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The Role of Resources and Mortality in Life-History Evolution: A Model of Optimal Reproductive Effort and Offspring Size in the Trinidadian Guppy

Farrah Bashey

Department of Biology, University of California, Riverside, USA

Goal

To improve understanding of life-history patterns in guppies by developing a model that predicts resource allocation decisions (interbrood interval, reproductive effort, and offspring size).

Background

The work of David Reznick and colleagues on life-history evolution in guppies (*Poecilia reticulata*) is viewed as strong support for age-specific demographic models for the evolution of reproductive effort (cf. Stearns 1992, p. 165). This work compares the life history of guppies from high- and low-predation sites. High-predation environments are those in which guppies co-occur with larger species of fish, such as the pike cichlid (*Crenicichla alta*), that frequently feed on guppies. Low-predation environments are found in the same drainages, but upstream of rapids or waterfalls that exclude the larger species of predators. At these sites, guppies co-occur with just the killifish (*Rivulus hartii*) that is limited to feeding on juvenile guppies (Liley and Seghers 1975). This difference in age-specific mortality risk leads to the prediction that guppies from high-predation locales should mature at an earlier age and have a higher reproductive effort than their counterparts from low-predation environment (following demographic models aligns such as Gadgil and Bossert (1970) and Law (1979)). These predictions have been well supported via comparative studies of the life-history phenotypes of wild-caught guppies (Reznick 1989; Reznick and Endler 1982; Reznick et al. 1996b) as well as through laboratory comparisons of the genetic basis of these life-history patterns (Reznick 1982; Reznick and Bryga 1996). Furthermore, replicated introduction experiments demonstrate that a change in predation environment is associated with the rapid evolution of life-history patterns in the predicted direction (Reznick et al. 1990; Reznick and Bryga 1987; Reznick et al. 1997). Nevertheless, our understanding of guppy life-history evolution is not complete.

In their analysis of age-specific mortality as the mechanism of selection on guppy life histories, Reznick et al. (1996a) found an overall difference in mortality rates between *Crenicichla* and *Rivulus* locales, but no difference in size-specific mortality. Classic demographic theory predicts that in density-independent populations or in populations where density-dependent regulation affects all ages equally, a uniform change in mortality rate will not select for any change in reproductive effort or age at maturity (Gadgil and Bossert 1970; Michod 1979). If size-specific mortality is equated to age-specific mortality, then a specific form of density-dependence must be operating in order for predator-mediated selection to favor the observed changes in life history (Charlesworth 1980).

Moreover, although predation is the dominant factor associated with differences in life-history phenotypes between low- and high-predation sites (Strauss 1990), low- and high-predation sites do differ significantly in factors relating to resource availability (Reznick et al. 2001). What effect does different resource availability have on evolution of life-history traits? Current theory does not yield a general prediction for how changes in resource availability affect the evolution of life-history traits. For example, while Gadgil and Bossert (1970) demonstrated that reduced resource availability would select for a later age at maturity and lower reproductive effort, the opposite change in life history is predicted by Kozlowski and colleagues (Kozlowski and Uchmanski 1987; Kozlowski and Wiegert 1987). The discrepancy between these predictions is due to the use of a different fitness criteria and different assumed relationships between resource availability and age-specific survival and fecundity.

Furthermore, current life-history models focus on *either* reproductive effort/age at maturity or offspring size. However, in the guppy system these traits are strongly correlated. As part of my dissertation work I have been evaluating adaptive hypotheses for the evolution of offspring size. Offspring size varies between populations as well as plastically with populations in response to food availability (Reznick and Yang 1993). The two adaptive hypotheses that I have been evaluating are (1) size-limited predation by *Rivulus* and (2) size-dependent competitive ability. To assess the importance of offspring size differences, I would like to incorporate the results I have on newborn and juvenile growth and survival to assess the effects on the entire life history. Additionally, most offspring-size theory starts with the assumption that reproductive effort is fixed; although, empirical evidence suggests that reproductive effort is more variable than offspring size (Stearns, 1992, p. 174). Only one theoretical study (Winkler and Wallin 1987) specifically examines the interplay between reproductive effort and effort per offspring. They conclude that as the optimal effort per offspring increases, the optimal total effort should decrease. Thus, selection of offspring size could constrain evolution of reproductive effort. Conversely, offspring size may be suboptimal if costs of reproduction are such that reproductive effort faces the higher selective pressure.

Research Questions

I would like to examine the evolutionary interplay of offspring size and reproductive effort in the context of the guppy system. Specifically, I would like to address how three decisions a female guppy must make affect her fitness. In every reproductive cycle, a female guppy must decide (1) how long to forage before fertilizing her litter, (2) how much of her surplus energy to put into her litter, and (3) how to partition that energy among offspring in her litter. These decisions can also be thought of as (1) interbrood interval, (2) reproductive effort, and (3) offspring size. I will explore how different patterns of resource availability and mortality affect the fitness consequences of these decisions.

Methods and Work Plan

To start I will examine the fitness consequences of having a fixed set of life-history decisions. In this oversimplified model, interbrood interval, reproductive effort and offspring size decisions will remain fixed throughout all reproductive cycles. In addition, to assess the fitness of these three decision variables, I will have to include a fourth, age at first reproduction. To find the best set of fixed life-history decisions, I will use numerical techniques to determine the combination(s) that maximize(s) lifetime reproductive success (R_0) and the intrinsic rate of growth (r). I will repeat this exercise with different patterns of size-specific mortality and resource availability. This fixed model will provide a good baseline for comparison with the more complex models that allow flexibility in life-history decisions.

I have used a dynamic optimization approach as outlined by Mangel and Clark (1988) and McNamara (1991; 1993; McNamara and Houston 1996) to develop a model assessing the optimality of reproductive effort and offspring size decisions. My plan for this summer is to revise and expand this model to include interbrood interval using the continuous-time algorithm developed by ADN. The dynamic optimization approach allows each of the three decisions to change at any reproductive cycle. Moreover, it allows for females of different sizes to make different decisions. My goal is to examine how life-history patterns will evolve in response to different mortality and resource availability regimes. This approach will not only allow me to address whether life-history patterns we see across populations of guppies are adaptive, but it can also address scenarios in which plasticity may be advantageous.

The final issue I would like to address is under what conditions density and frequency dependence can affect the fitness of life-history decisions in this system. When density and frequency dependence are introduced into a system, fitness measures like R_0 and r may be misleading and a more robust measure is the invasibility criterion (Metz et al. 1992; Mylius and Diekmann 1995). To this end, I hope to explore how favored life-history decisions change when feedbacks on population size, population structure, resource availability and predation risk are included.

Relevance and Link to ADN's Research Plan

The proposed research will examine how life-history decisions will evolve in response to changes in the environment. From an ecological perspective, accurately predicting changes in life-history traits will allow for better assessment of population growth and viability. From an evolutionary outlook, life-history traits are closely linked to fitness and thus provide the best traits for studying adaptive evolution in action. The proposed research aims to understand the evolution of life-history traits in a fish species that is well studied. By using a well-studied species, the effectiveness of our modeling can be assessed by comparison to empirical data. Furthermore the environmental changes this work addresses, mortality and resource availability, are general and relevant to many anthropogenic disturbances. Thus the goals of the proposed research are closely allied with ADN's interest in Fisheries Management and Evolutionary Conservation Biology.

Expected Output and Publications

The proposed research is expected to result in one chapter of my Ph.D. dissertation. This chapter will be submitted for publication as a jointly-authored paper early in 2002.

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Adaptive dynamics of life-history traits in harvested communities:
Evolutionary responses in mixed fisheries

Anna Gårdmark

Department of Theoretical Ecology, Lund, Sweden

Goal

To clarify whether and how the presence of co-harvested populations in mixed fisheries modifies the evolutionary response of exploited target populations.

Background and motivation

Over the past few years, concerns have risen about the evolutionary consequences of large-scale exploitation in commercial fisheries (*e.g.* Browman 2000, Law 2000, ADN workshop March 14th-17th, 2001). The high and selective mortality imposed by fisheries can cause evolutionary changes in size-dependent life history traits (Law and Grey 1989, Stokes et al. 1993, Heino 1998). This expectation is supported by observed trends of decreasing age at maturity and size at maturity in several exploited populations, such as North Sea plaice, Northeast Arctic cod, and Baltic cod (Rijnsdorp et al. 1993, Jørgensen 1990, and Cardinale and Modin 1999, respectively). These observations suggest that fisheries induce genetic changes that may be difficult to reverse, changes that will decrease the available fish biomass and thus also the long-term yield of fisheries.

With few exceptions (Gårdmark *et al.* in prep.) studies on evolutionary effects of population harvesting have neglected interactions between species and/or populations. Current harvesting practices, however, ensure that different species and populations are often caught simultaneously; this is due to non-discriminating fishing gear and to the targeting of areas where populations mix. In many species, populations mix during part of the year at feeding or spawning grounds. These mixing areas are often targeted by fisheries (*e.g.* Baltic cod (Aro 1989)), or fisheries might follow a migratory population into areas where they mix with local populations (*e.g.* herring fishery off Nova Scotia (Claytor 2000). Populations originating from different regions often have different life-history characteristics. Size-selective harvesting on mixed populations can therefore cause different evolutionary responses in the different populations. The mixing of populations therefore poses a problem for predicting evolutionary responses to harvesting.

Here, I propose to analyze how the evolutionary responses to harvesting might be altered under different types of population mixing and harvesting regimes. This work is designed as a continuation of a recent project on the evolutionary responses to harvesting in a population subject to different types of predation, conducted in collaboration with Ulf Dieckmann. In addition, the proposed research is an important application of adaptive dynamics theory that will contribute to the understanding of evolutionary effects of exploitation.

Research question

As populations of different origin often differ in their life-history traits, harvesting of mixed populations might have different evolutionary effects on these populations. If populations do not interact with each other when mixing, single-population models can be used and the evolutionary responses can be predicted by using methodology developed in earlier studies. However, there are several ecological settings in which the mixing populations influence each other, obvious examples being direct resource competition and apparent competition. Depending on the form of interaction and on the type of harvesting applied, the evolutionary outcome becomes harder to predict. For example, if individuals of two mixing populations are dependent on both population densities and if the harvesting regime cannot discriminate between these populations, harvesting could possibly initiate a co-evolutionary process in the two competing populations.

In this project I will analyze the evolutionary responses to harvesting in age-at-maturity in two age-structured populations that mix during part of the year. In particular, I will study how the evolutionary responses are dependent on

- the form of interaction between the populations and
- the harvesting regime (whether harvesting can discriminate between populations or not).

Methods and work plan

For the analysis of this problem I will construct a model of two age(/size)-structured populations that can interact and are subject to harvesting. I will then apply the techniques of adaptive dynamics to analyze the evolutionary change in age(/size)-at-maturity in response to harvesting. For each type of population interaction outlined below, I will analyze the effect of two harvesting regimes: (a) when harvesting on the mixed populations can selectively target the different populations and (b) when harvesting acts indiscriminately on both populations. In particular, pairwise invasibility plots will be constructed for each case.

The following three alternative assumptions on population interaction will be tested:

1. The two mixing populations do not affect each other. Starting with this simplest case provides baseline results to which outcomes in the following settings can be compared.
2. The interaction between the mixing populations is asymmetric, such that one of the populations influences the other negatively, but not vice versa. (Such amensalism could apply, for example, if mixing occurs when one population migrates into the area where the other population is resident and the resident population is very small compared to the migratory one, or if the migratory population is regulated by factors outside the mixing area.)
3. The interaction is symmetric, such that competition is equally strong within and between populations.

The analysis will focus on the relationship between the evolutionary outcome in the possible strategy space and the type of density-regulation, differences in life history parameters and differences in harvesting regimes.

Relevance and link to ADN's research plan

This project provides an innovative application of the theory of adaptive dynamics. Utilization of adaptive dynamics techniques for developing the theory of evolutionary effects of population harvesting is relevant for ADN's research on 'Fisheries-Induced Adaptive Change.'

The proposed research extends the application of adaptive dynamics techniques to previously untackled complex problems of evolutionarily sustainable fisheries management, thus supporting ongoing ADN projects.

This project is also related to research done by previous YSSP participants (Mikko Heino, Are Saltahug, Frode Lium, and Sondre Aanes) and strengthens the existing collaboration between the ADN project and the Department of Theoretical Ecology at Lund University.

Expected output and publications

The proposed research is planned to result in a jointly authored research paper. This work is also planned to be one of the articles in my PhD thesis, either as a manuscript or in its published form.

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Adaptive speciation in spatially structured environments

G. Sander van Doorn

Department of Biology, University of Groningen, The Netherlands

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.

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Behavioral changes in response to trawl fishing: A case study on the Northeast Arctic cod

Nils Olav Handegard

Institute of Marine Research, Bergen, Norway

Goal

To develop a model for estimating behavioral profiles of trawl avoidance and to use such a model to assess the potential for evolutionary adaptation in trawl-avoidance behavior.

Background

The stock assessment of Northeast Arctic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) is based on virtual population analysis (VPA). Landing statistics and relative abundance indices from scientific surveys, the swept area, and acoustic indices are the basic input data used for this analysis. In the tuning of the VPA, the two survey indices of fish density are used independently of each other. Both indices are assumed to reflect total stock abundance, but neither of the two survey methods samples the complete vertical distribution of the stock.

It is therefore desirable to combine the two estimates into one absolute abundance estimate, covering the whole water column (Godø and Wespestad, 1993, Michalsen 1999). In order to achieve this goal, several problems must be overcome, necessitating more knowledge on trawl performance (Engås *et al*. xx), fish behavior in response to trawling (Fernö & Olsen 1994), and trawl efficiency (Aglen *et al*. 1999, Ona 1988).

Research questions

The main question for this project is whether and how the fishing mortality on Northeast Arctic cod has affected behavioral patterns of individuals in this stock.

A change in the adaptive behavior to vessel and gear could introduce biases in the indices, since the indices rely on the catchability of fish to remain constant. In order to achieve absolute abundance estimation for a species, the reaction of fish to the approaching trawl gear is of importance. Such a reaction could change adaptively, either on a short-term scale (individual learning processes) or on a long-term scale (changes in the gene pool of the population).

Methods and work plan

This project is divided into three sub-tasks, focusing, first, on estimating the profile that describes the behavioral response of Northeast Arctic cod to trawling and, second, on understanding whether the estimated profile is compatible with predictions based on evolutionary modeling.

Step 1: Establish behavioral profile

The first step is to investigate behavioral data from experiments conducted by the Institute of Marine Research, Bergen, Norway, in order to determine a snapshot of the behavioral profile of the northeast Arctic cod in response to modern trawl gear.

The behavioral data is recorded by an echo sound beamer. The echo sounder is attached to a buoy and launched in front of the vessel. Then the vessel passes the buoy and the reaction for the individuals are recorded. Each individual is detected and tracked via the echo signal and a three-dimensional trajectory for each individual is obtained. From this information it is possible to extract swimming velocities and diving angles for the detected individuals.

The first step is to extract all fish trajectories from the buoy data. In addition, the estimated sound profile of the survey ship is used to determine the loudness or volume l of the noise generated by the vessel at the location of the focal fish.

Then the velocities of individual fish are estimated by the following linear model,

$$v = w_z(l)\, z + w_s(l)\, s \ ,$$

where v is the observed velocity vector of the focal fish, z is the unit vector pointing vertically downwards, and s is the unit vector pointing away from the source of the sound. The weights $w_z(l)$ and $w_s(l)$ of these two velocity components are dependent on loudness and constitute the behavioral profile of the fish.

One extension of this simple model incorporates the rate of change in loudness, c, in addition to the loudness l itself,

$$v = w_z(l,c)\, z + w_s(l,c)\, s \ ,$$

another extension incorporates either the direction of the local gradient in fish concentration or, alternatively, the direction towards the global centre-of-mass of the school,

$$v = w_z(l)\, z + w_s(l)\, s + w_g(l)\, g,$$

where g is a unit vector pointing in this direction and $w_g(l)$ is the weight associated with this component of the velocity v. For this extension to be feasible, the vector g must be estimated from the available data.

Since the linear systems above will be highly over-determined, we expect that these estimates can be obtained from the data through a technique known as singular value decomposition.

Another approach may be to divide each observed velocity vector into components that point, a, horizontally away from the vessel, *b*, vertically away from the vessel and, *c*, horizontally perpendicular to *a*. Then each observed velocity can be fitted to the following model,

$$v = w_a(l)\, a + w_b(l)\, b + w_c(l)\, c,$$

The weight functions estimated through these models provide a snapshot of the behavioural profile that describes the response to the approaching vessel. This profile is needed to proceed with Step 2 below.

Step 2: Compare observed and predicted profiles

In a second step we will try to explore whether the reconstructed behavioral profile or reaction norm is compatible with predictions obtained from individual-based simulations of fish schools exposed to trawling, shaped by the selection pressure for increasing escape probabilities.

The model estimated above already describes, to the extent it is valid, the individual-based three-dimensional movement behavior of schools in response to trawling. Combined with a three-dimensional model of trawl types (including information on average trawl speed), it should be possible to incrementally adjust the shapes of the weight functions to maximize escape probabilities for modern trawl gear. It will then be interesting to see how much the profiles that are obtained via this evolutionary optimization coincide with those directly reconstructed from the data.

The model uses the escape of the trawl as a selection pressure. Modeling the fish reaction to vessel and gear will make the foundation of such a model. The fish reacts to the vessel, warps, otter boards, and trawl. A model based on repulsion of these sources of stimuli has to be incorporated. The reaction thresholds of these stimuli are sensitive for the result (Handegard, in press), and most likely variable.

Step 3: Assess effects of different gear

If step 2 provides a significant result, a further step would be to carry out the same evolutionary optimization for the physical characteristics of traditional trawl gears and vessels. We will then "mismatch" a particular trawl gear with reaction norms adapted to a different gear and evaluate the expected loss in catchability that results from various such combinations. This will be a first step towards predicting the catch of a traditional gear operating on today's stock.

Relevance and link to ADN's research plan

Scientists at the Adaptive Dynamics Network (ADN) project at IIASA are experienced in the development and application of complex adaptive models. The Institute of Marine Research (IMR) has experience in analyzing the dynamics of fish stocks, including new techniques for examining fish behavior.

In this project I will try to connect the data from the experiments with an adaptive model of how the behavior of Northeast Arctic cod has evolved in response to sustained exploitation by trawling vessels. To connect empirical evidence with theory is essential for validation of the theory, and, at the same time, an underlying theory is valuable in order to explain the observed behavior. This is a two-way street. The first question is highly relevant for ADN, and the second is of value for the IMR.

Expected output and publications

If Step 1 above generates significant results, this project should lead to an interesting publication on the probability of vessel-induced behavioral changes resulting from high fishing mortality.

The investigation of behavioral patterns from buoy data developed in Step 1 could also help to define a more standardized post-processing routine for the buoy data. With such a tool, a more thorough study of the behavioral database could be carried out. This work could possibly lead to an additional publication.

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The impact of epidemiological parameters on the phylogeny of pathogen strains

Isao Kawaguchi

Department of Biology, Faculty of Science, Kyushu University, Japan

Goal

To develop a deeper understanding of how the polygenetic properties of disease strains are affected by underlying epidemiological detail.

Background and motivation

Currently, an enormous number of nucleotide sequences become available for viruses and infectious bacteria that cause major epidemiological outbreaks in humans. The phylogenetic relationships found *within* a species or a quasispeices of such pathogens vary greatly from pathogen to pathogen and might reflect their epidemiological and microevolutionary dynamics:

- The measles viruses were highly homogeneous for a long time and most subtypes have diverged only recently.
- For influenza A, new serotypes are continuously derived each year; yet, the phylogenetic tree reconstructed for the variants sampled over a few decades collapses to a single trunk (Fitch et al. 1997).
- The dengue virus quasispecies consists of four distantly related subtypes, which diverged a long time ago and have coexisted ever since (Zannoto et al. 1996, Gubler and Kuno 1997).

Little is known, at this stage, about how these striking differences in tree shapes are related to the underlying epidemiological parameters – like transmission rate, virulence, recovery rate – and to the populations' genetic setup.

Methods

I recently started to investigate these questions in collaboration with Dr. Akira Sasaki, Kyushu University. We focused on pathogen strains defined by epitope sequences of length *n*, and considered the competition between pathogen strains through the epidemiological dynamics with the host cross-immunity (Kawaguchi and Sasaki, manuscript). For this purpose, we have adopted an individual-based simulation model, rather than a traditional population-based SIR model, because in SIR models the number of dynamical variables (the number of immunological states of hosts) increases dramatically with the length of epitope sequences.

We consider a finite number of N host individuals and of $m=2^n$ viral serotypes, defined by binary epitope sequences of length n. The immunological status of a host with regard to each strain of the pathogen can change from S (susceptible) to I (infected and infectious), and from I to R (recovered and immune). With m serotypes of the pathogen, there are therefore 3^m different immunological host states. We also take into account the coinfection by multiple strains and the cross-immunity between pathogen strains. We allow for mutation at each site of the epitope sequence, and hence keep track of the microevolutionary change of the pathogen serotypes. We assume that the degree of cross-immunity mounted by hosts against a newly infecting strain is determined by the Hamming distance between the epitope sequence of this and the previously infecting strain.

The immune status of host individual i can be described by the vector $\mathbf{s}_i$ which has m columns, each indicating the immune status relative to a pathogen strain. Each element in $\mathbf{s}_i$ denotes either of three states, susceptible (0), infected (1), or recovered (2). Thus, the immune status of the individual i is specified by the vector $\mathbf{s}_i \in \{0,1,2\}^m$. The jth element of that vector, $\mathbf{s}_{ij}$, is 0 if the individual has never been infected by viral strain j; $\mathbf{s}_{ij} = 1$ if the individual is currently infected by the strain; and $\mathbf{s}_{ij} = 2$ if the individual is immune to the strain. The epitope sequence of strain j is denoted by a binary sequence x_j.

For viral strain j with serotype x_j infecting a host with immune status vector $\mathbf{s}_i$, the probability that the strain can escape the immune response acquired by a previous infection by strain l with the serotype x_l is assumed to be given by

$$\phi(x_j, x_l) = 1 - \exp[-d(x_j, x_l)^2 / 2\sigma^2] , \tag{1}$$

where $d(x_j, x_l)$ is the Hamming distance between serotypes x_j and x_l; σ gives the characteristic distance in serotype space over which the immune response mounted by a strain is effective. This infection probability is zero when two serotypes perfectly match and approaches one as the distance between them diverges to infinity. The infection probability of a new strain should be affected by all previously infecting strains and we therefore assume that the overall effect of previous infections is given by multiplying (1) for all previously infecting strains. Thus the probability that a pathogen serotype x can evade the immune response in host i (and hence can infect the host) is

$$\eta_i(x) = \prod_{\substack{j=1 \\ \mathbf{s}_{ij}=2}}^{n} \phi(x, x_j) , \tag{2}$$

where the product is taken for all j with $\mathbf{s}_{ij}=2$. The transition probability that the individual i becomes infected by viral strain j is then

$$P(\mathbf{s}_{ij} = 0 \rightarrow \mathbf{s}_{ij} = 1) = \beta u_j \eta_i(x_j) , \tag{3}$$

where $u_j = \sum_j \mathbf{1}(\mathbf{s}_{ij} = 1)$ is the total density of viral strain j in the population and β is the transmission rate. The transition probability that individual i currently infected by strain j is recovered and immune to the serotype is

$$P(\mathbf{s}_{ij} = 1 \rightarrow \mathbf{s}_{ij} = 2) = \gamma_{ij} \,, \tag{4}$$

where γ_{ij} is the recovery rate of host i from an infection by strain j. A healthy individual dies with natural mortality d, while an infected individual in general has a higher mortality that depends on the number of current infections,

$$\text{mortality of individual } i = d + v_i \alpha_0 \,, \tag{5}$$

where $v_i = \sum_j \mathbf{1}(\mathbf{s}_{ij} = 1)$ is the number of currently infecting strains in the individual i, and α_0 is the virulence of the pathogen.

From this model, we generated phylogenetic trees and identified statistics that characterize the shape of these trees as well as other phylogenetic relationships. We then analyzed how these statistics are related to the epidemiological parameters and genetic setup of the studied population.

Research questions and work plan

During the summer project, I plan to extend the basic model described above in two directions. Both extensions are intended to make the basic model more realistic.

- The first direction is to allow for variation in the virulence of strains. So far, the virulence α_0 is assumed to be constant, whereas the virulence of natural diseases can evolve over relatively short periods of time i (e.g. Fenner 1983; May and Anderson 1983). I plan to first analyze the model by assuming that the virulence is determined by the epitope sequence itself. In an alternative approach, I will then assume the virulence to be determined independently of the epitope sequence and will examine the joint evolution of virulence and epitope sequence (assuming partial linkage between them). As before, I will generate phylogenetic trees and epidemiological time series through simulation of the model and will analyze their relationship with the underlying epidemiological parameters.
- A second direction of extension is to introduce demographic change of total host population size, rather than assuming a constant host population size.
- In addition, I am planning to investigate the potential for developing analytical treatments of this system in collaboration with ADN Project Coordinator Dr. Ulf Dieckmann, who supervises my YSSP project.

Relevance and link to ADN's research plan

This study ties in with ADN's research focus on disease evolution and virulence management. It focuses on the relationship between phylogenic tree shape and epidemiological parameters. If we succeed in finding interesting tendencies in this relationship, this would open up possibilities for inferring epidemiological parameters from observed phylogenetic trees. The model will also allow for simulating how viruses evolve when host populations are treated with antibiotics or is vaccinated.

Envisaged publication

In collaboration with Ulf Dieckmann, a paper on the theoretical aspects of the developed model is planned to be submitted at the end of the YSSP period.

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Size Distribution and Dynamics of Patches in Fragmented Landscapes

Ádám Kun

Department of Plant Taxonomy and Ecology, Eötvös University, Budapest, Hungary

Goal

To understand the dynamics of spatially structured ecological populations in variable habitats by applying and extending results of percolation theory.

Introduction

Spatial and temporal heterogeneity applies to all aspect of life. From the major climatic changes, through the turning of seasons, to the fine-grained distribution of mineral nutrients in the soil organisms have to cope with heterogeneity. Bacteria changes huge part of their genome because of changes in the local availability of some resources. Some plant exhibit morphological changes in response to spatial heterogeneity. Most animals have to forage for food, which is heterogeneously dispersed in space. And sadly many organisms have to cope with the challenge of ever shrinking and fragmenting habitats.

Heterogeneity helps and forces organisms to evolve, to adapt. Major changes in composition and availability of resources; changes in the frequency, composition and abilities of other species forces organism to evolve. The challenge of the ever-present fluctuations and the inhomogeneity in resource distribution has to be dealt with by the organism every day of its life. It seems likely that spatial and temporal heterogeneity is a prerequisite for the complexity and diversity of life.

The myriad solutions to the challenge of life led to the staggering diversity of species we encounter. Careless human management - or lack of management - of resources threatens this diversity. Forest cuts, pollution, rubbish heaps and degradation of soils leads to fragmentation of n atural habitats (Primack 1998). More and more natural habitats are destroyed in order to be developed as agricultural fields. The shrinking habitats could not sustain their former species pool. Available food, shelter and territory dwindles and so do population sizes of species. The population size of species that are rare even in pristine habitats could shrink to the level where the population go extinct. Habitat destruction is the major cause of species extinction (Lawton and May 1995).

Generally an ecological landscape is a mosaic of different kind of A given habitat can be most accurately characterized by its flora. Plants - as they are sessile - are effected by spatial heterogeneity the most. In his pioneering paper in 1947, Watt named the study of spatio-temporal dynamics of populations as the main aim of ecology. Yet, the study of spatial processes only became the focus of researches in the past ten or fifteen years. The change of methodology in theoretical studies is even slower: most classical ecological model does not consider the importance of spatial heterogeneity. With the development of novel modeling techniques and with the increasing computational power of computers the construction and analysis of spatio-temporal models have became feasible. Theoretical ecology advanced considerably with the introduction of such techniques as these allow scientists to construct models that are increasingly realistic and informative (Czárán 1998).

Research questions

The proposed research project for the IIASA summer program will address two spatio-temporal problem of great ecological significance.

First, we are planning to complete an investigation on the role of percolation barrier (Stauffer and Aharony 1992) on plant populations, and the effect of temporal fluctuation on the percolation barrier, and thus on the spread and size of plant populations. This collaborative research is already under way, and it seems that the existence of percolation barrier and the alleviating of it by small fluctuation could be one of the explanations of why intermediate disturbance helps maintain diversity and large populations. A second investigation will commence during the summer period as is meant to focus on the dynamics of occupied and empty favorable patches on a fragmented and changing landscape. 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 Beáta Oborny.

Method

We plan to use the basic model of percolation theory to study important ecological questions.

Percolation theory was developed to describe physical properties of gels, polymers, and glassy materials and forms the basis for studies of flow of liquids through material aggregates. Percolation theory deals with movement on a two dimensional lattice consisting of enabled and restricted sites. Let p denote the proportion of enabled sites on the lattice. On a $m \times m$ lattice pm^2 sites are chosen randomly to be enabled, the rest [$(1-p)m^2$] are restricted. A set of enabled sites, where a given site could be reached from every other element of the set by only moving trough neighboring elements (the definition of neighbor is strongly dependent on the geometry of the lattice), is called a cluster. The number, size and shape of enabled clusters changes as a function of p. There is a critical value of p (referred as critical probability, p_c, or percolation barrier) above which the largest cluster theoretically span the infinite plane. In a finite lattice the largest cluster will cross the grid continuously from one side to the other.

In ecology percolation theory could be applied as follows: in a heterogeneous or fragmented habitat an organism with dispersal rate not greater than the grain of the habitat could only conquer every large resource cluster if percentage of resource patches are greater than a critical value. In other way, bellow a certain percentage of resource or natural patches some clusters could not be reached and exploited. This would result in a lower population size than the carrying capacity would indicate; or in fragmented landscape parts of a population could not mix with other parts.

There are numerous types of models for describing the spatial dynamics of populations (Dieckman et. al. 1997, Oborny and Cain 1997). Models can be based on either discrete or continuous space or states, and they can operate deterministically or stochastically. One of the most widely used spatially explicit modeling techniques is cellular automaton (Neumann 1951, Hogeweg 1988, Czárán 1998). Percolation has been studied many times by cellular automata (Neuhauser 1998, Tao 1999, Hiebeler 2000), and we plan to employ this modeling technique in our investigations.

A cellular automaton is a grid, where every cell is in one of the few predefined states, and the next state of a cell is dependent on the state of itself and its neighbors. Neighbors could be defined in many way: in the basic percolation theory models authors use the so called Moore neighborhood (the closest four cell in a square grid); in plant population models hexagonal lattice could be used so every neighbor is in the same distance from a given cell. Number of states of a cell is usually kept low. Populations spreading on a fragmented landscape could be described by 4 states: unoccupied restricted site (UR), occupied restricted site (OR), unoccupied enabled site (UE) and occupied enabled site (OE). The next state function could be generally described as follows:

An unoccupied enabled site could be colonized from neighboring occupied sites (UE → OE if there is OE in the neighborhood).

- o In percolation theory restricted site could not be colonized, so the UR → OR transition could not occur. With the implementation of this rule the OR state become non-existent.
- o Change of site quality from restricted to enabled (UR → UE)
- o Change of site quality from enabled to restricted, could result in loss of occupancy (UE → UR or OE → UR).

For completing the definition of a cellular automaton one need to state the initial state of every cell in the grid. All important characteristics of the system are dependent on the ratio of enabled to restricted site. At a given enabled to restricted site ratio we assign the states randomly to the field. One enabled site will be occupied.

This general method is the main link between the two proposed researches. While the two field of study might be well apart, the studied phenomena are only differing in their scale. Plant species could sense environmental heterogeneity on the scale of centimeters, and local dispersal means a few meters maximum. On the other hand landscapes are on the magnitudes of hectares, and sites are patches clear cuts or natural forests.

Research plan

The Percolation Barrier as a Challenge for Locally Dispersing Organisms

Motivation and background

Plants are essentially modular organism this trait is very pronounced in clonal species where the unit of iteration is the ramet. A ramet is a potentially physiologically independent unit. Spreading and growing in clonal species are horizontal, and local (Oborny and Bartha, 1995). Local spreading is not only the characteristic of clonal species, but many sexually propagating species disperse only locally (O'Connor, 1991). An environment that is heterogeneous on the scale comparable to the propagating distance of the species poses a particular challenge, which have to be addressed by the organism. Oborny (1994a,b) have compared a wide range of clonal morphological strategies in regard to their ability to selectively place their offspring to favourable patches.

For example in heterogeneous environments that are poor in resources wide unfavorable regions might prevent locally dispersing organisms to reach and conquer favorable sites (Oborny et. al. 2000). In my MSc thesis, I have studied the spatial behavior of a locally dispersing clonal plant population in a heterogeneous environment. I have shown that in relatively poor habitats, with only 10-40% of favorable sites, population size was equilibrating much below the actual carrying capacity of the environment: the population could not colonize all favorable patches since it was unable to cross unfavorable regions.

In general, the dynamics of population spread on a lattice that consists of favorable and unfavorable sites can be studied by percolation theory. The theory suggests that there is a certain ratio of favorable to unfavorable sites below which the population cannot spread indefinitely far from its point of origin. While this is a well-known phenomenon among physicist, ecologists have yet to realize the full importance of percolation.

Method

Cellular automata are not only fit to study percolation systems but also are geared to study next-neighbor interactions, which is the most prevalent type of interaction within plant communities.

The method employed in this investigation is basically the same as in the method section, but the implementation is a bit different: the cellular automata in our model had two layers: a population layer and a resource layer. Both layers consist of a 100×100 cell lattice. We used the von Neumann (4-neighbour) neighborhood. The topology of the automata was toroidal.

Resource layer

Each cell's state - the local environment - could be either favorable or unfavorable. The represented habitats were spatially and temporally heterogeneous. For modeling environmental heterogeneity, we used the following two parameters:
(1)   the average resource richness of the habitat (p),
(2)   the frequency of change in the local resource level (C_g).

The average resource richness of the habitat (p) determined how many percent of the habitat patches were favorable (and 1-p portion of the patches was unfavorable).

We introduced temporal heterogeneity by changing a portion of the favorable sites to unfavorable and a portion of the unfavorable sites to favorable. The parameter C_g gave the probability of resource level change from favorable to unfavorable. So in every step C_g percent of the favorable sites became unfavorable (we chose randomly from the available sites). C_b, the probability of an unfavorable site becoming favorable computed as follows to maintain that p percent of the sites are favorable:

$$C_g \times p = (1\text{-}p) \times C_b.$$

Population layer

In the population layer each cell represented enough space for one ramet, so a cell was either empty or occupied by a ramet. A ramet in a given cell encountered a microhabitat characterized by the quality of the resource layer in the same place (same co-ordinates).

In the beginning of each simulation we randomly placed 50 ramets to the population layer. All the other cells were unoccupied.

Favorable sites were colonized if there were neighboring favorable sites occupied by a ramet. Unfavorable sites could not be colonized.

If a favorable site become unfavorable, then the ramet occupying the site dies.

The parameters of the simulation

We followed the competition of the strategies for 500 time step. After the 500th time step we recorded the number of ramets in the field. The parameter values used in the simulations we the following:

- o the range of average resource availability (p) was from 10% to 65% by steps of 5%;
- o and the frequency of resource change (C_g) was 0%, 1%, 1.5%, 2%, 3%, 4%, 5%, 7%, 10%, 15% and 25%.

For each parameter combination we've made 10 replications and averaged the results.

Intermediate result

From my results I could establish that with a modest amount of temporal fluctuations in the environmental pattern the populations could spread over the entire habitat, thus partly alleviating the percolation barrier. The resulting effective rate of spread was maximal at an intermediate level of fluctuation. The exact magnitude of fluctuation where the population size was maximal was dependent on the average resource richness of habitats. With increasing resource richness the needed fluctuation decreased.

Research questions and work plan

During the summer project, we plan to investigate the implication of my findings on community level processes and its possible connections with the intermediate disturbance hypothesis. The required data are available we only have to re-examine them for our new questions. The intended work is in most part an analysis of literature on intermediate disturbance hypothesis and the writing of the proposed paper on the subject (see the *Envisaged publications* section)

Percolation in a fragmented habitat: a new tool for conservation biology?

Motivation and background

Vegetation patterns are the result of complex interaction between climate, terrain, soil, water availability and biota and alterations resulting from natural disturbances (like wind and fire). Alteration in landscapes as a result of urbanization, agriculture, and forestry management have significant effect on the pattern of vegetation as established systems are removed and replaced with managed ones. The surrounding matrix has a negative influence on natural habitats, and these effects are most severe at the edges of habitat fragments, and small fragments are comprised of nothing but edges. In this way reserves are nothing more that patches linked to a surrounding matrix (Hansson and Angelstam 1991). The number and size of natural patches required for the prevention of further loss of species is still hotly debated (see discussion of the 'One Large Or Several Small reserves - the 'SLOSS' - question by, *e.g.*, Soulé and Simberloff 1986).

Some of the inherent problems associated with fragmentation of natural habitats are the followings (for further information on habitat fragmentation and degradation see Primack 1998):

- o Fragments have a greater amount of edge for the area of the habitat, and the center of each habitat fragment is closer to an edge. Interior areas - those that have a certain distance from the perimeter - are valuable, and many species could only live in the interior. So the effective amount of lost natural habitat is greater than indicated only by measuring the managed/destroyed areas.
- o Dispersal of indigenous species (especially the specialized ones) through the matrix to distant biotopes of similar kind is very slow. So individuals are restricted to a few patches that are close enough. Genetic diversity could dwindle as effective population size decreases.
- o Available territories decreases and this most of the manifest itself in less available food. Large mammals are especially threatened by loss of natural habitats (like Grizzly bears in North America), as they need quite large areas for foraging for food.

The effect of habitat fragmentation could be lessened by the implementation of ecological corridors. Ideal size and distribution of ecological corridors are still and open question and depends strongly on the size of the gap to be bridged, the species to be preserved, etc.

In a static landscape the distribution of patch sizes is known from established theory. Moreover percolation systems have been proposed as neutral models for the analysis of broad-scale landscape patters (Gardner *et. al.* 1987).

On the other hand the distribution of patch sizes in a fluctuating environment is not known. Our aim for the proposed project is to study the spread of a locally dispersing model population on spatially and temporally heterogeneous (fragmented) landscapes. We plan to assess the proportion, size distribution, and temporal dynamics of favorable sites and compare it to the analogous quantities for occupied sites.

A related problem is concerned with the prevention of the invasion of alien species. Hopefully the results will allow us to better understand the type and magnitude of environmental change that foster or prevent invasion in a fragmented landscape.

Method

We will use the cellular automata described in the Method section with hexagonal lattice geometry. At the start of the simulation only one patch is occupied. Some of the favorable sites will be reached and occupied by locally dispersing individuals. By introducing fluctuation to the habitat pattern (by turning favorable sites into unfavorable ones and vice versa) some clusters of favorable sites will break up while others will coalesce. In our first model when an empty cluster of favorable sites coalesces with an occupied site, the population will colonize the formerly empty cluster. By implementing this rule we describe a system where the population propagate more frequently than the environment changes.

In a follow up investigation we can study population with comparable dispersal rate to environmental change. Also the initial pattern of enabled/restricted could be generated in many different ways. We could employ methods that generate more aggregated patches, and analyze their behavior.

It is desirable to record the generated landscape pattern in every time step so in future studies we could measure characteristics like edge/area ratios or fractal dimension of enabled clusters. These and other characteristics are frequently employed in describing real landscapes (Gustafson and Parker 1992).

Dynamics in individual based, stochastic models tend to fluctuate and only behave in a reproducible manner if the number of individuals is sufficiently large. Thus the numerical investigation of such systems could be 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. A system with infinitely fast spreading hypothetical species is probably easier to approximate. Individual-based simulations will allow us to determine the size distribution of clusters of favorable/unfavorable and of occupied/empty sites, as well as the temporal changes occurring in such a system.

Research questions and work plan

With this model, we plan to assess the spatio-temporal characteristics of ideal ecological corridors and the intensity of random environmental change that is necessary to ensure persistence of an endangered species or containment of an alien species. In general, we expect to gain insight into invasion processes in heterogeneous habitats, a topic of direct relevance for understanding the adaptation of spatially structured populations.

During the envisaged stay at IIASA, I plan to develop and refine the necessary simulation program, process the obtained data, and get acquainted with the relevant literature with the aim of preparing a publication for an international scientific journal.

Relevance and link to ADN's research

Devising innovative tools for modeling population dynamics in spatially heterogeneous habitats is of critical importance in modern applied and theoretical ecology. We expect the project proposed here to successfully contribute to ADN's research foci on simplifying spatial complexity. The established research priorities of ADN call for intensifying the research on the dynamics of spatially heterogeneous ecosystem, and the proposed project is definitely within this scope.

There exists a contact and collaboration between Dr Beáta Oborny, my supervisor at the Department of Plant Taxonomy and Ecology at Lóránd Eötvös University, and Dr Ulf Dieckmann, Project Coordinator of the Adaptive Dynamics Network Project of IIASA.

Envisaged publications

The proposed research is planned to result in at least two publications. The investigation on connecting percolation on a fragmented and temporarily heterogeneous landscape with the intermediate disturbance hypothesis will result in one paper. We also plan to write an additional paper on the dynamics of locally dispersing populations and of favorable patches in a fragmented landscape. We plant to apply our findings to conservation biology, and this is also expected to result in a publication that reports the spatio-temporal characteristics of ideal ecological corridors and the required intensity of random environmental change which ensure persistence of an endangered species or containment of an alien species.

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Improving the method of moments for two-species spatial Lotka-Volterra models

Péter Szabó

Department of Plant Taxonomy and Ecology, Eötvös University, Budapest, Hungary

Goal

To identify optimal moment closures for describing two interacting spatially structured populations.

Background and Motivation

Spatial models offer new insights and ideas in ecology and evolutionary biology. The rapid development of computer technology nowadays allows for the exploration of spatially explicit, site- or individual-based models that are designed to describe complex ecological processes in extrinsically or intrinsically structured populations (Levin 1976; Hamilton and May 1977; Crowley 1981). Local interactions and dispersal, often described by individual-based stochastic processes, result in new, and sometimes surprising departures from traditional mean-field descriptions. For instance, spatially explicit counterparts of mean-field models often predict the survival of apparently disadvantageous traits, the evolution of altruistic phenotypes, and reveal the macroscopic structure observed also in field-experiments (Nowak and Sigmund 1992; Durrett and Levin 1994; Oborny and Bartha 1995; Czaran 1997; Dieckmann, Law and Metz 2000).

However, realizations of spatially explicit models contain a vast amount of information. It is therefore difficult to extract those essential degrees of freedom that are needed to parsimoniously specify the current state of the system and to predict its expected change. Relaxation projections are used to identify suitable sets of state variables, which provide salient extra information beyond mean densities. Correlation densities have proven useful in providing such necessary additional information about the spatial structure of an ecological system (Dieckmann, Law and Metz 2000). By describing the dynamics of correlation densities it also becomes possible to predict the long-term dynamics of such systems. Moment closures, needed for describing the dynamics of correlation densities, play a central role in relaxation projections. It has been observed that under particular circumstances certain moment closures provide more accurate descriptions than others. Yet, the criteria for choosing the most appropriate moment closure for a given system currently are almost entirely unclear.

Research questions

For describing the correlation dynamics of a given order we must take into account higher-order correlation densities: correlation dynamics of order i depend on correlation densities of order 1, …, $i+1$. This recursive relation between correlation densities (or moments) is called a moment hierarchy. Fortunately, higher-order terms usually contain no essential extra information, so we may truncate the moment hierarchy by expressing correlation densities of order $i+1$ through correlation densities of order 1,..., i. Such a relaxation projection can be defined by using several alternative moment closures.

Here we focus on expressing triplet densities $\tilde{T}$ in terms of singlet densities N and pair densities $\tilde{C}$. There exist four such candidate moment closures:

1. $\qquad \tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)N_k + \tilde{C}_{ik}(\xi')N_j + \tilde{C}_{jk}(\xi'-\xi)N_i - 2N_iN_jN_k$

2.a $\qquad \tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')/N_i$

2.b. $\qquad \tilde{T}_{ijk}(\xi,\xi') = \frac{1}{2}\left[\tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')/N_i + \tilde{C}_{ij}(\xi)\tilde{C}_{jk}(\xi'-\xi)/N_j + \tilde{C}_{ik}(\xi')\tilde{C}_{jk}(\xi'-\xi)/N_k - N_iN_jN_k\right]$

3. $\qquad \tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')\tilde{C}_{jk}(\xi'-\xi)/(N_iN_jN_k)$

The indices i, j, and k refer to the different species that may coexist in the considered ecological system. Vectors ξ and ξ' denote the distances between individuals i and j, and between individuals i and k, respectively. The four closures above are referred to as the power-1, asymmetric power-2, symmetric power-2, and power-3 moment closure, respectively.

The above closures obey two consistency conditions, which provide criteria for valid moment closures:

- Condition (C1). In the absence of any pair correlations, individuals in triplets must also be assumed to be uncorrelated.
- Condition (C2). Because attention is focused on small-scale spatial structure, pairs of individuals separated by large distance are assumed to be uncorrelated.

These closures, originally introduced for continuous space, are easily applied to dynamics in discrete space. In this case elements of the distance vectors may take their values only from a discrete set, in our case they may take integer values.

In this project we plan to identify the most suitable moment closure for a flexible class of spatially explicit two-species Lotka-Volterra models on square lattices. For this purpose we will investigate the four candidate closures above, as well as variants that result from assigning different weights to the terms on the right-hand side of these closures. The goal is to determine how the considered ecological setting affects the optimal choice for these weights.

Method and work plan

We will study a two-species Lotka-Volterra model on a two-layered square lattice with asynchronous updating. There exist occupied and empty sites on the lattices of both species. The elementary ecological processes in this model are birth, death, and movement events. Each individual gives birth to a new individual, dies, or changes state with an adjacent site at constant rates, depending on whether their site on the other species' layer is occupied or not. By choosing different values for these rate parameters, a wide range of ecological interactions – including competition, mutualism, and predator-prey relations – can be investigated.

We will perform numerical simulations of these systems with different parameter settings. On this basis, we will measure average singlet densities, pair densities, and triplet densities. Values for the latter will then be compared to those obtained by different approximation methods (moment closures). In this way, optimal weights can be estimated through linear regression.

Previous studies suggest that power-2 provide the best match (Dieckmann, Law and Metz 2000). Specifically, we therefore plan to investigate this kind of closure in two ways. First, tentative evidence indicates that the optimal weight of the three terms in Equation 2.b depends on the relative demographic timescales of the two interacting species. To confirm this hypothesis we will simulate systems with such different relative demographic timescales and compare them by approximations that are based on different weight values. Second, weights can be assigned to the three terms in Equation 2.b in a configuration-dependent way by using different weight values for different triplet configurations. To clarify whether or not such a generalization is worthwhile will be one focus of our study.

Relevance and link to ADN's research plan

Obtaining better insight into criteria for choosing moment closures has important repercussions for the efficient modeling of spatial ecological systems. Moreover, pair approximation techniques and corresponding moment closures play a critical role in the studies on spatial invasion fitness conducted by the Adaptive Dynamics Network.

Expected output and publication

The proposed research is planned to result in a jointly authored paper by the end of the YSSP.

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