Young Scientists Summer Program 2002
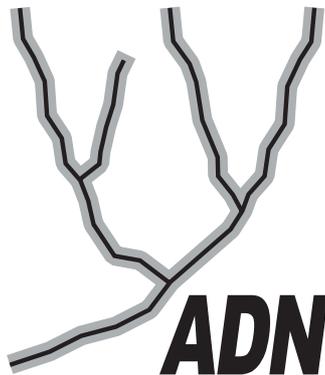
Two Research Projects

Adaptive Dynamics Network
International Institute for Applied Systems Analysis
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ADN

Adaptive Dynamics of Mutual Predation

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Goal

To explore the evolutionary origin and stability of mutual-predation food webs.

Background and motivation

There are more roles for an organism to play within a trophic system than those of competitor, predator, and prey. This realization leads to a transition from thinking in terms of food *chains* to thinking in terms of food *webs*. (Polis et al., 1995; Persson et al., 1995). Classical concepts from studies of linear food chains and of competitive interactions have thus been probed by theoretical and experimental studies on systems involving more complex interactions between organisms. This has led to insights into the role of intra-guild predation (Mylius et al., 2001) and cannibalism (Claessen et al., 2000) for the regulation of communities.

My PhD research focuses on one such complex interaction between organisms by investigating the ecological and evolutionary consequences of two mite species predating (a) on pollen and (b) on each other's larval stages. Since, with regard to the pollen resource, the two mite species form a guild, and since within this guild, the two mite species nevertheless predate on each other, such a complex interaction is called mutual intra-guild predation (MIGP).

Previous research (Mylius et al., 2001, Diehl and Feissel, 2000) has indicated that intra-guild predation (IGP) systems (consisting of a resource and two resource consumers, of which *one* is also an intra-guild predator that utilizes the other consumer as prey) exhibit diminished opportunity for coexistence when compared to classical linear food chains (consisting of a resource, a resource-consuming prey, and its predator). In particular, at increased primary productivity, the intra-guild predator excludes the prey.

In the case of MIGP, I have found that parameter combinations allowing for coexistence are further restricted compared to linear food chains and IGP systems. In addition, at increased primary productivity, *both* consumer species can exclude the other, resulting in ecological bistability. (R. HilleRisLambers, in prep.)

Research questions

Because of the notoriously fast evolution of arthropods species (illustrated, for example, by the problematic evolution of insect pest resistance to pesticides) the question is begged as to how evolutionarily stable such MIGP systems are. Furthermore, interesting questions arise from considering how such food web configurations could have evolved in the first place. Because of the ecological bistabilities involved in IGP and MIGP systems, evolution towards such complex configurations from other, simpler food web configurations are fraught with potential for evolutionary suicide. On the other hand, given the flexibility in feeding strategies and the substitutability of resources (both species can subsist on either a herbivorous/carnivorous diet alone) it would certainly be

relatively easy for mites to evolve, for example, towards a more specialist strategy, if such an adaptation would be advantageous. This project thus seeks to clarify if MIGP configurations of feeding strategies are robust to evolutionary change, and through which evolutionary pathway they are likely to have arisen.

Methods and work plan

I plan to describe the individual feeding strategy of a mite species by a single parameter that can vary under a trade-off between carnivorous and herbivorous strategies, i.e., between adaptation for predation on the other mite species or for harvesting of the pollen resource. Here we can either consider a simple linear trade-off, based on the assumption that time allocated to one feeding strategy is time *not* allocated to the other, or we can investigate slightly more complex trade-offs derived from physiological constraints.

By varying the two traits thus resulting for the two mite species we can capture a continuum of three-species food web configurations. Specific examples are (1) a classical linear food chain, (2) a classical two-competitor, one-resource system, (3) IGP systems, and (4) MIGP systems. Using techniques developed as part of the adaptive dynamics framework (Metz et al., 1996, Geritz et al., 1998, Dieckmann and Law, 1996, Dieckmann, 1997), we can then not only examine if and how MIGP systems will evolve *to* any of the other food web configurations, but also if and how MIGP systems could evolve *from* any of the other possible food webs, and under what ecological conditions.

I have already constructed and analyzed a stage-structured model of two size-structured generalist predators feeding on each other and on a common resource. In addition, I have already analyzed an unstructured version of this model. I have found that this simpler, and thus more analytically tractable model, exhibits the same qualitative behavior as the more complex structured model; in particular, it gives the some qualitative predictions about species replacements along a gradient of primary productivity. I therefore propose to first use the unstructured version of the model (possibly later extending the analysis to the structured version depending on time and computational ease). I then plan to follow a sequence of three steps:

- A first step will involve deriving the fitness functions for both species, given a trade-off between herbivorous and carnivorous feeding strategies. Due to the symmetry of interactions (both species are described by identical equations, and differ only in parameters involved) the fitness expressions will be identical. While I will eventually deal with linear, convex, or concave trade-offs between the two feeding strategies, initial analyses will focus on the linear case.
- In a second step I will study the potential for evolution towards MIGP systems by constructing pairwise invasibility plots (Metz et al., 1996, Geritz et al., 1998) for each of the possible food web configurations from which MIGP systems could evolve.
- The third step will involve studying the coevolutionary dynamics of both species's feeding strategies, using the canonical equation of adaptive dynamics (Dieckmann and Law, 1996).

The first two steps will also help me to familiarize myself with the methods of adaptive dynamics theory and may already be completed before the start of the summer program. The third step will be developed during the summer program in collaboration with Ulf Dieckmann.

Relevance and link to ADN's research plan

Understanding how different food webs are linked to each other through the evolution of feeding strategies would contribute to a greater understanding of community evolution. In addition there is a chance of increasing our understanding of arthropod feeding strategies and thus contribute to the current debate on the evolution of specialism vs. generalism. This study may also generate interesting insights into mechanisms of adaptive speciation. Other important applications may arise for applications in the field of biological control.

Expected output and publications

This work is expected to result in one chapter in my PhD thesis, which will also be submitted as a co-authored piece for publication late in 2002 or early in 2003.

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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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