Adaptive speciation in spatially structured environments

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Goal

To understand the structure of speciation processes in terms of ecological, sexual, and spatial differentiation and to thereby characterize the alternative qualitative pathways such processes can follow.

Background and Motivation

After many years of heated debate, speciation still remains one of the most exciting topics within evolutionary biology. One of the issues that particularly has received a lot of attention concerns the question whether species generally originate in allopatry (i.e. through divergence after geographical isolation) or in sympatry (i.e. through ecological or other interactions between individuals within a single population). Based on the forceful arguments of leading evolutionary biologists and the results of classical models of sympatric speciation (e.g. Maynard Smith, 1966), allopatric speciation has long been considered the only plausible general mode of speciation.

This has changed only recently, when the application of molecular biological techniques has revealed a number of instances where the resolved phylogenies could be better explained by sympatric rather than by allopatric speciation (e.g. Schliewen *et al.*, 1994). Moreover, renewed theoretical interest in sympatric speciation has resulted in important new insights in the mechanisms underlying speciation: evolutionary branching has been established as a paradigm for the evolution of stable ecological polymorphism (Dieckmann & Doebeli, 1999), solving the longstanding problem of the origin and maintenance of ecological variation under disruptive selection, and sexual selection has been used to explain the evolution of a mating system that allows for reproductive isolation, the second vital ingredient of sympatric speciation (Higashi *et al.*, 1999).

However, an important aspect that is missing from the recent theoretical models of sympatric speciation, is space. By definition, individuals are sympatric when their interactions depend on their genotypes only, and therefore, sympatric speciation can be studied only in a spatially homogenous, or well-mixed context. Notwithstanding this, there are at least three arguments in favor of considering spatial structure in speciation models:

- Most interactions between organisms occur locally in some spatial context. This allows for spatial pattern formation, even in a homogeneous environment. Moreover, also spatial heterogeneities may induce larger-scale spatial patterns. In most biological systems, such patterns are present and it is important to consider the effects of such spatial variation on evolution.

- Recent theoretical models of sympatric speciation have shown that speciation may crucially depend on stochasticity (Dieckmann & Doebeli, 1999; Van Doorn *et al.*, submitted; Van Doorn & Weising, submitted). In a well-mixed population, stochastic fluctuations will only be sufficiently large when the population size is sufficiently small. Yet, with spatial structure, fluctuations can be considerable, even in a large population, because of the stochasticity of local interactions with a limited number of neighbors. Therefore, a small spatial component may greatly enlarge the potential for speciation.
- The important issue in the allopatric/sympatric debate is not whether spatial processes are highly relevant or completely irrelevant, but, rather, whether speciation results from externally imposed events and neutral processes (e.g. geographical separation and the evolution of reproductive isolation due to genetic drift during allopatric speciation) or from internal selective processes (e.g. the evolution of assortative mating driven by sexual selection during sympatric speciation). Therefore, as soon as the mechanisms of speciation are concerned, a distinction between adaptive and non-adaptive speciation would be more useful than a distinction between sympatric and allopatric speciation, which merely reflects a mode, not a mechanism of speciation. From this point of view, it is immediately clear that the role of spatial structure in adaptive speciation should not be ignored.

Research question and work plan

During my stay at IIASA, I would like to consider the following questions: (1) what will be the effect of spatial structure on the potential for speciation, (2) are these effects different for different spatial processes (dispersal, local competition, local mate choice, spatial resource heterogeneity), and (3) what are the mechanisms through which spatial structure influences speciation?

These questions will be addressed by extending an existing theoretical model of sympatric speciation (Van Doorn & Weissing, submitted), which integrates ecological and sexual selection aspects of speciation. In this model, sympatric speciation is initiated by simultaneous evolutionary branching of an ecological strategy, leading to ecological differentiation, and mating strategies, resulting in assortative mating.

The model is made spatially explicit by implementing local resource variability, local competition for resources, local mating and limited dispersal. By varying the latter spatial scales with respect to the scale of resource heterogeneities, different regimes, corresponding to different amounts of spatial structure, can be explored.

The model will be analyzed by a combined analytical and individual-based computer simulation approach. Preliminary work suggests that an analytical treatment, aided by numerical analysis, is still attainable for this model. Using the methods of adaptive dynamics, I aim to derive parameter conditions necessary for evolutionary branching and subsequent speciation, and compare these conditions for different spatial scenarios.

Relevance and link with ADN's research

The project aims at exploring the effects of spatial structure on adaptive speciation. First, since I will investigate this aspect of speciation in a single framework together with ecological processes and sexual selection, the results of the analysis may serve to disentangle the multiple mechanistic pathways through which species can arise. Second, our approach separates patterns (sympatric or allopatric) from processes (adaptive or non-adaptive) involved in speciation. This may contribute to a more systematic study of speciation, which would be an improvement in the often-polarized speciation debate.

The ideas developed here build on, and extend ADN's research on adaptive speciation. The model structure is largely derived from Dieckmann & Doebeli (1999) and the methodology used to analyze the evolutionary dynamics in the model has been developed by ADN (Metz *et al*., 1996).

Envisaged publications

The proposed research is planned to result in a jointly authored paper, which will be integrated in my PhD thesis.

References

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