Analytical Solution of Metapopulation Dynamics in Stochastic Environment

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Abstract

We study a discrete stochastic linear metapopulation model to understand the effect of risk spreading by dispersion. We calculate analytically the stable distribution of populations in different habitats. The simultaneous distribution of populations in habitats has a complicated self-similar structure, but the population in each habitat follows a log-normal distribution. A class of discrete stochastic matrix models were mostly dealt numerically. Our analytical predictions are robust in the wide range of parameters. Qualitative predictions of the current results should hold in the case of multiple habitats. We thus conclude that environmental stochasticity always promotes dispersal.

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Environmental heterogeneity and fluctuations are both important in ecological and evolutionary biology [1, 2]. Assuming that populations face time-varying environmental conditions, environmental heterogeneity often gives rise to paradoxical behavior [3]. For example, Jensen and Yoshimura [4] present a discrete-time model of offspring allocation into two habitats, either of which is so poor that populations cannot survive if the two habitats are exclusive. The authors demonstrate that dispersal can lead to population persistence. Similar paradoxical behaviors have been attracting attention in various research fields such as ecological biology [5–8], financial economics [9–11] and information engineering [12]. In this paper, we study a discrete stochastic linear metapopulation model [7], which is given as discrete-time stochastic matrix models. This class of models have been mostly dealt numerically by simulations, because of the analytical difficulty in tracking the stochastic processes. Here, we present an analytical method and show that these models are principally tractable analytically. To characterize long-term behavior of the entire system, geometric mean of local growth rate has been often used [3, 4, 11]. However, this simple approach is not valid except for well-mixed cases. We present an accurate method to assess the long-term growth in this model. We derive analytically the stable distribution of populations.

Let us consider populations that inhabits in $n$ discrete habitats. Let $x_i(t)$ be the number of individuals in patch $i$ at time $t$. Thus, the state of the populations is described by a vector $x_i(t) = (x_1(t), x_2(t), \ldots x_n(t))^T$, where the superscript $T$ represents the transpose. In each habitat, the population reproduces at random growth rates. Then a fraction of the population disperses from a habitat to another habitat. The population dynamics is given by a discrete-time stochastic matrix model

$$x(t + 1) = DM(t)x(t),$$

where $D$ is a time-independent dispersal matrix, and $M(t)$ is a time-dependent diagonal matrix of local growth rate. In this paper, we focus on the case of two habitats for simplicity, but the results can be extended to a general case (i.e., $n > 2$). The dispersal matrix is given as

$$D = \begin{pmatrix} 1 - q & qs \\ qs & 1 - q \end{pmatrix}.$$  (2)

Here the parameters $q$ and $s$ are between 0 and 1. The migration rate $q$ represents the proportion of population that migrates from a habitat to the other habitat. When $q =$
0, the two habitats are isolated completely. The parameter $s$ is survival rate during the transportation between habitats. The matrix of growth rate is written as

$$M(t) = \begin{pmatrix} m_1(t) & 0 \\ 0 & m_2(t) \end{pmatrix}. \quad (3)$$

We assume that the local growth rate $m_i(t)$ ($i = 1$ or 2) is a stochastic variable which takes one of two values, $m_-$ with probability $p$ and $m_+$ with probability $1-p$. Here, we set $m_- < m_+$. This stochastic fluctuation of the local growth rate comes from environmental fluctuations. Here, we neglect the temporal correlation of the local growth rates. But we take into account the correlation between two habitats. We denote by $c$ the correlation coefficient between $m_1(t)$ and $m_2(t)$ at same time. If we denote by $p_{++}$ the probability that $m_1(t) = m_+$ and $m_2(t) = m_+$, we obtain

$$p_{++} = (1 - p)^2 + cp(1 - p)$$
$$p_{--} = p^2 + cp(1 - p)$$
$$p_{+-} = (1 - c)p(1 - p)$$
$$p_{-+} = (1 - c)p(1 - p). \quad (4)$$

The initial populations at $t = 0$ is set as $(x_1(0), x_2(0))^T = (1, 1)^T$.

To solve eq. (1), we consider the dynamics of the ratio of populations in two habitats

$$r(t) = \frac{x_2(t)}{x_1(t)}. \quad (5)$$

The dynamics of $r(t)$ is written as

$$r(t + 1) = f\left(\frac{m_2(t)}{m_1(t)} r(t)\right), \quad (6)$$

where $f(r)$ is defined as

$$f(r) = \frac{r(1 - q) + qs}{rqs + 1 - q}. \quad (7)$$

Equation (6) indicates that the future value $r(t + 1)$ depends only on the present value $r(t)$, that is, $r(t)$ follows one-dimensional Markov process. Thus, statistical state of $r(t)$ is characterized by its density distribution $\rho_t(r)$. The evolution of $\rho_t(r)$ is described by the Frobenius-Perron equation \cite{13, 14}. Using the probability $p_{--}, p_{+-}, p_{++}$ defined in eq. (4),
we have

\[
\rho_{t+1}(r) = p_+ \frac{m_+}{m_-} g(r) \rho_t \left( \frac{m_+}{m_-} f^{-1}(r) \right) \\
+ p_- \frac{m_-}{m_+} g(r) \rho_t \left( \frac{m_-}{m_+} f^{-1}(r) \right) \\
+ (p_{++} + p_{--}) g(r) \rho_t(f^{-1}(r)),
\]

where \( g(r) \) is the derivative function of \( f^{-1}(r) \):

\[
g(r) = \frac{1 - 2q - q^2(s^2 - 1)}{(rqs + q - 1)^2}. \tag{9}
\]

The density distribution \( \rho_t(r) \) converges to the stationary distribution \( \rho_*(r) \) (or invariant measure) eventually, regardless of where it begins. The distribution \( \rho_*(r) \) is determined by the recursive formula obtained by substituting \( \rho_*(r) \) for \( \rho_t(r) \) and \( \rho_{t+1}(r) \) in eq. (8).

Figure 1(a) shows an example of \( \rho_*(r) \) with a logarithmic scale. This distribution \( \rho_*(r) \) has a complicated self-similar structure. Figure 1(b) shows the time distribution obtained by simulation over 100000 time steps for the same parameter of Fig. 1(a). These two distributions agree exactly. Because of the ergodicity of a Markov process, the time average is equal to the ensemble average. The distribution of \( \ln r(t) \) is symmetric around the vertical axis \( \ln r(t) = 0 \) (Fig. 1), because this model is invariant under the permutation of \( r(t) \) and \( 1/r(t) \). This means that the distribution of \( r(t) \) coincides with that of \( 1/r(t) \). In the special case \( qs = 1 - q \), \( r(t) \) becomes one deterministically for \( t > 0 \), that is, \( \rho_*(r) = \delta(r - 1) \). This case represents well-mixed populations, which were examined by prior theoretical works [4, 7, 15, 16].

The dynamics of the populations \( x_1(t) \) and \( x_2(t) \) is described as

\[
x_1(t + 1) = x_1(t)[m_1(t)(1 - q) + m_2(t) qsr(t)], \tag{10}
\]
\[
x_2(t + 1) = x_2(t)[m_2(t)(1 - q) + m_1(t) qs/r(t)]. \tag{11}
\]

A very important point is that the stochastic variable \( r(t) \) is determined by eq. (8) and can be treated independent of \( x_1(t) \) and \( x_2(t) \). Thus, eqs. (10) and (11) are regarded as random multiplicative processes for \( x_1(t) \) and \( x_2(t) \), respectively. Taking into account the symmetry of \( r(t) \) and \( 1/r(t) \), it is obvious that the two processes (10) and (11) are identical. Hence, it is sufficient to consider only (10). Taking the logarithms of both sides of eq. (10) and
summing them from $t = 0$ to $t = T - 1$, we obtain

$$\ln x_1(T) = \sum_{t=0}^{T-1} \ln x_1(t + 1) - \ln x_1(t) = \sum_{t=0}^{T-1} \ln[m_1(t)(1-q) + m_2(t)qs r(t)].$$

Thus, $\ln x_1(T)$ is given by the sum of the time series of the effective growth rate $\ln[m_1(t)(1-q) + m_2(t)qs r(t)]$. Because the effective growth rate depends on $r(t)$, the effective growth rates have a temporal correlation. However, the auto-correlation function of the effective growth rates decays rapidly, as shown in Fig. 2(c). Thus, applying the central limit theorem, we expect the distribution of $\ln x_1(T)$ after a long time ($T \gg 1$) approaches a normal distribution. Thus, $x_1(T)$ follows a log-normal distribution. The mean value of $\ln x_1(T)$ is calculated by using the stationary distribution of $r(t)$. Moreover, in an approximation in which the temporal correlation of $r(t)$ is neglected, we can also estimate the variance of $\ln x_1(T)$. In Figs. 2(a) and (b), we show examples of the evolution of the actual ensemble distribution and the approximation results. The averages (or peaks) of the actual distributions agree exactly with the theoretical results. The actual variances are also equal to the theoretical results (Fig. 2(b)) when the auto-correlations are negligible (Fig. 2(c)). How-
FIG. 2. Evolution of probability distribution of $\ln x_1(t)$ for (a) $q = 0.2$ and (b) $q = 0.65$, when $t = 1000, 2000, \text{ and } 4000$. The other parameters are $m_+ = 3$, $m_- = 0.01$, $c = 0$, $p = 0.3$, and $s = 0.5$. The crosses stand for the distribution obtained by 100000 stochastic realizations. The lines stand for the approximation with neglecting time correlation of the effective growth rates. (c) The temporal correlation functions of the effective growth rates of $x_1(t)$ in the cases (a) and (b). We find a slight negative correlation at short time lags and rapid decay to zero. The negative correlation implies that the variance of the actual probability distribution tends to be smaller than the approximation with neglecting temporal correlation of the effective growth rate. (Color online)

However, the actual variances are smaller than the approximation results (Fig. 2(a)), when the auto-correlations are not neglected (Fig. 2(c)). Here the deviations are universally smaller because the growth rates tend to have a negative correlation in short-range intervals of time.

Because $x_1(t)$ and $x_2(t)$ obey the same stochastic process, $\ln x_2(T)$ follows the same normal distribution as $\ln x_1(T)$. At a glance, the difference $\ln x_2(T) - \ln x_1(T)$ looks like to follow a normal distribution. But this insight is not correct. Recall that $\ln r(T) = \ln x_2(T) - \ln x_1(T)$. We have concluded that this distribution has a complicated form (as is seen in Fig. 1). This indicates that the two variables $x_1(T)$ and $x_2(T)$ are not independent of each other but have a complex relationship. Thus, the simultaneous distribution of $x_1(T)$ and $x_2(T)$ has a complicated self-similar structure. For the well-mixed case ($qs = 1 - q$), $x_1(t)$ and $x_2(t)$ simply coincide. However, unless the populations are well-mixed, $\ln x_1(T) + \ln x_2(T)$ does not follow a normal distribution and furthermore resulting $x_1(T) + x_2(T)$ does not follow a log-normal distribution. The current result holds regardless of the shape of the distribution of $m_1(t)$ and $m_2(t)$, since it is not because of the restriction that $m_1(t)$ and $m_2(t)$ can have only two values.
Which population survives is assessed by the ensemble average of the long-term population growth
\[ \langle \frac{1}{T} \ln x_1(T) \rangle. \] (13)
For the well-mixed case \((qs = 1 - q)\), the long-term growth rate (13) is rewritten by the average of local growth rates
\[ \langle \frac{1}{T} \ln x_1(T) \rangle = p_{++} \ln(2m_+) + p_{--} \ln(2m_-) + 2p_{+-} \ln(m_+ + m_-) + \ln(1 - q). \] (14)
Contrarily, for the isolated case \((q = 0)\), it is calculated as \((1 - p) \ln m_+ + p \ln m_-\). For general cases, however, the long-term growth rate (13) cannot be written in a simple form. To obtain the value of (13), we need to calculate (12) by the stationary distribution of (8) with the help of computer.

Figure 3 gives a comparison between numerical simulations and analytical results. If the long-term growth rate (13) for \(q = 0\) is negative, the population cannot survive in a single habitat. As shown in Fig. 3(a), the growth rate increases with the migration rate \(q\) until the optimal migration rate \(q^*\), where the long-term growth rate has the maximal value. Consequently, the dispersal is advantageous for the populations to persist. Figure 3(a) shows that the effect of dispersal is strong (weak) when the environments of habitats have a negative (positive) correlation. In Fig. 3(b), we plot the optimal migration rate \(q^*\) as a function of survival rate \(s\) for five values of \(p\). The curves for \(p\) and \(1 - p\) coincide, because of the symmetry between the two habitats. Although the optimal migration rate \(q^*\) decreases with decreasing \(s\), \(q^*\) remains finite even for relatively small \(s\). Note that the average \(\langle \frac{1}{T} \ln x_1(T) \rangle\) is the logarithm of the geometric average of \(x_1(T)\). Since \(x_1(T)\) follows a lognormal distribution, the geometric average of \(x_1(T)\) coincides with the median of \(x_1(T)\). This means that when the long-term population growth (eq. (13)) is positive (negative), the population grows (decays) with a probability of more than half.

Risk-spreading phenomena have been treated in biology and economics applying discrete stochastic linear metapopulation models. Most these studies are based on numerical approaches, except well-mixed cases that can be solved by simple algebra. Here we have solved analytically the cases of non-well-mixed populations. Our approaches can be widely applicable for forecasting long-term trends not only in physical phenomena, but also in population biology and economic forecasting. Even complex stochastic problems may be
tractable and solved analytically in this approach.

We analyzed the case of two habitats for simplicity. In the case of more than two habitats, the qualitative prediction should be same as in the case two habitats. Here we could expect the same The above results are expanded to the case of networks with more than two habitats. Here, the ratios of populations among habitats have a complicated self-similar stationary distribution, while each population always has a log-normal distribution. In other words, the simultaneous distribution has a complicated structure, but its marginal distributions always follow a log-normal distribution. However, the numerical calculations become terribly cumbersome even in the case of three habitats. We should note here that this problem of multiple habitats may be treated in the framework of metapopulation dynamics because some analytical solutions are already acquired[17, 18]. We may also apply the current model to the studies of horizontal gene transfer in two distinctive environmental states[19, 20]. We can also add a nonlinear effect to the current linear model. Then, the stable distribution departs from a log-normal distribution. For example, the density dependent effect prevents a population from increasing to an infinitely large number. On the other hand, it is well-known that a finite injection leads to a power law distribution.
Although these cases have not been investigated here, we can conjecture that the simultaneous distribution may still show have complicated self-similarity. In addition, some environmental factors are naturally correlated in successive times, resulting in the temporal correlations in local growth rates. These cases are treated numerically [7], because temporal correlations are extremely complex and highly tedious to treat analytically. The current method may be applicable to solve these models analytically and we expect no qualitative differences from the current results. We also find robustness in environmental parameters $m_+$, $m_-$, $p$ and $c$. We generally could conclude that the stochasticity always promotes dispersal to ensure the long term survival even if the cost of migration is considerably high.

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