Ecology and evolution of clonal integration in heterogeneous environment

Ph.D. THESIS

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Introduction

Terrestrial plants are sessile, so individual plants have to cope with the conditions of the microhabitat where they are rooted. Besides seed dispersal, clonal growth offers a way to escape from locally bad conditions. Clonal plants produce genetically identical, vegetative offspring (ramets), each at a distance from the mother. Thus, the genetic individual (genet) can spread laterally, meeting a variety of microhabitat conditions.

In some of the clonal species, established ramets remain connected and share resources (e.g. water, mineral nutrients and photoassimilates), these species are called integrators. In other species, established ramets become physiologically independent (splitters).

The question has arisen already at the early clonal plant research: in what kind of habitats is clonal integration or splitting adaptive? Most hypotheses concerning the advantage or disadvantage of integration assume some kind of environmental heterogeneity. According to experiments there is no benefit of resource sharing (apart from the possible advantage of resource storage) in homogeneous environment. In the last two decades the adaptive advantage of integration or splitting in heterogeneous environments was the focus of many researches.

My aim is to study the effect of the presence or absence of resource sharing in spatially and temporally heterogeneous habitats on population dynamics in the framework of a spatially explicit model. I investigate the habitat criteria which select for integration in a more complex patch pattern than which can be realized in experiments. In the model I consider as much heterogeneity component as possible. To my knowledge the presented studies are the first to model physiological integration in a spatially explicit framework.

This thesis consists of six studies focused on answering the question posed above.

In the first study I investigate the behaviour of the strategies in an environment where it is assumed that good sites contain excess resource which can be used to further improve a ramet competitive ability or survival, but can be exported to ramets in unfavourable conditions.

The second study investigates the effect of percent cover of good sites on the spatial spread of a splitter and two integrator (Transient Integrator consisting of small clonal fragments and Permanent Integrator where all ramets of a genet remain connected) strategies in a fine-grained, non-changing environment.

The third study expands the investigations of the second study to other types of habitats. Beside resource availability, the effects of patch size, contrast and frequency of environmental change are studied.

The fourth study aims to answer whether the quality of good sites or the quality of bad sites has a greater effect on the outcome of competition.

In the fifth study I have used a chessboard-like landscape in order to directly compare my results with results obtained in experiment.

The sixth study is and evolutionary study of clonal integration. The evolvable trait is the amount (percentage) of resource pooled to be evenly distributed within the genet. I followed the evolution of this trait in spatially and temporally heterogeneous environments.

Methods

All members of the INTEGRID model family are stochastic cellular automata, thus they are discrete in time and space. The model is scaled to the plant: the ramet to ramet distance defines the size of the cells, and the time step corresponds to the establishment time of a new ramet generation. The automaton has two layers: the resource layers stores the state of the spatially and temporally heterogeneous environment, and the population layer stores the states of the clones.

Resource layer

There are two kinds of microsites: good (resource-rich, favourable) and bad (resource-poor, unfavourable). I used two landscapes (resource pattern): chessboard-like and percolation map. Each landscape can be defined by size of patches (s), average resource richness of the habitat (p), patch turnover rate (C), quality of the good sites (e_g) and quality of the bad sites (e_b). The difference of the two later parameters gives the contrast (m). In a *chessboard-like* landscape $s \times s$ sized good and bad patches alternate, so every good patch is neighboured by bad patches and *vice versa*. In changing environment the resource pattern turn into its opposite with probability C. In a *percolation map* a $s \times s$ sized patch is good with probability p, and bad with probability $1-p$. In changing environment a $s \times s$ sized good patch become a bad patch with C_g probability and a bad patch become a good patch with C_b probability (the two probabilities are chosen so that the average resource availability will not change). In the first study excess resource in the good patch is assumed. No such assumption is made in the other studies; a good patch holds at most enough resource for one ramet.

Population layer

I have used three strategies in the studies. The Splitter ramets become physiologically independent after their establishment. In the Permanent Integrator ramets belonging to the same genet share the available resource evenly. With regard to the Transient Integrator connections between ramets are recorded, and only connected ramets share their resources. A connection die with the death of a ramet, thus ramet death may result in the fragmentation of the Clonal fragment (set of physiologically connected ramets).

A site represents enough space for one ramet. A site can be occupied or empty. In every time step ramets can colonize neighbouring empty sites. If more than one ramet can colonize the same empty site, then the one with higher amount of resource available to it has a higher chance of colonizing the site. Ramets survive with probability related to their resource status.

I study the difference between the strategies in two ways. [a] First, I investigate the population sizes in various environments. I compare the case when the Splitter and Integrator are growing separately to the case of growing together, in competition. [b] Secondly, I consider only competition, but map the parameter space in more details.

There are four possible outcomes of competiton: (1) both strategies become extinct; (2) Integrator wins; (3) Splitter wins; (4) long-term coexistence.

Theses

Landscape Generating Algorithms

1. I provide a definition of environmental heterogeneity which can be used to generate heterogeneous landscape for models of spatially explicit population dynamics with as much heterogeneity components considered as possible. I show that the Ising model known from statistical mechanics can be used to generate heterogeneous landscapes.
2. I give a method to introduce temporal heterogeneity into landscape generating methods which have been only used so far to model spatial heterogeneity.

The Ecology of Clonal Integration

3. None of the considered heterogeneity parameters alone can explain the outcome of competition. Either of the strategies can win at low or high contrast, in fine or coarse-grained habitats, with or without temporal fluctuation, or at different resource availabilities. This result clearly shows the importance of identifying all the components of heterogeneity when predicting the effect of integration. [first, third, fourth and fifth study]

4. Integrators can successfully even out environmental heterogeneity. The strategy with larger clonal fragment is more efficient in evening out environmental heterogeneity. [from second to fifth studies]
5. Clonal integration, i.e. resource sharing, is advantageous in constant habitats if the resource is concentrated into few, small patches. In changing environment integration is generally advantageous but, but more advantageous if resource is concentrated into few, large patches. If the same amount of resource is spread more evenly among the sites or with the decrease of excess resource in one good site splitting become advantageous. [first study]
6. In constant, fine-grained habitats with high contrast the spread of the strategies is limited at low resource availability. Population sizes show a sudden increase at a given value of resource availability. This value is lower for the Integrators, thus the spread of Integrators are less limited. [second study]
7. Locally Splitters are at least as good competitors as Integrators in good sites. Splitters can exclude Integrators from good patches. [first and second studies]
8. Small environmental fluctuation helps the spread of populations, because by the change in the resource pattern "bridges" can form between clusters of good sites. The spread of Splitters are more limited, thus small fluctuation helps the Splitter to dominate. [third study]
9. The negative effect of environmental change is the disruption of established ramet is good sites. While Splitter ramets tend to be exclusively in good sites, thus it affects Splitter more. Integrators successfully even out the heterogeneity of the environment. [first and third sudies]
10. At high resource availability the small number of subsidized ramets in bad sites add to the success of Integrators, because with the change of the environment these ramet can change from resource importers to resource exporters. In such habitats then Integrator exclude the Splitter. [third study]
11. Increasing patch size results in the dominance of the Splitter in constant and in the dominance of the Integrator in fluctuating environments. [first and third studies]
12. The quality of the bad sites affect the outcome of competition more than the quality of the bad sites. Varying the contrast between good and bad sites has little effect. [third and fourth studies]

The Evolution of Integration

13. The ecological model predicts the optimal strategy well. Where the Splitter wins, there the little or no sharing evolved. Where the Integrator dominate, there the evolutionary optimum is considerable resource sharing. If the quality of the sites is negatively correlated in time, then full integration is the adaptive strategy.

Publications

1. Oborny B., **Kun Á.**, Czárán T. and Bokros Sz. (2000) The effect of clonal integration on plant competition for mosaic habitat space. *Ecology*, **81**(12), 3291-3304.
2. Oborny B., Czárán T. and **Kun Á.** (2001) Exploration of resource patches by clonal growth: a spatial model on the effect of transport between modules. *Ecological Modelling*, **141**:151-169.
3. Oborny B. and **Kun Á.** (2002) Fragmentation of clones: How does it influence dispersal and competitive ability? *Evolutionary Ecology*, **15**:319-346.
4. **Kun Á.** and Oborny B. (2003) Survival and competition of clonal plant populations in spatially and temporally heterogeneous habitats. *Community Ecology* **4**(1): 1-20 (accepted)

Conferences

1. Oborny B., **Kun Á.**, Bokros Sz. and Czárán T.: Spatial pattern formation in a community of clonal species. "Strategies in spatial ecological modelling" Workshop, Berlin. Organized by the Wissenschaftcolleg zu Berlin in June 1996
2. Oborny B., Bokros Sz., and **Kun Á.**: Dispersal strategies of plants (in Hungarian). 4th Hungarian Ecological Congress, Pécs. June 1997
3. Oborny B., Bokros Sz., **Kun Á.** and Czárán T.: Consequences of physiological integration on the spatial organization of clonal populations in heterogeneous habitats. "Clonal plants and environmental heterogeneity: Space, time and scale" – 5th International Clonal Plant Workshop, Bangor, UK. September 1997
4. **Kun Á.** and Oborny B.: The advantage of resource sharing in clonal plants - a Cellular Automata Model (in Hungarian). "Pattern and process in ecology" – Szegedian Ecological Days, Hungarian Academy of Science, November 1998
5. Oborny B., **Kun Á.** and Czárán T.: Competition of clonal plants for mosaic habitat space. "Ecological consequences of environmental heterogeneity", Annual Symposium of the British Ecological Society. Marc 1999.
6. **Kun Á.** and Oborny B.: Environmental heterogeneity and spatial competition in clonal populations - a cellular automata model. "Theory and mathematics in biology and medicine" conference. Amsterdam, the Netherlands. June 1999

7. Oborny B., **Kun Á.** and Czárán T.: Competition of clonal plants for mosaic habitat space - cellular automata simulations. “Theory and mathematics in biology and medicine” conference Amsterdam, the Netherlands. June 1999
8. Oborny B., **Kun Á.**, Czárán T., Meszéna G. and Mágori K.: Competition of clonal species for mosaic habitat space. “Theoretical Biology in Central Europe”, Collegium Budapest, Institute for Advanced Study. November 1999
9. Oborny B., Mágori K., Meszéna G. and **Kun Á.**: A step from modularity to clonality - Evolutionary dynamics of module autonomy. Clone 2000 - 6th International Workshop on Clonal Plants, Obergurgl, Austria. August 2000.
10. **Kun Á.** and Oborny B.: Competition between integrators and splitters in spatially and temporally heterogeneous habitats. Clone 2000 - 6th International Workshop on Clonal Plants, Obergurgl, Austria. August 2000.
11. Oborny B., Mágori K., Meszéna G., Dieckmann, U., **Kun Á.**: Competition and cooperation between parts of the same organism - An adaptive dynamic model on the evolution of modular growth in plants. Santa Fe Institute, USA. Marc 2001.
12. Oborny B., **Kun Á.**, Meszéna G.: Fine versus coarse-grained perception of habitat heterogeneity. - How does it influence species coexistence? ABUDIV Conference, Tihany, Augustus 2001.
13. Oborny B., Meszéna G., Dieckmann, U., Mágori K., **Kun Á.**: Adaptation to habitat heterogeneity by fragmentation. “Theoretical Biology of Adaptation”, ESF Conference, Tihany, September 2001.
14. Oborny B., Meszéna G., Dieckmann, U., Mágori K., **Kun Á.**: Falling apart - Can it be adaptive? Santa Fe Institute Seminar, 16/04/2002