Moment-closure Approximations to Levins Metapopulation Model

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Abstract

In this study, we apply the log-normal mixture and beta-binomial mixture approximations to the stochastic version of the Levins metapopulation model. Mixture approximations are able to capture the behaviour of the model around the threshold between persistence and extinction of occupied patches. Comparison with simulation results show that mixture approximations are able to predict extinction behaviour but on a shorter time scale than the simulations, describe meta-stable persistence of occupied patches but slightly underestimate the mean and describe quasi-equilibrium probabilities.

Introduction

We extend the application of closure approximations to the stochastic version of Levins metapopulation model widely used in ecology. A metapopulation refers to an aggregation of populations or species that inhabit small patches of an area. Each of the populations is called a 'local population' and have a substantial probability of becoming extinct (Hanski, 1999). In order for the species to persist, they may migrate or colonise empty patches so that long-term persistence can only occur at metapopulation level (Hanski, 1999). Thus, at any given time a non-zero proportion of patches is occupied. However, the metapopulation will eventually go extinct if each occupied patch is desolated. This is an interesting property and important phenomenon in ecology. Stochastic techniques have been used in ecological studies previously (Isham, 1995; Levin and Durret, 1996; Keeling, 1997; Bolker and Pacala, 1997; Keeling, 2000a,b, 2002; Ovaskainen and Hanski, 2004). Particularly in the application of moment-closure techniques to metapopulation ecology, Keeling (2000b) developed the concept of multiplicative moments for the third-order cumulant and this technique was used to consider the behaviour and persistence of a finite sized metapopulation. This multiplicative concept is equivalent to assuming a log-normal distribution for the population size. However, it is difficult to describe extinction behaviour by any existing closure schemes. It is natural to consider the log-normal mixture and beta-binomial mixture approximations (Krishnarajah et al., 2005) for this purpose.

Levins metapopulation model is described in section 2 and analysed by mo ment closure schemes in section 3. The conclusion is presented in section 4 with a discussion of the results.

Levins metapopulation model

We consider the concept of metapopulations (Levins, 1969) which has been important to ecologists in describing the patch occupancy dynamics. "In 1970, Richard Levins coined the term metapopulation to describe a 'population' consisting of many local populations, in the same sense in which a local population is a population consisting of individuals" (Hanski, 1999). When the local population moves or local extinction occurs, then an occupied patch becomes unoccupied. Colonisation by individuals from an occupied patch in the system makes an unoccupied patch occupied. Levins (1969) illustrated the fact that in order to control the persistence or extinction of any species, populations at the metapopulation level need to be considered. In particular local extinctions must be balanced by immigration from other patches. The Levins model gives the rate of change in the number of occupied local populations, n (t), as

$$\frac{dn}{dt} = r_c n\left(1 - n / N\right) - r_e n \qquad (1)$$

where r_c is the colonisation or migration rate parameter and re contributes to the extinction rate for a local population. N denotes the total number of potential patches or habitats that can support local populations. When $r_e / r_c > 1$, the metapopulation goes extinct rapidly. The essential condition for the metapopulation to persist is $r_e / r_c < 1$ (Hanski, 1999). This model is deterministic and assumes that extinction occurs independently in different patches. Migration and recolonisation of empty patches is important to ensure dynamic equilibrium of occupied patches and the persistence of a species at metapopulation level.

Using the deterministic Levins model in equation (1), we formulate the stochastic model (Keeling, 2002) in which extinction and colonisation of a patch is described by the following transition probabilities

$$\text{Prob}\left[\delta_n(t+\Delta t)=1\right]=r_c n\left(1-\frac{n}{N}\right)\Delta t \qquad (2)$$

$$\text{Prob}\left[\delta_n(t+\Delta t)=-1\right]=r_e n\Delta t \qquad (3)$$

We create the equilibrium distribution as shown in Keeling (2002) and apply the log-normal mixture and beta-binomial mixture approximations (Krishnarajah et al., 2005) to the two different cases, namely N = 10 and N = 100 fixing the parameters r_e = 0.17 and r_c = 0.5 with an initial condition of five occupied patches (n_0= 5). The stochastic process is simulated with the inter-event time exponentially distributed with rate $R = r_c n(1-n/N)+r_e n$ and a patch is colonised with probability $r_c n(1-n/N)/R$ or an occupied patch becomes extinct with probability $r_e n/R$ (Renshaw, 1991; Krishnarajah, 2005).

Graphs (a) and (b) of Figure 1 show the simulation results of single realisations of the stochastic Levins metapopulation model. When N = 10 (10 potential patches or habitats) with 5 populated patches initially, the simulation results show that the population is unable to persist for a long period of time as seen in graph (a). The extinction of each local population leads to global extinction or extinction at metapopulation level rather quickly. Whereas, the process reaches equilibrium quickly when there are 100 patches that can support local populations, with the number of occupied patches fluctuating around 60 (graph (b). In this case local extinction seems rare thus making global extinction impossible for the finite time considered.

The histograms, graphs (c) and (d), of Figure 1 were obtained from 105 simulations for t = 100 in which the system is allowed to reach equilibrium. From the histogram representing the distribution of occupied patches, we can see that when N is small (10 potential habitats) the distribution is bimodal with a mode at n = 0. Thus, when there are just a few potential habitats, global extinction is frequent. When N is large (N = 100), global extinction of occupied patches are rare and the histogram approaches normality as it moves away from 0 (Keeling, 2002). Thus, as the number of potential habitats increase, there is more chance for migration and new colonisation. This reduces the chance of a species becoming extinct as there is always a large proportion of occupied habitats in the metapopulation.

In the following sections we perform the moment closure analysis to see if this sort of bimodality and persistence behaviour of an ecological system is predicted by the moment equations derived using the mixture approximations.

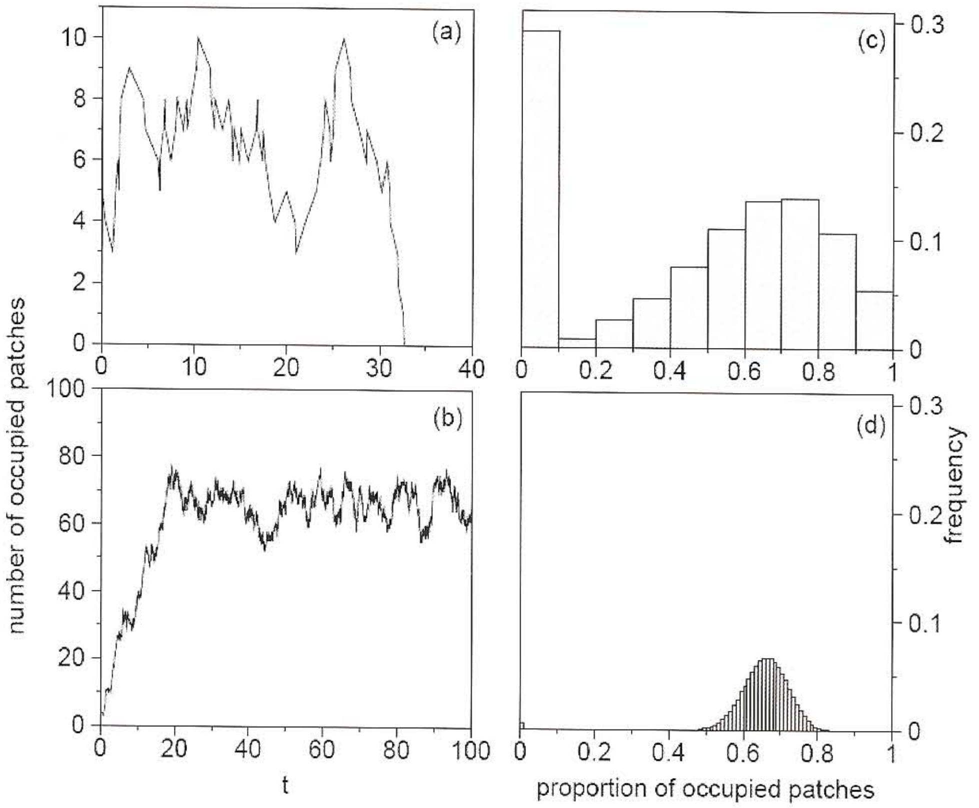

Figure 1: Single realizations (a-b) show the number of occupied patches, n, over time, t, and histograms (c-d) show the proportion of occupied patches, n/N

Moment evolution equations

We study the stochastic version of Levins metapopulation model in terms of a system of moment equations with the first moment $E[n(t)]$, describing the expected number of occupied patches. The three differential equations describing how the first moment, $E[n(t)]$, second moment, $E[n^2(t)]$ and third moment $E[n^3(t)]$ equations of the stochastic process evolve over time, are

$$\frac{dE[n(t)]}{dt} = (r_c - r_e)E[n(t)] - \frac{r_c}{N}E[n^2(t)] \quad (4)$$

$$\frac{dE[n(t)]}{dt} = (r_c - r_e)E[n(t)] + \left(2r_c - 2r_e - \frac{r_c}{N}\right)E[n^2(t)] - \frac{2r_c}{N}E[n^3(t)] \quad (5)$$

$$\frac{dE[n(t)]}{dt} = (r_c - r_e)E[n(t)] + \left(3r_c - 3r_e - \frac{r_c}{N}\right)E[n^2(t)] + 3\left(r_c - r_e - \frac{r_c}{N}\right)E[n^3(t)] - \frac{3r_c}{N}E[n^4(t)] \quad (6)$$

These equations are open, meaning that the differential equation for the lower moments depend on higher order terms. Thus closure scheme is needed, so that they can be solved numerically. Hence, we apply the log-normal mixture and beta-binomial mixture approximations to close the system of equations. A detailed description of the derivation of these mixture approximations is given in Krishnarajah et al. (2005). The probability density function of the log-normal mixture distribution is

$$P_t(n) = p\pi_1(n) + (1-p)\left(\frac{1}{n\sqrt{2\pi k_2}}\exp\left(\frac{-(\log n - k_1)^2}{2k_2}\right)\right) \quad (7)$$

where $\pi_1(n) = \delta_{n,0}$ and p is the probability of extinction, k_1 is the mean and k_2 is the variance of the log-normal (Kendall, 1994). The log-normal is defined on $0 \le n \le \infty$ where n is the number of occupied patches and N denotes the number of potential patches. The symbol $\delta_{n,0}$ is the Kronecker delta (Arfken, 1985) defined by

$$\delta_{n,0} = \begin{cases} 1 & \text{if } n = 0 \\ 0 & \text{otherwise} \end{cases} \tag{8}$$

The probability mass function of the beta-binomial mixture distribution (Krishnarajah, 2005) is

$$P_t(n) = p\pi_1(n) + (1-p)\left(\frac{N!B(n+a, N+b-n)}{n!(N-n)!B(a,b)}\right) \tag{9}$$

where

$$\pi_1(n) = \begin{cases} 1 & \text{if } n = 0 \\ 0 & \text{for } n = 1, 2, \dots, N. \end{cases} \tag{10}$$

$B(a,b)$ is the beta function given by

$$B(a,b) = \int_0^1 n^{a-1}(1-n)^{b-1}\,dn \tag{11}$$

The beta-binomial is defined on n = 0, 1, 2,..., N where n and N are as defined previously in the text. a and b are the shape parameters of the beta-binomial distribution.

Results and discussion

The results of both mixture approximations for the stochastic model described by equations (2) and (3), are compared with the simulation results and shown in Figure 2.

Graph (a) shows the expected number of occupied patches over time and (c) shows the estimated variances over time for N = 10 potential patches. These results match with the description of bimodality as shown in Figure 1 (a) and (c) in which some of the patches are colonised and remain occupied for a considerable period of time although ultimate global extinction is assured over time. Both the log-normal mixture and beta-binomial mixture approximations are able to estimate new colonisation and the rise in number of occupied patches as shown by the stochastic model. They are also able to show that after a period of time local extinctions (extinction of local populations) occur leading to global extinction of the metapopulation. Unfortunately, extinction of the metapopulation is predicted on a shorter time scale compared to the simulations. The mixture approximations are able to mimic the behaviour shown by the stochastic model but predict extinction to occur too quickly. The variance of the system is slightly overestimated in the beginning of the process but eventually underestimated over time (graph (c)) due to overestimation of extinction.

When the number of potential patches are increased to N = 100, global extinction becomes rare. Meta-stable equilibrium is reached meaning that there is a balance between patch extinction and patch colonisation that remains constant over a long period of time. The mixture approximations are able to predict this persistence of the metapopulation as shown by simulations (graph (b) of Figure 2) but slightly underestimate the expected number of occupied patches. The variance of the process is overestimated by both the log-normal and beta-binomial mixture approximations. The mixture approximations are able to predict the qualitative behaviour of this ecological system but the overall temporal evolution of the process does not agree well with the simulation results in both cases.

Figure 3 shows the theoretical, beta-binomial mixture and log-normal mixture probabilities for the stochastic Levins model conditioned on extinction not having occurred. The equilibrium probabilities computed from the beta-binomial mixture distribution agree well with the computed theoretical probabilities in both cases. The log-normal mixture form gives a fair description of the equilibrium probabilities when N = 100. The beta-binomial mixture is more flexible in approximating the probabilities of the model conditional on non-extinction. It is able to capture the dynamics of the theoretical probability mass function of the stochastic model better than the log-normal mixture distribution.

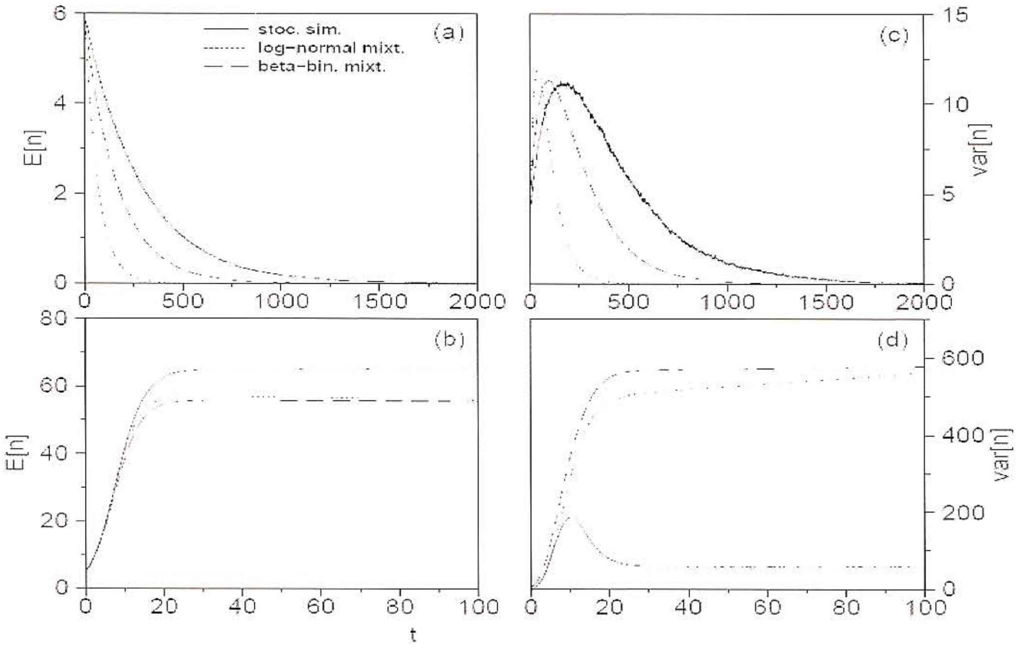

Figure 2: Mixture approximation and simulation results for N = 10 (a and c) and N = 100 (b and d). Expectednumber of occupied patches (a and b) and variance (c and d) obtained from the mixture approximations and stochastics simulation over time.

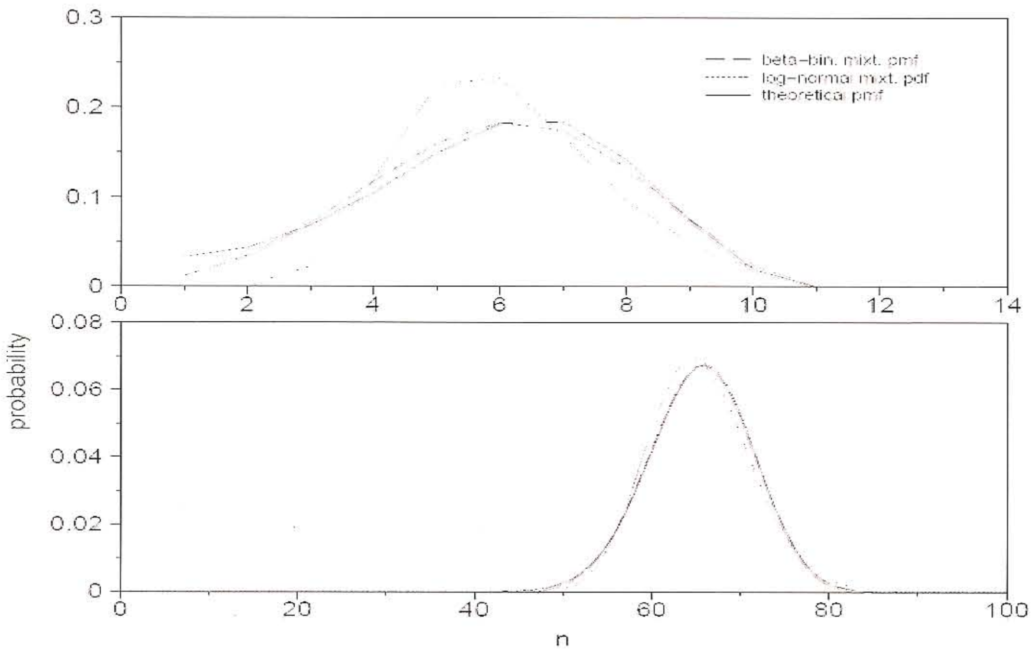

Figure 3: Comparison of theoretical, beta-binomial mixture and log-normal mixture quasi-equilibrium probabilities in the cases of 10 and 100 potential patches.

Conclusion

In this study we applied the mixture approximations in an ecological context. In case of the stochastic Levins metapopulation model, we applied the log-normal and beta-binomial mixture approximations. The mixture approximations are able to predict extinction behaviours of the occupied patches and global extinction of the population seen for small N, but do so on a shorter time scale than that predicted by the simulations. The mixture approximations are also able to mimic the persistence of the colonised patches as seen in the simulations (for large N=100) but slightly underestimates the mean. The behaviour shown by the mixture approximations are qualitatively correct. However, the beta-binomial mixture approximation is able to predict the quasi-equilibrium probabilities conditioned on non-extinction very well.

Both log-normal mixture and beta-binomial mixture approximations overes timate the rate of extinction in case of the Levins metapopulation model. However, the beta-binomial mixture distribution gives a better description of quasi-equilibrium probabilities of the Levins model than the log-normal mixture.

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