Evolution of Resource Competition between Mutually Dependent Digital Organisms

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Abstract We study the emergence and dynamics of competing strains of digital organisms in a world with two depletable resources. Consumption of one resource produces the other resource as a by-product, and vice versa. As a consequence, two types of mutually dependent organisms emerge that each prey on the waste product of the other. In the absence of mutations, that is, in a purely ecological setting, the abundances of the two types of organisms display a wide range of different types of oscillations, from regular oscillations with large amplitude to irregular oscillations with amplitudes ranging from small to large. In this regime, time-averaged abundance levels seem to be controlled by the relative fitness of the organisms in the absence of resources. Under mutational pressure, on the other hand, populations evolve that seem to avoid the oscillations of intermediate to large amplitudes. In this case, the relative fitness of the organisms in the presence of resources plays an important role in the time-averaged abundance levels as well.

1   Introduction

In nature, organisms almost never evolve in a fixed, constant environment, but evolve in an ecosystem in which their niche is affected not only by their own actions but also by the actions of other organisms occupying different niches. Most theoretical or modeling studies, however, either address evolutionary dynamics while neglecting ecological interactions, or study ecological interactions in the absence of evolution. The reason for this separation of fields is that the evolution of ecosystems is even more complex than the already very complex field of community ecology. One particularly useful approach to study the evolution of ecosystems is to study abstract ecosystems that have had most of their complexity stripped away. Such approaches are usually entirely mathematical in nature, but can lead to important insight into fundamental properties affecting ecosystem evolution. But even in field ecology, the idea that evolutionary time scales are too large to affect ecological dynamics has given way to the recognition that some systems have ecological and evolutionary time scales of the same order [2].

Rapid evolutionary adaptation that drives ecological dynamics in a predator-prey model has recently been observed in an experimental system involving planktonic rotifers and green algae [13]. In this study the authors observed predator-prey cycles that were exactly out of phase by a half cycle, and explained them by the rapid adaptation of

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the prey that becomes resistant to the predator (standard Lotka-Volterra type predator-prey cycles without adaptation are only a quarter cycle out of phase). When predators are forced to low numbers due to this resistance, the non-resistant prey outcompete the resistant ones, allowing the predator population to rebound [10]. In the present article, we show that a similar out-of-phase dynamics occurs—for very different reasons—in mutually dependent digital organisms, who compete not directly but via the substrates on which they cross-feed.

While evolutionary biology has traditionally been a field dominated by observation and theory, experimental evolution has grown in importance in the last 15 years (see, e.g., [5] for a recent review). Moreover, experiments with digital organisms (that is, self-replicating computer programs) rather than microorganisms are becoming more and more common, which adds a dimension to experimental research that was previously only available in theoretical modeling: With digital organisms, we can easily construct various test environments, over which we have perfect control, and can repeat experiments many times to obtain good statistics. The origins of digital life research and more recent developments are reviewed in [12]. See also the description of the Avida system in this issue, and references therein [9]. In the past, digital life experiments have focused mainly on the dynamics of asexual replicators in a single niche. Lately, however, multi-niche systems have been explored with the Avida digital life platform [4, 3].

The concept of a niche emerges in digital life systems such as Avida if a metabolic fitness landscape is superimposed on the purely replicative fitness requirement. The metabolism of a digital organism is that part of its genetic sequence that exploits the computational environment for extra CPU time. (CPU time here plays the role of the basic resource necessary for the survival of a self-replicating computer program: Without CPU time, the program is not executed, and therefore does not leave any offspring.) The organisms can gain extra CPU time by evolving the code necessary to perform logical and mathematical operations on random numbers that are supplied by the environment. In a single-niche system, all organisms gain the same amount of extra CPU time whenever they carry out particular computations. A multi-niche system is created by associating a depletable resource with each possible type of computation, and then limiting the availability of this resource by creating a chemostat in which inflow and outflow of resources are regulated [1]. In this setting, different species inhabiting the different niches emerge spontaneously, and can coexist indefinitely [4, 3]. These species interact entirely via the process of negative frequency-dependent selection (the fitness of a particular phenotype decreases as it becomes more common), which as a consequence creates selective pressure for further and sustained differentiation of the species.

To set the stage for the present study, let us imagine a simple world that has two resources termed A and B. Two metabolic pathways are allowed: Organisms can consume A, leaving B as a by-product, and organisms can consume B, thereby turning it into A. These reactions are each associated with a particular logical operation; here we chose the NAND and NOT operations:

$$A \xrightarrow{\text{NOT}} B \,,$$
$$B \xrightarrow{\text{NAND}} A \,.$$
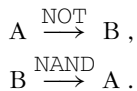
Each pathway is exclusive, that is, we prevent any organism from simultaneously taking both paths and becoming self-sufficient. Both reactions convert one unit of one resource into one unit of the other resource, so that the total quantity of resources is conserved. Note that this setup is different from the standard chemostat implementation

of depletable resources, where a constant inflow and outflow of resources ensures that the level of resource consumption is related to the equilibrium resource concentration in the system. Instead, here we provide an initial amount of resource that is simply converted back and forth between the species.

We set up the world in such a manner that initially only resource A is present, and no organism is naturally capable of using it. After an initial period of adaptation, digitals with the capability of utilizing A do evolve (they perform the NOT operation to trigger the benefit if A is present). As the A-consumers prosper in their new-found energy source, they deplete the supply. Eventually, all A will be converted into B, and it will remain that way until a type evolves with the capability of carrying out the reverse metabolic pathway, that is, performing the NAND operation and converting B back to A. At this point, if any A-consumers are still alive, they begin a symbiotic relationship with the B-eaters. In the following sections, we describe in detail the nature of this symbiotic relationship.

2   Materials and Methods

All experiments were conducted using Avida version 1.99, available from http://www. sourceforge.net/projects/avida. All parameters in the genesis file (see [9])—except those mentioned below—were kept at their default settings.

The setup of the environment is shown in Figure 1 for a bonus value of $k_A = 2^4 = 16$ for reaction A→B (corresponding to the NOT computation), and a bonus value of $k_B = 2^7 = 128$ for reaction B→A (corresponding to the NAND computation). We held the bonus value for the first reaction fixed in all experiments, and varied the

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  RESOURCE A:initial=3600
  RESOURCE B:initial=0

  REACTION ECHO
  REACTION AtoB
  REACTION BtoA

  REACTION ECHO echo \
          process:value=0.2:type=pow \
          requisite:max_count=3

  REACTION AtoB not \
          process:resource=A:value=4:type=pow:product=B \
          requisite:noreaction=BtoA:max_count=1

  REACTION BtoA nand \
          process:resource=B:value=7:type=pow:product=A \
          requisite:noreaction=AtoB:max_count=1
```

Figure 1. Environment file for bonus pair 2^4 and 2^7. An explanation of how environments are defined in Avida can be found in [9] in this issue.

bonus value for the second reaction from 2^3 to 2^{10}. Organisms were prevented from carrying out both reactions, and could successfully complete the reactions only once per replication cycle. In addition to the two reactions A→B and B→A, we also rewarded a simple computation, ECHO, with a small bonus irrespective of resource abundances. This additional bonus facilitates the evolution of the more complex reactions NOT and NAND, without substantially altering the ecological dynamics among organisms once the two reactions A→B and B→A are established in the population.

2.1 Adaptation Runs
First, we carried out experiments in which the organisms were allowed to evolve. We used the mutation settings of the default genesis file, that is, the organisms experienced a probability of copy mutations of 0.0075 per instruction copied, and a probability of insert or delete mutations of 0.05 per generation. We seeded the runs with the length-15 default organism, which consists of only a simple copy loop. We carried out between 15 and 40 replicates for each bonus setting, and considered bonuses 8, 16, 32, 64, and 128 for the reaction B→A (the reverse reaction always had bonus 16). We let the runs continue for between 10,000 and 15,000 updates (10 updates corresponded to 5–8 generations). We averaged abundances of organisms performing A→B (type-A organisms, for short) and organisms performing B→A (type-B organisms) for the last 200 updates in order to estimate the proportion of type-A and type-B organisms in the population. (By abundance of organisms of a given type, we mean the number of organisms of that type in the population.) The evolved populations consisted of type-A and type-B organisms exclusively in all cases, that is, no other organism types evolved, and the original ancestor had disappeared.

2.2 Ecology Runs
We carried out additional runs with mutations turned off, in order to study the types of ecological interactions that are possible in this two-resource system. In all ecology runs, we studied the competition of a pair of organisms (one of type A, and one of type B). These organisms were extracted from the final populations of the earlier adaptation runs.

We studied 10 different pairs of organisms (two different organisms of type A paired each with five different organisms of type B). The seven organisms in these pairs had been previously evolved at various bonus values, and were chosen such that the ratios in basic fitness across the 10 pairs was considerable. We carried out for each pair five replicates for each bonus setting, with bonuses 16, 128, and 1024 for the reaction B→A (a total of 150 runs). We let the runs continue for 5,000 updates, and averaged abundances of organisms for the last 200 updates.

3 Results

3.1 Adaptation Runs
In all experiments with mutations turned on, we started with populations unable to perform either NOT or NAND, and with resource A present and resource B absent. This setup dictates that organisms of type A have to emerge first, followed by organisms of the B type. We did observe occasionally that the A type evolved, but that the B type did not follow suit. In those cases, the incipient type-A population quickly used up its resources and became extinct after a short amount of time. However, at this point resource B was present in the environment at a high level, which meant that organisms of type B could evolve now. In all of our experiments, we found that eventually both types of organisms would evolve and stably coexist. After some transient time, both
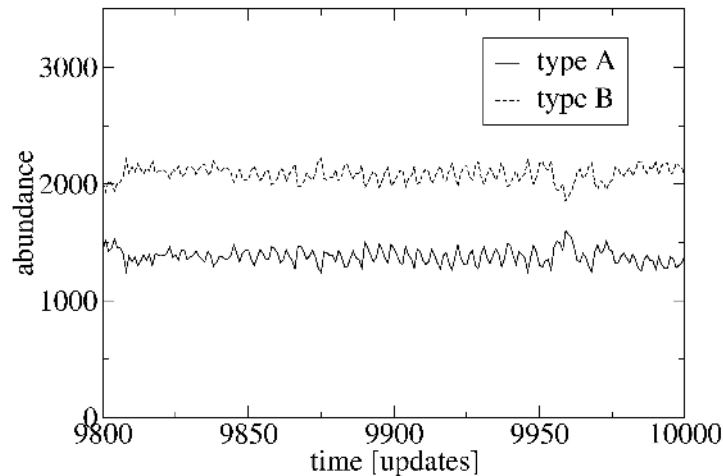
Figure 2. Abundances of organisms of type A and B as functions of time, for the last 200 updates of an evolution run (bonus ratio $k_A/k_B = 0.125$). Type-B organisms are consistently more abundant than type-A organisms.

organism abundances and resource levels fluctuated with small amplitude around a well-defined equilibrium value (see Figure 2 for organism abundances).

Next, we studied how the equilibrium levels of types A and B changed as a function of the ratio of the bonuses we handed out for reactions A or B. We held the bonus for reaction A fixed at $k_A = 2^4 = 16$, and varied the bonus for reaction B from $k_B = 8$ to $k_B = 128$. We found that there was a general tendency for the organism type reaping the higher bonus to have a higher abundance (see Figure 3). This result is not surprising, as the organism type with the higher bonus is replicating faster than the other one. What we did find surprising was that the ratio of the abundances of the two types of organisms changed only very slowly with the ratio of the bonuses. Naively, one would assume that if type B replicates twice as fast as type A, then it should also reach twice as high an abundance, since it gets the double award for each resource unit it uses up. However, as can be seen in Figure 3, changing the ratio in bonuses from 1 to 0.125 (almost a factor of ten) changes the mean ratio of abundances not even by a factor of two.

The argument presented in the previous paragraph for why abundance ratios should scale with the bonus ratios makes an important implicit assumption: We assume that the basic fitnesses of the organisms in the absence of the resources are comparable. (Remember that the digital organisms in Avida can always reproduce, even in the absence of a resource. However, here we gave quite high bonuses for resource consumption, so that, for example, an organism of type A would reproduce 16 times faster in the presence of resource A than in its absence.) A detailed analysis of several evolved populations showed that this assumption was not justified. When the B organisms had a higher bonus than the A organisms, then their basic fitness was substantially—up to a factor of two or more—lower than that of the A organisms. In other words, in the absence of both resources, the organisms that were adapted to the resource with the higher bonus had a substantially lower fitness than the organisms adapted to the resource with the lower bonus. Nevertheless, even though this difference in basic fitness
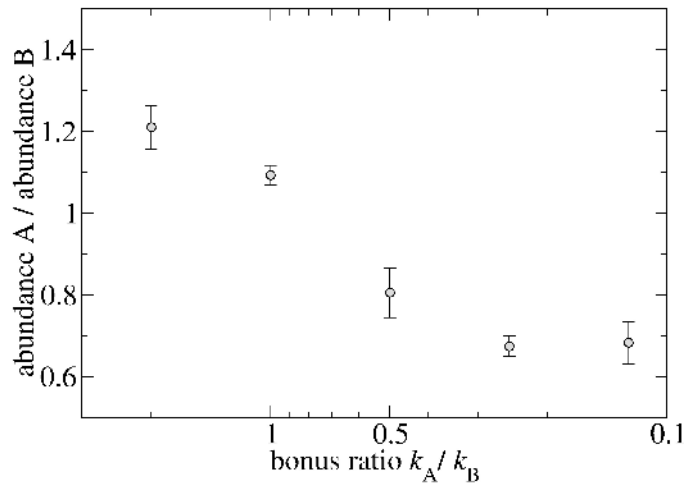
Figure 3. Equilibrium ratio of abundances of organisms of type A and type B versus ratio of bonuses k_A/k_B in adaptation runs.

was substantial, it was not sufficient to explain the difference in equilibrium levels of the two organisms.

We made a second interesting observation: Not only were the basic fitnesses of the two types of organisms different, there also tended to be substantial diversity in the basic fitnesses of the two types. These differences could be up to 20–50% of the basic fitness of the respective type of organism.

In order to understand better how exactly equilibrium values are regulated in this system, we carried out additional, highly controlled experiments without mutations.

3.2 Ecology Runs

We selected two organisms of type A, and five organisms of type B, and studied all possible pairings at three different bonus ratios, $k_A/k_B = 1$, $k_A/k_B = 0.125$, and $k_A/k_B = 0.016$. The organisms were selected such that we had a substantial spread in basic fitness ratios among the ten possible pairs of organisms.

Our results were partly as expected, and partly surprising. First, we noticed that the ratio of abundances was roughly given by the ratio of basic fitnesses, but that there were also some outliers that clearly did not follow this trend (Figure 4). We carried out an analysis of variance (ANOVA), and found that the ratio in basic fitnesses, the bonus ratio, and the interaction between those two ratios all contributed significantly to the overall variance (Table 1), with the basic fitness ratio making the largest contribution.

The observation that the ratio of the abundances is approximately proportional to the ratio of the basic fitnesses is in agreement with our naive model, according to which the faster replicator should make up the larger fraction of the population. However, we did not expect that the bonus ratio would make a smaller contribution to the overall variance than the basic fitness ratio, as we varied the bonus ratio by a factor of 64 and the basic fitness ratio only by a factor of approximately 4. Also, naively we would think that basic fitness ratio and bonus ratio should independently contribute to the final abundance ratio, whereas the highly significant interaction between the two
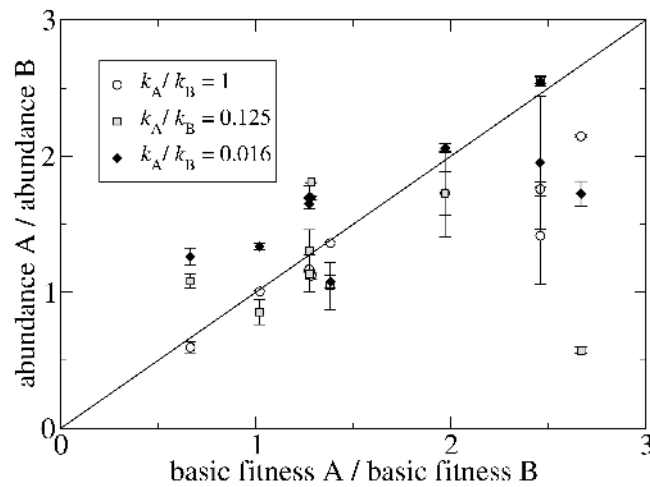
Figure 4. Equilibrium ratio of abundances of organisms of type A and type B versus ratio of the basic fitnesses of the organisms in ecology runs. The solid line indicates the set of points at which the abundance ratios and the basic fitness ratios agree.

Table 1. ANOVA table for ecology runs. The contributions of the basic fitness ratio, the bonus ratio, and their interaction to the overall amount of variance in the abundance ratios are all highly significant.

	Df	Mean squares	F	p
A (basic fitness ratio)	6	3.76	33.3	$< 2.2 \times 10^{-16}$
B (bonus ratio)	2	1.63	14.4	2.2×10^{-6}
A × B	12	1.07	9.5	5.3×10^{-13}
Residuals	129	0.11	N/A	N/A

suggested otherwise. Finally, we were surprised to find that a large fraction of the abundance ratios was now above 1 (Figure 4), even though the organisms had been extracted from populations in which the abundance ratio was well below 1 (but with mutations present). The populations seemed to be experiencing substantially different dynamics depending on whether mutation pressure was present or not: In the absence of mutations, the ratio of the basic fitness seemed to have the most influence on the abundance ratio, whereas in the presence of mutations, the ratio in bonuses seemed to have a substantial influence on the abundance ratio as well, but not as large as the naive model would predict.

When studying the abundances of type-A and type-B organisms as a function of time, we made another interesting observation: Unlike in the adaptation runs, we now observed a wide range of different types of oscillations—for some parameter settings, irregular with moderate to large amplitudes (e.g., Figure 5a); for some parameter settings, irregular with small amplitudes, interspersed with intermittent bursts of large-amplitude oscillations (e.g., Figure 5b); and for some parameter settings, regular with large amplitudes (e.g., Figure 5c).

These different types of oscillations are caused by synchronization effects between the organisms. For certain ratios of bonuses and basic fitnesses, the two types of organisms are perfectly synchronized, so that first type-A organisms use up all of resource
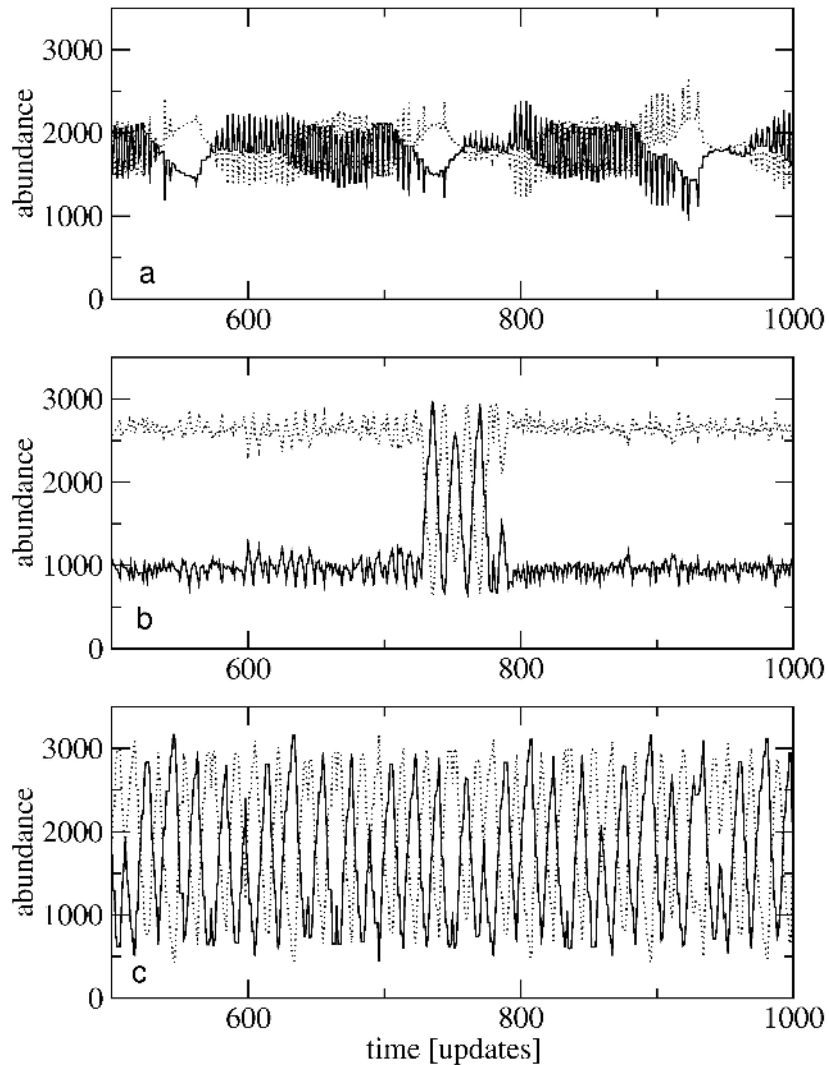
Figure 5. Abundance of organisms of type A (solid lines) and B (dotted lines) versus time in ecology runs. Ratio of bonuses is (a) $k_A/k_B = 1$, (b) $k_A/k_B = 0.125$, (c) $k_A/k_B = 0.016$.

A producing resource B, while type-B organisms are running idle, and then type-B organisms use up all of resource B producing resource A, while type-A organisms are running idle. This situation leads to regular oscillations with large amplitude. There are two reasons why the organisms go through this kind of a boom-and-bust cycle. First, the organisms receive a large bonus in the presence of the resource, which makes them operate much faster after resource consumption than before. Therefore, organisms running on bonus speed can operate with almost no interference from organisms running on basic speed. This separation of time scales allows one type of organism to consume all of its resource before the other type has even realized that its own

resource has been replenished. Second, the separation of time scales is augmented by a special modus operandi of the Avida software: The organisms never receive their bonus during their lifetime, but hand it over to their children, who then run at the new speed (see [9]). Therefore, the reaction to a newly present resource is always delayed by one generation.

Figure 6 illustrates this synchronization effect. We display organism abundances (solid lines in parts b and d), as well as numbers of organisms currently running on bonus speed (dashed lines in parts b and d). We see that the time point at which the largest fraction of organisms are running on bonus speed always coincides with the time point at which the organisms' resource is used up. Likewise, their resource always reaches its maximum level when not a single organism is running on bonus speed.

We now also understand why the ratio of the basic fitnesses is such a good predictor of the organisms' abundance ratio, as shown in Figure 4: The bottleneck for reproduction is how fast an organism type can react to a replenished resource reservoir, and that time depends on the basic fitness rather than on the bonus value, because the organisms are running idle at their basic fitness while the resource is being replenished.

Depending on the exact values of basic fitnesses and bonuses, however, the two types of organisms can lose their synchronization. The cases of incomplete synchronization or no synchronization at all create the other types of oscillations as we have demonstrated in Figure 5. Of particular interest is the case of Figure 5b. In this case, synchronization is completely lost most of the time (when the amplitude of the oscillation is small). Then, organisms of type A are always in low abundance, so that their resource is always sufficiently abundant, and all type-A organisms run on bonus speed. Type-B organisms are in high abundance, and their resource is drawn down almost to zero. However, since all type-A organisms run at bonus speed, they constantly produce some of resource B, and therefore there are always some type-B organisms that run at bonus speed. As a result, in this case the type-B organisms do actually get an advantage from having the higher bonus, and reach a higher abundance than the type-A organisms.

Finally, we were interested in the phase shift between the two oscillations. In order to examine the phase shift, we studied phase plots of the organism abundances (see for example Figure 7). We found that after a very short transient, all points in the phase diagram fell on the line $y = 3600 - x$, meaning that the two oscillations were a half cycle out of phase. (The phase diagram of the Lotka-Volterra model, which shows a phase shift of a quarter cycle, is an ellipse.) Surprisingly, this result was independent of the particular type of oscillation (regular or irregular, small or large amplitude) that we observed. Moreover, even in the adaptation runs with mutations, we found that the phase shift was a half cycle.

4 Discussion

We have found that a simple system of two types of digital organisms cross-feeding on each other's metabolic waste products can exhibit a quite complex array of different types of oscillations. Originally, we had thought that it should be fairly simple to predict analytically the time-averaged abundances of the organisms, but the complex synchronization issues made a simple prediction impossible. Moreover, while it may be possible in principle to understand all aspects of synchronization for a particular pair of organisms in the absence of mutations, in the case of the highly diverse populations that evolve under mutation pressure, this kind of detailed understanding will probably always remain elusive.

Interestingly, the evolved populations learned to avoid synchronization effects, and displayed fairly stable equilibrium concentrations with only small fluctuations. By avoiding synchronization, the population can make maximal use of the available re-
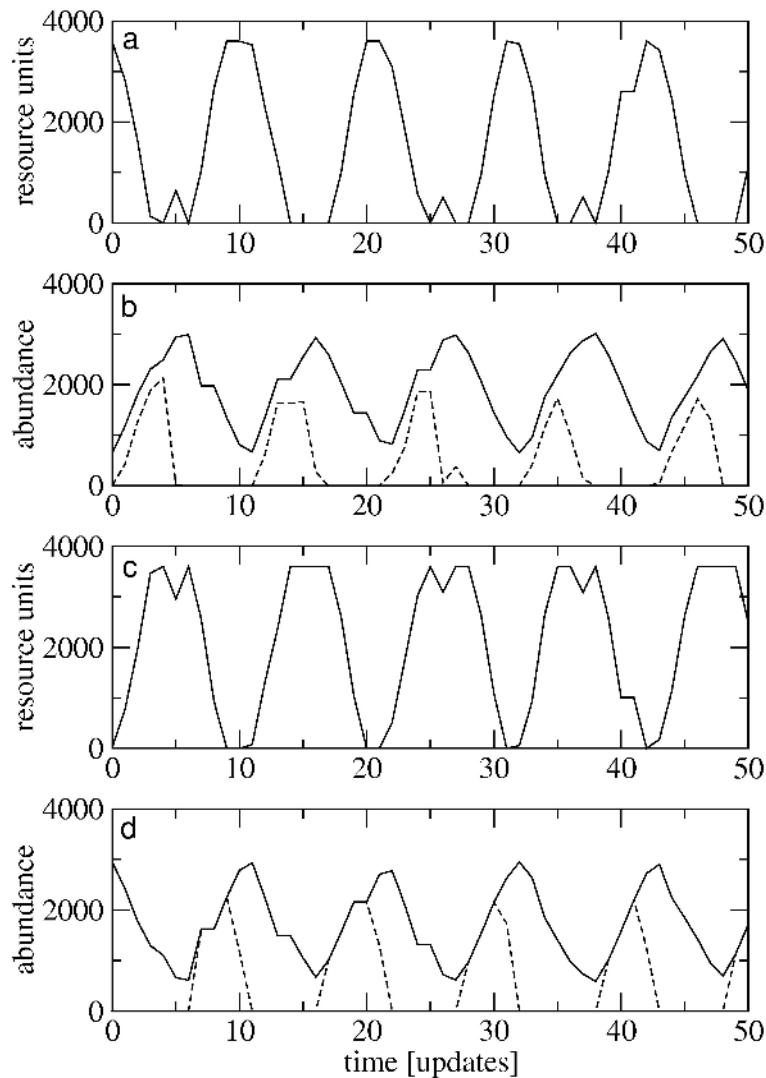
Figure 6. Resource level (a, c) and abundance of organisms (b, d) as a function of time. (a) Level of resource A. (b) Total abundance of type-A organisms (solid line), and abundance of type-A organisms running at bonus speed (dashed line). (c) Level of resource B. (d) Total abundance of type-B organisms (solid line), and abundance of type-B organisms running at bonus speed (dashed line).

sources: Without synchronization, a large fraction of both types of organisms never run idle at their basic fitness, so that the overall number of reproductive events per unit time is much larger than in the synchronized populations. Furthermore, in non-synchronized populations the type with the higher bonus can occupy a higher fraction of the population than the type with the lower bonus. Therefore, at first glance one might say that it is in the best interest of the type with the higher bonus to avoid synchronization, while it is in the best interest of the other type to create synchronization, because it would reach the higher abundance in this case. However, this reasoning
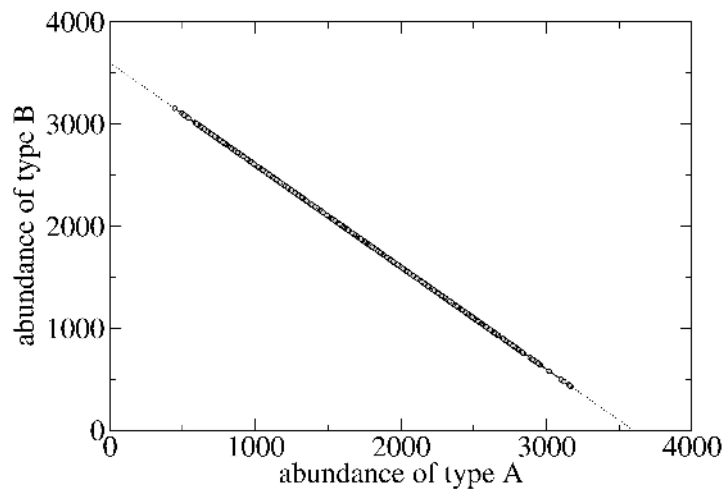
Figure 7. Phase diagram of the oscillation dynamics. The dotted line indicates the set of points that satisfies $y = 3600 - x$. The phase diagram corresponds to the run shown in Figure 5c.

is not correct: The resource corresponding to the lower bonus is in non-synchronized populations typically sufficiently abundant to feed all the organism type specialized on it, so that the organisms of this type would decrease their reproductive success if they reestablished synchronization. Therefore, it is in the interest of both types of organisms to maintain the non-synchronized state, and thus non-synchronization is an evolutionarily stable strategy [8] in this system.

Synchronization effects similar to those we observed here in the Avida system might also appear in bacterial systems. When bacteria grow, they move through several stages that are characterized by different growth rates. When food first becomes available, the bacteria do not respond immediately, but start dividing very slowly (lag phase). After a while, the bacteria start to divide rapidly (log phase), until the resources become scarce. At that point, the bacteria enter the stationary phase, in which they stop replicating. In a system of two mutually cross-feeding strains of bacteria, we can imagine that under certain circumstances, one strain is always in log phase at the time when the other is in stationary or lag phase, and vice versa. This situation would correspond directly to the situation we observed here in Avida.

Yoshida et al. [13] found that adaptation can lead to a phase shift of a half cycle in a predator-prey system, whereas normally the predator lags only a quarter cycle behind the prey [7, 11, 6]. Here, we also found a phase shift of a half cycle, but we saw it even in the absence of adaptation, in pairwise competitions of type-A and type-B genotypes. The reason for this difference is that our system is symmetric, whereas there is an inherent asymmetry in the predator-prey system. In the classic predator-prey system, without adaptation, the predator can rebound as soon as the prey starts to rise in abundance, while the prey cannot rebound before the predator starts to fall in abundance. Moreover, the prey can grow (and grows best) when the predator is absent, while the predator grows best at a high abundance of prey, and cannot grow at all when prey is absent. In a system of mutual cross-feeding, such as the one studied here, each type has to wait for the other type to produce the resource it needs, and

neither can grow on its own. Moreover, each grows best when the other is at a high abundance. For these reasons, we expect that a phase shift of a half cycle should be a common observation in all systems of mutual cross-feeding, and is not restricted to digital organisms or the particular system we have studied here. We should also mention that the predator-prey system is two-dimensional, whereas the system we studied here is inherently four-dimensional (two types of organisms, and two resources). Therefore, differences in the types of attractors of the two systems are to be expected.

Acknowledgments

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