Mutualism Promotes Diversity and Stability in a Simple Artificial Ecosystem

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Abstract This work investigates the effect of ecological interactions between organisms on the evolutionary dynamics of a community. A spatially explicit, individual-based model is presented, in which organisms compete for space and resources. We investigated how introducing the potential for mutualistic relationships (where the presence of one type of organism stimulates the growth of another type, and vice versa) affected the evolutionary dynamics of the system. Without this potential, one or a small number of individual types of organisms dominated the simulated community from the onset. When mutualistic relationships were allowed, many persisting types arose, with new types appearing continually. Furthermore, we investigated how the stability of the community differed when mutualistic relationships were allowed and disallowed. Our results suggest that the existence of mutualistic relationships improved community stability.

Keywords
ecosystem, evolution, ecological interaction, mutualism, ecosystem diversity, ecosystem stability

1 Introduction

Since the publication of Darwin's *The origin of species*, it has been widely appreciated that the "infinitely complex relations" that exist between organisms have played a crucial role in shaping the dynamics of biological evolution [11]. Such interactions can lead to the formation of diverse communities [9] and can, in some situations, introduce drives for ongoing evolution rather than stasis [12, 18, 25]. Despite this, much of the existing literature on creating artificial evolutionary systems has concentrated on the properties of the individual replicators, rather than on how individuals interact with each other.

Von Neumann was interested in systems capable of an evolutionary increase in complexity, but his work focused exclusively on the properties required of an individual self-replicating machine [26]. He did not consider interactions between replicators as a driving force for increased complexity. Rather, the little mention he did give to such interactions concerned their potential harmful effect in disrupting the functioning of self-replication within an individual machine. Von Neumann considered a system that had the *potential* for an evolutionary increase in complexity. But he did not address the question of where the *drive* for such an increase might arise from within an evolutionary system itself.

However, some early implementations of artificial evolutionary systems did consider interorganism interactions. Both Barricelli [3, 4] and Conrad and Pattee [10] designed

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systems where mutualistic symbioses could arise. Although both systems exhibited some interesting ecological and evolutionary dynamics, attempts to evolve complex organism behaviors met with limited success in both cases. Conrad and Pattee [10] remarked: "It is evident that the richness of possible interactions among organisms and the realism of the environment must be increased if the model is to be improved." They continued: "One point is clear, that the processes of variation and natural selection alone, even when embedded in the context of an ecosystem, are not necessarily sufficient to produce an evolution process" (pp. 407–408).

More recently, one of the most notable attempts to create an artificial evolutionary system that displays the kind of ongoing dynamics evidenced by biological natural history has been Ray's Tierra [22]. This work studied the evolution of a population of self-replicating computer programs. Most of the interesting results in Tierra were due to ecological interactions (parasitism in particular, where short programs emerged that could only reproduce with the help of longer "host" programs). As impressive as these results were, it is difficult to draw any general conclusions from them about ecological interactions and evolvability; the complexity of the system's design, and the difficulty of implementing control scenarios against which to test hypotheses, combine to make Tierra a somewhat unwieldy platform for scientific investigation [24].

If research in the synthesis of open-ended evolutionary systems is to progress beyond these rather specific results and lead to a general understanding of how such systems should be constructed, we need to elaborate the theoretical grounding upon which they are designed. This must include a more explicit understanding of how the low-level design of the system, in terms of the particular kinds of interaction allowed between individuals, affects the emergent evolutionary dynamics.

Some advances in this direction have been made using Holland's Echo model of complex adaptive systems [14, 15]. The design of Echo emphasizes the role of ecological interactions and exchange of resources. In particular, in Echo, Holland takes the view that it is the "market" that emerges from exchanges of resources between individual agents that is the source of much of the interesting behavior of a complex system. Schmitz and Booth used Echo to model food web complexity [23]. Their simulation demonstrates that "individual physiological capacity and behavior can have a profound effect on the character of higher-scale interactions." In particular, they found that "persistence of complex organizational structure (i.e. full 3-level chains) when trophic efficiencies were of the magnitude observed in real systems ... was only possible if heterotrophic agents could perceive and intentionally select the most nutritious prey agents within their neighbourhood."

In the present work, we concentrate not on the sensory and intentional capacities of individual agents, but rather on their roles as consumers (ingestion), processors (digestion), and producers (excretion) of abiotic resources. Specifically, we investigate how these processes can promote community diversity through the emergence of ecological dependencies (specifically mutualism) between different kinds of agents. Our model presupposes that mutualistic relationships between agents are possible; given this possibility, we study how such relationships affect community diversity and its evolution in time. In addition, we show that mutualistic relationships also affect the stability of the system (although, in contrast to other work such as [19], analysis of ecosystem stability was not our primary goal).

The structure of the article is as follows. In the next section we introduce the model used in these experiments. The experimental design is described in Section 3, and a sensitivity analysis on the effects of varying the main parameters in the model is presented in Section 4. The results of the experiments are given in Section 5. A discussion of the model and results, along with possibilities for future experiments, are presented in Section 6.

2 The Model

2.1 Model of Organism Interactions

In the model,[1] organisms compete for space and resources but can also form mutualistic relationships. A biological system corresponding to the model is one where one type of organism produces something useful to another organism and vice versa, for example, the mycorrhizal relationships (mutualistic relationships observed in roots) [2]. The organisms are sessile and have no sensory or information-processing capabilities. Reproduction occurs when organisms accumulate a certain amount of nutrition (referred to here as "utility points," as explained later in this section) from resources, and this amount is the same for all organisms. Mutation in the model ensures that new varieties of organisms continually enter into the system and therefore affects the probability of (potentially) mutualistic pairs of organisms coexisting and interacting with each other. The model is comparable to various other simple individual-based evolutionary models proposed in the artificial life literature, such as Packard's Bugs model [21]. Some of the more important features that, in combination, distinguish it from these other models include: (a) a variety of different resources exists in the environment; (b) organisms have individual specificity for particular resources; (c) organisms not only ingest resources but also excrete waste products; (d) organisms are sessile but can capture resources over an extended area of the lattice. These features are explained fully in the following sections.

2.2 Substrate

Space is represented by a two-dimensional lattice. There are eight types of resources available on the lattice. The resources are distributed in packets, with each packet potentially able to contain all eight types of resources. A resource packet is represented by an ordered binary string of length 8. A 1 in the nth position corresponds to the presence of the nth resource in the packet, and a 0 corresponds to its absence. For example a resource packet "0011 1100" contains resource types 3, 4, 5, and 6 and does not contain resource types 1, 2, 7, and 8. Since there are eight resource types possible, there are 256 possible resource packets. The number of resource packets at a single lattice cell can vary from 0 to the maximum number per cell R_{cell} (a model parameter). A representation of a section of the lattice of the model is shown in Figure 1.

The model is initialized with resource packets randomly distributed on the lattice. The number of resource packets is defined by $R_{\text{init}}X$, where R_{init} is the initial proportion of resources placed on the lattice, and X is the size of the lattice. At each time step a proportion R_{re} of resource packets present on the lattice is randomly removed, and the same number is distributed randomly over the lattice. (The constitution of these new resource packets is described in the next paragraph.) This represents a resource flow through the system and a disturbance in the environment that can be important for maintaining diversity.

Whenever a new resource packet is placed on the lattice in this way, its constitution is either: (a) with probability $(1 - P_{\text{br}})$, a random string of 0s and 1s, or (b) with probability P_{br}, a distinguished type of resource packet. The latter is the "basic" resource packet, toward which the environment is biased. This ensures that a population of organisms on the lattice is under some pressure to adapt to this combination of resource packets. This drives the system to a state of low diversity since organism types best adapted to digesting the basic resource packet will outcompete other types. Therefore, if mutualistic interactions increase diversity, the effect will be stronger. The basic resource packet in simulations (unless specified otherwise) was arbitrarily set to "1111 1111."

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[1] The model was an adaptation of that described by Pachepsky et al. [20], and its development was also influenced by Jones [16].

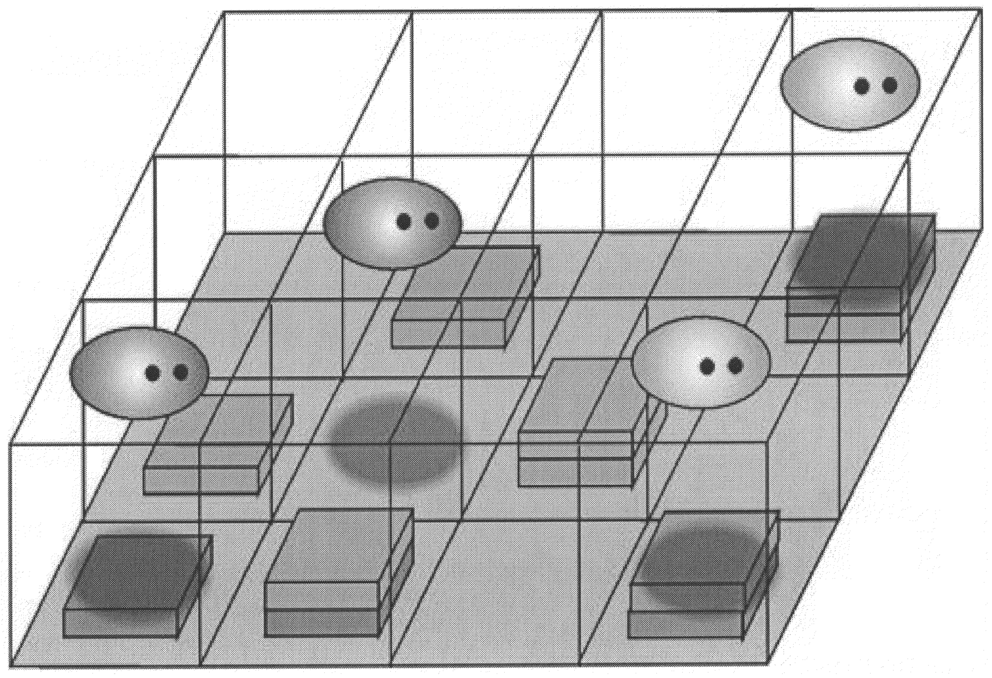

Figure 1. A representation of part of the lattice. The ovals represent the different types of organisms. The bricks represent the different types of resources.

2.3 Organisms

Each cell on the lattice can be occupied by at most one organism. The organisms are distributed on lattice cells, take up resources, digest and metabolize them, produce waste, reproduce, and die. Time in the model is discrete. These processes are characterized in the following manner.

2.3.1 Uptake of Resources

An organism can obtain resource packets from its lattice cell and the cells around it in a square area. For an organism i, this resource catchment area, A_{r}^{i}, is

$$A_{\mathrm{r}}^{i} = (2A_{n}^{i} + 1)^{2}$$

where A_{n}^{i} can take on integer values between 0 and $A_{n\_\max}$ (a parameter of the model). A_{r}^{i} represents the area over which an organism can collect resources. At each time step, organisms place a request for a number of resource packets defined by the parameter O_{r}. The location of each resource packet that each organism requests is picked randomly within the organism's catchment area. Therefore, each cell may receive requests for zero, one, or more resource packets from each of the organisms that have that cell within their catchment area. At each cell, the packets are then allocated to the organisms according to availability.

When demand for resource packets at a particular cell exceeds the number available, competition occurs in the following way. Let x be the total number of resource packets demanded, and k the total number of resource packets available, at the cell. At each time step, the packets at a given cell are distributed among the organisms requesting packets from it using "roulette wheel" selection, as follows: Each organism is assigned

Table 1. Correspondence of the number of matches—between an organism's template and a resource—to the number of utility points obtained.

Number of matches	0	1	2	3	4	5	6	7	8
Utility points	−3	−2	−1	0	+1	+2	+3	+4	+5

an area of the wheel that is proportional to its demand from that cell relative to x. The roulette wheel is then spun k times, and after each spin one resource packet is transferred from the cell to the organism selected.

However, if one of the organisms requesting resources for a particular cell resides in that cell, it gets all of the resource packets it requests (or however many there are available if there are insufficient resource packets to fulfill the request). The rest of the packets are then distributed among the remaining organisms using the roulette wheel selection as described above. This allows organisms with small resource catchment areas to compete with those with larger resource catchment areas. It also represents a situation in which the organism physically located in a particular space has access to all of the resources there; for example, if it is a plant, it has an extensive root structure in that location.

2.3.2 Resource Digestion

Each organism has a "template" associated with it. The template, like the resource packet, is an ordered 8-bit string of 0s and 1s (e.g., "1110 0111"). In an organism, the template represents the organism's preference for different types of resources. The digestion of a resource consists of matching the template to the resource bit by bit, and counting the number of matched bits (i.e., "1" in the template and "1" in the resource, or "0" in the template and "0" in the resource). In other words, an organism gets a match each time a preferred resource type is present in the resource packet, and also for each time a disfavored resource type is absent. Depending on the number of matches, the organism is assigned utility points, which are used by the organism for metabolism and reproduction. The correspondence of matches to utility points is shown in Table 1. In an environment with random resource packets, organisms will get one utility point on average (which is spent on metabolism as explained below). Each organism is initially assigned a number of utility points, defined by the parameter U_{init}.

The product of digestion, "waste," is then deposited in place of the digested resource packet. Waste is the logical NOT of the template (i.e., for template "1111 0000," the waste is "0000 1111").[2] This means that after digesting a resource packet, the organism removed from the resource packet the resource types that it preferred and output the resource types that it did not prefer. This matching scheme gives rise to the possibility of mutualistic relationships between organisms developing. For example, two organisms with templates "1100 0011" and "0011 1100," respectively, get eight matches from digesting each other's waste, giving them the maximum possible utility points (Figure 2). Of course, this can only occur if by chance one of the organisms is in a position to take up a resource that is the "waste" of the other.

The utility points obtained from digesting resources are "spent" on metabolism and reproduction. Metabolic processes cost organisms a given number of utility points per time step, defined by the parameter M. Reproduction occurs when a number of utility

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[2] The scheme employed here for determining the composition of the waste product represents a situation where an organism always produces a certain type of waste product, no matter what its diet. However, the precise details of this scheme are essentially arbitrary, and no specific analogy with a biological system is intended.

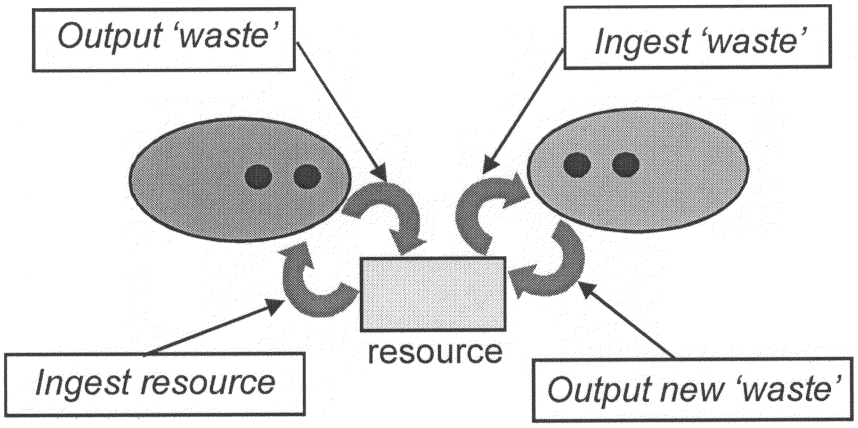


Figure 2. Interactions between organisms through resources. One individual can digest a resource and output a "waste," which can be ingested by another organism. If the "waste" of one organism is beneficial to another organism, then mutualistic interactions can occur.

points T_{rep} is achieved, where

$$T_{\mathrm{rep}} = 2NU_{\mathrm{init}}$$

and N is the number of offspring that organisms must produce at each reproduction. This means that an organism has to accumulate twice the amount of utility points necessary to produce offspring, half of which is spent on reproduction and half of which stays with the organism.

2.3.3 Organism Type

We define an "organism type" as a collection of organisms with the same template and catchment area.

2.4 Reproduction and Death

When an organism reproduces, its offspring are dispersed randomly over a square region centered upon the lattice cell of the parent organism. The area of this region is $(2D+1)^2$, where D is a parameter of the model. At each time step, eligible organisms reproduce in random order. The parent organism gives each of its offspring a number of utility points defined by U_{init}. If the cell on which the offspring lands is occupied, the offspring dies. When created, each offspring can mutate with some probability P_{m} in which case its template and resource catchment radius A_n^i may change values in the following manner. The catchment area and each bit of the template have an equal probability to mutate. The number of mutations, from zero to nine (eight bits and one resource catchment radius) is chosen randomly. The bit in the template is changed from "0" to "1" or vice versa, and the radius of the resource catchment area mutates to a random value between 1 and A_{n_max}. At each time step there is a probability, P_{d}, that each organism may die.

3 General Experimental Design

For all simulations, the initial population size was set to $X/2$ (= 450 organisms for the X value used in the experiments; see Table 2). These organisms were randomly distributed on the lattice. Each organism is assigned a random template and catchment

Table 2. The basic set of values for the model parameters.

Parameter	Value
Environment	
Environment size, X	30 × 30
Random death probability, P_{d}	0.001
Resources	
Maximum number of resource packets per cell, R_{cell}	7
Initial resource distribution proportion, R_{init}	0.5
Resource renewal proportion, R_{re}	0.3
Basic resource probability, P_{br}	0.05
Organisms	
Total resource packet request per organism, O_{r}	7
Maximum resource catchment radius, $A_{n\_\max}$	4
Initial utility points, U_{init}	10
Metabolic rate, M	1
Dispersal distance, D	10
Number of offspring, N	3
Mutation	
Mutation probability, P_{m}	0.025 (or 0.0 for no-mutation simulations)

radius A_n^i. The state of each organism (template and resource catchment radius) and locations were recorded every 100 time steps throughout the simulation. The simulation length was based on the number of generations it spanned, where a generation was defined to be the mean across all organisms of the time between reproductive events.

3.1 Measures of Community Dynamics

To quantify and compare the community dynamics under different conditions, the following four measures were used. Cumulative measures were used instead of average measures to avoid problems with obtaining averaged statistics from time series data: If temporal autocorrelation in data is observed (and it was) the simple mean and the standard deviation cannot be used for statistical reasons, and more sophisticated time series analysis has to be employed (which is outside the scope of this article) [8].

The cumulative number of individuals, C_{ind}, during a simulation was used to estimate the abundance of the community. The value of C_{ind} was calculated by adding the number of individuals present on the lattice at each recorded time step. In other words, C_{ind} at time i was found by

$$C_{\mathrm{ind}} = \sum_{t=0}^{t=i} N_{\mathrm{tot}}(t)$$

where $N_{\mathrm{tot}}(t)$ is the total number of individuals present on the lattice at time t.

The cumulative number of types C_{type} and number of persisting types were used to estimate the diversity in the system. The value of C_{type} was calculated in a similar manner to the cumulative number of individuals. In particular, C_{type} was calculated by adding the number of organism types present on the lattice at each time step.

This measure is problematic because it does not give an idea of the persistence of some types versus others. For example, this measure may not distinguish between a situation where different types arose with relatively small abundances throughout the simulation, and a situation where a smaller number of types persisted with higher abundances consistently through time. Therefore, an additional measure of diversity, the number of persisting types T_p, was used.

The number of persisting types T_p was defined to be the number of types that persist on the lattice for a time equal to, or greater than, 10,000 time cycles (which corresponds to about 63 generations on average). The number of persisting types and the time period of their persistence contain information about whether new persistent types arise in the system continually. A potential problem with using this measure is that the state of the system was only recorded once every 100 time steps. This means that some of the types may have disappeared and returned between the two points when the state of the lattice was recorded. To assess the importance of this problem, the state of the system was recorded every time step for two simulations. In these simulations, the same number of persisting types was obtained either based on records for each time step or every 100 time steps. This suggests that recording the state of the lattice every 100 time steps does not affect the counted number of persisting individual types.

The average number of "1"s in the templates of the persisting types T_{ones} was used as a characterization of the composition of the community. This gives a measure of how adapted the organisms are to the basic resource packet (which was arbitrarily picked to be all "1"s). For example, if the average number of "1"s is close to eight then most of the surviving types are adapted to the basic resource packet.

4 Sensitivity Analysis

Before obtaining results from the model, the sensitivity of the model to the parameter values was investigated. This was done to determine whether the conclusions we draw are general, and how the results might change as parameter values are varied. This section describes the sensitivity analysis. The length of the simulations for the sensitivity analysis was set to 200,000 time steps, which corresponds to between 660 and 10,000 generations depending on the value of the number of offspring N, which largely determines the generation length (see Section 3, General Experimental Design, for the definition of a "generation"). First, the sensitivity analysis is performed on the parameters relating to the organism properties: the dispersal distance D, the number of offspring N, and the total resource request per organism O_r. Next, the effect of variation in mutation rate P_m is explored. Finally, the sensitivity analysis is conducted on the parameters describing resource properties: the proportion of the lattice initially filled with resources R_{init}, the basic resource bias P_{br}, and the substrate renewal rate R_{re}.

4.1 Sensitivity to the Parameter Values of Organism Properties

The sensitivity analysis was performed for the following parameters: the dispersal distance D, the number of offspring N, and the total resource request per organism O_r. These were chosen since they were interrelated, and the effect of simultaneously varying them was not obvious. The two organism parameters that were held constant were U_{init} and M. These had a straightforward effect on the dynamics. Initial utility points controlled the ability of an organism to persist in unfavorable conditions. Metabolic rate raised the pressure on organisms to find better-suited resource packets (i.e., it increased competition).

Table 3. The minimum value of total resource request per organism O_r necessary for survival of the population for a range of values of dispersal distance D and the number of offspring N.

	D		
N	3	10	30
1	4	3	3
3	4	3	3
5	4	4	4

The sensitivity analysis was performed as follows. The dispersal distance D was set to 3, 10, and 30 cells away from the location of the parent. The number of offspring produced at a reproduction N was set to 1, 3, and 5 offspring. The total resource request per organism at each time step O_r was set to 4, 7, and 81 requests. The upper limit of 81 requests was chosen to correspond to the largest catchment area possible. One simulation for each configuration was conducted, for a total of 27 simulations. Since the variability between simulations was not drastic between configurations, one simulation for each configuration was deemed sufficient.

For each configuration the following were recorded: cumulative number of individuals C_{ind}, cumulative number of types C_{type}, and number of persisting types T_{p}. The results are summarized in Figures 3, 4, and 5. Variation in the number of offspring N and the dispersal distance D did not have an effect on the measured quantities, whereas variation in the number of requested resources O_r had a substantial effect. The minimum number of requested resources that was necessary for community survival is presented in Table 3. High values of N and low values of D both increased the local density of organisms. This increased competition for resources and therefore meant that the minimum threshold value of O_r necessary for survival was higher. C_{ind} (Figure 3) responded to an increase of O_r, the number of requested resources, by increasing toward a maximum value (defined by the number of resource packets available in the environment). On the other hand, T_{p} and C_{type} (Figures 4, 5) increased toward the maximum when the number of requested resources was at the intermediate value of 7. This may be because high numbers of requested resources reinforced the persistence of dominant types in the model in the following way. When two organisms were in a mutualistic relationship with each other, they benefited from digesting the "waste" products of each other. The higher the number of resource packets that organisms requested, the more "waste" they produced and the more beneficial resource packets they could digest. In this way, if a mutualistic relationship became established in the model, it was stronger when the number of requested resource packets was higher, leading to improved success for the mutualistic partners and therefore to lower diversity in the population as a whole.

4.2 Sensitivity to Mutation Rates

To estimate the effect of mutation on community dynamics, the mutation rate P_{m} was varied. P_{m} was assigned values of 0.0014, 0.025, and 0.5. Table 4 shows the response of the cumulative number of individuals, and of diversity, both in terms of the cumulative and persisting number of types. For both diversity measures, the number of types increased with increasing mutation rate. This is not surprising, as higher mutation increases the rate of new types created in a community.

4.3 Sensitivity to Resource Composition

For one selected configuration of organism properties, $(D, N, O_r) = (10, 3, 7)$, three resource properties were varied: the proportion of the lattice initially filled with resources

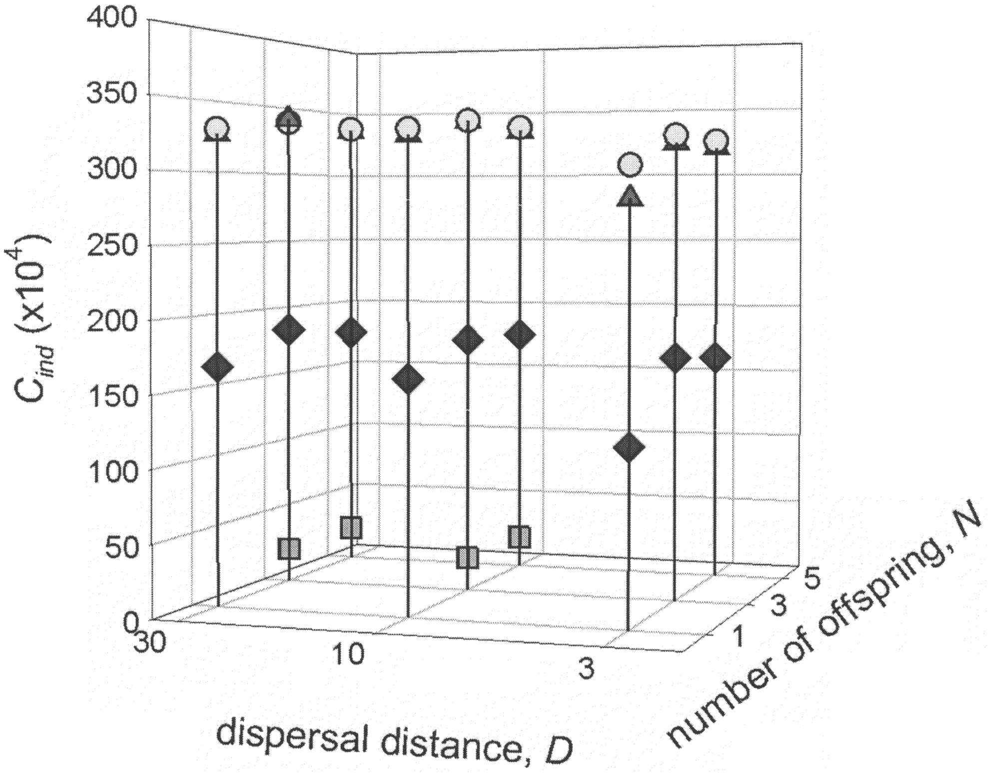


Figure 3. Cumulative number of individuals C_{ind} for the range of values of D, N, and O_r. Square symbol corresponds to $O_r = 3$; diamond to $O_r = 4$; triangle to $O_r = 7$; circle to $O_r = 81$. Where the squares are not shown, the populations did not survive (see Table 3).

Table 4. The response of the number of persisting types T_p, cumulative number of individuals C_{ind}, and cumulative number of types C_{type} to changes in the mutation rate P_m.

P_m	$C_{ind}(\times 10^4)$	$C_{type}(\times 10^4)$	T_p
0.0014	338.8	7.9	17
0.025	336.8	20.7	61
0.5	333.6	146.4	117

R_{init}; the substrate renewal rate R_{re}; and the basic resource bias P_{br}. The parameter R_{init} was set to 0.3, 0.5, and 0.7; R_{re} was set to 0.1, 0.3, and 0.7; and P_{br} was set to 0.5, 0.1, 0.05, and 0.01. Each parameter was varied individually, with the other two being set to the values of $(R_{init}, R_{re}, P_{br}) = (0.5, 0.3, 0.05)$.

The response of the model to variation in R_{init} is shown in Table 5. The value of R_{init} was directly proportional to the cumulative number of individuals and both diversity measures. A larger initial proportion of resources on the lattice predictably led to a larger population size. The positive effect of R_{init} on diversity implies that, within the range of values explored, increasing substrate richness improved conditions for diversity.

The results of varying R_{re}, the proportion of resources renewed every time step, are presented in Table 6. The cumulative number of individuals, C_{ind}, was directly proportional to the replenishment rate. The diversity measures C_{type} and T_p, on the

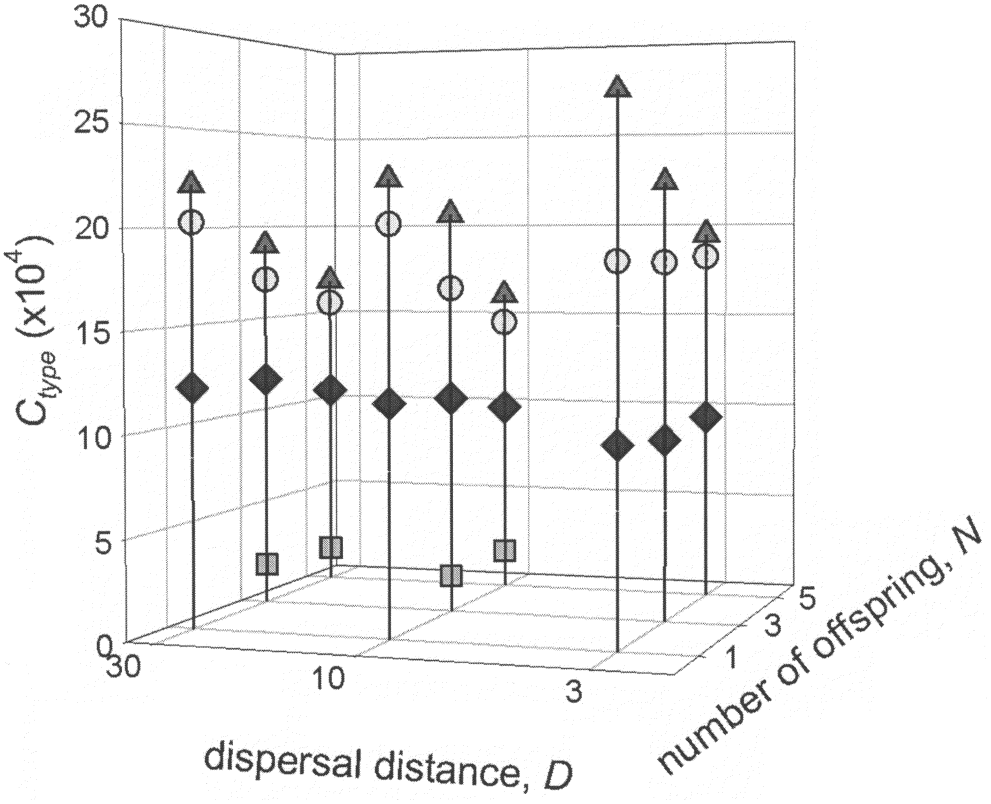


Figure 4. Cumulative number of types C_{type} across the range of values of D, N, and O_r. Square symbol corresponds to $O_r = 3$; diamond to $O_r = 4$; triangle to $O_r = 7$; circle to $O_r = 81$. Where the squares are not shown, the populations did not survive (see Table 3).

Table 5. The effect of variation in the initial resource distribution proportion R_{init}.

R_{init}	$C_{\text{ind}}(\times 10^4)$	$C_{\text{type}}(\times 10^4)$	T_{p}
0.3	233.7	5.6	5
0.5	336.8	20.7	61
0.7	671.7	40.0	146

other hand, peaked at the intermediate value ($R_{\text{re}} = 0.3$). This can be explained by the fact that for high values of the renewal rate, mutualistic relationships failed to establish themselves, since an increase in replenishment rate R_{re} increased the probability that the "waste" of organisms would be renewed to a random resource packet. This led to the domination of types with templates consisting predominantly of "1"s. This, in turn, led to higher C_{ind}, since the survival of organisms adapted to the basic resource was not dependent on the presence of specific other organisms in the vicinity (as is the case for mutualistic partners).

The results of varying P_{br} are presented in Table 7. Varying P_{br} did not seem to affect the cumulative number of individuals. Nor did it have a drastic effect on diversity, although a general unimodal (humped) relationship was observed, with higher values of diversity measures, C_{type} and T_{p}, observed for intermediate values of P_{br} (0.1 and 0.05). This relative independence of C_{ind}, C_{type}, and T_{p} to P_{br} suggests that the organisms

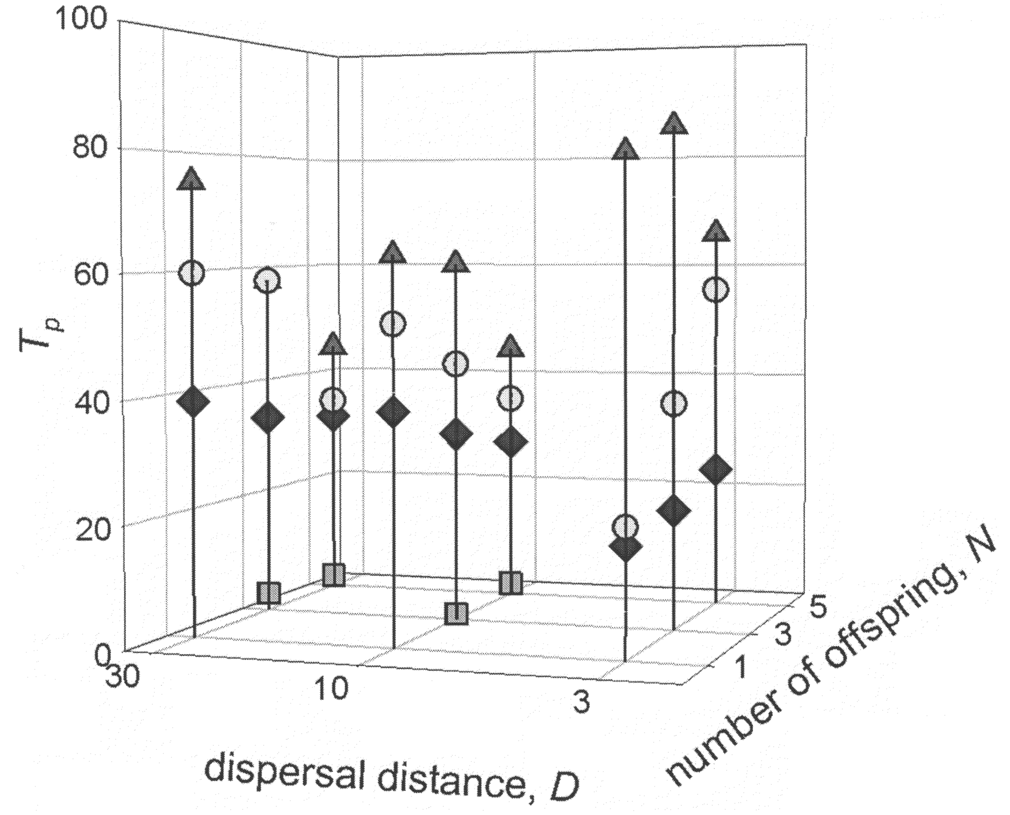


Figure 5. Number of persisting types T_p for the range of values D, N, and O_r. Square symbol corresponds to $O_r = 3$; diamond to $O_r = 4$; triangle to $O_r = 7$; circle to $O_r = 81$. Where the squares are not shown, the populations did not survive (see Table 3).

Table 6. The effect of variation in the resource renewal proportion R_{re}.

R_{re}	$C_{ind}(\times 10^4)$	$C_{type}(\times 10^4)$	T_p
0.1	322.1	15.3	26
0.3	336.8	20.7	61
0.7	653.5	8.4	8

are adapting more to other organisms than they are to the composition of the abiotic resource supply (i.e., resources directly introduced into the environment by the resource renewal process). However, a clear trend was observed in the average number of "1"s in the templates of persisting types T_{ones}; T_{ones} approached 8 with an increasing bias toward the basic resource packet P_{br}. For the intermediate values of the resource bias, T_{ones} was close to 4 (which means that the templates were, on average, half "1"s and half "0"s). This shows how the composition of a community responds to the level of bias toward a particular basic resource packet, so the population was still showing some adaptation to abiotic resources.

Sensitivity analysis showed that, while parameter values affected the extent of diversity and the population levels, diversity in the system is present across a wide range of values for the model parameters. Using this information, we selected parameter values that gave rise to high diversity in the system (Table 2) and used these for a more

Table 7. The effect of variation in the basic resource probability P_{br}.

P_{br}	$C_{ind}(\times 10^4)$	$C_{type}(\times 10^4)$	T_p	T_{ones}
0.5	334.4	15.8	50	6.4
0.1	337.7	19	60	4.9
0.05	336.8	20.7	61	4.1
0.01	337.6	19.3	51	3.7

detailed analysis of the temporal behavior of the system in the presence and absence of mutualistic interactions. This analysis is presented in the next section.

5 Experiments

5.1 Effects of Organism Interactions and Mutation on Diversity

The possibility of interactions between organisms in the model was introduced by allowing the waste of an organism to be a potential resource to other organisms. To explore the effects of organism interactions on diversity, the model was run with and without waste production with the parameter values listed in Table 2. To investigate the effects of waste production and mutation in combination, simulations were performed with the following configurations: mutation and waste production, mutation and no waste production, no mutation and waste production, and finally, no mutation and no waste production. For each scenario, 10 simulations were performed. For simulations without waste production, the organism's "waste" was a random resource packet. To investigate the long-term evolutionary dynamics of the system, the simulations were run for 1,000,000 time cycles, which corresponds to about 6,250 generations (see Section 3, General Experimental Design, for the definition of a "generation"). For each configuration, each sample of 10 simulations was tested for normality using the Kolmogorov–Smirnov test. This showed that the hypothesis that the samples were normal could not be rejected at the 5% significance level for all samples. To compare simulations with different configurations, the samples were subjected to an independent *t*-test. All differences mentioned in the text were significant at the 1% level.

The results of the simulations are summarized in Table 8. With no mutation, community diversity was much lower. For simulations without waste production, simulations with mutation had a higher cumulative number of individuals than in those without mutation. In the presence of waste production, the cumulative numbers of individuals with and without mutation were not significantly different. Mutation was important when no waste was produced because it allowed better-suited types to evolve in the course of a simulation. In the simulations with waste production, however, evolution promoted not only the best-suited type but also mutualistic pairs. If placed in close proximity, mutualistic pairs of organisms could compete well with organisms adapted to the basic resource. However, this dependence on the spatial proximity of specific other organisms meant that the total number of individuals on the lattice was not as high.

There were significant differences between simulations with and without waste production. In simulations without waste production, one or a few types soon established themselves and dominated the community dynamics. In simulations with waste production, the overall picture is dynamic—many types persisted for a significant length of time, the dominant types changed—and this process did not seem to end. To visualize the evolution of diversity in the model, a cumulative evolutionary activity measure was used. The cumulative evolutionary activity of an individual type j at a time t_i is given by $\sum_{t=0}^{t=t_i} N_j(t)$ where $N_j(t)$ is the number of individuals of type j at a time t

Table 8. Comparison of simulations with and without waste production and with and without mutation. The values shown are means (with standard deviations in parentheses) of 10 simulations. For each configuration, each sample of 10 simulations was tested for normality using the Kolmogorov–Smirnov test. This showed that the hypothesis that the samples were normal could not be rejected at the 5% significance level for all samples. To compare simulations with different configurations, the samples were subjected to an independent *t*-test. All differences mentioned in the text were significant at the 1% level.

	$C_{\mathrm{ind}}(\times 10^4)$	$C_{\mathrm{type}}(\times 10^4)$	T_{p}	T_{ones}	Average A_{r} of persisting types
With mutation					
With waste	338.2	17.8	226.3	4.3	66.3
	(0.6)	(0.5)	(17.0)	(0.2)	(0.7)
No waste	463.2	6.7	14	7.1	9.2
	(0.1)	(0.1)	(4.2)	(0.1)	(0.6)
No mutation					
With waste	339.1	5.7	13.5	4.3	68.1
	(2.1)	(1.1)	(1.7)	(0.2)	(2.8)
No waste	442.1	1.3	1.7	7	9.8
	(10.6)	(0.1)	(0.7)	(0.4)	(2.5)

[5, 7]. Figure 6 (top) shows the development of diversity in a simulation without waste production, and Figure 6 (bottom) in a simulation with waste production. In the latter case, among persisting types each type could be matched up to other types with which mutualistic relationships were possible. For example, during a simulation one of the dominant types had a template "1111 1010." During the same time, its exact opposite "0000 0101" (i.e., the best partner for mutualism) existed on the lattice in similar abundance, and four of its close opposites, with only one defective bit, existed on the lattice as well. This situation was typical for all persisting types.

Comparison of community characteristics in the cases with and without waste production is shown in Table 8. Both cumulative number of types and number of persisting types are higher in the cases with waste production. This indicates that waste production promoted community diversity. Both with and without mutation, the number of "1"s in templates of persisting types T_{ones} was lower with waste production than without (Table 8). This means that with waste production, the persisting templates were not as adapted to the basic resource, as they could "adapt" to each other. That is, with waste production, the range of diversity in a community was wider. The cumulative number of individuals, however, was lower with waste production. This was because the survival of organisms that persisted due to mutualistic relationships was dependent on the presence of mutualistic partners in their vicinity. Moreover, these types produced waste that was detrimental to themselves (see the description of the matching scheme).

The average resource catchment area of persisting types tended to be large in cases with waste production, and small in cases without (Table 8). The large resource catchment area was advantageous when mutualistic relationships were possible, as this increased the chance of acquiring resource packets that were the "waste" of another organism. Without waste production, no such pressure existed. In this case, the advantage of having a small resource catchment area was that an organism had a high chance of requesting a resource packet from its own cell, thus avoiding competition.

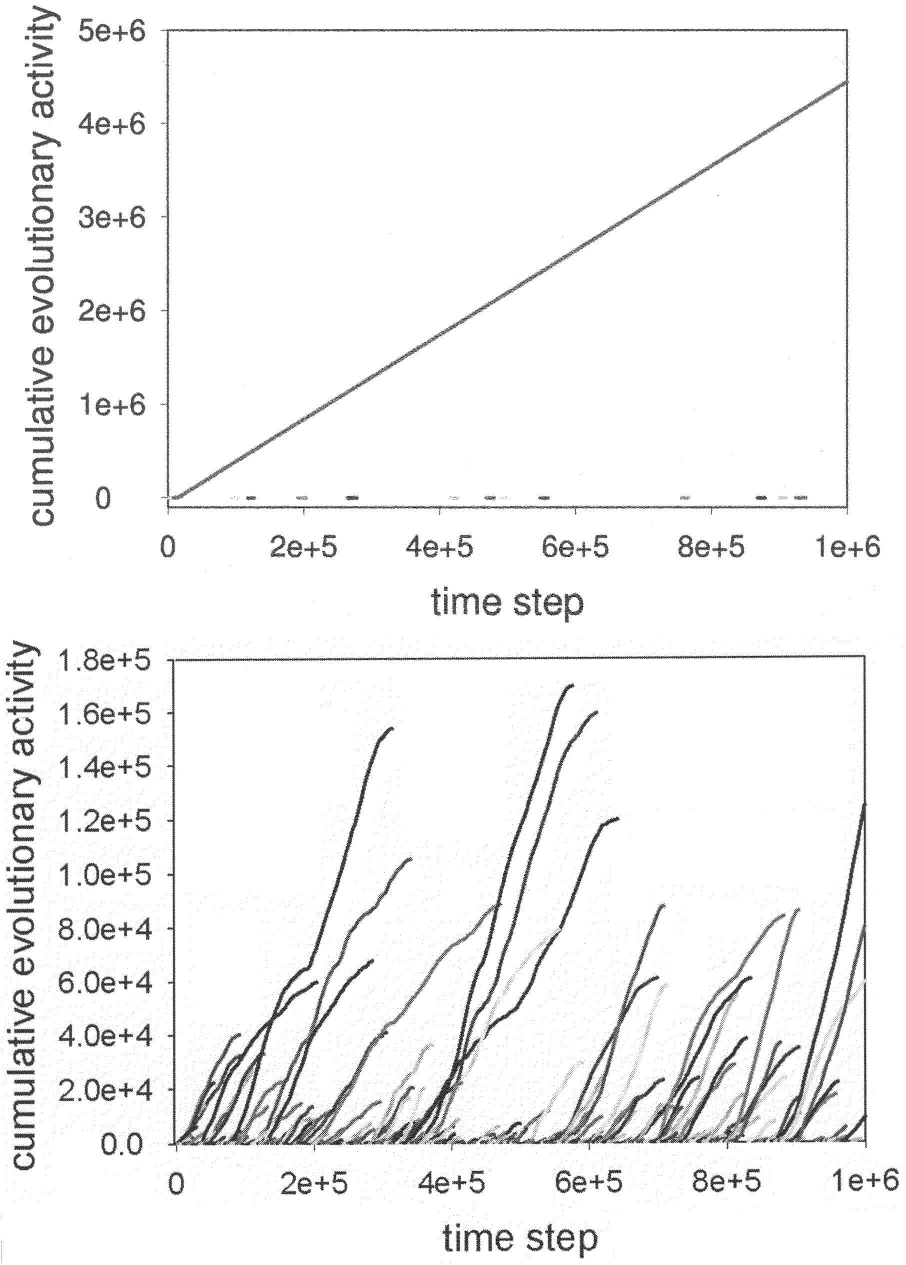


Figure 6. Comparison of simulation output with and without waste production (both with mutation). The simulation with waste production is much more dynamic. (top) Example of a cumulative evolutionary activity plot for a simulation without waste production. One type (with template of "1111 1111") dominates, with a few closely related (Hamming distance of 1 or 2) types arising in small numbers. (bottom) Example of a cumulative evolutionary activity plot for a simulation with waste production.

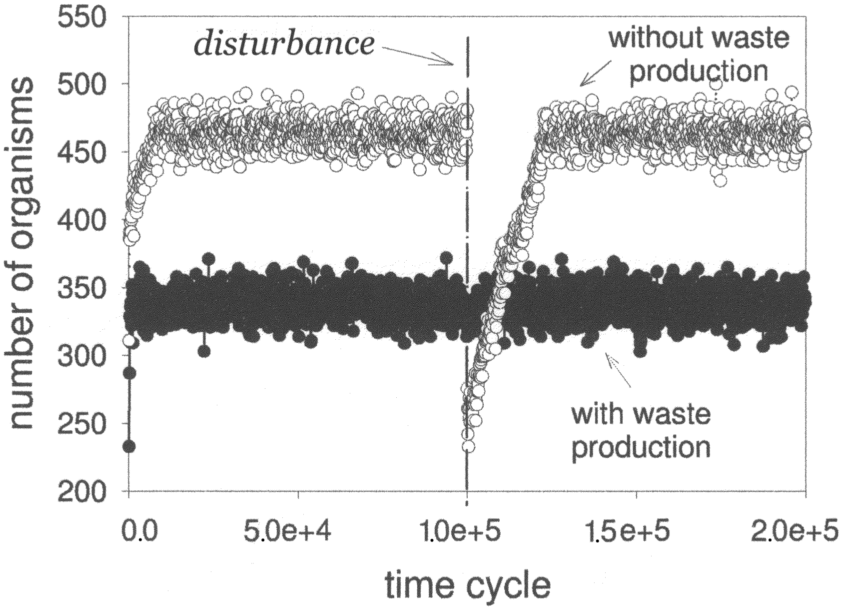


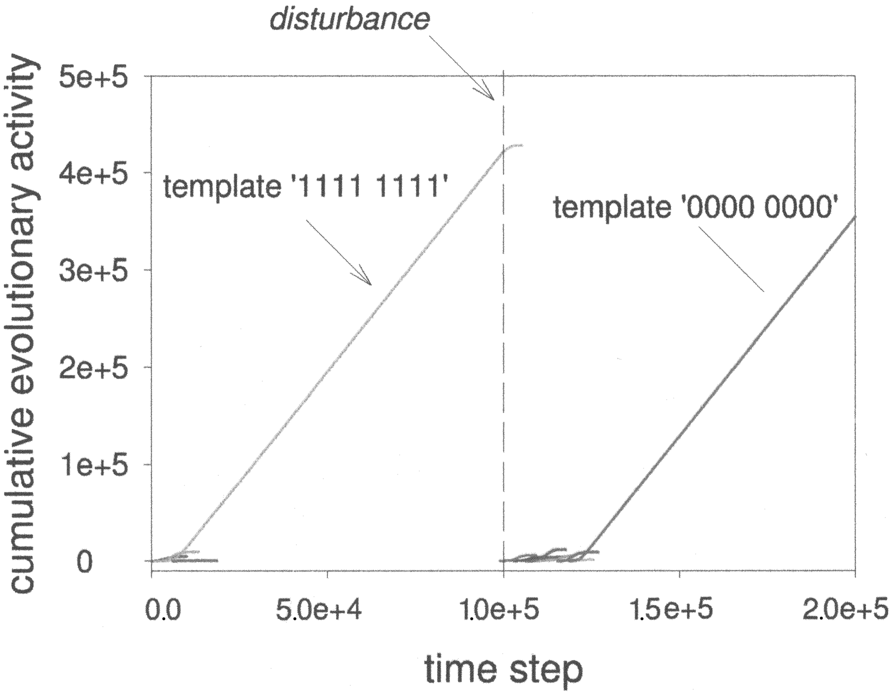
Figure 7. Response of communities to a change in the basic resource bias in the middle of a simulation (results for other simulations were similar).

5.2 Effects of Mutualistic Relationships on Community Stability

The previous results show that mutualistic relationships in the model expanded the range of individual types able to persist in a community. To investigate whether such an expansion had any effect on the stability of the system, the system was subjected to an environmental disturbance. This was achieved by switching the basic resource packet from “1111 1111” to “0000 0000” in the middle of a simulation. Five simulations were performed for each of two configurations: with waste production, and without waste production (with mutation in both cases). The simulations were run for 200,000 time steps. Figure 7 shows the number of individuals on the lattice over time in one simulation (results were similar in the other four runs). In both cases communities survived the disturbance, but communities with waste production were less affected by the change. Figure 8 shows the cumulative evolutionary activity plots in two cases. Figure 8 (top) shows that in a case without waste production, one dominant type changes to another once the bias in the type of basic resource packet is changed. On the other hand, Figure 8 (bottom) shows that, in a case with waste production, activity is not as affected by the change in the resource bias. Some of the types do go extinct when the disturbance is introduced, but some do not. Since the types in mutualistic relationships do not rely on the basic resource packet to the same extent, the type composition does not change as drastically with the change in the basic resource packet.

6 Discussion

A model with the possibility of simple mutualistic interactions among individuals was presented. The mutualistic interactions occurred through resource interactions. Individuals digested resources and deposited “waste,” which could be used by other individuals (Figure 2). In some cases, the “waste” of one organism was beneficial for



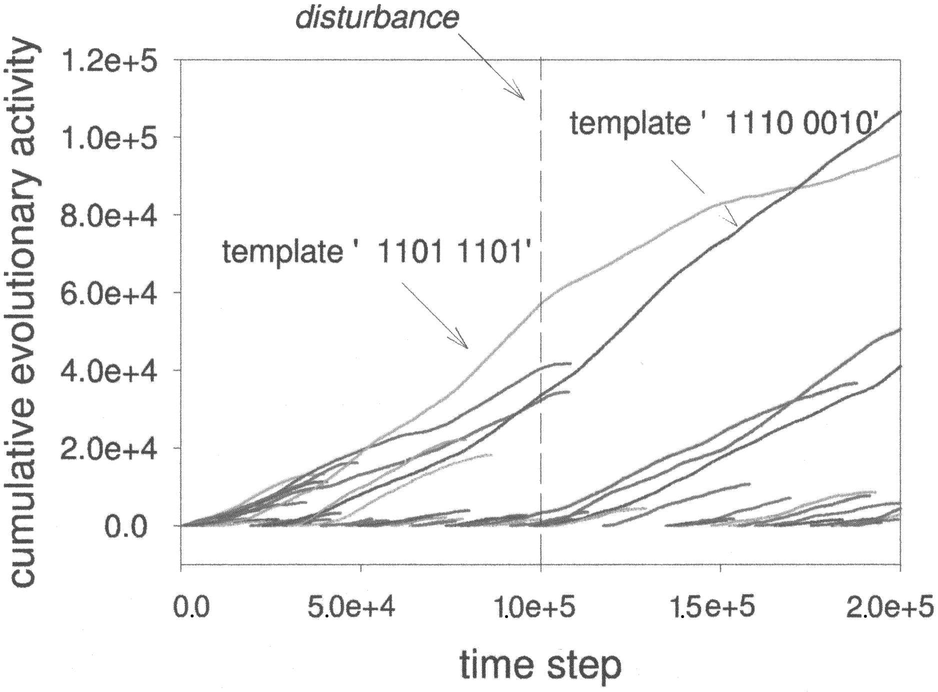


Figure 8. Cumulative evolutionary activity in simulations with disturbance of communities without (top) and with (bottom) waste production. (top) In the first half of the simulation the basic resource packet is "1111 1111," and therefore the dominant type has a template "1111 1111." In the second half of the simulation the basic resource packet is changed to "0000 0000," and the dominant type emerges with template "0000 0000." (bottom) In the first half of the simulation the basic resource packet is "1111 1111," and in the second half of the simulation the basic resource packet is changed to "0000 0000." While some types go extinct after the disturbance, some of the types persist (e.g., two types with templates "1101 1101" and "1110 0010").

another organism and vice versa. This allowed mutualistic interactions to occur. However, since the organisms took up resources locally and at random, it was not obvious whether the mutualistic relationships could be established. The fact that they were shows that individuals did not need sensory perceptions or mobility (although organism types "move" when organisms disperse seed) to form relationships. It was enough to have a sufficient area over which the individuals could look for resources.

Mutualistic relationships formed within a wide range of parameter values and affected population size, community diversity, and community composition. The dynamics of communities was explored when an environmental pressure on a community was imposed: A certain type of resource packet was more abundant than others. In a situation without mutualistic interactions, the community diversity quickly disappeared and the type most adapted to the environment survived. The possibility of mutualistic relationships broadened the range of types of organisms that survived in a particular environment. This occurred because the organisms in mutualistic relationships could compete with organisms of the type that was most adapted to the abiotic environment. This had an interesting effect on population. In particular, the size of the populations was smaller when the mutualistic relationships formed. This was because the success of the relationships depended on mutualistic organisms being spatially well mixed, but the model lacked a mechanism by which an optimum spatial mix could be reliably attained. This being the case, the organisms had to rely on the fortuitous placement of offspring at reproduction to achieve an adequate spatial mix between mutualistic types.

In the presence of mutualistic interactions, the community was continually evolving. Instead of some relationships establishing and remaining dominant, many types became dominant and then went extinct, and this process did not seem to end [Figure 6 (bottom)]. Since the dominance of the mutualistic relationships depended on organisms finding the "waste" of their counterpart, there was a stochastic element in the process. This was sufficient to generate instabilities that allowed other dominant types to arise.

The organism interaction model presented here is very simple. It includes only a few basic mechanisms of individual interaction, which is far removed from the complexity of reality. The aim of this study was to explore whether it was possible for mutualistic interactions to affect diversity in simple systems: It was. This knowledge can be used to extend the model to more complex situations. It can be enriched to include the possibility of larger mutualistic webs and other individual interactions, such as predation. To make such interactions possible, it is necessary to define a system with more flexible interactions, possibly adding mobility or sensory ability to an individual's capabilities.

These investigations would be most beneficial if coupled with biological studies, so that the modeling could be informed, guided, and checked. The model could be informed by biological systems where mutualistic interactions play a central role such as tree–mycorrhizal and plant–bacterial communities (as described in [17, 28]).

The organism interaction model resides in the realm between artificial life and ecology. The present model was easily developed from an existing model of plant communities [20]. Although the models describe two seemingly very different systems, in the basic structure they are quite similar. The ecological and artificial life models often have a similar basic setup, but there have been few connections between them. In general, individual-based ecological population models have concentrated on smaller-scale populations with a rather detailed description of the individuals [13]. The artificial life models, on the other hand, have concentrated on processes on evolutionary scales, with the main questions centering around the evolution and persistence of diversity and complexity [1, 6]. Since models in the two areas are similar in their basic structure, it may be fruitful to investigate possible connections between them [27]. It will also lead to the question of how the two scales of population dynamics and evolutionary dynamics can be connected, and whether population dynamics has lasting consequences for evolutionary dynamics. Such knowledge will be fruitful both for the analysis and understanding of biological ecosystems, and for the synthesis and evolution of artificial ecosystems.

Acknowledgments

We would like to thank John Crawford for insightful discussion. Leeza Pachepsky gratefully acknowledges support from a SERAD studentship.

References

1. Adami, C., Belew, R., Kitano, H., & Taylor, C. (Eds.). (1998). *Artificial life VI: Proceedings of the Sixth International Conference on Artificial Life*. Cambridge, MA: MIT Press/Bradford Books.
2. Allan, M. F. (1996). *The ecology of mycorrhizae*. Cambridge: Cambridge University Press.
3. Barricelli, N. A. (1962). Numerical testing of evolution theories Part I. Theroetical introduction and basic tests. *Acta Biotheoretica, XVI*(1/2), 69–98.
4. Barricelli, N. A. (1963). Numerical testing of evolution theories Part II. Preliminary tests of performance. Symbiogenesis and terrestrial life. *Acta Biotheoretica, XVI*(3/4), 99–126.
5. Bedau, M. A., & Brown, C. T. (1999). Visualising evolutionary activity of genotypes. *Artificial Life 5*, 17–35.
6. Bedau, M. A., McCaskill, J. S., Packard, N. H. & Rasmussen, S. (Eds.). (2000). *Artificial life VII: Proceedings of the Seventh International Conference on Artificial Life*. Cambridge, MA: MIT Press/Bradford Books.
7. Bedau, M. A., Snyder, E., & Packard, N. H. (1998). A classification of long-term evolutionary dynamics. In C. Adami, R. Belew, H. Kitano, & C. Taylor (Eds.), *Artificial life VI: Proceedings of the Sixth International Conference on Artificial Life* (pp. 228–237). Cambridge, MA: MIT Press/Bradford Books.
8. Box, G. E. P., Jenkins, G. M., & Reinsel, G. C. (1994). *Time series analysis—Forecasting and control* (3rd ed.). Englewood Cliffs, NJ: Prentice Hall.
9. Christensen, K., di Collobiano, S. A., Hall, M., & Jensen, H. J. (in press). Tangled nature: A model of evolutionary ecology. *Journal of Theoretical Biology*.
10. Conrad, M., & Pattee, H. (1970). Evolution experiments with an artificial ecosystem. *Journal of Theoretical Biology, 28*, 393–409.
11. Darwin, C. (1859). *The origin of species*. London: John Murray.
12. Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society London B, 205*, 489–511.
13. Grimm, V. (1999). Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecological Modelling, 115*, 129–148.
14. Holland, J. H. (1995). *Hidden order: How adaptation builds complexity*. Boston: Addison-Wesley/Helix Books.
15. Hraber, P. T., Jones, T., & Forrest, S. (1997). The ecology of Echo. *Artificial Life 3*, 165–190.
16. Jones, S. (2000). Evolvability in the context of the biosphere. In C. C. Maley & E. Boudreau (Eds.), *Artificial Life 7 Workshop Proceedings* (pp. 41–44). Unpublished.
17. Kiers, E. T., Lovelock, C. E., Krueger, E. L., & Herre, E. A. (2000). Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: Implications for tropical forest diversity. *Ecology Letters, 3*, 106–113.
18. Marrow, P., Law, R., & Cannings, C. (1992). The coevolution of predator-prey interactions: ESSs and Red Queen dynamics. *Proceedings of the Royal Society London B, 250*, 133–141.

19. May, R. M. (1973). *Stability and complexity in model ecosystems.* Princeton, NJ: Princeton University Press.

20. Pachepsky, E., Crawford, J. W., Bown, J. L., & Squire, G. (2001). Towards a general theory of biodiversity. *Nature, 410*, 923–926.

21. Packard, N. (1989). Intrinsic adaptation in a simple model for evolution. In C. G. Langton (Ed.), *Artificial life* (pp. 141–155). Redwood City, CA: Addison-Wesley.

22. Ray, T. S. (1991). An approach to the synthesis of life. In C. G. Langton, C. Taylor, J. D. Farmer, & S. Rasmussen (Eds.), *Artificial life II* (pp. 371–408). Redwood City, CA: Addison-Wesley.

23. Schmitz, O. J., & Booth, G. (1996). Modeling food web complexity: The consequence of individual-based spatially explicit behavioral ecology on trophic interactions. *Evolutionary Ecology, 11*, 379–398.

24. Taylor, T. (1999). *From artificial evolution to artificial life.* Unpublished doctoral dissertation, Division of Informatics, University of Edinburgh, UK.

25. Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory, 1*, 1–30.

26. von Neumann, J. (1966). *The theory of self-reproducing automata.* Champaign: University of Illinois Press.

27. Wheeler, M., Bullock, S., Di Paolo, E., Noble, J., Bedau, M., Husbands, P., Kirby, S., & Seth, A. (2002). The view from elsewhere: Perspectives on ALife modeling. *Artificial Life, 8*, 87–100.

28. Wilkinson, H. H., & Parker, M. A. (1996). Symbiotic specialization and the potential for genotypic coexistence in a plant-bacterial mutualism. *Oecologia, 108*, 361–367.