Ultimate Ecology

How a Socio-Economic Game Can Evolve into a Resilient Ecosystem of Agents

Yannick Oswald

Institute of Systems Sciences, Innovation and
Sustainability Research
Karl-Franzens University Graz
Graz, Austria
yannick.oswald@edu.uni-graz.at

Thomas Schmickl

Artificial Life Lab of the Institute of Zoology
Karl-Franzens University Graz
Graz, Austria
thomas.schmickl@uni-graz.at

Abstract — **This article introduces a novel approach towards modeling evolutionary game-theoretical systems by creating a self-regulating societal ecosystem. We here develop a very simple model of a cooperating agent population that interacts with a dynamically changing environment. These interaction patterns are initially random but adapt with time in a process mimicking natural adaptation and selection in biological evolution: Ultimately, a homeostatic system emerges from scratch that regulates the growth of populations and environmental resources in a sustainable way, exhibiting strong resilience to perturbations. Moreover, the agent population exhibits horizontal social behavior represented by the Ultimatum Game but also vertical evolution-relevant behavior represented by reproductive strategies. The interplay between these horizontal and vertical mechanisms is in the focus of the analysis presented here. We found emergence of co-dependent horizontal and vertical norms. Ultimately, we analyzed the interplay between micro- and macro-properties and found significant effects, suggesting occurrence of emergence within the system: Micro properties are local and individual while macro properties are global and population-wide. We show that both levels interact and influence each other bilaterally as a result of the nonlinear and complex system behavior.**

Keywords — Evolutionary Game Theory, Ultimatum Game, Co-evolution, Emergence, Dynamic Equilibrium, Ecosystem Models, Evolutionary models, Nonlinear complex systems.

I. INTRODUCTION

Understanding why, how and under which conditions unselfish-cooperative behavior emerges is a fundamental research target in biology, sociology and economics. This is a challenging endeavor, as the evolution of natural organisms and ecosystems, as well as the evolution of societal and economical systems are both complex and intrinsically dynamic. Complex macro behavior emerges from a set of relatively simple microscopic key interactions that ultimately govern the global dynamics. A classical approach to study those patterns of interaction is the Ultimatum Game (UG) that empirically studies social interaction patterns among living agents (humans and animals) world-wide. It is widely discussed in evolutionary game theory and experimental economics. In the rudimentary version of the game, the rules are as follows: There are two players, a proposer and a responder. The proposer receives a certain amount of money and has the obligation to share a deliberate proportion with the responder. It is then up to the

responder to accept or deny this offer. Upon acceptance both parties can keep their shares, otherwise the money is lost for both. We here regard the UG as a generic representation for cooperative or uncooperative behavior between two or more individuals, similar to [1]. In contrast to [1], we do not distinguish between human interactions or cooperation in the animal kingdom. Thus, we use the UG as a general simple model of interactive individual-level behavior from which a systematic collective cohesion, a social norm, can emerge. Collective cohesion is not limited to humans but a characteristic property throughout the realm of life [2].

The literature on evolutionary spatial games is extensive and so is the discourse on evolution in the spatial UG [3]. In [3] a classification system for evolutionary UG models is suggested: There, specific classes emphasize different aspects of the UG. The classes include 1. alternating-role models, 2. reputation based models, 3. noise-based models, 4. spite-based models, 5. spatial- population and structure based models and 6. empathy-based models. In summary, the characteristics of the agents, their relations among each other and the game rules themselves can be varied in order to test their impact on the resulting level of cooperation. In addition to this classification in [3], a lot of research has been dedicated to the relationship between network topology, networked populations and the respective level of cooperation in the UG [4-6]. Moreover, more exotic and more complex games like multiple-player-games recently have been attracting attention [7]. While these model varieties represent important aspects of reality, no UG has yet been embedded into a dynamic but self-stabilizing ecosystem. In order to be considered a reasonable approximation for interactions among
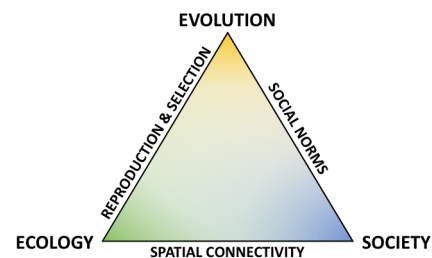

Fig. 1.   The interplay between ecology, evolution and society as the crucial factors of development in our model system.

individuals, an evolving UG playing population needs to satisfy ecological population dynamics. In precise terms, it needs to be able to exhibit density-dependent, thus self-regulating, logistic population growth in the fashion of Verhulst [8-9]. We emphasize that a natural population is able to enter a dynamic equilibrium respecting the environment's carrying capacity [10]. Such dynamic equilibria are fundamental for evolving populations and thus for the evolution of life itself. In order to respect these natural aspects, we model a system that can show emergence of cooperative behavior and that is as "life-like" as possible. Fig. 1 subsumes our concept to model the interplay between ecology (the flow of resources and populations), evolution (reproduction, mutation and selection) and the social and economic interactions of agents, which are represented by the UG. The importance of such a threefold approach, considering genetic, cultural and environmental co-evolution, for the purpose of investigating human sociality has for example been stressed by Herbert Gintis [11]. Yet it has not been brought forward into evolutionary game theory. Concerning these three perspectives, we ask the following research questions:

1. **Ecological Perspective:** Can the Ultimatum Game be the basis for a self-stabilizing population and environment? If so, what equilibria are obtained? Which constraints do these equilibria depend on?

2. **Social Perspective:** Does a certain social norm that governs UG behavior emerge within the population? Is the emerging behavior cooperative or uncooperative? Do ecological or evolutionary factors influence this social norm? Are the emerging norms in accordance with existing literature reports?

3. **Evolutionary Perspective:** Does dominant reproductive behavior emerge within the population? Is the system converging towards a certain number of offspring per agent? Is the system converging towards a certain paternal share of resources with agents' offspring? Are those reproductive strategies tied to certain ecological conditions?

Firstly, the ecological perspective asks whether it is possible at all to set up the UG as a novel self-stabilizing ecosystem, including a dynamic but self-regulating population and environment. Secondly, the social perspective asks whether a certain social norm concerning cooperativeness emerges. Finally, the evolutionary perspective investigates the life cycle of individuals, i.e. birth, death, reproduction and especially the inheritance of characteristics by the offspring.

II. THE MODEL

The agent-based model is implemented in Netlogo 5.3.1. Agents represent socially interacting humans, animals or organisms that depend on an act of agreement among each other. "Patches" represent the underlying and enclosing environment. Thus "patches" are the atomic elements representing space in a lattice-like discrete way in our model. The initial population density (*D*) of agents is the number of agents over the number of patches. Density values above 1.0 indicate that more than one agent is present on each patch on average. However, the agents are homogenously distributed across space. The patches only own one variable which is called energy $(E_j(t))$. Energy represents the free energy within the system. It is used by the agents to play the UG with each other. Fig. 2 depicts the fundamental mechanisms of the model. The basic unit of energy in our system is one "*e-unit*". Our system has a steady influx of energy added to each patch every time step, homogenously distributed in space. This way, a renewable but limited energy resource upholding the system is modeled, as it is also found within natural ecosystems, like our sun is providing ecosystems on earth with a constant and homogenously distributed radiation rate. The modeled agents move in an uncorrelated random walk in space. In Fig. 2 the accumulated energy resources on patches are represented as grass. Agents cannot access those resources alone, they have to cooperate pairwise in order to harvest those local resources. However, after the harvesting, they have to agree on sharing those collectively harvested resources to gain their individual shares of nutrients. In case they cannot agree those harvested resources get ultimately lost. This social interaction mechanism is very similar to the UG: An agent finds a partner for interaction randomly within a given radius in each time step and plays the UG for the resources it finds on the local patch. This way the agents sustain themselves and are able to pay their "living-costs (*c)*" that represent any sort of metabolic expenditures. The harvested resources are removed from the patches after each UG in any case. The focal agent acts as "proposer" and the local partner as a "responder" in the UG. Thus, each agent acts as "proposer" once per step but can be selected several times or never as a "responder". The population remains spatially well mixed by moving randomly over time, thus no preferred proposer-responder pairings are evoked. We set our living costs to *c=100* e-units/step and, in consequence, the maximum amount of energy that can be harvested to $g_{max}=300$ e-units/step. This combination allows each one of the two cooperating agents to gain 150 e-units/step on average, which is 50% above their metabolic expenditure rates. This means that 2 out of 3 games have to be played successfully by agents to stay on their energy levels in case that patches contain on average 300 or more e-units. These settings allow balanced system dynamics but put also strong selection pressure to play the game efficiently. Each agent *i* is fully described by eight variables: A genome consisting of 4 genes, gene#1 to gene#4 $(\gamma_1-\gamma_4)$, the level of individually stocked resources $(R_i(t))$, the agent's position $(<x_i(t), y_i(t)>)$ and orientation $(\varphi_i(t))$. In the genome, γ_1 determines the willingness to share and γ_2 represents the willingness to accept an offer in the UG. The higher those values, the smaller the share offered by the proposer and the larger the demanded share that can be accepted by the responder: If 1 - γ_1 of a proposer is greater or equal than γ_2 of the responder, then the game will be successful. For instance, if γ_1 of the proposer is 0.8 and γ_2 of the responder is 0.2, then the proposer will receive 80% of the resources and will hand over 20% of the resources to the responder. If 1 - γ_1 < γ_2, then the game will always be unsuccessful and nobody will receive anything. Furthermore, γ_3 is the share of individually stocked resources passed over to an agent's offspring and γ_4 determines the number of offspring produced. These progeny then have to share those inherited resources equally among each other. γ_4 is modeled as an integer number between 0 and *f*, with *f* being the maximum number of offspring each agent can produce per reproduction event.
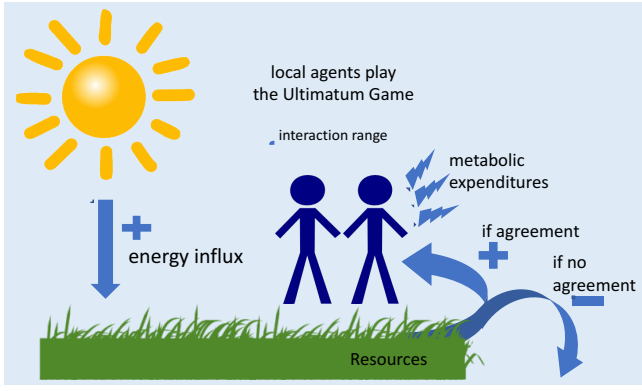
Fig. 2. Schematic representation of the model. Our model assumes a constant energy influx, comparable to our sun in natural ecosystems. This energy influx manifests in the form of persistent environmental resources, depicted as grass. The agents in our model move randomly within this environment, they encounter energy and play the Ultimatum Game for these harvested resources. If successful, they store these resources into their own stocks, otherwise those resources get lost. Over time agents loose stocked resources due to their metabolism. *Graphics from http://www.clker.com/*

Moreover, the agents are subject to a density-independent death rate (μ_i), determining each agent's probability to die in each time step. The agents in the initial population have an initial resource endowment which covers the first occurring living-costs. From the second time-step onwards, they have to successfully play the UG in order to gain new resources and to stay alive. If its individual resources store falls to zero, an agent will die. Above a certain resource threshold ($\Theta_{reproduction}$) an agent reproduces and lives on afterwards, thus we model overlapping generations.

TABLE I.   KEY PARAMETERS

Variables & constants	Description	Initial Value	Dimension
$< x_i(t), y_i(t) >$	Position of agent i at time step t	$< [x_{max}, y_{max}] \epsilon Z^2 >$	length units, length units
$\varphi_i(t)$	Orientation of agent i at time step t	$[0, 360] \epsilon R$	degree
t_{max}	Simulation runtime	$\epsilon \{1700, 2500\}$	steps
t	Time step	$[0, t_{max}] \epsilon Z$	steps
$G_i = < g_1, g_2, g_3, g_4 >$	Genome of each agent i	$< [0,1]^3 \epsilon R^3, [0,1] \epsilon Z >$	dmnl[4]
$R_i(t)$	Resources of agent i at time t	R_0	e-units
$E_k(t)$	Energy stored as resources in patch k at time t	E_0	e-units
r	Interaction radius of agents	4	length units
D	Population density	$\epsilon \{0.5, 1.25, 1.5\}$	agents/patch
$I_k(t)$	Energy input on each patch k	$\epsilon \{75, 150, 250\}$	e-units/step
R_0	Initial resources of each agent	1000	e-units/agent
E_0	Initial energy on each patch	500	e-units/patch
$\Theta_{reproduction}$	Reproduction threshold	$\epsilon \{3000, 10000\}$	e-units
μ	Mortality rate of agents	1%	dmnl
f	Max. # of offspring (DOF)	10	dmnl
c	Energy cost of living	100	e-units/step
g_{max}	Energy gain of successful	300	e-units/game
$\gamma 1$	Value of gene 1: Willingness to share	$[0,1] \epsilon R$	dmnl
$\gamma 2$	Value of gene 2: Willingness to accept	$[0,1] \epsilon R$	dmnl
$\gamma 3$	Value of gene 3: Willingness to give to offspring	$[0,1] \epsilon R$	dmnl
$\gamma 4$	Value of gene 4: Number of offspring per reproductive act	$[1,10] \epsilon Z$	dmnl

Agents reproduce asexually. Through reproduction they pass on a certain amount of their stocked resources (γ_3) to their offspring.

For instance, if γ_3 is 0.8 then the agent will pass on 80% of its resources to all offspring with an equally divided share among them. Agents not only pass on resources to their offspring but also their individual values of γ_1 - γ_4. These genes are subject to mutation which makes our model stochastic in character. The mutational rate has a uniform distribution ±x around a mean value of zero. Table 1 summarizes the key parameters of our model, their set initial values and their dimensions.

III. METHODS

Our experimental study layout is structured along the three research perspectives and thus along the research questions discussed in section I. In all experiments, the habitat was modeled as a connected lattice of 16 by 16 patches.

A. Ecological Perspective

In order to find out whether the system enters a self-regulating ecological equilibrium, we ran the model in the long-term. Furthermore, we evaluated the population density and the amount of free energy inflow into the system and checked for stable equilibria. Afterwards we investigated the effects of individual and environmental factors. At first, we evaluated whether or not different starting population sizes yield the same population equilibrium. In order to do so, we initialized our system with initial densities of 50% (small population), 125% (close to equilibrium population) and 250% (very large population) and observed the consecutive population dynamics with 100 repetitions each. Secondly, we tested whether or not the emerging population density equilibria are dependent on the energy abundance in the system, which is in turn determined by the current energy influx. Therefore, we perturbed this influx $I_k(t)$ during specific periods of time. We expected a positively proportional relationship between $I_k(t)$/c and the resulting population density. In total, we conducted 300 runs, 100 for each setting with a duration of 1700 time steps.

B. Sociological Perspective

At first, our goal was to see whether or not a social norm can evolve in the system over time at all. Therefore, we analyzed the final values of γ_1 and γ_2 in the *"genospace"* for whole populations at the end of each run. Secondly, we investigated whether or not this social norm depends on ecological and evolutionary factors by analyzing γ_1 and γ_2 after 2500 time steps in environments with different energy influxes (75, 150 and 250 e-units/step) and different reproduction thresholds ($\Theta_{reproduction} \in \{3000, 10000\}$ e-units) of agents. For each configuration, we conducted 500 simulation runs of our model.

C. Evolutionary Perspective

In order to investigate the dominant reproductive strategy emerging in our system, we measured how much progeny successfully proliferating agents produce per reproduction event and how much of their stocked resources they inherit to them. Importantly, we also analyzed if this reproductive strategy is influenced by micro- and macro-constraints, such as the reproductive threshold agents exhibit or the amount of energy influx into the environment. For all runs the parameter f has been set to 10, therefore γ_4 could take any integer value

between 1 and 11, giving agents 10 degrees of freedom concerning their reproduction. We ran the model for 2500 time steps in three different energy influx settings (75, 150 and 250 e-units/step) and for two different reproduction thresholds ($\Theta_{reproduction} \in \{3000, 10000\}$ e-units). Each combination of parameters was simulated 500 times.

IV. Results

A. Ecological Perspective

Fig. 3A shows the first 200 time steps of our simulation runs. Testing three different initial population densities we see that all runs converged to the observed long-term average of 1.32 agents/patch. Fig. 3B shows that also the resource abundance converged to the same long-term equilibrium of 225.78 e-units/patch with all initial population densities, after a period of initial deviation due to those differing initial agent populations. These equilibria were stable no matter from which initial population the system came from, given that all other conditions were held constant. Fig. 3C and Fig. 3D show the population and resource dynamics in the long-term run. During the period of $t \in \{500, 501, ..., 799\}$ and $t \in \{1100, 1101, ..., 1399\}$ we perturbed the system by decreasing the energy influx into the habitat by 100 e-units (first period) or increasing it by 100 e-units (second period) respectively to a base value of 150 e-units. Population dynamics and resource dynamics almost immediately found an alternative equilibrium, thus we observed self-regulation of the emerging ecosystem to compensate for these new situations.

Our statistical analyses of the data in Fig. 3C and D show that in periods of enriched energy input ($I_k(t) = 250$ e-units/step) the mean agent density (Mann-Whitney U-test, $N_1=200$, $N_2=500$, $W=2.09*10^5$, $p<10^{-4}$) and the mean resource density in the environment (Mann-Whitney U-test, $N_1=200$, $N_2=500$ $W=2.05*10^5$, $p<10^{-4}$) were significantly elevated above the level of standard energy input ($I_k(t)=150$ e-units/step). Analogously, there was a significantly lowered mean agent density (Mann-Whitney U-test, $N_1=200$, $N_2=500$, $W=2.09*10^5$, $p<10^{-4}$) and a significantly lowered mean resource density in the environment (Mann-Whitney U-test $N_1=200$, $N_2=500$, $W=129.5$, $p<10^{-4}$) in periods of low energy influx ($I_k(t)=50$ e-units/step for each patch k in our model world).

B. Social Perspective

In order to answer research question number two, we plotted phase plots of γ_1 versus γ_2. Fig. 4 shows the means of the distribution of these genes finally emerging in populations in 500 independent runs. We observed the distribution of these means in three different levels of energy influx $I_k(t)$ (75, 150 and 250 e-units/step) and with two different reproduction thresholds $\Theta_{reproduction} \in \{3000, 10000\}$ e-units). Overall, we found that the social behavior of agents clustered in a very specific region of our genospace, somewhere between a completely rational and a completely fair behavior.
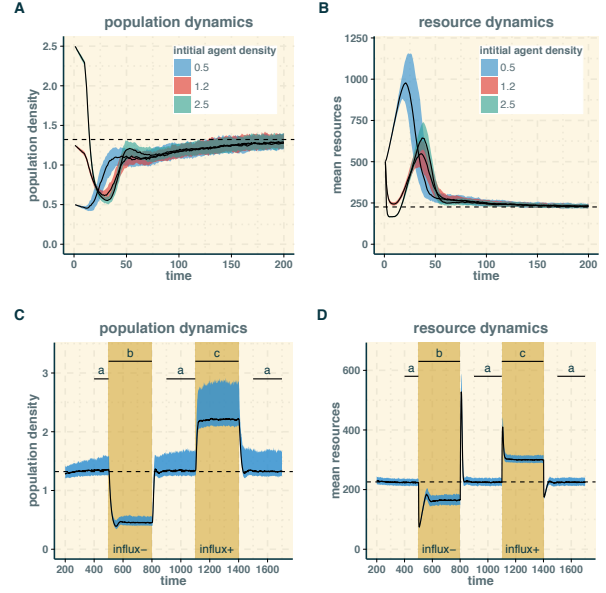

Fig. 3. Ecosystem dynamics established by cooperating agents. A+B: The effect of initial starting populations on population dynamics (A) and on environmental resource dynamics in the first 200 time steps (B). C+D: The effect of perturbations of energetic inflow into the system on population dynamics (C) and on environmental resource dynamics in long-term simulation runs. Dark solid lines indicate medians, blue ribbons show the span between 10th and 90th percentile (90% of all results). Vertically shaded golden areas indicate perturbation periods, during which the energy influx was altered. Dashed horizontal lines indicate the observed median values during undisturbed periods in long-term runs (1700 time steps), thus they indicate an emergent "carrying capacity" of the system. N=100 simulation runs for each setting in (A) and (B) and 300 simulation runs for (C) and(D). Horizontal bars indicate the periods we statistically analyzed against each other (Mann-Whitney U-test) and different letters at these bars indicate significantly different medians of system variables during these times.

No clusters of irrational strategies emerged. There always emerged a certain benefit bias towards the proposer, as all data points reside in the lower left triangle area of the phase plots in Fig. 4. Moreover, the emerging strategies were found to be rather insensitive to the level of energy coming into the system. On the contrary, there seems to be a clear difference of strategies that emerged from a system with a reproduction threshold of 3000 e-units (blue triangles) and a system where this parameter was set to 10000 e-units (red squares).

In the latter configuration agents tended to lean slightly towards fairer strategies having a considerable amount of population-wide mean values below 0.75 for γ_1 and around 0.25 for γ_2. Additionally, we plotted the estimated density distributions of these observed mean values across the population (Fig. 5), where the blue areas depict densities for $\Theta_{reproduction} = 3000$ e-units and the red areas depict densities for $\Theta_{reproduction} = 10000$ e-units. In this visualization, the emerged differences between the observed distributions are even more obvious. With a higher reproduction threshold, the social behavior of the agents tends towards more fairness and cooperation. With a lower reproduction threshold, the social behavior of the agents tends towards more 'rational', uncooperative and egoistic behavior.
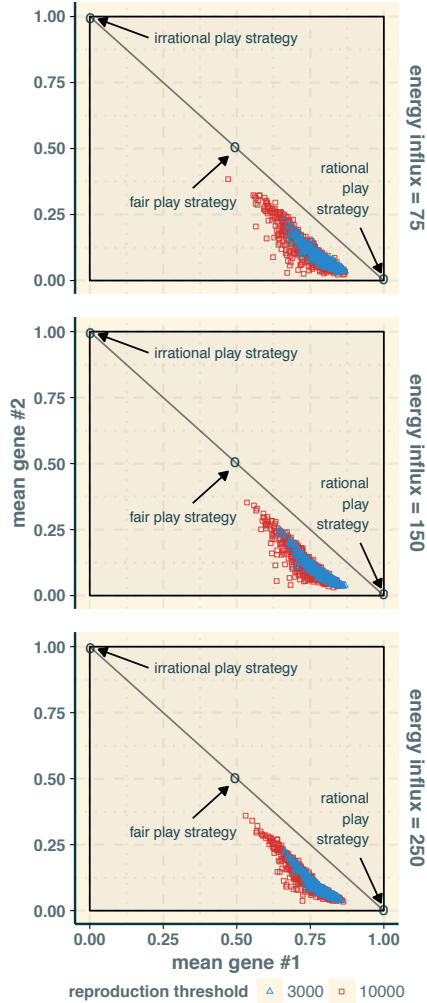
Fig. 4. Evolved social norm with different reproductive energy thresholds and different environmental conditions (energy infux differs) after t=2500 time steps. N=500 repetitions for each setting. Red squares: Population means at $\Theta_{\text{reproduction}}$=10000 e-units. Blue triangles: Population means at $\Theta_{\text{reproduction}}$=3000 e-units.
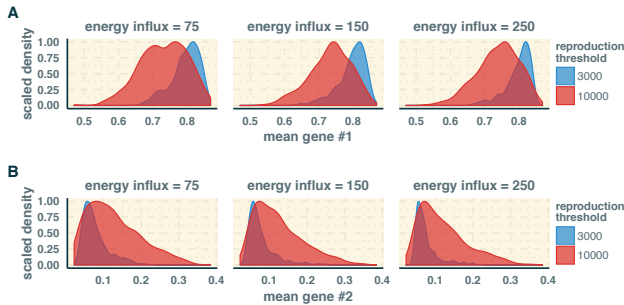

Fig. 5. Density estimates (normalized to 1.0) of the evolved social norms with different reproductive energy thresholds and different environmental conditions (energy infux differs)) after t=2500 time steps. N=500 repetitions for each setting. Red areas: Observed density distributions for $\Theta_{\text{reproduction}}$=10000 e-units. Blue areas: Observed density distributions for $\Theta_{\text{reproduction}}$=3000 e-units.

C. Evolutionary Perspective

In order to answer the third research question, we produced phase plots of γ_3 versus γ_4 (Fig. 6). We distinguished in our analysis three different levels of energy influx and the two different reproduction thresholds, similar as in section IV-B. We plotted the finally emerging population-wide mean values of γ_3 and γ_4 for each population in all 500 runs for each setting. Concerning the different rates of energy influx, we found that the spread of means in the population was larger with lower energy influx and the results were more tightly clustered with higher energy influx. However, even more notable are the two clusters emerging from two different reproduction thresholds. With $\Theta_{\text{reproduction}}$=3000 e-units, γ_3 clustered around high values, meaning these agents handed over larger shares of their own stocked resources to their offspring. For $\Theta_{\text{reproduction}}$=10000 e-units, these gene values clustered at lower values, meaning that these agents handed over smaller shares of their reserves. Besides that, it is notable that with a higher energetic threshold for reproduction the agents evolved to have either a lot more offspring per reproduction event, or they evolved to have considerably less offspring with a lower energetic threshold. Looking at details, we found that agents evolved towards extreme values over time, thus they evolved differing reproductive strategies. For instance, in the case of an energy influx at 75 e-units/step, the largest population-wide mean number of offspring was above 8.0 offspring/event and the minimum value was very close to zero. Contrarily, with a lower threshold the maximum value was only around 6.0 offspring/event and the minimum resided around 2.5 offspring/event, thus the mean values and the variances within such agent populations differed concerning the offspring numbers. To get a clearer picture on these findings, we plotted the estimated density distributions of these results (Fig. 7) showing these differences of medians and variances clearly.

We found that higher offspring numbers tended to be paired with low parental supply for offspring while in strategies with lower numbers of offspring more supplies were passed over across generations. These reproductive strategies are known as r-strategy and K-strategy in biology. They emerged in our system induced by different biological clocks: Agents which reproduced early with low amounts of stocked resources developed a strategy of 'cheap mass production' (r-strategists), while long-lived agents, that reproduce only after longer times of resource accumulation, tended to produce fewer but better equipped offspring (K-strategists).

D. Macroscopic effects emerging from microscopic mechanisms

Finally, we investigated whether or not the individual evolutionary mechanisms are connecting the microscopic (proximate) mechanisms to the observable macroscopic (ultimate) properties of our modeled system. With different reproduction thresholds of agents, different population density equilibria and different resource equilibria of the habitat emerged (Fig. 8). Therefore, not only macro-ecological conditions, as shown in subsection IV-A, were found to

determine the state of the system but also the local and individual characteristics of the agents. Our statistical analyses show that both the reproduction threshold as well as the tested environmental influx rates have a significant effect on the macroscopic global properties of the system: A higher reproduction threshold led to a significantly lower agent density (Kruskal-Wallis test X^2=183.26, N_1=N_2=500, df=1, p<10^{-4}) and to a significantly higher level of standing resources in the environment (Kruskal-Wallis test, X^2=393.08, N_1=N_2=500, df=1, p<10^{-4}). An increased inflow of energy into every patch at every time step led to an increased density of agents (Kruskal-Wallis test, X^2=2631.6, N_1=N_2=500, df=2, p<10^{-4}) and, despite this higher number of consumers, also to a significantly higher environmental resource abundance (Kruskal-Wallis test, X^2=2314.8, N_1=N_2=500, df=2, p<10^{-4}).
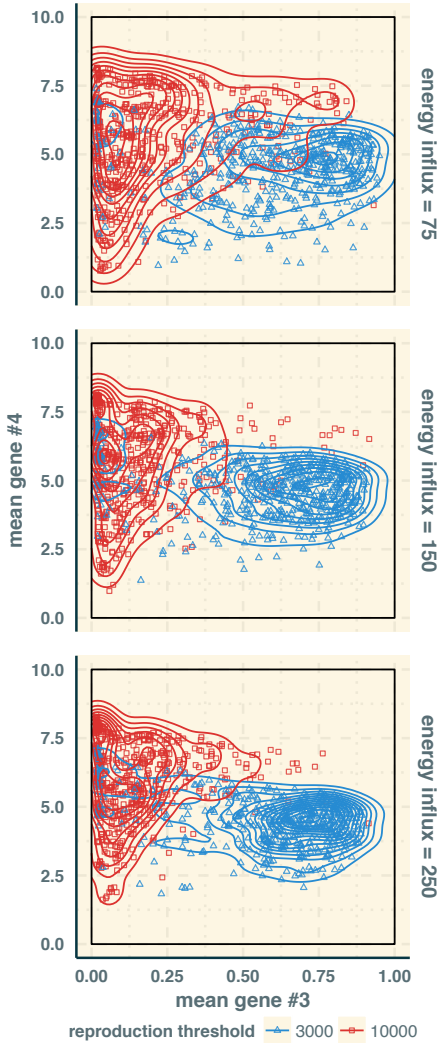

Fig. 6. Evolved evolutionary/reproductive strategies with different reproductive energy thresholds and different environmental conditions (energy infux differs) after t=2500 time steps. N=500 repetitions for each setting. Red squares: Population means at $\Theta_{reproduction}$=10000 e-units. Blue triangles: Population means at $\Theta_{reproduction}$=3000 e-units.
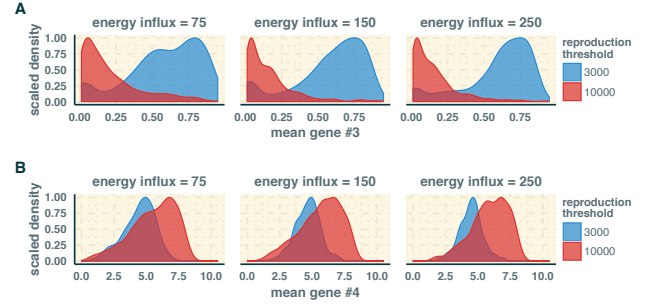

Fig. 7. Density estimates of evolved reproductive strategies with different reproductive thresholds and different environmental conditions (energy infux differs) after t=2500 time steps. N=500 repetitions for each setting. Red areas: Observed density distributions for $\Theta_{reproduction}$=10000 e-units. Blue areas: Observed density distributions for $\Theta_{reproduction}$=3000 e-units.

ANOVA indicates a strong combined effect of the energy influx and of the reproductive threshold on the median agent population density (F=131.4, df=2) and on the median resources on each patch (F=20.88, df=2, p<10^{-4} for both tests).

V. DISCUSSION

Page, Nowak and Sigmund [12] pioneered models of evolutionary spatial Ultimatum Games. They modeled an agent population with agents conceptualized as neighboring squares in a grid. All agents play exhaustively with each other at every time step, accumulating their payoffs. The next generation is produced proportionally to each agent's respective share of the cumulative payoff. Such global "fitness-function" approaches to evolution prevail in most recent work [4, 13, 14, 15]. In contrast to these approaches, our model presented here depicts agents as dynamic individuals which interact not only with each other but also with their environment. Thus, the environment takes on a crucial role in determining the agents' fate, but so do the agents take on a crucial role in determining the state of the environment. Not only is this feedback, between agents and environment, a new mechanism in evolutionary UGs, but also the approach to reproduction is novel here. In previous work, the "fitness-function" reproduction was essentially a global procedure which acted upon the system as a whole. However, in real eco-systems every individual takes care of its own reproduction under consideration of the local conditions it faces and independently from the overall global population. Our model mimics this localization and individualization of reproduction. What happens to the overall population and the overall system are emergent consequences and not global prescriptions. Furthermore, we have investigated a system in which a social norm evolves that regulates horizontal resource sharing among the agents (UG, γ_1 and γ_2) but also vertical resource sharing among generations (reproductive strategy, γ_3 and γ_4). This combination of horizontal and vertical cooperation is, to the best of our knowledge, an entirely novel approach to evolutionary Ultimatum Games. The evolutionary process modeled here was used without a model of evolving cooperative social interaction in the studies of [17] and [18] for animal predator-prey systems.
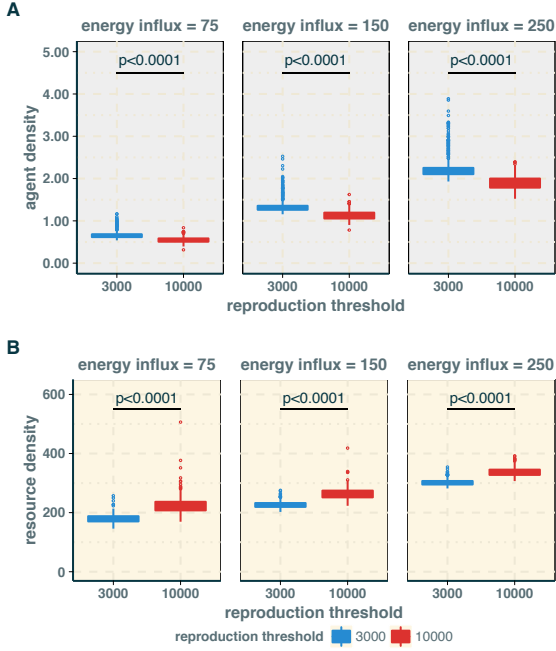
Fig. 8. Effect of the microscopic reproductive resource threshold on (A) the emerging population density and (B) on the final resource abundance in the environment under different energy influx conditions after t=2500 time steps. N=500 repetitions for each setting. Red box plots: Population medians and IQR of populations with $\Theta_{reproduction}$=10000 e-units. Blue box plots: Population medians and IQR of populations with $\Theta_{reproduction}$=3000 e-units.

The resulting range in γ_1 and γ_2 to which our populations converge is 2% to 25% for γ_2 and 15% to 45% for (1-γ_1), thus it is closer to rational behavior than reported in [12, 14]. It also includes less cooperative values than the average of the empirically measured values for (1-γ_1) in human populations ($\approx$ 42%) around the globe [16]. Regardless, our evolved behaviors are still significantly different from completely rational behavior. The model results attained by [15], for instance, are very similar to ours and will only show more cooperation if the probability for ongoing role switching from proposer to responder becomes very high. However, these models are based on different assumptions and procedures. For example, in our case the population converges towards a level of cooperation that is necessary to sustain itself. In the models of [12, 14, 15] the continued existence of the population is a pre-programmed global property of the system. Systems in which resources are shared among a population of agents are often the basis of bio-inspired swarm algorithms, for example in [19, 20] whereby sometimes even the evolution of interaction norms is pursued in robotic swarms as the ultimate goal to produce long-lasting physically embodied agent societies that develop and adapt collectively over time [21]. Evolutionary robotics exploits the fact that robots (often also in groups) adapt their behaviors in a process roughly matching biological evolution. In a recent project [19] a swarm of robots evolves over time its mechanisms of interaction and habitat exploitation, to the best of our knowledge yielding the first physically embodied population of agents conducting cultural

evolution in order to optimize overall and individual performance. It is surprising that despite these conceptual differences the emerging social strategy is fairly similar. The range of the horizontal γ_1 is consistent over different initial resource conditions either. Consequently, the ecological perspective together with the social perspective suggest that there is a necessary minimum level of cooperation to sustain a functioning eco-system. Modeling the reproductive strategies into the evolutionary perspective is a novel feature. Therefore, there are no previous results we can compare them to. Nevertheless, we can identify some quite promising relationships between the vertical degree of cooperation and the horizontal one. We could demonstrate that as soon as reproduction requires more resources (because of higher reproduction thresholds), the overall population becomes horizontally more cooperative. While a higher reproduction threshold leads to more horizontal cooperation (Fig. 4), it does lead to a lower vertical cooperation, as is expressed by γ_3 (Fig. 6). In both cases individual agents maximize their long-term resource access, either by cooperating with other individuals or by limiting the resources given to offspring to the necessary. On the other hand, a lower reproduction threshold is clearly connected to more vertical and less horizontal cooperation. Importantly, the value of γ_3 displays a relative number between 0.0 and 1.0. For example, a value of γ_3=0.1 means that an agent with high reproduction threshold, which has therefore accumulated many resources, may inherit a similar amount of resources to its offspring than an agent with a value of γ_3=0.3 and a low reproduction threshold. Thus, horizontal and vertical sharing exhibit an inversely proportional relationship. It is also noteworthy that the evolutionary process in our model occurs in parallel to ecological perturbations. This is a feature that has not been investigated in comparable systems yet. Such a parallelism of processes is closer to the natural situation of both focal systems: genetic evolution in animals and memetic or cultural evolution in humans are both not happening isolated from an intrinsically dynamic environment.

Despite the insights we have gained here, many questions have been left untouched. Throughout previous work, microscopic mechanisms, that are properties of the evolving agents, have been evaluated on their effect on the evolving degree of cooperation within the population. These micro-mechanisms include the mutational rate of offspring genes, the degree of randomness while assigning the role of proposer and responder, the reputation individual agents own, the degrees of freedom for the willingness to share and the willingness to accept and so forth. Likewise, macro-mechanisms and their effect on the degree of cooperation have been investigated such as the size of the model world, the size of the population or the role of social network topologies. For example, already the study of [12] could show that smaller neighborhoods lead to more cooperative populations because of the higher pressure to play successfully with the few interaction partners available. These studies showed that the higher the mutational rate of the offspring, the more cooperative the population becomes due to a larger diversity in the population, what demands more

willingness to cooperate. So far, we have constructed a functioning societal ecosystem. In the future, we want to test our societal ecosystems on the above-mentioned mechanisms. First and foremost, we would like to follow up on the influence of differently sized environments. We would like to see various populations evolve within a single system but with separated environments and to investigate whether distinct horizontal and vertical norms of cooperation emerge. Thereupon, we also would like to explore migration between the different environments and the effect of migration on the evolution of norms. In future extensions of the model we plan to include spatial and temporal heterogeneity of resources in order to represent cycles like day and night, winter and summer or diverse geographic resource conditions. As was recently shown by [22], there is a significant difference between equal sharing and fair sharing, an issue we plan to further investigate with our model presented here. Certainly, the Ultimatum Game is not the only possible way to model interactions within a population of agents. Other games from game theory, such as the Dictator Game, the Prisoner' Dilemma and so forth could be evaluated as basis for a societal ecosystem and be compared to the Ultimatum Game regarding applicability and effectiveness. However, the Ultimatum Game combines several important aspects for the purpose of modeling cooperation. It puts bilateral importance to proposer and responder unlike for example the Dictator Game, in which only the proposer is relevant for the outcome. It also is an adequate choice to model material interactions among agents and resource flows within an ecosystem unlike the Prisoners' Dilemma, in which immaterial goods such as freedom, are the subject-matter.

VI. CONCLUSION

We modeled a functioning societal ecosystem in which horizontal and vertical interactions between individuals evolve. Horizontal and vertical norms of cooperation and behavior emerge as well. The only horizontal and individual-based mechanism to sustain this societal ecosystem is the Ultimatum Game from economic game theory. Hence, we demonstrated that at least one economic game can be used as the basis to model a self-regulating, interactive and dynamic population. This effectiveness in being a basis for a self-regulating population is in our view evidence for the reasonability of representing social and economic interactions by the Ultimatum Game. We used a novel approach to combine the horizontal interactions of the agents with the vertical and intergenerational interactions. We showed that under different reproductive conditions, for instance different reproduction thresholds, different vertical but also different horizontal behaviors emerge within the population. At this point, we not only open the door for further investigation and discussion in evolutionary game theory but also in the discourse of gene-culture co-evolution.

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