SPATIALLY EXPLICIT POPULATION MODELS

During the last decade, ecologists and particularly mathematical ecologists have focused on different approaches to the problem of spatial distribution of species. When the spatial distribution is not considered explicitly, the mathematical models are called spatially implicit. They consider the proportion of territory occupied by given species, but there is no information on which particular sites this occupation takes place (*Caswell & Cohen, 1991; Barradas & Cohen, 1994; Barradas et al., 1996; Barradas & Cohen, 1997; Hanski, 1999; Federico & Canziani, 2000*). When the spatial distribution of the species is specified, the models are called spatially explicit (*Turner et all., 1995; Marquet & Velasco-Hernández, 1997; Hanski, 1999; Neubert & Caswell, 2000; Ruiz-Moreno et al., 2001*).

Here we have developed a methodology that allows us to link the information available through vegetation maps, soil maps, and distributed hydrological models to the definition of Habitat Quality Indices for each species of interest. In this way, the population models are not general, but the dynamics of the species is related to each particular environment at a very local scale.

One way to link habitat information (present in the classified synthetic maps or 10-Classes images) with mathematical ecology models is through Spatially Explicit Models. Hence, we developed Spatially Explicit Models based on a Metapopulation approach and from a Cellular Automata perspective. This type of model can describe the spatial distribution of a species in a landscape. The landscape is divided into cells that can be occupied (by a given species) or void. The dynamics of the model results from processes such as Colonization, Persistence, and Dispersion. Both Colonization and Persistence processes are subject to disturbances that can occur with either constant or density dependent probabilities. Several different functional forms that are ecologically meaningful can be considered. Dispersion processes can have global or local range.

Development of the Model

The Model was developed in four progressive stages.

In a first stage, the model was developed taking into account colonization and persistence processes, both affected by disturbance processes, and considering a **global dispersion** process *(Figure 61).* This *configuration* makes this model comparable with that developed by Federico (1997). This was done in order to verify the performance of the cellular automata. The results of simulations of the cellular automata model for different cases and functional forms show a behavior that coincides to that of the analytical model.



Figure 61. First Stage Cellular Automata Model : Global Rules for Colonization, Persistence and Disturbances

In a second stage, the model was enhanced with **local dispersion** processes. This restricted range on the dispersion process was necessary because the species can not always spread from one extreme to the other end of the landscape. Clearly, the range allowed for the dispersion depends on the capacity of movement of the species and the time step considered. Under this restriction, all three processes, Colonization, Persistence and Disturbance, in a given cell depend on the state of its neighbors *(Figure 62).*



Figure 62. Second Stage Cellular Automata Model: Restricted Neighborhood

Habitat quality affects all the processes (Colonization, Persistence and Disturbance). Hence, the third stage was the incorporation of theoretical habitat qualities, as a first step to the definition of heterogeneity in the landscape. At first, it was necessary to work with a theoretical spatial distribution of habitat quality in order to evaluate the behavior of the model. In Figure 63 a landscape divided into two types of habitat is shown: the red portion has a higher habitat quality than the blue portion. At this point, it is not always possible to use analytical results for a comparative analysis.



Figure 63. Third Stage Cellular Automata Model: Different Theoretical Habitat Quality in the same Landscape (black points represent species presence)

The fourth stage includes the possibility of running the model on a real landscape. This is done by using a fragment of a 10-Classes image in order to establish the spatial distribution of habitat quality for a given species *(Figure 64).* This fragment of image is accompanied by a text file were the different habitat quality values are specified. It is appropriate to note that the values of habitat quality should be specified for each species to be modeled. In the case of the species modeled for this project, the capybara and the caiman, it was not possible to establish true habitat quality indices, due to the lack of specific biological and/or ecological information.



Figure 64. Fourth Stage Cellular Automata Model: Landscape with Habitat Quality from a Synthetic map (black points represent species presence, i.e. here artificial reintroduction)

First Stage Cellular Automata Model

As mentioned earlier, the Analytical Model *(Federico, 1997, Federico & Canziani, 2000)* and the First Stage Cellular Automata Model have very similar behaviors, since from a numerical viewpoint the steady states are almost identical. In fact, the slight differences are due to the introduction of a discretization of the space in the latter relative to the continuous approach in the former model. The most interesting Main result is the possibility of following visually the dynamics of spatial occupation of the landscape.

As an example, consider the following simulation, where the colonization occurs with probability $C(y) = 1 - e^{(-d \cdot y)}$ and where the dispersion coefficient of the Poisson distribution is d=5. Disturbances in the colonization process occur with a probability f(y) representing a Type III functional response. Disturbances in the persistence of the species in a patch occur with constant probability. The metapopulation model reaches a stable equilibrium when approximately 51% of the patches are occupied.

First Stage Cellular Automata Simulation
Colonization Process $C(y) = 1 - e^{(-d \cdot y)}$ with $d = 5$
Disturbances in Colonization $f(y) = 1 - \frac{y^2}{k + y^2}$ with $k = 0.2$
Disturbances in Persistence $g(y) = 0.5$
Analytical Steady State = 0.5107807 Steady State from Simulation = 0.51651712

In the following graphics, it is possible to see how the distribution in space evolves before an equilibrium is reached.





Second Stage Cellular Automata Model

Second Stage Cellular Automata Model have similar behavior to the previous model and the type and value of the steady states are similar to those of the previous one. The main result is that now we have the possibility of evaluating how the initial spatial distribution of the species in the landscape affects the time to reach steady states.

Consider the following second stage cellular automata simulation, where the probability of colonization is no longer Poisson, but constant, all the other functions remaining as in the previous example. We can observe in the figures that it takes a much longer time to occupy the landscape.













This model is a good approximation to many real life situations, where the processes are local but their consequences are observed at the global scale. At this stage, the model has some significant theoretical applications, because it allows to observe some interesting effects, such as the formation of some areas of higher density, where the species can consolidate its presence and from which it becomes easier, either to colonize or to resist extinction.

As mentioned earlier, the model can be used as a tool to select the location or locations of a re-introduction of a species in a given homogeneous area, in order to insure a better probability of success, as can be observed in *Figure* 65.

Dynamics of Occupational Proportion



Figure 65. Notable Differences in the time needed to reach a steady state depending on the initial location (random in blue, from a corner in rose, from the center in green)

Cellular Automata with Heterogeneous Habitats

Although the construction of spatially explicit population models is flourishing, very little has been done regarding the inclusion of habitat heterogeneity. We believe that the cellular automata approach is very appropriate for the study of this type of problems because it simplifies the formulation of the interactions between cells *(Wolfram, 1986).* The recent literature shows some intents of formulating models that are continuous in time and discrete in space, as well as others that are discrete in time and continuous in space, but the mathematical treatment becomes cumbersome very rapidly, and can not be applied to real-life situations.

The behavior of the **Third and Fourth Stage** Cellular Automata Models here developed strongly depends on habitat quality indices, distribution, and relative abundance of the species. Using third stage models we can develop theoretical computational experiments that help understand at a smaller scale the processes involved. These are useful to study afterwards the behavior of the fourth stage models that involve several different habitat qualities from satelital images. Otherwise, the complexity of the interactions occurring at that stage could hinder the interpretation. Consider now a simulation example for the third stage model. As previously, all the functions remain the same, but the landscape is now defined into two different regions with a higher quality for the red one and a lower quality for the blue one. Now it is possible to observe the differences in movements of the species and the time needed to expand, based not on the species ability but only on habitat factors.











Step Time = 188



A similar experiment can be carried on now for the fourth stage model, taking as landscape a sector of the classified synthetic map of the Esteros del Ibera, near the Parana Lagoon, on the western region of the system. The habitat classification corresponds tentatively to capybara populations.

Fourth Stage Cellular Automata Simulation

Colonization Process $C(y) = \mu = 0.92$ Disturbances in Colonization $f(y) = 1 - \frac{y^2}{k + y^2}$ with k = 0.2Disturbances in Persistence g(y) = 0.5Neighborhood Definition : Moore Region Habitat Quality from Synthetic Maps



Step Time =10





Both types of model allow to analyze the time required to reach steady states and how the initial spatial distribution can have an influence on it. It is also possible to perform experiments regarding the implementation of controls over any given area within the landscape considered.

Any of these Cellular Automata Models can be a decisive tool in situations such as the re-introduction of species. The models we developed are the first link between ecological data and an integrated management tool that provides analysis of spatial distribution, efficiency and efficacy of reintroduction, economic issues, and control of the presence of a species in specific places.

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