

The evolution of metapopulation migration

Kalle Parvinen

*Department of Mathematical Sciences,
University of Turku, Finland*

In recent years there has been an increasing interest in the study of metapopulation models. Metapopulation models are a type of spatially heterogeneous population models particularly suited to study implications of habitat fragmentation. In conservation biology the most important question is to study conditions for metapopulation persistence. One method for the metapopulation to avoid extinction is dispersal.

In different environments we observe different dispersal behaviour. Dispersal behaviour is adapted, since all individuals try to use as good strategy as possible in the present environment. The change of strategies used has an effect on the population dynamics and to the environment. Geritz *et. al* (1997,1998) presented *adaptive dynamics* as a new analytical framework for studying invasion problems in population models. See also Dieckmann (1997). This framework can also be used in examining invasion processes in metapopulations. Two questions are of particular interest: How are changes in environmental conditions affecting evolutionarily stable dispersal strategies? What are the consequences of resulting adaptations for metapopulation persistence?

In the paper Parvinen (1999) I studied the evolution of migration in a general discrete-time metapopulation model with finitely many patches using the framework of adaptive dynamics.

The following system of equations constitutes the model for monomorphic situation.

$$x'_i = (1 - m_{x,i})f_i(x_i + y_i)x_i + \sum_{j=1}^n m_{x,j}\alpha_{x,ij}F_{ij}f_j(x_j + y_j)x_j \quad (1)$$

Here $'$ indicates the state of the metapopulation at the next time step and x_i is the size of the resident population in patch i . The numbers $m_{x,j}$ and $\alpha_{x,ij}$ are the migration parameters. The survival probability during migration is denoted by F_{ij} and the functions f_i describe reproduction in the patches. Migration is not uniform in the patches and survival probabilities between the patches are not necessarily equal. Therefore the patch locations are not neglected.

If the resident is assumed to have settled down in a stable fixed point or cyclic orbit, then the model becomes linear with respect to the sizes of the mutant population. Then the success of invasion can be determined from the dominant Lyapunov exponent of the mutant. In the article Parvinen (1999) I have shown analytically that if the equilibrium of the resident population is a fixed point then (i) the strategy not to migrate is an evolutionarily stable strategy (ESS) (ii) a mutant population with no migration can invade any resident population in a fixed point state (iii) in the uniform migration case the strategy not to migrate is attractive under small mutational steps so that selection favors low migration.

If the resident population is in a two-cyclic orbit, then the situation is different. In the uniform migration case the invasion behaviour depends both on the type of the residents attractor and the survival probability during migration. If the survival probability during migration is low, then the system evolves towards low migration. If the survival probability is high enough, then evolutionary branching can happen and the system evolves to a situation with several co-existing types. In the case of out-of phase attractor, evolutionary branching can happen with significantly lower survival probabilities than in the in-phase attractor case. Most results in the two-cyclic case are obtained by numerical simulations. Also when migration is not uniform

we observe in numerical simulations in the two-cyclic orbit case selection for low migration or evolutionary branching depending on the survival probability during migration.

The model in Parvinen (1999) provides interesting results and helps us to understand the evolution of migration. To gain better understanding it is important to study extensions of this approach. One extension is to study structured metapopulation models, where instead of a finite number of patches we have a distribution of patches of different quality. This extension allows us to study the combined effect of local catastrophes and habitat fragmentation to the evolution of the metapopulation. I am currently doing this analysis in collaboration with Dr. Ulf Dieckmann and Prof. Hans Metz from IIASA and Prof. Mats Gyllenberg from the University of Turku, Finland.

We have studied two models for the local population growth either with or without demographic stochasticity. The local population growth in the deterministic case is described by

$$\frac{dx}{dt} = g(x)x - k(x)x + \alpha D, \quad (2)$$

where $g(x)$ corresponds to population growth via births and deaths, $k(x)$ is the per capita emigration rate and α is the immigration rate from the dispersal pool. The corresponding stochastic model is illustrated in Figure 1.

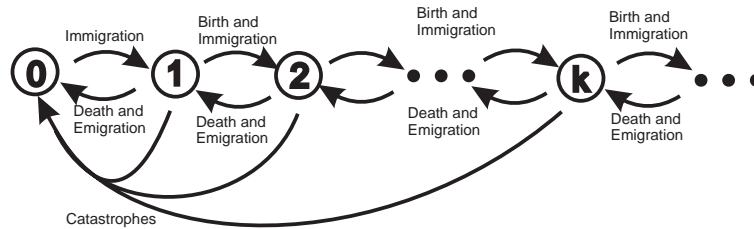


Figure 1: State transition diagram for a single patch in a model with demographic stochasticity

We have already the following results: The evolutionarily stable dispersal rates do not necessarily increase with rates for the extinction of populations in habitable patches. Instead, without demographic stochasticity, adapted dispersal rates exhibit a maximum for intermediate levels of disturbance and fall off for both higher and lower rates of local extinction. Second, we describe how the demographic stochasticity that inevitable occurs in finite populations affects the evolution of dispersal rates. Contrary to predictions from deterministic models, evolutionarily stable dispersal rates in small local populations can remain high even when rates of local extinction are low. The first manuscript containing these results will be submitted soon.

Several extensions can be made to this model:

- In this study the catastrophe rate has been assumed to be constant. In practice this may be too restrictive assumption. Therefore I want to study the model with catastrophe rate depending on the local population size.
- Non-constant catastrophes may be enough to observe special evolutionary cases. In this study only evolutionarily stable strategies were found. In Parvinen (1999) evolutionary branching was observed under certain conditions. Adaptive suicide is another interesting phenomenon. Its occurrence has been found in some models. It would be very interesting to find branching or evolutionary suicide also in this model.
- In this study the emigration rate has been the only evolutionary variable. The immigration rate and a variable describing local adaptation could also be taken as evolutionary variables.

Further study of these topics would be very interesting and I am expecting to obtain better understanding of metapopulations via this collaboration, which started during my 3,5 months visit in IIASA as a guest research scholar. In practice good collaboration requires frequent meetings and joint work. Therefore participating IIASA Young Scientists Summer Program in ADN would be an optimal way to ensure the substantial continuation and the expected good results from this collaboration.

References

- Dieckmann, U (1997). *The Dynamical Theory of Coevolution*, PhD Thesis, University of Leiden, The Netherlands.
- Geritz SAH, Kisdi É, Meszéna G and Metz, JAJ (1998). Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree, *Evolutionary Ecology*, **12**:35-37.
- Geritz SAH, Metz JAJ, Kisdi É and Meszéna (1997). Dynamics of adaptation and evolutionary branching, *Physical Review Letters*, **78**:2024-2027.
- Parvinen K, (1999). Evolution of migration in a metapopulation, *Bulletin of Mathematical Biology*, **61**:531-550.