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 versions, 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 possible 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 De- partment of Biological Physics at Etvs 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 com- paring 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 ex- tended ecological system can belong to this universality class.

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