

Size Distribution and Dynamics of Patches in Fragmented Landscapes

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Goal

To understand the dynamics of spatially structured ecological populations in variable habitats by applying and extending results of percolation theory.

Introduction

Spatial and temporal heterogeneity applies to all aspect of life. From the major climatic changes, through the turning of seasons, to the fine-grained distribution of mineral nutrients in the soil organisms have to cope with heterogeneity. Bacteria changes huge part of their genome because of changes in the local availability of some resources. Some plant exhibit morphological changes in response to spatial heterogeneity. Most animals have to forage for food, which is heterogeneously dispersed in space. And sadly many organisms have to cope with the challenge of ever shrinking and fragmenting habitats.

Heterogeneity helps and forces organisms to evolve, to adapt. Major changes in composition and availability of resources; changes in the frequency, composition and abilities of other species forces organism to evolve. The challenge of the ever-present fluctuations and the inhomogeneity in resource distribution has to be dealt with by the organism every day of its life. It seems likely that spatial and temporal heterogeneity is a prerequisite for the complexity and diversity of life.

The myriad solutions to the challenge of life led to the staggering diversity of species we encounter. Careless human management - or lack of management - of resources threatens this diversity. Forest cuts, pollution, rubbish heaps and degradation of soils leads to fragmentation of natural habitats (Primack 1998). More and more natural habitats are destroyed in order to be developed as agricultural fields. The shrinking habitats could not sustain their former species pool. Available food, shelter and territory dwindles and so do population sizes of species. The population size of species that are rare even in pristine habitats could shrink to the level where the population go extinct. Habitat destruction is the major cause of species extinction (Lawton and May 1995).

Generally an ecological landscape is a mosaic of different kind of A given habitat can be most accurately characterized by its flora. Plants - as they are sessile - are effected by spatial heterogeneity the most. In his pioneering paper in 1947, Watt named the study of spatio-temporal dynamics of populations as the main aim of ecology. Yet, the study of spatial processes only became the focus of researches in the past ten or fifteen years. The change of methodology in theoretical studies is even slower: most classical ecological model does not consider the importance of spatial heterogeneity. With the development of novel modeling techniques and with the increasing computational power of computers the construction and analysis of spatio-temporal models have become feasible. Theoretical ecology advanced considerably with the introduction of such techniques as these allow scientists to construct models that are increasingly realistic and informative (Czárán 1998).

Research questions

The proposed research project for the IIASA summer program will address two spatio-temporal problem of great ecological significance.

First, we are planning to complete an investigation on the role of percolation barrier (Stauffer and Aharony 1992) on plant populations, and the effect of temporal fluctuation on the percolation barrier, and thus on the spread and size of plant populations. This collaborative research is already under way, and it seems that the existence of percolation barrier and the alleviating of it by small fluctuation could be one of the explanations of why intermediate disturbance helps maintain diversity and large populations. A second investigation will commence during the summer period as is meant to focus on the dynamics of occupied and empty favorable patches on a fragmented and changing landscape. 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 Beáta Oborny.

Method

We plan to use the basic model of percolation theory to study important ecological questions.

Percolation theory was developed to describe physical properties of gels, polymers, and glassy materials and forms the basis for studies of flow of liquids through material aggregates. Percolation theory deals with movement on a two dimensional lattice consisting of enabled and restricted sites. Let p denote the proportion of enabled sites on the lattice. On a $m \times n$ lattice pm^2 sites are chosen randomly to be enabled, the rest $[(1-p)m^2]$ are restricted. A set of enabled sites, where a given site could be reached from every other element of the set by only moving through neighboring elements (the definition of neighbor is strongly dependent on the geometry of the lattice), is called a cluster. The number, size and shape of enabled clusters changes as a function of p . There is a critical value of p (referred as critical probability, p_c , or percolation barrier) above which the largest cluster theoretically span the infinite plane. In a finite lattice the largest cluster will cross the grid continuously from one side to the other.

In ecology percolation theory could be applied as follows: in a heterogeneous or fragmented habitat an organism with dispersal rate not greater than the grain of the habitat could only conquer every large resource cluster if percentage of resource patches are greater than a critical value. In other way, below a certain percentage of resource or natural patches some clusters could not be reached and exploited. This would result in a lower population size than the carrying capacity would indicate; or in fragmented landscape parts of a population could not mix with other parts.

There are numerous types of models for describing the spatial dynamics of populations (Dieckman et. al. 1997, Oborny and Cain 1997). Models can be based on either discrete or continuous space or states, and they can operate deterministically or stochastically. One of the most widely used spatially explicit modeling techniques is cellular automaton (Neumann 1951, Hogeweg 1988, Czárán 1998). Percolation has been studied many times by cellular automata (Neuhauser 1998, Tao 1999, Hiebeler 2000), and we plan to employ this modeling technique in our investigations.

A cellular automaton is a grid, where every cell is in one of the few predefined states, and the next state of a cell is dependent on the state of itself and its neighbors. Neighbors could be defined in many way: in the basic percolation theory models authors use the so called Moore neighborhood (the closest four cell in a square grid); in plant population models hexagonal lattice could be used so every neighbor is in the same distance from a given cell. Number of states of a cell is usually kept low. Populations spreading on a fragmented landscape could be described by 4 states: unoccupied restricted site (UR), occupied restricted site (OR), unoccupied enabled site (UE) and occupied enabled site (OE). The next state function could be generally described as follows:

An unoccupied enabled site could be colonized from neighboring occupied sites (UE → OE if there is OE in the neighborhood).

- In percolation theory restricted site could not be colonized, so the UR → OR transition could not occur. With the implementation of this rule the OR state become non-existent.
- Change of site quality from restricted to enabled (UR → UE)
- Change of site quality from enabled to restricted, could result in loss of occupancy (UE → UR or OE → UR).

For completing the definition of a cellular automaton one need to state the initial state of every cell in the grid. All important characteristics of the system are dependent on the ratio of enabled to restricted site. At a given enabled to restricted site ratio we assign the states randomly to the field. One enabled site will be occupied.

This general method is the main link between the two proposed researches. While the two field of study might be well apart, the studied phenomena are only differing in their scale. Plant species could sense environmental heterogeneity on the scale of centimeters, and local dispersal means a few meters maximum. On the other hand landscapes are on the magnitudes of hectares, and sites are patches clear cuts or natural forests.

Research plan

The Percolation Barrier as a Challenge for Locally Dispersing Organisms

Motivation and background

Plants are essentially modular organism this trait is very pronounced in clonal species where the unit of iteration is the ramet. A ramet is a potentially physiologically independent unit. Spreading and growing in clonal species are horizontal, and local (Oborny and Bartha, 1995). Local spreading is not only the characteristic of clonal species, but many sexually propagating species disperse only locally (O'Connor, 1991). An environment that is heterogeneous on the scale comparable to the propagating distance of the species poses a particular challenge, which have to be addressed by the organism. Oborny (1994a,b) have compared a wide range of clonal morphological strategies in regard to their ability to selectively place their offspring to favourable patches.

For example in heterogeneous environments that are poor in resources wide unfavorable regions might prevent locally dispersing organisms to reach and conquer favorable sites (Oborny et. al. 2000). In my MSc thesis, I have studied the spatial behavior of a locally dispersing clonal plant population in a heterogeneous environment. I have shown that in relatively poor habitats, with only 10-40% of favorable sites, population size was equilibrating much below the actual carrying capacity of the environment: the population could not colonize all favorable patches since it was unable to cross unfavorable regions.

In general, the dynamics of population spread on a lattice that consists of favorable and unfavorable sites can be studied by percolation theory. The theory suggests that there is a certain ratio of favorable to unfavorable sites below which the population cannot spread indefinitely far from its point of origin. While this is a well-known phenomenon among physicist, ecologists have yet to realize the full importance of percolation.

Method

Cellular automata are not only fit to study percolation systems but also are geared to study next-neighbor interactions, which is the most prevalent type of interaction within plant communities.

The method employed in this investigation is basically the same as in the method section, but the implementation is a bit different: the cellular automata in our model had two layers: a population layer and a resource layer. Both layers consist of a 100×100 cell lattice. We used the von Neumann (4-neighbour) neighborhood. The topology of the automata was toroidal.

Resource layer

Each cell's state - the local environment - could be either favorable or unfavorable. The represented habitats were spatially and temporally heterogeneous. For modeling environmental heterogeneity, we used the following two parameters:

- (1) the average resource richness of the habitat (p),
- (2) the frequency of change in the local resource level (C_g).

The average resource richness of the habitat (p) determined how many percent of the habitat patches were favorable (and $1-p$ portion of the patches was unfavorable).

We introduced temporal heterogeneity by changing a portion of the favorable sites to unfavorable and a portion of the unfavorable sites to favorable. The parameter C_g gave the probability of resource level change from favorable to unfavorable. So in every step C_g percent of the favorable sites became unfavorable (we chose randomly from the available sites). C_b , the probability of an unfavorable site becoming favorable computed as follows to maintain that p percent of the sites are favorable:

$$C_g \times p = (1-p) \times C_b.$$

Population layer

In the population layer each cell represented enough space for one ramet, so a cell was either empty or occupied by a ramet. A ramet in a given cell encountered a microhabitat characterized by the quality of the resource layer in the same place (same co-ordinates).

In the beginning of each simulation we randomly placed 50 ramets to the population layer. All the other cells were unoccupied.

Favorable sites were colonized if there were neighboring favorable sites occupied by a ramet. Unfavorable sites could not be colonized.

If a favorable site become unfavorable, then the ramet occupying the site dies.

The parameters of the simulation

We followed the competition of the strategies for 500 time step. After the 500th time step we recorded the number of ramets in the field. The parameter values used in the simulations we the following:

- the range of average resource availability (p) was from 10% to 65% by steps of 5%;
- and the frequency of resource change (C_g) was 0%, 1%, 1.5%, 2%, 3%, 4%, 5%, 7%, 10%, 15% and 25%.

For each parameter combination we've made 10 replications and averaged the results.

Intermediate result

From my results I could establish that with a modest amount of temporal fluctuations in the environmental pattern the populations could spread over the entire habitat, thus partly alleviating the percolation barrier. The resulting effective rate of spread was maximal at an intermediate level of fluctuation. The exact magnitude of fluctuation where the population size was maximal was dependent on the average resource richness of habitats. With increasing resource richness the needed fluctuation decreased.

Research questions and work plan

During the summer project, we plan to investigate the implication of my findings on community level processes and its possible connections with the intermediate disturbance hypothesis. The required data are available we only have to re-examine them for our new questions. The intended work is in most part an analysis of literature on intermediate disturbance hypothesis and the writing of the proposed paper on the subject (see the *Envisaged publications* section)

Percolation in a fragmented habitat: a new tool for conservation biology?

Motivation and background

Vegetation patterns are the result of complex interaction between climate, terrain, soil, water availability and biota and alterations resulting from natural disturbances (like wind and fire). Alteration in landscapes as a result of urbanization, agriculture, and forestry management have significant effect on the pattern of vegetation as established systems are removed and replaced with managed ones. The surrounding matrix has a negative influence on natural habitats, and these effects are most severe at the edges of habitat fragments, and small fragments are comprised of nothing but edges. In this way reserves are nothing more that patches linked to a surrounding matrix (Hansson and Angelstam 1991). The number and size of natural patches required for the prevention of further loss of species is still hotly debated (see discussion of the 'One Large Or Several Small reserves - the 'SLOSS' - question by, *e.g.*, Soulé and Simberloff 1986).

Some of the inherent problems associated with fragmentation of natural habitats are the followings (for further information on habitat fragmentation and degradation see Primack 1998):

- Fragments have a greater amount of edge for the area of the habitat, and the center of each habitat fragment is closer to an edge. Interior areas - those that have a certain distance from the perimeter - are valuable, and many species could only live in the interior. So the effective amount of lost natural habitat is greater than indicated only by measuring the managed/destroyed areas.
- Dispersal of indigenous species (especially the specialized ones) through the matrix to distant biotopes of similar kind is very slow. So individuals are restricted to a few patches that are close enough. Genetic diversity could dwindle as effective population size decreases.
- Available territories decreases and this most of the manifest itself in less available food. Large mammals are especially threatened by loss of natural habitats (like Grizzly bears in North America), as they need quite large areas for foraging for food.

The effect of habitat fragmentation could be lessened by the implementation of ecological corridors. Ideal size and distribution of ecological corridors are still an open question and depends strongly on the size of the gap to be bridged, the species to be preserved, etc.

In a static landscape the distribution of patch sizes is known from established theory. Moreover percolation systems have been proposed as neutral models for the analysis of broad-scale landscape patterns (Gardner *et. al.* 1987).

On the other hand the distribution of patch sizes in a fluctuating environment is not known. Our aim for the proposed project is to study the spread of a locally dispersing model population on spatially and temporally heterogeneous (fragmented) landscapes. We plan to assess the proportion, size distribution, and temporal dynamics of favorable sites and compare it to the analogous quantities for occupied sites.

A related problem is concerned with the prevention of the invasion of alien species. Hopefully the results will allow us to better understand the type and magnitude of environmental change that foster or prevent invasion in a fragmented landscape.

Method

We will use the cellular automata described in the Method section with hexagonal lattice geometry. At the start of the simulation only one patch is occupied. Some of the favorable sites will be reached and occupied by locally dispersing individuals. By introducing fluctuation to the habitat pattern (by turning favorable sites into unfavorable ones and vice versa) some clusters of favorable sites will break up while others will coalesce. In our first model when an empty cluster of favorable sites coalesces with an occupied site, the population will colonize the formerly empty cluster. By implementing this rule we describe a system where the population propagates more frequently than the environment changes.

In a follow up investigation we can study population with comparable dispersal rate to environmental change. Also the initial pattern of enabled/restricted could be generated in many different ways. We could employ methods that generate more aggregated patches, and analyze their behavior.

It is desirable to record the generated landscape pattern in every time step so in future studies we could measure characteristics like edge/area ratios or fractal dimension of enabled clusters. These and other characteristics are frequently employed in describing real landscapes (Gustafson and Parker 1992).

Dynamics in individual based, stochastic models tend to fluctuate and only behave in a reproducible manner if the number of individuals is sufficiently large. Thus the numerical investigation of such systems could be 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. A system with infinitely fast spreading hypothetical species is probably easier to approximate. Individual-based simulations will allow us to determine the size distribution of clusters of favorable/unfavorable and of occupied/empty sites, as well as the temporal changes occurring in such a system.

Research questions and work plan

With this model, we plan to assess the spatio-temporal characteristics of ideal ecological corridors and the intensity of random environmental change that is necessary to ensure persistence of an endangered species or containment of an alien species. In general, we expect to gain insight into invasion processes in heterogeneous habitats, a topic of direct relevance for understanding the adaptation of spatially structured populations.

During the envisaged stay at IIASA, I plan to develop and refine the necessary simulation program, process the obtained data, and get acquainted with the relevant literature with the aim of preparing a publication for an international scientific journal.

Relevance and link to ADN's research

Devising innovative tools for modeling population dynamics in spatially heterogeneous habitats is of critical importance in modern applied and theoretical ecology. We expect the project proposed here to successfully contribute to ADN's research foci on simplifying spatial complexity. The established research priorities of ADN call for intensifying the research on the dynamics of spatially heterogeneous ecosystem, and the proposed project is definitely within this scope.

There exists a contact and collaboration between Dr Beáta Oborny, my supervisor at the Department of Plant Taxonomy and Ecology at Lóránd Eötvös University, and Dr Ulf Dieckmann, Project Coordinator of the Adaptive Dynamics Network Project of IIASA.

Envisaged publications

The proposed research is planned to result in at least two publications. The investigation on connecting percolation on a fragmented and temporarily heterogeneous landscape with the intermediate disturbance hypothesis will result in one paper. We also plan to write an additional paper on the dynamics of locally dispersing populations and of favorable patches in a fragmented landscape. We plant to apply our findings to conservation biology, and this is also expected to result in a publication that reports the spatio-temporal characteristics of ideal ecological corridors and the required intensity of random environmental change which ensure persistence of an endangered species or containment of an alien species.

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