

Ecological Risk Assessment by the Use of the Probability of Species Extinction.

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Abstract

I first overview the researchs in this CREST project on establishing ecological risk concept based on the probability of population extinction. We then propose a new method to estimate the risk of population extinction based on the time series of fluctuating population size fitted to a stochastic differential equation model. This method can be used to estimate the extinction risk of natural populations, but it also provides a method to estimate the extinction risk in realistic population models with structures (space, age, or size) that make analytical solutions impossible. We first derive a formula of the expected time to extinction for a population with logistic growth and environmental and demographic stochasticities (*canonical model*). The predictions of the formula with three parameters (intrinsic population growth rate, carrying capacity, and environmental noise) estimated from time series data was close to the mean extinction time of the computer simulation results of the model in detail. We then analyze the population dynamics in two habitats connected by migration using fitting to the canonical model.

1. Ecological Risk and Population Extinction Risk

Harm to human health is a plausible and well established criterion of the environmental risk of toxic substances. However, the single concern of the impact on human health has sometimes caused undesirable outcomes by underestimating destructive effects to environment and ecosystems. To overcome this problem, the "ecological risk" concept has been proposed in environmental risk evaluation. Nakanishi (1995) in particular advocated the use of ecological risk as a criterion separate from the threat to the

human health, with the hope of a better balance between the welfare of the current human generation and that of future generations.

Nakanishi (1995) further proposed that the risk of extinction of animals and plants might be used as the basis for quantifying ecological risk. The extinction of species, race, or any taxonomic unit is an unrecoverable and deprives future human generations of the opportunity to enjoy its potential use. The loss of biodiversity may threaten the ecosystem stability and function (Schulze & Mooney 1993). Even if most species that have been lost and will be lost are of no direct economical value, their loss serves as a good measure of ecological risk because it is likely to be correlated with the magnitude of the general threat to the environment and ecosystem.

But how can we measure the risk of population extinction in the field? Even if there are methods to evaluate extinction risk, are they sufficiently reliable and robust so that environmental risk assessment can be based on them? Are they simple enough to be applicable to many species for which little ecological study has been carried out? A very exact method of estimating extinction risk might not be useful if it requires many years of careful and laborious study.

Once the extinction risk, or the probability of population extinction to occur within a specified time frame, is adopted as a criterion for ecological risk, the study of environmental risk assessment immediately becomes close to several disciplines of applied ecology. For example, conservation biology is a science studying how species extinction occurs, and determining methods to mitigate the loss of biological diversity (Ginzburg *et al.* 1982; Primack 1993). Sustainable management of biological resources, such as fishery and hunting, has also started to considering the risk of extinction of the resources species in recent years (Lande *et al.* 1995; Saether *et al.* 1996).

In this paper, I overview the research effort in this CREST project on establishing an ecological risk concept based on the probability of population extinction.

1.1 From toxicity to diversity loss

Study of the risk of diversity loss caused by environmental release of toxic chemicals includes several steps (Fig. 1).

First, the toxicity of potentially harmful chemicals is normally measured for its effects on the survivorship, fertility, and growth rate of test organisms. Since the reduction of these demographic parameters can only be observable at much higher concentrations than that in the field, we must do some extrapolation of the effect at low concentration. We must then combine these measurements with demographic parameters (e.g. age-specific mortality) to the effect on the aggregate statistics, such as intrinsic growth rate r . Y. Tanaka has studied potential problems with these procedures and worked out solutions (Tanaka 1997). He has been also reviewed the laboratory measurements of toxicity.

The second step is to evaluate the population extinction risk once intrinsic growth rate r , carrying capacity K , and environmental fluctuation are known. This has been studied by H. Hakoyama and Y. Iwasa. The largest problem is the difficulty in the estimation of parameters, especially the estimate of the magnitude of environmental fluctuation, which is

essential in extinction risk assessment and yet is very difficult to determine. Dr. Hakoyama has developed a new strategy to cope with this problem, as explained below.

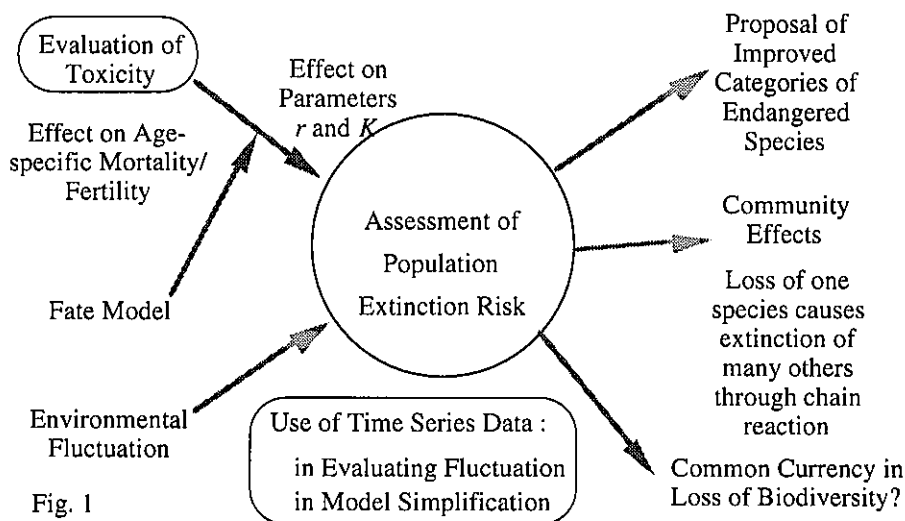


Fig. 1

Once we have a method to estimate the risk of population extinction, we can then need to convert it the general loss of biodiversity. It is well known that the perturbation of one species in an ecosystem will propagates through the networks of species interaction and might cause the extinction of several other species. Such a "community effect" has been studied in theoretical ecology (Pimm 1982), but the study is often limited to a highly idealized model of species interaction, such as Lotka-Volterra equations. Even so it is concluded that we can make no general conclusion on the direction and the magnitude of community effects. K. Miyamoto has been working on this community effects in the ecosystem model for the Lake Biwa community, including many speices of phytoplankton, zooplankton, fish. He observed an unexpected drop of biomass caused by toxic chemicals in his simulation model.

Population extinction risk has been used in categories of endangered species (Mace and Lande 1991). H. Matsuda and his colleagues have been pointed out potential problems of the criteria (Matsuda *et al.* 1998).

2. A New Method of Evaluating Population Extinction Risk.

Central to this research program is the estimate of population extinction risk and its increase due to various kinds of threat (e.g. habitat size reduction, habitat fragmentation, toxic chemical release, recurrent spread of epidemics, invasion of competitors, genetic deterioration). To evaluate the extinction risk of natural populations, computer simulation models are constructed, which are flexible and can incorporate realistic structures. However, realistic simulation models have a large number of parameters, many of which are often difficult to estimate accurately from available data. In particular, an estimate of the

magnitude of the environment fluctuation of demographic parameters is normally unavailable, but it is essential in extinction risk estimate.

Here we focus on a new method to evaluate the risk of population extinction by using a formula derived from a simple model. We first choose a mathematically tractable case as a "canonical model". If a time series of the population size over the years is available, we can estimate the three corresponding parameters in the canonical model to fit the time series. This method provides a way to estimate the extinction probability for a given field population of animals or plants. It may also give a way of aggregation (model simplification) from a complex realistic model to a simple one including a few parameters.

2.1 Canonical model

Let X be the population size at time t . The dynamics of the population size are expressed in terms of stochastic differential equation:

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right) + \sigma_e \xi_e(t) X + \xi_d(t) \bullet \sqrt{X}, \quad (r, K, \text{ and } \sigma_e > 0), \quad (1)$$

where the first term in the right hand side indicates the logistic growth in the absence of stochasticity. r is the growth rate when population size is small, and K is the carrying capacity that is the population size maintained in stable habitats.

The second term in the right hand side of the equation indicates the fluctuation of the growth rate caused by environmental stochasticity. If survivorship or fertility fluctuates between years, the average is included in the first term of Eq. (1) and the deviation from the average is expressed in the second term of Eq. (1). We assume that this fluctuation is irregular and occurs very quickly. $\xi_e(t)$ is called white noise, and indicates the source of stochastic changes with mean zero and quickly changing sign randomly between positive and negative within any short time interval. Since the fluctuation of environmental quality is common to all the individuals in the population, its contribution to the population increase is simply proportional to the current population size X . σ_e is the intensity of the environmental fluctuation.

The third term in Eq. (1) indicates the demographic stochasticity caused by the stochasticity of survival and reproductive success that is independent between individuals. $\xi_d(t)$ is the white noise that is independent of $\xi_e(t)$. Since the demographic stochasticity of different individuals tends to cancel with each other, its contribution is proportional to the square root of population size.

2.2 The average extinction time

Here we concentrate on the extinction risk of a long-term sustainable population. If the population starts at the carrying capacity, the extinction time follows an exponential distribution, and we can treat extinction events as if they occur at random (Quinn & Hastings 1987; Halley & Iwasa 1997). The average time to extinction for a population following the stochastic differential equation (1) can be calculated as,

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

where $R \equiv \frac{2r}{\sigma_e^2 K}$ and $D \equiv \frac{1}{\sigma_e^2}$. (see; Lande *et al.* 1995).

We carried out computer simulations. For each set of parameters, more than 500 (sometimes 1000) replicates were made in calculating the time to extinction, leading to an estimate of reliability interval of about 12%. Equation (2) was always consistent with computer simulations.

The mean extinction time T_K increases with K at an increasing rate, if the environmental stochasticity is small. On the contrary, the mean extinction time only slightly increases at a decreasing rate with the carrying capacity when the environmental fluctuation is sufficiently large (Fig. 2).

To obtain a formula showing explicit dependence on the parameters, we derived an approximate expression that gives T_K in terms of r , K , and σ_e^2 . We calculated the integral Eq. (2) numerically for a range of parameters and derived two regression formulas, differing in simplicity and accuracy. In deriving these, we note scaling property of the model. The regression of logarithmic extinction time and the logarithmic carrying capacity K gives a simple linear relationship:

$$\log_{10} T_K = \frac{2r}{\sigma_e^2} \log_{10} K + [\text{terms independent of } K], \quad (3)$$

(see Ludwig 1976; Lande 1993). The mean extinction time is a power function of the carrying capacity. Suppose that the habitat change in size without changing in quality. Then the logarithm of the mean extinction time change can be calculated from Eq. (3) simply by knowing $2r/\sigma_e^2$.

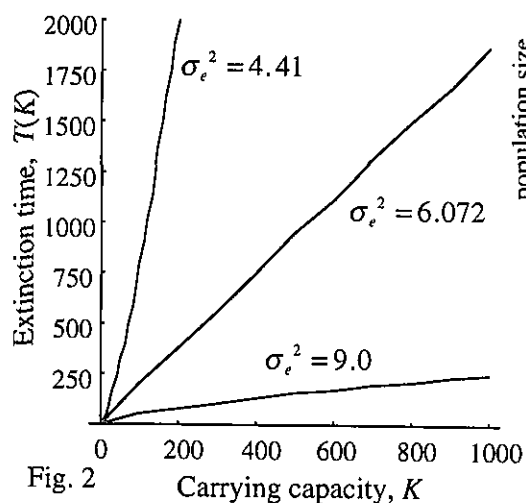


Fig. 2

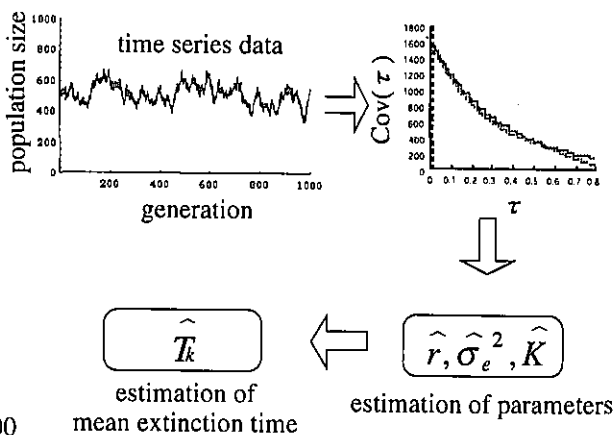


Fig. 3

3. Estimate of Mean Extinction Time from Population Fluctuations

To apply the model to field populations, we need three parameters. The estimate of the intrinsic rate of population growth r obtained in a habitat or in a laboratory may be used in a different population with proper care. The carrying capacity K and the magnitude of environmental variation σ_e^2 must be measured from the data on the population studied.

Assuming small fluctuations around the population mean ($\sigma_e^2 \ll r$) and positive intrinsic growth rate ($r > 0$), we can pick up a period of population fluctuation which the population size staying near K , in which the population is controlled by the systematic forces of logistic growth and environmental stochasticity. Under this approximation, the average population size and the variance of the population fluctuations are:

$$E[X(t)] = K, \quad \text{and} \quad \text{Var}[X(t)] = \frac{\sigma_e^2 K^2 + K}{2r}, \quad (4)$$

respectively. The carrying capacity can be estimated simply from the average population size.

If the intrinsic growth rate r is known from some separate sources, we can estimate the environmental variance σ_e^2 by fitting to the observed variance of the population fluctuation.

If a reliable estimate of intrinsic population growth rate r is not available, we may use the following formula for the autocovariance function of population size:

$$AC_x(\tau) = \text{Cov}[X(t), X(t + \tau)] = \frac{\sigma_e^2 K^2 + K}{2r} e^{-r|\tau|}, \quad (5)$$

where τ is time lag. In addition to the nonlinear fitting to the autocovariance function Eq. (5), we developed a maximum likelihood estimate of r and σ_e^2 from the time series data. These gave very similar results.

We have carried out computer simulations to examine the accuracy of the method.

[1] If we know the correct value of intrinsic growth rate r , the maximum likelihood estimate of environmental variation σ_e^2 from time series is very accurate, so is the estimate of the mean extinction time T_K .

[2] On the other hand, if we do not have information on r separately, the maximum likelihood estimate of r is based on the time series $\{X(t_0), X(t_0 + \tau), X(t_0 + 2\tau), \dots,$

$X(t_0 + n\tau)\}$. But this estimate includes relatively large variance and some bias. However the estimated average extinction time is not very poor if we use a log-log plot.

[3] Sometimes, a relatively long time series of catch in fishery or hunting is available but conversion of the data to the actual population size might be difficult. In such cases, we can calculate environmental fluctuations σ_e^2 from the time series of relative population size.

If r is estimated separately, we have quite reliable estimate of σ_e^2 , but even if no separate information of r is available, we can still use time series data of the catch or hunting and estimate of both r and σ_e^2 . But the estimate of extinction time itself requires on estimate of carrying capacity K .

4. Aggregation of the Dynamics in Two Populations to a One-Population Model

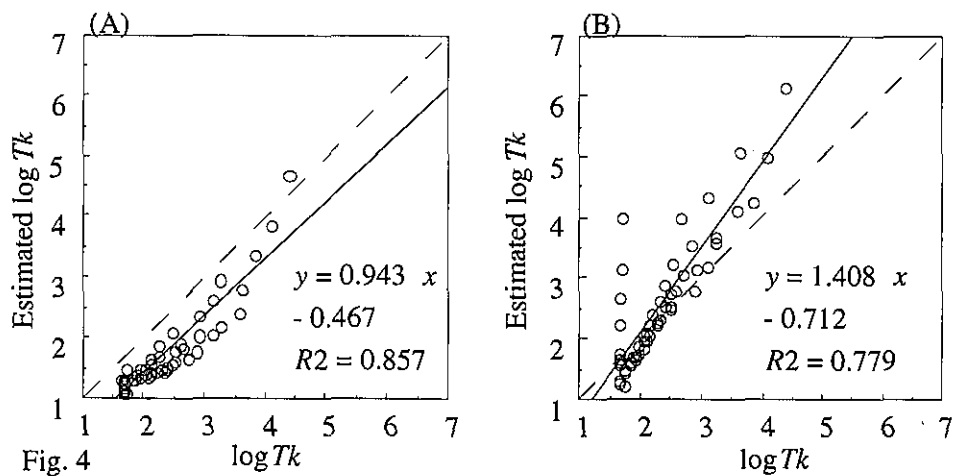
This method can be used to aggregate a complex model to a simple model, Eq. (1). As an example, we study a metapopulation composed of two local populations. Let X_1 and X_2 be the size of two populations, each following a stochastic model with logistic equation:

$$\frac{dX_1}{dt} = rX_1\left(1 - \frac{X_1}{K}\right) + \varepsilon_1(t) \circ X_1 + \xi_{d1}(t) \circ \sqrt{X_1} + m(X_2 - X_1), \quad (6a)$$

$$\frac{dX_2}{dt} = rX_2\left(1 - \frac{X_2}{K}\right) + \varepsilon_2(t) \circ X_2 + \xi_{d2}(t) \circ \sqrt{X_2} + m(X_1 - X_2), \quad (6b)$$

where $\varepsilon_1(t)$ and $\varepsilon_2(t)$ are white noise for environmental stochasticity with magnitude of σ_e^2 . Let ρ be the correlation coefficient between these two. $\xi_{d1}(t)$ and $\xi_{d2}(t)$ in Eq. (6) are independent white noises of demographic stochasticity, and m is the migration rate. The intrinsic growth rate, r , and the carrying capacity, K , are the same in two local populations.

For different values of migration rate between the population m and correlation ρ of the environmental fluctuations in the two habitats, we did computer simulation. For each set of parameter values, we calculated 500 replicates, and then estimated the extinction time.



Now we apply an aggregation method. We first generated a sample path of population sizes in the two habitats, then estimated three parameters, \hat{r} , \hat{K} , and $\hat{\sigma}_e^2$ by fitting to the sampled population fluctuations to the canonical model, and calculated the mean extinction time T_K using Eq. (2), finally compared it with T_K obtained from computer simulations.

Given the time series data of the population sizes in the two habitats, there are two different methods to fit to the canonical model. We may fit the total population size $X_1(t) + X_2(t)$ to the canonical model. The second method is to sample the population size in one habitat, say habitat 1, and fit the population size $X_1(t)$ to the canonical model Eq. (1). Figures 4A and 4B give the estimate of extinction time $\log T_K$ using parameters estimated from $X_1(t) + X_2(t)$ and $X_1(t)$, whilst the horizontal axis is the value from computer simulations. Both figures give a highly significant positive correlation, though they include considerable variances. The prediction of Eq. (3) with parameters estimated by $X_1(t) + X_2(t)$ tends to underestimate $\log T_K$, and the prediction with parameters estimated by $X_1(t)$ tends to overestimate it.

The slope of regression for Fig. 4A (estimate from $X_1(t) + X_2(t)$) was not statistically significantly different from 1. The extinction time estimate T_K may deviate systematically from the true values from the direct computer simulation, the difference in $\log T_K$ is a constant. For the purpose of evaluating the risk factor causing the decrease in $\log T_K$, the aggregation method is quite applicable.

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