

Evolutionary branching in a coevolutionary model for mutualism

Rahel Luethy

Zoology Institute, University of Basel, Switzerland

Discussions with my diploma supervisor Dr. Michael Doebeli (University of British Columbia, Vancouver, Canada) have motivated the writing of this research proposal. It has been jointly developed with Dr. Ulf Dieckmann, Coordinator of the IIASA Adaptive Dynamics Network, ensuring a good integration of the proposed project into ADN's research program.

Background

Introduction

Understanding speciation remains one of the fundamental problems in evolutionary biology. Classically, it is believed that most species originated in allopatry (i.e. through divergent evolution after geographic isolation) while the possibility of sympatric speciation has often been dismissed. At least partly, this was due to a lack of a coherent theoretical framework. Metz and his collaborators remedied this problem by introducing their theory of adaptive dynamics (Metz et al. 1992, Geritz et al. 1998). This framework offers a possibility for studying phenotypic evolution driven by ecological interactions. One of the central phenomena of adaptive dynamics is evolutionary branching. It occurs when frequency-dependent selection splits an initially monomorphic population into two distinct clusters in phenotype space. Essentially, adaptive dynamics is an asexual theory without any population genetic background. This seems to make it irrelevant for the analysis of sexual populations. Recently, Dieckmann and Doebeli have addressed this criticism (Dieckmann and Doebeli 1999). They have shown that the evolution of assortative mating in respect to the trait under study makes evolutionary branching possible in sexual populations. It therefore holds as a general theory for sympatric speciation. Evolutionary branching has been observed in a number of classical models describing a wide range of ecological interactions. Among them, a model for mutualism has been shown to offer a selection regime leading to evolutionary branching (Doebeli and Dieckmann, submitted).

Interspecific mutualistic interactions are widespread in nature and play fundamental roles in all ecosystems (see e.g. Boucher 1985). While their evolution is an ongoing challenge for theoreticians (see e.g. Doebeli and Knowlton 1998) much less attention has been given to their role in processes of diversification. Doebeli and Dieckmann (submitted) deal with this question by studying evolutionary branching in a model for mutualism.

Model for mutualism

The classical model for mutualism (Vandermeer and Boucher 1978) is developed by adding a second term to the basic Lotka-Volterra equation for one species:

$$\begin{aligned}\frac{dN_1(x, t)}{dt} &= r_1 \cdot N_1(x, t) \cdot \left(1 - \frac{N_1(x, t)}{K_1(x)} + \alpha_{12} \cdot N_2(u, t) \right) \\ \frac{dN_2(u, t)}{dt} &= r_2 \cdot N_2(u, t) \cdot \left(1 - \frac{N_2(u, t)}{K_2(u)} + \alpha_{21} \cdot N_1(x, t) \right).\end{aligned}$$

The added terms α_{12} and α_{21} are positive real numbers describing the mutualistic support the two species give each other. This approach is very similar to two-species competition models,

where the α -values are negative and represent competitive strength. In extension to classical models for mutualism (e.g. Vandermeer and Boucher 1978) the interaction coefficients α_{ij} are determined by quantitative characters. One of the few other studies that do consider coevolution of quantitative traits affecting mutualistic interactions is Kiester et al. (1994). Kiester et al. (1994) considered a pair of mutualistic species in which quantitative characters determine the amount of mutualistic support. One example of such a system is a flowering plant and its pollinator, where the mutualistic support depends on the flower morphology and the feeding apparatus. In the model described by Doebeli and Dieckmann (submitted), individuals do not vary in overall mutualistic support they give but in how they allocate it to their interspecific partners. This allocation is determined by a Gaussian function of phenotypic distance (with a maximum at distance 0), which leads to frequency-dependent selection in the mutualistic partner-species. The functions $K_1(x)$ and $K_2(u)$ define the carrying capacities of different phenotypes in the two species. Biologically, this can be thought of as how effectively a certain phenotype is able to use a given resource. These functions are again assumed to be of Gaussian form $N(x_0, \sigma_{K1})$ for species 1 and $N(u_0, \sigma_{K2})$ for species 2. Thus, $K_1(x)$ and $K_2(u)$ have a stabilizing effect on each species. The frequency-dependent effect of the mutualistic interaction combined with the stabilizing effect of the carrying capacity leads to a conflict between "being close to the mutualistic partner" and "efficiently use the resource present". In its simplest, symmetric form (if the two species only differ in their resource maxima, i.e. $x_0 \neq u_0$) this results in evolutionary branching in both species, i.e. each initial species splits into two phenotypic branches as soon as the maxima x_0 and u_0 lie far enough apart. Doebeli and Dieckmann (submitted) point out that this result is robust in the sense that introducing asymmetries in the system will not change the outcome qualitatively as long as the asymmetries are small. As soon as the introduced asymmetries are large, new interesting phenomena such as sequential evolutionary branching arise. The aim of the research proposed here is to give a detailed classification of the possible coevolutionary dynamics in this model.

Research questions, personal interests and work plan

While Doebeli and Dieckmann confined themselves to pointing out that evolutionary branching is a generic feature of their model, the aim of my diploma work (started December 1999) is to give a detailed classification of its coevolutionary dynamics. In order to do so, I will predominantly rely on Dieckmann and Law (1996) who provide a general framework for this kind of analysis. They investigate evolutionary dynamics of a predator-prey community as an individual-based birth-death-mutation process and develop deterministic approximations of the stochastic process that describe the mean evolutionary path of the system. In the first part of my diploma work (until May 2000) I will continue to get acquainted with the literature as well as improve my modeling skills. This is directly connected to projects I was involved in prior to the start of my MSc work. Supervised by Dr. Michael Doebeli, I was engaged in modeling evolutionary branching in a competition model, and as his research assistant I investigated experimental evolution of speciation in yeast. In November 1999 I worked on object oriented design and programming patterns (in collaboration with Benjamin Rosenbaum, Senior Software Architect). The research proposed here will represent the second part of my diploma work. YSSP and especially the contact to IIASA senior research staff will facilitate solving specific questions that certainly arise during the work planned as well as help me to strengthen my mathematical and computational background.

Relevance and link with ADN's research

Both the model for mutualism as well as the framework for the analysis of coevolutionary dynamics were co-developed by ADN Project Coordinator Dr. Ulf Dieckmann. Thus, the project proposed here continues and extends previous and ongoing research of the ADN. In general, a detailed knowledge of a model's evolutionary dynamics is crucial to decide about its role and importance in the field it is situated in. I refer to Doebeli and Dieckmann (submitted) who have emphasized that a comprehensive analysis of their model for mutualism would be a "worthwhile and interesting endeavor".

Envisaged publication(s)

It is planned that the coevolutionary analysis of the model for mutualism will result in at least one publication (in collaboration with Dr. Ulf Dieckmann and Dr. Michael Doebeli).

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