

Author's Notes: This paper, written in 1975, derives a mathematical criterion that reveals which new behaviours can "invade" a system. It establishes therefore what characteristics a new behaviour must have if it is to grow from an initial unique occurrence to become a population described by its own population dynamics. It defines what successive evolutionary steps must be, and provides an objective definition of "better" for the behaviour characterising some particular role in an ecosystem. It equates "better" with "able to invade in the face of the pre-existing behaviours", and is not intended as a "value judgement". The same criterion is also used to establish whether an invading behaviour will necessarily replace a pre-existing type, or whether it will simply find its own niche and add to the diversity of behaviours present. The "cunning" part is that it avoids attempting to say exactly in what way a mutation differs from its contemporaries, whether it runs faster, digests better etc., but simply uses its resulting "performance" in the birth and death stakes to say what **MUST** be true if it is to invade. Unfortunately, Maynard-Smith's *Evolutionary Stable Strategies* work was published at the same time as this, and got all the attention, as it was coming from someone well-known in Ecology. However, ESS is really a very "closed" vision of evolution with known pay-offs for given strategies. The "forgotten theory" presented here was about the necessary effect of whatever mutations or innovations occurred. It still offers lots of room for further development in human systems, since this has not been done.

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Evolution, population dynamics, and stability

(Ecology/fluctuations/predator-prey relationships)

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ABSTRACT. By treating mutant populations as fluctuations relating to the structural stability of the equations of population dynamics, a criterion is developed permitting the prediction of long-term population trends in an evolving ecosystem, As an illustration it is shown that the ratio of predator to prey biomass increases under the effects of their combined evolution,

It is widely recognized that in complex systems, described by interdependent macroscopic variables obeying non-linear equations, fluctuations can play a vital role, complementary to that of the macroscopic average values (1, 2). This phenomenon has been called "order through fluctuation" and has been shown to be the motor behind a wide range of physical phenomena.

A most important contribution to the understanding of pre-biotic evolution was made when Eigen (3) showed that a system containing autocatalytic polymerization processes could exhibit an evolution when subject to a flux of monomers. The evolution was towards the formation of replicating polymers with the most accurate replication mechanism. Prigogine *et al.* (4) have pointed out that this type of evolution belongs to the scheme of "order through fluctuation," where the latter is not

just fluctuations of a component density, but also is the appearance in small quantities of new substances.

They showed that the mathematical analysis characterizing this type of evolution is that of the "structural stability" of the chemical kinetic equations,

In this article we wish to show that biological evolution due to selective advantage can be described by just such a mechanism, whereby the equations describing the population of interacting genotypes in an ecosystem must be unstable to the appearance of a new genotype or species if evolution is to occur. The mean value of each population is described by dynamics involving such concepts as birth rate and death rate, which will *be* characteristic of the competition for vital factors, the reproductive mechanisms, and the form of the trophic network describing the ecosystem. An individual event, however, such as the spontaneous mutation of a single individual, corresponds to a different level of description from this "average density" dynamics (5).

The representation of mutation or speciation

Let us suppose that there are S species present, each of which contains n_i different genotypes within it. Our equation, therefore, describes different genotypes, whose densities we will simply label as x_1, x_2, \dots, x_n in order to simplify the notation. The most general equations describing the evolution of these variables is, in a steady homogeneous environment:

$$\frac{dx_i}{dt} = G_i(x_1, x_2, \dots, x_n) \quad (1)$$

for $i = 1, 2, 3, \dots, n$

where each G_j is some function of the constituent genotype densities. The G_i expresses the constraints of the i -th genotype due to itself and the other genotypes of its own species with which it is in genetic "contact," as well as the other species present in the ecosystem. Thus, these equations reduce under restrictive assumptions to those of Volterra-Lotka for competitive systems, of Levin (6), and of Leon (7).

How are we to introduce the concept of spontaneous mutation into such equations? Clearly, such an event corresponds to the sudden appearance of a hitherto absent genotype or species. However, such an event concerning an individual will not initially figure in our general Equation 1 which is a statistical average over a large number of volume or surface elements. Thus, if we consider the probability of a particular new genotype's appearing as a result of a spontaneous mutation to be small compared with that of the processes of normal birth and death in the system, we can de-couple the source of fluctuation from the average level of description. The new genotype must spread its influence over a sufficient volume or area before it can appear in the average density description,

It will then constitute a macroscopic fluctuation of the previously existing dynamics and we wish to show that evolution occurs because the previously existing dynamics is not stable to the fluctuation from zero of certain genotypes previously absent.

In dealing with ecosystems we have to allow for the fact that new "behaviours" may arise from the appearance of a new gene. Because of this the invasion may lead to more than one new genotype, and therefore to more than one new behaviour. This means that our criterion of "invasion" must encompass whatever new behaviours result.

In sexually reproducing species the mutation of a particular allele will provoke the appearance of more than one new genotype. For example, if a particular locus is initially in a State of balanced polymorphism with AA, AB and BB types, then the introduction of an allele C will result in the appearance of three new genotypes, AC, BC and CC. In general, therefore, we will suppose that the mutation manifests itself at the macroscopic level by the sudden appearance of small amounts of new genotypes, These populations modify the equations for the n previously existing genotypes and obey new differential equations for their time rate of change.

A criterion of evolution

The system of equations representing a real ecosystem must permit at least one stable solution. This will either be a stable steady state or a stable limit cycle (8). In nature, no other result could persist. If the S species, within all n genotypes, of Eq. 1 are to coexist, then these are the only possible solutions. We shall therefore assume that our system has attained one of these two states before the new genotypes appear. This assumes in the case of genetic mutation that the length of time separating the arrival, on the macroscopic level, of successive mutations is greater than that characterizing the relaxation of the system to its stable condition. We will discuss this point again later. The moment before the new genotypes appear the system is therefore described by x_1, x_2, \dots, x_n populations at their steady-state values or having a periodic form characteristic of their limit cycle. The populations of the genotypes which will appear are still zero and the question we ask is: *under what conditions will this state of affairs be unstable to the small fluctuations of x_{n+1}, \dots, x_{n+h} from zero?*

In order to answer this, we must study the stability matrix of the population dynamics of the complete system, with the new genotypes present. The new equations we will write as,

$$\frac{dx_i}{dt} = G_i'(x_1, x_2, \dots, x_n, x_{n+1}, \dots, x_{n+h}) \quad (2)$$

and from this we may calculate the elements of the community matrix

$$A_{ij} = \frac{\partial G_j}{\partial x_i} \quad \text{for } i, j = 1, 2, \dots, n, n+1, n+\eta \quad (3)$$

If the new populations are to grow, then we need "instability" for the new equations

The stability of the equations is obtained by solving the equation,

$$\text{Det } |A_{ij} - \delta_{ij}\lambda| = 0 \quad \text{for } i, j = 1, 2, \dots, n, \dots, n+\eta \quad (4)$$

for the roots λ . For instability λ must have a positive real part.

Let us now consider what we mean by "mutation" or "genetic error". Generally, in a system described by statistical variables we must realize that an "error" is not an event that should never occur i.e., probability zero. It is simply an event with a considerably smaller probability than other events occurring in the system. The

difference between what is "systematic" and what is "unexpected" is thus quantitative, not qualitative. This is how the dynamics has been framed. The n-genotype dynamics, before a mutation, represents the effects of all the systematic interactions {large probabilities} between the n, while a mutation corresponds to an error, and hence to an event of much smaller probability which is not explicitly in the n-genotype dynamics. This means that there are no terms in the kinetic equations of the new genotypes {mutants} of the form $f\{x_i\}$ for $i = 1, 2, \dots, n$, since such a term would correspond to a systematic production of a mutant from one of the n types, and this contradicts our definition of mutant, which is an error or small probability event.

Examining the determinant 4 with this in mind, we realize that the terms A_{ij} , where: $i = n + 1, \dots, n + \eta$ and $j = 1, 2, \dots, n$, are zero, and therefore the determinant reduces to the multiple of two sub-determinants: .

$$\text{Det} | A_{ij} - \delta_{ij} \lambda | = \text{Det} | A_{kl} - \delta_{kl} \lambda | * \text{Det} | A_{pq} - \delta_{pq} \lambda | \quad (5)$$

Where

$$i, j = 1, 2, \dots, n, n+1, \dots, n+\eta$$

$$k, l = 1, 2, \dots, n$$

$$p, q = n+1, n+2, \dots, n+\eta$$

The first determinant of the right hand side is identical to that determining the stability of the system before the appearance of the mutants because it is evaluated at $x_{n+1}, x_{n+2}, \dots, x_{n+\eta} = 0$, and this we have assumed either to be described by a stable steady state or a limit cycle. Thus this situation will only be unstable if the second determinant possess a root having a positive real part.

Summarizing then, our criterion for an evolutionary step to occur following a genetic error is that the determinant,

$$\text{Det} | A_{pq} - \delta_{pq} \lambda | = 0 \text{ for } p, q = n + 1, n + 2, \dots, n + \eta \quad [6]$$

should lead to a root having a positive real part, when evaluated at the previously existing steady-state $x_1^0, x_2^0, \dots, x_n^0$ and $x_{n+1}, x_{n+2}, \dots, x_{n+h} = 0$ or over the periodic values corresponding to the previously stable limit cycle behaviour.

This criterion, therefore, enables us to see what new genotypes could find a niche in the ecosystem. It, therefore, permits us to draw many interesting conclusions concerning the long-term trends in an evolving ecosystem. In order to illustrate the criterion in a nontrivial case we will study the problem of a sexually reproducing predator-prey system where occasionally new alleles appear in both species.

A predator-prey ecosystem

Let us first define the equations governing the genotype population densities initially present. We will suppose that in the absence of the predator the prey would proliferate according to some logistic growth, expressing the effect of the saturation of some vital material. As a first step we will study the appearance of a mutant allele in the prey population which will be described by diploid genetics where the rate of reproduction is not proportional to the probability of random encounter between

male and female. This would only be the case for a very sparsely scattered species. We will assume that the birth rate of X_{AA} offspring from X_{AA} and X_{AB} parents is, for example,

$$(X_{AA}X_{AB})/2(X_{AA} + X_{AB} + X_{BB}) \quad \text{etc.}$$

Apart from these genetic effects there will be some characteristic constant describing the dependence of the populations on purely ecological factors. Thus the birth rate above must be multiplied by a constant k expressing the ability of the couple $X_{AA}X_{AB}$ to find the necessary food to maintain themselves and to produce their offspring, to defend their territory, and to assure the survival to adulthood of their young. The death rate will reflect the ability of each genotype to avoid predators or starvation. The equations governing the dynamics of the prey genotype densities are, supposing for clarity that they have equal ecological. Effectiveness:

$$\frac{dX_{AA}}{dt} = k * \left(\frac{X_{AA}^2}{2} + \frac{X_{AA} * X_{AB}}{2} + \frac{X_{AB}^2}{8} \right) * \left(\frac{N}{X} - 1 \right) - s * X_{AA} Y$$

$$\frac{dX_{AB}}{dt} = k * \left[\frac{X_{AA}^2}{4} + \frac{X_{AA} X_{AB}}{2} + \frac{X_{BB} X_{AB}}{2} + X_{AA} X_{BB} \right] * \left[\frac{N}{X} - 1 \right] - s * X_{AB} Y$$

$$\frac{dX_{BB}}{dt} = k * \left[\frac{X_{BB}^2}{2} + \frac{X_{BB} X_{AB}}{2} + \frac{X_{AB}^2}{8} \right] * \left[\frac{N}{X} - 1 \right] - s * X_{BB} Y$$

$$X = X_{AA} + X_{AB} + X_{BB}$$

We have a corresponding equation for the predator Y , which could also, if necessary, be written in terms of the separate equations of its constituent genotypes.

$$\frac{dY}{dt} = -dY + s * \{X_{AA} + X_{AB} + X_{BB}\} * Y \quad [8]$$

The equations show that the population densities relax to a stable steady state, $X_{AA} = X_{BB} = d/4s$; $X_{AB} = d/2s$; $Y = k(N - d/s)/2s$. We wish now to consider what will happen if a mutant allele C appears in small quantities in the system. It will manifest itself in three new genotypes, X_{AC} , X_{BC} , and X_{CC} . In the evolution criterion then, $\eta = 3$, and we must resolve the equation,

$$\text{Det } |A_{ij} - \delta_{ij}\lambda| = 0 \quad [9]$$

where $A_{ij} = dG_i/dx_j$ for $i, j = AC, BC, \text{ and } CC$.

In order to do this we need to write the equations governing the change in the densities X_{AC} , X_{BC} , and X_{CC} in which, it must be supposed, the mutant allele C causes different "performances". of the three new genotypes. In fact it is only necessary to write the equations to first order in X_{AC} , X_{BC} , and X_{CC} because Equation 9 is evaluated at the steady state values $X_{AA}^0, X_{AB}^0, X_{BB}^0$ and Y^0 and for $X_{AC} = X_{BC} = X_{CC} = 0$. We therefore have,

$$\begin{aligned} \frac{dX_{AC}}{dt} &= \left[\frac{k_{AC}X_{AC}}{2} * (X_{AA} + \frac{X_{AB}}{2}) + \frac{k_{BC}}{2} X_{BC} * (X_{AA} + \frac{X_{AB}}{2}) + k_{CC} * X_{AA} * X_{CC} \right] * \left[\frac{N}{X} - 1 \right] - s_{AC} X_{AC} Y \\ \frac{dX_{BC}}{dt} &= \left[\frac{k_{BC}X_{BC}}{2} * (X_{BB} + \frac{X_{AB}}{2}) + \frac{k_{AC}}{2} X_{AC} * (X_{BB} + \frac{X_{AB}}{2}) + k_{CC} * X_{ABB} * X_{CC} \right] * \left[\frac{N}{X} - 1 \right] - s_{BC} X_{BC} Y \\ \frac{dX_{CC}}{dt} &= -s_{CC} X_{CC} Y \end{aligned} \quad (10)$$

The determinant 9 can now be evaluated, and the first important simplification arises because $dG_{cc}/dX_{AC} = dG_{CC}/dX_{BC} = 0$ and $dG_{cc}/dX_{cc} = -s_{cc}y_0$. Hence the genotype X_{cc} only contributes a negative root to the equation and evolution, therefore, depends on the part of the determinant referring to X_{AC} and X_{BC} . If the allele C is not to be rejected by the system there must be a positive root to this remaining part of the determinant. The latter can be calculated by substituting the steady state values of $X_{AA} 0$, $X_{AB} 0$, $X_{BB} 0$, and y_0 . We then obtain from 9 a quadratic equation for λ .

$$I^2 + I * \left[\frac{(k_{AC} + k_{BC}) - (s_{AC} + s_{BC}) * k}{4} \right] * \left(N - \frac{d}{s} \right) + \frac{s_{AC}s_{BC}k}{4s} \left[\frac{k}{s} - \frac{1}{2} \left(\frac{k_{AC}}{s_{AC}} + \frac{k_{BC}}{s_{BC}} \right) \right] * \left(N - \frac{d}{s} \right)^2 = 0$$

The condition for a positive root to this equation is

$$\frac{1}{2} \left[\frac{k_{AC}}{s_{AC}} + \frac{k_{BC}}{s_{BC}} \right] > \frac{k}{s}$$

We, therefore, can deduce the fact that only a mutant allele C leading to heterozygotes X_{AC} and X_{BC} satisfying this condition can invade the system. If it is not fulfilled, then the allele is rejected and disappears. We deduce then that evolution may only proceed in this case when the new heterozygotes have a better average "performance" than the previously existing species.

The genetic case is more "difficult" to prove than a simpler non-genetic one. In academic terms (and also since genes really exist in reality) therefore this is more convincing. However, we now turn to the simpler case to show how generic and simple the overall result

In order to see the generality of this result let us study the simpler case of a prey species which does not reproduce sexually. The equations before the appearance of a mutation are:

$$\begin{aligned} \frac{dX_i}{dt} &= k_i X_i (N - X_i) - s X_i Y \\ \frac{dY}{dt} &= -dY + s X_i Y \end{aligned} \quad (13)$$

and the equation governing the mutant density is:

$$\frac{dX_2}{dt} = k_2 X_2 (N - X_1 - X_2) - s_2 X_2 Y \quad (14)$$

Our criterion of evolution tells that only a mutant that satisfies the condition,

$$\frac{k_2}{s_2} > \frac{k_1}{s_1} \quad (15)$$

can appear in the system. If we suppose an evolutionary mechanism based on the sudden appearance, in small quantities, of new species as Stanley has recently proposed (9), then clearly its genetic isolation confers on it a formal similarity to the case of asexual reproduction. Our criterion, therefore, takes on its simplest form for this case, although it would be necessary to include the possibility that the new species may introduce entirely new interactions into the ecosystem rather than being simply a slightly different version of an existing type. Even so, our criterion permits us to analyze possible avenues of evolutionary development, and hence predict trends in the system.

So far, we have simply considered the initial moment of "take-off" when an ecosystem leaves its previously stable state. Our criterion can help us to decide what state the system will move to after take-off. To do this, we apply the criterion "backwards" to possible final states and thus discover which are stable. For example, in the asexual example 13 if we have instability with respect to the appearance of species 2, then we must have:

$$\frac{k_2}{s_2} > \frac{k_1}{s_1} \quad (16)$$

and applying our criterion to the state $X_1 = 0$, $X_2 = d/s_2$: $Y = k_2/s_2(N - d/s_2)$ we find that condition 16 is exactly that required to ensure the stability of this state. Therefore, we may conclude that the species 2 replaces 1.

In the genetic case, the analysis is more complicated but an application of the criterion to possible final states again can tell us what will happen. For example, in the case where an allele C appears in a population of homozygotes X_{AA} . the condition for instability is:

$$\frac{k_{AC}}{s_{AC}} > \frac{k_{AA}}{s_{AA}}$$

and if we have:

$$\frac{k_{CC}}{s_{CC}} > \frac{k_{AC}}{s_{AC}} > \frac{k_{AA}}{s_{AA}}$$

then the allele C replaces A completely in the population. Thus if C is associated with a dominant or partially dominant increase in the value of k/s we will have total replacement. If, on the other hand, we have:

$$\frac{k_{AC}}{s_{AC}} > \frac{k_{AA}}{s_{AA}}, \frac{k_{CC}}{s_{CC}}$$

then the final state will be a balanced polymorphism with all three populations present.

The evolution of the **prey** species is thus characterized by steps which can only increase the **"effectiveness" of the population on the average**, by increasing the value of k/s associated with it. Following a similar analysis, one can also show that evolution can only lead to new types which are described by equations where the saturation level N increases. *This corresponds to prey species who can either exploit new resources of vital matter, or use the old ones more efficiently.*

An analysis of the evolution of the **predator** can be performed using criterion 6 and leads to the result that the predator evolution is characterized by steps in which the value of d/s decreases. Again this result is true for a sexually or asexually reproducing population. From this we see that the evolution of the coefficient s , describing the facility with which the predator feeds on the prey, is in opposite directions for the two species. This is entirely logical and describes successive moves and counter-moves which are analogous to an armaments race. We, therefore conclude that over a long period the evolutionary changes will result in s remaining reasonably constant, k and N increasing, and d decreasing.

Having deduced the trends in the interaction coefficients, the long-term population trends become evident. After each step the populations tend to:

$$X = d/s \text{ and } Y = k(N - d/s)/s$$

and the ratio of predator to prey to

$$\frac{Y}{X} = \frac{k}{d} * (N - \frac{d}{s})$$

which *increases* as evolution proceeds.

In conclusion then, stability considerations of a predator- prey ecosystem tell us that errors in the genetic matter *lead to a steady increase in the consumer/producer ratio*, and that the consumer and producer will undergo an "arms race" where successive improvements in the "hunting" techniques of the predator will be countered by improvements in the avoidance techniques of the prey.

Discussion

A general criterion has been proposed for evolution through selectively advantageous mutations. It is based on the stability requirements of ecosystems and permits the prediction of long-term population trends in a given ecosystem. In reality, evolution is probably to be described in terms of three mechanisms corresponding to different scales and "mixing" properties of the species. For example, if the system is such that the average mating distance includes only a small number of individuals, then local inhomogeneity will be frequent and **genetic drift** relatively important. However, these inhomogeneities concern neutral mutations, that is, ones not affecting the interaction coefficients k , s , d , etc. The evolution of these coefficients will still obey our criterion,

since only mutations which **do** alter the interaction coefficients in accordance with our criterion can spread into large areas of the system. However, it would be necessary to correct slightly our criterion for spatial effects, as the area invaded by the mutant will not be homogeneous, and our condition for "take-off" will be slightly too restrictive. In a system in which the average mating distance includes many individuals, ensuring good "mixing," the area invaded by the mutant will be almost homogeneous and our criterion is therefore perfectly correct. It also applies without reserve to asexual species, and this case formally resembles that of evolution through speciation (9). Speciation in fact corresponds to a problem of the "nucleation" of a finite fluctuation such as has recently been studied in chemical systems (10).

In the illustration given above of a predator-prey ecosystem the theory predicts that the ratio of consumers to producers will increase with evolution. Is there any evidence for this in nature?

We must first emphasize that this tendency is calculated assuming that the environment remains unchanged. Any climatic or geological changes may interrupt this process. We therefore look for confirmation first by studying oceanic populations, whose environment has remained unchanged for a very long time. *Surveys (11) show that the biomass of the phytoplankton (producers) is often only as large, and sometimes less than that of the trophic chain depending on it (the consumers)! This result is explained by ecologists as being due to the extraordinary effectiveness of the phytoplankton. This is precisely what our theory predicts. The long stable period has permitted the phytoplankton to evolve a very high productivity, which results not in a high producer population, but, as we have seen, in a high consumer population.*

Qualitatively we may understand the appearance of an agricultural society on the basis of these ideas. Because of his ability to learn, man can change his coefficients of interaction with the environment faster than nature can evolve (genetically) countermeasures. Thus, a human society that devotes all its inventiveness to improving hunting techniques and avoiding death through unnatural causes simply diminishes the quantity d/s , the "prey" population. This can lead to the extinction of both prey and predator. Agriculture, on the other hand, corresponds to the use of man's abilities to increase k , the "prey" birthrate, and N . The benefits of this action are, as we have seen, passed on to the consumer, and man's population increases as a result.

The method presented here can also be used to study such questions as the evolution of "specialists" or "generalists" in a given environment, or the division of labour within, for instance, an insect colony, as well as these same questions applied to societies where non-genetic innovations are possible and where imitative and anti imitative mechanisms decide their repression or amplification.

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This paper establishes what error making changes in individuals in a population can invade the system. This can also clearly include INNOVATIONS. Whatever new behaviours are tried out, whether random or calculated, only those that fulfil the criterion of evolution proved here can actually grow to any significance in the system. Furthermore, since the evolutionary process over the long term must therefore be made up of successive such invasions, we can therefore use our criterion to reveal the long-term trends in such ecosystems. This reveals a steady transfer of "biomass" from the producers to the consumers of an ecosystem. In human systems this may correspond to the higher rewards available in "high level" economic functions (e.g. traders in financial options) compared to those working in farming or mining. This reflects the emergence of temporary, partial monopolies of new knowledge in which only certain locations and people can exploit the new ideas. They are high in the "value chain" of the economy and benefit from any improvements occurring in the knowledge base up-stream in the value chain, at the producer end. Innovations in the primary and secondary sectors is rapidly communicated around the globe and leads to competition that soon takes away the excess profits. What this paper foreshadows, therefore is the fundamental reason why we move to a "knowledge economy", since with emergent clusters of innovation in the upper reaches of the economic system.

The ideas presented here have never really been developed properly and applied in the economic and business context.