

## QUANTUM EVOLUTION AND THE FOLD CATASTROPHE

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ABSTRACT: Given some mild mathematical and biological assumptions, it is shown that under a gradual secular change in the environment, quantum evolution can arise in essentially only one way, from the fold catastrophe of topology. A new representation of adaptive peaks incorporates a phenotype  $\times$  environment space and other features. Consequences of the theory include a 'square root' law and can in principle be tested.

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## Introduction

The fossil record shows that the evolution of a population from one form to another can take place relatively suddenly with the intermediate forms not persisting. This sort of evolution, called quantum evolution, is well documented at intermediate or low taxonomic levels and although the record is poor has been shown to have occurred at high taxonomic levels (e.g. origin of classes) as well. Quantum evolution has been discussed in detail by Simpson (1944, pp. 206 ff., 1953, pp. 389 ff.) and usually involves pronounced and radical morphological changes once a threshold has been crossed. It is irreversible and is commonly preceded by preadaptation and it is possible that species often arise in this way. It can be associated with sudden, pronounced environmental changes (Axelrod, 1967, p. 201) but in this paper it is shown using Rene Thom's profound ideas of structural stability and morphogenesis that, in the absence of environmental discontinuities, it can be safely assumed that quantum evolution can arise only from the fold catastrophe. Thom, in his important and highly original book Stabilité Structurelle et Morphogénèse (1973b, 1974), has placed biology and other subjects which because of their complexity and discontinuous nature have so far resisted an adequate mathematical treatment, into a topological framework, which enables him to classify the manner in which sudden and substantial (or 'catastrophic') changes can occur in quite general processes without having to have an explicit knowledge of the process itself. Consequently his results can be applied to a wide variety of phenomena, particularly in biology (which in fact provided an important stimulus to his thinking) (Dodson, in press, Thom, 1969 or 1970a, 1971a, 1973b, 1974, Waddington, 1974, Zeeman, 1972, 1974). The application of Thom theory to populations subject to natural selection is discussed more generally in another paper by the author (Dodson, in press), which also contains a brief account of quantum evolution.

## The Environment

We are going to consider populations in uniform or homogeneous environments, i.e. environments which are the same for each individual in the population. Thus the ranges of populations under consideration will not be too extensive or varied. The environment, which will be denoted by  $e$ , can be described or specified adequately by a sufficiently long list or  $m$ -tuple of real numbers, so that the environment  $e = (e_1, e_2, \dots, e_m)$ , where  $e_1$  might be the mean temperature,  $e_2$  the rainfall and so on, can be regarded as a vector in  $m$ -dimensional Euclidean space  $R^m$ . Plainly the set  $E$  of all possible environments is a bounded subset of  $R^m$ .

In this paper we are concerned with populations which display quantum evolution while the environment varies steadily, smoothly and slowly (just how slowly will be discussed in the next section) with time. This affords a reasonable description of the environment of many populations (Simpson, 1953, p. 385). The variation with time implies that the environment can be specified by the time  $t$  and we write symbolically

$$e = \phi(t).$$

It suffices for our purposes not to have an explicit knowledge of the environment but simply to know that in principle it can be specified at each time  $t$ .

The condition that the variation is smooth implies that the environment  $e$  traces out a smooth curve in  $R^m$  as time passes and the condition that the change is steady implies that the  $m$ -dimensional environment  $e$  can be replaced in the subsequent analysis simply by  $t$ . The duration of the steady secular change in the environment will be denoted by  $I$ , so that the set of corresponding environments will be  $e(I)$ . In addition the assumption of smooth secular environmental variation excludes sudden geological upheavels, bursts of cosmic radiation, etc. Thus our model should be applicable to marine environments (which are usually homogeneous with few geographic barriers) during periods in which there is a gradual, steady secular environmental change.

#### The Phenotype

Now we give a precise definition of the phenotype of a population in an environment  $e$ . At a given time  $t$ , the phenotype of an individual in the population can be described, as in the case of the environment, by listing phenotypic parameters  $p_1, p_2, \dots, p_n$ , where for example  $p_1$  might be the height,  $p_2$  the weight and so on. Providing its length is finite, this list can be as long as is necessary to describe the phenotype. We define the mean phenotype of a population at a time  $t$  by the list or  $n$ -tuple or  $n$ -dimensional vector  $(\bar{p}_1, \dots, \bar{p}_n)$ , where each  $\bar{p}_i$  is the mean of the phenotypic parameters measured for a suitably representative sample of the population. Thus when we speak of the mean phenotype of a population we are really referring to a distribution of phenotypes about some mean. We drop the bar and denote the mean phenotype by  $p = (p_1, \dots, p_n)$  and for convenience we shall refer simply to the phenotype of the population.

Plainly the phenotype  $p$  depends on both the environment  $e$  and the time  $t$  of measurement. The set  $\{(p_1, \dots, p_n)\}$  of all possible phenotypes corresponding to the range of different environments and times is a bounded subset of  $n$ -dimensional Euclidean space  $R^n$  and will be called the phenotype space, denoted by  $P$ . In reality the phenotype of a population is represented by a small  $n$ -dimensional ball centred at the mean  $p$  but except where this distribution is relevant, the phenotype will be approximated by the point  $p$  in  $P$ . We note that when the environment  $e$  is determined by the time  $t$ , the phenotype  $p$  depends on the time  $t$  alone.

The phenotypic variability of an isolated inbreeding phenotypically monomorphic population in a fixed environment, after long and highly effective selection, will be small and the greater part of the population will have phenotypes which are very close to an optimally fit form (Simpson, 1953, p. 71). Indeed it has been observed that the phenotypes of wild populations, which are subject to natural selection, are highly uniform with only small individual variations occurring about a mean (Maynard Smith, 1962, p. 285, Waddington, 1942) and we note that the phenotype just defined will give an accurate description of a uniform population. Of course to some extent the uniformity is

arbitrary and depends on the discrimination of the observer, and in fact in a population there must be some spread of phenotypes with a genetic component for natural selection to act on and produce evolution. This variation may have a significant effect on the response of population's phenotype, by analogy with phase transitions, and it is hoped to investigate this possibility further. We note that the genotype is not required to be uniform.

A population in stable equilibrium with its environment under natural selection (i.e. no longer evolving) is in general canalised or displays homeostasis, so that despite individual genetic and environmental differences, the population remains extremely uniform phenotypically (Eldredge and Gould, 1972, pp. 114-115, Maynard Smith, 1962, p. 285, Waddington, 1942). That is the population has a range of environmental and genetic stability inside which the phenotype remains unaltered, with phenotypic change only occurring once a threshold is passed. We shall assume that the populations considered in this paper are canalised, partly because canalisation is so common and partly because it simplifies the analysis. (Of course canalisation is to some extent a consequence of the fitness being locally maximal). Thus our model conforms to the picture of stasis punctuated by episodic quantum evolution (cf. Eldredge and Gould, 1972, p. 98). However even if a uniform population did exhibit a secular phenotypic trend, the small standard deviation enjoyed by such a population would mean that the phenotypic trend would be moderate. In any case the general picture of the response of the phenotype near a threshold would be very similar.

#### Fitness

We assume that the fitness of a population with phenotype  $p = (p_1, \dots, p_n)$  in an environment  $e = (e_1, \dots, e_m)$  is given by a real number  $f(e, p)$  and we assume further that  $f(e, p)$  depends smoothly on the environment  $e$  and the phenotype  $p$ . In mathematical language this means that we assume the fitness is given by a smooth, real-valued function  $f : E \times P \rightarrow R$ . Since Darwin's law of natural selection implies that natural selection tends to increase the fitness (or decrease the misfitness) of a population in a given environment  $e$  by modifying the phenotype  $p$ , the fitness can be compared with a potential function. The definition of fitness introduced here is similar to that of Levins (1968, p. 14) and of the 'fitness function' used by Wright (1970, p. 18) and is not defined in terms of off-spring (though it could be providing it were 'smoothed' appropriately). It is also closely connected with the "selection landscape" discussed by Simpson (1953, p. 155).

As we have pointed out above, since it is varying smoothly and steadily with time, the environment is determined by time and so we can speak of the fitness  $f(t, p)$  of a population with a phenotype  $p$  at a time  $t$ , instead of the fitness  $f(e, p)$  at an environment  $e (= \phi(t))$ . (Strictly speaking we should use a different symbol, say  $F$ , where  $F = f \circ (\phi \times 1)$ , or  $F(t, p) = f(\phi(t), p)$ , for the fitness at time  $t$ , but it is not necessary for our purposes). Thus we have the fitness  $f(t, p)$  given by a smooth, real function  $f : I \times P \rightarrow R$ , where  $I$  is the time interval corresponding to steady secular change in the environment.

If the environment  $e$  remains fixed for long enough, the population will attain stable equilibrium with its environment (i.e. the phenotype will not vary significantly for small changes in the environment) by modifying its phenotype so that the fitness will be locally maximal or, to use Simpson's terminology, so that the population is at an adaptive peak. Now the time scales involved in evolution are very great and it is thought that in general the selective advantage offered by mutations important for evolution is very small (Wright, 1940, p. 178). Hence if the environment changed sufficiently slowly, it is reasonable to assume (as do Eldredge and Gould, 1972, p. 94) that, providing no environmental thresholds were crossed, wild populations have evolved while in stable

equilibrium with their altering environments or have remained at an adaptive peak (i.e. have remained maximally fit). That is we shall assume that the environment changes sufficiently slowly for the population to adapt immediately to the small extent required to stay at the slowly altering fitness (or adaptive) peak which determines the phenotype. Of course inside the stability range of a particular phenotype of a canalised population, there is little or no phenotypic change and so this question does not arise. At a threshold (where the fitness peak disappears) the population may well take considerable time to evolve to the significantly different new stable form. However, since they are not maximally fit, the intermediate forms will not persist.

We have assumed tacitly that the populations are capable of evolving to fitter forms. This will be the case if the distribution of the phenotypes includes a sufficiently numerous genetically determined component which is fitter. To some extent this question is one of time scale, which if it were sufficiently long, would make the response seem immediate. In any case we shall assume that the populations under consideration in this paper have the requisite phenotypic and genetic variability to enable them to evolve to a maximally fit form. Thus our analysis should hold for moderate intraspecies evolution, and so should be relevant for example to bivalve taxa which have a low degree of interspecific competition (Stanley, 1973).

Since the fitness is assumed to be smooth, we can use the language of the differential calculus to express the fact that the fitness  $f(t,p)$  of a population with a phenotype  $p$  at time  $t$  is at a peak or local maximum as follows: For a population with phenotype  $p = (p_1, \dots, p_n)$  in equilibrium with its environment  $e$  at time  $t$  (i.e. which is maximally fit at time  $t$ ), we have that

$$\frac{\partial f}{\partial p_1} = \frac{\partial f}{\partial p_2} = \dots = \frac{\partial f}{\partial p_n} = 0. \quad (1)$$

The set of points  $(t,p) = (t, p_1, \dots, p_n)$  (which includes the fitness peaks) in  $I \times P$  for which (1) holds is called the critical set of  $f$  with respect to  $p$  and is denoted by  $M_f$ . Thus to use Simpson's terminology, the critical set includes the adaptive peaks.

The critical set also includes points where the fitness is locally minimal or at a saddle point i.e. points at which the population is in unstable equilibrium with its environment. However the variation in phenotype which populations exhibit, small though it may be, prevents a population from remaining in unstable equilibrium, since any individual with a phenotype differing from the mean phenotype of the population will be fitter than individuals with the mean phenotype. Similar considerations hold for points of neutral equilibrium (which should not be confused with neutral mutations) and so populations can remain only in stable equilibrium with their environment.

If we could describe the critical set  $M_f$  then we would know what the phenotype could be at a given time  $t$ , i.e. in an environment  $e = \phi(t)$ , for under natural selection the phenotype  $p$  will evolve so that the point  $(t,p)$  lies in  $M_f$ . There may be more than one possible stable phenotype for a particular environment and we discuss which one the population would assume in the following section. In general little can be said about  $M_f$ , since the phenotype of an organism or species depends on a great many factors and, apart from the simple case of effects arising from a few genes, is not susceptible to exact mathematical analysis. However by imposing a second mild restriction on the fitness (the first was that the fitness should be smooth) namely structural stability, it is possible to describe  $M_f$  qualitatively near points (i.e. environments) associated with sudden and substantial (or 'catastrophic') phenotypic change.

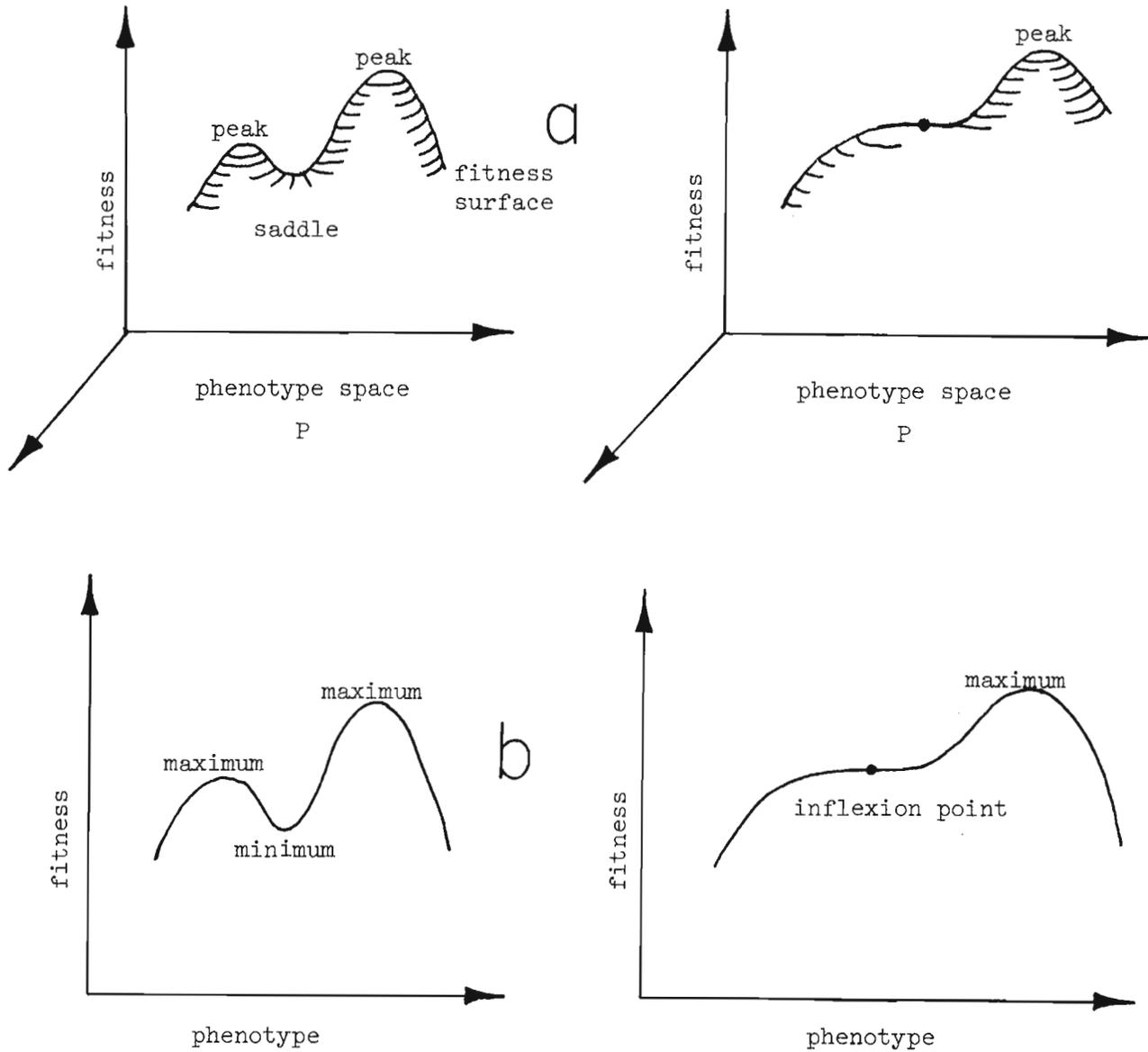


Fig. 1. The fitness surface when the phenotype space P is two-dimensional is shown in (a). On the right hand side a saddle and a peak have annihilated each other. In (b) the phenotype space is one-dimensional and the fitness surface becomes a curve.

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The Governing Fitness Peak and Quantum Evolution

In general at a given time  $t$ , i.e. at  $e = \phi(t)$ , there will be more than one phenotype  $p$  which maximises the fitness locally and the question arises of which local maximum or peak the fitness assumes. The uniformity of the phenotype of a wild population implies that a population will evolve to a new form that is more fit only if the new peak is separated from the old peak by a saddle sufficiently close in height to the old peak. (In Fig. 1(a) the case when the dimension  $n$  of the phenotype space is 2 is shown. In Fig. 1(b) the one-dimensional case is shown, when the saddle becomes a simple minimum and the peak a maximum.) This can be shown to be a consequence of having a gradient system but it follows in

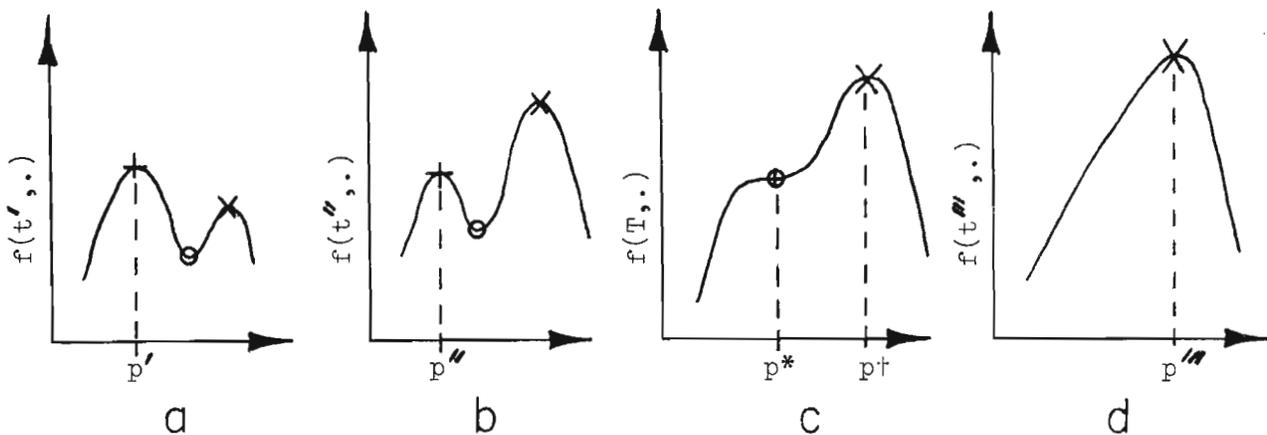


Fig. 2. Fitness curves corresponding to environments  $t'$ ,  $t''$ ,  $e_T$  and  $t'''$ . The disappearing maximum is marked with a +, the appearing maximum with an x and the minimum with an o. At environment T, the maximum + and the minimum o coalesce at  $\oplus$  to give a point of inflexion. The corresponding value of the phenotype is  $p^*$ .

this case since otherwise members of the population would pass through a stage in which they were less fit than the original population and so would be eliminated. Thus we see that the fitness stays at a particular peak until owing to some appropriate environmental variation the peak is annihilated by a saddle and disappears. This is called the delay rule and gives rise to quantum evolution, for as soon as the peak disappears the population will no longer be maximally fit and so will evolve until it reaches a new fitness peak, the intermediate forms being transient since they are not maximally fit.

In the ideal situation where the population always remains in stable equilibrium with its steadily varying environment (or maximally fit), there would be an actual discontinuity in the phenotype immediately the peak disappeared. In reality the discontinuity would correspond to the population not being maximally fit and so undergoing evolution to a maximally fit form. Also the slight spread of distribution of phenotypes in the population would mean that the population would start to evolve just before the peak disappeared, the actual threshold depending on the variability of the population, to a new optimally fit form. If the evolution were sufficiently rapid, the transient intermediate forms might well be actually absent from the fossil record. We note that just prior to its annihilation, the peak becomes less pronounced and so this model suggests that just before quantum evolution occurs there should be increased variability in the phenotype of the population. This increased variability could be connected with the onset of comparatively rapid evolution.

This representation of the response of a population under selection exhibiting quantum evolution was suggested by Simpson (1953, p. 155) with his 'selection landscape'. However our point of view differs from Simpson's in four respects: first we consider the mean phenotype and so in our case the population is represented by a point instead of a small area. Secondly we are assuming that the population is in equilibrium with its environment except at thresholds, so that the point representing the phenotype will be located at a peak except where the peak is annihilated by a saddle. Thirdly, we consider the selection landscape to be varying slowly and smoothly with time and fourthly we are more concerned with the critical set in  $E \times P$  or  $I \times P$  than with the fitness surface or selection landscape.



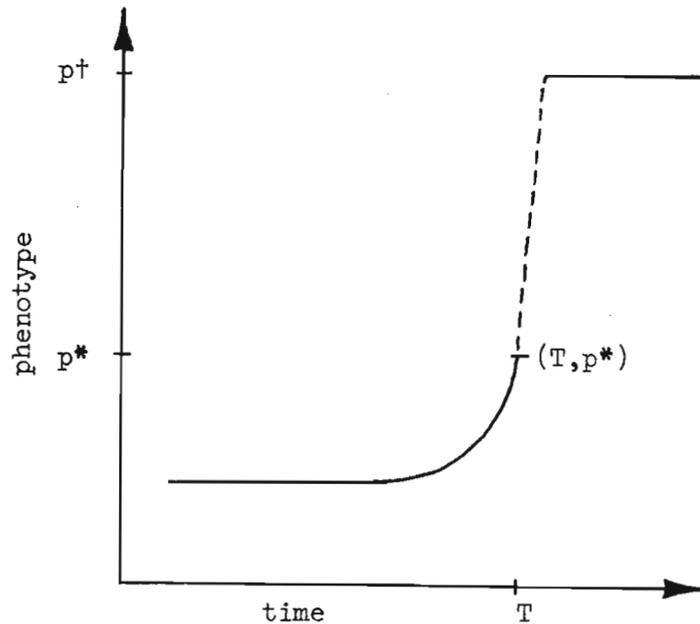


Fig. 4. The graph of the phenotype  $p$  plotted against time as the environment crosses the threshold at time  $T$ . The solid lines correspond to the population having a phenotype which maximises the fitness, i.e. to the population being in stable equilibrium with the environment  $e$ . The dotted lines correspond to phenotypes for which the population is not maximally fit and so not in equilibrium with the environment.

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for the response of the phenotype to the varying environment. Populations with phenotypes between  $p^\dagger$  and  $p^*$  (dotted line in Fig. 4) will not be in stable equilibrium with their environment and so will be transient. We repeat that no matter how slowly or slightly the environment passes the threshold  $e_T$ , the population will not be maximally fit until its phenotype is given by  $p^\dagger$ . Moreover this is so even if the change in the environment reverses in direction and re-crosses the threshold, so that in this model, quantum evolution is irreversible once the threshold has been crossed. The rate of evolution  $\frac{dp}{dt}$  of the population depends on the population's variability and genetic structure and will not be discussed in this paper beyond pointing out that the rate might well be relatively rapid compared to the rate of change in the environment or even virtually instantaneous in terms of geological time.

Finally, canalisation implies that the phenotype curves (drawn solid) in  $I \times P$  will be horizontal away from thresholds, so that there will be little difference between  $p^\dagger$  and  $p'''$ , unless there is another threshold near  $T$  (or  $e(T)$ ) (corresponding to the new fitness peak being close to annihilation by another saddle).

#### Structural Stability and Thom's Theorem

So far we have done little more than restate Simpson's analysis of quantum evolution, (1953, pp. 389-393), except that the populations under consideration are in a slowly and steadily varying homogeneous environment. Thus the conclusions reached here should be of particular relevance to those marine invertebrates which display quantum evolution in the absence of any environmental discontinuities. In order to say more about the phenotypic response associated with quantum evolution occurring in a steadily changing environment we need to introduce the idea of structural stability. The fitness function  $f : I \times P \rightarrow R$  is said to be (locally) structurally stable if any sufficiently small perturbation

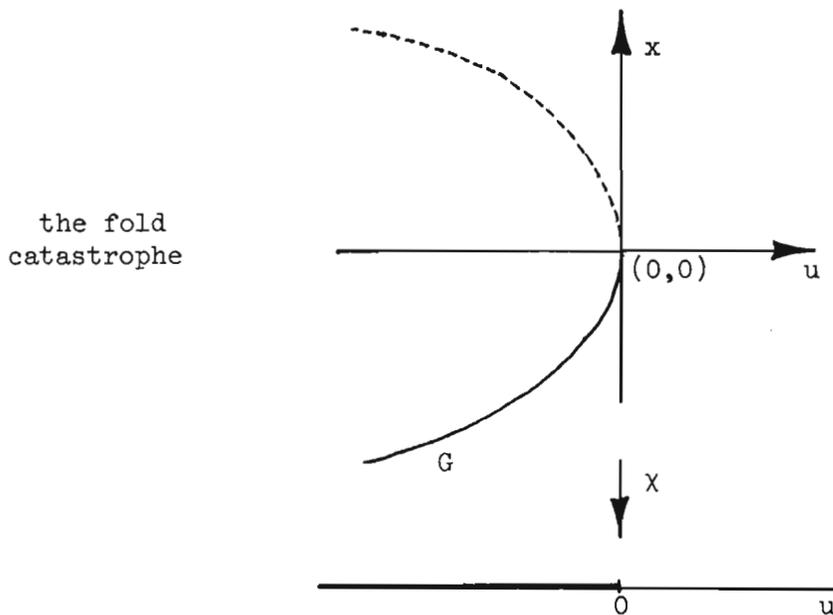


Fig. 5. The curve G is given by the parabola  $x^2 + u = 0$ . A point  $(u,x)$  on the solid part of the parabola maximises  $V(u,x) = \frac{1}{3}x^3 + ux$  locally, a point on the dotted part minimises  $V(u,x)$  locally and the origin corresponds to a point of inflexion of  $V$ . The point  $u = 0$  is a threshold. Note that  $V(u,x)$  has no critical points near the origin when  $u$  is positive.

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or variation  $g$  of  $f$  (i.e. if  $g$  is sufficiently 'close' to  $f$ ) has essentially the same shape or, more precisely, if the structure of the critical points of  $g$  is essentially the same as that of  $f$  (technically, if  $g$  is equivalent to  $f$ ). Thus this property is analogous to the homeostasis or canalisation commonly enjoyed by biological systems. We shall not define structural stability fully (the interested reader is referred to Dodson, in press, Thom 1969 or 1970 or Zeeman 1972) as it suffices for our purposes to know that 'almost all' functions are structurally stable and that excluding the possibility that the fitness function is structurally unstable is analogous to excluding the possibility of balancing a pin on its point. Hence the assumption which we now make that the fitness function is structurally stable is not very restrictive but it allows us to invoke Thom's theorem. This in a simple form appropriate for our purposes states that for a uniform (canalised) population with phenotype  $p$  subject to natural selection in a slowly and smoothly changing environment  $e$ , we have

1. the critical set  $M_p$  is a one-dimensional smooth curve embedded in  $I \times P$ ,
2. any quantum evolution (i.e. any significant change in phenotype associated with an environmental threshold) must arise from the fold catastrophe, to be explained in the next section.

The first assertion has already been assumed in Figs. 3 and 4. The theorem does not exclude the possibility of the critical set being very complicated in its entirety but there will be just two free ends with no reticulation. Moreover the assumption that the population is canalised implies that away from thresholds, curves of points corresponding to local maxima of the fitness are horizontal.

#### The Fold Catastrophe

The second assertion needs more explanation. The fold catastrophe is the graph  $G$  of the parabola given by  $x^2 + u = 0$ , together with the projection  $\chi : G \rightarrow R$  given by  $\chi(u,x) = u$  (Fig. 5). We note that the image  $\chi(G)$  of the parabola  $P$  under the projection  $\chi$  is the negative part of the  $u$ -axis up to the origin (heavy line in Fig. 5). Also it is readily checked that the parabola  $x^2 + u = 0$  is the critical set of the function  $V(u,x) = \frac{1}{3}x^3 + ux$ . The lower half of the parabola

consists of points  $(u,x)$  for which  $V(u,x)$  is locally maximal, the upper half consists of points for which  $V(u,x)$  is locally minimal and the origin  $(0,0)$  is a point of inflexion where a local maximum and minimum annihilate each other. It is evident that the fold catastrophe has a number of features in common with the curves discussed in the section on thresholds. In fact more is true.

Let there be a threshold at time  $T$ , corresponding to an environmental threshold at  $\phi(T) = e_T$  and the population having a phenotype  $p^*$  (i.e. we suppose that at the critical point  $(T,p^*)$  the peak in the fitness surface is annihilated by a saddle). Then the second part of the theorem says that near the point  $(T,p^*)$  in  $I \times P$  the critical curve looks like the parabola  $x^2 + u = 0$  (Fig. 4). Moreover points on the lower half of the parabola correspond to points on the critical curve of the fitness for which the fitness surface has a peak, the upper half to points where the fitness surface has a saddle and the origin to the point  $(t,p^*)$ . The real variable  $u$  is a smooth diffeomorphic function of the time  $t$ , i.e.  $u = u(t)$  and the point  $u = 0$  corresponds to the temporal threshold  $T$ , i.e.  $u(T) = 0$ . The single real variable  $x$  corresponds to the  $n$ -dimensional vector  $p = (p_1, \dots, p_n)$  representing the phenotype and the response of  $x$  as  $u$  varies is qualitatively the same as that of  $p$  as the time  $t$  varies, that is the two curves are, in a sense that can be made precise, similar and  $p$  maximises the fitness  $f(t,p)$  locally when and only when  $x$  maximises  $V(u(t),x)$  locally. Thus as the time  $t$  passes  $T$ , the environment  $e(t)$  crosses the threshold  $e(T) = e_T$  and the variable  $u(t)$  crosses the origin, passing from negative to positive values. As soon as  $u$  becomes positive (i.e. as soon as  $t$  exceeds  $T$ ) the variable  $x$  is no longer at a local maximum of  $V$  and will increase in value some distance from the origin until it reaches a new local maximum. This corresponds to the population being no longer maximally fit past the environmental threshold  $e_T$  and consequently evolving to a new stable maximally fit form with phenotype  $p^+$  given by  $p^+$ , significantly different from  $p^*$ . It is not possible to say much about the difference between  $p^*$  and  $p^+$  but canalisation implies that it is unlikely that the new phenotype  $p^+$  will vary much subsequently.

Thus, to sum up, prior to the threshold at time  $T$ , the response of the phenotype will be qualitatively parabolic (technically equivalent to a parabola) with a vertical tangent at the threshold. The lower solid line in Fig. 4 shows the phenotypic response prior to the threshold. This response of the phenotype up to the threshold at  $T$  can be discussed in terms of an exact model, namely the fold catastrophe, shown in Fig. 5, which should be compared with Fig. 4.

It is possible to be more explicit about the response of the phenotype  $p = (p_1, \dots, p_n)$  at a time  $t$  just prior to a threshold at time  $T$ , where we can neglect powers of  $(T - t)$ ,  $(p_1^* - p_1)$ ,  $\dots$ ,  $(p_n^* - p_n)$  higher than the first to obtain the formula

$$a_1(p_1^* - p_1) + \dots + a_n(p_n^* - p_n) = (T - t)^{\frac{1}{2}}, \quad (2)$$

where  $a_1, \dots, a_n$  are real constants. Thus our model predicts that just prior to a threshold, a 'square root' law should hold for the phenotypic response, but we cannot say for what range it would be valid. Nor as we have said can we say much about the difference between  $p_T$  and  $p^*$ , although by invoking canalisation one would expect that if the formula (2) held for  $t > t_0$ , then we would have that

$$\sum_{i=1}^n |p_i^* - p_i| \geq \frac{1}{A} (T - t_0)^{\frac{1}{2}},$$

where  $A = \text{maximum}(|a_1|, \dots, |a_n|)$ . Of course an inequality giving the range of validity of (2) in terms of the difference between  $p_T$  and  $p^*$  would be of much more interest.

The response of the phenotype of a population is commonly discussed in terms of a single phenotypic feature (e.g. Eldredge and Gould, 1972, figures 5-4, 5-5, 5-6, 5-8). Under the various hypotheses given above, any mean phenotypic change associated with a threshold must arise from the fold catastrophe. It is worth repeating that if at a time  $t$  just prior to a threshold at time  $T$ , the mean phenotypic parameter  $y$  say is plotted against  $t$ , the resulting graph should be parabolic, given by

$$y = y^* - K(T - t)^{\frac{1}{2}},$$

where  $K$  is a constant. This implies that the rate of change of phenotype

$$\frac{dy}{dt} = \frac{K^2}{2(y^* - y)},$$

whence  $\frac{dy}{dt}$  increases hyperbolically prior to the phenotypic

threshold  $y^*$ .

#### Conclusion

We have shown that under a number of realistic assumptions any significant phenotypic response to a gradual secular environmental change of a canalised uniform population subject to natural selection, which is associated with a threshold, can only arise from the fold catastrophe. Thom theory predicts a 'square root' law prior to the threshold which at least in principle can be looked for, although admittedly the practical difficulties are very great. Possible candidates might be the early history of the mammalian order Taeniodonta, which has been discussed by Patterson (1949), or the change from brachydonty to hypsodonty in the Equidae, discussed by Simpson (1953, p. 389).

The theory does not say much about the difference between the original and final stable forms, nor when or why thresholds occur. It says that if they occur then they must have a certain structure. To obtain information about the difference in phenotype or the location of the thresholds, more information would have to be incorporated into the theory. Also, the theory can only be applied to a single population and although it could be extended under rather unrealistic and uninteresting conditions to cover a predated population, it cannot be applied to two or more competing populations. However, this might be possible using Smale's theory of optima.

Equation (2) is formally similar to equations in the mean field theory of phase transitions. This theory is inadequate near a threshold since the variability, which is neglected in the mean field theory, becomes important there. This suggests that using the mean phenotype may also be inadequate very near the threshold.

Lastly, A. Hallam and the author are preparing a paper which discusses allopatric speciation in the context of Thom theory. In this case, instead of just a secular change, we consider a population subject to an environmental gradient as well. There is some overlap with this paper and indeed the formalism is almost identical, but we believe that Thom theory gives additional insight into this very important type of evolution as well as into quantum evolution.

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