Ulf Dieckmann, Tomáš Herben, Richard Law
(alphabetical order)

Strategies in Spatial Ecological Modeling: Reliability, Robustness and Generality*

Participants and Programme

Tamás Czárán (University of Budapest):
Coexistence in one-sided competition: the temporal refuge effect in a stochastic cellular automaton model and its mean-field approximation.

Ulf Dieckmann (Wissenschaftskolleg zu Berlin):
Towards the low-dimensional analysis of spatial ecological processes.

Volker Grimm (Umweltforschungszentrum Leipzig):
Pattern-oriented modeling.

Tomáš Herben (Wissenschaftskolleg zu Berlin):
Interactions at the level of plant individuals: building blocks of spatially extended models of community dynamics.

Florian Jeltsch (Umweltforschungszentrum Leipzig):
Tree spacing and coexistence in semi-arid savannas: a model-based analysis.

Richard Law (Wissenschaftskolleg zu Berlin):
Spatio-temporal processes in plant communities.

Beáta Oborny (University of Budapest):
Spatial pattern formation in a community of clonal species - a cellular automaton model.

Armin Ratz (Umweltforschungszentrum Leipzig):
Reproducing pattern in fire ecosystems: a simulation model.

Eckhard Winkler (Umweltforschungszentrum Leipzig):
A combination of continuous and discrete features in the modeling of clonal plant spread.

Christian Wissel (Umweltforschungszentrum Leipzig):
Spreading of rabies: from a pattern to control strategies.

---

* Seminar under the auspices of *Otto und Maria Fischbeck-Stiftung* held at the Wissenschaftskolleg from July 10–11, 1996

Introduction

The workshop "Strategies in spatial ecological modeling: reliability, robustness and generality" was intended to discuss and assess the current state of ecological modeling in the spatial domain.

The meeting further served to establish closer contacts and cooperation between three research groups at Leipzig, Budapest, and at the Wissenschaftskolleg in Berlin. In particular, the different priorities and strategies on which research in the groups is based became a major focus for discussions during the workshop.

A lively exchange of ideas and evaluations was organized around the following questions.

– Based on the participants' experiences, what are the advantages and shortcomings of different formal paradigms for spatial ecological modeling?
– What are reliable methods for the calibration of spatial ecological models? How is the accuracy of such calibrations to be assessed?
– How stable are the qualitative conclusions drawn from these models? Which are the relevant perturbations for checking robustness?
– What is the meaning of genericity in modeling spatial ecological systems? How can we go beyond inductions based on individual simulation runs? Can we arrive at more general conclusions and more systematic insight regarding spatially complex ecological dynamics?

Pattern and process

In his introductory lecture, Richard Law emphasized the long-lasting challenge in ecological research to achieve a synthesis of the analyses of patterns and processes observed in biological communities. This difficult problem – posed by S.A. Watt as early as 1947 and still largely unsolved – requires the integration of two historically rather separate branches of ecological research.

On the one hand, spatial patterns typical for many ecological systems have been characterized by statistical methods, without encompassing the dynamics of such patterns and their corresponding statistical measures through time. On the other hand, in descriptions of temporal dynamics, attention typically has been confined to quantities that do not reflect spatial pattern, like the overall abundance of individuals in a population.

These approaches taken separately focus either on the spatial or on the temporal domain, and prevent a deeper understanding and a more accurate forecasting of dynamics in many ecosystems. Only on a short time scale, when spatial patterns can be assumed not to change significantly, or on an extreme spatial scale, where temporal dynamics may be assumed not to depend on the details of the spatial structure, are these two approaches viable on their own. In contrast, on scales intermediate in time and space, the temporal process will be contingent on the spatial pattern and vice versa.

Whereas neglecting temporal variation in ecological systems is seldom warranted, ignoring spatial variation can be justified if individuals in the system are well mixed among each other. Processes like wind dispersal of seeds and movement of animals tend to destroy spatial variation and, in the extreme, lead to a state in which each individual experiences a similar local environment. Following a tradition in physics, this typical local environment is called the "mean field." In consequence, the corresponding "mean-field assumption" holds for well-mixed systems and moreover serves as an approximation for systems with little spatial heterogeneity.

Although mean-field approximations have pervaded most of ecological research over the past few decades, they are of limited value. It has been shown empirically for a variety of ecosystems that predictions based on such approximations can go widely astray relative to the actual change in the system. In addition to such quantitative deviations, qualitative discrepancies between mean-field forecasting and actual observations have also been found.

In his contribution, Christian Wissel outlined instances of spatio-temporal dynamics (i.e. of the combined consideration of pattern and process) that have helped to improve predictability and understanding of the complicated behavior within particular ecological systems. Focusing on the spread of rabies in foxes, he demonstrated how spatially explicit models may open up new perspectives in ecological management and may provide answers unattainable within the classical mean-field paradigm. These simulation models of spatio-temporal dynamics can be used successfully to assess the impact of management strategies like vaccination or hunting schemes.

The inadequacies of the mean-field approximation had repercussions on most of the talks given at the workshop. Ulf Dieckmann underpinned the theme with a formal analysis of the role that spatial correlations and fluctuations play in the composition of ecosystems; the presence of either of these indicates a departure from the mean-field assumption. Richard Law and Tomáš Herben referred to the empirical knowledge available on plant reproduction, growth and interaction. The local character of these processes, in combination with the sessile nature of plants, stresses the need for explicit consideration of spatial pattern in decribing their dynamics. Tomáš Herben and Eckhard Winkler pointed out that plant architecture is particularly important for understanding the vegetative growth of clonal plants; the resulting non-isotropies as well as small-scale heterogeneities require special attention. In a study on fire spread in forest ecosystems, Armin Ratz showed that simple rules describing the interactions of ecological individuals can give rise to complex spatio-temporal heterogeneities, rendering mean-field approximations inappropriate.

Goals of ecological modeling

The need to describe ecosystems in a way explicit both in time and in space is becoming more and more recognized in the ecological literature. Unfortunately, from a practical viewpoint, the approaches to achieve this goal are as yet disparate and un-integrated. This led to vigorous discussions during the workshop on the question: what properties characterize good ecological modes?

Several different perspectives were suggested. Christian Wissel and Florian Jeltsch argued in favor of carefully constructed computer simulation models that capture many of the essential processes and features underlying real-world ecosystems. The overall behavior of such models is determined by rules that implement knowledge of or assumptions about specific systems. Based on such models, practical questions concerning ecosystem management and control can be addressed and a close link established between field ecologists and the modeling scientists.

Ulf Dieckmann and Richard Law advocated an approach that, while starting from known properties of individuals, systematically tries to bridge the different levels of organization. These levels separate the microscopic interaction of individuals from the mesoscopic dynamics of local environments and the macroscopic change of the community as a whole. The method holds the promise of providing a simplified but analytic description of the macroscopic spatio-temporal process that can foster new insights and that allows for comprehensive analyses beyond the investigation of individual simulation runs.

Volker Grimm addressed the issue of which systems in nature should be the targets of our models. As a guideline he suggested that modelers should focus on "real patterns observed in nature". Starting from such patterns has three advantages. First, the potentially novel concepts or measures needed to characterize the ecosystem under consideration immediately suggest themselves once the pattern has been recognized. Second, the question of whether the observed pattern is recovered in the model's dynamics serves as a simple qualitative criterion for validating the model. Third, the presence of a particular spatial pattern implies the existence of a specific spatial scale which can be used to interpret predictions from the model in terms of actual spatial distances in the real ecosystem.

Paradigms for modeling ecological space

In devising models for spatio-temporal ecological dynamics another dichotomy becomes relevant. For certain systems it can be advantageous to describe the dynamics of spatially extended ecological systems on a grid. Such grid-based models were employed in the contributions of Tamás Czárán, Florian Jeltsch, Beáta Oborny, Armin Ratz, and Christian Wissel. This type of approach amounts to partitioning physical space into a set of discrete cells. Typically, cells have the shape of squares, but also hexagonal or triangular cells can be used. The state of a cell is characterized by either the number or the density of individuals in the cell or, alternatively, just by the type of individuals predominant in the cell. Models based on this paradigm are called coupled-map lattices or cellular automata, respectively. On such grids the ecological dynamics is represented by rules which specify the conditions for and the rates of transitions in cell states depending on the cell's immediate neighborhood. Advantages of a discrete-space representation are its simplicity and flexibility. Implementing models of this type on a computer is also straightforward.

For some ecosystems, however, the discretization of physical space into regular cells seems rather arbitrary. It introduces a particular spatial scale into the modeling process, the specific choice of which can be far from obvious. Moreover, in describing the processes of interaction occurring in ecological communities it is often advantageous and more natural to directly consider these interactions between ecological individuals rather than constructing interactions between artificially introduced cells. In this case, spatially continuous models may be prefered. Such models, in which individuals are represented in space as points or by means of specific shapes, are called individual-based. A model of this type was presented by Tomáš Herben, Ulf Dieckmann and Richard Law to capture the spatio-temporal dynamics observed in a montane grassland community comprising four vegetatively growing grass species.

A hybrid approach to spatial representation was proposed by Eckhard Winkler. In the context of vegetative growth in plant communities, he contrasted the cell-oriented perspective of grid-based models with the plant-oriented representation of individual-based models, referring to the latter as reflecting the "plant's eye view." In his model, the growth of clonal plants was modeled on two separate spatial scales: juvenile plant modules move large distances and are essentially represented as points in continuous space, whereas the clonal growth of adult plant modules is described on a discrete grid of neighboring cells.

The calibration problem

One of the major problems in understanding the dynamics of spatial ecological systems is the estimation of model parameters. Models for spatio-temporal processes tend to have more parameters than those that aim only capture temporal processes in ecosystems. Parameters of spatio-temporal models include quantities like local interaction coefficients, competition ranges, movement radii, and local carrying capacities, reflecting fine details in the ecological and physiological properties of the natural system. These quantities have to be specified correctly before the model can be expected to produce predictions that match the observations.

So how should values for the model parameters be estimated? Three distinct approaches to this question were discussed at the workshop. First, the parameters could be obtained from independent experiments. Such a direct approach is sometimes feasible and if so always the preferred option. Tomáš Herben, for instance, described measurements of the survival probabilities of plants in grassland communities and outlined how to obtain empirical estimates of interaction coefficients by means of plant removal and implant experiments. Unfortunately, direct measurements of model parameters are not always possible. Either there exists no manageable experimental protocol, or the experimental design would impose perturbations into the system so large that the resulting numerical estimates would be unreliable.

An alternative approach was proposed by Florian Jeltsch. His spatio-temporal model of trees, shrubs, grasses and annual plants in the semi-arid savannas contained a relatively large number of parameters, many of which were not accessible to direct measurement. Although exact values for these quantities could not be obtained, experienced field ecologists from the area were able to estimate feasible parameter ranges. By providing probable upper and lower bounds for parameters, a set containing realistic parameter combinations could be delineated. This estimation procedure was then followed by a sensitivity analysis of the model relative to this set, allowing the identification of critical parameters and their likely values.

A third method, suggested by Richard Law, Ulf Dieckmann and Tomáš Herben, tried to overcome the limitations of direct measurements while avoiding some of the subjectivities when guessing parameter ranges. This method used statistical measures to characterize certain important properties of a spatio-temporal process. These measures were then applied both to an observed spatio-temporal pattern and to one predicted by the model. The resulting differences in these measures were used to construct a single function, the "pattern-deviation function," that measures the "distance" between the two spatio-temporal processes. This distance was then minimized by altering the parameter values of the model. The combination of parameter values yielding the smallest distance between the observed and the predicted process, corresponding to the lowest value of the pattern-deviation function, is then used for further validation tests and predictions.

Several statistical measures can be used to characterize patterns in space. Canonical summary statistics like correlation functions were proposed and applied by Ulf Dieckmann. As an alternative, Beáta Oborny suggested a set of information-theoretical statistics, originally introduced by P. Juhasz-Nagy, which capture aspects of spatial heterogeneity, diversity and association in terms of entropy measures. Using these statistics she was able to extract the salient features that distinguish the changing spatial patterns in a three-species community of clonal plants when altering the quality of the ecological habitat. For particular ecological systems, however, more specialized measures may be more appropriate. In his study of spatial patterns generated by forest fires, Armin Ratz employed spatial statistics for fire patterns to calibrate and validate his model. Measures investigated were the proportion of perturbed area within a fire patch, the median size of islands left unperturbed by the fire within such patches, the density of these islands, as well as shape indices and edge indices for fire patches. All the different statistical measures discussed during the workshop capture particular features of spatial patterning and amount to filtering the large amount of information contained in a given spatial pattern. However, in general, no small number of such measures will suffice to exhaustively summarize all of this information.

Generality and its limitations in ecology

Improvements in modern computer technology today make detailed spatio-temporal models of ecological systems possible. But the conclusions that can be safely drawn from simulation studies are limited. First, it is hazardous to generalize from single simulations. Unless backed by sound analytic reasoning, conclusions can only be taken for granted to the extent that they have been underpinned by explicit simulation runs. Second, a comprehensive understanding of critical mechanisms and causal pathways in the dynamics of spatial systems is far from complete. This is the case even though spatially explicit simulation models of ecological communities are already fairly successful in exploring, and sometimes even in forecasting the macroscopic consequences of microscopic processes. There is a pronounced discontinuity between today's simulation studies and the formal analytical tools available for deriving more general conclusions about the dynamics of spatially extended ecological systems.

Conclusions of the most general kind are of course unlikely to hold in ecology. Few if any results have been found in ecology that would apply without qualification to all ecosystems observed. If insufficient care is exercised in stating the prerequisites for a conclusion or the assumptions entering into a derivation, general statements quickly become void of content. Moreover, ecological forecasting cannot normally match the accuracy of predictions achieved in physics or chemistry. The inherent stochasticity of ecological dynamics, the relatively small numbers of discrete individuals involved, and the unforeseeable fluctuations induced by the environment of an ecological system, all mean that quantitative predictions typically carry substantial margins of error. In view of these fundamental constraints, ecological theory needs to give attention to predictions and conclusions that are both explicitly conditional and qualitative.

One response to these considerations is a sensitivity analysis. Once an ecological model has been formulated (and possibly calibrated), the parameters are perturbed and the response of the model's dynamics to these perturbations observed. Qualitative features of the dynamics that remain unchanged by the perturbations can then be regarded as robust conditional on the range of perturbations applied. An analysis of this type has been conducted, for instance, for Christian Wissel's rabies model and by Florian Jeltsch on his savanna model. Some statistical features of certain systems, for example in the dynamics of forest fires investigated by Armin Ratz, turn out to be extremely insensitive to alterations of the modeling structure. The existence of robust predictions of this type is known in the physical theory of phase transitions and critical phenomena as "universality." The concept of "self-organized criticality," originally introduced by P. Bak, tries to provide an explanation why such remarkable robustness may be more wide-spread. Universalities of this kind are good examples of qualitative rules with surprisingly weak conditionals.

A second type of qualitative reasoning often is applied implicitly when trying to understand the global behavior of a complex ecological model. Instead of predicting the system's dynamics in a single step, a decomposition is devised based on a set of individual if-then relations. These relations in turn result from the identification of characteristic processes or entities in the system together with observations on the critical conditions for their occurence. The conditional of the conclusion then is the union of the assumptions entering into all the if-then relations invoked. This type of reasoning goes beyond treating the ecological model as a "black box" and amounts to a first step in gaining insight into the causal pathways reflecting the dynamics of a spatio-temporal process.

However, two problems remain. First, it is not always easy to decide what the relevant types of perturbations for checking robustness are. Second, even if attention is eventually confined to a limited set of parameters, the range of values over which tests are performed may be questionable. Analytic methods, where available, avoid these problems and provide an alternative way forward. If an analytic derivation can be provided, it is no longer necessary to test for robustness under a plethora of possible perturbations; rather, the derivation process itself serves to delineate those specific perturbations that are challenging robustness.

The field of devising sufficiently powerful methods for tackling the complex dynamics of spatial ecological systems is wide open and no conclusive answers on this matter could be given in the course of the workshop. Nevertheless, several promising approaches in this direction have been reported. (i) In his contribution Tamás Czárán provided an extended mean-field analysis of a cellular automaton model, an analysis that explicitly takes into account fluctuation corrections relative to the standard mean-field dynamics. These corrections arise because an individual in its local environment only interacts with a relatively small number of partners, giving rise to sampling variation of binomial type. He was able to demonstrate the superiority of the extended analysis in reflecting the actual dynamics of the full spatial model. (ii) In his study of clonal plant growth Eckhard Winkler observed significant departures from mean-field predictions resulting from the presence of strong spatial correlations between individuals of the different species. By introducing correction coefficients that reflect the deviations from complete spatial randomness, he could modify the standard mean-field model, resulting in an improved fit to the full spatial model. The correction coefficients, however, have to be estimated numerically from simulation runs. (iii) A potentially generic path toward obtaining analytical methods for the study of spatially explicit, ecological dynamics was outlined by Ulf Dieckmann. Whereas mean-field approximations of spatio-temporal processes are tractable analytically, they can fail to capture the dynamics of the full spatial system for two reasons. First, fluctuations, inevitable in finite systems with local interactions, are ignored. Second, no account is taken of spatial correlations resulting from heterogeneities in the system. An expansion scheme in both the fluctuations and the correlations was proposed to overcome these limitations. The resulting two-fold moment hierarchy may provide viable and meaningful approximations for ecological systems not respecting the mean-field assumption.

Conclusions

The discussions during the workshop demonstrated that methodological pluralism remains an essential ingredient for progress in spatial ecological modeling. This pluralism extends at least into three different dimensions.

First, ecological models that are closely tied to the dynamics of specific ecological systems and to the empirical expertise of field ecologists are needed as well as much more simplified, abstract models. Whereas challenging phenomena and patterns may crop up in the former, we would be lost in the space of possibilities without the clarifications of the latter. Second, with respect to the different modeling paradigms for spatial ecological dynamics no objective preference can be established. What we do need are more precise theoretical links between the paradigms to avoid duplication of effort and unnecessary discussion about the relevance of phenomena predicted from one paradigm but not from another. Third, all the three different modes of reasoning about spatio-temporal processes in ecosystems – from the sensitivity analysis of black-box models, to establishing sets of lower-level, qualitative if-then relations, and eventually to the method of analytic derivations – can contribute to our understanding of complex processes in the spatial domain.

It will help to direct the efforts within this spectrum toward the central goal that makes ecology so interesting and different from some other sciences: to obtain qualitative conclusions with minimal conditionals. The workshop at Berlin endeavored to foster this goal by improving connections and coherence within a wide spectrum of options.