Final report

Subproject 1.

We entered a collaboration with spider ecologist Leticia Avilés (UBC, Vancouver) to study the ecological constraints on spider sociality. Avilés has been studying social and subsocial spider species for decades and has accumulated vast amounts of data on their life history, biogeography, behavior, etc. Using these data and her unmatched expertise in the topic, we created a spatial model to test how the varying environmental factors influence social tendencies in the modeled spider species. We modeled the Eastern slopes of the Andes by introducing distinct environments with varying disturbances and insect sizes. With the model we could reconstruct the naturally occurring species distribution patterns. We tested two previously published hypotheses on the geography of spider sociality, and found supportive evidence for both: i) we have shown that social spiders are mainly limited by the available insect sizes, as large colonies cannot be maintained without large insects, and that ii) subsocial species are limited by environmental disturbances, as their costly webs are impossible to maintain in heavy rains or wind. This work has been published in *The American Naturalist*.

We created a dynamical model to investigate the evolution of division of labor by cross feeding in bacterial communities. We pointed out that this type of mutualistic interaction can stably be present if producing the common good serves a density dependent private benefit. Furthermore, we have shown that coexistence of generalist and specialist producers is a typical outcome of selection. This paper is published in *Evolution*.
Syntrophic cooperation among prokaryotes is ubiquitous and diverse. It relies on unilateral or mutual aid that may be both catalytic and metabolic in nature. We constructed a simple mathematical framework of the ecology and evolution of these types of syntrophic partnerships. We have shown that cooperation is stable both ecologically and evolutionary. Studying in the case where partners cross-feed on each other's self-inhibiting waste. By contrast, systems where producers actively secrete enzymes that cross-catalyze their partners' resource consumption are not robust against non-producer cheaters. We conclude that if a pairwise cooperative interaction is expected to transform into a more intimate interaction, for example to ectosymbiosis and then endosymbiosis, cross-feeding type of associations are more likely to serve as a starting point for such an evolutionary scenario. The work is accepted by the *Scientific Reports* and will be published in the following months.
We have reviewed the major ideas proposing potential evolutionary routes from a cross-feeding, or syntrophic, community to the emergence of endosymbiosis, and beyond to organellogenesis. We raise the paradox of why there have been no observations of symbioses like those that produced the mitochondria and chloroplasts. We review the conditions where mutualisms (as an interspecific division of labor) can arise through multilevel selection that results in community-wide genetic inheritance leading to multilevel selection and heritable multispecies phenotypes. We ask the question, can such a unit be selected for and carry sufficient amount of information given that majority of the species are replaceable since there is a great redundancy in terms of the functional roles they perform in a community. We conclude that lack of such events indicates that microbes can only

undergo major evolutionary transition in individuality via endosymbiosis. This work is published in *Frontiers of Evolution and Ecology*.

We had two investigations focused on the general aspects of cooperation and communication. We have studied a simple public goods game 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 in the vicinity of the steady state. 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. This work was published in *Journal of Theoretical Biology*.
The other work considered the role of communication and coordination in the evolution and stability of cooperation within the framework of a strategic model. Our basic question was whether signaling cooperative intentions by employing both honest and dishonest cost free signaling strategies (cue), promotes or hinders the success of collective actions. We conducted our numerical investigations in an agent-based model and also made some analytical studies as well. We have shown that under reasonable environmental conditions cheaters cannot wipe out cooperation; in fact, cooperators may even exclude non-investing cheaters at high cooperation thresholds. If signaling is an inevitable side effect (cue) of cooperation, lying almost never pays off: even very cheap fake signals are selected against. Cue-driven threshold cooperation is a viable evolutionary strategy even for microbes that cannot keep track of past behavior of their potential cooperating partners and is free to mutate into any kind of cheater. Currently the manuscript is close to the phase for submitting.

Unfortunately, one planned part of the subproject needed to be brought to a halt. The reason for this is that concerns were raised about the authenticity of the data our models were based on, along with the integrity of our foreign collaborator.

Subproject 2.

We collected the data of the studied sport-charity campaign. We recorded the fundraisers' running distance and the amount of donated money and the information whether the name of the donor and/or the donated money were published. After the analysis of the data we pointed out that humans apply an egalitarian strategy in managing reputation in the studied sport-charity campaign. Donors can publish or hide their name and the amount in this campaign. We have found that donors giving less than the average amount prefer to hide the donated amount compared to donors giving average or high amounts. Further, donors giving very high amounts tend to hide their name from the public. Further, we have shown that athletes running longer distances collect more money for the organization. We think

that this correlation is present since running can be considered as a costly signal of altruistic behavior which is rewarded. This work was published in the journal of *Evolution Mind and Behavior*.
In the second phase public data of the fundraisers and donors were collected using web scraping techniques. The age of the fundraisers were estimated based on their photos using a deep learning algorithm. Further, we estimated the subjective cost of the fundraising (running) by using sentiment analysis of the introductory text of the fundraisers. We focused on how the communicated cost and goal of a charity run affected the potential donors. We analyzed the introductory texts of the runners presented online according to the cost and the social benefit of the fundraising communicated by them. We have shown that emphasizing more the subjective cost of running and the social benefit of the goal, or writing a longer text, attracted more donors, and even though the average amount of donation per donor did not increase, still led to a greater amount of donations collected overall by the fundraiser. It was also shown that a higher communicated subjective cost resulted in a higher ratio of opposite-sex donors, both in the case of male and female runners, suggesting that the communication of the cost of an altruistic act might be the object of sexual selection. Rather surprisingly we found that younger fundraisers tend to communicate a higher subjective cost than older ones. This work was accepted by *Behavioral Ecology and Sociobiology* and will be published in the near future.

Subproject 3.

In our original project outline we proposed an experiment to study whether charity behavior, through increasing the donor's reputation, could lead to increased cheating. We developed the experimental protocol for the planned experiments and received the ethical permissions from the authorities (EPKEB). We developed and implemented the software for the experiment, estimated the effect size, designed a statistical pipeline for the study and performed the pilot studies. We preregistered our study, including approaches, methods, and study plan (see https://osf.io/vsfnd/files/). By the end of the project we collected the necessary amount of data. However, due to an administrative error, the treatment distribution is still not balanced, thus we have to collect data from further ten or twelve subjects. We will collect the missing data, analyze them and write the publication in the beginning of the next year.

We note here that we faced various challenges throughout the experiment. First, we were forced to have a long break in data collection because of the covid pandemic. Further, we also had to move the experiment to another room, and to prepare a new student for being the experimenter, all of which caused further delay. Last, but not least, as a show-up fee we could only pay a symbolic amount of money for participation, which made the recruitment extremely (and unexpectedly) difficult.

Other satellite works connected to the projects

One of our members (JM) was involved in a project which investigated how working time reduction affects CO2 emission and ecological footprints. She collected the data, carried out

the statistical analysis, and provided professional support as a data scientist for a review article published in *Environmental Research Letters*. (Since reduction of CO2 emission is one of the most important recent collaborative challenges of the world this work is clearly connected to the general aims of the project.)
We studied the evolutionary background of parental care as a specific case of division of labor with the help of a comparative study. We found significant correlation only between parental care and sexual selection, while anisogamy and sexual selection seemed to be uncorrelated. Our result which was published in *Scientific Reports* questions the validity of the Darwin Bateman paradigm.
Microbiomes provide key ecological functions to their host. The intestinal microbiota of salmonids is characterized by few dominating species. Healthy fish coexist with a mutualistic *Mycoplasma* sp. species, while stress allows the spread of pathogenic strains, such as *Aliivibrio* sp. and after the stress, the *Mycoplasma* does not recover. *Aliivibrio* sp. often remains the dominant species, or *Mycoplasma–Aliivibrio* coexistence was occasionally observed. We devised a model involving interactions among the host immune system, *Mycoplasma* sp. and a toxin-producing pathogen. Our model is in harmony with experimental results that host–*Mycoplasma* mutualism prevents the spread of pathogens. Contrary, stress suppresses the host immune system allowing dominance of pathogens, and *Mycoplasma* does not recover after stress disappears. This work was issued in *Frontiers in Microbiology*.

Investigations motivated by the COVID-19 pandemic

The COVID pandemic significantly modified our life and this situation encouraged us too to help the fight against this pandemic with our research.
We investigated how the presence and size of groups where lockdown does not prevail (nursing homes, meat factories, schools, etc.) modifies the total number of infected people and the decay rate of infection. We pointed out that the number of these groups has a smaller effect on the dynamics than their size, so decreasing the number of persons in the same airspace is an effective strategy against the spread of the infection. This work is issued in *Biophysics Journal*.
Another work in this topic which has shown that the mobility drop in the cell-phone data is a good proxy for the main characteristics of the country level epidemics was published in the *Scientific Reports*. According to the number of citations within two years we can say that this paper has a significant impact on the field.
Intensified anxiety responses and even symptoms of post-traumatic stress are commonly observed under quarantine conditions. One of our members collaborated in a study where they measured the effects on fear, anxiety and wellbeing of the pandemic in a sample of Hungarians. The work was published in *Psychologia Hungarica Caroliensis* and we plan to publish the results in an international journal as well (https://psyarxiv.com/feth3).

Popular science, science communication, conferences

We have organized and carried out two personal and two online workshops within the framework of the Evolution is fun project. https://www.evolutionisfun.hu/index.html. Three

of us (AF, JM, IS) wrote six popular science papers connected with human cooperation or COVID pandemics in *Qubit*. IS wrote a paper in *Természet Világa* about the evolutionary origin of human musicality, which is again related to human cooperation. JM was a coauthor of the Covid: Olyan, mint az influenza csak halálosabb (Covid is like a flu but more deadly) titled popular science book about COVID pandemics which was issued by Typotex publisher in 2021.
JM and her colleagues created a webpage (https://koronavirus-kisokos.eu) that provides easy to understand information about SARS-CoV-2 and Covid-19. Members of the group had taken part in the Researchers' Night program every year within the project period. The members of the group had 7 interviews in various Hungarian media within the period of the grant. Further, we presented our results on 15 national and international conferences and workshops within the period of the project.