# Final report of NKFI project # **K140901**
2017-2022

# „Cooperative and competitive ecological and evolutionary dynamics on different organizational levels ”

| | |
|---|---|
| *Principal investigator:* | Tamás Czárán |
| *Participating researchers:* | András Szilágyi<br>Balázs Könnyű<br>Beáta Oborny<br>György Barabás<br>Dániel Vörös |

## *Introduction*

This was a theoretical research project with the inclusion of diverse topics from the chemical origin of life through subsequent major evolutionary transitions like the assembly of the first eukaryotic cell, game theoretical models of bacterial evolution, and spatio-temporal ecological processes, to certain aspects of the socio-ecological evolution of neolithic hominins. The common denominator of all these radically different problems is the role of cooperative and competitive interactions among simpler system components in the construction of new organizational levels by evolution.

The original plan of the research program aimed at less diverse topics, but – as it often happens with theoretical investigators – answers to questions regarding a certain field of research yielded, by analogy or homology, questions on a different (sometimes very different) field. This is what actually happened to our project as well, resulting in the extension of our model for the coevolution of bacterial cooperation and communication into another modelling project on fungal evolution or the coevolutionary origins of human cooperation and communication, and yet another one on the evolution of social structure in early hominin populations. At the same time, one of the research themes originally aimed at in the project plan (the 2. phage-bacterium coevolution module) could not be pursued and published, because the PI returned from Copenhagen University (earlier than originally planned) where both the theoretical and the virology laboratory support for the subproject were given. However, the topic of bacterial coevolution of cooperation, communication and cheating still has been investigated in detail, and those results are published in high-ranking journals.

Below we will list and briefly discuss the publications related to each of the three major topics of the original project plan. The number of publications is **26**; the overwhelming majority of these papers appeared in **D1 or Q1** journals. The cumulative impact factor of the publications supported by this project is **141.713.**

## *Results*

### *I. Prebiotic evolution and major evolutionary transitions:*

1. A. Szilágyi, I. Zachar, I. Scheuring, Á. Kun, B. Könnyű & T. Czárán: Ecology and evolution in the RNA World Dynamics and stability of prebiotic replicator systems. Life 7:48, 2017 doi: 10.3390/life70400048.

The many different incarnations of nucleotide sequence (string) replicator models proposed recently are all attempts to explain on this basis how the genetic information transfer and the functional diversity of prebiotic replicator systems may have emerged, persisted and evolved into the first living cell. We have postulated three necessary conditions for an RNA World model system to be a dynamically feasible representation of prebiotic chemical evolution: (1) it must maintain and transfer a sufficient diversity of information reliably and indefinitely, (2) it must be ecologically stable and (3) it must be evolutionarily stable. In this review, we discuss the best-known prebiotic scenarios and the corresponding models of string-replicator dynamics and assess them against these criteria. We suggest that the most popular of prebiotic replicator systems, the hypercycle, is probably the worst performer in almost all of these respects, whereas a few other model concepts (parabolic replicator, open chaotic flows, stochastic corrector, metabolically coupled replicator system) are promising candidates for development into coherent models that may become experimentally accessible in the future.

2. Zsuzsanna Vig-Milkovics, István Zachar, Ádám Kun, András Szilágyi, Eörs Szathmáry: Moderate sex between protocells can balance between a decrease in assortment load and an increase in parasite spread. Journal of Theoretical Biology 462:204-310 (2019)

Sexual reproduction is widespread in nature despite the different kinds of cost that it entails. We do not know exactly when the first sexual process took place and especially why it was beneficial at first. It is clearer why sex is advantageous for the prokaryotes and eukaryotes but the benefit of sex for protocells with individually replicating ribozymes is not yet fully understood. In this context sex is the simple horizontal gene transfer among two protocells that undergo transient fusion. Many authors argue that horizontal gene transfer (HGT) was very common in the early stage of evolution. However, HGT is a risky mechanism considering both the disruption of optimal compositions and the spread of parasites among protocells. In order to test the effects of HGT on the fitness of a protocell population, we explored by numerical simulations those conditions under which fusion might have been beneficial. We investigated multiple conceivable types of fusion in the stochastic corrector model framework and we considered the spread of parasites in every case. Protocells contain up to five species of unlinked, essential ribozymes; if a protocell has the same amount of each, it reaches maximum fitness. Fusion is dangerous not only due to the spread of parasites but also because it can ruin the cells with balanced ribozyme composition. We show that fusion can restore the ribozyme composition of the protocells under certain circumstances (high gene count, intermediate split size and low rate of fusion) and thus it can decrease the effect of the genetic load. Fusion could have been a useful early mechanism in contributing to the reliable coexistence of the different ribozymes before the spread of the chromosomes.

3. István Scheuring, András Szilágyi: Diversity, stability, and evolvability in models of early evolution Current Opinion is Systems Biology 13:115-121. (2019)

Based on the RNA world hypothesis, we outline a possible evolutionary route from infrabiological systems to early protocells. To assess the scientific merits of the different models of prebiotic evolution and to suggest directions for future research, we investigate the diversity-maintaining ability, evolutionary/ecological stability, and evolvability criteria of existing RNA world model systems for the origin of life. We conclude that neither of the studied systems satisfies all of the aforementioned criteria, although some of them are more convincing than the others. Furthermore, we found that the most conspicuous features of the proposed prebiotic evolutionary scenarios are their increasing spatial inhomogeneity along with increasing plasticity, evolvability, and functional diversity. All of these characteristics change abruptly with the emergence of the protocells.

4. Adamski, P., Eleveld, M., Sood, A., Kun, Á., Szilágyi, A., Czárán, T, Szathmáry, E., Otto, S.: From self-replication to replicator systems en route to de novo life. Nat Rev Chem 4, 386–403 (2020). https://doi.org/10.1038/s41570-020-0196-x

The process by which chemistry can give rise to biology remains one of the biggest mysteries in contemporary science. The de novo synthesis and origin of life both require the functional integration of three key characteristics — replication, metabolism and compartmentalization — into a system that is maintained out of equilibrium and is capable of open-ended Darwinian evolution. This Review takes systems of self-replicating molecules as starting points and describes the steps necessary to integrate additional characteristics of life. We analyse how far experimental self-replicators have come in terms of Darwinian evolution. We also cover models of replicator communities that attempt to solve Eigen's paradox, whereby accurate replication needs complex machinery yet obtaining such complex self-replicators through evolution requires accurate replication. Successful models rely on a collective metabolism and a way of (transient) compartmentalization, suggesting that the invention and integration of these two characteristics is driven by evolution. Despite our growing knowledge, there remain numerous key challenges that may be addressed by a combined theoretical and experimental approach.

5. A. Szilágyi, B. Könnyű & T. Czárán: Dynamics and stability in prebiotic information integration: an RNA World model from first principles. Scientific Reports 10:51, 2020. doi: 10.1038/s41598-019-56986-8

The robust coevolution of catalytically active, metabolically cooperating prebiotic RNA replicators were investigated using an RNA World model of the origin of life based on physically and chemically plausible first principles. The Metabolically Coupled Replicator System assumes RNA replicators to supply metabolically essential catalytic activities indispensable to produce nucleotide monomers for their own template replication. Using external chemicals as the resource and the necessary ribozyme activities, Watson-Crick type replication produces complementary strands burdened by high-rate point mutations (insertions, deletions, substitutions). Metabolic ribozyme activities, replicabilities and decay rates are assigned to certain sequence and/or folding (thermodynamical) properties of single-stranded RNA molecules. Short and loosely folded sequences are given replication advantage, longer and tightly folded ones are better metabolic ribozymes and more resistant to hydrolytic decay. We show that the surface-bound MCRS evolves stable and metabolically functional communities of replicators of almost equal lengths, replicabilities and ribozyme activities. Being highly resistant to the invasion of parasitic (non-functional) replicators, it is also stable in the evolutionary sense. The template replication mechanism selects for catalytic "promiscuity": the two (complementary) strands of the same evolved replicator will often carry more than a single catalytically active motif, thus maximizing functionality in a minimum of genetic information.

6. B. Könnyű & Á. Kun: Surfaces, the missing link in the origins of life. Journal of Systems Chemistry 8: 95-106, 2020.

In this article, we argue for the necessity of a surface-bound stage in the origin of life. Accordingly, at least the polymerization of the biologically active polymers (RNA) was produced on mineral surfaces, which then could also retain functional ribozymes. Functional ribozymes could then form communities, which, on surfaces, due to limited mobility and local interaction, can co-exist and be resistant to parasitic replicators. An example of such a system, the Metabolically Coupled Replicator System (MCRS) is discussed in detail.

7. D. Vörös, B. Könnyű, T. Czárán: Catalytic promiscuity in the RNA World may have aided the evolution of prebiotic metabolism. 2021. Plos Computational Biology 17: e1008634, doi: 10.1371/journal.pcbi.1008634

The Metabolically Coupled Replicator System (MCRS) model of early chemical evolution offers a plausible and efficient mechanism for the self-assembly and the maintenance of prebiotic RNA replicator communities, the likely predecessors of all life forms on Earth. The MCRS can keep different replicator species together due to their mandatory metabolic cooperation and limited mobility on mineral surfaces, catalysing reaction steps of a coherent reaction network that produces their own monomers from externally supplied compounds. The complexity of the MCRS chemical engine can be increased by assuming that each replicator species may catalyse more than a single reaction of metabolism, with different catalytic activities of the same RNA sequence being in a trade-off relation: one catalytic activity of a promiscuous ribozyme can increase only at the expense of the others on the same RNA strand. Using extensive spatially explicit computer simulations we have studied the possibility and the conditions of evolving ribozyme promiscuity in an initial community of single-activity replicators attached to a 2D surface, assuming an additional trade-off between replicability and catalytic activity. We conclude that our promiscuous replicators evolve under weak catalytic trade-off, relatively strong activity/replicability trade-off and low surface mobility of the replicators and the metabolites they produce, whereas catalytic specialists benefit from very strong catalytic trade-off, weak activity/replicability trade-off and high mobility. We argue that the combination of conditions for evolving promiscuity are more probable to occur for surface-bound RNA replicators, suggesting that catalytic promiscuity may have been a significant factor in the diversification of prebiotic metabolic reaction networks.

8. Szilágyi A, Kovács VP, Szathmáry E, Santos M (2020) Evolution of linkage and genome expansion in protocells: The origin of chromosomes. PLOS Genetics 16(10): e1009155. https://doi.org/10.1371/journal.pgen.1009155

Chromosomes are likely to have assembled from unlinked genes in early evolution. Genetic linkage reduces the assortment load and intragenomic conflict in reproducing protocell models to the extent that chromosomes can go to fixation even if chromosomes suffer from a replicative disadvantage, relative to unlinked genes, proportional to their length. Here we numerically show that chromosomes spread within protocells even if recurrent deleterious mutations affecting replicating genes (as ribozymes) are considered. Dosage effect selects for optimal genomic composition within protocells that carries over to the genic composition of emerging chromosomes. Lacking an accurate segregation mechanism, protocells continue to benefit from the stochastic corrector principle (group selection of early replicators), but now at the chromosome level. A remarkable feature of this process is the appearance of multigene families (in optimal genic proportions) on chromosomes. An added benefit of chromosome formation is an increase in the selectively maintainable genome size (number of different genes), primarily due to the marked reduction of the assortment load. The establishment of chromosomes is under strong positive selection in protocells harboring unlinked genes. The error threshold of replication is raised to higher genome size by linkage due to the fact that deleterious mutations affecting protocells metabolism (hence fitness) show antagonistic (diminishing return) epistasis. This result strengthens the established benefit conferred by chromosomes on protocells allowing for the fixation of highly specific and efficient enzymes.

9. Szilágyi A, Szabó P, Santos M, Szathmáry E (2020) Phenotypes to remember: Evolutionary developmental memory capacity and robustness. PLOS Computational Biology 16(11): e1008425. https://doi.org/10.1371/journal.pcbi.1008425

There is increased awareness of the possibility of developmental memories resulting from evolutionary learning. Genetic regulatory and neural networks can be modelled by analogous formalism raising the important question of productive analogies in principles, processes and performance. We investigate the formation and persistence of various developmental memories of past phenotypes asking how the number of remembered past phenotypes scales with network size, to what extent memories stored form by Hebbian-like rules, and how robust these developmental “devo-engrams” are against networks perturbations (graceful degradation). The analogy between neural and genetic regulatory networks is not superficial in that it allows knowledge transfer between fields that used to be developed separately from each other. Known examples of spectacular phenotypic radiations could partly be accounted for in such terms.

10. Zachar, I. 2022. Closing the Energetics Gap. Nature Ecology & Evolution, August.

A modelling *study suggests that the proposed energetic barrier between prokaryotes and eukaryotes may not be relevant to the complexity gap between the two domains. The energetic advantage of early mitochondria was probably small, and eukaryotes likely emerged without the help of an endosymbiont.

11. Zachar I and Boza G. 2022. ‘The Evolution of Microbial Facilitation: Sociogenesis, Symbiogenesis, and Transition in Individuality’. Frontiers in Ecology and Evolution 10 (April)

In certain cases, syntrophic cooperation can lead to a transition in individuality, when freely reproducing, unrelated entities (genes, microbes, etc.) irreversibly integrate to form a new evolutionary unit. The textbook example is endosymbiosis, prevalent among eukaryotes but virtually lacking among prokaryotes. We set out to distinguish syntrophy-specific aspects of major transitions, to investigate why a transition in individuality within a syntrophic pair or community is so rare. Community properties, like joint metabolic capacity, functional profile, guild composition, assembly and interaction patterns are important concepts that may provide the heritable information at a higher level of selection. We explore these ideas, relating to concepts of multilevel selection and of informational replication, to assess their relevance in the debate whether microbial communities may inherit community-level information.

12. Boza, G*, G Barabás*, I Scheuring, and I Zachar. 2022. Eco-Evolutionary Modelling of Microbial Syntrophy Indicates the Robustness of Cross-Feeding over Cross-Facilitation. Scientific Reports [under review].

Syntrophic cooperation among prokaryotes relies on unilateral or mutual aid that may be both catalytic and metabolic in nature. Hypotheses of eukaryotic origins claim that mitochondrial endosymbiosis emerged from mutually beneficial syntrophy of archaeal and bacterial partners. However, there are no other examples of prokaryotic syntrophy leading to endosymbiosis. One potential reason is that when externalized products become public goods, they incite social conflict due to selfish mutants that may undermine any mutualistic interactions. Studying the case where partners cross-feed on each other’s self-inhibiting waste, we show that cooperative partnerships will eventually dominate over selfish mutants. By contrast, systems where producers actively secrete enzymes that cross-facilitate their partners’ resource consumption are not robust against cheaters over evolutionary time. We conclude that cross-facilitation is unlikely to provide an adequate syntrophic origin for endosymbiosis, but that cross-feeding mutualisms may indeed have played that role.

## *II. Coevolution of cooperation and communication (in bacteria, fungi and hominin populations)*

13. T Czárán, I Scheuring. 2022. Weak selection helps cheap but harms expensive cooperation in spatial threshold dilemmas. Journal of Theoretical Biology 536:110995

We have studied a simple Public Goods Game (PGG) scenario played out by cooperating (C) and defecting (D) agents, applying the highly nonlinear threshold benefit function in an individual-based lattice model. A semi-analytical approximation of the lattice model has been developed and shown to describe the dynamics fairly well in the vicinity of the steady state. Besides the expected outcomes (i.e., the negative effect on cooperator persistence of higher cooperation costs and/or more intensive mixing of the population) we have found a surprising, counter-intuitive effect of the strength of selection on the steady state of the model. The effect is different at low and high cooperation costs, and it shows up only in the lattice model, suggesting that stochastic effects and higher order spatial correlations due to the emergent spatial clustering of cooperators (not taken into account in the semi-analytical approximation) must be responsible for the unexpected results for which we propose an intuitive explanation, present a tentative demonstration, and shortly discuss their biological relevance.

14. B Auxier, TL Czárán, DK Aanen. 2022. Modeling the consequences of the dikaryotic life cycle of mushroom-forming fungi on genomic conflict. Elife 11, e75917

A fascinating exception to the usual diploid life cycle of most organisms is Basidiomycete fungi, where two haploid genomes remain separate in a dikaryon, retaining the option to fertilize subsequent monokaryons. We test the consequences of the dikaryotic life cycle for mating success and myceliumlevel fitness components, assuming a trade-off between mating fitness at the level of the haploid nucleus and fitness of the fungal mycelium. The maintenance of fertilization potential by dikaryons leads to a higher proportion of fertilized monokaryons, but the ensuing intradikaryon selection for increased nuclear mating fitness leads to reduced mycelium fitness relative to a diploid life cycle. This fitness reduction is lower compared to a hypothetical life cycle where dikaryons can also exchange nuclei. Prohibition of fusion between dikaryons therefore reduces the level of nuclear parasitism.

15. Szilágyi A, Kovács V, Czárán T*, Szathmáry E* 2022. Evolutionary ecology of language origins through confrontational scavenging. Phil.Trans.Roy.Soc.Lond. (in press)

A dynamic model and an agent-based simulation model implementing the assumptions of the confrontational scavenging hypothesis on early protolanguage as an adaptive response of Homo erectus to gradual change in their habitat has been developed and studied. The core assumptions of the hypothesis and the model scenario are the pre-adaptation of our ancestors to occupy the ecological niche that they constructed for themselves by having evolved displaced communication and a rudimentary tool manufacture, two features allowing them to utilize a new, concentrated and abundant resource - megafauna carrion - on the savannas replacing arboreal habitats due to the drying climate of East Africa about two million years ago. The shift in diet requires coordinated cooperation by the hominin scavengers confronted with concurrent predators. Power scavenging compels displaced symbolic communication featuring a limited semantic range; syntax is not yet required. We show that phenotypic evolution on the accuracy of information transfer between cooperating hominins is a necessary and sufficient condition for the population of agents to survive the diet shift. Both the individual and the group fitness of the hominin horde increases with the accuracy of their protolanguage, with decreasing time allocated to foraging and thus more time left for culture.

16. Andersson C and Czárán T. 2022. The transition from animal to human culture – simulating the social protocell hypothesis. Phil.Trans.Roy.Soc.Lond. (in press)

The social protocell hypothesis (SPH) proposes that human culture originates in cumulative integration of simple animal-style traditions into simple "institutions" and "cultural lifestyles." The proposed mechanism (the social protocell) explains these origins as an initially coincidental provision of group-level cultural evolutionary individuality as (i) a side-effect of social group behavior (observable also in modern-day Pan,) driven by (ii) the pursuit of resources amenable to complex cultural strategies, namely carnivory directed at large carcasses (unique to hominins). We test the SPH using a model of the social protocell. We ask whether cumulative systems of traditions (institutions) for resource exploitation arise, whether institutions improving evolutionary individuality can co-evolve. We introduce a genetic feature of agents to test the plausibility of a mutualistic partnership between Homo and sociont. The model produces the predicted behavior and reveals several additional behaviors as fodder for future work.

17. Számadó, Sz*, I Zachar*, D Czégel, and DJ Penn. 2022. General Solution to Biological Signalling Games: Honesty Is Maintained by Trade-Offs Rather than Costs. BMC Biology [under review].

Our model clarifies the relationship between signalling costs at equilibrium and the conditions for reliable signalling. It shows honest signals at the equilibrium can have any cost value, even negative, being beneficial for the signaller independently of the receiver's response at equilibrium and without requiring further constraints. Our results are general and we show how they apply to seminal signalling models, and refute the claim that signals must be costly at the evolutionary equilibrium to be reliable, as predicted by the so-called "costly signalling" theory. We argue that the evolution of reliable signalling is better understood within a Darwinian life-history framework, and that the conditions for honest signalling are more clearly stated and understood by evaluating their trade-offs rather than their costs per se. Our results highlight why signals are expected to be efficient rather than wasteful.

## *III. Spatio-temporal integration of cooperative and competitive efforts in clonal plants*

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

The growth and development of plants from the perspective of network theory have been reviewed. The main focus was on foraging behaviour, by which the plant explores and exploits resources in the habitat. I 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 operates through distributed control. Accordingly, I described the plant as a network of agents, and mentioned some examples for questions which could typically be answered by network modelling. I also pointed out some unexplored areas, in which a dialogue between plant science and network theory could be mutually inspiring. Finally, I discussed some general issues (e.g., cooperation versus competition between the agents) which are applicable to other, similar systems, too.

19. Kun Á., Oborny B., Dieckman U. (2019) Five main phases of landscape degradation revealed by a dynamic mesoscale model analysing the splitting, shrinking, and disappearing of habitat patches. Scientific Reports 9: 11149.

To understand adaptation to the environment (e.g., by various strategies of plant growth) it is necessary to give an accurate description of the spatial and temporal pattern of the habitat. We investigated habitats which consisted of two kinds of discrete patches (e.g., rich vs. poor in a resource), and described the dynamics of these patches on the basis of elementary events (splitting, shrinking, disappearance; and the opposite, merging, expanding, and appearance). Our aim was to provide an organism-centered viw of habitats. Theoretical polulation biology and landscape ecology had provided many methods of habitat description on the local and global scales (for example, on the basis of percolation theory). We complemented this view by a meso-scale description, focussing on the individual patches. We think that this is particularly relevant for the organisms that live in patchy habitats, because the events that happen to the actual patch, in which the individual lives (splitting, merging, etc.) determines its opportunities for survival and reproduction. We demonstrated this by the example of an organism which required a minimum patch size for survival. When habitat loss exceeded a threshold, patch splitting became dominant among the events, which threatened the survival of the organism considerably. The results suggest that the meso-scale dynamics of patches are potentially significant selective factors, and should be considered in the study of adaptive movement/growth strategies.

20. Oborny, B. (2019) The plant body as a network of semi-autonomous agents: a review. Phil. Trans. Roy. Soc. B. 374(1774): 1-11.

The growth and development of plants from the perspective of network theory are reviewed. The main focus was on foraging behaviour, by which the plant explores and exploits resources in the habitat. I 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 operates through distributed
control. Accordingly, I described the plant as a network of agents, and mentioned some examples for questions which could typically be answered by network modelling. I also pointed out some unexplored areas, in which a dialogue between plant science and network theory could be mutually inspiring. Finally, I discussed some general issues (e.g., cooperation versus competition between the agents) which are applicable to other, similar systems, too.

21. Juhász R., Oborny B. (2020) Percolation theory suggests some general features in range margins across environmental gradients. Ecological Complexity 42, 100814.

The margins within the geographic range of species are often specific in terms of ecological and evolutionary processes, and can strongly influence the species' reaction to climate change. One of the frequently observed features at range margins is fragmentation, caused internally by population dynamics or externally by the limited availability of suitable habitat sites. We study both causes, and describe the transition from a connected to a fragmented state across space by means of a gradient metapopulation model. The main features of our approach are the following. 1) Inhomogeneities can occur at two spatial scales: there is a broad-scale gradient, which can be patterned by fine-scale heterogeneities. The latter is implemented by dispersing a variable number of small obstacles over the terrain, which can be penetrable or unpenetrable by the spreading species. 2) We study the occupancy of this terrain in a steady-state on two temporal scales: in snapshots and by long-term averages. The simulations reveal some general scaling laws that are applicable in various environments, independently of the mechanism of fragmentation. The edge of the connected region (the hull) is a fractal with dimension 7/4. Its width and length changes with the gradient according to universal scaling laws, that are characteristic for percolation transitions. The results suggest that percolation theory is a powerful tool for understanding the structure of range margins in a broad variety of real-life scenarios, including those in which the environmental gradient is combined with fine-scale heterogeneity. This provides a new method for comparing the range margins of different species in various geographic regions, and monitoring range shifts under climate change.

22. Ishida K., Oborny B., Gastner, M. (2021) Agent-based neutral competition in two-community networks. Phys. Rev. E 104: 024308.

Competition between alternative states is an essential process in social and biological networks. Neutral competition can be represented by an unbiased random drift process in which the states of vertices (e.g., opinions, genotypes, or species) in a network are updated by repeatedly selecting two connected vertices. One of these vertices copies the state of the selected neighbor. Such updates are repeated until all vertices are in the same "consensus" state. There is no unique rule for selecting the vertex pair to be updated. Real-world processes comprise three limiting factors that can influence the selected edge and the direction of spread: (1) the rate at which a vertex sends a state to its neighbors, (2) the rate at which a state is received by a neighbor, and (3) the rate at which a state can be exchanged through a connecting edge. We investigate how these three limitations influence neutral competition in networks with two communities generated by a stochastic block model. By using Monte Carlo simulations, we show how the community structure and update rule determine the states' success probabilities and the time until a consensus is reached. We present a heterogeneous mean-field theory that agrees well with the Monte Carlo simulations. The effectiveness of the heterogeneous mean-field theory implies that quantitative predictions about the consensus are possible even if empirical data (e.g., from ecological fieldwork or observations of social interactions) do not allow a complete reconstruction of all edges in the network.

23. Oborny B., Zimmerman D. (2022) Advancing and retreating fronts in a changing climate: a percolation model of range shifts. Ecography [under review].

Climate change causes considerable shifts in the geographic distribution of species worldwide. We propose a new method for movement range delineation based on percolation theory. We suggest marking the boundary between the connected and fragmented occurrence of the species (the hull). We demonstrate the advantages of this connectivity-based method on simulated examples in which a metapopulation is advancing vs. retreating along an environmental gradient with different velocities. The simulations show that the hull is a fractal and has the same dimension (7/4) even when the front is advancing or retreating relatively fast, compared to the generation time. It is particularly robust in the retreating (trailing) edge. Accordingly, we propose marking the range edge at the mean position of the hull, the 'connectivity limit' of the species. Theoretical considerations suggest that the connectivity-based method is broadly applicable to real-life data.

*IV. Other publications supported by the project:*

24. Csákvári, E., Fabók, V., Bartha, S., Barta, Z., Batáry, P., Borics, G., Botta-Dukát, Z., Erős, T., Gáspár, J., Hideg, É., Kovács-Hostyánszky, A., Sramkó, G., Standovár, T., Lengyel, Sz., Liker, A., Magura, T., Márton, A., Molnár V., A., Molnár, Zs., Oborny, B., Ódor, P., Tóthmérész, B., Török, K., Török, P., Valkó, O., Szép, T., Vörös, J., Báldi, A. (2021) Conservation biology research priorities for 2050: a Central and Eastern European perspective. Biological Conservation 264: 109396.

One of the main goals of the EU Biodiversity Strategy for 2030 is to avoid further loss of biodiversity and to restore ecosystems in the future. For effective conservation it is essential to bring together the policy makers, researchers and society on national and as well as international levels. These efforts can be facilitated if we collect the main research topics related to conservation biology to provide new evidence for the most urgent knowledge gaps. We used possible future statements from the Environmental Foresight – Hungary 2050 report to highlight likely future environmental and conservation problems and ask the experts to define research questions addressing these future statements. The study resulted in fourteen priority research topics. The main overarching themes include innovative technologies, involvement of local stakeholders and citizen scientists, legislation, and issues related to human health. We believe that our prioritisation can help science–policy discussion, and in the long run will eventually contribute to healthy and well-functioning ecosystems.

25. János Podani, Lajos Rózsa, András Szilágyi (2021) Annual plants, pigeons and flies: first signs of quantitative ecological thinking in Linnaeus’s works, Archives of Natural History 48(1): 94-110

Thinking about the dynamics of populations of plants and animals goes back to Linnaeus. He used at least three examples to show what happens when the population of a species grows without limitations and to illustrate the potential reproductive capacity of organisms. We examined the mathematical precision of calculations Linnaeus used in presenting these examples and reviewed the assumptions under which Linnaeus's conclusions are valid. In the case of a slowly reproducing annual plant, additionally cited by Darwin, the final result was incorrect, although little different from the true value. In the example of a pair of pigeons, the calculations were accurate, although the well-known fact that pigeons breed several times throughout their lifetime was ignored. Though the input parameters must have been unknown to Linnaeus, a short statement in Systema naturae regarding the population increase and feeding capacity of bluebottle flies was found fairly correct and robust enough to withstand minor changes in input parameters.

26. Gastner M.T., Takács K., Gulyás M., Szvetelszky Zs., Oborny B. (2019) The impact of hypocrisy on opinion formation: a dynamic model. PLOS ONE 14(6): e0218729.

We studied neutral competition by means of the voter model. We built and analyzed a two-layered network model of neutral competition between two alternatives (e.g., opinions or species). We compared the process from various initial conditions, varying the proportions between the two opinions in the external (revealed) and internal (hidden) layer. According to our results, the existence of the hidden layer always prolonged the extinction time. In a complete graph, this time span increased linearly with group size. We found that the group-level process consists of two steps: (1) fast and directional change, and (2) a slower, random drifts. During stage (2), the ratio of opinions in the external layer is approximately equal to the ratio in the internal layer; that is, the hidden opinions do not differ significantly from the revealed ones at the group level. We furthermore find that the initial abundances of opinions predicts the mean extinction time and determines the opinions’ probabilities of winning.