Mathematical analysis of three species model and introduction of the canonical model.

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Suggestions from Tatiana

- a) could you transform your experimental model into a generic model with competing preys and a predator (all exposed to chronic irradiation)
- b) It would be most interesting to apply the canonical model of population to the case of chronic radiation exposure, could you do it?
- c) The concept of metapopulation with extinction of some sub-populations and their repopulation due to migration seems to be very promising, it would be nice if you make a presentation about this concept; will you?

Three species model

Microcosm (Kawabata microcosm)



We developed a simulation model of microcosm.s



Chronic exposure on SIM-COSM



In chronic exposure, Tetrahymena (most resistant species in individual level) is the most sensitive.

Assumptions

- To develop a simple mathematical model, we focused on the direct interaction between species, and indirect interactions are ignored.
 - whereas each species depends on metabolites from the others in microcosm and SIMCOSM.
- The ecosystem is not closed.
 - Microcosm and SIMCOSM are self sustainable system and closed system.
- Spatial effects are omitted.
- Stochasticities are ignored.

Deterministic model



 r_i : growth rate of organism *i* h_i : handling time of species *i* α_i : mortality of organism *i*

a: predation rate of E. coli*b*: predation rate of Tetrahymena

Analytic results

- The model has four equilibria
 - All of species were extinguished.
 - Euglena (producer species) was only existing.
 - Only predator species (Tetrahymena) was extinction.
 - All species were coexisted.
- Hysterisis (or resume shift) was not existed (No bistable cases were existed).
- Prey and predator populations were dynamically fluctuated when handling time of prey species is long.

Chronic irradiation

- LD₅₀ values with single species cultured are 4000Gy for Tetrahymena, 330 Gy for Euglena and 13 Gy for E. coli.
- From the analysis of the model, in chronic low dose rate irradiation, Tetrahymena who is the most resistant species in individual level is the most sensitive species.
- The analytical result is consistent with simulation results.

the canonical model

The canonical model

Hakoyama, H. and Iwasa, Y., J. Theor. Biol., 204, 337-359, 2000.

The canonical model is developed to calculate the extinction risk of stable population

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) + \begin{cases} \sigma_e \xi_e(t) \circ X \\ \text{environmental} \\ \text{stochasticity} \end{cases} + \begin{cases} \sigma_d \xi_d(t) \bullet \sqrt{X} \\ \text{demographic} \\ \text{stochasticity} \end{cases}$$

r: intrinsic growth rate,

K: carrying capacity,

 σ_e : intensity of the fluctuation of growth rate by environmental stochasticity, σ_d : intensity of the fluctuation of growth rate by demographic stochasticity (can be set as 1)

 ξ_e and ξ_d : white noise which corresponding to fluctuation of environment and demographic process,

Environmental stochasticity: the environment quality fluctuates year-to-year and the effects of fluctuation is common among the population.

Demographic stochasticity: number of offsprings is different between individuals.

Estimation of parameters of the canonical model

- Time unit is mean generation time.
- Intensity of demographic stochasticity(σ_d) can be set as 1 if number of offspring per female follows a Poisson distribution.
- Intensity of environmental stochasticity(σ_e) is estimated from time series data.
- Carrying capacity *K* is equivalent to mean population density.
- Intrinsic growth rate *r* should be obtained from other source, because growth rate is small when population at equilibrium.



Estimation of intrinsic growth rate *r* of the population which is consisted of multiple age.

Using Leslie matrix which describes life cycle of the organisms $\begin{pmatrix}
n_0(t+1) \\
n_1(t+1) \\
\vdots \\
n_w(t+1)
\end{pmatrix} = \begin{pmatrix}
f(0) & f(1) & f(a) & f(w) \\
p_1 & 0 & \cdots & 0 \\
p_2 & & & & \\
p_2 & & & & \\
& & p_{a-1} & & \\
0 & & p_w & 0 & \\
& & n_w(t)
\end{pmatrix}$ $\frac{n_a(t): \text{ population density of age } a \text{ at time } t \\
f(a): \text{ fertility at age } a \\
p_a: \text{ survival rate per year at age } a
\end{cases}$

Averaged growth rate *r* of the population is obtained from solution of Euler-Lotka equation

$$1 = \sum_{a=0}^{w} e^{-(a+1)r} f(a) p_1 \cdots p_a$$

Chronic radiation

$$\frac{dX}{dt} = (r - \Delta r(D)) \left(1 - \frac{X}{K}\right) X + \sigma_e \xi_e(t) \circ X + \xi_d(t) \bullet \sqrt{X} - \alpha(D) X$$

$$\Delta r(D): \text{ reduction of reproductive success.}$$

$$\alpha(D): \text{ mortality per capita}$$

morbidity and genomic damage should be converted to
reduction of reproductive success or mortality.

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Risk evaluation of the radiation

"average sustainable time (extinction risk)" can be calculated.

$$T_{control} = \frac{2}{\sigma_{e}^{2}} \int_{0}^{x_{0}} \int_{x}^{\infty} e^{-R(y-x)} \left(\frac{y+D}{x+D}\right)^{R(K+D)} \frac{dy}{(y+D)y} dx$$

$$T_{exposed} = \frac{2}{\sigma_{e}^{2}} \int_{0}^{x_{0}} \int_{x}^{\infty} e^{-R'(y-x)} \left(\frac{y+D}{x+D}\right)^{R'(K'+D')} \frac{dy}{(y+D)y} dx \quad \begin{array}{l} D = \sigma_{d}^{2} / \sigma_{e}^{2} \\ R = 2r / (\sigma_{e}^{2} K) \\ R' = 2r_{exposed} / (\sigma_{e}^{2} K_{exposed}) \end{array}$$

Endpoint of the population risk is reduced mean extinction time $\Delta T = T_{control} - T_{exposed}$ $\Delta \log T = \log T_{control} - \log T_{exposed}$ for very large population $\Delta 1/T = 1/T_{control} - 1/T_{exposed}$ for endangered species

Meta-population

Meta population

 Population separated sub-populations and sub-Populations are connected each other.



Subpopulation A can be sustained due to migration from population B at high dose. However, when migration rate is very high, total population goes extinction

Generic formulation for metapopulation

$$\frac{dX_i}{dt} = r_i X_i \left(1 - \frac{X_i}{K_i} \right) - \sum_{i \neq j} m_{ji} \left(X_j - X_i \right)$$

 X_i : population density of sub-population *i* r_i : intrinsic growth rate of sub-population *i* K_i : Carrying capacity of sub-population *i* m_{ji} : migration rate from population *j* to *i*

Implications for meta-population

Hakoyama and Iwasa J. Theor. Biol., 232, 203-216, 2005

- Hakoyama and Iwasa applied the canonical model to metapopulation.
- Endpoint is extinction time of total population $(X_{total} = \Sigma X_n)$.
- Parameters (r, K, σ_e^2) are estimated from time series data of total population.
- Estimated parameters have many biases, so that the biases are removed by Monte Carlo bias-correction method using approximate maximum likelihood.
- Comparing with computer simulation and estimation from parameter aggregated canonical model, the estimation was very well when migration rate is not low.