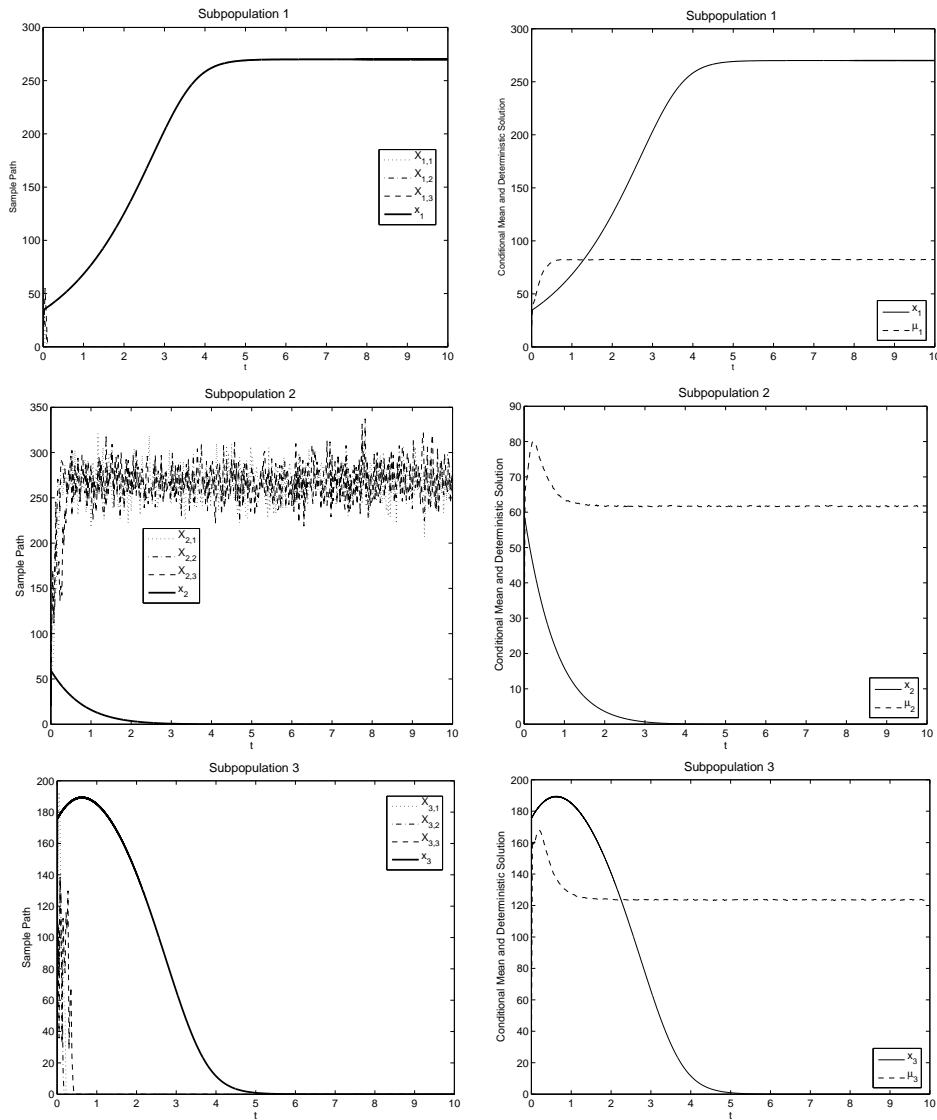


FIGURE 3. (left column) Three randomly chosen stochastic realizations and the solution to the deterministic model with $(a_1, a_2, a_3) = (270, 540, 1080)$, $(b_1, b_2, b_3) = (1, 2.01, 4.01)$ and $P = I$. The initial population size for both stochastic model and deterministic model is $(20, 20, 20)$. (right column) The solution to the model (1) and the mean conditioned on nonextinction.

the choice of parameters. Both plots indicate that the stochastic model disagrees with the deterministic model much more in the middle than in the tails.

To get a better understanding of the stochastic model dynamics, we consider three values of λ , $\lambda = 20, 100, 180$, with initial condition $(20, 20, 20)$, and plot the frequency histograms for $X_1(10)$, $X_2(10)$ and $X_3(10)$ out of these 1000 sample paths in Figures 6, 7 and 8. We repeat the same numerical experiment for the initial

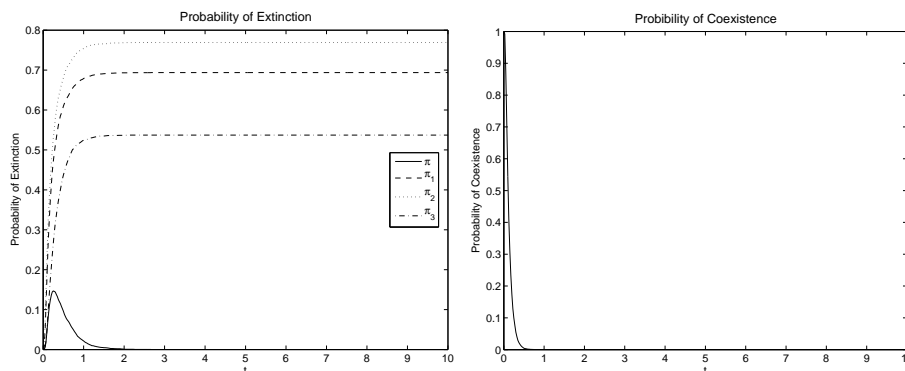


FIGURE 4. (left) The probability of extinction for each population and the probability that all subpopulations are driven to extinction. (right) The probability of coexistence.

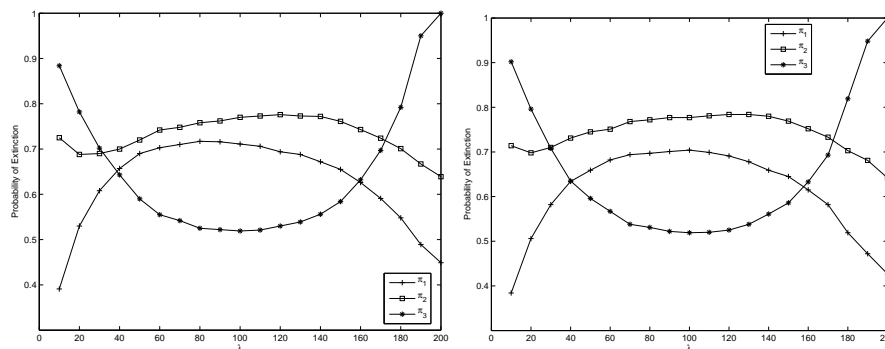


FIGURE 5. (left) Probability of extinction $\pi_1(0, 10)$, $\pi_2(0, 10)$ and $\pi_3(0, 10)$ for λ values between 10 and 200 with initial condition $(20, 20, 20)$. (right) Probability of extinction $\pi_1(0, 10)$, $\pi_2(0, 10)$ and $\pi_3(0, 10)$ for λ values between 10 and 200 with initial condition $(20, 40, 80)$.

condition $(20, 40, 80)$. Figures 6 and 8 show that subpopulation 1 has a greater chance to win the competition than subpopulations 2 and 3, which agrees with the deterministic case since subpopulation 1 has the highest growth-to-mortality ratio. However, Figure 7 indicates that subpopulation 3 has greater chance to win the competition than subpopulations 1 and 2. Hence, it is not possible to determine a priori which subpopulation will win the competition if the difference in the growth-to-mortality ratios are small.

From these two examples, we can see that the agreement between the stochastic model and the deterministic model is better if the difference among the ratios (a_i/b_i) are bigger.

5.2. Selection-mutation case. In this section, we consider a selection-mutation case. We choose $n = 3$, $T = 10$, and we use *ode15s* in Matlab to solve numerically

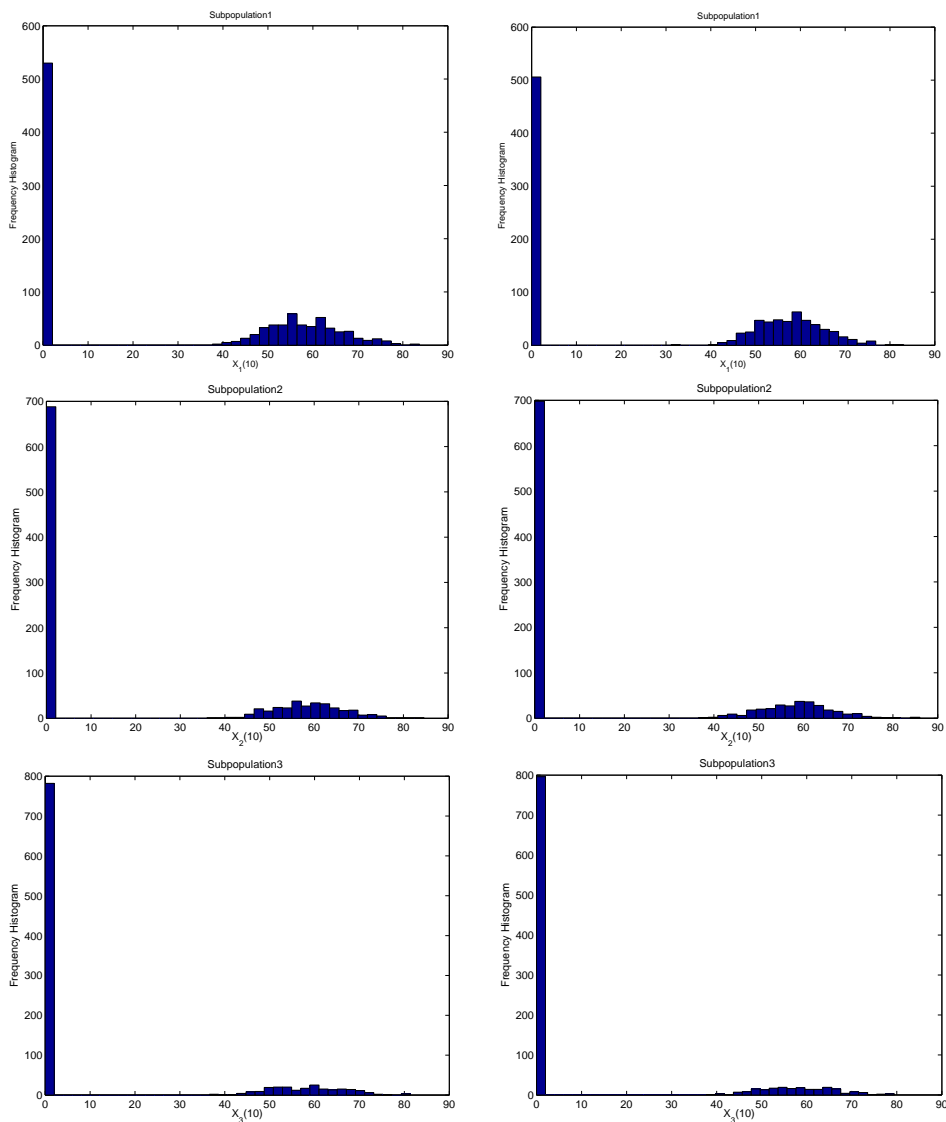


FIGURE 6. Frequency histograms for $X_i(10)$, $i = 1, 2, 3$ out of the 1000 sample paths with $\lambda = 20$. (left column) Initial condition is $(20, 20, 20)$. (right column) Initial condition is $(20, 40, 80)$.

the deterministic model (1). The matrix P is chosen as

$$P = \begin{pmatrix} 0.6 & 0.2 & 0.2 \\ 0.2 & 0.6 & 0.2 \\ 0.2 & 0.2 & 0.6 \end{pmatrix}.$$

Hence, P is an irreducible matrix. The initial population size is set to $(10, 10, 10)$. The values for all the other parameters are chosen to be $a_1 = 8$, $a_2 = 10$, $a_3 = 17$, $b_1 = 0.1$, $b_2 = 0.1$ and $b_3 = 0.1$. We simulate 7000 ($N = 7000$) sample paths for the corresponding stochastic model. Three randomly chosen stochastic realizations

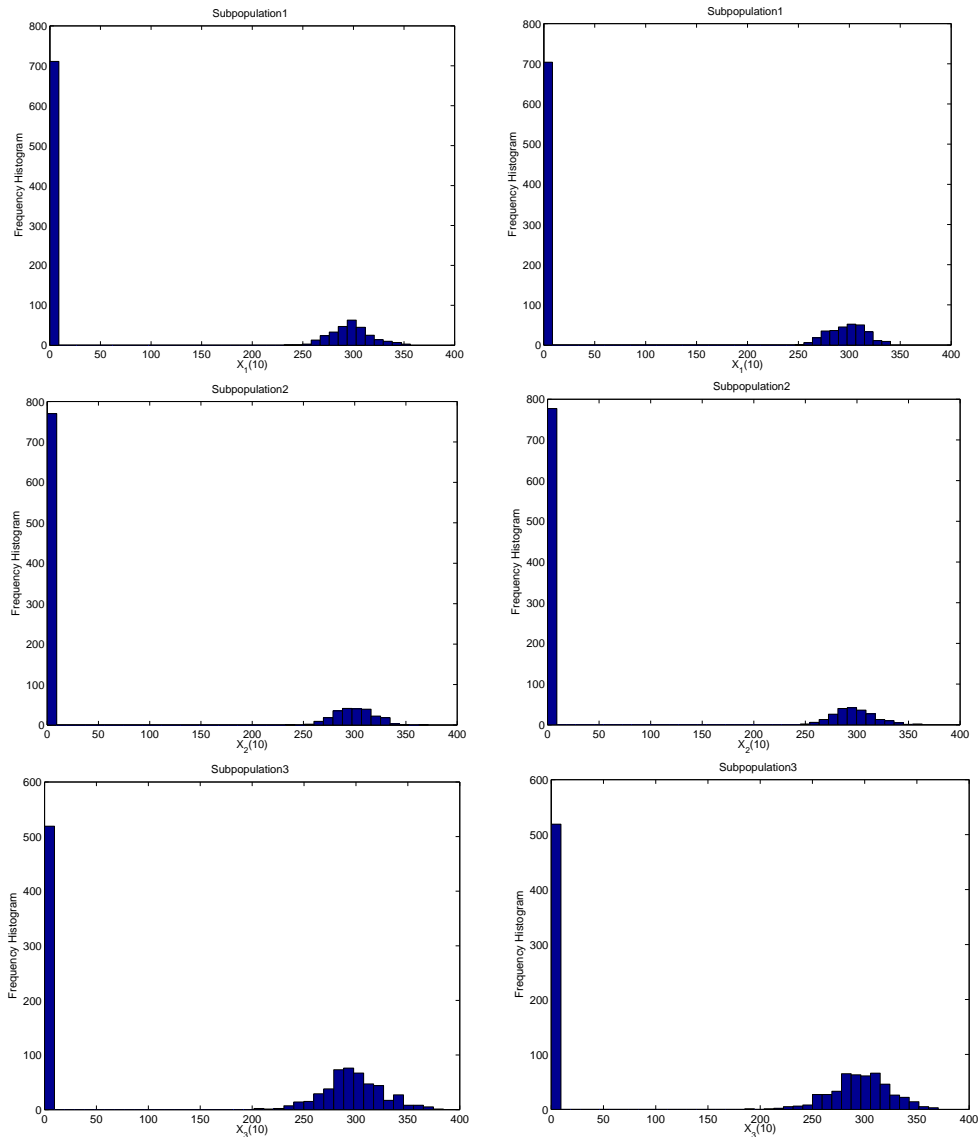


FIGURE 7. Frequency histograms for $X_i(10)$, $i = 1, 2, 3$ out of the 1000 sample paths with $\lambda = 100$. (left column) Initial condition is $(20, 20, 20)$. (right column) Initial condition is $(20, 40, 80)$.

and the solution to the deterministic model for each subpopulation were plotted in Figure 9 (left column). The results show that all subpopulations survive for these three realizations. We also observe that the sample variance is a bit large. To test whether the variance depends on the initial condition, we repeat the same numerical experiment with initial condition $(20, 20, 20)$ and present the results in Figure 9 (right column), which indicate that the large sample variance does not depend on the choice of the initial condition. We point out that since the case considered in this example is a selection-mutation case and all the populations

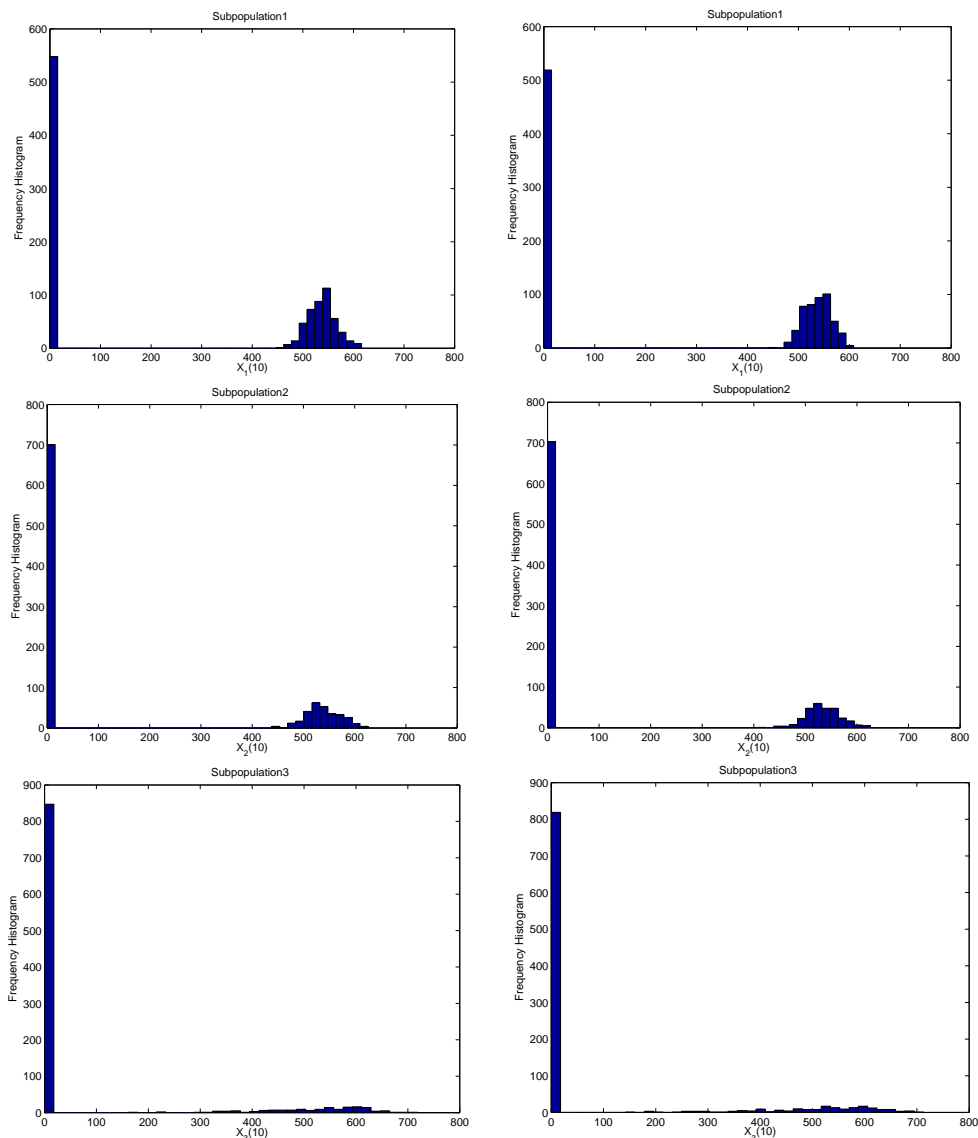


FIGURE 8. Frequency histograms for $X_i(10)$, $i = 1, 2, 3$ out of the 1000 sample paths with $\lambda = 180$. (left column) Initial condition is $(20, 20, 20)$; (right column) Initial condition is $(20, 40, 80)$.

coexist, the covariance is a function of all the subpopulations (see (4.1)), which may be the reason for such large sample variance.

The mean conditioned on nonextinction $(\mu_1(t), \mu_2(t), \mu_3(t))$ and the solution to the deterministic model with initial condition $(10, 10, 10)$ are plotted in Figure 10, which suggests the mean conditioned on nonextinction is very close to the deterministic equilibrium. The sample standard deviation $(\sigma_1(10), \sigma_2(10), \sigma_3(10))$ is approximately equal to $(5.3518, 6.3403, 10.0541)$. The probability of extinction $\pi_i(0, t) \equiv 0$ for $i = 1, 2, 3$, $\pi(0, 0, 0, t) \equiv 0$, and the probability of coexistence

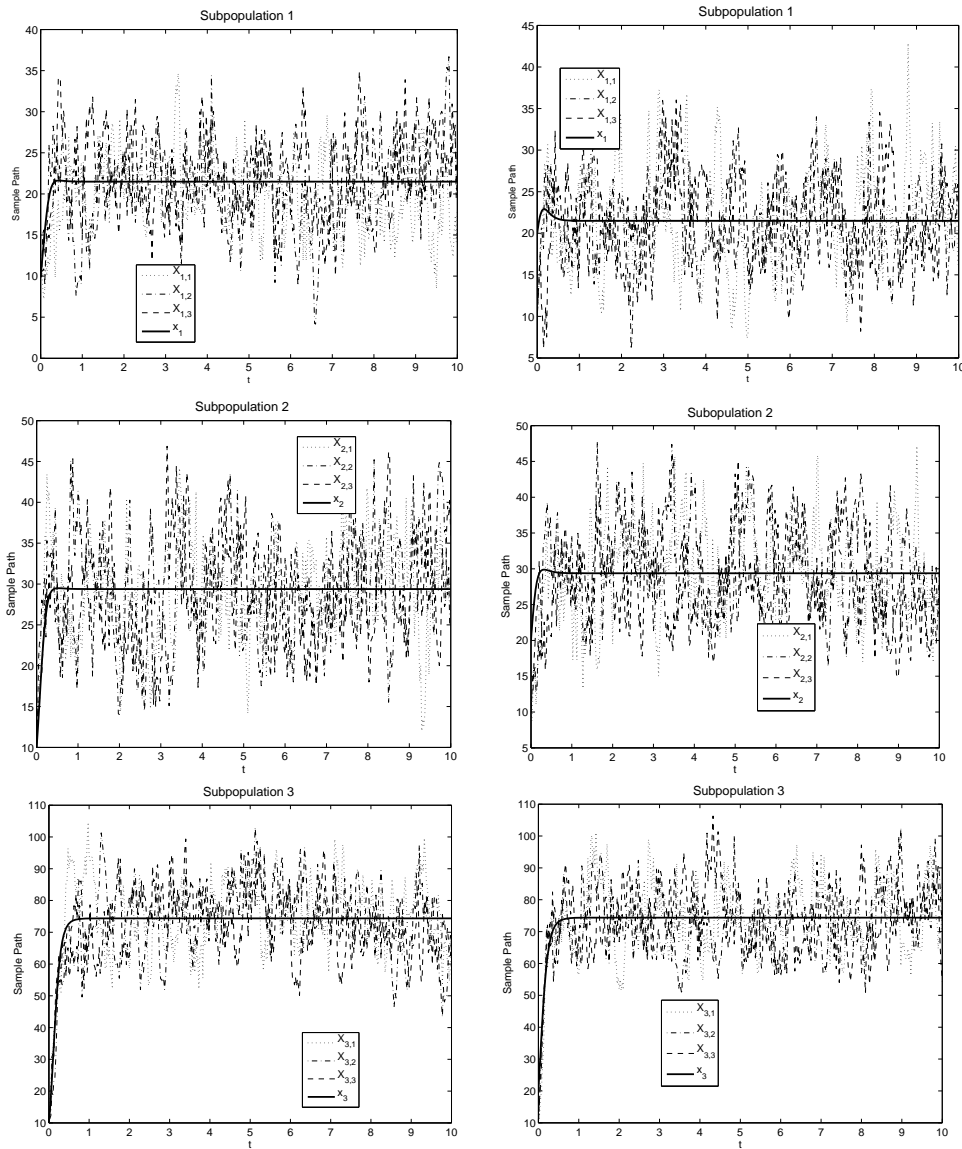


FIGURE 9. Three randomly chosen stochastic realizations out of 7000 sample paths and the solution to the deterministic model with $(a_1, a_2, a_3) = (8, 10, 17)$ and $(b_1, b_2, b_3) = (0.1, 0.1, 0.1)$ under selection-mutation case. (left column) The initial population size for both stochastic model and deterministic model is chosen to be $(10, 10, 10)$; (right column) The initial population size for both stochastic model and deterministic model is chosen to be $(20, 20, 20)$.

$\pi_c(t) \equiv 1$, which means that the populations coexist. Hence, the stochastic model and deterministic model have similar behavior in this case.

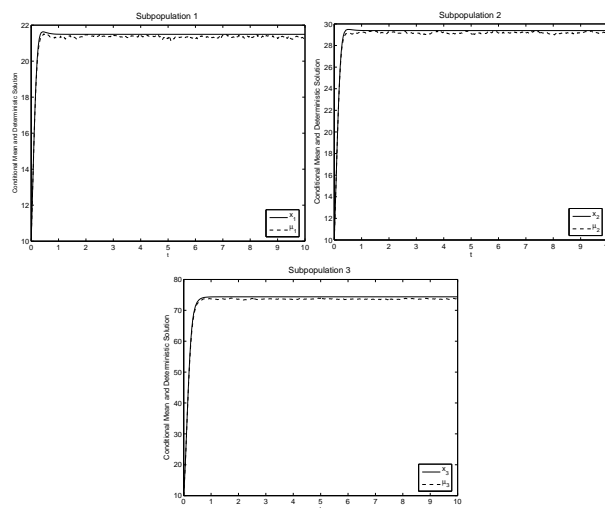


FIGURE 10. The solution to the model (1) and the mean conditioned on nonextinction.

We performed many simulations for other selection-mutation examples with an irreducible matrix P . The results were always in agreement with the deterministic model (1).

6. Concluding remarks. In this paper we compared a stochastic and deterministic selection-mutation models. For the most part the behavior of the mean conditioned on nonextinction of stochastic model follows that of the deterministic model. In particular, in the case of open reproduction (selection-mutation) all subpopulation survive in both the stochastic and deterministic models. In the case of closed reproduction (pure selection) one population survives in both models. However, a main difference is that if subpopulation have growth to mortality ratios that are close to each other then in the deterministic case the one with the highest ratio will win the competition but it is not so in the stochastic model. Perhaps this is due to an Itô diffusion effect. Recall that in our simulations we set the population size to be zero if the population size $X_i^k \leq 0$. Thus, X_i^k values in the interval $(0, 1)$ may contribute to the growth in the stochastic differential equation model rather than becoming extinct in a continuous-time Markov chain model.

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