Final report about the NKFIH-OTKA project No. K109215

Critical transitions and emergent boundaries in ecosystems: computer simulations

The research was conducted by one senior researcher (Dr Beáta Oborny) and her students (from BSc to PhD level).

We investigated a key problem in the protection of natural populations and communities: ecological *threshold phenomena*. It is a frequent observation that gradual changes in the environment, e.g., climate changes, can cause abrupt transitions in the states of populations; for example, result in species extinctions or outbreaks of invasions. Our basic idea was to view these transitions in a unified framework based on the theory of *critical transitions*. Thus, we transferred knowledge from statistical physics to ecology, and developed a set of new models, concerning the *structure and dynamics* of 1) habitats, 2) populations, and the interaction between 1) and 2). Examples include the transitions

1) from a connected to a fragmented state (in a habitat and/or population), and
2) from a living to an extinct state (in a population).

Emphasizing the broad applicability of this theoretical framework, we studied various ecological phenomena from a fine spatial scale (centimeters) to broad scales (hundreds of meters or kilometers). We investigated the

I. *growth of individual plants among habitat patches,*
II. *spreading of populations in patchy landscapes, and*
III. *range dynamics across broad geographic scales.*

We present the results below according to these categories. It is important to note that the results obtained at one spatial scale can often be generalized to other scales. The main tools in the studies were spatially explicit dynamic models, primarily stochastic cellular automata. The practical relevance of the models was discussed in research papers, and also in separate review papers.

I. Growth of individual plants across habitat patches

The use of space by various growth forms is a key to understanding the self-organization of plant communities, and thus, the structure and function of ecosystems. It is crucial how the plants' developmental modules are arranged in space; and thus, how they explore and exploit resources (light, soil nutrients, etc.). In the interaction between the plant individual and the environment, one of the key factors is the plant's ability to percolate within and between the suitable habitat patches, which contain resources and are unoccupied by other individuals. Several growth strategies, including phenotypically plastic ones, have been described. The ecological literature on *clonal* plants is especially rich in exciting examples on foraging and spatial competition. We re-considered these phenomena in the framework of *percolation theory*. Our objective was to better understand a) plant adaptation to various habitat types, and b) the spatial structure and dynamics of plant populations.

I.1. Transitions in the habitat structure: patch sizes and distances

We modelled various patchy habitats, which consisted of suitable patches interspersed by unsuitable regions. We varied the proportion of suitable sites (*p*), and observed the size distribution of the patches (percolation clusters) that were formed by the suitable sites, and also the nearest-neighbor distances between the patches. Thus, we described the availability of the suitable sites from the aspect of a plant that lives in this this habitat. Our computer simulations were in accordance with the earlier results in *percolation theory*: the mean patch size showed an abrupt increase as *p* surpassed 0.5. In addition, they yielded a new result: the mean distance also had a *sharp (but not critical) transition* at a value of *p* that was much lower than the percolation threshold (between p=0.2 and 0.3). This suggest that there is a broad range of habitats (0.2<p<0.5) in which leaving a habitat patch offers high benefit with low risk.

I.2. Consequences for a plant that forages for resources by clonal growth

We tested the effect of patch sizes and distances on a plant that forages for resource patches. Numerous experiments have demonstrated that different clonal plant species show diverse reactions to patch boundaries (see a review in Oborny and Hubai 2014, cited below). In some species, the individual tends to avoid the unsuitable region by withdrawing resources through the internal connections (e.g. stolons) from those modules (ramets) that are in resource-poor sites. We called this the Avoiding strategy (A). Others tend to cross the boundary, because resource-rich modules subsidize the resource-poor ones (Entering strategy, E). We compared the extreme cases of A and E to an intermediate mixed strategy (M), in various habitats, modelled as described in I.1. The results demonstrated the importance of the *percolation transition* (at *p*=0.5) in the optimal strategy. Below the threshold, E was more efficient than A in foraging for the resource; above the threshold, the opposite was found. Interestingly the efficiency of the mixed strategy (M) was not intermediate, but proved to be higher than either of the pure strategies across a broad range of *p*. The lower threshold, related to the patch distances, limited the survival of M. We conclude that a smooth change in the total amount of a resource over an area can lead to an *abrupt change* in the structure of resource patches, and that strongly influences the optimal foraging strategy.

<u>*Publication and oral presentations about I.1-2*</u>

<u>Research paper:</u> Oborny B., Hubai A.G.: ***Patch size and distance: modelling habitat structure from the perspective of clonal growth***, Annals of Botany 114(2), 389-398. old., 2014. IF: 3.295.

<u>Conference talk (with Abstract):</u> Oborny B., Hubai A. G.: ***Az élőhely növény-perspektívából: foltméretek, távolságok és növekedési válaszok***, XV. Kolozsvári Biológus Napok, 2014

I.3. Invasion by clonal growth

We applied further computer simulations to investigate the dynamics of plant invasion in the habitats described above. We varied the proportion of suitable sites (*p,* as before), and also the plant's ability to penetrate into the unsuitable region (*e*). Thus, we could compare various mixed strategies ($0<e<1$). Another addition to I.2. was the observation of the time-dependence of the invasion process. By definition, plants with higher *e* moved more biomass out of the suitable portion of the habitat into the unsuitable one. The expected gain from this risky behavior was a) to reach sites that would be unreachable otherwise, and b) to speed up spreading by making shortcuts. The simulations confirmed the significance of a) below the *percolation threshold* ($p<0.5$) and of b) in the whole parameter space. The same relative advantages were observed in pairwise simulations as well, when clones with different *e* values competed for a resource.

Presentations about I.1-2

Conference talks (with Abstracts):

Hubai A.G., Oborny B.: ***Térhódítási vágta: kockázat és siker a klonális növekedésben***, A 10. Magyar Ökológus Kongresszus absztraktjai, 2015

Hubai A.G., Oborny B.: ***The invasion race: speed and persistence in clonal expansion***, Abstracts of the 11th Clonal Plant Workshop, Trebon, Czech Republic, 2015

I.4. "The plant in the labyrinth"

In the afore-mentioned simulations, the population of modules was spreading by a simple contact process, in which the branching structure of the plant was not represented. As a next step, we developed a more advanced model, in which the placement of new modules was constrained by the architecture of the plant (branching angle, branching probability, and the distance between branching points). Thus, we made a „plant in the labyrinth" model. It was based on an old problem in statistical physics, the "ant in the labyrinth". In contrast with an animal-like agent (an "ant"), a clonal plant can stay in a place and move at the same time: some parts can develop roots, while others move on by horizontal growth and branching. Like in the classical, "ant in the labyrinth" model, space was represented by a lattice, which consisted of open and closed sites (i.e., resource-rich and poor sites). The organism could move from open to open sites only. Each simulation was initiated from a single seed in an open site. In the set of simulations, we varied the proportion of open sites (*p*) in the lattice, and observed the plant's ability to reach the open sites that were in the same percolation cluster as the initial site. The simulations revealed *a new kind of threshold* (the '*tracking threshold*', approximately p_t=0.73), that was higher than the classical *percolation threshold* (p_c=0.5). At $p_c<p<p_t$ the habitat contained a giant component (open patch), but the plant could not spread successfully, because the pathways were too narrow, compared to the scale of growth. We demonstrated that by varying the grain of the habitat pattern relative to the distance between two branching points. The simulations suggest that fine-grained habitats can be "labyrinths" for a plant in a broad range of *p*. Within that range, the plant individual is likely to utilize only a small fraction of the available resource, leaving gaps open for colonization by other individuals. Therefore, the "labyrinth effect" is a considerable factor in the self-organization of plant communities.

Publication and oral presentations about I.4.

Research paper: Oborny B., Benedek V., Englert P., Gulyás M, Hubai A.G.: ***The plant in the labyrinth: adaptive growth and branching in heterogeneous environments***, Journal of Theoretical Biology 412: 146-153, 2017. IF: 1.833.

Conference talk (with Abstract): Oborny B., Kun Á., Hubai A.G., Gulyás M., Benedek V., Englert P.: ***Adaptation to patchy environments by modular growth***, Abstracts of the European Conference on Complex Systems 2014, Lucca, 2014

Conference posters (with Abstracts):

Benedek V., Englert P., Oborny B.: ***„Plant in the labyrinth" – A környezeti heterogenitás és a növekedési lépték viszonya***, A 10. Magyar Ökológus Kongresszusz absztraktjai, Veszprém, 2015

Benedek V., Englert P., Oborny B.: ***„Plant in the labyrinth" – Patch structure and plant architecture limiting clonal growth***, Abstracts of the 11th Clonal Plant Workshop, Trebon, Czech Republic, 2015

I.5. Effects of the branching angle

Our previous studies suggested that varying the branching angle could have a non-trivial effect on the efficiency of space-filling in the aforementioned "labyrinth" situation. Studying this phenomenon further, we found that limiting the range of the angle (from 120^o to 60^o) did not decrease the efficiency, and could even increase it in some habitat types. Interestingly, this effect was the strongest around the '*tracking threshold*'. That is, less turning helped filling the "labyrinth" space.

Publication and oral presentations about I.5.

Research paper: Benedek V., Englert P., Oborny B.: ***The effect of branching angle on adaptive growth in patchy environments***, Evolutionary Ecology, DOI: 10.1007/s10682-016-9873-0, 2016. IF: 1.875

Conference poster (with Abstract): Benedek V., Englert P., Oborny B.: ***Klonális növekedési jellegek hatása a terjedésre és térkitöltésre***, A 6. Kvantitatív Ökológiai Szimpózium absztraktjai, 2017

I.6. Effects of the ramets' demography

In contrast with the previous studies, the habitat in this study was not patchy, i.e., we investigated the invasion of homogeneous space. We were interested in some internal (within-plant) effects. Two kinds of ramets were distinguished: (1) terminal ramets were recently produced at the end of a branch, thus, they were directly neighbored by the growing tip(s); while (2) internal ramets were not neighbored by any region of growth. The death rate could differ in the terminal vs. internal ramets. An additional cause of mortality was also considered: the tip of a branch could die due to intraclonal competition. We studied how the death rates at the terminal and internal ramets influenced the shape of the growing clone, and how this affected the final occupation of space. The simulations showed that intraclonal competition could seriously hinder the invasion process, and created considerable gaps in the clonal plant's canopy. This effect was particularly strong when the terminal mortality was high, and the internal mortality was low. In this case, the clone had only a relatively small number of growing points, and growth was restricted to the forward direction; it was difficult to turn back due to a „wall" of surviving, old ramets. This caused a characteristic, „fan-shaped" pattern of ramets (which has also been observed in real clonal plants). The results suggest that the maintenance of the terminal vs. internal ramets are not equally valuable for clonal plants. It is advantageous to maintain the terminal ramets as long as possible, but not the internal ramets. Their long-term maintenance, that is observable in some species, requires another explanation (e.g., on the basis of competition between clones).

Publication and oral presentations about I.6.

Submitted manuscript (in review): Benedek, V., Englert, P.: ***The effect of ramet mortality on clonal growth***, Theory in Biosciences (in review)

<u>**Conference talk (with Abstract):**</u> Benedek V., Englert P., Oborny B.: ***Képes-e a növény elfoglalni az összes, számára alkalmas szabad helyet? - A növekedést korlátozó tényezők***, XV. Kolozsvári Biológus Napok, 2014

<u>**Conference posters (with Abstracts):**</u> Benedek V., Englert P., Oborny B.: ***Klonális növények térfoglalása különböző növekedésmintázatok esetén***, A XI. Magyar Természetvédelmi Biológiai Konferencia absztraktjai, 2017

I.7. Physiological integration in clonal plants: a review

Physiological integration between ramets is a ubiquitous phenomenon among clonal plants; but we find a large variation in the degree of integration. Understanding the adaptive significance of integration is still a challenge in clonal plant research. One of the important factors in natural selection for/against integration is resource use: integrators/splitters sense the resource pattern in a coarse/fine-grained manner. The paper reviewed seven computer models on this phenomenon. In summary, integration proved to be advantageous in two, contrasting cases: A) when the total amount of resource was low, and it was distributed in a fine-grained, constant pattern, or B) when the total amount was high, and it was coarse-grained and variable over time. Starting from case A, and increasing the total amount of resource gradually, we experienced an abrupt change in the optimal strategy from splitting to integration at a well-defined *critical threshold*. Further tests revealed that only radical splitting was favorable; even very small integrated fragments, which consisted of two ramets, produced the same result as extensively integrated clones. This suggest that in fine-grained environments evolution can hardly “fine-tune” the fragment sizes. Another plant parameter is more easily tunable: the shared resource relative to the total amount of resource in a ramet. Altogether, the results suggest that changes in the spatial and/or temporal distribution of resources can explain evolutionary transitions in both directions: from splitting to integration and back. The transition can be *abrupt or gradual*, depending on the environmental parameter that is changing.

<u>*Presentations about I.7.*</u>

<u>**Conference talks (with Abstracts):**</u>

Oborny B.: ***Mi kell a vegetatív szaporodáshoz? - A forráshasznosításon alapuló érvek áttekintése***, A 10. Magyar Ökológus Kongresszus absztraktjai, 2015

Oborny B.: ***United we stand, divided we fall? - a summary of seven models on physiological integration***, Abstracts of the 11th Clonal Plant Workshop, Trebon, Czech Republic, 2015

<u>Conference talk (without Abstract):</u> Oborny B.: ***United we stand, divided we fall? Competition and cooperation within modular organisms.*** ELTE Evolúcióbiológiai Nap, Budapest, 2018

I.8. The plant body as a network of semi-autonomous agents: a review

The above-mentioned results were summarized in a review paper on the growth and development of plants from the perspective of network theory. The main focus was on foraging behavior, by which the plant explores and exploits resources in the habitat. The review presented some typical challenges posed by the environment, and discussed the plants' potential and limitations in solving these tasks. The plant's constructional units (modules) were considered as a group of cooperating agents, which operate through distributed control. Some unexplored areas were also highlighted, in which a dialogue between plant science and network theory could be mutually inspiring.

Publication about I.8.

Review paper: Oborny B.: ***The plant body as a network of semi-autonomous agents: a review***, Phil. Trans. Roy. Soc. B. (in press), 2019. IF: 5.666.

To summarize section I., the adaptation of plants to patchy resources strongly depended on the connectivity of resource patches. In particular, the optimal value of several plant traits showed an abrupt change at the percolation threshold.

II. Spreading of populations across patchy landscapes

In this part of the project, we studied landscape-level phenomena related to critical transitions. In general, the viability of a species in a landscape hinges on its ability to disperse or migrate across suitable habitat patches. One of the serious anthropogenic problems is the fragmentation of natural habitats, which is often exacerbated by disturbances within the remaining fragments. For many species, it is a considerable challenge to 'track' the suitable habitat when it is scattered and changes over time. We studied various landscapes from an organism-centered view, on the basis of percolation theory.

II.1. Splitting, shrinking, and disappearing patches: a dynamical meso-scale view of habitats

The new model was based on our previous investigations on percolation phenomena in patchy landscapes. The novelty of the model was a meso-scale approach: we studied the effects of habitat loss on the scale of individual patches. Each patch was modeled as a contiguous assemblage of discrete habitat sites. The removal of a single site necessarily caused one of the following elementary events in the patch: (a) splitting, (b) shrinkage without splitting, or (c) complete disappearance. We investigated the probabilities of these events, and their effects on various species that differed in the minimum patch area required for persistence. To study this, we introduced a new dynamical neutral landscape model (DNLM). In each set of simulations, the total habitat cover p was constant, but the locations of the individual habitat sites changed. Habitat loss was implemented by decreasing the value of p from 1 (pristine land) to 0 (no habitat available). The simulations revealed five main phases of landscape degradation: (1) when there was little habitat loss, the most frequent event was the shrinkage of a large, spanning patch; (2) then splitting became significant; (3) splitting peaked; (4) the remaining patches shrank; and (5) gradually disappeared. Organisms which required relatively large patches were particularly sensitive to phase (3). This phase emerged at a value of p that was well *below the percolation threshold*. In conclusion, the effective habitat loss caused by the removal of a single habitat site could be several times higher than the actual habitat loss. The amplification of loss depended on the organism's habitat requirement, and on the actual phase of landscape degradation.

Submitted manuscript about II.1.

Research paper: Kun Á., Oborny B., Dieckmann, U.: ***Splitting, shrinking, and disappearing patches: a dynamical view of habitat loss***, Scientific Reports (submitted in August, 2018).

Summary of Section II: in the case of serious dispersal limitation, not only the global characteristics of the habitat pattern matter (e.g., the overall percolation structure), but a meso-scale description of the habitat is also needed for understanding the populations' survival and spreading.

III. Range dynamics across broad geographic scales

A fundamental goal of ecological research is to understand the distribution of organisms in space and time. A lot of effort has been devoted to the study of populations at the edges of spatial distributions (range margins), where the conditions gradually worsen and, thus, the abundance vanishes. We contributed to these studies by suggesting that the theory of critical transitions is a powerful tool for understanding the structure and dynamics of range margins. In particular, we suggested to view the vanishment of the population density at the margin as a spatial manifestation of a critical transition. We investigated this transition by gradient contact processes.

III.1. Populations across environmental gradients

First we investigated the structure and dynamics of steady-state range margins, assuming that the environment changed across space (i.e., there was an environmental gradient), but was constant over time. Even these steady-state margins were complex. As the environmental conditions worsened, the population's spatial structure typically showed a percolation transition from a connected to a fragmented phase. Within the fragmented phase, the population 'islands' decreased, and their fluctuations increased, until the population underwent another transition from the living to the extinct state. We prepared a software for studying these changes at different environmental gradients, varying the demographic parameters of the population across space. Then we identified the percolation clusters (i.e., the population fragments) within the occupied terrain, and delineated the hull of the largest cluster. Our earlier studies had shown a robust property of the hull: it was a fractal with a dimension 7/4. This and some other scaling laws applied in a broad parameter range due to universality in the percolation transition. We reviewed these results, and related them to other models of range edges. The review and the simulation software served as a basis for further investigations, in which we relaxed the assumption of constant environment (see III.2).

Presentations about III.1

Talks (with Abstracts):
Oborny B.: ***Kihalási küszöbök és éles határok az ökológiai rendszerekben***, Az MTA Biológiai Osztály ülésén elhangzott előadások kivonatai, 2017

Oborny B.: ***Határzónák és végvárak - Demográfiai és térbeli terjedési tulajdonságok hatásai az elterjedési terület szélén***, A 6. Kvantitatív Ökológiai Szimpózium absztraktjai, 2017

III. 2. Shifting species' ranges in a changing climate

In this study, we assumed that the climate was changing, and thus, the demographic parameters were changing not only across space, but also over time. Thus, we could model the shifts of the ranges of distribution. The primary question was whether the population's spreading was fast enough to move together with the moving habitat (the problem of 'habitat tracking'). We also tested whether the shift would distort the fractal edge. A manuscript about the results is in preparation. Meanwhile, we wrote a review about the potential methods of delineating the range edges, in order to detect their shifts precisely. Theoretical considerations (on the basis of models of directed percolation) suggest that the most external, “island-like” occurrences of a species are statistically unreliable for this purpose. We recommended to monitor another kind of boundary: the so-called hull, which is the border between the fragmented and the connected occurrence of the species. We showed that the hull had some intriguing geometric characteristics, which were preserved a) when we varied the details of the population dynamic process, b) when the gradient was not constant, but the environment changed in space in more complex ways, and importantly, c) when the environment was gradually changing over time, i.e., the range was shifting. On this basis, we recommended the hull for delineating a range edge reliably.

Review, dissertation, and oral presentation about III.1

Review paper: Oborny B.: ***Scaling laws in the fine-scale structure of range margins***, MDPI Mathematics 6, 315: 1-13, 2018

BSc Thesis: Haraszti H.: ***Milyen módszerekkel állapítják meg a fajok elterjedési határát?***, ELTE TTK Biology BSc Thesis, supervisor Beáta Oborny, 2017. Evaluation: excellent.

Conference talk (with Abstract): Oborny B.: ***Advancing vs. retreating fronts: The fine-scale dynamics of treeline shifts***, Abstracts of the 1st International Conference on Community Ecology, Budapest, 2017

III.3. Boundaries between species

We investigated some characteristic cases in which interfaces were formed between two competing species. Model 1 was a continuation of the gradient contact process study, extending it for three states (empty, occupied by species 1 or 2). This work is in progress. To better understand the results obtained in Model 1, we analyzed and published the results from a simpler model first. In this model, only two states were distinguished (site occupied by species 1 or 2), and the environment was homogeneous. Our aim was to better understand the geometry and fluctuations of the interface between competing species in neutral competition, which is going to serve as a reference for further studies on non-neutral competition (e.g., between species with different strategies of spreading). We applied a well-known model of neutral competition, the voter model in regular lattices and in mean field approximations. The expected time to extinction is an important characteristic in these systems. The average time in the mean field had been published earlier in mathematical papers. Our investigations added the higher moments in the mean field, by which the whole distribution of the extinction time can be constructed. We complemented these results with the distribution of the consensus time in square lattices, obtained from computer simulations. We characterized the dependence of the extinction time on the system size and initial conditions. The results have were published in mathematical papers (Gastner et al. 2018 and 2019 in the list of publications). The first parts of these papers, about the basic voter model (BVM), are applicable to ecological competition; the second parts are specific for social systems (which is reflected in the titles of the papers). Beside this theoretical groundwork, the PI made a literature review about some characteristic cases in which sharp (but winding) boundaries emerge between two species or vegetation types with or without an environmental gradient.

Research papers, review article, and oral presentation about III.3

Research papers:

Gastner, M., Oborny B., Gulyás M.: ***Consensus time in a voter model with concealed and publicly expressed opinions***, Journal of Statistical Mechanics 2018/063401: 1-21, 2018

Gastner, M., Takács, K., Gulyás, M., Szvetelszky, Zs., Oborny, B.: ***The impact of hypocrisy on opinion formation: a dynamic model***, PLOS ONE (elfogadott cikk), 2019

Conference talk (with Abstract): Gastner, M., Oborny B., Gulyás, M.: ***A voter model with concealed and publicly expressed opinions***, Abstracts of the 2018 Conference on Complex Systems, Thessaloniki., 2018

Review article: Oborny B.: ***Kritikus küszöbök és hirtelen összeomlások. Miért nehéz előrejelezni a környezetváltozások ökológiai hatásait?***, Természet Világa 2018(2): 69-73, 2018

Summary of section III: margins of the geographic distributions of species are important regions in terms of ecological and evolutionary processes, including the species' response to climate change. Our results suggest that (meta)populations across environmental gradients share some common features, which allow for generalizations within a broad variety of species and environments: (1) sharp edges can emerge even across relatively smooth environmental gradients; (2) intraspecific competition combined with dispersal limitation is a sufficient condition for the sharpening; (3) at the margin, the "mainland" of continuous occurrence splits into "islands"; and the structure of the hull of the mainland obeys some characteristic scaling laws. These general features follow from a second-order phase transition from a connected to a fragmented state. The results contribute to understanding the origin of vegetation zones and the spatial pattern of ecotones.

Dissemination of the results

We gave talks addressed to broader audiences. Both the PI and the students participated in the dissemination of the results.

Hubai A.G.: ***Játékos útkeresés***. Előadás a XIX. Bolyai Konferencián, 2014. márc. 22-23.

Benedek V.: ***Sakkoznak-e a növények?*** Előadás az Eötvös József Kollégium Diákbizottsága által szervezett XV. Eötvös Konferencián, 2014. ápr. 25-27.

Oborny B.: ***Mit tanulhatunk a növényektől?*** Előadás az Internet Hungary Konferencián, Siófok, 2014. okt. 14-15.

Oborny B.: ***Alkalmazkodás, átrendeződés és közösségszerveződés ökológus-szemmel.*** Előadás a Nokia Talent Program keretében a Kürt Akadémián, Budaörs, 2014. jan. 23.

Oborny B.: ***Özönlények.*** Előadás a Szép Galériában, Nagy András képzőművészet-költészet-tudomány programjának keretében, Budapest, 2017. júl. 3.

Oborny B. és Szvetelszky Zs.: ***Nem tudja a jobb kéz, mit csinál a bal? Modularitás és startégia***. Előadás a 28. Országos Marketing Konferencián, Budapest, 2017. november 15.

Oborny B.: ***A bőség zavara - avagy meg tudjuk-e érteni a diverzitást?*** Előadás a Magnet Házban, Budapest, 2018. jún. 7.

Oborny B.: ***"The ant in the labyrinth" versus "the plant in the labyrinth"***. Előadás a Szegedi Eötvös Kollégiumban, 2018 március 18.

We prepared a website for the project: https://sites.google.com/view/ecologicalboundaries/publications

Budapest, 30 January, 2018.