The Interplay between Sexual Selection and Ecological Differentiation in Sympatric Speciation

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Goal

To elucidate the interaction of different mechanisms promoting speciation, and, in particular, to study how joint evolution in ecological and mating traits leads to reproductive isolation.

Background and motivation

Speciation is the process by which a species splits into two species that cannot interbreed, and which consequently remain distinct and reproductively isolated in the future (Maynard Smith, 1998, Bulmer, 1994, TREE, 2001).

In the wake of work by Mayr (1942), allopatric speciation (speciation due to prolonged geographical isolation and separate evolution) has come to be accepted as the most likely speciation mechanism. Recent field studies, however, have suggested that sympatric speciation (speciation without geographical isolation of the incipient species) might be more widespread than was previously thought, as in the case of the explosive speciation of cichlids in Lake Malawi and other African lakes. The growing interest in mechanisms of sympatric speciation has fostered a variety of theoretical analyses (TREE, 2001, Payne and Krakauer, 1997, Dieckmann and Doebeli, 1999, Kondrashov and Kondrashov, 1999, Higashi et al., 1999). Collectively, these have lend support to the notion that sympatric speciation can be expected to occur under certain, not too restricted conditions.

The most important driving forces of sympatric speciation are

- ecological differentiation through natural selection, leading to divergence and dimorphism in an adaptive trait that affects the ecological function and behavior of its bearer, and
- mating differentiation through sexual selection, leading to divergence and dimorphism in an adaptive trait that affects the mating function and behavior of its bearer.

Selection on ecologically relevant traits is one of the most frequent evolutionary mechanisms in natural sexual or asexual populations. It occurs when bearers of different adaptive traits are not equally well adapted to their ecological environment. In theoretical models this can be represented, for example, by carrying capacities depending on adaptive ecological traits (Dieckmann and Doebeli, 1999).

Sexual selection is natural selection applied to sexual traits. For example, males or females having certain traits may mate more successfully than those who do not, without the traits under consideration themselves conferring better adaptation to the ecological environment (Andersson, 1994). This situation can lead to a Fisher runaway process, by which genetic correlations (linkage disequilibria) emerge, for instance, between male traits and female preferences (Higashi et al., 1999, Payne and Krakauer, 1997, Gavrilets, 2000a,b, Tregenza et al., 2000, Gavrilets et al., 2001).

While these two mechanisms have been analyzed in some detail separately, studies that combine ecological and mating differentiation in a single model so far are rare (see Dieckmann and Doebeli, 1999). Yet, such analyses are needed in order to better understand the variety of evolutionary pathways that can lead to sympatric speciation, as well as their prerequisites and robustness.

Even when speciation is allopatric, minimal amounts of gene flow between the incipient species usually cannot be excluded. To account for this complication, speciation is formally considered to be sympatric when it occurs within the dispersal range of the species. It is clear that most natural populations are spatially structured, and in most cases, contrary to assuming a well-mixed population, this structure cannot be thought of as being homogeneous. Those theoretical studies of sympatric speciation in which space is not made explicit and populations are assumed to be well-mixed obviously meet the refined definition of sympatric speciation. But even spatially extended models can be used to investigate processes of sympatric speciation, as long as dispersal is frequent or far enough for speciation, if it occurs, to be considered sympatric. The spatial structure of populations and environments underlying speciation processes therefore is an important element of models that assess alternative mechanisms of sympatric speciation. In other words, spatial differentiation (at least initially almost absolute in allopatric speciation and almost absent in sympatric speciation) has to be considered in conjunction with ecological differentiation and mating differentiation.

Research questions

The topics I plan to tackle during my stay at IIASA are as follows:

- To study the interaction between natural and sexual selection in processes of sympatric speciation.
- In this context, to analyze the importance of self-generated spatial structure underlying the speciation process.
- If time permits, to examine the impact of externally imposed spatial heterogeneity (in particular, in the form of environmental gradients) on the sympatric emergence of species.

Methods and work plan

For this purpose, I intend to combine two different theoretical approaches recently proposed (Payne and Krakauer, 1997, Dieckmann and Doebeli, 1999), into a single model that integrates both natural and sexual selection.

I will first analyze the joint evolution of an ecological trait and two mating traits (one expressed only in males, the other only in females) in a spatially unstructured population. Retaining the same ecology and mating structure, I then plan to extend this model to make space explicit. A specific aim for this extension is to study the effects of conditional dispersal. In particular, dispersal can depend on mating success, on local carrying capacity, and/or on effective resource availability. I will investigate how these dependences affect the potential for sympatric speciation.

This agenda will be carried out based on an (ecological) extension of the model introduced by Payne and Krakauer (1997), by means of numerical simulations and analytical treatment where possible (see Dieckmann and Doebeli, 1999, and references therein).

Relevance and link to ADN's research plan

In this project, we aim to build a framework for the study of sympatric speciation, which integrates both natural and sexual selection. We expect that a systematic study of this mode of speciation with the inclusion of the two main driving mechanisms, together with spatial effects, will contribute to the present debate by giving a more complete and realistic picture of the possible directions that may promote sympatric speciation.

The programme of research planned here will extend the ideas of the previous studies on adaptive speciation carried out in ADN. The model envisaged will contribute as an alternative extended model to the one proposed by Dieckmann and Doebeli (1999), with the use of the ideas and methods presented there, as well as in other ADN studies (i.e., Metz et al., 1996).

Expected output and publications

The study envisaged here is expected to be published in a jointly authored paper, and this might be integrated in one chapter of my PhD thesis.

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