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Seven Research Projects

Adaptive Dynamics Network
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A model for evolving fish stocks in a stochastic environment: the example of the North-east Arctic cod

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Background

After the introduction of heavy exploitation, a number of fish stocks have shown large changes in age and size at maturity (Law and Grey 1989, Jrgensen 1990). For the North-east Arctic cod there has been observed a decrease in age at maturation (Jrgensen, 1990). A decrease in age at maturation and the possible decrease in size at maturation can reduce the total biomass of the population and thereby reduce the long term yield of the population (Law and Grey, 1989). Knowledge about the population structure is also crucial in the quantitative assessment of a population such as the North-east Arctic cod. Heino (1998) showed that harvesting can select for life history changes in an exploited population with an age-structured population model. This model was extended by Salthaug (in prep.) by incorporating size and genotype structure in addition to age structure. If evolutionary changes in a population are caused by the harvesting regime and/or trends and fluctuations in the environment, these should indeed be taken into account by quantitative models.

Problem

Extend the existing model by incorporating environmental variations and trends in order to explain the observed changes in the North-east Arctic cod stock in a more realistic way.

Task:

It is known that the structure of a population might be influenced by the environment (Jrgensen, 1990), and thus, in order to construct a more realistic model environmental variations should be accounted for in the model. The general goal of this extension is twofold:

1. Reduce uncertainties in predictions of cod population structure and adaptation by accounting for known variability in environmental conditions and fishing pressures.
2. Analyse whether evolutionary changes in central life history traits should be taken into account in the management of renewable resources by predicting their expected rates under realistic conditions.

Approach

There exists some knowledge about which environmental factors can affect the structure in populations. Environment will, in this approach, include changes in the ocean climate, variation in the biological environment and changes in exploitation. For the North-east Arctic cod the temperature seems to affect larval and juvenile growth (Ottersen and Sundby, 1995). There is a relationship between prey abundance (e.g. capelin) and growth of cod (Bogstad et al., 1995). There has been a change in fishing effort because of more efficient vessels and fishing gears (Nakken, 1994). Fishing gears are selective, that is, fish with certain phenotypic properties such as size are more likely to be caught than others. When introducing variations and trends in the

environment we will use the observed (known) changes in environmental conditions and fishing pressures;

1. Variations in temperature (and, maybe, other climatic variables such as the North-Atlantic oscillation index)
2. Variations in fishing effort
3. Variations in fishing selectivity
4. Variations in prey abundance

Existing and documented relationships will be used. In addition, such relationships might be investigated using the theory of generalised linear models or multivariate time series. I will try to match the described variation statistics by analysing variances, auto-correlations and cross-correlations. More specifically this means that we have to formulate and fit plausible functions of the model parameters, i.e. the growth rate, as a function of the environmental variables described above.

Further, in order to investigate the described problem, we will try to find a model which:

1. Mimics observed time series for variations in stock abundance and composition as closely as possible
2. Mimics observed time series for age and size at maturation as closely as possible

In particular, I intend to follow the following progression of steps:

1. Decide which environmental variables to use. Then construct a matrix where the rows consists of the time series of observed or estimated values for each chosen variable. Of course we want as long time series as possible, but the longest possible time series for cod is from 1932 until now.
2. Determine the best possible functional forms of the model parameters as functions of the environmental variables, or use known relationships if possible.
3. Simulate the extended model by the same procedure as described by Salthaug (in prep.), but now introduce the observed variations in environmental conditions as explained. More specifically this means: i) simulate the model with no fishing pressure, ii) introduce fishing pressure and simulate the model over the time span where the changes in the population structure have been observed.
4. Based on defined test statistics, investigate how the model recovers the observed data (that is the data described by God, 2000). This will indicate where we have to focus our attention in the search for a model which describes the observed changes in the population structure for cod. When this is done, we have to consider further adjustments or extensions of the model that will help to improve the accuracy of predictions with respect to observed data.

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Adaptive dynamics of size-structured populations: ontogenetic trade-offs and speciation in piscivorous fish

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The lectures and discussions at the IIASA workshop on Adaptive Speciation (December 1999) have motivated the writing of this research proposal, which has been jointly developed with Ulf Dieckmann, Project Coordinator of the IIASA Adaptive Dynamics Network, ensuring that the proposal is well integrated into ADN's research program.

Background

There are several examples of sibling fish species that appear to have speciated by means of specialization on two different resources ('resource polymorphism'), e.g. in cichlids (Schliewen et al. 1994; D. Tautz, pers. com.), sticklebacks (Rundle et al., in press) and Arctic char (Skúlason and Smith 1995). In these cases, like in many other size-structured populations, resource use is strongly correlated to individual body size. One of the resources is a 'basic' resource that both specialists use when small, whereas the second resource is used more or less exclusively by only one specialist (the bigger one). Hence, the second 'specialist' is in fact an ontogenetic omnivore. Moreover, it is likely that their common ancestor was also capable of such ontogenetic omnivory.

Population dynamics of piscivorous fish

In the first part of my PhD project I have studied the population dynamics of such an ontogenetic omnivore, focusing on the Eurasian perch (*Perca fluviatilis*). Small perch are mainly planktivorous but, as their size increases, they become increasingly piscivorous (Persson et al. in press). Together with André de Roos and Lennart Persson I developed a physiologically structured population model (PSPM) (Metz and Diekmann 1986, De Roos 1997) to study the impact of size-dependent competition and cannibalism on population dynamics (Claessen et al. 2000). The PSPM has been used successfully to predict population dynamics and individual development of perch. Moreover, this study offers a population dynamical (i.e. environmental, non-genetic) explanation for the occurrence of a frequently observed resource polymorphism. In populations of piscivorous fish often two distinguished life histories occur in a population: giant cannibals and planktivorous dwarfs (Smith and Skúlason 1995). Our study shows that this phenomenon emerges from size-structured population dynamics with size-dependent cannibalism and competition.

Here, I propose to extend this study by including evolution of an 'ontogenetic strategy'. Incorporation of this well-studied PSPM into the framework of adaptive dynamics will provide a sound, mechanistic platform to address questions of evolution in size-structured populations, such as the above mentioned examples.

Ontogenetic trade-off and ontogenetic strategy

The required morphologies for efficiently capturing and processing different prey types, e.g. fish and zooplankton, differ. It is reasonable to assume that an individual cannot be maximally

adapted to feeding on both prey types simultaneously. Moreover, the ability to be piscivorous later in life imposes constraints on the efficiency of planktivory earlier in life (L. Persson, pers. comm.). In other words, there is an ontogenetic trade-off between piscivory and planktivory, that results from morphological constraints. The resource polymorphism in Arctic char illustrate that individuals may differ in their ‘ontogenetic strategy’. The piscivorous morph is a worse planktivore early in life but a voracious piscivore when big, and vice versa for the planktivorous morph.

In the proposed research, an ontogenetic trade-off will be defined as a negative relation between the maximum planktivorous attack rate (at the optimal size for planktivory) and the maximum cannibalistic attack rate (at any given size). Thus two parameters in the original model will be parameterized as functions of an additional i -state variable, the ontogenetic strategy z . The value of $z \in [0, 1]$ is an index of developmental investment in morphological structure that increases the ability to capture and process fish prey. Thus $z = 0$ corresponds to the planktivorous specialist, and $z = 1$ to the piscivorous specialist. An intermediate z obviously represents a generalist strategy.

Research question and work plan

My question focuses on (1) the direction of evolution of the ontogenetic strategy, depending on the pattern of population dynamics, and (2) the role of developmental flexibility in the evolution of size-structured fish populations. Specifically, (2) addresses the question whether the possibility of a size-dimorphism given by population dynamics facilitates evolutionary branching.

(i) The population dynamics in the possible strategy space will be explored, charting the regions with different population dynamical attractors. (ii) With standard methods from adaptive dynamics theory, the direction of the evolution of z will be determined in these different regions in strategy space. To this end pairwise invasibility plots will be constructed. (iii) The potential of evolutionary branching will be investigated. In the neighborhood of evolutionary singular points I will study frequency-dependent selection on the strategy z , resulting from population dynamical feedbacks. (iv) Finally, the question will be addressed whether the size-dimorphism is a *substrate for* rather than a *result of* evolution.

During my March-May 2000 work visit with Lennart Persson, Umeå University, Sweden, I plan to make a start with the project. This will mainly concern the formulation of the ontogenetic trade-off based on empirical data and the above mentioned point (i).

Relevance and link with ADN's research

In order to confront the theory of adaptive dynamics with empirical data one has to formulate testable hypotheses. A mechanistic way is to identify ecological factors that promote or inhibit evolutionary branching (Dieckmann and Doebeli 1999, and the Adaptive Dynamics workshop at IIASA). In order to do so, one has to be specific about the ecological processes in the studied system. The research proposed here is expected provide a platform for such a ‘case study’ to test the theory of adaptive dynamics. The PSPM for perch has been shown to correctly predict both qualitative and quantitative aspects of population dynamics of an empirical lake population (Claessen et al. 2000). Using this model, the proposed research hence potentially result in testable predictions regarding adaptive dynamics in this system.

Another interesting potential test case is provided by the suggested ongoing speciation process in Arctic char in some Icelandic lakes. The research group of Skúlason has provided evidence for a genetic basis of the resource polymorphism in certain lakes (e.g. Thingvallavatn).

Yet, on the same island there are also lakes where a size-dimorphism of piscivorous giants and planktivorous dwarfs occurs, yet without the genetic differentiation (S. Skúlason, pers. comm.). The hypothesis that the dimorphism may be induced by population dynamics is confirmed by preliminary results of the PSPM parameterized for Arctic char (Jens Andersson, unpublished results). The mechanistic approach of the proposed research may provide tools to identify the ecological factors or population dynamical patterns that promote adaptive speciation in one lake and inhibit it in another lake.

In general, an understanding of life-history adaptation in a physiologically structured population with environmental feedback extends classical life-history theory in a critical manner and is an important prerequisite for the analysis and management of many ecological systems. In this vein, the proposed research allows for applying, testing, and extending the required mathematical tools for this purpose in a well-specified ecological setting.

Finally, the research proposed here relates obviously to the research completed by last year's YSSP participant Janica Ylikarjula. Hence, this YSSP project continues and extends previous and ongoing research in the ADN project.

Envisaged publication(s)

The proposed research is planned to result in at least one chapter in my PhD thesis. The evolution of an ontogenetic strategy in the above mentioned PSPM of perch will result in a jointly authored paper. Eventually, the case study of speciation in Arctic char, in collaboration with S. Skúlason, may lead to a second publication.

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Three applications in evolutionary dynamics

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This research proposal is motivated by ongoing work on evolutionary dynamics jointly developed with Sergio Rinaldi, my PhD Tutor at the Politecnico di Milano, and Régis Ferrière, member of the IIASA Adaptive Dynamics Network. My interest in the subject is recent and has been reinforced by attending the Winterschool on Mathematical Modelling in Ecology and Evolutionary Biology, at Paris.

Background

Ecological interactions among genetically invariant populations easily lead to cyclic or chaotic regimes at the fast ecological timescale. By contrast, modelling studies often support the idea that genetical processes tend to stationary regimes. Genetical changes are frequently considered separately, occur simultaneously in systems of coevolving populations. In complex cases, ecological and genetical characteristics continue to vary, even when external conditions remain constant (*Red Queen Dynamics*).

The main problem in evolutionary dynamics is to derive the equations that describe the time evolution of the populations' genetical traits. These dynamics are the result of the random appearance of a mutant followed by the competition between the mutant and the resident individuals. Since the mutant is rare initially, it must be able to spread at low density, i.e. to invade. But the fate of an initially successful mutant depends on its interactions with the resident population. Either it replaces the former resident, or both the mutant and the resident stay in the system at finite densities, giving rise to a branch in the evolutionary dynamics (*polymorphism*).

Most of the studies developed in the last years focus on cases in which

1. the resident population has a single attractor
2. the attractor is an equilibrium
3. an invading mutant always replaces the former resident

Thus, if successful mutations are small and occur rarely enough, there are monomorphic evolutionary dynamics within species, and the state equations describing such dynamics, are called *monomorphic model*. This monomorphic model is often derived by explicitly taking into account the mutant characteristics, like in but sometime even without taking care of the mutant at all, like in

Research questions and work plan

The research plan is in three parts, each one dealing with a problem in which one of the three above conditions is not satisfied.

Evolutionary dynamics of populations with multiple attractors

Assumption (1) does not always hold, since many populations have multiple attractors. For this reason we first intend to explore the consequences that such a property may have on evolutionary dynamics. To this aim, we will consider the simplest case in which the population can have two alternative stable equilibria and determine if this condition can trigger cyclic evolutionary dynamics. Technically, this will be done by using the so called *separation principle* a condition for the existence of slow-fast limit cycles.

Evolutionary dynamics of predator-prey systems

The second (major) research topic concerns the evolutionary dynamics of predator-prey systems described, in ecological time, by a couple of ordinary differential equations. Evolutionary dynamics of predator-prey systems have already been studied in terms of simple Lotka-Volterra models. Here, more realistically, we assume that the predator has a saturating functional response. Thus, the model is the standard Rosenzweig-MacArthur model (logistic prey and Holling type II predator), where parameter values depend upon two phenotypes, one for each species.

The derivation of the monomorphic model is not easy, since for fixed phenotype values, the attractor of the predator-prey model can be a limit cycle, which is not known analytically. In turn, this implies that the monomorphic model cannot be specified analytically. In order to avoid this difficulty, we plan to consider the particular but meaningful case in which preys are much faster than predators in growing and reproducing. This implies that the limit cycle becomes a slow-fast limit cycle which is completely known and, one would hope, allows the derivation of the monomorphic model analytically.

The analysis of the monomorphic model and, in particular, the determination of all its attractors, will be solved numerically by using advanced software for bifurcation analysis. The main task of this analysis is to check if under suitable environmental conditions one of the following two properties holds:

- (i) coevolution can be a never-ending process
- (ii) coevolution can find its end at a point where the two populations are at the edge of their most complex dynamic behavior (a cycle in the present case)

Proving that case (ii) is possible, would be because, on one hand, recent analyses of field data support the idea dynamic behavior, while, on the other hand, ecosystems often hold at the edge of the most complex dynamic behavior

Evolutionary dynamics in information technology

A third (minor) research topic concerns the area of *information technology*, where remarkable new ideas have emerged in the last fifty years. Given a fixed state of science and technology, producers and consumers interact and quickly tend to an equilibrium. But, once in a while, one of the many new ideas go through and produces a technological innovation, which, in turn, entrains a new supply-demand equilibrium. Thus, the appearance of a new idea is like the appearance of a mutant with a new technological trait, and the success of the idea is characterized by the substitution of the old technological trait to a rest, but under to diversified the birth of PC points in the history of information technology.

Some preliminary but rewarding discussions on this problem are certainly possible at IIASA, where various projects are focussing on industrial innovation. Régis Ferrière and Sergio Rinaldi

will initiate contacts with researchers in the groups that are potentially interested. If clear signs of interest come from one or more research devoted to the topic.

Envisaged publications

The proposed research is planned to be part of my PhD thesis or, alternatively, be one of my two minors in my PhD program at the Politecnico di Milano. The study on evolutionary dynamics of predator-prey systems will result in a jointly authored paper, hopefully by the end of the YSSP. The studies on populations with multiple attractors and information technology may also lead to independent publications.

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Adaptive dynamics of spatially-structured sessile populations: life-history evolution and competition for space in the rocky intertidals

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Background

Intertidal communities of sessile organisms are strongly determined by the outcome of an evolutionary game of competition for space. Different organisms can adopt different strategies from a continuum. Some organisms grow fast, very soon produce huge amounts of propagules and disperse them very far. These organisms usually have poor competitive ability and invasion success. Other organisms grow slow, live longer, and produce a few propagules that disperse very locally. These organisms tend to be good competitors.

Mean-field models of competition for space

Inspired by space-limited systems—such as the intertidal—Hastings(1980) studied disturbance, coexistence, history and competition for space using a theoretical framework derived from a competitive-hierarchy assumption. A competitive-hierarchy means that types can be ordered in a hierarchical way based only in competitive abilities. In other words and without losing generality, if $i < j$, then a type i will replace type j with probability one. Thus, the model studied by Hastings (1980) is

$$\frac{d}{dt}p_i = \beta_i p_i \left(1 - \sum_{j=1}^i p_j\right) - \left(\delta_i + \sum_{j=1}^i \beta_j p_j\right) p_i. \quad (1)$$

In this equation, β_i and δ_i represent respectively, the propagule production rate per site (or patch) and the disturbance rate for a species indexed by i . The function (of time t) p_i represents the proportion of occupied sites.

This model (equation 1) is a generalization of Levins' (1969) patch-occupancy metapopulation model

$$\frac{d}{dt}p = \beta p(1 - p) - \delta p. \quad (2)$$

Hastings' (1980) investigations lead him to conclude: "*to survive, a poorer competitor must be a better colonizer*" (Hastings, 1980 p.366). Mathematically, in the case of two species where species 1 is a better competitor than species 2 (*i.e.*, $\beta_1 < \beta_2$ assuming $\delta_1 = \delta_2 = \delta$),

$$\beta_2 > \frac{\beta_1^2}{\delta}. \quad (3)$$

Here better colonizer has a larger rate of offspring production. Notice that space is not considered explicitly. In this case, types spread along the fecundity axis (β).

The sequence $\beta_1 < \beta_2 < \beta_i < \dots < \beta_n$ of fecundity values, determines a hierarchy of species competitive ability: species 1 > species 2 > ... > species n . By studying the high-diversity limit of this colonization-extinction model (equation 1) Kinzig and collaborators (Kinzig *et. al.*, 1999) showed the occurrence of unusual behavior including infinitesimally

close species packing, pathologically slow dynamics, and regularities in trait-abundance relationships.

Collaborators¹ and I developed an evolutionary version, with sequential invasions with species chosen at random (uniformly) from $[\beta_{min}, \beta_{max}]$. We are currently studying this system and seem to agree with Kinzig *et. al.* (1999). However, I think a better way to investigate the evolutionary dynamics of this system would be through the application of adaptive dynamics techniques. The spatial model I will study in my YSSP project will reduce in the mean-field and for hierarchical cases to equation (1).

Spatially explicit models of competition for space

So far, the models described above only consider space in an implicit way. Spatially explicit frameworks are essential for the understanding of competition for space (Durrett & Levin, 1994). Based on Silvertown *et. al.*'s (1992) model of competition in grasslands, Durrett and Levin (1998) introduced a spatial stochastic process to describe a simple but complete scenario of competition for space in the language of continuous-time Markov chains.

(i) An individual of species i produces new offspring of its type i at rate β_i . That is, the times t_n between the production of the offspring are independent and have $P(t_n > t) = e^{-t \cdot \beta_i}$. (ii) An offspring of type i produced at x (site in a two dimensional lattice) is sent to y with probability $\phi_i(|x - y|)$ where $|x - y|$ is the distance from x to y . We consider, finite dispersal ranges. Thus, there is an R so that $\phi_i(r) = 0$ when the distance $r > R$. (iii) If the site y is occupied by type j , and type i dispersed to that site, a successful invasion (*i.e.*, the state of y changes from j to i) occurs with probability $\alpha_{i,j}$; if invasion does not occur, the site y remains unchanged.

Using this model, the authors concluded "long-range dispersal of a resident type can overcome a modest competitive advantage for an invader that has a more narrow dispersal range" (Durrett & Levin, 1998 p.35). In other words—when space is considered—a better colonizer not only may coexist but resist invasion from better competitors. However, notice that here better colonizers have a wider dispersal range.

Currently I am involved in a collaboration with Bruce Menge's group at Oregon State University. In that collaboration we are developing models of the kind described above trying to understand the onshore variation in community structure along the coast of Oregon and its relationship with offshore variations in oceanographic conditions. I hope to use the results of the research proposed here as a tool to understand empirical patterns of community organization in the rocky shores of the Western US.

Proposed research

Intertidal organisms conquer space by growing, spreading to new areas, and by overgrowing other organisms. Thus, a trait space is defined by variations in offspring production rate β , individual mortality δ , competitive ability α , and dispersal capacity R .

A strategy $w \in [0, 1]$ consist of a set of values $\beta(w)$, $\delta(w)$, $\alpha(w)$, $R(w)$ determined by ontogenetic trade-offs. We could think of w as the organism's efficiency to capture space. Low w , corresponds to species with high offspring production rates, high mortality, large dispersal capacity, and low competitive ability. On the other hand, high w corresponds to species with low offspring production rates, low mortality, small dispersal capacity, and high competitive ability.

¹Jonathan Dushoff, Lee Worden, and Simon Levin

The model I propose to study

The model I propose to study during my participation in IIASA's YSSP program is a game-theoretic extension of Durrett & Levin's (1998) model of competition for space.

(i) An individual of type w produces new offspring of a close-by type w' at rate $\beta(w)$. (ii) An offspring of type w produced at x is sent to y with probability $\phi_w(|x - y|)$ where $|x - y|$ is the distance from x to y . I consider $\phi_w(r) = 0$ when the distance $r > R(w)$ and $\phi_w(r) = [2R(w) + 1]^{-2}$ if $r \leq R(w)$. (iii) If the site y is occupied by type w , and type w' dispersed to that site, a successful invasion (*i.e.*, the state of y changes from w to w') occurs with probability $\alpha_{w,w'} = \alpha(w)/[\alpha(w) + \alpha(w')]$; if invasion does not occur, the site y remains unchanged. (v) Individuals die at rate $\delta(w)$.

The functions $\beta(\cdot)$, $\delta(\cdot)$, $R(\cdot)$, and $\alpha(\cdot)$ will obey the constraints $\frac{d\alpha}{dw} > 0$, $\frac{d\beta}{dw} < 0$, $\frac{d\delta}{dw} < 0$, $\frac{dR}{dw} < 0$. More concrete functional forms have to be defined from empirical insights. However, to start the theoretical investigation, simple general forms will be assumed.

Research questions

My question focuses on the life-history evolution of sessile organisms and the interaction between spatial correlations and evolutionary dynamics. The questions I will focus on during my research at IIASA are:

- (1) What is the relationship between the spatial pattern of population dynamics and evolutionary stability and dynamics of w ?
- (2) How can multi-type assemblages self-organize in their usage of space-time to avoid competitive exclusion? How do these populations of coexisting types use spatial and temporal scales?
- (3) Are the statistical properties of coexisting types (proposed by the model) present in real community patterns?
- (4) What are the statistical properties of the spatial mosaics? This may give insight into the landscape ecology of intertidal communities.

Plan of work

To study the model proposed I plan to:

(i) Explore the population dynamics within the possible trait space. This will be done by numerical simulations of the interacting particle system and by its analytical approximations (pair-approximations, correlation and moment equations).

(ii) Apply the standard methods of adaptive dynamics (pairwise invasibility plots, characterize evolutionary attractors, and evolutionary branching points) to understand the evolutionary dynamics of the model proposed.

Relevance and link to ADN's research

The proposed research links to ADN's interests at least in one. At the *foundational* level, the model I propose in this project will contribute to ADN's research as an operational tool to test adaptive dynamics' axiomatic theory. The proposed research also constitutes an interesting *application* to understand the organization of sessile intertidal communities of the Western United States at multiple scales of space and time, where spatial invasion dynamics are being monitored for different species of sessile organisms. Finally, the proposed research also is an *extension* of the scope of adaptive dynamics theory to evolving spatial systems. The mathematical analysis of the proposed model will enlarge the scope of adaptive dynamics theory and contribute to its expansion to spatial evolutionary games.

Envisaged publication(s)

The proposed research is expected to result in one chapter of my Ph.D. thesis. The analysis—numerical explorations and analytical approximations—of the spatio-temporal dynamics of the the population and evolutionary model will result in a jointly authored paper.

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Evolutionary branching in a coevolutionary model for mutualism

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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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Ecology and evolution of spatially extended populations

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Motivation and background

Life on earth is essentially spatial. While on some parts of the globe volcanoes erupt, destroying all life in their vicinity, other parts are completely quiet and stable, creating a safe heaven for life to prosper. Spatial heterogeneity, however, applies not only at the global level, but also at smaller spatial scales. Even single populations often live in spatially heterogeneous habitats. It seems likely that spatial heterogeneity is a prerequisite for the complexity and diversity of life that we encounter. Yet, most classical ecological models consider space as being homogeneous. It only has been over the past few years that development of modeling tools in ecology has reached a point at which comprehensive analysis of the ecological and evolutionary implications of spatial heterogeneity becomes feasible. This allows scientists to construct models that are increasingly realistic and informative. Resulting individual-based and spatially explicit models, however, are difficult to analyze conclusively. Dynamics in these models tend to fluctuate and thus require statistical methods for analyzing simulation results. Moreover, stochastic individual-based models behave in a reproducible manner only if the number of individuals is sufficiently large and the numerical investigation of such systems is therefore extremely expensive in terms of computation time. For this reason, it is often desirable to find analytic approximations for predict the behavior of such systems. Numerous types of models exist for describing spatial systems. Models can be based on either discrete or continuous space, and they can operate deterministically or stochastically. Discrete-space models, like cellular automata, are geared to study next-neighbor interactions, but rest on a discretization of space that, for most ecological systems, is artificial. Continuous-space models, on the other hand, are well suited to investigations of diffusion processes, and of distance-dependent interactions. Deterministic models in continuous space produce predictable dynamics but are based on assuming infinitely large local densities. In contrast, stochastic models are based on individual probabilistic events, but are affected by the problem of potentially large fluctuations. The proposed research project for the IIASA summer program will address these fundamental challenges of ecological theory at two different levels. First, we are planning to complete an investigation on the evolution of integration strategies in clonal plants. This collaborative research is already well under way. A second investigation will commence during the summer period as is meant to focus on extinction processes of ecological populations that live in spatially continuous habitats. The relative amount of time that will be allocated to these two investigations during the summer will be decided in agreement with Dr Ulf Dieckmann and Dr Gza Meszna.

Evolution of integration strategies in clonal plants

The first investigation will study the evolutionary ecology of clonal plants by considering adaptations in their integration strategies and by exploring how the resulting adaptive outcomes are depending on environmental conditions.

Background on clonal plants

Clonal plants constitute a major part of terrestrial and continental vegetation (van Groenendael, 1996). The transport system of many clonal plants is integrated, yet many of them lose these connections after the juvenile settlement. The genetic individuals of plant populations, called genets, consist of several potentially independent physiological individuals; these are called ramets. The degree of resource transfer between ramets is determined by the genets integration strategy. There are two extreme types of genets: the splitter type, whose ramets do not integrate at all, and the integrator type, whose ramets are totally integrated, creating one giant organism (Room, Mailette and Hanan, 1994). This strategy defines the fate of the genet in a given environment as well as its capacity to cope with given rates of environmental fluctuations. We assume that different patches of the plants habitat can be of one of two types: good patches, on which ramets can persist without resource integration, and bad patches that can only be inhabited by ramets if neighboring ramets, themselves situated on good patches, offer resources integration. We use stochastic cellular automaton models (Oborny & Cain, 1992) and mean-field models, together with adaptive dynamics methods, like pairwise invasibility plots (Geritz et al., 1998), to analyze the adaptation of integration strategies to environmental fluctuations at different temporal scales. Results obtained so far suggest that low levels of environmental change allow the splitter type to control all good patches in the plant's habitat and to amount to an evolutionarily stable strategy (ESS). However, as the rate of fluctuation grows, the splitter type loses its patches, while the integrator type is suffering less. At very high rates of environmental fluctuations, the integrator strategy eventually becomes evolutionary stable, while intermediate levels of fluctuation result in an intermediate evolutionary outcome. So far, we have utilized a model in which environmental changes are independent of the neighborhood and integration of resources occurs globally, i.e., throughout the entire habitat. In this setting, we have observed significant differences between the results of the cellular automaton model and of the mean-field approximation provided that resource levels were low. In such cases, migration to nearby good patches became important. In more resource-rich scenarios, however, the mean-field approximation was successful in estimating the adaptive outcome observed in the spatially explicit model. Recently, the following extensions of our initial model have been analyzed. First, the process of resource integration has been to those next neighbors of a given focal cell that belong to the same genet as the focal cell. This modification makes our model more realistic and is expected to better demonstrate the limitations of from mean-field approximations. Second, we have also implemented a new, neighborhood-dependent version of environmental change by using Ising-type dynamics. This modification results in a more patchy distribution of environmental quality, again making the model more realistic. On this basis, we can calculate correlation lengths in space and in time for the pattern and process of environmental heterogeneity, respectively.

Research questions and work plan

During the summer project, we plan to compare the results of different versions of our model to determine their quantitative differences. Our aim is to construct phase diagrams of adaptive outcomes that show the changes in evolutionarily stable integration strategies in response to different scales of environmental heterogeneity, measured in terms of correlation lengths in space and in time. These phase diagrams will give us a very compact way of summarizing the adaptive behavior in these systems of clonal plants. The model versions to be investigated are based on cellular automata with four, six, and eight nearest neighbors and on analytic methods based on one-point approximation, pair approximation, and mean-field approximation. These analytic methods should bridge the gap between the spatially explicit cellular automaton ver-

sions, and the mean-field approximation (Law, Dieckmann, 1998). By studying these methods of approximation we expect to identify the simplest approximation that can fully capture the results of the original model (Dieckmann, Herben, Law 1997). In a recent paper Beta Oborny and Tams Czrn have investigated similar problems related to clonal integration (Oborny et al., 1999). They have analyzed the behavior of different strategies for such clonal integration as a function of two factors: the total resource input into the habitat and the grain size of the distribution of environmental quality. This model is different from our one in important respects: integration of resources is global and patch dynamics are not of the Ising type. One aim of our study is to compare our results with this previous investigation. In this context, we plan to construct an integrative model that unites the two different approaches into a common framework, thus allowing for the comprehensive examination of the various factors involved.

Directed percolation in continuous space: a new tool for conservation biology?

The second investigation will study the persistence of ecological populations distributed across a spatial habitat by utilizing on methodological tools from the theory of directed percolation.

Background on directed percolation

In this investigation we aim at increasing our theoretical insight into the pressing problem of species extinction. In industrialized environments, the continual degradation and fragmentation of habitats pushes countless species over the brink of extinction. In this context, we will apply the framework of directed percolation, originally developed in statistical physics; to study spatially extended populations on the verge of extinction. A better understanding of these extinction processes may eventually allow for better strategies of control and management for threatened populations. Percolation phenomena occur in physics when a block of material possesses tunnels or connections that are suitable to be occupied by another substance. The system is percolating if the substance can connect remote locations in the block via these tunnels or connections. The percolation probability of the system is a function of the fraction of the tunnels, compared to the impermeable parts of the block. If there are very few tunnels, the system does not percolate. As the fraction of tunnels grows, the size of the clusters connected by the substance increases. At a certain level of tunnels, called the percolation threshold, many of these clusters unite, and the system percolates (Stauffer, Aharony, 1995). A physical example of this phenomenon is an imperfect electrical conductor. For general percolation processes, the percolating substance can move in any direction throughout the block. In contrast, phenomena of directed percolation can be exemplified by water trickling through sand in only one direction, directed by the force of gravity as an external force (Hinrichsen, Koduvely, 1998). The analogy to ecological systems arises by considering the spatial environment of a given species and by adding the time dimension in which the system evolves as an extra direction to this space. We can then study the populations fate in terms of a process of directed percolation of individuals surviving from the past into the future. If that process percolates, the population persists.

Research questions and work plan

The main goal of this second investigation is to create an additional tool for conservation biology that may help to estimate the survival probabilities of endangered species under different environmental conditions. While classical percolation theory focuses on spatially discrete systems, a realistic description of ecological populations requires consideration of continuous space. We

plan to investigate whether ecological extinction processes in continuous space belong to the universality class of directed percolation. For this purpose, we will analyze individual-based models of species with movement, clonal reproduction, and death. In an analogous process from physics that already has been shown to belong to the universality class of directed percolation, particles can hop between discrete sites, can branch by pair formation, and die by pair annihilation. At the percolation threshold, the scaling properties of this physical system turn out to be universal and also apply to all other kinds of models of directed percolation. Likewise, the ecological system can only escape extinction beyond a certain threshold where the rate of reproduction becomes larger than the death rate. The open question is whether, around that extinction threshold, the risk of extinction exhibits the same universal scaling behavior as has been found in a plethora of physical systems. After implementing a model of the ecological population in continuous space, we will therefore study its behavior and, in particular, test whether it belongs to the directed percolation universality class or not. If the answer is positive, it will be interesting to find empirical support for such universal behavior. The potentially resulting universal law of population extinction is expected to offer qualitative as well as quantitative insight into the population dynamics of endangered species.

Relevance and link to ADN's research

Devising innovative tools for modeling spatially heterogeneous populations is of critical importance in modern ecology and evolutionary biology. Our first investigation is addressing the architecture of clonal plants. Since a very large number of plants on our planet reproduce clonally, improving our understanding of their adaptive responses to different ecological conditions is very important. The second investigation proposed here will possibly lead to establishing a universal law for the extinction patterns of spatially extended populations and may thus contribute to better strategies for the control and management of populations on the verge of existence. There exists a long-standing contact and collaboration between Dr Gza Meszna, my supervisor at the Department of Biological Physics at Eötvös University, and Dr Ulf Dieckmann, Project Coordinator of the Adaptive Dynamics Network Project of IIASA. Both of them had a significant role in the very first steps in the development of adaptive dynamics theory, and have been continuously cooperating on extending this theory. Ulf Dieckmann visited Hungary several times during the last few years, and Gza Meszna has paid several visits to IIASA. I also had a chance of working at IIASA for a while in 1999. On this basis, we expect the project proposed here to successfully contribute to ADN's research foci on (i) Foundations of Adaptive Dynamics and on (ii) Simplifying Spatial Complexity.

Envisaged publications

The proposed research is planned to result in at least two publications. The investigation on the evolution of integration strategies in clonal plants will result in a paper on the effect of the ecological scales in space and time on plant adaptation, based on the phase diagrams mentioned above. We also plan to write an additional paper on comparing the different approximation schemes for the spatially explicit model, focusing on those scenarios that are not well captured by existing mean-field approximations. The investigations on the application of directed percolation to conservation biology are also expected to result in a publication that reports under which conditions spatially extended ecological system can belong to this universality class.

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The evolution of metapopulation migration

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In recent years there has been an increasing interest in the study of metapopulation models. Metapopulation models are a type of spatially heterogeneous population models particularly suited to study implications of habitat fragmentation. In conservation biology the most important question is to study conditions for metapopulation persistence. One method for the metapopulation to avoid extinction is dispersal.

In different environments we observe different dispersal behaviour. Dispersal behaviour is adapted, since all individuals try to use as good strategy as possible in the present environment. The change of strategies used has an effect on the population dynamics and to the environment. Geritz *et. al* (1997,1998) presented *adaptive dynamics* as a new analytical framework for studying invasion problems in population models. See also Dieckmann (1997). This framework can also be used in examining invasion processes in metapopulations. Two questions are of particular interest: How are changes in environmental conditions affecting evolutionarily stable dispersal strategies? What are the consequences of resulting adaptations for metapopulation persistence?

In the paper Parvinen (1999) I studied the evolution of migration in a general discrete-time metapopulation model with finitely many patches using the framework of adaptive dynamics.

The following system of equations constitutes the model for monomorphic situation.

$$x'_i = (1 - m_{x,i})f_i(x_i + y_i)x_i + \sum_{j=1}^n m_{x,j}\alpha_{x,ij}F_{ij}f_j(x_j + y_j)x_j \quad (1)$$

Here $'$ indicates the state of the metapopulation at the next time step and x_i is the size of the resident population in patch i . The numbers $m_{x,j}$ and $\alpha_{x,ij}$ are the migration parameters. The survival probability during migration is denoted by F_{ij} and the functions f_i describe reproduction in the patches. Migration is not uniform in the patches and survival probabilities between the patches are not necessarily equal. Therefore the patch locations are not neglected.

If the resident is assumed to have settled down in a stable fixed point or cyclic orbit, then the model becomes linear with respect to the sizes of the mutant population. Then the success of invasion can be determined from the dominant Lyapunov exponent of the mutant. In the article Parvinen (1999) I have shown analytically that if the equilibrium of the resident population is a fixed point then (i) the strategy not to migrate is an evolutionarily stable strategy (ESS) (ii) a mutant population with no migration can invade any resident population in a fixed point state (iii) in the uniform migration case the strategy not to migrate is attractive under small mutational steps so that selection favors low migration.

If the resident population is in a two-cyclic orbit, then the situation is different. In the uniform migration case the invasion behaviour depends both on the type of the residents attractor and the survival probability during migration. If the survival probability during migration is low, then the system evolves towards low migration. If the survival probability is high enough, then evolutionary branching can happen and the system evolves to a situation with several co-existing types. In the case of out-of phase attractor, evolutionary branching can happen with significantly lower survival probabilities than in the in-phase attractor case. Most results in the two-cyclic case are obtained by numerical simulations. Also when migration is not uniform

we observe in numerical simulations in the two-cyclic orbit case selection for low migration or evolutionary branching depending on the survival probability during migration.

The model in Parvinen (1999) provides interesting results and helps us to understand the evolution of migration. To gain better understanding it is important to study extensions of this approach. One extension is to study structured metapopulation models, where instead of a finite number of patches we have a distribution of patches of different quality. This extension allows us to study the combined effect of local catastrophes and habitat fragmentation to the evolution of the metapopulation. I am currently doing this analysis in collaboration with Dr. Ulf Dieckmann and Prof. Hans Metz from IIASA and Prof. Mats Gyllenberg from the University of Turku, Finland.

We have studied two models for the local population growth either with or without demographic stochasticity. The local population growth in the deterministic case is described by

$$\frac{dx}{dt} = g(x)x - k(x)x + \alpha D, \quad (2)$$

where $g(x)$ corresponds to population growth via births and deaths, $k(x)$ is the per capita emigration rate and α is the immigration rate from the dispersal pool. The corresponding stochastic model is illustrated in Figure 1.

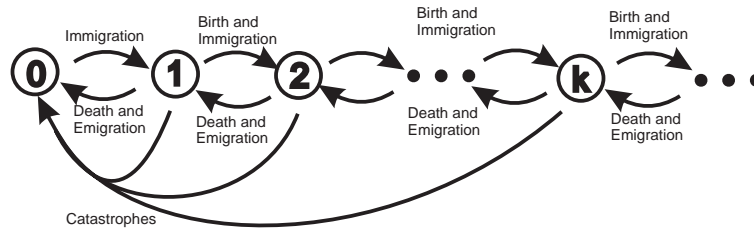


Figure 1: State transition diagram for a single patch in a model with demographic stochasticity

We have already the following results: The evolutionarily stable dispersal rates do not necessarily increase with rates for the extinction of populations in habitable patches. Instead, without demographic stochasticity, adapted dispersal rates exhibit a maximum for intermediate levels of disturbance and fall off for both higher and lower rates of local extinction. Second, we describe how the demographic stochasticity that inevitable occurs in finite populations affects the evolution of dispersal rates. Contrary to predictions from deterministic models, evolutionarily stable dispersal rates in small local populations can remain high even when rates of local extinction are low. The first manuscript containing these results will be submitted soon.

Several extensions can be made to this model:

- In this study the catastrophe rate has been assumed to be constant. In practice this may be too restrictive assumption. Therefore I want to study the model with catastrophe rate depending on the local population size.
- Non-constant catastrophes may be enough to observe special evolutionary cases. In this study only evolutionarily stable strategies were found. In Parvinen (1999) evolutionary branching was observed under certain conditions. Adaptive suicide is another interesting phenomenon. Its occurrence has been found in some models. It would be very interesting to find branching or evolutionary suicide also in this model.
- In this study the emigration rate has been the only evolutionary variable. The immigration rate and a variable describing local adaptation could also be taken as evolutionary variables.

Further study of these topics would be very interesting and I am expecting to obtain better understanding of metapopulations via this collaboration, which started during my 3,5 months visit in IIASA as a guest research scholar. In practice good collaboration requires frequent meetings and joint work. Therefore participating IIASA Young Scientists Summer Program in ADN would be an optimal way to ensure the substantial continuation and the expected good results from this collaboration.

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