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I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

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"Individual-based ecological models for spatially-explicit investigation and computational ecology"

Louis J. Gross
Institute for Environmental Modeling
Department of Mathematics
Dept. of Ecology and Evolutionary Biology
University of Tennessee
Knoxville, TN 37996-1300
U.S.A.

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MAIN BUILDING STRADA COSTIERA, 11 TEL. 2240111 TELEFAX 224163 TELEX 460392 ADRIATICO GUEST HOUSE VIA GRIGNANO, 9 TEL.224241 TELEFAX 224531 TELEX 460449
MICROPROCESSOR LAB. VIA BEIRUT, 31 TEL. 224471 TELEFAX 224600 TELEX 460392 GALILEO GUEST HOUSE VIA BEIRUT, 7 TEL.2240311 TELEFAX 2240310 TELEX 460392

Individual-based ecological models for spatially-explicit investigation and computational ecology

Louis J. Gross
Departments of Mathematics and Ecology and Evolutionary Biology
University of Tennessee, Knoxville, TN 37996-1300
gross@math.utk.edu

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An ongoing discussion amongst those who work on theory in biology deals with the relative benefits of reductionist versus holistic viewpoints. Reductionists tend to argue for breaking systems down to their smallest feasible objects of interest, trying to build up from mechanisms at this small scale to larger scale phenomena. Those with a more holistic view prefer to deal with aggregated properties of systems first, and then add to it complications imposed by smaller scale structure within the system. These contrasting views of the process of theory construction are mirrored in the general process of model construction in any field. There are those who much prefer to build highly simplified models first, and then add new variables and constructs in order to increase the realism, while others prefer to start by including every aspect of the system which may be important, perhaps eventually discarding much of it as the process proceeds. The alternative views may thus converge towards similar models (as measured by the number of state variables say), but not necessarily. My experience is that, at least in theoretical biology, those trained as mathematicians tend towards the holistic end of this spectrum (and it is indeed more of a continuum than just two distinct contrasting views), while those with more of an engineering background tend towards the reductionist view.

A prime example of the contrast between these approaches occurs in population biology. The vast majority of theory in population biology has started from very simple differential equations in which a single variable represents population density, solutions of these are analyzed mathematically, and potentially compared to abundance estimates from field or lab observations. Although these models have had a great influence on theory in ecology, their aggregated form is particularly difficult to relate to observational biology. As this aggregated view of a population is highly simplified, a wide variety of extensions have been made to incorporate (1) size, age or physiological structure (leading to coupled systems of differential equations or partial differential equations); (2) space (leading to metapopulation models in which a population is broken down into distinct patches, or in the continuous space case to partial differential equations); (3) discrete generations (leading to difference equation models and matrix models); (4) stochastic effects (leading to birth and death processes and stochastic differential equations). In all these cases, as extensions are added, the models become less analytically tractable, and become considerably more difficult to analyze except numerically. The use of such extensions may well be required however, if we wish to ensure our models are sufficiently realistic to be applicable to specific problems in managing natural systems. Modern theory construction should not be bound by the limits of analytical mathematics.

The new field of computational ecology is an attempt to combine more realistic models of ecological systems with the often large data sets available to aid in managing these systems, utilizing techniques of modern computational science to manage the data, visualize model behavior, and statistically anayze the complex dynamics which arises. This often involves the use of Geographic Information Systems (GIS) to provide underlying static or dynamic maps of abiotic and biotic factors which are of importance in the natural system of particular interest. I believe that computational ecology will continue to grow in importance, as a necessary means to analyze complex problems of natural system management involving the coupling of detailed, spatially-explicit ecological models with physical models for abiotic components (such as soil, and hydrology), and the attendant effects on the system, of human actions.

One recent reductionist approach in ecology analyzes systems based upon the actions of individuals. These individual-based models track the behavior, growth, reproduction and death of individuals, from which they build up the dynamics of aggregated units such as populations and communities. These individual-based models are beginning to have significant impact on a variety of theoretical and practical questions in ecology, and there are now a few such models which are available for teaching purposes. One program we will use in this Workshop is EcoBeaker, written by Eli Meir and published by Sinauer Press, which has associated with it a variety of ecological scenarios preprogrammed to illustrate key ecological concepts (see the WWW site http://www.webcom.com/sinauer/EcoBeaker.html). Other individual-based modeling resources include those at the National Micropopulation Simulation Resource (with a biomedical emphasis - see http://www.nmsr.labmed.umn.edu/nmsr/NMSR.html), the Swarm program based at the Sante Fe Institute (see http://www.santafe.edu/projects/swarm/), David Griffeath's Ecomachine project (see his Primordial Soup Kitchen Page at http://math.wisc.edu/~griffeat/kitchen.html), and Rick Durrett's stochastic spatial models (see http://www.tc.cornell.edu/er94/ff02spring/ff04models.html). A basic, but now outdated, reference is DeAngelis, D. L. and L. J. Gross (1992) (editors) (1992) Individual-Based Models and Approaches in Ecology, Routledge, Chapman and Hall, New York.

There are several ways to construct individual-based models. My purpose here is to just mention the basics for models with explicit spatial structure. In this case, some type of spatial grid is set up, in which each location (or pixel in a computer map) corresponds to a spatial location with a certain spatial extent for each grid cell. Each grid cell then is characterized by a state, with each state corresponding to (a) presence or absence of a given species, (b) number of a given species present in the cell, (c) numbers of each of several species present in the cell, etc. There are then two basic approaches: (i) model how each grid cell changes based upon some set of rules and the states of surrounding grid cells, or (ii) model how each individual organism being considers moves among the grid cells and how the organisms state changes through time. Type (i) is the cellular automata approach, in which each cell is in one of a relatively small number of states and the rules for changes in state depend on the current state and that of nearest neighbors. The program SimLife from Maxis is of this type, in which each grid location consists of a single individual of a given species. Type (ii) is a truly individual-based approach, in which individual organisms can move anywhere across the spatial set of grid cells, change their respective states (e.g. size, fat content, number of offspring, etc.) and have their location attached to them as just another state variable. In this approach, each grid cell just combines the individuals located in it at any particular time.

Key questions in developing an individual-based model involve setting an appropriate spatial and temporal scale, deciding what individual-level state variables should be included and how to model them, and how to model movement, growth, mortality and reproduction of individuals. These are not independent issues of course, since setting the scale affects all aspects of the model. The appropriate spatial scale would depend upon (a) the activity pattern of an individual over the shortest time period of interest; (b) the availability of spatially-explicit information on habitat preferences, food resources, shelter and other spatial components affecting individual behavior; and (c) the availability of information to accurately model individual behavior. If activities at the shortest time scale of interest all occur within the smallest spatial scale at which you have habitat information, then there is little advantage to modeling behaviors which occur within that time step. If behaviors over the smallest time period of interest range over several spatial locations for which you have habitat information, then including state variables which measure such behaviors are appropriate. Driving all this is the set of questions you wish the model to address, which will no doubt lead to an appropriate temporal scale. Activities which occur on a time scale which significantly affect the aspects of individual behavior directly related to the questions of interest should be included, while those with small effect may be ignored or averaged.

There are two basic methods to track time sequences of behavior in these models. In one case there is a fixed underlying time step at which one censuses all inviduals, considering changes in behavior or state variables for all individuals. If this is done sequentially, then care must be taken to randomize the ordering of the individuals chosen in different time periods in order to avoid bias. Alternatively, event-based models take each individual, determines a time at which the next behavior or state variable change occurs, and ignores that individual until such a time is reached. Such event-driven approaches may be more computationally efficient , as not every individual needs to be investigated each time period. Though their investigation is still rather limited, parallelization methods for individual-based models have been developed and indicate thatbasic model assumptions made for sequential versions may well need to be modified in order for efficient parallel algorithms to be utilized. The assumptions that may be modified concern the ordering of interactions between individuals, and parallel implementations may well handle these in a more realistic manner than sequential implementations. Therefore there is no inherent reason why one should expect exactly the same model output from sequential and parallel implementations.

The program EcoBeaker allows one to combine grid-based and individual-based approaches. It allows one to set up changes in states of a grid cell as a simple transition matrix (possibly dependent on neighboring cells) as for example used in the Situation File to illustrate the Intermediate Disturbance Hypothesis. In this File, each grid cell is assigned to a state based upon the species present (e.g. Grasses, Blackberry Bushes, Oak Trees, Fire, etc.), with a certain probability of transition to a new state the following year. Alternatively, the program allows species to be set up as Individualistic, in which they have certain movement rules, and in which there can be several individuals of different species extant in a given grid cell at any particular time. The Situation File to Illustrate Competitive Exclusion is one example of this, in which the various Rabbit species have differing daily energy requirements, and movement rules. In addition to allowing users to change the parameters associated with any particular species, to add new species, and to code entirely new scenarios (admittedly this is something very few students would attempt), EcoBeaker also allows oneto investigate the effects of different sampling methods.

While EcoBeaker is structured to be a very easily applied tool, the complexity of model output is also instructive. A user has to decide what are the appropriate output variables to plot, and to come up with their own methods to summarize results, Though reminiscent of real field experiments, the program output is obviously more constrained. It does serve to illustrate however that, though such models are not that difficult to construct, the interpretation of results is non-trivial, particularly when trying to pick apart the effects of different model parameters. This is of course just as true for more realistic individual-based models, designed not for education but for application to ecosystem management. On this point, see L. J. Gross (1994) Limitations of reductionist approaches in ecological modeling: model evaluation, model complexity and environmental policy. In Wildlife Toxicology and Population Modeling: Integrated Studies of Agroecosystems (Eds. R. J. Kendall and T. E. Lacher), pp. 509-518. Lewis Publishers and CRC Press, Boca Raton. For additional comments on validation methods for individual-based models, see J. Bart (1995) Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* 5: 411-420.