

Evolution Experiments with an Artificial Ecosystem

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The technique of ecosystem reconstruction provides a mechanism for examining assumptions about natural ecosystems and their evolution. A hierarchical computer program has been developed with genetic, organismic and population levels embedded in an ecosystem. The program consists of a population of cell-like organisms subject to a strict materials conservation law. The conservation law induces a competitive interaction among organisms. Organisms can also participate in co-operative interactions and are capable of executing representative biological strategies, such as genetic recombination and modulation of the expression of the genome. Preliminary experiments with the system show that the efficiency of individual organisms may be restricted, but with a concomitant increase in the utilization of the environment. The nature of the restrictions probably differs from those that occur in natural biology, due to specializing assumptions in the model, but the mechanism of their appearance may be a general ecosystem process.

1. Introduction

The present theory of evolution is concerned primarily with the statistics of populations of genes. The statistical behavior of these populations is dependent on what are called *fitness* criteria. Unfortunately, fitness functions are not a part of the theory itself, but must be inferred from observation, experience, and intuition. In order to improve the predictive capacity of the theory of evolution, many attempts have been made to define general aspects of fitness, but this has always proved exceptionally difficult. We believe that this difficulty is a reflection of our lack of understanding of the origin of hierarchical organizations—that is, collections of units which exhibit short term *deterministic* mechanisms in the individual which are to a large degree the long term result of the *statistical* behavior of large groups of these individuals. In evolutionary theory this is often expressed by the statement that evolution operates on populations of phenotypes, not on the genotype or the individual, but at the same time it is the gene which constructs the individual

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according to deterministic mechanisms which are not dependent at the time of construction on any of the statistical behavior of populations. We know that in nature the behavior of living systems involves many hierarchical levels of interaction, from the genetic level up through the individual, the population, and ultimately to the entire ecosystem. A theory of evolution which does not reflect this hierarchical level structure cannot be expected to give a clear picture or to give useful predictions.

In this paper we describe preliminary evolutionary experiments using a computer program in which three hierarchical levels of biological organization are distinguishable. We call these the *genetic*, the *organismic* and the *population* levels. Furthermore, we do not introduce any fitness criteria as an explicit part of the program. Instead, we interpret the computer in this experiment as an ecosystem in which the various interactions within and between levels must take place. This means that we must introduce certain constraints which correspond in some sense to the real ecological conditions in the physical world. The two most important which we consider are: (1) the way the world is spatially divided, i.e. how the individual organisms can occupy the world; and (2) the closure of this world to matter, i.e. the conservation of matter. Notice that these are not fitness criteria, but are the most general conditions which collections of organisms must satisfy.

A number of programs have already been developed which use some features of natural evolution. In particular, Bremermann (1962, 1967) has applied evolution techniques to optimization and search processes. The work of Reed, Toombs & Barricelli (1967) uses a fixed pattern of numbers, determining certain strategies that develop in the context of a game situation. Programs or designs have also been published which incorporate the detailed dynamics of self-reproduction. For example, see Stahl (1967) for a simulation of the bacterial cell and Arbib (1967) for the design of a more general self-reproducing system. However, the complexity of such programs precludes the possibility of extending them to the population dynamics level on present day computers.

To our knowledge the program which will be described in the present paper is the first which allows individual organisms with a genotype and phenotype to evolve within the general constraints of an ecosystem. Our approach is intermediate between those in which organisms evolve in relation to arbitrary fitness criteria imposed by the programmer and those in which the dynamics at the level of the individual organisms are so detailed that evolution processes are precluded on present day computers. Hopefully this intermediate approach will provide a tool for examining many problems in evolutionary biology which are intractable from an analytical or natural experimental point of view.

While it may be clear that a multilevel hierarchical structure is a characteristic of living systems, it is by no means clear how these levels should be represented in a computer program. As a practical matter we cannot represent all the molecular details of the genetic level and still have time or room in the computer for the direct multiplication of these detailed individuals up to the population level. To avoid this problem the present program uses a common, fixed set of features or routines which can be used by all "organisms". The phenotype (or phenome) of an organism determines the way in which these routines are used. Of course this places restrictions on possible modes of evolution, restrictions not present in nature, where new functions or hierarchical levels of organization can always emerge. However, it is just these features or conditions for evolution which are the important unknowns. The use of common routines allows these unknowns to be manipulated directly. This would not be possible if each organism carried its own private program.

The features which are included in the common set of routines are to a certain extent arbitrary. This is not necessarily a defect as long as the process of modifying these features produces a system whose behavior converges to that of a natural ecosystem. It is difficult to define the characteristics of an evolution process precisely. However, we consider it a step in the right direction if the artificial ecosystem exhibits certain behavior characteristic of the natural system—for example, behavior characteristic of ecological succession processes, with the provision that the origin of new types, of crucial importance in evolution, is possible (see Margalef, 1958; Odum, 1969). We have also adopted two other ground rules. First, the processes of evolutionary search must agree with biological fact, even if unbiological search techniques are more effective. This is important, since breakdowns in the analogy between computers and biological systems might lead to such a divergence. Second, the artificial ecosystem must be as simple or primitive as possible. We are working for the minimum or necessary conditions for evolution. We hope that this is a useful strategy for distinguishing the essential properties of ecosystems from the frozen accidents. In fact, the present project grew out of an attempt to determine what observed conditions should be considered as significant in an abiogenic experiment, if the origin of life is identified with the origin of systems capable of supporting evolution (Pattee, 1966, 1969).

2. Biological Fundamentals

In order for a lineage to persist the organisms of this lineage must, on the average, produce at least one offspring before they die. Individual organisms have various strategies for achieving this. Also, lineages or species have

various survival strategies. Organisms, for example, may be well adapted to a given environment, or they may be adaptable, in the sense that they can respond flexibly to a variety of environments. This is also true at the level of the species, and at other levels of biological organization. In general adaptability and adaptedness interfere with each other at a given level of organization, in the sense that an increase in adaptability results in a decrease in adaptedness. This interference can also occur between levels of organization. For example, the adaptability of a species depends on the variability of its gene pool. If the organisms of the species have complicated adaptations, however, the variability of the gene pool will be restricted. This follows because the genes of more complicated organisms must be more integrated, or adapted to one another, and therefore rearrangements of these genes are more likely to produce nonfunctional forms.

Thus the set of strategies characterizing a biological system cannot be arbitrary—only certain sets of strategies will be consistent. This is important because it means that the evolutionary search strategy of a system depends on the characteristics of organisms. At the same time, the evolution of these characteristics depend on the search strategies. This is one statement of the apparent paradox of the origin of hierarchical control.

These search strategies cannot be described without describing the spatial organization of the population. This organization, together with species specificity, influences the pattern of gene flow, and therefore the search strategy. Extensive gene flow within a population tends to keep the population homogeneous. In order for the population to differentiate, gene flow between subpopulations must be prevented. Such blockage usually, and perhaps always, follows isolation of the subpopulations. In any case it is evident that isolation would facilitate the speciation process.

The formation of species is restricted by the niches, or spheres of existence which are available. These, in turn, are modified by the formation of new species. Such niche multiplication is most evident in relation to the appearance of trophic levels. Of course species with certain types of strategies may be able to colonize new niches more rapidly than other types of species, or migrate into similar niches in different locations. The sequential change of the ecosystem will decrease only as niches are filled and as mechanisms evolve to reset the environment. The development of such stability in an ecosystem is often associated with the development of a high degree of symbiosis.

Most of the mechanisms which have been discussed are present in bacteria. Here there are three important levels of organization: the genetic, the cellular (or organismic) and the population levels. Bacteria have a variety of homeostatic or adaptability mechanisms at the organism level—for example induced enzyme synthesis. In general the presence of an unnecessary inducible enzyme

places a bacterial strain at a disadvantage. The bacterial population can also exhibit a greater or lesser degree of adaptability. Since many bacteria have a high growth rate, mutation is of course an important mechanism of search. Bacteria are also capable of exchanging genetic material through conjugation and transduction. Ravin (1960) has suggested that such processes may play an important role in the life of micro-organisms, and that bacterial populations could support a wide variety of breeding structures. Of course the main processes of present day microbial ecology may involve the culturing of already existing types in different environments. It is likely, however, that sexuality played an important role in relation to the origin of these types.

Bacteria participate in symbiotic relationships in the sense that certain types may require substances produced by other types. There are no trophic levels in the sense in which they occur in metazoan populations, but a number of species may be required to cycle materials back to their original form. The organization of the bacterial population, as a whole, may be controlled by chemical messages between units. For example, bacterial populations often reach a certain size and stop growing, despite the fact that nutrients are not limiting and poisons have not accumulated. This fact turns out to be pertinent when the behavior of the model ecosystem is analyzed.

3. Representing the Fundamentals

The significance of the facts reviewed in the previous section may not be universally agreed upon, but that is not crucial for our purposes. Most of the features discussed are present in micro-organisms. Presumably these are most similar to primitive life forms and it is possible that any systems capable of supporting evolution would rapidly develop a spectrum of processes including those discussed. The question we are asking is whether or not these processes, or some subset of them, can actually produce evolution. It is possible that not all of these processes are essential. It is also possible that some important processes in nature have been overlooked. The only way to approach this problem is to design an artificial ecosystem which we can test and modify.

We shall only describe this evolution program at a functional level since a listing of the program and a detailed description of its operation is given elsewhere (Conrad, 1969). It is written in LISP, a list processing language, and in the LISP assembly language. The program and its variations have been run for about three hours on the IBM 360/67 computer at the Stanford Computation Center.

The events in the evolution program take place in what we call the *world*. The world is a one-dimensional string of *places*. The string is closed, or forms

a loop, to avoid end effects. Each place in the world is characterized by a state (A or B) and a certain number of material parts called *chips*. Organisms (or cells) may be viewed as selective catalytic shunts in a cycle of these parts, i.e. cells control the rate of flow of matter. The world, as a whole, is subject to a strict materials conservation law. This induces the fundamental competitive interaction among the organisms.

Each organism is attached to some place in the world. It should be emphasized that the organism is not located only at this place, and the place does not correspond to an ecological niche. (Certainly such niches must not be artificially imposed by the programming.) Rather, the organism is allowed to operate over a certain number of contiguous places (its territory), but is associated with the place of attachment for certain of its activities and at the end of every period or cycle of the program.

The temporal organization of the model is not in real physical time since events occur at discrete periods. The periods are not generation times, and the lifetime of an organism can extend over any number of these periods. However, the consequences of an organism's behavior must depend on the behavior of other organisms—that is, it must appear as if organisms are functioning simultaneously. This is achieved, inside the computer, by using the device of a *two-pass* system, allowing interaction among processes arbitrarily separated by the sequential operations of the computer. In the first pass organisms interact with the environment and with other organisms in local sequence time. The consequences of an organism's behavior in what corresponds to global, physical time are determined during the second pass. Here chips are collected, organisms reproduce, and chips from decaying organisms (detritus chips) are returned to the matter pool. The net effect of birth and decay determine the composition of the new biota, and the process is repeated. In the actual program the second pass consists of a number of sub-passes. The overall flow of information in the program is illustrated in Fig. 1.

The organisms have a genome and a phenome. The genome is mapped into the phenome according to a doublet code. This mapping is not designed to represent the known processes of protein synthesis, or embody any particular logic of self-reproduction. However the genotype-phenotype distinction serves as a basis for efficiently describing various representative strategies of construction and interaction, which is the same function it performs in real cells.

There are 16 possible codons or pairs of genome symbols. These are usually mapped into six types of phenome symbols. The sequence of phenome symbols determines how an organism uses common routines. The immediate behavior of an organism depends on its *internal state* and on its *input state*. The first input state is the state associated with the organism's attachment

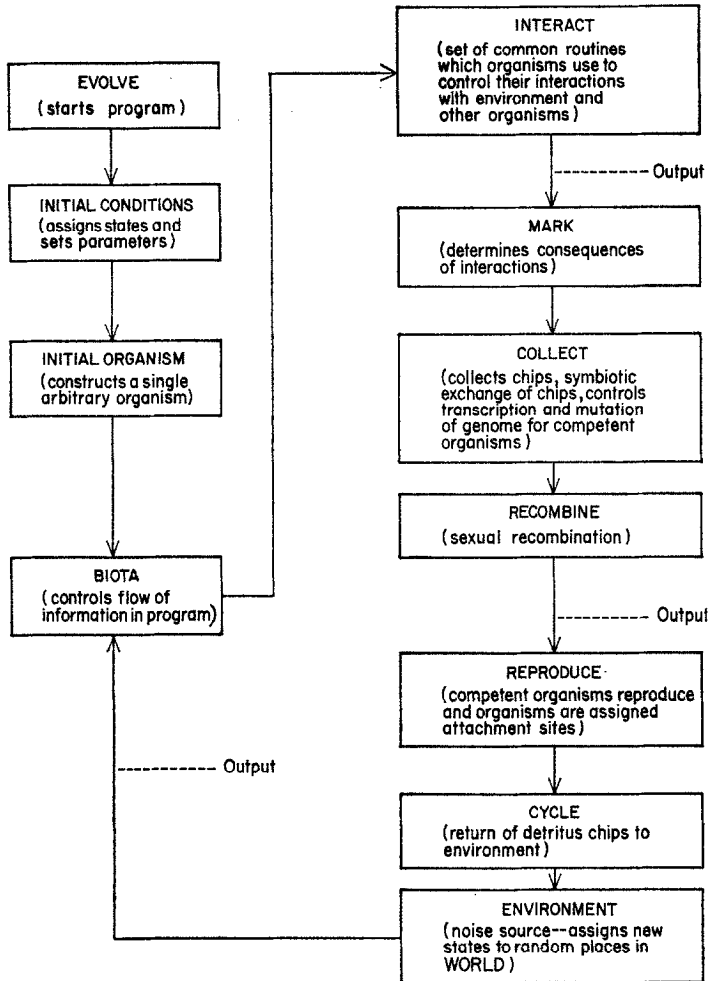


FIG. 1. Flow of control in evolution program. The diagram is highly simplified. A new period is initiated when BIOTA is re-entered after ENVIRONMENT is executed. The second pass begins with MARK.

site. The organism's first internal state is the first symbol on its phenome. The second input state is the state immediately to the right of the first input state, and the second internal state is the next symbol on the organism's phenome, and so forth.

Six routines are possible. When the organism is in state A or B it compares itself to the input state, or tries to match the environment. When it is in state

C it looks for a conjugate, or organism with which it can recombine. When it is in state D it allocates a chip to a repair process—that is, to its self-maintenance—if it in fact succeeds in collecting this chip. When it is in state F it looks for a symbiont, or organism with which it can share chips. When it is in state E it jumps into a mode in which the rule determining the next internal state is somewhat more complicated. We call this the parametric mode. Here the system can select the next phenome symbol from a pair of possible phenome symbols on the basis of the state of the environment. This represents a modulation of the genome or an inducible property, in the sense that the genome can express itself differently in different environments. The organism must pay for the extra genetic material, but only for the part of the phenome which it uses. The operation of an organism is illustrated in Fig. 2.

WORLD	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
INPUT STATE	A	A	B	A	B	B	B	A	B	A	A	A
INTERNAL STATE	A	C	B	D	F	E	AB	AA	E	D		
—————ORGANISM—————												

FIG. 2. Representative organism. The organism is attached at place P2. The first internal state is A and the first input state is A. The organism records this fact, and will collect a certain number of chips during the second pass. The second internal state is C. The organism will later look for a conjugate at position P3. The third internal state is B and the input state is A. These do not match and the organism goes to its next internal state. This is D, and the organism can allocate a chip to repair processes, assuming that it collects a chip. The fifth internal state is F, and the organism will later look for a symbiont at place P6. The next internal state is E and the organism goes into a parametric mode. The seventh internal state is one of the pair A or B. Thus the organism will always match place P8. The internal state which follows is also one of a pair, but in this case both members of the pair are A's. This is wasteful and, in fact, the organism does not match place P9. The organism now goes into an E state and jumps out of the parametric mode. Thus the next state is D and the organism is entitled to another repair chip. In general, if the second alternative in the parametric mode is a non-matching type symbol it cannot be used. Also it is wasteful if the E symbol signalling the parametric mode occurs in an odd position, since the immediately following symbol will not be used.

Each organism carries a record of its own activities. The record is an accounting device and not part of the structure of an organism. During the first pass each organism marks all the places which it utilizes and stores the names of these places on its record. It also stores the location of possible symbionts and conjugates, as well as some other accounting information. After each organism in the system has interacted with the environment, the number of chips returned at each place is determined. This is the quotient of the number of chips and the number of marks associated with the place. Only a whole number of chips can be withdrawn and therefore a certain

number of chips, associated with an unusable remainder, may be unavailable. In the second pass each organism collects chips from the places it has matched. The symbiotic exchange of chips with other organisms takes place at this time. Organisms can develop recognition codes enabling them to exert some selective control over their symbiotic interactions. A certain number of chips which are collected are used for repair and are immediately returned to the matter pool. Repair chips represent energy which an organism uses for its maintenance. The probability that an organism will decay depends on the number of repair chips which it collects.

Chips which are not used for repair are allocated to reproduction. When an organism doubles its size, in terms of chips, it becomes competent to reproduce or fission. In this case the genome is copied and mutated. Both point and size (increment or decrement) mutations are possible. Redundancy in the code allows some control over the effective mutation rates of phenome symbols. If the organism has the sexual property it looks for a conjugate in the appropriate places. Recombination consists of breaking and splicing genomes at random places. Organisms can develop recognition codes which enable them to exert some selective or specific control over the flow of genetic information.

The transcribed genome is translated into a phenome and a daughter cell is produced. The daughter cell may be attached at the same place as the parent, or one place to the right or left. In most versions of the program the probability of dispersing or migrating in this sense is under genetic control. If the parent organism decays, chips must be returned to the environment. This is also true if an organism collects more chips than it can use. This replacement is achieved by dividing the number of chips to be returned by the length of the phenome. The quotient (rounded to the lower integer) is returned to each place corresponding to the position of a phenome symbol. The remainder is also returned to the environment, one chip at a time starting at the attachment site of the organism. Chips are strictly conserved, but the pattern of replacement is, in general, not the same as the pattern of withdrawal. This is important because it means that the environment is not automatically reset by the program. If resetting the environment is important for survival, then organisms must evolve mechanisms for achieving this themselves.

Thus, the redistribution of chips in the environment is affected only by the activities of organisms. The distribution of A and B states, on the other hand, may be affected by noise. A and B states can be interpreted as representing sets of environmental conditions, such as temperature or salinity, which are reasonably independent of the structure of the matter cycle. Organisms can withdraw chips if they are in a state which allows them to function under the given conditions.

4. Some Comments on the Model

The present model establishes a one-dimensional biology. There is a discrete one-dimensional world with one-dimensional organisms. The ecology, physiology and genetics of these organisms are therefore as simple as we can imagine.

The discreteness and relatively rigid form of this model at both the organism and population levels is clearly an imperfect representation of biological systems. Within this framework, however, there is a remarkable degree of internal freedom and behavioral flexibility. The reproductive success of organisms, or groups of organisms, depends on both the biological and physical environments. These change in the course of evolution, and consequently the criteria of fitness are subject to evolutionary change. Likewise, the processes of speciation and niche selection are not imposed by the programming. For example, the sexual recognition codes control the flow of genetic information in the population. Speciation occurs (in the biological sense) when subpopulations are genetically isolated. Such isolation cannot arise from a single change in a sexual recognition code; in fact, the population could maintain a range of such codes. Thus the possibility of speciation or development of disjoint sets of codes is present in the model, but whether or not this possibility will be used is not known in advance. It should be remarked that the present program does not use any external mechanisms for spatially isolating populations. In fact, this may be an unrealistic freedom in the model.

The amount of information which can be processed in the environment of the computer is much smaller than can be processed by natural systems. For example, in the experiments to be described the average population ranged from 200 to 400 organisms, depending on the number of chips initially assigned to the world. This point should be kept in mind when interpreting the statistical behavior of the system. It should also be remembered that the organisms are operating in the information-rich constraints of the computer environment, and can therefore evolve free of many of the internal constraints necessary for the self-reproduction of organisms in the present day environment. Furthermore, the types of organisms which can evolve are limited by the fixed nature of the common routines. For example, there are severe restrictions on the trophic structure of the system. In fact only a single trophic level is possible, along with symbiotic interactions at this level. The system could be modified to accommodate an arbitrary number of trophic levels, but we felt that this complication might obscure the minimum initial constraints required for evolution.

These minimum conditions can be studied by further simplifying the system. For example, any particular organism strategy can be removed by altering the code. The evolution process can begin with a single arbitrary organism. The program is also capable of accepting populations of organisms as inputs, and most of the parameters in the system are under operator control.

5. Experimental Results

(A) GENERAL COMMENTS

Several variations of the evolution program have been prepared. The behavior of the program is very complex, and it is neither practical nor instructive to follow the dynamics in detail. Rather, a mode of description must be adopted which gives a simple, but not overly distorted, picture of the system. The data analysis associated with the evolution program has proved to be somewhat difficult, since it is hard to know in advance what features of the system will be significant.

The program reports vital statistics of organisms, as well as statistics regarding the matter pool, the size of organisms, and the fraction of organisms executing various strategies. The *utilization* of the matter pool is expressed by the ratio of chips bound in organisms to chips free in the environment. The *matching ratio* is the quotient of the number of successful matches to the number of attempted matches. The relative changes in size of the population can be expressed as a *survival curve*.

The system has also been examined relative to certain classification schemes. For example, organisms can be classified in terms of the types of strategies which they execute, in terms of size, in terms of the functionality of the parametric strategy, and so forth. It should be emphasized that these classification schemes are arbitrary, and the accuracy of the picture which they provide cannot exceed the extent to which they express important elements of the system. The data provided by the various population quantities and classification schemes must always be considered in conjunction with one another.

The only way of understanding the causal relations of the system with certainty is by controlling its dynamics through alterations in the programming. In practice, experiments focused on limited aspects of the system's behavior, and many variations on the program were run relative to these.

The behavior of the program will be summarized in the remainder of this section. A detailed presentation of results and data analysis, as well as a description of all alterations in the programming, can be found elsewhere (Conrad, 1969).

(B) TYPICAL BEHAVIOR

The first evolution program (system I) was run for only 41 periods. The interpretation of its behavior, however, is clear cut and establishes a good perspective.

The system I environment was noiseless, and organisms were allowed to persist indefinitely if they could allocate a sufficient number of chips to repair processes, a condition rapidly discovered by the population. The matching ratio increased as the run progressed, and the organisms became increasingly efficient with respect to the relative number of matching type symbols on their phenomes (see Fig. 3). However, the behavior of system I was in many ways the antithesis of evolution. Both birth and death rates became very small. Organisms maintained themselves by withdrawing

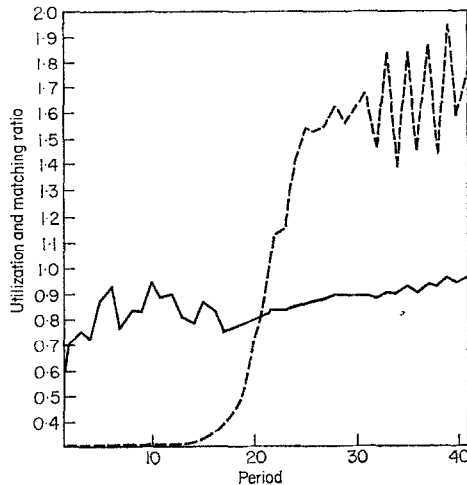


FIG. 3. Utilization and matching ratio curves for system I. The growth phase ended in the neighborhood of period 25. ----, Utilization curve; —, matching ratio curve.

repair chips; only a small number of chips were used for self-reproduction. Inefficient organisms were eliminated (most markedly) when the number of free chips fell below a critical level. As a consequence the population became homogeneous, one type tended to predominate, and chips in certain places were never utilized. This was associated with the fact that the dispersion of the population was retarded, due to the low reproduction rate. Essentially, the collectively stable behavior of the population precluded its further evolution.

Subsequent versions of the program were therefore modified in a variety of ways. In particular, a noise level was established and repair strategies were

designed so that the probability for an organism to decay is never zero. These are certainly more realistic conditions. One version (system III) was run for 251 periods. This was the longest run, and is the only one which will be described here.

The composition of the system III biota showed a succession of patterns. The diversity of types, as with system I, increased to a maximum at the end of the growth phase. Aside from this, and in contrast to system I, there is no indication that the composition of the population will cease to change. The size of organisms, as well as the diversity of sizes, also tended to increase, allowing organisms to interact with a greater number of places. The changing composition of the population is associated with this size increase, since the probability distribution for different types of organisms is related to average size (in the absence of selection).

The various strategies show stretches of overall increase or decrease; in general trends cannot be extrapolated. The symbiosis property often occurred with a frequency above its equilibrium value, and the symbiosis codes tended to concentrate, increasing the efficiency with which this strategy was utilized. In general the sexual property was not favored, and the sexual codes tended to spread out, thus reducing the probability of recombination. However, the sexual property exhibited stretches of consistent increases. These were associated with consistent increases in the parametric property. This pattern was always observed immediately following perturbation experiments in which the logic of the program was modified, presumably changing optimum strategies. In one case, however, system III exhibited a stretch of consistent decreases in the sexual property, with concomitant increases in the parametric property, indicating a possible competitive exclusion of types.

On the average, utilization of the environment increased as the run progressed.

(C) CO-ADAPTIVE PROPERTIES

Some of the organisms in system III were efficient, and well-organized parametric types did occur. However, the predominant types of organisms were definitely inefficient. Many organisms carried phenome sequences of no apparent selective value, and the parametric property was by and large non-functional, in the sense that it was rarely used to increase the organism's ability to match the environment. Organisms with efficiently placed parametric symbols exhibited no clear advantage over those with inefficiently placed symbols. Also, organisms with a conservative dispersal strategy (whose offspring have a better chance of retaining correlations with the environment) did not predominate over dispersive types. The matching ratio showed con-

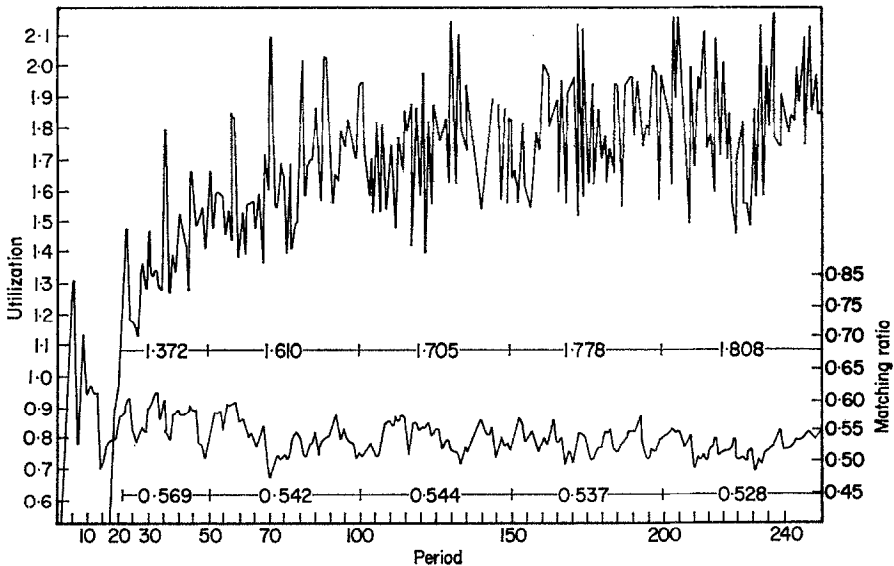


FIG. 4. Matching ratio and utilization curves for system III. The scale on the left is for the utilization (upper curve). The scale on the right is for the matching ratio (lower curve). Average values for representative blocks of the run are shown under each curve. Note decreasing average matching ratio and increasing average utilization. The growth phase ended sharply at period 20.

siderable fluctuation, but declined slightly, on the average, as the run progressed (see Fig. 4).

The low efficiency of organisms and the decline in the matching ratio are somewhat surprising since improvement in these properties would often be regarded as a criterion for evolution. Yet system I, which had a steadily increasing matching ratio, did not exhibit behavior at all characteristic of evolution.

The low efficiency and decline in the matching ratio were not artifacts, since these were exhibited by many arbitrary variations of the system. The decline is associated with the fact that the number of chips returned to an organism for matching a particular place is the quotient (rounded to the lowest integer) of the number of chips and the number of matches for that place. Thus a decrease in the number of matches may increase the utilization of the environment, and conversely. This is a feature of the programming, but it is not unrealistic, since overly severe competition usually reduces the efficiency of populations in nature. In fact, the matching ratio can be induced to increase by cycling chips more rapidly through the system.

Adaptations which confer an advantage on the population, rather than on the individual, will be called co-adaptations. We have oriented our preliminary experiments with the evolution program around the working assumption that the decline in the matching ratio and low efficiency are co-adaptive in this sense. Such co-adaptations arise from the effect of overcompetition on the relative reproduction rates of organisms with different efficiencies. All population quantities in the evolution system exhibit oscillations. When chips become scarce, selection presumably becomes more intense. This is associated with a contraction in the population. In the case of system III (but not of system I) this contraction is often associated with a decrease in the matching ratio. In such a situation the organisms which succeed in reproducing form the most efficient group, but the predominant contribution to the population comes from organisms which just survive. Apparently the intensity of selection reduces the capacity of selection to distinguish between efficient (but not extremely efficient) organisms and inefficient organisms. This follows because efficient organisms are not likely to reproduce, and are therefore at no advantage relative to less efficient organisms.

This mechanism is sufficient to explain some of the fluctuations of the matching ratio, but it does not account for the overall decrease. Organisms in the evolution program may be grouped together on the basis of the places they match. In fact, associations of less efficient organisms have been found which make a greater contribution to the subsequent population than comparable associations of more efficient organisms. This raises the possibility that group or interdeme selection is operating, but the relative importance of this mechanism is not yet clear. It might be remarked that removal of all unnecessary strategies (by an alteration of the code) increases the fluctuation of the matching ratio, suggesting that these strategies helped to retain co-adaptations.

6. How Useful is this Model?

This simple evolution program shows many analogies to natural evolution, but the departures from natural evolution are also striking. Different types of organisms may develop, but there is no evidence that speciation, in any biological sense, is taking place. Mutual dependencies may exist among some of these types, but there does not seem to be any niche multiplication in the sense of the developing biota creating roles for widely different organisms. The system applies some of the built-in routines in unexpected ways, but of course there is no possibility for new routines to appear.

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 im-

proved. For example, the system exhibited some integration or coadaptive behavior at the population level. However, this integration was slight by comparison to that which develops in the course of natural evolution, and quite different in character. Natural biological systems are not known to control competition by developing disorganized phenotypes. Ordinarily such systems prevent overutilization of the environment through mechanisms of inter- or intraspecies communication, e.g. control of predator-prey relationships, regulation of growth rates, territoriality, self-thinning, etc. Natural systems may also increase stability by rapid cycling of materials back to the environment through the detritus pathway. The evolution program did not allow good internal control in this respect, and, in fact, the elastic growth characteristics of the population would have reduced the importance of such control. However, oscillations in population quantities are decreased by imposing an increase in the rate at which chips are cycled through the system.

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. This was evident in the case of system I. This would imply that variation and selection processes associated only with replicating nucleic acid molecules (as distinct from systems capable of using such a store of instructions to control specific reactions) would probably not evolve in any effective way (see Mills, Peterson & Spiegelman, 1967).

7. Conclusions

It is, of course, not yet clear what necessary conditions are to be associated with evolution processes. However, we have shown how assumptions about such conditions can be examined through the technique of ecosystem reconstruction. We feel that the present study indicates the feasibility and usefulness of this synthetic approach as a source of new ideas and information about fundamental problems in evolutionary biology.

In addition to their use as models of biological evolution, the behavior of such programs, especially their shortcomings, appear to us as potentially valuable for understanding the general theory of the origin of hierarchical control at all levels, including the design of computers with more creative or life-like problem-solving abilities. Most current efforts at problem solving are still algorithm-oriented rather than evolution-oriented; that is, we tend to concentrate on procedures which can be definitely specified rather than on general search and selection strategies.

Experience with the present model re-enforces our feelings that the most profound and significant processes of evolution—the innovations, the origins

of new hierarchical levels of organization—are still outside the scope of this type of program and remain to be discovered. Experience with other computer programs intended to model higher mental processes, such as general problem solving and artificial intelligence studies, have shown similar weaknesses. As one might expect, true acts of creation at all levels remain difficult to imitate.

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