Conditions for Evolutionary Branching in Two-dimensional Trait Spaces

Hiroshi Ito

Department of Systems and Sciences, University of Tokyo, Japan

Goal

To investigate the conditions for evolutionary branching in two-dimensional trait spaces without assuming infinitesimal mutation probabilities and step sizes.

Background and motivation

Speciation by ecological interaction (Schluter 1994; Feder et al. 1997; Orr and Smith 1998) is one of the important processes underlying the generation of biodiversity. Recently, theoretical studies based on adaptive dynamics theory (Metz 1996; Dieckmann & Law 1996; Dieckmann 1997) have provided a general framework for understanding this phenomenon by introducing the concept of evolutionary branching in a trait space (Geritz et al. 1998; Dieckmann & Doebeli 1999; Doebeli and Dieckmann 2000). These studies proposed analytical conditions for branching at evolutionarily singular points (called evolutionary branching points) in one-dimensional trait spaces, under the assumption that both the mutation probability and the mutation step size are infinitesimally small. An asexual monomorphic population situated in the vicinity of a branching point can then be shown to first converge to that point and then to diverge into two subpopulations driven by frequency-dependent disruptive selection. Evolutionary branching points thus are convergence stable fitness minima.

In multidimensional trait spaces, the branching condition is still expected to be similar to that derived for one-dimensional trait spaces (Dieckmann 2000; Vukics et al. 2003; Egas and Dieckmann, submitted), since a population under the aforementioned infinitesimal assumptions experiences disruptive selection only if the fitness gradients in all directions vanish. This formal reasoning, however, implies a serious problem: evolutionary branching in a focused trait cannot occur if the population simultaneously experiences directional selection in any other trait that is not considered.

My previous research, and my recent investigations with Ulf Dieckmann, addressed the adaptive dynamics in two-dimensional trait space and showed that if either mutation probability or step are not infinitesimally small, evolutionary branching can still arise, if only the magnitude of the fitness gradient in the other trait is small enough relative to the curvature of the fitness valley at the branching point in the focal trait,. There appears to exist a certain threshold for evolutionary branching under such conditions, which depends on the relationship among the fitness curvature in the focal direction, the fitness gradient, mutation probabilities, and mutational step sizes. Since both mutation probabilities and mutational step sizes are not infinitesimally small in real populations, and since such populations tend to evolve in multidimensional trait spaces, understanding that threshold is necessary for understanding the mechanism of evolutionary branching in real populations (Schliewen et al. 1994; Schluter 1994; Feder et al. 1997; Losos et al. 1998).

Research questions

For simplicity, I will focus on two-dimensional trait spaces and on situations in which a population experiences frequency-dependent disruptive selection on one trait and directional selection on the other trait. In this system, I will try to determine the threshold condition for evolutionary branching.

Methods and work plan

To understand the branching mechanism in detail, I will investigate branching conditions along an artificial two-dimensional fitness landscape for an asexual population. This landscape is constructed by combining two one-dimensional fitness landscapes. Evolution in the first trait is modeled according to a resource competition model in a one-dimensional trait space that brings about evolutionary branching (Dieckmann & Doebeli 1999). Evolution in the second trait simply follows a constant fitness gradient, which can prevent evolutionary branching in the first trait when mutation probabilities and mutational step sizes become too small.

For this project, I plan to utilize three alternative descriptions of the evolutionary process unfolding in asexual populations:

1. *Monomorphic and polymorphic stochastic model on artificial fitness landscape.*
   To analyze the effects of mutation probability and mutation step separately, I will calculate evolutionary dynamics based on the polymorphic stochastic model and on the monomorphic stochastic model introduced by Dieckmann & Law (1996). The purpose of these analyses is to approximate the branching threshold, based on the shape of the fitness landscape and on the mutation probabilities and steps.

2. *Individual based model on natural fitness landscape.*
   To examine the usefulness of the threshold condition thus obtained, I will apply it to two different individual-based models defined on two-dimensional trait spaces. These models were previously constructed in my PhD research project, and are based on resource competition and predator-prey interactions, respectively.

3. *Deterministic description of dynamics based on canonical equation.*
   I will also try to deterministically describe evolutionary dynamics including evolutionary branching in the resource competition model and the predator-prey model, based on the canonical equation of adaptive dynamics.

Relevance and link to ADN's research plan

This project aims to bridge a gap between analytical predictions and numerical studies of evolutionary dynamics involving evolutionary branching, and thus directly links to ADN's research foci on *Adaptive Speciation* and on the *Foundations of Adaptive Dynamics*.

Expected output and publications

This work is intended for publication as a co-authored research article and will also be included in my PhD thesis.

References

Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34: 579-612.

Dieckmann, U. (1997). Can adaptive dynamics invade? Trends Ecol. Evol. 12: 128-131.

Dieckmann, U. and Doebeli, M. (1999). On the origin of species by sympatric speciation. Nature 400:354-357.

Dieckmann, U. Adaptive dynamics in two dimensions. (powerpoint slide 2000)

Doebeli M and Dieckmann U. (2000). Evolutionary branching and sympatric speciation by different types of ecological interactions. Am. Nat. 156: S77-S101.

Egas, M., Sbelis, M. W. and Dieckmann U. (submitted) Evolution of specialization and ecological character displacement of herbivores along a gradient of plant quality.

Feder, J.L., Roethele, J.B., Wlazlo, B. and Berlocher, S.H. (1997). Selective maintenance of allozyme differences among sympatric host races of the apple maggot fly. Proc. Natl. Acad. Sci. U. S. A. 94:11417–11421.

Geritz, S. A. H., Kisdi, E., Meszéna, G. and Metz, J. A. J. (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12: 35-57.

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. and Rodríguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115-2118.

Metz JAJ, SAH Geritz, G Meszéna, FJA Jacobs and JS van Heerwaarden. (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In Stochastic and spatial structures of dynamical systems, J van Strien & SM Verduyn Lunel, eds. KNAW Verhandelingen, North Holland, Amsterdam, pp 183-231.

Orr, M. R. & Smith, T. B. Ecology and speciation. (1998). Trends Ecol. Evol. 13:502-506.

Schliewen, U. K., Tautz, D. and Pääbo, S. (1994). Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368:629-623.

Schluter, D. (1994). Experimental evidence that competition promotes divergence in adaptive radiation. Science 266:798-801.

Vukics, A., Asboth, J and Meszéna, G.. (2003). Speciation in multidimensional evolutionary space. Phys. Rev. E. 68:041903.