

Evolutionary Drive: The Effect of Microscopic Diversity, Error Making, and Noise

By

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AUTHOR'S Comments: This paper sets out the lessons derived from several pieces of work. These are that in order to understand some real world situation, we must necessarily reduce it to some simpler representation than all its trillions of molecules. This reduction process proceeds by assuming some spatial boundary, eliminating "irrelevant" descriptors and accepting a classification of the types of things present, and then aggregating both spatially and taxonomically. These are the steps necessary to reach a probabilistic description of the events that occur in the system, and a stochastic model of evolution was developed in an earlier paper (Allen and Ebeling, 1984). However, in order to move from a probabilistic description to one of smooth, differential equations, we need to assume also that processes occur at their average rates. This final assumption leads us to a representation that we know of as System Dynamics, and in ecology and demography as "population dynamics".

System dynamics is a mechanical representation of the situation, and hence appears to allow prediction of the future. However, a system governed by such equations cannot spontaneously change its regime of operation (self-organisation) nor its qualitative structure with new behaviours and types of variable. In other words, such a model, in which the non-average fluctuations, and individuals have been "removed", cannot either self-organise its collective structure, or evolve qualitatively. In this paper we show how microscopic diversity (the different attributes, skills and quirks of individuals) actually drives evolutionary change. *We show that evolution will select for populations which retain "variability," even though this is, at any given time, loss-making, predicting that we shall not observe populations with "optimal behaviour," but populations which can "learn."* Because evolution selects for populations with sub-optimal current performance, this in turn allows greater micro-diversity by a reduced selective pressure. Indeed, evolution is seen to be "driven" by the "noise" (fluctuations and micro-diversity) to which it leads.

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Evolutionary Drive: The Effect of Microscopic Diversity, Error Making, and Noise

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In order to model any macroscopic system, it is necessary to aggregate both spatially and taxonomically. If average processes are assumed, then kinetic equations of "population dynamics" can be derived. Much effort has gone into showing the important effects introduced by non-average effects (fluctuations) in generating symmetry-breaking transitions and creating structure and form. However, the effects of microscopic diversity have been largely neglected. We show that evolution will select for populations which retain "variability," even though this is, at any given time, loss-making, predicting that we shall not observe populations with "optimal behavior," but populations which can "learn." This lesser short-term efficiency may be why natural diversity is so great. Evolution is seen to be "driven" by the noise to which it leads.

1. INTRODUCTION

Evolutionary theory is today at the beginning of an exciting new phase. From fresh discoveries and insights that have emerged over recent years in physics and chemistry, an evolutionary synthesis which will at last unite the so-called "hard" and the "soft" sciences now seems very near. A key factor in this is the new understanding of the limitation of the "Newtonian model." In this view, understanding of a system was to be obtained by identifying its "parts" together with the causal connections between them. The resulting assemblage of mechanisms then constituted a "model" of the system, and provided a tool for understanding observations and making predictions.

However, evolution in biology or the human sciences does not concern so much the simple functioning of the existing system, although this is interesting. Instead, it is primarily concerned with how the system *became* what it is, and how it will *evolve* in the future. In other words, if the world is viewed as some kind of "machine" made up of component parts which influence each other through causal connections, then instead of simply asking how it "works," evolutionary theory is concerned with *how it got to be as it is*. It is fundamentally about the origins of *qualitative change* in things, and how the "parts" of a system came into being, and are maintained.

The new ideas that have emerged in the physical sciences are also about just these issues. The "mechanical paradigm" of Newton has at last been put in perspective. It is right for certain situations, for example when describing the behavior of a frictionless, reversible system such as the planets revolving around the sun. Furthermore, even when dissipation and friction are present and irreversible evolution occurs, it is right for the case of an isolated system or one placed in a uniform environment. More precisely then, it is right for systems which go to thermodynamic equilibrium, because their behavior is *predetermined* by the appropriate thermodynamic potential such as the entropy or free energy. For such systems, evolution, the action of spontaneous natural processes, will be such that at best existing structure is only preserved, while in general it will tend to be eroded by the action of dissipative forces.

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But we know that it is inappropriate for systems which are out of thermodynamic equilibrium, where exchanges across the boundaries can occur. As recent discoveries have shown⁽¹⁻³⁾ evolution can quite well lead to the emergence of structure and form and to qualitative change even in relatively simple physical systems.

One of the important aspects of the work of Prigogine was to realize and point out that the study of nonequilibrium systems gives a new scientific basis with which to understand the emergence of complexity and the processes and rules which may govern the "self-organization" which has led to the present biological and human realities. Now we can begin to link the theories of biological, social, cultural, and economic evolution to physics and chemistry, not just in a trivial way by possibly spurious analogy, but by the profound unity of an evolutionary synthesis.

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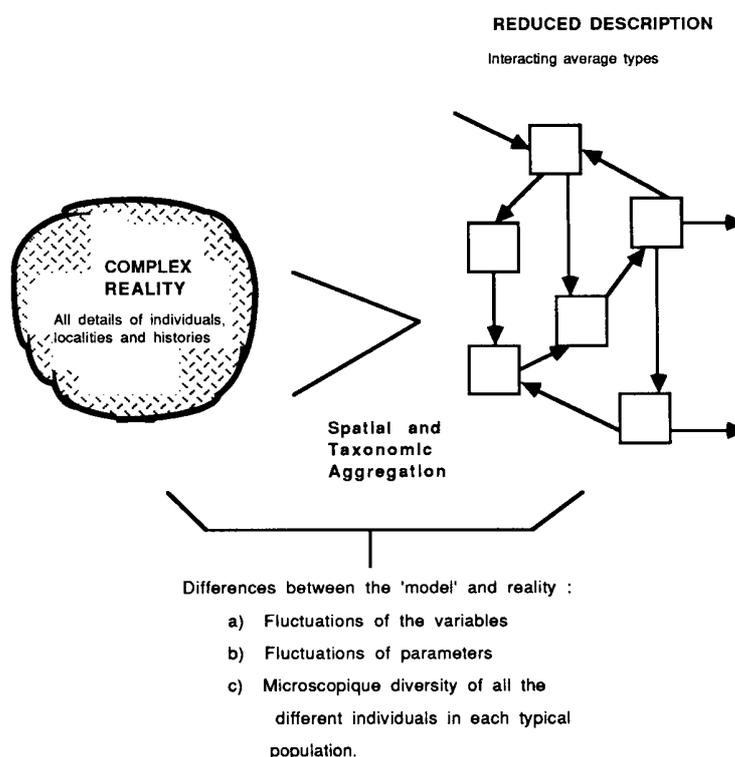


Fig. 1. Modeling, and even thinking about a complex system, necessitates a simplification into categories which constitute the system. The difference between reality and the model shows itself in fluctuations and in microscopic diversity.

The key element in this new understanding can be seen in Fig. 1. What this stresses is that any "model" of reality can only be conceived in terms of "typical elements" of the system, where classifications and both spatial and taxonomic aggregations have been carried out. However good the choice of variables, parameters and laws of interaction may be, these concern only the average behavior, and to establish a closer link with reality we must therefore study the effects of "fluctuations" of variables and parameters around average values and in the existence of *microscopic diversity* far greater than that considered at the level of the macroscopic model. Such models therefore correspond to reduced descriptions of reality, assuming that only average types are present. If, in addition, it is supposed that only *the most probable events occur*, then evolution is completely deterministic and is represented by the behavior of the differential equations which then characterize the particular system.

The work of many authors on self-organization and synergetic phenomena has demonstrated the fact that, for systems far from equilibrium, basic physical non-linearities can in fact amplify fluctuations of variables and lead to symmetry-breaking instabilities in which structure and organization appear or, if already present, evolve qualitatively.

However, an aspect that has been relatively neglected is that of the effects on the system of *microscopic diversity*. As will be shown, just as fluctuations in variables and parameters can radically affect the evolution of the spatial and structural organization of complex systems, so, the real microscopic diversity underlying simplified kinetic models is the real source of innovation and change in the nature of the elements which make up the system. And this will make a more solid bridge between physics, living systems, and the ideas of Darwin.

Perhaps because of this missing synthesis, if we examine the theory of biological evolution, then we find that still one hundred years after Darwin's death disagreements flourish both as to the theoretical basis on which evolutionary change should be understood and also on the evidence in support of one or another idea⁽¹⁻²²⁾.

However, broadly speaking, the generally accepted view is that of "gradualist neo-Darwinism," which is often compressed into the statement "As a result of evolution, every individual maximizes his inclusive fitness." The message is one of *materialistic* optimization resulting from the evolutionary process, a message which reflects thinking based on the "Newtonian model" of system evolution to a global equilibrium. In this view survival is reserved for those who best monopolize and make use of the sources of material existence--energy and the biological building materials, and the evolutionary wisdom derived from past experiences is "stored" in the genes of each population. Observed behavior is then "explained" on that basis.

Clearly, the evidence for evolution itself is undeniable, but the correctness of the particular view expressed above is very hard to prove or disprove, since it does not really make predictions which can be tested. When we examine mathematical models purporting to describe such processes, however, we see that they contain mechanisms of reproduction and mortality whose repeated action over time leads some population types to flourish and others to decline. Apart from the models of Eigen and Schuster⁽²⁴⁾ these models of evolution do not ask where new "behaviors" come from, but simply show that, if several are present, then under competition some will grow at the expense of others. The idea is that, in the natural world which surrounds us, such eliminations have already occurred, and what we see is the "outcome" of such a process, which is all the marvellously adapted, mutually interdependent behaviors of living creatures. The image that this presents is one of evolution as a "blind watchmaker"⁽²⁵⁾, where the intricate machinery of the living world is seen as being comparable to that of a watch whose cogs and bearings are the fruit of the selection in the past of unspecified random mutations. Behind this is the idea of evolution as an optimizing "force," which has led to the retention of the organisms we see because of their functional superiority. In other words, in this view, behavioral optimality should characterize the organisms that inhabit a "mature" system. An additional twist to this results from supposing that it is true and from using optimization (of whatever fits) as a basis for the explanation of behavior.

But we disagree with this view. In general, each species is in interaction with others, and therefore evolutionary improvements will lead to counter measures and to an "arms race" without any obvious end. And if there is no end, then the most that can be said of the behavior of any particular individual or population is that its continued existence proves *only* that it is *sufficiently effective-not* optimal.

Our aim here is to show how a model can be developed which takes into account both the "selective" effects of interactions between species and the simultaneous need to *discover* new "strategies" or "niches."

This model should also throw some light onto another persistent problem—that is, understanding the origin of the observed amount of natural diversity. In practice, if a set of differential (mechanical) equations is set up which try to represent a real ecosystem, then, when they are run forwards in time on a computer, most of the species present are eliminated, and a radical simplification occurs. Somehow, the selection which occurs is much too harsh in such an artificial system of differential equations, and we believe that this is due to the reduced description in terms of only "average types." We shall examine the effect introduced by the presence of microscopic diversity in reality.

Since the natural systems which surround us do in reality maintain their complexity, we may conclude that the mechanical equations which are used in such models obviously do not capture the real interactions and adaptability of the natural system! This topic has been the subject to much study ⁽²⁶⁾, but the central problem remains that species in an ecosystem are not "randomly assembled," but in fact result from a co-evolutionary process, and this is what is not being modeled.

In this paper we shall present a simple model which attempts to generate an "evolutionary population dynamics," where the parameters involved have a plasticity which is the result of evolutionary processes of "phenotypic discovery" and "systematic selection."

2. A SIMPLE MODEL OF CO-EVOLUTION

We shall study the evolution of a particular population as it feeds on resources, reproduces, and dies, either of natural causes or because of some predator. But "evolution" implies some changes of form, character, or behavioral strategy, which affects the manner in which individuals perform in capturing prey, reproducing, and avoiding death. Clearly, there are many "dimensions" of behavior or morphology which can affect these mechanisms, but here we shall only consider a simple case of two dimensions. In Fig. 2 we see two-dimensional space of possible morphologies or strategies for a population. Each point corresponds to a particular blend of the two dimensions of character. Below it, we may imagine a surface on which we represent the "resources" (generally prey species) available to each particular character. In this way, a population with characteristics of the point *i*, say, can "feed on" the resources below *at and around* the point *i*, depending on the degree of specialization. Above the two-dimensional "character space" of the population considered, we can also imagine a surface which expresses the "dangers" which will result from a given morphology or strategy—that is, from predator populations which consider the population we have chosen as a "resource."

For any particular "character" of our population, there is a *relief map* of possible rewards and dangers which could result, given the prey and predator species that exist in the system at that time. This means that the "character space" is spanned by a kind of "contour map" of potential "Malthusian parameter" (birth rate-death rate), which will show the "selective advantage" of any particular character choice, given the existing circumstances. In this paper we shall simply examine the simplest problem of how an evolution leads a population to "climb" a hill in the evolutionary landscape.

Let us consider the simplest possible case of a single population *x*. According to its "situation" in character space, it will have a certain birth rate and mortality, and we shall suppose that the limits of the resource on which it feeds will give rise to a logistic-type population dynamics. The equation will be :

$$\frac{dx}{dt} = bx\left[1 - \frac{x}{N}\right] - mx$$

where N is the limiting resource related to the prey species in the level below, and b , and m , the birth and death rates which correspond to the position in "character space"- that is, on the evolutionary landscape.

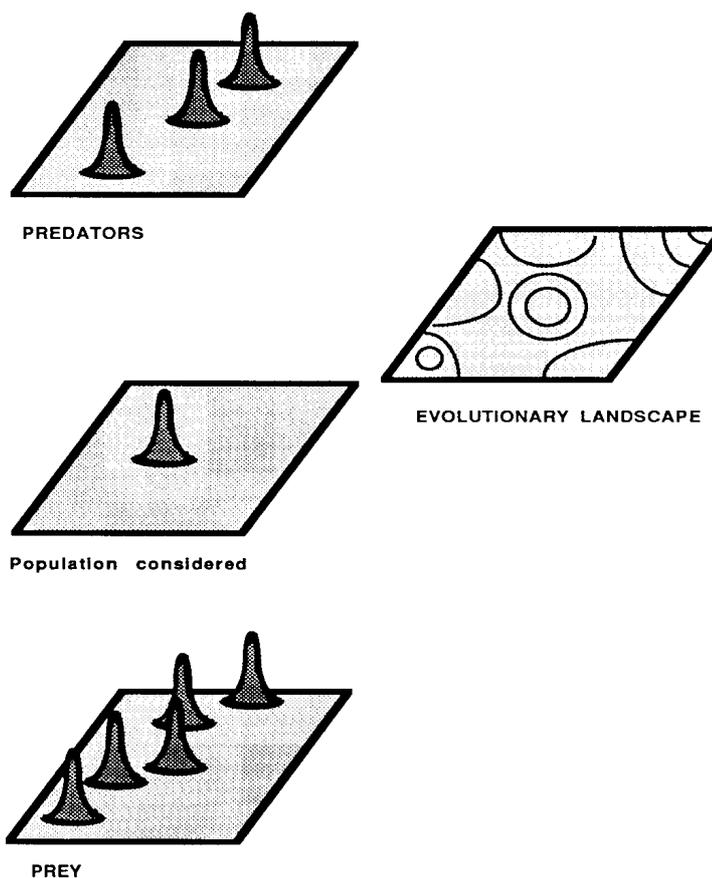


Fig. 2. A two-dimensional space of morphology or character for a population feeding on prey and fed on by predators.

Now, what interests us here is the question of "evolution." How does the "character" of a population change over time in response to the "rewards and dangers" of particular strategies? In order to examine this, we must consider two important aspects:

- (a) Imperfect reproduction leading to "diffusion" in character space.
- (b) The operation of selection in amplifying "favorable" mutations and suppressing unfavorable ones.

Usually, the models of population genetics or of neo-Darwinian evolution simply consider the *second term*. That is, they assume that all strategies are present initially, and examine the "selection" of the "fittest." We shall attempt to retain both aspects.

We can construct a parameter space of the effectiveness of the two species. For this, we have to consider two indices, i and j , which characterize the effectiveness of b and m , respectively. So, we have

$b(i)=b^0 (1+\alpha i)^\gamma$ and $m(j)=m^0 [1/(1+\beta j)]^\epsilon$ and different values of $\beta^0, \mu^0, \alpha, \beta, \gamma,$ and ϵ correspond to different "evolutionary landscapes" which all show increasing effectiveness in a diagonal direction toward the bottom right-hand corner, as in the Fig. 3.

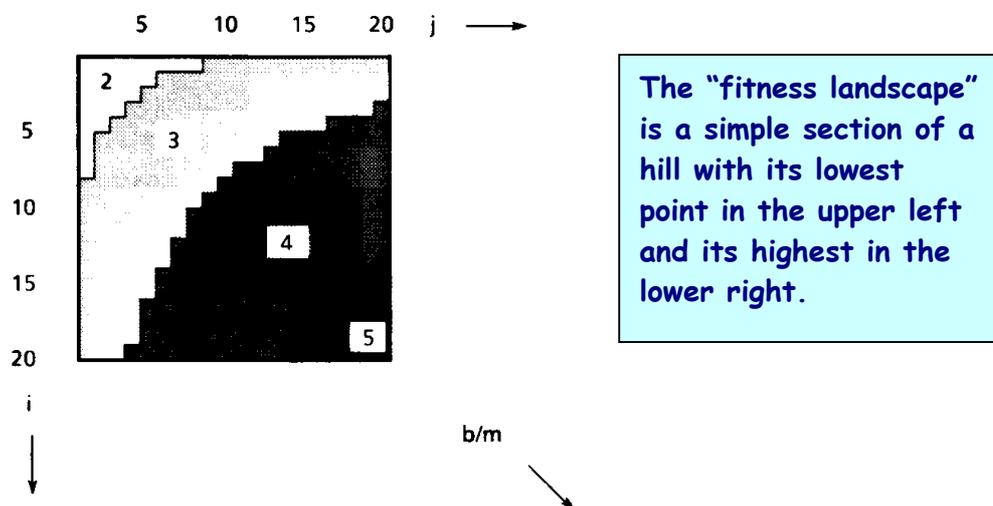
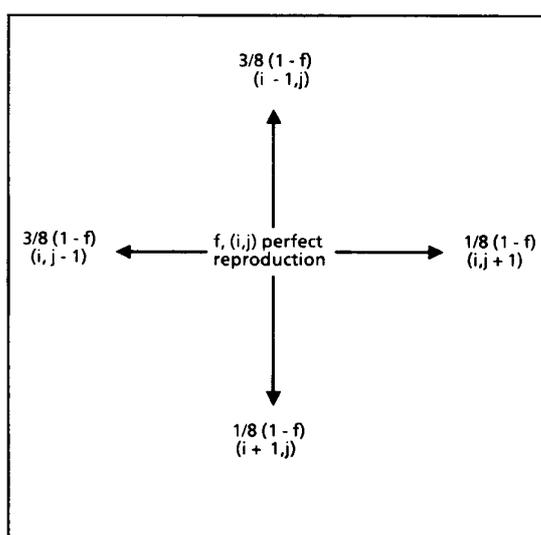


Fig. 3. The parameter space in which we can study co-evolution of x and y .

In this simple example then, we are assuming that the characteristics corresponding to the two dimensions chosen for the "evolutionary landscape" happen to be such that they affect reproduction and longevity separately.

For species which reproduce perfectly, coexistence is only possible if the two species are of exactly equal effectiveness, b/m . They are at the same "altitude." But let us suppose that only a fraction (f) of the births of x are "perfect" reproductions of the parents. On average, this would give rise to a negative effect. That is, the births of "mutant" types would be biased toward the less effective.



Error making diffusion, because it is essentially random, is viewed as being more often "worse" (downhill) than "better" (uphill) in character space. Therefore on average, any such exploration is a net cost in the present. It is only over time that there is perhaps a "pay-off".

Fig. 4. The pattern of reproduction of each population $x(i, j)$ and $y(il j)$, linking all points of the evolutionary landscape.

We shall suppose, as a first assumption, that 3/4 of the mutants are characterized by a *lower* value of i and j , while only 1/4 have *higher values* as in Fig. 4.

Each point in parameter space is connected to its vertical and horizontal neighbors through mutations or stochasticity of behavior. Diagonal mutations are excluded because we assume that reproduction and longevity are independent.

The equation for the dynamics of a species is

$$\frac{dx(i, j)}{dt} = \left[\{b(i)(fx(i, j) + \frac{3}{8}(1-f)x(i, j+1) + \frac{1}{8}(1-f)x(i, j-1))\} + \right. \\ \left. b(i+1)\frac{3}{8}(1-f)x(i+1, j) + b(i-1)\frac{1}{8}(1-f)x(i-1, j)\right].C - m(j)x(i, j)$$

where f is the fraction of perfect reproduction (e.g., 90%) and C is the "crowding" factor taking into account competition with other species.

Now let us examine first the possibility that a perfectly reproducing species ($f(x) = 1$) could be "invaded" by an imperfectly reproducing one ($f(y) = 0.9$). In Fig. 5 we show the result of initially placing 200 units of x at position (10, 10) and then seeing if 2 units of y placed also at (10, 10) can invade.

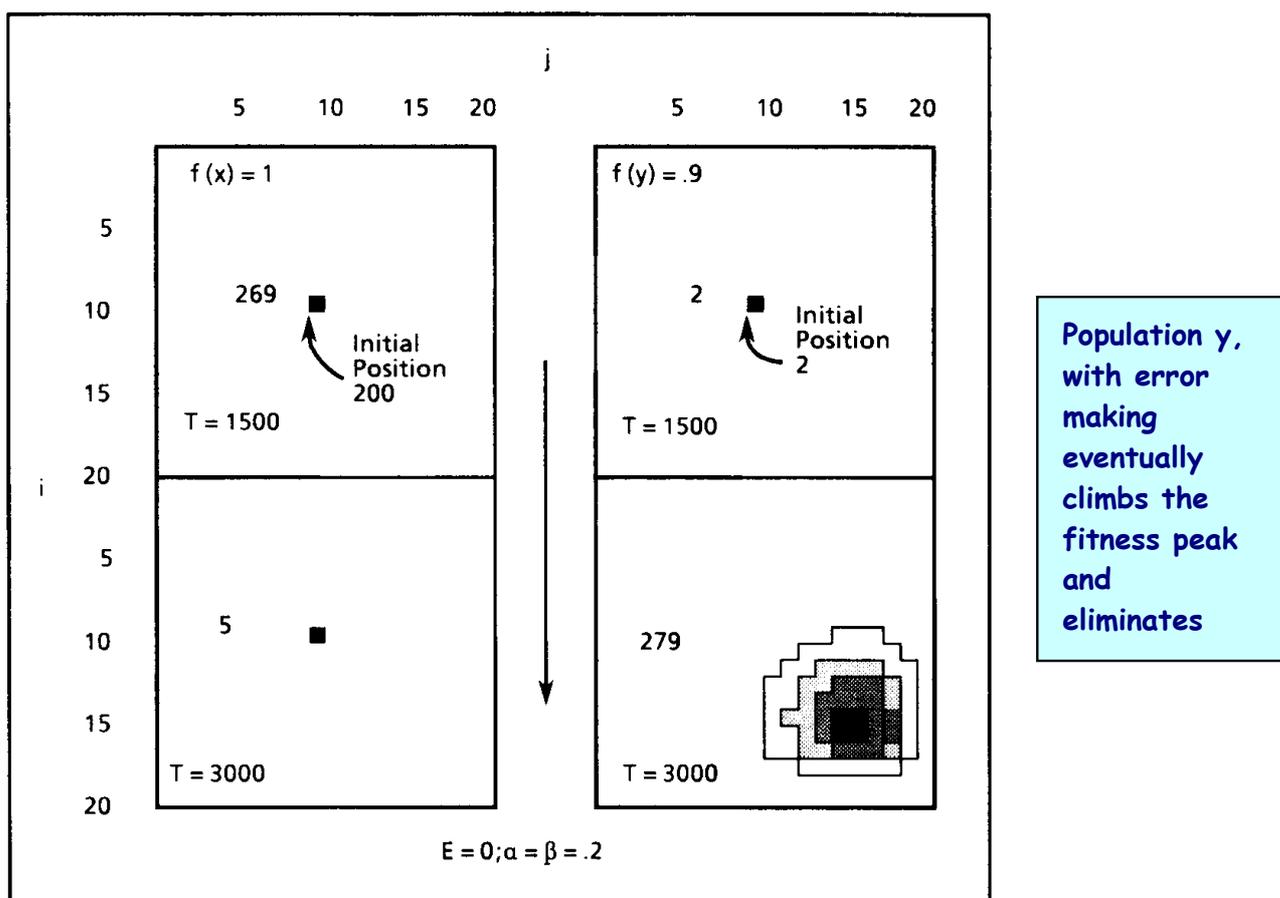


Fig. 5. The competition between a perfect reproducer (left) and an imperfect one (right) goes in favor of the imperfect one, given sufficient time. At time 3000 population $x = 5$ and $y = 269$.

Initially, as can be well imagined, the species x grows, while y remains at a low value. However, the errors in reproduction of y lead to a "Cloud" of small populations around its

initial position (10, 10). These are mostly at lower values of i and j , but some are higher. As the selection operates, the least effective populations of y are eliminated rapidly, but gradually small amounts of mutant populations "invade" the more effective regions of the parameter space (3), and after some time they start to multiply at the expense of x , and then rapidly eliminate the perfect reproducer. His "perfect reproduction" allows no possibility of an adaptive response.

The simulation above showed that even if a population of "perfect reproducers" had ever evolved, it would have been invaded and replaced by error makers. We can also examine the effect of "error making" on a species' ability to maintain itself or evolve in its evolutionary landscape.

We find that if the slope is sufficiently large, then error making is advantageous, and we find a forward evolution whose rate depends on the slope of the landscape. Therefore if the slope decreases as b/m increases, then at the "top of a hill," selection will operate in favor of lower error rates, because local exploration and discovery have yielded all there is to "know" about that resource.

But if we are to adopt a properly "ecosystemic" view of evolution, then we must admit the fact that, as our "error making" species climbs a "hill" in his evolutionary landscape, the "hill" itself will *move away* as the "characteristics" of the prey and predators change in view of the success of our "hill climber." In--this first study, we can represent this complex phenomenon in a rather simple way. We assume that there is a backward diffusion from $i + 1$ and $j + 1$ to i and j , and from there to $i - 1$ and $j - 1$. In this manner we can say that, in order simply to maintain its position on slope of increasing success, the combination of error making and selection must succeed in countering this backward blowing wind.

We can account for this by adding a term:

$$E(x(i+1),j)+x(i,j+1) - 2.x(i,j)$$

to Eq. (2).

The term E is a measure of the instability of the environment and the rate of evolution of the other species in the system. If it is large, then a species which does not evolve in its behavior will rapidly become less and less effective over time. This term sets the natural limit to evolutionary progress in terms of "effectiveness." An equilibrium distribution of populations is attained, and the larger the value of E , the lower the values of i and j for the centroid of the population.

The value of E which a species must counteract will result from the evolution of the other species in the system. In this way, there is a kind of "11 competition" between the different levels which will ensure that E will not go to zero. This is why evolution can probably never be viewed as being "11 over." In reality, the mutual linkages will ensure that each population maintains a variability as part of its strategy enabling survival. And this variability will be seen at each instant as being *inefficient and sub-optimal!*

Whatever the precise fraction of superior and inferior "mutants" is (and this is determined by the natural world, not the species or the ecologist), there will exist an "optimal" rate of mutation which will be selected for by evolution, and our model can be used to find this. The evolutionary process will therefore lead quite naturally to a rate of evolution which is itself regulated by the evolutionary process elsewhere in the system, so that the "progress" being made in each level of the system is just counteracted by that in the others!

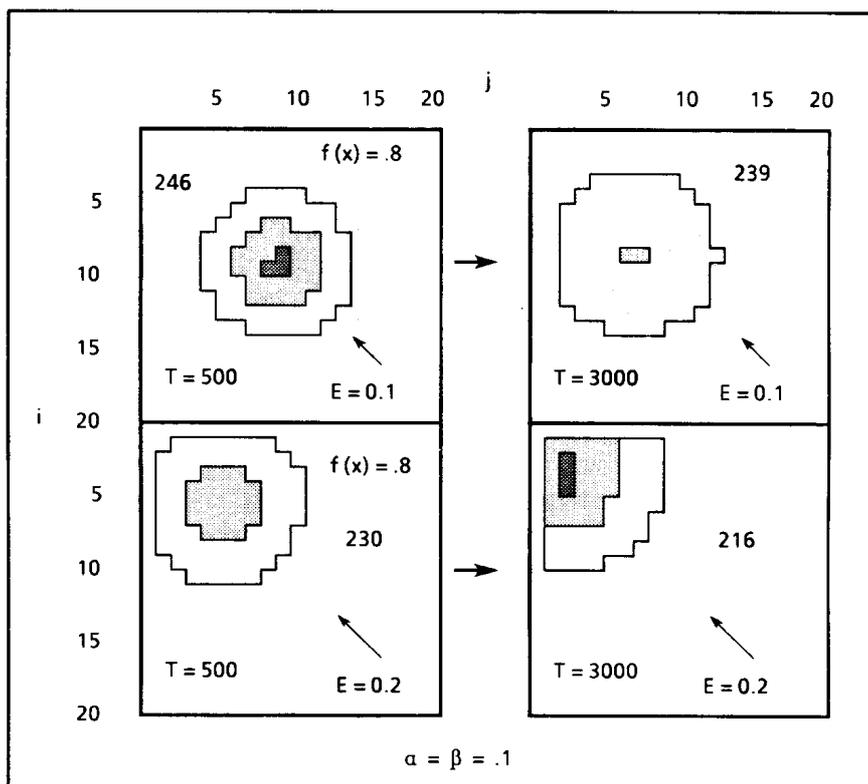


Fig. 6. With an environmental wind E of 0.1, the equilibrium position of the population centroid is at (8, 8). With $E = 0.2$, it is at (3, 3).

Not only that, but perhaps evolution itself could set these rates. In order to explore this possibility, we can suppose that the "fidelity" of reproduction of a population is *hereditary characteristic which could itself vary*.

For these simulations the vertical i -axis will still represent the rate of reproduction of any subpopulation, and will still serve to represent the "hill" up which evolution is struggling to climb. Clearly, the higher the value of i attained, the higher the birth rate. However, the value of j will indicate how "true" replication is ($j = 0, f = 0\%$; $j = 19, f = 100\%$). In this way *selection itse@y* will act on the system to decide the degree of "variability" that is the most effective in climbing the hill.

In Fig. 7 with $a = f_l = 0.1$ for species with initially equal values of b but different values of f (for x , 95%: for y , 85%) we see that the species with initially the lower fidelity "wins." On its way to "winning," however, the species goes through an "identity crisis" and plunges to very low average fidelity, but then gains until it has only a distribution of fidelity that ranges from 85% to 100%.

From these simulations we see that, if a certain amount of "random variability" is a property of a particular population, then selection can operate on it to regulate the variability that is "necessary" for "hill climbing" or countering the evolution of other species represented by E .

We see that variability itself is part of a species' strategy. In other words, what we see as the result of evolution are not populations with optimal behavior, but rather populations which can *learn!!*

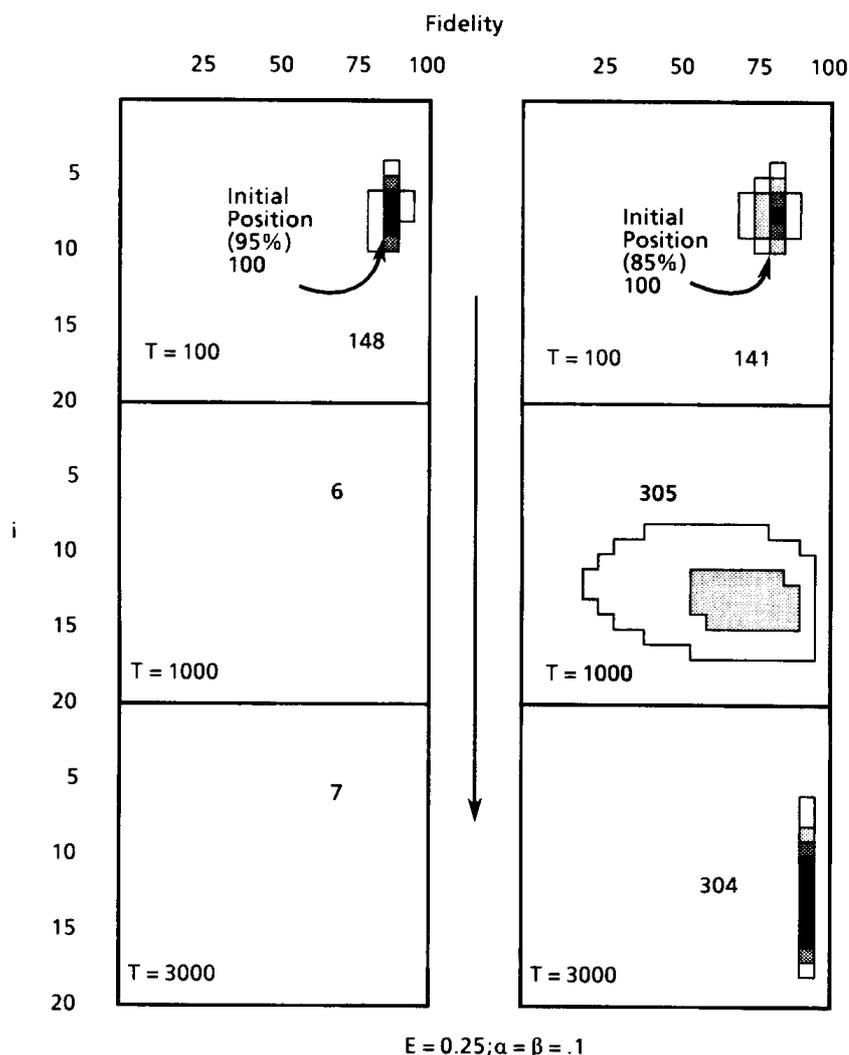


Fig. 7. Evolution of fidelity in an evolutionary landscape with a steep slope and strong environmental wind. Here in order to move forward "variability" is strongly selected for, then high effectiveness is maintained by high fidelity.

3. DISCUSSION

The model which we have presented above corresponds to a new "adaptive" version of population dynamics, in which the parameters that characterize a population can change as a result of evolutionary processes. These processes include not only the *selection* of more advantageous individuals, but also the *creation* of new types. In this way, the system is not looked at as if its evolution were over. This means that we have not supposed that at some prior time all possible population types have been present, and evolution has already acted to "retain" the "Fittest." In such a view, evolution simply selects for those types which are sitting on a 'b-m' hill—a peak of their Malthusian parameter—their adaptiveness.

This idea is similar to that used by Eigen and Schuster for describing the evolution of competing polymers in their theory of the hypercycle. They retain both "mutations" and "selection," and obtain a similar kind of result to the one we establish here. They show that evolution should not be looked at in terms of single population types, but instead in terms of a successful quasi-species, whose average behavior is the most effective. In the system that they discuss, a chemical reactor into which flow carefully controlled fluxes of monomers,

there is in fact only a single "evolutionary hill" to climb, and the polymers duly perform this task. The hill itself does not move, because there are no other levels of population involved, and in consequence it is certainly correct to say that evolution will come to an end when the quasi-species is at the top of the adaptive landscape.

Very recently, Ebeling and Engel have also proposed a model which retains both variability and selection⁽²⁷⁾. They discuss their application to the solving of optimization problems, and fundamentally they adopt the view that evolution leads to "hill-climbing."

However, we feel that when we consider the natural evolution of ecosystems, then the need to adapt and to change will be a permanent feature, owing to the evolution of other levels (prey and predators) of the system, and that therefore the ability to adapt will remain as part of the evolutionary strategy.

Because of this, we believe that evolutionary models must contain both "discovery" and "selection," and should be likened to a problem of "fishing"⁽²⁸⁾. That is, evolution is about *discovering* hills in the evolutionary landscape, and climbing toward the top. However, an "arms race" with the prey and predators of each species will result. This means that as a population climbs a hill in the evolutionary landscape, so the hill and the evolutionary landscape move!

We have presented here only the very simple problem of climbing a particular "hill," and have explored how small mutations or errors in reproduction could achieve this. Obviously, other landscapes and mutation patterns can and will be modeled. We find that variability is necessary to success in hill-climbing, even though this necessarily implies a certain level of "waste" or "sub-optimality" at any given instant. Furthermore, we show how the mechanism of variability itself could be adjusted by the evolutionary process itself, leading to the idea that *evolution is driven by the noise to which it leads*. It is driven from within, each species being part of the environment of others, and strongly connected to a changing physical environment as well. Evolution is no longer simply the selection of "optimal behavior", but the selection of species that can both produce and cope with change.

Co-evolution within an ecosystem will lead to behavior on the part of individuals and species that is *not optimal* in terms of the simple rationality of maximal exploitation of known resources or maximal avoidance of death. However, the variability in behavior and phenotype will ensure the longer-term survival of the species.

Because behavior is sub-optimal at any given instant, with loss making parts, selection is relaxed and the species remaining in competition are not operating a "knife-edge" selection. In this way, partly, the rigors of the mechanical models of population dynamics are relaxed, and we can better imagine the emergence and maintenance of the complex and diverse systems of reality.

The usual mechanical equations of population dynamics give rise to "razor sharp" selection, because each "strategy" breeds "pure." This is why such models collapse down to an unrealistic simplicity. In our view, strategies or characteristics do not "breed pure." The "fitness" of a single population type is linked to that of all the types to which it is connected through its "errors." Since "fitness" can only be judged over time, then, since population types are connected together by their "future variabilities," we cannot consider them apart. We must consider the "population cloud" with its average performance and its variability. We have a kind of "group selection," in that the future of each member of a population is intertwined with that of the others. Similarly, in thinking of the whole ecosystem, we see that the progress made in one sector will set the standard for the others, and again the evolution of a population, or a strategy, cannot be considered in isolation.

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SUMMARY: This paper is fundamental in setting out exactly how and why evolution occurs at all. It shows us that although "hill-climbing" seems a simple idea for improving something, in evolutionary processes it has important consequences. Firstly, for it to happen at all, there must be "exploration" in character, behaviour or strategy space. This exploration must be allowed to occur in the absence of proof about the pay-off that WILL result. It means that if "evolution" had to put ideas for exploration to a Board of Directors then it would have no pie charts or spreadsheets to justify, rationally the expense. Fortunately, evolution does not have to do this, and so essentially random based explorations happen all the time, keeping the system currently "sub-optimal" on any single criterion, but allowing it to evolve creatively. This is of enormous importance. Creative, adaptive responses only arise for these loose, micro-diverse, open and sub-optimal organisations.