Extinction risk of a meta-population: aggregation approach

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Abstract

Aggregation of variables of a complex mathematical model with realistic structure gives a simplified model which is more suitable than the original one when the amount of data for parameter estimation is limited. Here we explore use of a formula derived for a single unstructured population (canonical model) in predicting the extinction time for a population living in multiple habitats. In particular we focus multiple populations each following logistic growth with demographic and environmental stochasticities, and examine how the mean extinction time depends on the migration and environmental correlation. When migration rate and/or environmental correlation are very large or very small, we may express the mean extinction time exactly using the formula with properly modified parameters. When parameters are of intermediate magnitude, we generate a Monte Carlo time series of the population size for the realistic structured model, estimate the “effective parameters” by fitting the time series to the canonical model, and then calculate the mean extinction time using the formula for a single population. The mean extinction time predicted by the formula was close to those obtained from direct computer simulation of structured models. We conclude that the formula for an unstructured single-population model has good approximation capability and can be applicable in estimating the extinction risk of the structured meta-population model for a limited data set.

Keywords: Aggregation; Extinction; Mean extinction time; Correlation of environmental fluctuation; Migration rate

1. Introduction

In practical ecological risk assessment (e.g., Primack, 2002; Nakanishi et al., 2003), aggregating components in realistic and complex models is beneficial to estimate the extinction risk of populations using a limited data set. The theory of model selection (Akaike, 1973; Linhart and Zucchini, 1986; Burnham and Anderson, 2002) supports the use of simplified and aggregated models. An “operating model” gives an accurate and detailed representation of nature. If we had the exact values of all the parameters, the complex operating model should be the best one for predictions and decisions in risk assessment. However, in reality, we have to use uncertain parameter values estimated from limited data. If we estimate too many parameters from limited data, complex models perform, on average, worse than simple models. This is because complex models show instability for each repeated sample and the output of models reflects the particularities of data set more than the underlying phenomenon. The optimal size of models is much smaller than intuition dictates (Hilborn and Mangel, 1997). In general, the “accuracy” of prediction depends on the amount of data relative to the number of parameters, and for a small sample size a model aggregated appropriately shows the best performance for prediction. A problem of model selection is to find such an approximate model for a given sample size (Linhart and Zucchini, 1986).

There are many ways to aggregate a given complex model, and approximated models differ in performance. We ask whether an aggregated simple model with a
small number of variables can be used as a good surrogate to a realistic and complicated model. The approximation capability of an aggregated model is measured by the discrepancy between the complex model and the approximating model with the parameter set chosen to fit the complex model (Linhart and Zucchini, 1986). There have been studies on perfect aggregation condition for a simple deterministic model (Hakoyama and Iwasa, 1986). However these results of aggregation theory are at this moment too general to be practical, and the method of useful aggregation must be studied separately for each problem (e.g., Michalski et al., 1997; Lett et al., 2003).

In this paper we apply the aggregation idea in evaluating population extinction risk. We study the mean extinction time for a meta-population, which consists of local populations linked each other by migration (MacArthur and Wilson, 1967; Levins, 1969, 1970, see also Hanski and Gilpin, 1991; Hastings and Harrison, 1994; Hanski and Ovaskainen, 2003 for reviews). We use a single population model (canonical model: Hakoyama and Iwasa, 2000a) as the one approximating the meta-population (operating model). We first explain the single population model and the estimate procedure, and then consider a population living in two separate habitats. The two subpopulations are similar in size and local populations are connected by migration. The environmental fluctuation can be correlated. The estimate of mean extinction time of the whole population strongly depends on the migration rate and the correlation coefficient of the environmental fluctuation in these two. We show mathematically that, in the limit of very fast migration, the two populations can be considered as a single population if parameters (intrinsic rate of natural population growth, carrying capacity and environmental stochasticity) are replaced properly. We also derive the mean extinction time in the case in which environment is uncorrelated and migration is non-existent between populations. When parameters are of intermediate magnitude, we need to use computer simulation to know the mean extinction time of the two patches model. To examine the approximation capability of the canonical model to the meta-population model in terms of the accuracy of estimating the mean extinction time, we use the parameter fitting by Monte Carlo time-series data. We generate a time series of population size from the structured population (i.e. meta-population), then find “effective parameters” by fitting to the canonical model, and calculate an estimate of the mean extinction time using a formula (estimator) derived for a single unstructured population model (the canonical model), studied in Hakoyama and Iwasa (2000a). By comparing these results with the direct computer simulation of meta-population model, we can discuss the accuracy and failure of the aggregated model. This procedure is an example of model simplification, or “aggregation” (see Discussion and Fig. 5 of Iwasa et al., 2000). We also discuss the extension to a meta-population composed of more than two local populations.

2. Canonical model and parameter estimation from time series

In previous papers, we studied a single density-dependent population with logistic growth and environmental and demographic stochasticities (canonical model), and we developed a method to estimate the mean extinction time from the time series of population fluctuation (Hakoyama and Iwasa, 2000a; Hakoyama et al., 2000; Iwasa et al., 2000). The decline of the sustainability of populations by human activities (or management options) is evaluated by the decrease of the mean extinction time, and it can be used in comparing different options of environmental management (Hakoyama and Iwasa, 2000a; Hakoyama et al., 2000, Iwasa et al., 2000; Nakamaru et al., 2002, 2003). For example, Hakoyama et al. (2000) have compared the risk of habitat destruction and toxic-chemical exposure by using the relative increase of extinction risk. Nakamaru et al. (2002, 2003) have assessed the risk of DDT and its metabolites for birds by using the enhanced extinction risk. They expressed it in terms of “risk equivalent”; the reduction of carrying capacity $K$ that causes the same enhancement of the extinction risk.

A single population model, called “canonical model” is represented by the following stochastic differential equation:

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) + \sigma_e \xi_r(t) + \xi_d(t) \cdot \sqrt{X},$$

$$\quad (r, K \text{ and } \sigma_e > 0), \quad (1)$$

where $X$ is the population size at time $t$. The first term on the r.h.s. is the logistic growth with intrinsic rate of natural growth $r$ and the carrying capacity $K$. $\xi_r(t)$ and $\xi_d(t)$ are independent white noises for environmental and demographic stochasticities, respectively. $\sigma_e$ is the intensity of the environmental fluctuation. Environmental stochasticity caused by large-scale fluctuations in conditions (e.g., climate) is common to all the individuals, but demographic stochasticity arises from independent chances of individual fitness (Lande, 1993; Hakoyama and Iwasa, 2000a). We can model these stochasticities as a diffusion process like Eq. (1), if the fluctuation of the population size is not catastrophic.
Stratonovich-calculus is assumed for the environmental fluctuation (indicated by a small open circle) and Ito-calculus in the demographic stochasticity (indicated by a solid circle) (see Hakoyma and Iwasa, 2000a for detail). This choice was made for the convenience of parameter fitting to time-series data. Ito-calculus for the environmental fluctuation is adopted in other works (Ludwig, 1976; Lande, 1993; Lande et al., 1995), but these two are mathematically equivalent if parameters are replaced in a correct manner (Hakoyma and Iwasa, 2000a).

In a density-dependent population, such as Eq. (1), after the initial transient period, the population size may stay around the carrying capacity fluctuating for a long time before extinction. Therefore, the extinction time follows an exponential distribution approximately, and we can treat extinction events as if they occur at random (Quinn and Hastings, 1987). In such a situation, the extinction risk can be characterized well by a single quantity—the mean time to extinction. The mean extinction time of Eq. (1) is

$$T = \frac{2}{\sigma_e^2} \int_0^\infty \int_x^\infty e^{-R(y-x)} \left( \frac{y+D}{x+D} \right)^{R(D+1)} \frac{dy}{(y+D)^y} \, dx,$$

(2)

where $R \equiv \frac{2r}{\sigma_e^2}$ and $D \equiv \frac{1}{r}$ (Hakoyma and Iwasa, 2000a). We use the average extinction time starting from the carrying capacity $x_0 = K$ in the following analysis (see Shaffer, 1987; Lande, 1993; Lande et al., 1995). Eq. (2) is then a function of the parameters $r$, $K$ and $\sigma_e^2$. It is denoted by $T = \varphi(r, K, \sigma_e^2)$. The dependence of $T$ on the carrying capacity $K$ is

$$\ln T \approx \frac{2r}{\sigma_e^2} \ln K + \text{[terms independent of $K$]}$$

(Hakoyma and Iwasa, 2000a; see also Ludwig, 1976; Lande, 1993).

To apply the model to a field population, we need to estimate three parameters. The intrinsic rate of population growth $r$ may be available from demographic and ecological studies, or knowledge of experts (Foley, 2000; Etienne et al., 2003). However, the carrying capacity and the environmental fluctuation $\sigma_e^2$, sometimes $r$ as well, need to be estimated from the population fluctuation. Hakoyma and Iwasa (2000a) developed the estimate of unknown parameters from a given time series of population size $\{X(t)\}$. As mentioned above, for density-dependent populations, the population size fluctuates around the carrying capacity for a long time before going extinct. In this case, we may consider quasi-equilibrium probability distribution of population size controlled by logistic growth and environmental stochasticity. If the demographic stochasticity is much smaller than the environmental stochasticity, as is the case if the population size is moderately large, carrying capacity $K$ and environmental stochasticity $\sigma_e^2$ are related to the mean and the variance of the population size:

$$K = E[X(t)],$$

$$\sigma_e^2 = 2r \cdot Var[X(t)]/E[X(t)^2],$$

(4a)

(4b)

in which the expectation can be replaced by the average over the years. Eq. (4a) implies that the carrying capacity can be estimated simply from the average population size. This is possible even if the magnitude of fluctuation in the population size caused by environmental stochasticity is large. Eq. (4b) indicates that the environmental stochasticity can be estimated from the magnitude of population fluctuation, if $r$ is known. If a reliable estimate of $r$ is not available, we can still estimate $r$ from only a time series of population size. If $r$ is larger, autocovariance drops faster, i.e. the population fluctuates more quickly over time.

Hakoyma and Iwasa (2000a) developed the approximate maximum likelihood estimator. To know the reliability of the estimation method, Hakoyma and Iwasa (2000a, b) carried out Monte Carlo analyses, and derived a new method (Monte Carlo Bias Correction, MCBC) of removing the bias in estimates and the estimating the confidence interval of the parameters. The confidence intervals are asymptotically exact and the bias-corrected estimator is almost an unbiased estimator even for small sample size. Satake et al. (2004) adopted MCBC in removing the bias in spatio-temporal dynamics and analysed the vegetation height dynamics of tropical rain forests. In the following, we adopt the MCBC based on the approximate maximum likelihood estimate when we need to estimate parameters from time-series data.

3. Two populations model

Let $X_1$ and $X_2$ be the sizes of two populations, each following a stochastic model with logistic equation:

$$\frac{dX_1}{dt} = rX_1 \left( 1 - \frac{X_1}{K} \right) + \varepsilon_1(t) \cdot \sqrt{X_1 + m(X_2 - X_1)},$$

(5a)

$$\frac{dX_2}{dt} = rX_2 \left( 1 - \frac{X_2}{K} \right) + \varepsilon_2(t) \cdot \sqrt{X_2 + m(X_1 - X_2)},$$

(5b)

where $\varepsilon_1(t)$ and $\varepsilon_2(t)$ are Gaussian white noises of environmental stochasticity with magnitude of $\sigma_e^2$. These satisfy

$$E[\varepsilon_1(t)] = E[\varepsilon_2(t)] = 0,$$

(5c)

$$\text{Cov}[\varepsilon_1(t), \varepsilon_1(t+\tau)] = \text{Cov}[\varepsilon_2(t), \varepsilon_2(t+\tau)] = \sigma_e^2 \delta(\tau),$$

(5d)
where \( \delta(\tau) \) is the delta function. Environments in the two habitats may be correlated if they receive a common large-scale climatic fluctuation. In the extreme case of strong covariance in environmental fluctuation, \( \xi_1(t) = \xi_2(t) \). On the other hand, if the two habitats are at a great distance, independent environmental fluctuations may occur in each habitat. The alternative extreme is perfect independence of \( \xi_1(t) \) and \( \xi_2(t) \). In between these two, there is a spectrum of situations with intermediate degree of correlation of these two. The environmental correlation represents implicitly the effect of the distance between habitats and the scale of various environmental fluctuations. Let \( \rho \) be the correlation coefficient between \( \xi_1(t) \) and \( \xi_2(t) \). Correlated environmental fluctuation can be represented by considering three independent white noises \( \eta_1(t) \), \( \eta_2(t) \), and \( \eta_3(t) \), each with auto-covariance function \( \delta(\tau) \). Then we set

\[
\begin{align*}
\xi_1(t) &= \sigma_1(\sqrt{1 - \rho \eta_1(t)} + \sqrt{\rho \eta_3(t)}) \\
\xi_2(t) &= \sigma_2(\sqrt{1 - \rho \eta_2(t)} + \sqrt{\rho \eta_3(t)}).
\end{align*}
\]

(5e)

\( \xi_1(t) \) and \( \xi_2(t) \) have auto-covariance function \( \sigma_i^2 \delta(\tau) \) each, and their cross-covariance function \( \text{Cov}[\xi_1(t), \xi_2(t + \tau)] = \rho \sigma_1^2 \delta(\tau) \).

\( \zeta_{d1}(t) \) and \( \zeta_{d2}(t) \) in Eq. (5a) and (5b) are independent white noises of demographic stochasticity. Demographic stochasticity is clearly independent between local populations, because it arises from independent variabilities of individual fitness. \( m \) is the migration rate.

The intrinsic growth rate, \( r \), and the carrying capacity, \( K \), are the same in two patches of this model.

For general values of migration rate between the populations \( 0 \leq m < \infty \) and different correlation \( \rho \) of the environmental fluctuations in two habitats \( (0 \leq \rho \leq 1) \), we carried out computer simulation using the following Euler method.

### 3.1. Computer simulation—population dynamics in two habitats

During a short time interval of length \( \Delta t \), the change in the population sizes \( \Delta X_1 \) and \( \Delta X_2 \) is given as follows:

\[
\begin{align*}
\Delta X_1 &= \left[r X_1 \left(1 - \frac{X_1}{K}\right) + \frac{1}{2} \sigma_1^2 X_1 + m (X_2 - X_1)\right] \Delta t \\
&\quad + X_1 \Delta \xi_1 + \sqrt{X_1} \Delta \zeta_{d1},
\end{align*}
\]

(6a)

\[
\begin{align*}
\Delta X_2 &= \left[r X_2 \left(1 - \frac{X_2}{K}\right) + \frac{1}{2} \sigma_2^2 X_2 + m (X_1 - X_2)\right] \Delta t \\
&\quad + X_2 \Delta \xi_2 + \sqrt{X_2} \Delta \zeta_{d2}.
\end{align*}
\]

(6b)

Here, we generate the fluctuations of environment that is correlated between the two habitats:

\[
\begin{align*}
\Delta \xi_1 &= \sigma_1(\sqrt{1 - \rho \Delta \eta_1} + \sqrt{\rho \Delta \eta_3}) \quad \text{and}
\Delta \xi_2 &= \sigma_2(\sqrt{1 - \rho \Delta \eta_2} + \sqrt{\rho \Delta \eta_3}) \quad (i = 1, 2),
\end{align*}
\]

(6c)

where \( \Delta \eta_1 \), \( \Delta \eta_2 \), and \( \Delta \eta_3 \) are stochastic variables with mean 0 and variance \( \Delta t \) and are independent of each other and over time.

For each set of parameter values, we calculated at least 1000 replicates (mean \( \pm \) SD: \( 2723.3 \pm 865.7 \)), and then estimated the extinction time. The results are shown in Fig. 1a as a density plot. It indicates that the extinction time is the largest when migration rate is large \( (m = 1) \) and correlation of environmental fluctuation is weak \( (\rho = 0) \). Smaller migration rate and stronger correlation make the extinction time shorter.

\[
\begin{align*}
\text{Fig. 1. The density plot of the common (i.e. base 10) logarithm of mean extinction time of the population in two habitats. Dark color indicates long mean extinction time. Horizontal axis is for the migration rate \( m \) and vertical axis is for the correlation coefficient of environmental fluctuation \( \rho \).} \quad \text{\( r = 0.1 \), \( K = 100 \), \( \sigma_1^2 = 1 \). (a) Computer simulation ("true" value): The time increment \( Dt \) is 0.001. (b) Aggregation estimates: We estimated \( T \) from Monte Carlo sampling paths of the total population size \( X_1(t) + X_2(t) \) using the formula Eq. (2) derived for a single population model with the parameters estimated from time series. Sample path in quasi-equilibrium includes 50 years with 0.001 intervals \( (50 \times 1000 = 50000 \) points). We generated 10000 sample paths and estimated \( T \) for each path, and calculated the average of \( T \) as "estimated" \( T \).}
\end{align*}
\]
The two-habitats model is similar to that of Hill et al. (2002), which is a meta-population model that considers the regional and local dynamics simultaneously. In the continuous-time model, Hill et al. (2002) assume that there is no correlation in environmental fluctuation between patches. They also have examined a discrete-time meta-population model to examine the effect of the environmental correlation. Hill et al. (2002) have found that the mean extinction time with a small dispersal rate is considerably longer than the one without migration.

4. Soluble cases with very large or very small parameters

For several cases in which correlation coefficient $\rho$ or migration rate $m$ are extreme values, we can express the mean extinction time of coupled populations in terms of the formula for a single well-mixed population, given by Eq. (2), provided that we replace the parameters by suitable values (Fig. 2).

4.1. Very strong migration

If migration rate $m$ is very large, we expect that the two population sizes are kept equal, which allows some simplification of the analysis. By assuming Eqs. (5a) and (5b), the migration between habitats is canceled and the total population size $Z = X_1 + X_2$ follows:

$$\Delta Z = rZ \left(1 - \frac{Z}{2K}\right) + \frac{1}{2} \sigma_2^2 Z + \frac{\varepsilon_1(t) + \varepsilon_2(t)}{2} \cdot Z + \xi_3(t)\sqrt{Z},$$

in which $X_1$ and $X_2$ are replaced by $X_1 = X_2 = \frac{Z}{2}$. Note that the r.h.s. of Eq. (7) is a function of the variable $Z$ only (not $X_1$ or $X_2$ separately). The aggregated dynamics of the variable $Z$ is, therefore, completely self-described—or perfect aggregation holds (Iwasa et al., 1987; Gard, 1988). The arithmetic average of the environmental stochasticities of the two populations $\bar{\varepsilon} = \frac{\varepsilon(t) + \varepsilon(t)}{2}$ controls the environmental fluctuation of the total population. The mean and variance of this quantity are:

$$E[\bar{\varepsilon}(t)] = 0,$$

$$Cov[\bar{\varepsilon}(t), \bar{\varepsilon}(t)] = \frac{1}{4} \left( Cov[\varepsilon_1(t), \varepsilon_1(t)] + 2 Cov[\varepsilon_1(t), \varepsilon_2(t)] + Cov[\varepsilon_2(t), \varepsilon_2(t)] \right)$$

$$= \frac{1}{2} \sigma_2^2 (1 + \rho),$$

where $\rho$ is correlation coefficient between the environmental fluctuations, $\varepsilon_1(t)$ and $\varepsilon_2(t)$, in the two populations. We can express $\bar{\varepsilon}$ using a white noise $\xi_2$; $\bar{\varepsilon} = (\frac{\varepsilon}{2}) \xi_2$. Using Eqs. (8a) and (8b), Eq. (7) is rewritten as:

$$\Delta Z = \tilde{r} Z \left(1 - \frac{Z}{K}\right) + \tilde{\sigma}_e \xi_2(t) \cdot Z + \xi_3(t) \cdot \sqrt{Z},$$

where $\tilde{r} = r \left(1 + \frac{\sigma_1^2 (1 - \rho)}{4r}\right)$, $\tilde{K} = 2K \left(1 + \frac{\sigma_2^2 (1 - \rho)}{4r}\right)$, and $\tilde{\sigma}_e^2 = \frac{\sigma_2^2 (1 + \rho)}{2}$. This implies that the total population size of meta-population $Z$ follows the single-population model exactly. Then, the mean extinction time of the metapopulation in the strong migration limit is given by:

$$T[m = \infty, \rho] = \phi(\bar{\varepsilon}, \tilde{K}, \tilde{\sigma}_e^2), \quad 0 \leq \rho \leq 1,$$

where function $\phi(r, K, \sigma_e^2)$ is given by Eq. (2). Hence the effective size of carrying capacity is more than twice as large as the original value but the size of this excess is larger when the environment are less strongly correlated. The same is true for the effective value of intrinsic natural increase $r$. The stochastic chain rule known as Ito’s formula explains the dependencies of the effective parameters on the correlation coefficient. From the stochastic chain rule, there is a term $\frac{1}{2} \sigma_e^2 Z$ on the r.h.s. of Eq. (7), which depends on the intensity of the environmental stochasticity $\sigma_e^2$. Therefore, environmental correlation affects not only the effective intensity of environmental stochasticity $\sigma_e^2$, but also the effective size of carrying capacity $\tilde{K}$ and that of intrinsic natural increase $\tilde{r}$.

If the environmental fluctuation in two habitats is perfectly synchronized ($\rho = 1$), the mean extinction time with infinitely large migration rate ($m \to \infty$) is the same as that with doubled carrying capacity $\phi(r, 2K, \sigma_e^2)$, which is Eq. (10) with $\rho = 1$. As the correlation coefficient becomes smaller, the mean extinction time becomes longer. The longest mean extinction time is achieved when $m \to \infty$ and $\rho = 0$, in which the mean extinction time is $\phi \left( r + \frac{\sigma_1^2}{4} + 2K + \frac{\sigma_2^2}{2} \right)$.
As we can see from Fig. 1a, there is a threshold value of dispersal, and if \( m \) is greater than the threshold, the mean extinction time is independent of \( m \) and is affected only by changes in the environmental correlation \( r \). This implies that Eq. (10) gives a good approximation for the case when \( m \) is larger than the threshold. Hill et al. (2002) also found a similar threshold effect of \( m \).

4.2. No migration and no correlation in environmental quality

If there is no migration between the two populations \((m = 0)\) and if the environmental fluctuations are independent \((\rho = 0)\), then extinction occurs independently between the two populations. The average time to extinction of either one of the two populations is simply half of the average time to extinction of one population \( \frac{1}{2} \phi(r, K, \sigma_e^2) \), because we can regard the extinction of the canonical model as a Poisson process (Quinn and Hastings, 1987; Hakoyama and Iwasa, 2000a). Hence the extinction rate is doubled. The additional time to extinction for the remaining population is the same as one population, \( \varphi(r, K, \sigma_e^2) \). Thus the extinction time for both populations to go extinct is 50% longer than that for one patch:

\[
T[m = 0, \rho = 0] = \frac{3}{2} \phi(r, K, \sigma_e^2). \tag{11a}
\]

Using the scaling law \( \frac{\phi(r, K, \sigma_e^2)}{r} = \phi(r/k, K_2, \sigma_e^2/\sigma_e^2) \) studied in Hakoyama and Iwasa (2000a), Eq. (11a) becomes

\[
T[m = 0, \rho = 0] = \varphi \left( \frac{3}{2} r, \frac{3}{2} K, \frac{3}{2} \sigma_e^2 \right). \tag{11b}
\]

Note that the total population size \( Z = X_1 + X_2 \) does not perfectly aggregate the two-habitats model Eq. (5), because \( \Delta Z \) is not a function of \( Z \), but that of \( X_1 \) and \( X_2 \). This means the dynamics of \( Z \) does not follow the canonical model.

4.3. No migration and perfectly synchronized environmental fluctuations

If there is no migration \((m = 0)\), the mean time to extinction of the whole system should be longer than that of a single population separated \( \varphi(r, K, \sigma_e^2) \), because the second population may not be extinct when the first one has just become extinct. Even if the environmental quality is perfectly synchronized between the two habitats and the initial population size of two habitats is the same \( x_0 = K \), extinction in one habitat does not imply the extinction in the other because demographic stochasticity needed for population extinction is independent between the two habitats. Probably the extinction of the population in the second habitat is quite likely if the environmental fluctuation is perfectly synchronized. Since both the synchronization of the environment and weak migration make the extinction faster, \( T[m = 0, \rho = 1] \) is the shortest mean extinction time for the parameter range. It should be shorter than \( T[m = 0, \rho = 0] \) and \( T[m = \infty, \rho = 1] \) (Fig. 2). From these considerations we conjecture

\[
\varphi(r, K, \sigma_e^2) < T[m = 0, \rho = 1] < \min \{ \frac{\varphi(r, K, \sigma_e^2), \varphi(r, 2K, \sigma_e^2)}{2} \}. \tag{12}
\]

We confirmed these formulas (Eqs. (10)–(12)) by direct computer simulations of the stochastic metapopulation model.

5. Model simplification from time-series data

To estimate the mean extinction time, formula Eq. (2) is available only for a simple population expressed by Eq. (1). For a meta-population, we can write down the corresponding diffusion equation, but it is difficult to obtain an analytical solution for the mean extinction time and to construct the appropriate procedure for parameter estimation. We adopted aggregation based on parameter estimation methods for Eq. (1). We first generated a sample path of population sizes for the complex structured model, then estimated three parameters, \( \hat{r} \), \( \hat{K} \), and \( \hat{\sigma_e^2} \), from the sample population fluctuations, and calculated mean extinction time \( T \) using Eq. (2), finally compared it with \( T \) obtained from computer simulations.

Now we apply the aggregation method based on the time series of population size. Since the model including two habitats does not satisfy canonical model Eq. (1) exactly, aggregation includes some error. We are concerned with the magnitude of the error and the condition in which error is small. We first generated a time series of population sizes in the two habitats, and fit the total population size \( X_1(t) + X_2(t) \) to the canonical model Eq. (1). We adopted the Monte Carlo bias-correction method using approximate maximum likelihood estimate which is very effective in removing the bias in the estimates of parameters (Hakoyama and Iwasa, 2000a,b). We, then, derive the extinction time from the formula Eq. (2) with the three estimated parameters. These predictions (Fig. 1b) were compared with the results of computer simulations (Fig. 1a). The overall pattern of a density plot in Fig. 1b looks similar to Fig. 1a. We can see that the estimate using Eq. (2) with parameters obtained by fitting to the total population size was accurate for most of parameter regions, but the discrepancy is larger for slow migration than fast migration. Since the aggregation is perfect for infinite migration rate, the total population size follows the canonical model, and aggregation for significantly high migration rate is very good. For the case of no migration and no environmental correlation, the discrepancy was relatively large (data not shown). As explained earlier, if we can estimate the effective
parameters exactly for the case of no migration and no environmental correlation, the estimation of the mean extinction time will be accurate. However, the time series of total population size do not follow the single population model Eq. (1) with the three effective parameters, and the estimate procedure failed to estimate the exact effective parameters.

Fig. 3a shows the relation between the mean extinction time of the direct computer simulation of meta-population and the one predicted by the formula based on the method explained above. The aggregation gives fairly accurate prediction of the mean time to extinction.

5.1. Variation in patch sizes

We can expand the two habitats model, Eq. (5) into a case with different patch sizes. Let $K_i$ be the carrying capacity of habitat $i$ ($i = 1, 2$), and let $p$ be the fraction of emigrants per unit time. If the local population sizes are $X_1$ and $X_2$, the number of emigrants per unit time are $pX_1$ and $pX_2$, respectively. The emigrants become immigrants. We assume the total number of the emigrants $p(X_1 + X_2)$ is redistributed according to the size of each habitat. So, the numbers of the immigrants to each habitat are $\frac{K_1}{K_1 + K_2}p(X_1 + X_2)$ and $\frac{K_2}{K_1 + K_2}p(X_1 + X_2)$. Then, total migration fluxes for each habitat are $-pX_1 + \frac{K_1}{K_1 + K_2}p(X_1 + X_2)$ and $-pX_2 + \frac{K_2}{K_1 + K_2}p(X_1 + X_2)$. Rewriting $p = 2m$ to be consistent with Eq. (5), we have

$$\frac{dX_1}{dt} = rX_1 \left(1 - \frac{X_1}{K_1}\right) + \epsilon_1(t) \circ X_1 + \xi_d(t) \cdot \sqrt{X_1}$$
$$+ 2m \frac{K_1X_2 - K_2X_1}{K_1 + K_2},$$

(13a)

$$\frac{dX_2}{dt} = rX_2 \left(1 - \frac{X_2}{K_2}\right) + \epsilon_2(t) \circ X_2 + \xi_d(t) \cdot \sqrt{X_2}$$
$$+ 2m \frac{K_2X_1 - K_1X_2}{K_1 + K_2}.$$  

(13b)

Note that if the habitat size is identical between habitats, Eq. (13) becomes to Eq. (5). If $K_2 \to 0$, Eq. (13) becomes the canonical model Eq. (1); in which aggregation is perfect. Hence we expect that the aggregation of Eq. (13) to the canonical model becomes more accurate as the two habitats differ in size more significantly. The worst case is constant carrying capacity $K_1 = K_2$. Fig. 3b shows a result of aggregation of the meta-population model with different patch sizes to the canonical model. The aggregation also gives accurate prediction of the mean time to extinction.

5.2. Asymmetric migration

Let $m_{ji}$ be the migration rate from patch $i$ to $j$ ($i = 1, 2$). The difference in $m_{21}$ and $m_{12}$ indicates the extent of asymmetric migration. Substituting $m$ of Eq. (5a) and (5b) to $m_{21}$ and $m_{12}$, we have a model with asymmetric migration. Fig. 3c and d show results of aggregation of the model to the canonical model. The aggregation gives good estimate of the mean extinction time (Fig. 3c, d), although it tends to be overestimated when the extent of asymmetric migration is large (Fig. 3d).

5.3. Variation in growth rates

Let $r_i$ be the migration rate of patch $i$ ($i = 1, 2$). Substituting $r$ of Eq. (5a) and (5b) to $r_1$ and $r_2$, we have a model with different growth rates. Fig. 3e and f show results of aggregation of the model with different growth rates to the canonical model. The aggregation gives considerably accurate prediction of the mean time to extinction (Fig. 3e, f), even when $r_2$ is twice as large as $r_1$ (Fig. 3f).

6. $n$ Populations

The two habitats model can be extended to a model with $n$ habitats ($n > 2$). Let $X_i$ ($i = 1, 2, \ldots , n$) be the sizes of the habitats. The dynamics of $n$ habitats model is given as follows:

$$\frac{dX_i}{dt} = rX_i \left(1 - \frac{X_i}{K_i}\right) + \epsilon_i(t) \circ X_i + \xi(t) \cdot \sqrt{X_i}$$
$$+ \sum_{j \neq i} m_{ij}(X_j - X_i).$$  

(14)

Demographic noises $\xi(t)$ ($i = 1, 2, \ldots , n$) are mutually independent stochastic variable with mean zero. Environmental noises $\epsilon_i(t)$ ($i = 1, 2, \ldots , n$) are correlated environmental fluctuation as the sum of independent stochastic variables (similar to Eq. (5e)). For example, we can produce three correlated random variables for the three habitats model using three independent random variables ($\eta_1(t), \eta_2(t)$ and $\eta_3(t)$):

$$\epsilon_1(t) = \sigma_x \eta_1(t),$$

$$\epsilon_2(t) = \sigma_x (\rho_{12} \eta_1(t) + \sqrt{1 - \rho^2_{12}} \eta_2(t)), $$

$$\epsilon_3(t) = \sigma_x \left( \frac{\rho_{13} \eta_1(t) + \rho_{23} - \rho_{12} \rho_{13}}{\sqrt{1 - \rho^2_{12}}} \eta_2(t) + \sqrt{1 - \rho^2_{12} - \frac{(\rho_{23} - \rho_{12} \rho_{13})^2}{1 - \rho^2_{12}}} \eta_3(t) \right).$$  

(15)
Similar to the case of the two habitats model, we can express the mean extinction time of the \(n\) habitats model in terms of the formula for a single population for several cases with extreme correlation coefficient \(\rho_{ij}\) or migration rate \(m_{ji}\) (Appendix A). For intermediate parameter values, we conducted
simulations of a model with 3 and 5 habitats for aggregation study.

Fig. 4 gives the relationship between the estimates and the results of computer simulations. Horizontal axis is for the logarithmic mean extinction time log \( T \) obtained from computer simulations (true values), whilst vertical axis is for the prediction by formula Eq. (2) using parameters estimated from total population size of meta-population. As a simplest case, we show cases that the migration rate and correlation coefficient are common for all connections between given two patches (Fig. 4a, b). In Fig. 4a and b, we show the cases of 3 and 5 habitats. Fig. 4c and d show cases of 3 habitats that the correlation coefficient is common for all associations, but the migration rates are various in each connection. Fig. 4e and f show cases of 3 habitats that both the correlation coefficient and migration rate are various in each connection. The graphs demonstrate a highly significant positive correlation, although there are some deviations.

6.1. Fit to the dynamics of local habitats

In practice of conservation management, the total population size of meta-population is not always available. In such a case, we may fit the size of a part of the meta-population \( \sum_{i=1}^{j} X_i(t) \) (\( j < n \)) to the canonical model to estimate the mean extinction time of the whole meta-population in \( n \) habitats. This corresponds to the case in which a population under study might be connected by rare migration with other populations on which we do not have enough information. For example, for the three habitats model, we may use the partial time-series data \( X_1(t) \) or \( X_1(t) + X_2(t) \) instead of the total population size \( X_1(t) + X_2(t) + X_3(t) \) to estimate the mean extinction time. Fig. 5 gives the relationship between the computer simulations and the estimates from \( X_1(t) + X_2(t) + X_3(t), X_1(t) + X_2(t), \) and \( X_1(t) \). All cases give a highly significant positive correlation, and slopes of linear regression are close to 1, although they include considerable error and systematic bias. The estimates from \( X_1(t) + X_2(t) \) and \( X_1(t) \) significantly underestimate the mean extinction time of the whole population, and the extent of the underestimate is larger for the estimates from \( X_1(t) \) than those from \( X_1(t) + X_2(t) \).

7. Discussion

Classical meta-population models are the “occupancy model” (e.g., MacArthur and Wilson, 1967; Levins, 1969, 1970; Day and Possingham, 1995; Etienne et al., 2003), in which each local population is either filled (including a positive number of individuals) or extinct (no individual). On the other hand several authors have studied more realistic meta-population model that considers both regional and local dynamics simultaneously (e.g., Drechsler and Wissel, 1997; Frank and Wissel, 2002; Hill et al., 2002). The occupancy model can be regarded as the one produced by aggregation of the model considering the dynamics within local population. Drechsler and Wissel (1997) showed that the occupancy model can be a good approximation for the meta-population model with detailed local dynamics, if the variances of environmental fluctuations and the rates of dispersal are small. Frank and Wissel (2002) demonstrated that the occupancy model can reproduce the behavior of the complex spatial model in term of the mean extinction time. In the present paper, we examined an alternative way of aggregation of a meta-population model to a spatial-unstructured population model.

Only scant data are usually available for a complex model such as metapopulation (e.g., Etienne et al., 2003). In the viewpoint of model selection (Linhart and Zucchini, 1986; Burnham and Anderson, 2002), finding the candidates for a good simplified model is particularly important to obtain a reliable prediction based on observed data. Some aggregations are more effective than the others, but we cannot know a priori the approximation capability of different aggregated models. We, therefore, must study the capability of simplified models for each important case separately. In the aggregation study, we may find a robust and effective model that is simplified suitably. In this paper, we found that a single population model (canonical model; Hakoyama and Iwasa, 2000a) is exact (perfect aggregation) in the case with very large migration rate, and is very accurate in the case with intermediate parameters. This indicates a high potential and usefulness of the canonical model to aggregate meta-population models. Model selection using an observed (or artificial) data and some criterion, such as AIC (Akaike, 1973), is beyond the scope of the present study (see e.g., Ludwig and Walters, 1985; Foley, 2000). However, if we compare the canonical model and the meta-population model using some criterion of model selection, the canonical model might be the best possible model to estimate the extinction risk of the meta-population model for a realistically small data set that are usually available.

Several authors have carried out population viability analyses (PVA) to investigate confidence intervals of the long-term extinction probability for realistically small data; for density-dependent population (Ludwig, 1999), density-independent population (Fieberg and Ellner, 2000) and reddened environmental noise (Halley, 2003). Ludwig (1999) and Fieberg and Ellner (2000) have found that the confidence intervals are so wide as to be almost meaningless. Halley (2003) has found confidence intervals for the model with the reddened noise is...
narrower than that with white noise, concluding knowledge of environmental noise may still be meaningful to carry out PVA even for long-term prediction. Although it is often difficult in estimating precise extinction risk for small sample, several authors have a view that PVA can be used for comparing the effectiveness of different
management scenarios (e.g., Fieberg and Ellner, 2000; Hakoyama et al., 2000; Iwasa et al., 2000; Coulson et al., 2001; Nakanishi et al., 2003). However, even when we carry out PVA to compare ecological risks instead of discussing the precision of extinction probability, we should use an approximating model which is suitable for a limited data set.

In this paper, we also showed that even the size of a partial population is useful in estimating the relative extinction risk of the whole metapopulation. Fitting to time series of the local population size, the absolute value of mean extinction time is significantly underestimated, but the slope of linear regression between the true and estimated log $T$ seems to be close to 1 (see Fig. 5). This means the estimate of $\Delta \log T$ is relatively accurate. Therefore, the aggregation method using the partial population size may be applicable for the purpose of evaluating risk factors that cause the decrease in $\log T$.

7.1. Perspectives

In establishing the use of aggregation method, we can do the same procedures for other types of aggregation as used for meta-population model studied in the present paper—we can generate a time series of the population size from the models including various structures, and then obtain the “effective” parameters $r$, $K$, and $\sigma^2$ by fitting to the canonical models, and then predict the mean extinction time $T$ by Eq. (2). We then compare this estimate with the direct computer simulations. We do not expect that this method of estimate is always accurate, but we would like to see when this is very inaccurate, and when it is usable in further theoretical study. Wilcox and Possingham (2002) have studied the validity of the diffusion approximation in extinction models comparing an individual-based stochastic population model and a diffusion model (Foley, 1994), and concluded that the diffusion approximations are likely to be inaccurate in some parameter regions (see also Ludwig, 1996). This also can be regarded as a study of model aggregation. In the following, we list up several examples of situation in which the effectiveness of the aggregation method of extinction risk estimate should be examined usefully: (1) First, we can study more realistic meta-population models. Variation in migration pattern (network) and patch position (Day and Possingham, 1995; Frank and Wissel, 1998) are important factors to be considered, which we considered specific cases in this study. A different starting point of a discrete time model is also a research direction. (2) Second, we can study the simplification of age and size structured models. (3) Third, if environmental parameters fluctuate with auto-covariance instead of white noise, effective intensity of fluctuation, defined as the parameter $\sigma^2$ estimate using the time-series fitting, will be larger than the variance itself, such auto-correlated environmental variance would cause a faster extinction (Johst and Wissel, 1997). If the yearly correlation in environment is very strong, we need to express the environmental fluctuation by a deterministic model. If the environmental condition is poor at first and changes to good condition after a while, the mean population size is expected to decrease at first and to recover afterward, but extinction is caused by the demographic stochasticity when population size becomes very small temporally. The extinction probability accompanying such a temporary reduction in size is a function of the minimum level of the population and the length of the minimum level period (Iwasa and Mochizuki, 1988). (4) Fourth, the population dynamics of resource species, predator, or pathogens cause time-delay in the population regulation, and the interaction between species can have a large influence on the extinction risk. (5) Fifth, a clear drop in next generation by over-exploitation, a large explosion of a population in a generation are not described by diffusion approximation in Eq. (1), but a different approximation can be available (Halley and Iwasa, 1998). It is probably not applicable to fit the dynamics to Eq. (1) and use Eq. (2) if they include large jumps in population size between years. We conjecture high performance might hold in these ways of model aggregations. The limitation of the method for more diverse population models would be important subjects of further theoretical study.
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Appendix A

A.1. Population dynamics in n habitats

During a short time interval of length $\Delta t$, the change in the population size $\Delta X_i$ $(i = 1, 2, \ldots, n)$ is given as follows:

$$\Delta X_i = \left[ r X_i \left( 1 - \frac{X_i}{K} \right) + \frac{1}{2} \sigma_e^2 X_i + \sum_{j \neq i} m_{ji}(X_j - X_i) \right] \Delta t$$

$$+ X_i \Delta \xi_i + \sqrt{X_i} \Delta \xi_{di}. \quad (A.1)$$

Demographic noise $\Delta \xi_{di}$ $(i = 1, 2, \ldots, n)$ are mutually independent stochastic variable with mean zero. Environmental noise $\Delta \xi_i$ $(i = 1, 2, \ldots, n)$ are mutually correlated stochastic variables with mean zero, but are independent of $\Delta \xi_{di}$ $(i = 1, 2, \ldots, n)$, and have mean zero. Both of these are independent of current population sizes $X_i$ $(i = 1, 2, \ldots, n)$. Variances and covariances of these are

$$\text{Cov}[\Delta \xi_{di}, \Delta \xi_{di}] = \begin{cases} 1 & \text{if } i = j, \\ 0 & \text{if } i \neq j, \end{cases} \quad (A.2a)$$

$$\text{Cov}[\Delta \xi_i, \Delta \xi_j] = \sigma_e^2 \rho_{ij}, \quad (A.2b)$$

in which the correlation coefficient between population $i$ and population $j$ is denoted by $\rho_{ij}$.

In a simple case, all the pairs of populations may have the same correlation coefficient:

$$\rho_{ij} = \begin{cases} 1 & \text{if } i = j, \\ \rho & \text{if } i \neq j, \end{cases} \quad (A.3)$$

in which $0 \leq \rho \leq 1$. Or when the populations are arranged in a lattice and the correlation coefficient is a decreasing function of the distance between them, we have

$$\rho_{ij} = \rho(||x_i - x_j||), \quad (A.4)$$

in which $x_i$ is the coordinate of the population $i$ in the lattice.

A.2. Solvable cases

If migration rates $m_{ji}$ are very large, we expect that the $n$ population sizes are kept equal, which allows some simplification of the analysis. By summing up Eq. (A.1), the migration between habitats is canceled and the total population size $Z = \sum_{i=1}^{n} X_i$ follows:

$$\Delta Z = \left[ r Z - \frac{r}{K} \sum_{i=1}^{n} X_i^2 + \frac{1}{2} \sigma_e^2 Z \right] \Delta t + \sum_{i=1}^{n} X_i \Delta \xi_i$$

$$+ \sum_{i=1}^{n} \sqrt{X_i} \Delta \xi_{di}. \quad (A.5)$$

As we consider the case in which migration rates are very strong in which $X_i$ is replaced by $X_i \approx \frac{1}{2} Z$. The variance of environmental stochasticity and demographic stochasticity are:

$$\text{Var} \left[ \sum_{i=1}^{n} \frac{Z}{n} \Delta \xi_i \right] = Z^2 \frac{\sigma_e^2}{n} (1 + (n-1)\rho). \quad (A.7)$$

In a similar way, we have

$$\text{Var} \left[ \sum_{i=1}^{n} \sqrt{X_i} \Delta \xi_{di} \right] = Z^2 \frac{\sigma_e^2}{n} (1 + (n-1)\rho). \quad (A.8)$$

Hence we have

$$\Delta Z = \left[ r Z - \frac{r}{K} Z^2 + \frac{1}{2} \sigma_e^2 Z \right] \Delta t + Z \Delta \xi_{\text{total}} + Z \Delta \xi$$

$$= \left[ r Z + \frac{1}{2} (\sigma_e^2 - \sigma_e^2) Z - \frac{r}{nK} Z^2 + \frac{1}{2} \sigma_e^2 Z \right] \Delta t$$

$$+ Z \Delta \xi_{\text{total}} + Z \Delta \xi. \quad (A.9)$$

Using Eqs. (A.7) and (A.8), Eq. (A.9) is rewritten as:

$$\Delta Z = r Z \left[ 1 - \frac{Z}{K} \right] + \bar{\sigma}_e \bar{\xi}_{\text{total}}(t) \circ \bar{Z} + \bar{\zeta}(t) \cdot \sqrt{\bar{Z}}, \quad (A.10)$$

where $\bar{\xi}_{\text{total}}(t) = \bar{\xi}_{\text{total}}(t)/\bar{\sigma}_e$, $\bar{r} = r \left( 1 + \frac{\sigma_e^2 (n-1) (1-\rho)}{2n} \right)$, $\bar{K} = nK \left( 1 + \frac{\sigma_e^2 (n-1) (1-\rho)}{2n} \right)$, and $\bar{\sigma}_e^2 = \sigma_e^2 (1 + (n-1)\rho)$. $\bar{\xi}_{\text{total}}(t)$ and $\bar{\zeta}(t)$ are independent white noises. Then, the mean extinction time of the meta-population in the strong migration limit is given by $\phi(\bar{r}, \bar{K}, \bar{\sigma}_e^2)$:

$$T[m = \infty, \rho] = \phi(\bar{r}, \bar{K}, \bar{\sigma}_e^2), \quad 0 \leq \rho \leq 1. \quad (A.11)$$

If there is no migration between the $n$ populations ($m_{ji} = 0$) and if the environmental fluctuations are
independent \((\rho_y = 0)\), then the extinction in the \(n\) populations occurs independently. The average time to extinction of either one of the \(n\) populations is 
\[
\frac{1}{2} \phi(r, K, \sigma^2),
\]
and the average time to the next extinction is \(\frac{1}{n-1} \phi(r, K, \sigma^2)\), which is the mean waiting time for one of the remaining \(n - 1\) populations to go extinct. In the same way, the waiting time to extinction is longer, and the total time for all of these go extinct is
\[
T = \left(1 + \frac{1}{2} + \frac{1}{3} + \cdots + \frac{1}{n}\right) \phi(r, K, \sigma^2),
\]
(A.12a)

(Quinn and Hastings, 1987; McCarthy and Lindenmayer, 1999). From 
\[
1 + \frac{1}{2} + \frac{1}{3} + \cdots + \frac{1}{n} \approx \ln n + \gamma,
\]
we have
\[
T \approx \phi(r, K, \sigma^2)(\ln n + \gamma),
\]
(A.12b)
where \(\gamma \approx 0.5772\) is the Euler’s constant. This implies that the extinction time \(T\) increases in proportional to the logarithm of the number of local populations.

References


