Rock-Paper-Scissors dynamics in a digital ecology

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Abstract

In this paper we present an Alife-platform named *Urdar* aimed at investigating dynamics of ecosystems where species engage in cross-feeding, i.e. where metabolites are passed from one species to the next in a process of sequential degradation. This type of interactions are commonly found in microbial ecosystems such as bacterial consortia degrading complex compounds. We have studied this phenomenon from an abstract point of view by considering artificial organisms which metabolise binary strings from a shared environment. The organisms are represented as simple cellular automaton rules and the analogue of energy in the system is an approximation of the Shannon entropy of the binary strings. Only organisms which increase the entropy of the transformed strings are allowed to replicate. We find that the system exhibits a large degree of biodiversity and a non-stationary species distribution, especially during low rates of energy inflow, and that the time spent in each species configuration exhibits power-law statistics. Investigating the interaction between different species in the system by invasion experiments we observe that co-existence is a common feature and that some triplets of species exhibit intransitive, i.e. rock-paper-scissors like, interactions.

Introduction

The origin and maintenance of biodiversity has been a long standing question among ecologists (Hutchinson, 1959). One of the simplest ecological system where biodiversity emerges, and is stably maintained, is in populations of *E. coli* growing in a homogeneous environment limited by a single resource, usually glucose. The diversity is facilitated by cross-feeding (syntrophy), where one strain partially degrades the limiting resource into a secondary metabolite which is then utilised by a second strain. This phenomenon was first observed by Helling et al. (1987) and has since been reported to occur in other systems such as methanogenic environments (Stams, 1994), bacteria engaging in nitrification (Costa et al., 2006) and degradation of xenobiotic compunds (Dejonghe et al., 2003; Katsuyama et al., 2009).

The evolution of cross-feeding has been investigated by Pfeiffer and Bonhoeffer (2004) using a theoretical model, and their results showed that cross-feeding naturally emerges under the assumption that ATP production is maximised while the total concentrations of enzymes and intermediates are minimised. Further they showed that the evolution of cross-feeding depends on the dilution rate in the chemostat, and that a stable polymorphism is more likely to emerge at low dilution rates.

A different approach was taken by Doebeli (2002) who investigated the emergence of cross-feeding in the framework of adaptive dynamics. In this case the conditions for evolutionary branching and the appearance of cross-feeding are that there is a trade-off between uptake efficiency of the primary and seconday metabolites, and that this trade-off function has a positive curvature. The model also makes the correct prediction that cross-feeding is less likely to occur in serial batch culture, in which the primary resource is not replenished (Rozen and Lenski, 2000). This highlights the necessity of the secondary metabolite being present for an extended period of time for cross-feeding to evolve.

In this study we present a recent Alife-platform (Gerlee and Lundh, 2010) aimed at investigating the evolution of cross-feeding, but not in the context of a specific biological system, but instead we extract and analyse the general principles governing systems where cross-feeding might emerge. In its abstract nature the model will be more akin to an artificial chemistry (Dittrich et al., 2001), but with the difference that we make a distinction between the agents subject to an evolutionary process and resources which they consume for reproduction. The aim of this paper is to describe the new platform, present some new results, and discuss future investigations and possible extensions of the system.

The Model

To explain the motivation behind the plaform *Urdar*, let us consider the following thought experiment: a population of different species of bacteria inhabit a petri dish continually supplied with a given nutrient. The bacteria only partially metabolise the nutrient, which is added at a certain rate, so other bacteria might extract energy from the "left-overs" of this successive degradation. Assume that this experiment is carried out for a long period of time, so that species that do well will increase their share of the total population. Since we can imagine that different strains of bacteria have variations to their metabolism, we have that if a single species dominates the population, a certain type of left-overs will be abundant in the free pool of metabolites. Hence that would lead to higher number of offsprings of a species that is specialised on extracting energy from that kind of left-overs.

Please note that the model we will present is not specific to bacteria, but could represent any ecosystem where resources are consecutively degraded by several species, creating a network of interdependence. We set up such an experiment using artificial organisms or agents that are capable of successive degradation (transformation) of metabolites from which they extract energy used for self-maintenance and reproduction.

In our model we will use binary strings as the "foodstuff", and we will view the metabolic process as the degradation of ordered strings into strings with a higher degree of disorder. More specifically, let R be a pool of resources (or metabolites) $\{\mathrm{r}_i\}$ where each r_i is a binary string of length L, as for example $r_i = 00101\ldots01110$. Let A be the population $\{a_j\}$ of agents (or organisms), where each agent a_j is represented by a function that transforms binary strings into new binary strings, $a_j : R \rightarrow R$. We can view this mapping as a "metabolic digestion" of the string being transformed. More precisely the agents in A transforms resource strings from R in the following way

$$r_i^{\text{new}} = a_j(r_i^{\text{old}}).$$

Let now a positive function E on the binary strings in R represent the "energy state" of such a string. If the agent a_j is able to extract energy from the resource string r_i, we have that $E(r_i^{\text{new}}) < E(r_i^{\text{old}})$, and the amount of energy extracted is given by

$$\Delta E_j = E(r_i^{\text{old}}) - E(r_i^{\text{new}}).$$

The evolutionary dynamics are then introduced by a possible replication of the agent a_j to a daughter agent whenever $\Delta E_j > 0$. Replication in the current model is asexual and offsprings have just a single parent organism. The offspring is mutated with probability μ, and replaces another agent in the population, thus keeping the population size constant. The constant population size can be thought of as either being imposed by a space constraint, or by the carrying capacity of an additional nutrient required for biomass synthesis (assuming that the evolutionary dynamics related to this trait occurs on a much slower time-scale). The probability for a reproduction to take place is an increasing function of ΔE_j with zero probability if $\Delta E_j \leq 0$. Hence a successful type of agent, is one which is able to effectively extract energy from the binary resource strings in R, and the content of R in turn depends on which agents constitute the population. In order to feed the system with energy, strings in the resource pool R are continually being replaced with new high-energetic strings at a rate γ, representing a flow of energy into the system. A schematic of the modelling framework is shown in fig. 1, which illustrates how binary strings are metabolised by the organisms and flow through the system.

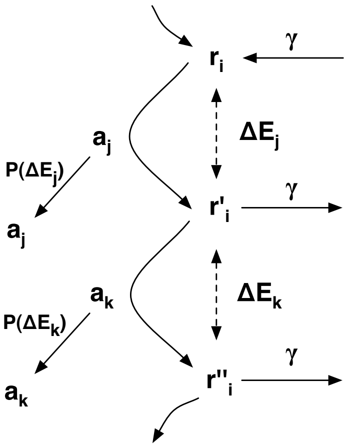

Figure 1: A schematic view of the model. The agents in the model digest binary strings by applying CA-rules, transforming r to r'. To each such metabolic step we can associate a difference in energy ΔE (visualised with dotted lines). The reproduction of each agent depends on how much it can decrease the energy of the binary string and occurs with probability $P(\Delta E)$ (represented by the arrows on the left hand side). The binary strings exist in a common pool which they enter (and leave) at a rate γ, as shown by the arrows on the right hand side.

The frame-work described so far is quite general, and we will in the following describe the particular choices we have made in the current study. Firstly, the agents a_j are chosen to be nearest-neighbour one-dimensional elementary cellular automata (CA), one of the simplest notions of digital algorithms. The reason for that particular choice in *Urdar* is that such functions are well studied in the literature starting from the work of Wolfram (1983). They are simple, but still shows a surprisingly wide range of complexity. The second choice we made was using an approximated Shannon Entropy as the energy function E, which gives an estimate of the amount of disorder a binary string contains (Shannon, 1948), associating a low entropy (low level of disorder) with a high "energy" state of the string, i.e. we set $E = 1 - s$. To motivate such a choice, one can see organismal metabolism as degradation of ordered structures into less ordered configurations. Entropy is a measure of such disorder. This viewpoint is both common and well established:

> “Thus the device by which an agent maintains stationary at a fairly high level of orderliness (= fairly low level of entropy) really consists in continually sucking orderliness from its environment.” (Schrödinger, 1944)

One could of course make use of a more sophisticated “artificial chemistry” by assigning higher energy, and hence fitness, if an organism is able to transform strings into certain patterns, instead of just increasing the entropy; but in our effort for simplicity and a more open-ended fitness function we have chosen the current set up.

Finally, the probability for agent a_j to reproduce, as a function of the energy it extracts from a binary string, is given by

$$P(\Delta E) = \begin{cases} \frac{1-\exp(-\Delta E/\beta)}{1-\exp(-\beta)}, & \text{if } \Delta E > 0 \\ 0, & \text{if } \Delta E \leq 0. \end{cases} \quad (1)$$

where β is a positive parameter indicating the level of competitive pressure among the agents. When β tends to zero, selection is weak as any $\Delta E > 0$ gives a probability of reproduction very close to unity, while for larger β selection is stronger as the magnitude of ΔE is more important for determining the value of $P(\Delta E)$ and hence the reproductive success of the organisms.

An example of applying CA-rules to binary strings is shown in fig. 2, where three rules**, i.e. three different species, digest a string** with a low entropy to binary strings with successively increasing entropy. This is the type of interactions we can expect in the model, in particular at low γ when the strings are replenished at a low rate. This figure also illustrates the fact that the CA-rules in general make small changes to the food string during digestion. In fact there is no CA-rule which can, in a single metabolic step, increase the entropy of a fairly ordered string to the maximum attainable entropy. This is similar to individual metabolic reactions in real organisms which generally only change the free energy of the metabolites a small amount, while the metabolism as a whole is responsible for the major difference in free energy between the nutrients taken up by the organism and the waste products being excreted. This fact also suggests that *Urdar* can be viewed as a model of the early stages of life on earth when the metabolic repertoire of organisms was much smaller and cross-feeding was possibly more prominent.

Note that in the current set up, the mapping between the genotype and phenotype of the agents is one-to-one, where the genotype corresponds to the integer value representing the rule (ranging from 0 to 255), and the phenotype simply is the action of the rule on the strings which are metabolised. All organisms implementing the same CA-rule are consequently referred to as belonging to the same species. In the current set up, we have chosen not to explicitly model self-replication in order to keep things simple. In future extensions of the model both sex and self-replication can be included.

The implementation of the model

To conclude the model description, let us sum up the main features of the model[1]. The dynamics, depicted schematically in fig. 1, in the model during one update can be described in the following way:

1. Each agent in the population picks randomly a resource string r_j from the **well mixed** resource pool R and transform it accordingly to its CA-rule and then puts the transformed string back into the resource pool.

2. The efficiency of the “metabolic process” just occurred is evaluated by measuring the energy difference ΔE of the string before and after the ”digestion/transformation”. This is done by drawing a random number x uniformly between 0 and 1, and if $P(\Delta E) > x$ the agent reproduces.

3. With probability μ the offspring will be mutated uniformly to another CA-rule.

4. In order to keep energy flowing into the system, after all agents have been updated, a fraction γ of the strings are replaced with high energy binary strings.

The replacement rate γ can be seen as a flow rate of energy into the system. If that rate is high, there will be less interaction through cross-feeding among the agents in A, as strings are flushed out at high rate, but if on the other hand γ is set to zero, the whole process will slow down to a halt. The strings introduced into the system are random binary strings, however with a low entropy (high degree of order). The new strings are constructed by at each position adding a 1 with probability p_0 and a 0 with the complementary probability $1 - p_0$. The Shannon entropy of such strings is given by

$$E_0 = p_0 \log_2 \frac{1}{p_0} + (1 - p_0) \log_2 \frac{1}{1 - p_0}, \quad (2)$$

where $\log_2$ is the logarithm with base 2, i.e. $2^{\log_2 x} = x$. By setting p_0 close to unity we can create strings which, although being random, have a low entropy. In order not to bias the resource pool to strings which are dominated by ones, at an equal rate we add strings which have the probabilities reversed, i.e. are dominated by zeros instead.

The parameters

We here briefly recapitulate the main parameters of the system and their significance.

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[1] An online version of the platform is available at: http://www.math.chalmers.se/∼torbjrn/Urdar/urdar.html

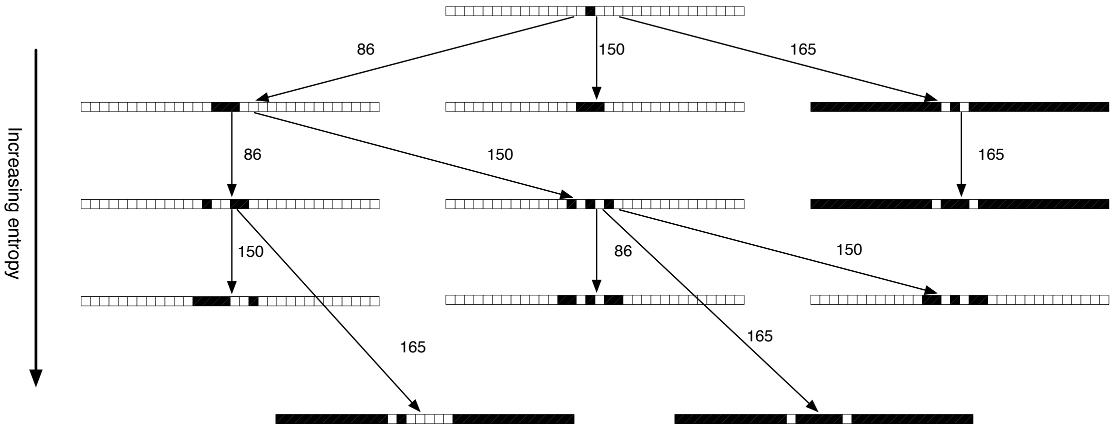

Figure 2: The transformation of binary food strings by three CA-rules. Only transformations that increase the entropy are shown and they have been truncated at a metabolic depth of four. The number of possible transformations is greater for the three rules together than for a single isolated rule suggesting the possible advantage of cross-feeding among the species in the model.

γ is the inflow rate of new high energetic binary resource strings into the pool R. After each update, i.e. after all agents have digested a resource string, the probability for each resource string in the pool to be replaced by a new fresh one, keeping the total number of resource strings constant, is γ. Here we will typically set $\gamma \in [0.003, 0.3]$.

μ is the mutation probability during reproduction, where an agent is uniformly changed to another of the 256 CA-rules. We will use $\mu = 0.01$ as a default value of the mutation rate.

β is the level of selective pressure, as it determines the importance of ΔE in calculating the reproductive rate, see eq. (1). The default value of in the current study is $\beta = 0.1$.

The population size is set to $N_A = 1024$, and the number of binary strings in the resource pool is $N_R = 5N_A = 5120$. The size of the binary strings is set to $L = 100$, and level of order in the inflowing strings is $p_0 = 0.95$, which gives, through eq. (2), an initial energy of $E_0 = 1 - s_0 \approx 0.8$. The initial condition of each simulation is a uniform distribution of species, i.e. 1024/256 = 4 organisms of each species, and a resource pool consisting of strings with the initial energy E_0.

Results

All ecosystem on earth are driven by energy entering the system either in the form of sunlight or in some chemical form such as glucose or ironsulphide. Similarly the dynamics in *Urdar* are driven by the flow of food strings with a high energy into the system, and if γ is set to zero the dynamics will eventually grind to a halt when all possible energy has been extracted from the resource pool **, i.e. no new agents will be generated**. The rate of energy supply is known to be of great importance to real ecosystems (Waide et al., 1999), and it is therefore of interest to analyse how the dynamics in our system depend on the flow rate of energy γ. **This relation is investigated in detail in Gerlee and Lundh (2010) and we will here focus on ecosystem stability and species interactions.**

The most straight forward way of characterising the dynamics is to look at the time evolution of the species distribution. This is shown in fig. 3 for two different values of the flow rate, in (a) $\gamma = 0.003$ while in (b) $\gamma = 0.3$. The striking difference between these two simulations **implies the interesting statement** that the number of co-existing species in the low flow case is considerably higher. **Hence one might say that a relative supply shortage encourages species diversification and cooperation.**

Ecosystem stability

These plots also show that at low flow rates the species distribution does not settle in a steady state but seems to fluctuate with different species dominating the ecosystem at different times. This shows that the dynamics of the system does not converge to a fixed-point, but instead obeys oscillatory or even chaotic dynamics. **If the mutation rate is set to zero similar dynamics are observed, although with a lower level of species diversity.**

The dynamics of the system can be visualised more easily if instead of viewing the frequency of all species in a 2-d plot as in fig. 3, pick a reference state $\mathbf{F^0} = (f_0^0, f_1^0, ..., f_{255}^0)$, and plot the L_1-distance from the reference state as a function of time, i.e.

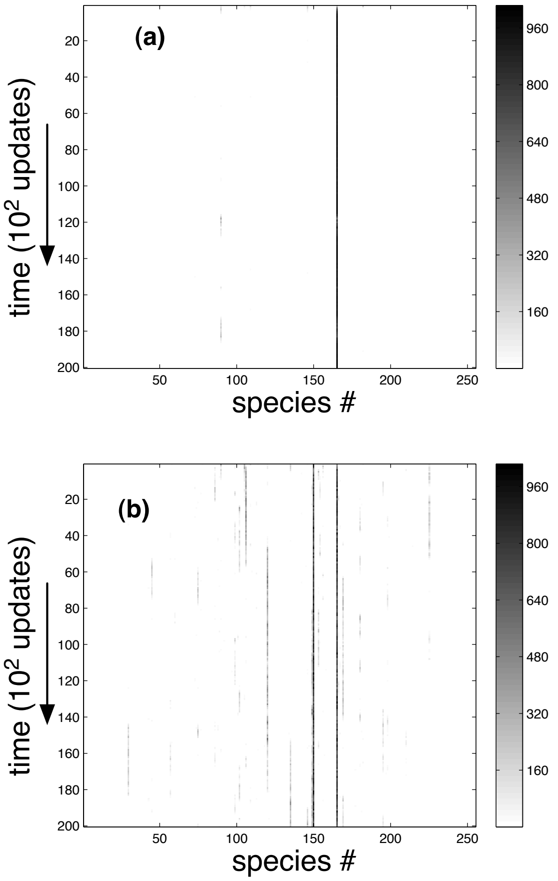

Figure 3: The time evolution of the species distribution for (a) $\gamma = 0.3$ and (b) $\gamma = 0.003$.

$$\Delta F(t) = \sum_{i=0}^{255} |f_i^0 - f_i(t)|, \tag{3}$$

where $f_i(t)$ is the fraction of the agents belonging to species i (i.e. performing the elementary CA-rule i) at time t. An example of such a plot is shown in fig. 4, which illustrates the same simulation as in fig. 3b, where the reference state was picked as the final state of the system at $t = 2 \times 10^4$. From this point of view we can clearly see how the system exhibits long periods of **stasis and seems to jump** between different states corresponding to specific species configurations**; as in so called punctuated equilibria introduced in Eldregde and Gould (1972)**. This can be compared to different epochs in the history of the ecosystem, and is thus comparable to paleontological data, which we will return to in the discussion. The time spent in these states seems to vary heavily and in order to quantify this we measured the waiting time distribution, i.e. the probability of the species distribution remaining in the same state a time T. The mutations present in the system, together with the relatively small population size, introduces fluctuations into the system, and in order to avoid these the projected time series $\Delta F(t)$ was binned into 20 equal sized bins (as shown in fig. 4).

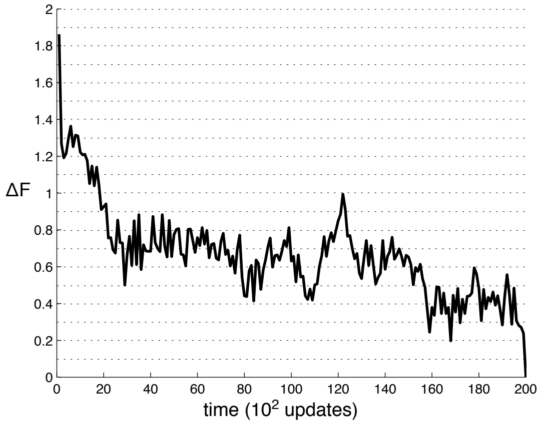

Figure 4: The species distribution shown in fig. 3b projected down to a one-dimensional state using (3). The dotted horizontal lines indicates the bins used for calculating the waiting times shown in fig. 5 below. **The reference state $\mathbf{F^0}$ was picked as the final state of the system at $t = 2 \times 10^4$.**

From this discretised data we calculated the cumulative probability $P(x > T)$ of finding the system in the same bin for at least T time steps. This was calculated from 50 different simulations each lasting $t_{max} = 2 \times 10^4$ times steps for $\gamma = 0.3$, 0.03 and 0.003. The result is shown in fig. 5, where the curves corresponding to the lower flow rates appear approximately as straight lines in a loglog-plot. This suggests that the waiting time scales as a power-law, and a linear regression showed that $P(T) \sim T^{-\alpha}$, where $\alpha \approx 2.6$ and 3.5 for $\gamma = 0.03$ and 0.003 respectively. On the other hand, the curve corresponding to $\gamma = 0.3$ is closer to a straight line in semilog-plot (see inset), and from this we found that $P(T) \sim e^{-\varepsilon T}$, where $\varepsilon \approx 0.04$. The exact slope of the curves naturally depends on the number of bins (a smaller bin size gives steeper curves), but the difference between the functional forms of the curves is robust. Please note that the waiting time for a random walk is exponential, which gives an indication of the difference in dynamics between the high and low flow rate.

Pair-wise species interactions

A natural question that arises is what kind of underlying dynamics gives rise to these transition patterns. If there existed for a fixed flow rate a single dominant species among the 256 possible then we would expect the evolutionary dynamics to converge to a species distribution and remain there. This is clearly not the case, at least not for the lower flow

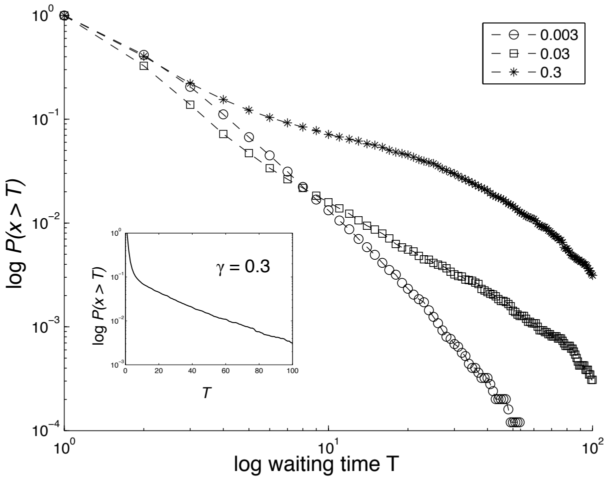

Figure 5: The cumulative distribution of waiting times plotted in a loglog-diagram for three different values of γ. For low flow rates the waiting **times appear to scale as a power-law**, while for high flow it seems to follow an exponential distribution as **indicated in the inset where the graph follows approximately a straight line over a long period in the semilog-diagram.**

rates, which suggests that more complicated dynamics than simply the selection for the best metaboliser occurs in the system.

This is in fact obvious if we return to the schematic of the model and also realise that different species have varying capacity to metabolise different strings. The fitness of a species depends on its ability to extract energy from the strings in the resource pool, but the composition of the resource pool in turn depends on what species are present in the ecosystem. This means that the fitness of a species depends on state of the entire ecosystem and will therefore change as the system evolves.

The simplest possible way to analyse the species interactions is to simulate the dynamics when only a pair of species are present and the mutation rate is set to zero. This of course neglects higher-order interactions, between conglomerates of species, which might influence the dynamics, but at least it represents a starting point for a deeper understanding of the system. We probed these species interactions by initialising the system with a 9:1 ratio in the abundance of a pair of species and then ran the simulation (without mutations) for 1000 time steps or until only one of the species remains. At the end of the simulation we recorded the abundance of the species and stored the frequency of the initially abundant species in a matrix C. Element c_{ij} thus holds the equilibrium frequency of species i when the initial ratio between $i : j$ was $1 : 9$. This experiment was carried out for all possible pairs of species in the range 90-164 of which there are $74 \times 74 = 5476$, and an excerpt of the resulting matrix is shown in fig. 6. Here white and black correspond to complete dominance, while any shade in between signifies stable co-existence between the species.

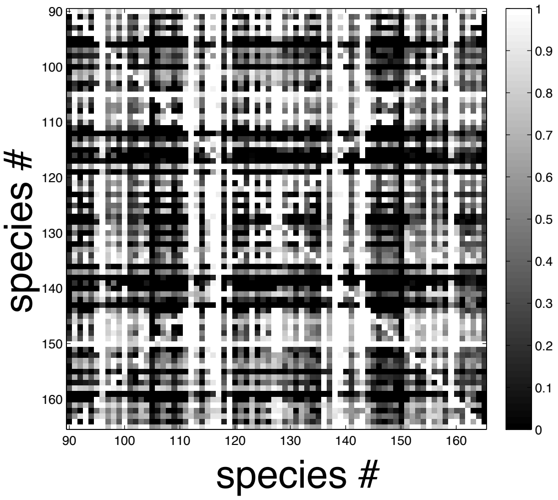

Figure 6: Excerpt of the matrix C describing the pair-wise species interactions in the system. **White and black correspond** to complete dominance, while any shade of grey corresponds to co-existence.

A striking feature is that co-existence seems to be a common mode of interaction. This emphasises what was discussed before, namely that the replication rate of species depends on the totality of species present (including itself) in the ecosystem. In the case of co-existing species, the increase in abundance is balanced by a reduction in reproduction rate, a phenomenon known as negative frequency-dependent selection (Huisman and Weissing, 1999), and when the replication rate of both species is balanced a steady-state is attained.

The interaction matrix in most cases satisfies $c_{ij} + c_{ji} = 1$, which means that the equilibrium concentration of the species is independent of the initial condition, but there are some interesting exceptions from this rule. Firstly we have the anti-diagonal of the matrix where $c_{ij} + c_{ji} \approx 2$, and this is due to the underlying symmetry of the cellular automaton rules. The pairs on the anti-diagonal are in fact rules that are inverses of each other when viewed in binary representation. For example rule 145 = 10010001_2 and its anti-diagonal partner is rule $255 - 145$ = 110 = 01101110_2. When these rules are applied to a generic binary string the output strings they yield are inverses of each other, which by symmetry of the entropy function imply that they have the same entropy. This means that the two rules, when competing in isolation, are neutral and the only evolutionary force acting on the system is random drift. The consequence of this is that the initially dominant rule is more likely to win and therefore we observe $c_{ij} \approx c_{ji} \approx 1$ (or visually a white line) on the anti-diagonal. Note that this does not imply that the two species are identical in their competition with other rules, and this has some important consequences for the dynamics of the model.

Secondly we have the cases where $1 < c_{ij} + c_{ji} < 2$, which indicates that the initial condition in fact influences the equilibrium concentration. Upon further inspection we found that the dynamics of these pair-wise interactions contain two stable fixed-points, as opposed to one which is the case in all other interactions. Typically the only fixed-point lies either, in the case of co-existence, in the interior of the phase space at $(i, j) = (c, 1 - c)$, for the equilibrium concentration c, which satisfies $0 < c < 1$, or in the case of dominance at (0,1). In the above mentioned cases both an interior and a boundary fixed-point are present, and this implies that the dynamics can converge either to co-existence or dominance depending on the initial frequencies of the species.

Rock-Paper-Scissors

The presence of co-existence in the pair-wise experiments gives a reasonable explanation of the large degree of co-existence in the full simulation (cf. fig. 3), but it does not explain why the species configuration never settles into a steady state. The lack of stability must be an inherent in the species configuration itself, and one possible explanation is that the property of being able to invade another species is not transitive. By this we mean that if a_i invades a_j, and a_j invades a_k, then it is not necessarily so that a_i invades a_k. If on the contrary a_k invades a_i we have what is called an intransitive cycle, similar to the Rock-Paper-Scissors game.

In order to investigate this possibility we searched the matrix C for species triplets which satisfy the above condition, and found 59 unique triplets (containing 44 different species) which satisfied the condition of intransitivity. A suitable way to illustrate this is with a network where the species are represented as nodes and a directed link connects node A and B if species A can invade species B. This is shown in fig. 7, and in this figure the intransitive relations appear as directed triangles of which there are plenty. For clarity we have only included species involved in at least one intransitive interaction. The network consists of 4 connected components suggesting a certain degree of modularity, which could allow for independent competition occurring simultaneously in the well-stirred environment. Further analysis showed that all except two triplets exhibited the double fixed-point property discussed above, and thus exhibit a weaker form of intransitivity. The two fully intransitive triplets where given by (120,145,158) and (120,131,158) and are highlighted in fig. 7. Mathematical analysis has suggested that RPS-dynamics can give rise to oscillatory behaviour due to the cyclic replacement of the species (Laird and Schamp, 2009). We investigated this possibility by performing experiments where the 3 members of an intransitive cycle were present in equal proportion in the initial population and the system was run without any mutations. We did however now observe oscillatory behaviour, but instead the dynamics converged on either a pair of species co-existing (and one species going extinct) or one single species dominating the system. This discrepancy from the analytical result is most likely due to a difference in the rates of replacement of the species, which in the analytical treatment is set to be equal for all interactions, and has also been observed in a bacterial system exhibiting RPS-dynamics (Kerr et al., 2002).

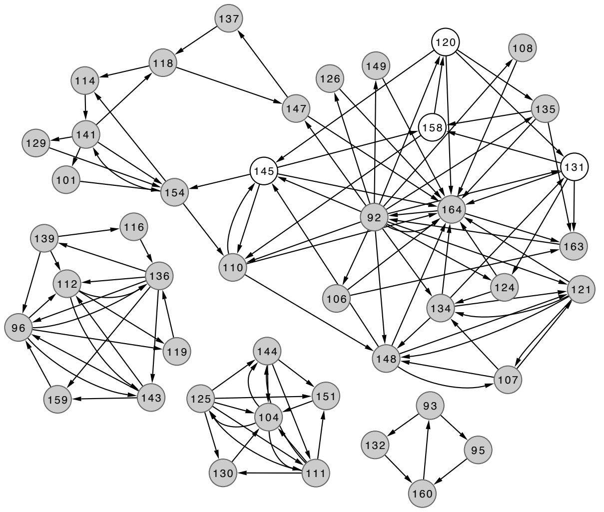

Figure 7: Network illustrating the intransitive species interactions. An edge points from node a to b if species a wins over b in a pair-wise invasion experiment, i.e. $C_{ab} > 0.75$. Intransitive triples are seen as cyclic triangles in the network. **The species involved in fully intransitive competition (not involving multiple fixed-points) are highlighted.**

Discussion

In this paper we have presented an Alife-platform *Urdar*, based on the mechanism of cross-feeding, which is observed in many microbial ecologies. The components of the platform are fairly simple consisting of elementary CA rules that transform binary strings. **Similar systems have been analysed by for example Dittrich et al. (2001) and Ikegami and Hashimoto (1995). The former considered a matrix multiplication chemistry, where binary strings could act both as agents and substrate, and in which stable autocatalytic cycles emerged. In the latter a different formalism was applied, where agents defined as Turing Machines acted on tapes represented as binary strings. What these systems did not include was a notion of energy necessary for replication, which is a central feature**

in *Urdar*.

Energy is obtained by increasing the entropy (disorder) of these strings. Despite of its simplicity the system exhibits surprising features such as a high degree of species diversity, non-stationary dynamics, and periods of stasis with broad distribution of waiting times.

The latter have also been observed in other evolutionary models such as Bak and Sneppen (1993) and Sole and Manrubia (1996), and relates to the punctuated equilibrium hypothesis put forward by Eldregde and Gould (1972). In the original conception of the hypothesis it was believed that geographic separation was a necessary condition. Our results show that long periods of stasis of stasis can appear in cross-feeding ecosystem that lacks any spatial component, and where the dynamics are driven by the mutual dependence between the species.

The above mentioned features are all driven by the cross-feeding interactions between the species and are more pronounced at low flow rates of high energy strings into the system. One way to study these interactions is to perform pair-wise invasion experiments captured in the matrix C (see fig. 6), which reveal that co-existence is quite common in the system. Studying this matrix we also found intransitive relations between three different species similar to the Rock-Paper-Scissors game. This type of interactions are commonly found in real ecosystems, and are know to promote biodiversity (Kerr et al., 2002; Laird and Schamp, 2009), suggesting a source of the observed non-stationarity in our system.

However, preliminary results indicate that removing the 44 species involved in intransitive relations from the ecosystem (and prohibiting mutations to them) does not reduce species diversity nor increases ecosystem stability. This suggest that higher-order interactions not captured by the pair-wise invasion experiments are responsible for the inherent instability of *Urdar*.

Future work

The experiments presented in this article only scratch the surface of this surprisingly complex ecosystem, and whole host of interesting questions remain to study. One obvious question that remains unanswered regards the underlying mechanism driving the above mentioned non-stationarity. One should also investigate the dynamics from a different point of view by making use of the metabolic history of all food strings (i.e. the list of species each string has been metabolised by). This makes it possible to map out which species engage in cross-feeding, and from this information generate a network of ecological interactions. Another possibility is to examine to which extent the process of evolution maximises productivity from an ecosystem point of view, i.e. how well does the evolved species composition do compared to an optimal species composition which maximises productivity (for a given flow rate). Further, the model could also be extended to include features present in real biological systems, such as a distinction between the genotype and phenotype of the organisms and a spatial dimension which would impact the nature of the species interactions.

Aknowledgement

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