International Congress on Environmental Modelling and Software

1st International Congress on Environmental Modelling and Software - Lugano, Switzerland - June 2002

Jul 1st, 12:00 AM

Avenues of Spatially Explicit Population Dynamics Modeling — A par excellence Example for Mathematical Heterogeneity in Ecological Models?

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Abstract: This contribution discusses different approaches to spatially explicit modeling of population dynamics of the intrusion of non-endemic species into patched habitats. Different modeling approaches such as cellular automata, partial differential equations and hybrid Petri nets are summarized. An application of a meta–population model for the Galapagos archipelago is described using a partial differential equation and a Petri net model. A detailed comparison of both models in terms of simulation results and methodology shows how different building blocks of ecological models can be. And the question is raised, how far the integration of models is at all possible and should be aimed at. Results of the investigation give a detailed insight into the problem of scaling ecological models and the core question of what processes should be considered in which scale in terms of space, time or complexity.

Keywords: Population Dynamic Modeling, Meta-Population, hybrid Petri Nets, PDE, Habitat Patches

1 INTRODUCTION

1.1 Mathematical Heterogeneity in Ecological Models

Modeling ecological processes often leads to simulation models which may by characterized as mathematically heterogeneous [Seppelt 2001]. This means, simulation models consist of different mathematical structures such as ordinary and partial differential equations, stochastic elements as well as matrix equations.

One main reason for this is that ecological models are a product of interdisciplinary research. Models comprise approaches from biology, chemistry, physics, ecology etc. Besides, physically based models – so called white box models – are not available for every scale in terms of space, time or complexity. Ecological models comprise physical models as well as statistical and phenomenological models – black- and gray-box models. Finally, different modeling environments or software-tools are used for model development.

1.2 Spatially Explicit Population Dynamic Models

Spatially explicit population models encompass the processes of

- spatial spread of individuals by migration or distribution by wind
- population dynamics, and
- depend on a spatially explicit habitat suitability model.

Different methodologies were presented in recent literature. Cellular automation models seem to be the most common solution. This approach represents the landscape by a regular mesh of equally sized grids. Information exchange (migration, habitat suitability) is possible between two neighbored cells. A population model is attributed to each cell and parameterized by associated habitat parameters. This model of population dynamics may be of any kind (Matrix, Lesli Model), c.f. for example [Schröder & Söndgerath, 2002, Richter et al. 2002].
Other approaches vary in mathematical as well as spatial structure. Obviously, all models depend on the specific problem to solve. However, two distinct approaches can be identified when looking at the representation of the landscape: a continuous and a discrete parameterization of the habitat properties in space.

1.3 Aim and Scope

For detailed analysis two entirely different modeling approaches are chosen here to model spatially explicit population dynamics:

1. Based on a modified McKendrick–Foerster–equation, a partial differential equation (pde) covering the physical processes of migration, growth and wind-spread solved by a dynamic finite element solver, and

2. A phenomenological model using the meta-population approach by McArthur et al., describing the processes of migration, growth, and spread solved by an invent based modeling environment using hybrid Petri-nets.

These models are applied to a non-endemic grasshopper species entering the Galapagos archipelago.

2. MODELLING APPROACHES

2.1 Hybrid Petri-Nets

A Petri net (pn) is a directed graph with two types of nodes, i.e. places p_i and transitions t_j. Alternate nodes are connected with arcs α_{ij}. Places are locations that hold information or data, within Petri net theory called "tokens". The transition nodes of the net transform the information carried by tokens. For each transition a rule is specified, that determines the conditions when all input tokens can be taken from the input places and tokens can be transformed to the output token. For standard Petri nets the number of input and output tokens are defined by weights w_{ij} which are associated with the arcs. Petri nets are capable of simulating dynamic processes, especially event based simulations.

Event based processes can be identified in ecological modeling. Examples are migration modeling in patchy or fragmented habitats or modeling population dynamics if distinct development stages of a population are considered.

The use of Petri nets in ecological modeling necessitates some extensions to the standard Petri net concept. These extensions concern

- Time marking of transitions, which allow different time periods for switching,
- Stochastic and dynamic behavior of transitions,
- Estimation of the number of output tokens by nonlinear transition functions, as well as differential equations together with ordinary differential equation solver.

Seppelt & Temme [2001] presented this concept and introduced a detailed theoretical section on the formal definition of hybrid Petri nets.

2.2 Meta Population Modeling of the Galapagos Archipelago

A meta–population model for a non–endemic species entering the Galapagos archipelago requires to set up models for the two processes of growth and migration. MacArthur & Wilson [1963] described migration from one habitat to another with the equation

$$n_{1,2} \propto A\left(p_2\right) e^{-\frac{d_{2,1}}{D}} \frac{1}{\pi} \arctan\left(\frac{1}{2}\frac{diam_{1,2}}{d_{1,2}}\right) \quad (1)$$

where $n_{1,2}$ denotes the number of individuals moving from island p_1 to island p_2. This number depends on the area $A(p_2)$ of the source habitat p_2, the „visible arc" of the destination island p_1 derived from the arctan–function of the quotient of diameter of the destination island p_1 taken at a right angle to the direction of p_1 to p_2. The exponential term introduces the decreasing success of migration with increasing distance $d_{1,2}$ from p_1 to p_2, where D denotes a mean travel distance parameter. Figure 1 illustrated Eqn. (1).

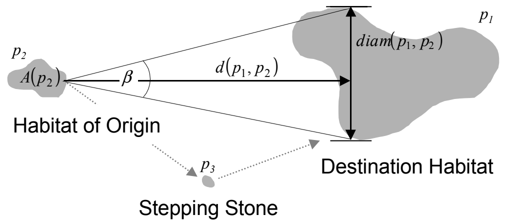

Figure 1: Visualization of Eqn. (1). Abbreviations: $diam_{1,2}$=$diam(p_1,p_2)$ and $d_{1,2}$=$d(p_1,p_2)$

For the growth of the grasshopper population on an island p_i the well known logistic growth function is assumed:

$$\frac{dP_i}{dt} = f\left(p_i\right) = rP\left(1 - \frac{p_i}{C_i}\right) \quad (2)$$

P_i denotes the population on island p_i. Habitat suitability may be introduced by habitat dependent growth rate r and/or habitat dependent carrying capacity C_i. The growth rate r is assumed to be constant for the entire study area. The carrying capacity depends on the size of the island $C_i \propto A(p_i)$.

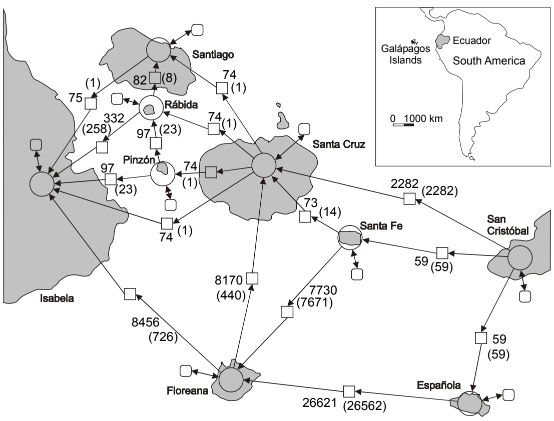

Figure 2: Map of Galapagos archipelago with the Petri net. The numbers at the arcs denote the first possible colonization of an island. The numbers in

brackets denote the average time in yeas grasshoppers need to migrate.

Figure 2 shows a map of the larger islands of the Galapagos archipelago overlaid by the Petri net developed to estimate the expansion and population dynamics. The places represent the species' population on an island. The transitions with rounded corners are connected to a logistic growth model (non-standard Petri net extension).

The arcs between the islands in the Petri net specify the probability of migration from one island to another according to Eqn. (1). The parameters of Eqn. (1) such as diameter, distance or area are obtained from the digital map of the Galapagos archipelago using a Geographic Information system. Another non–standard extension of the Petri net is the use of stochastic transitions for the migration process with an equal distribution and the expectancy value $1/n_{1,2}$.

2.3 Partial Differential Equation

Following for instance Henson [1999] the process of spatially explicit population dynamics of a population P can be described by the partial differential equation

$$\frac{\partial P}{\partial t} - \nabla \cdot (D \nabla P) + v \cdot \nabla P = f(P) \tag{3}$$

With the notations

P : Population at location x depending on time t (individuals per area)
D : coefficient of migration
v : vector of wind

Information on the geometry, topology and the habitat properties of the study area is introduced to the model as follows: For the ocean the function f describes a process of mortality. On an island p_i the function f defines a process of logistic growth with the rate r with a habitat dependent carrying capacity, cmp. Eqn. (2)

$$f(P) = \begin{cases} -\mu P & \text{open water} \\ rP\left(1 - \dfrac{P}{C_i}\right) & \text{for island } p_i \end{cases} \tag{4}$$

Migration is assumed to be constant over the entire study area and is equal to the average travel distance of a grasshopper in a time step.

Extensions can easily be introduced to the model. The diffusion term D may depend on gradients in the landscape to cover the process of migration to more suitable habitats. To be comparable to the approach used for the pn-model these topics are neglected.

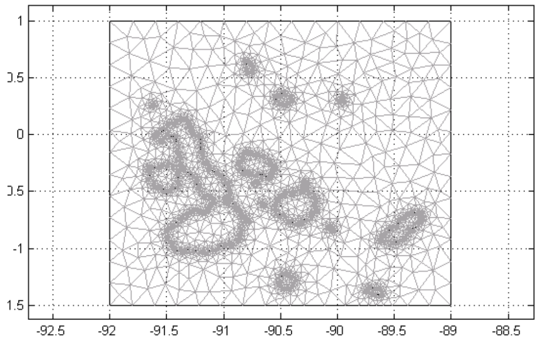

Figure 3: Finite element mesh for Galapagos–Archipelago. On x- and y-axis latitude and longitude are noted in degrees. The adaptively generated FEM mesh consist of 15437 triangles

A tool for numerical solving partial differential equations is required to derive solutions of Eqn. (3). FemLab®, an extension to MatLab® [Comsol 2001], is used. The tool bases on the technique of finite element methods (FEM). An important step of pre-processing is the set up of the geometry of the study area. Based on a digital map of the Galápagos archipelago a finite element mesh was generated using a Geographic Information System, c.f. Fig. 3. Based on these parameters of Eqn. (3) were specified using the information on habitat size derived from the GIS.

3. RESULTS

3.1 Dynamic Simulation

First topic of interest when running these different simulation models is their dynamic behavior. A starting population at the island San Cristóbal gives the initial condition for both model types.

Running the hybrid Petri net results in a set of time series with the abundance for each island. Figure 4 displays the results of a typical simulation run. Left part of the figure shows the populations on the larger, the right part shows the population sizes (below 20) of the smaller islands. Temporarily extinction on these islands is possible. Nevertheless these islands are important to support survival of the meta–population of the entire archipelago. These islands are called *stepping stones* and enable or help individuals to migrate from one larger island to another. Finally, the main island Isabela carries a population half of the carrying capacity after 250 years.

The results of the partial differential equation model are entirely different. This model calculates a fully spatially explicit population for every location of the study area (89° to 92° West, 1.5° south to 1° north). Contour plots are used to display the population density, c.f. Fig. 5.

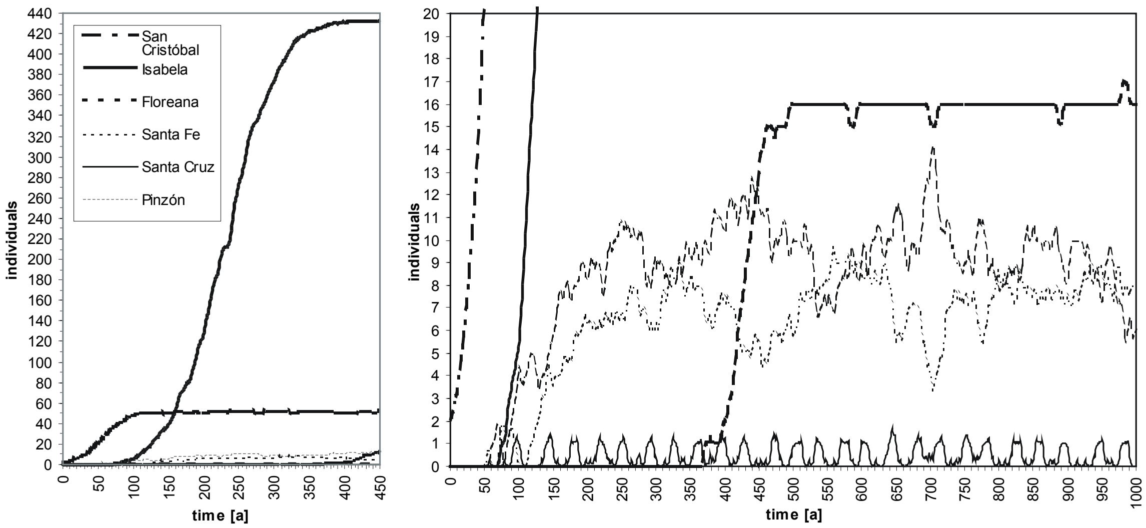

Figure 4: Population dynamics on different islands. The left figure shows the population size on the larger, the right figure shows the populations of smaller — possible stepping stone — islands.

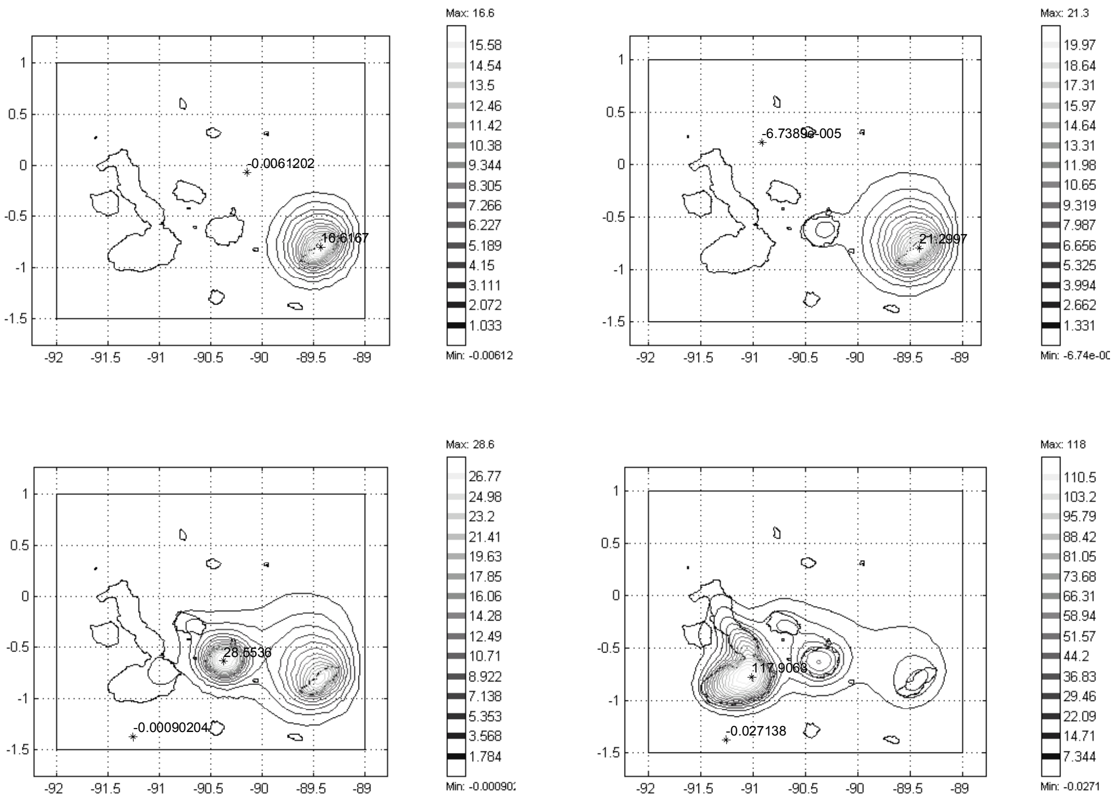

Figure 5: Simulation results of spatially explicit population dynamics of grasshopper species in Galápagos archipelago based on partial differential equation (3).

Assuming a grasshopper to be able to move 11 km per year leads to small but positive population sizes — even below unity — for ocean areas. However, this is essential to allow migration to a different island. Extinction on smaller islands is possible. On these island the process of migration overwhelms the growth process. Focusing on the population dynamics on the islands, the simulation results of both model types are comparable. For instance, on Isabela Island a population half of the carrying capacity is reached after 250 years. Population sizes and migration times are comparable. However, this comparison can only be interpreted qualitatively. The partial differential equation model gives a continuous distribution of grasshoppers for one time step. The time the first grasshopper reaches an island is somehow a fuzzy value compared to the results of the Petri net, c.f. Fig. 4.

3.2 Analysis

A second important step are the qualitative results on meta–population stability and migration pathways. Which islands are responsible for a spatial spread of the population over the entire islands? Which are the migration pathways? Both models give answers to this question.

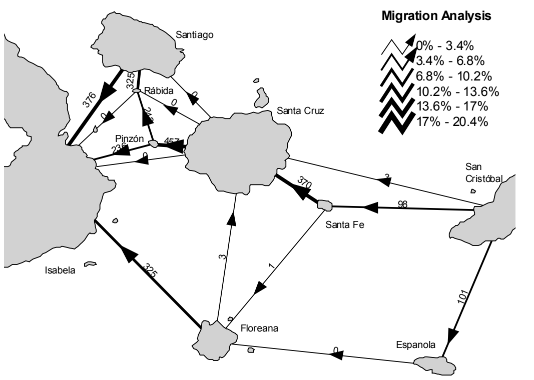

Figure 6: Analysis of migration pathways derived from Petri net analysis.

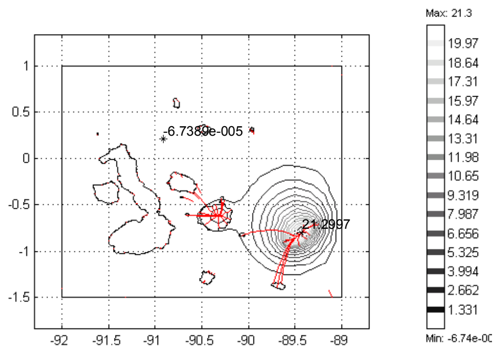

Figure 7: Results of a "grasshopper"-tracking analysis based on the pde–model, Eqn. (3)

Using the Petri net the vector of the switching frequencies of every transition is one starting point for the analysis. Based on this *net comitant*, a pathway analysis can be derived. Figure 5 displays the results of this analysis. The most frequent stepping stone islands can be identified (Santa Fe, Pinzon). However, direct migration pathways are also used, e.g. San Cristobal to Santa Cruz.

Using the partial differential equation model, these results are derived by a „grasshopper"–tracking analysis, a function most FEM-solver programs are capable of, usually known as „particle tracking". Figure 7 shows such a „grasshopper"-tracking analysis for a time step t=62.5 a. Each line displays the migration pathway for an interval of 25 years. A general statement like the one we get from Fig. 6 cannot be derived from the pde–model. In the simulation the most frequent (San Cristobal, Santa Fe, Santa Cruz, Isabela) paths are displayed, which is in accordance to the pn-Model.

Both modeling approaches may be applied to the problem in hand. Both methodologies show the advantages and their disadvantages. For detailed comparison of both modeling approaches Table 1 gives a summary of different aspects. In terms of science theory, the partial differential equation system is the more concise one. It produces a more aggregate model with a broad range of resulting explanations (compared to the parameters fed into the model). This equation Eqn. (3) collects the processes into one core equation. On the other hand, with this model we can run into more problems concerning numeric methods and interpretation. For instance, how shall we interpret positive population values (below unity) for open water regions? Shall we suggest the more phenomenological Petri net model, which has no physical explanation of Eqn. (1)? Or, is Eqn. (1) the „building block" for the migration process in patchy habitats?

4. DISCUSSION

Modeling biological systems requires the development of mathematically heterogeneous or so-called hybrid systems. This is either because of temporal or spatial processes show both, a discrete and a continuous behavior. Note that our perception of a process recognized as discrete or continuous depends also on the considered (spatial or temporal) scale. Hybrid models based on different mathematical modeling languages are the common result in ecological modeling.

Many authors suggest that integration of different existing models is a way to build complex models for a process of interest. An integration requires at least a flexible (possible object-oriented, as suggested by Villa [2001]) documentation together with a framework of data exchange to assist model coupling, c.f. [Maxwell, 1997]. Besides these more technical aspects knowledge on the suitability of model integration is required. The presented case study gives some hints on the spectrum of problems one is faced with when aiming at integration or coupling of different models.

Consider, for example, an integration of the pde-model — simulating population dynamics and migration on the islands — with the pn-model — simulating the migration across the ocean.

	Petri-Net	Partial Differential Equation
Processes		
- Dynamics	Continuous (growth)	Continuous
- Spatial	Stochastic, discrete, event based (migration)	Continuous
Data		
- Topology of habitats	Topological relation between the habitats/islands is the only information implemented into the Petri net	No information on topology of habitat patches deducible from FEM–mesh
- Geometry of habitats	Only aggregated indication on the geometry of the archipelago are fed into the PN-model: distance, diameter of a habitat.	FEM–mesh directly derived from habitat borders, imported from GIS.
Analysis Results	- Stochastic Analysis, Monte-Carlo Simulation - Event based model - Stepping Stones - Migration distance	- Numerical Solution by FEM using adaptive mesh generation - Experimental migration pathways - Migration distance - Non-zero abundances for open water regions
Classification	Empirical approach	Foundation on migration- and growth-models.

Table 1: Comparison of both modeling methodologies.

This avoids non-negative abundances of dragonflies for the open water areas, offers an event-based simulation of overseas migration and a continuous migration on the islands. For this integration at least two major problems have to be solved: First, boundary conditions of pde-model are time and event depending! Second, which region of an island is identified as a starting point for overseas migration? What is the input for the place in the pn-model?

The hypothesis is that it might be impossible to couple certain models, if these differ too much in structure. If this is the case, the general question is, which is the appropriate model to chose and how can we compare these different approaches?

For this case study it is an interesting starting point for research to investigate if for instance (properties of) Eqn. (1) might be derived from an analytical (stability) analysis of the partial differential equation system Eqn. (3). This analysis might clarify the questions when to use which model, and which parts of the model can be coupled or integrated. An analysis of the dynamic behavior of systems is indispensable to compare and assess different modeling approaches. The examples in this contribution showed that entirely different modeling approaches produced qualitatively and to a certain degree quantitatively similar dynamic behavior.

However, this can only be a starting point. Analysis of dynamic behavior includes concepts of stability analysis and dynamic and spatial invariant properties. This may be achieved by comparing the topologies derived from different dynamic simulation models. This might be a fruitful research topic, as it offers a deep insight into the relationship between different approaches in ecological modeling and might help to identify building blocks of ecological models.

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