

COEVOLUTION IN ECOSYSTEMS: RED QUEEN EVOLUTION OR STASIS?

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Ecosystems are assumed to have certain persistent characteristics in the kinds of species present, in their diversity, and their relative abundances (Preston, 1962; MacArthur and Wilson, 1967; Webb, 1969; Odum, 1971; Pielou, 1975; Rosenzweig, 1975a; Whittaker, 1977). It is important to ask what these constancies are. What, for example, do the temperate forests, the deserts or the rain forests of the New and Old World have in common? What can the fossil record tell us about long-term constancies? These are empirical questions (for recent discussions, see e.g., Cody, 1966, 1975; MacArthur, 1969, 1972; Van Valen, 1973; Boucot, 1975, 1978; Niklas, 1978; Levinton, 1979; Stanley, 1979; Niklas et al., 1980; Jones, 1981; Williamson, 1981a, 1981b). There is also the theoretical question of how the complex structure of a community is maintained over evolutionary time: this is the question addressed in this paper.

One approach, much encouraged by May's (1973) demonstration that stability is not a necessary consequence of complexity, has been to analyze pairwise interactions between species and to seek for processes which might stabilize such interactions (e.g., Pimentel, 1961; Rosenzweig, 1973; Slobodkin, 1974; Lawlor and Maynard Smith, 1976; Schaffer and Rosenzweig, 1978; for reviews, see Roughgarden, 1979; Slatkin and Maynard Smith, 1979; Futuyma and Slatkin, 1983; May and Anderson, 1983). This approach has two drawbacks. First, it is far from clear, particularly for predator-prey interactions, that evolution will lead to stability (Rosenzweig, 1977; Rough-

garden, 1977, 1979). Second, even if it does, it is not clear how the persistence of the whole community could arise from the stability of pairwise interactions.

Hence we need a theory of communities with the following characteristics: i) It should describe the whole community, and not subsets of species within it. ii) It should describe both the densities of genetically constant species, and evolutionary changes in those species. iii) It should describe how the number and types of species in the community change.

In this paper, we describe a first step towards such a general theory. It is based on three concepts: Van Valen's (1973) Red Queen hypothesis, MacArthur and Wilson's (1967) theory of island biogeography, and—to a lesser extent—the concepts of species packing and limiting similarity (MacArthur and Levins, 1964; May and MacArthur, 1972).

The main conclusion to emerge is that ecosystems are expected to approach one of two evolutionary modes. The first mode, corresponding to the Red Queen condition, is a steady state of change (even in a constant physical environment) characterized by continuing evolutionary change, extinction and speciation. The other is one of evolutionary stasis, with zero rate of evolution and no extinction or speciation; evolutionary change occurs only in response to changes in the physical environment.

Which of these pictures is more nearly correct depends on the assumptions of the model; in particular, it depends on whether, and if so how, one modifies Van Valen's (1973) "zero sum" assumption. Clearly, it would be desirable if this de-

cision could be based on an analysis of past and present communities. Unfortunately, such a decision is not easy.

Three Time Scales

It is useful to distinguish three different time scales. i) The ecological time scale, in which the variables are the species abundances. ii) The gene-frequency time scale, in which the number of species, and the nature of the interactions between them, are treated as constants, but the species are evolving through gene frequency changes. iii) The speciation-extinction time scale.

Basically, our time scales correspond to Valentine's (1972) classification of the types of changes occurring in communities: i) changes that alter the proportional representation of the populations present; ii) changes that alter the quality of the populations; iii) changes that alter the diversity of populations.

These distinctions are to some degree artificial. In particular, as gene frequencies change on time scale ii) the relative abundances of species will change, and this in turn will alter the strengths of the interactions between species. Nevertheless, we treat these interactions as constants on this time scale, and as variables only on scale iii). Some simplification of this kind seems necessary if progress is to be made, because it enables us to study separately the processes occurring on different time scales.

The Rate of Evolution and the Evolutionary Lag

The rate of evolution of any particular species will depend on how far the species is from a local adaptive peak. Maynard Smith (1976), adopting an idea suggested by Felsenstein (1971), attempted to make this idea more precise by defining the evolutionary lag, or "lag load":

$$L = \frac{\hat{W} - \bar{W}}{\hat{W}}, \quad (1)$$

where \bar{W} is the mean fitness of the present population, and \hat{W} the fitness of the

fittest possible genotype, incorporating all mutations favorable in the *contemporary* environment, whether they are already present in the population or have yet to occur.

The meaning of L can be made clearer by an imaginary experiment, which could perhaps be performed on a single species in a chemostat, but only in imagination on species in a real ecosystem. We wish to measure L_i for a species i at time T . At time T , we stop all evolutionary change in species other than i , and all changes in the environment. While preserving an unchanged sample of species i , we then permit species i to evolve, and wait until evolutionary changes in i have ceased. Then we introduce individuals from this final population of species i , of fitness \hat{W} , into the unchanged sample of species i , of fitness \bar{W} . It is then possible to measure \hat{W}/\bar{W} , and hence to calculate L_i .

The point of this Gedanken experiment is to establish that L is well defined, even if it cannot in practice be measured. However, our "example" requires that there *is* a local adaptive peak; that is, L is well defined provided that, in a constant environment (both physical and biological), evolutionary change of a given species would eventually slow down and stop. We return to this point in the Discussion.

Next, we need to define, for a given species, the rate of evolution, V . As we are only interested in adaptive genetic changes, and not neutral ones, we define V as the rate of change of \bar{W} :

$$V = d\bar{W}/dt. \quad (2)$$

With this definition, V will be defined as a monotonically increasing function of L . The claim that V increases with L is a vaguer but more general version of Fisher's (1930) "fundamental theorem of natural selection."

The Gene-Frequency Time Scale

The Lag-load Model.—The essential feature of Van Valen's Red Queen hy-

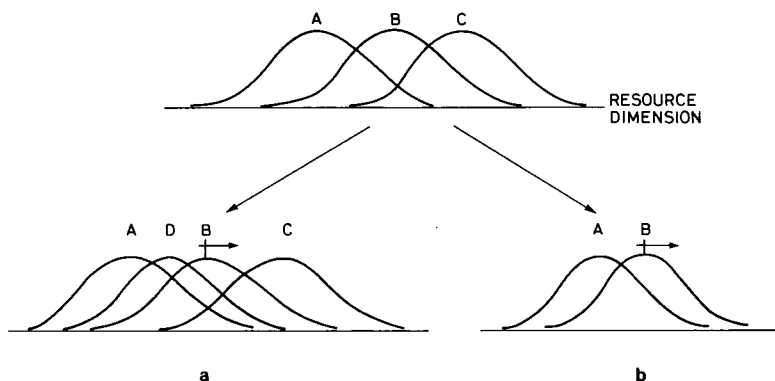


FIG. 1. The initial state is shown in the top diagram with three species uniformly spaced along a resource axis. This can be altered in two ways: (a) by the addition of species D; or (b) by the removal of species C. Change (a) would deprive species B of resources, and change (b) would provide species B with additional resources, yet both would result in a similar increase in the lag, L_B , of species B.

pothesis was as follows: the major component of the "environment" of any species consists of the other species in the ecosystem. Therefore, any evolutionary change in one species will be experienced as a change in the environment of others. Typically, the change experienced will involve an increase in L , because most species, most of the time, are assumed to be close to their local adaptive peaks: hence, an arbitrary change in the environment will usually move a species further away from its peak.

Consider a community with a fixed number S of species in an *unchanging* physical environment. Let the lag of the i th species be L_i . Then, following Maynard Smith (1976), the change in L_i in unit time is

$$\delta L_i = \delta_e L_i - \delta_g L_i, \quad (3)$$

where $\delta_e L_i$ is the increase in the lag of the i th species caused by evolutionary changes in others, and $\delta_g L_i = V_i$ is the reduction in lag caused by changes in species i itself. Hence,

$$\delta L_i = \sum_j \beta_{ij} \delta_g L_j - \delta_g L_i, \quad (4)$$

where β_{ij} is the increase in L_i caused by a unit change in L_j ; all $\beta_{ii} = 0$. If species i is at its local adaptive peak ($L_i = 0$), then β_{ij} is necessarily positive; in general, the closer species are to their adaptive

peaks, the more likely the β 's are to be positive.

We have used β rather than α to emphasize the difference between these β -coefficients and the α 's which appear in ecological models (e.g., May, 1973). The distinction is crucial to our argument. In particular, we emphasize that a community may change in such a way as to increase the lag load of species B, and yet this change may confer an ecological advantage on species B (in the sense of increasing the numbers of species B) or an ecological disadvantage on species B. This is illustrated in Figure 1: changes (a) and (b) both increase the lag load of species B, but change (a) would reduce the numbers of species B and change (b) would increase them. Hence, the commonly used ecological coefficients, α , define the type and strength of the ecological interactions influencing population densities in a community (on time scale i), whereas the β 's define the type and strength of interactions influencing the genetic constitution of populations (on time scale ii).

For each species,

$$V_i = \phi_i(L_i), \quad (5)$$

where $\phi(0) = 0$, and ϕ is a monotonically increasing function.

Initially, we assume linearity:

$$V_i = k_i \cdot L_i \quad (6)$$

Then, from (4),

$$dL_i/dt = \sum_j \beta_{ij} \cdot k_j \cdot L_j - k_i \cdot L_i. \quad (7)$$

These equations describe the behavior of the system on the gene frequency time scale, ignoring speciation and extinction. Since the equations are linear, their behavior after a sufficient period of time is given by

$$d\tilde{L}/dt = R \cdot \tilde{L}, \quad (8)$$

where \tilde{L} is a vector. That is, the loads will either increase indefinitely, or tend to zero, depending on the sign of R .

It is convenient to introduce as a variable the mean lag load, $\bar{L} = \sum L_i/S$. \bar{L} is a measure of the extent to which species, on average, depart from their adaptive peaks, and hence of the rate at which they are evolving. For the linear case, it follows from (8) that after a sufficiently long period of time,

$$d\bar{L}/dt = R \cdot \bar{L}. \quad (9)$$

To gain some insight into how the sign of R is determined, we consider the case in which all the k 's are equal and constant over time. Then, from (7)

$$d\bar{L}/dt = k \cdot \sum_i \left(\sum_j \beta_{ij} \cdot L_j - L_i \right) / S.$$

That is,

$$\begin{aligned} d\bar{L}/dt &= k \cdot \left(\sum_i \sum_j \beta_{ij} \cdot L_j - \sum_i L_i \right) / S \\ &= k \cdot \left(\sum_j \left(L_j \cdot \sum_i \beta_{ij} \right) - \sum_j L_j \right) / S. \end{aligned}$$

Writing

$$D_j = \sum_i \beta_{ij} \quad (10)$$

we obtain

$$d\bar{L}/dt = k \cdot \sum_j (D_j - 1) \cdot L_j / S. \quad (11)$$

Equation (11) can be rewritten as

$$d\bar{L}/dt = k(\bar{D}\bar{L}/\bar{L} - 1) \cdot \bar{L},$$

where $\bar{D}\bar{L} = \sum_i D_i \cdot L_i / S$. Hence, after a sufficiently long period of time, R can be specified as

$$R = k \cdot (\bar{D}\bar{L}/\bar{L} - 1). \quad (12)$$

Hence, it follows that R depends on k as well as the elements of the β -matrix and the L -vector.

It is clear from (11) that if the values of D_j are in general greater than 1, R will be positive, and the system will diverge (i.e., the average load will increase without limit); if, on the other hand, the D_j are in general less than 1, R will be negative, and the system will converge (i.e., the average load tends to zero). The value of k cannot alter the sign of R , and hence does not affect the stability of the system, but only the rate at which convergence or divergence proceeds.

The quantity D_j represents the "distributed decrement" associated with species j ; it is the summed increment of the loads experienced by other species caused by a unit reduction in the load of species j . The essential feature of Van Valen's (1973) Red Queen hypothesis was that such decrements occur, and maintain evolutionary change in the community; each species evolves because the others evolve. However, he made an additional "zero sum" assumption, that "a proportional amount w of successful response by one species produces a total negative effect $v = w$ on other species jointly." He used this assumption to argue that rates of evolution would be constant. In our notation, the "zero sum" assumption is the same as saying that $D_j = 1$ for all j . If this is true, then it does follow that all loads, and hence rates of evolution, are constant and different from zero (Maynard Smith, 1976). Van Valen (1976) defended the assumption on the grounds that the total resources available in the system are constant. However, the loads which determine the rates of evolution are not the same as the resources available (as explained in connection with Fig. 1); hence that argument fails.

If we reject the "zero sum" assumptions, as seems necessary, two possibilities remain: i) R is negative. In a uniform physical environment, evolution will cease. Evolution is maintained only by changes in physical conditions. ii) R is positive. If so, we must take into account the non-linearities which arise as loads increase—i.e., R is a function of the L 's. This is considered in the following section.

More generally, as pointed out by Stenseth (1979), R is also a function of the number of species in the community; this is considered in the section on "The speciation-extinction time scale."

Evolutionary Interactions Between Species Varying Over Time.—The assumption that all β 's are positive holds when all species are at their adaptive peaks (i.e., when all lags are zero). As species i moves further from its adaptive peak, it is more likely that changes in other species will reduce its lag; that is, some β_{ij} will be negative. Hence, as lags increase, values of β and hence of the distributed decrements D_i will tend to decrease. Since, for the linear case, the sign of R depends on whether, for most species, $D_i > 1$ ($R > 0$) or $D_i < 1$ ($R < 0$), we expect R to decrease with increasing \bar{L} . Hence we can replace (9) by

$$d\bar{L}/dt = (a + b \cdot \bar{L}) \cdot \bar{L}, \quad (13)$$

where $b < 0$.

Hence the system can reach a steady state of continued but non-accelerated evolution, in a community consisting of a fixed set of species. However, for reasons discussed in the next section, continued evolution would almost certainly lead to extinction and to speciation.

The Speciation-Extinction Time Scale

In the long run, the number of species, S , may alter, and this in turn will affect the β 's and hence R . Unfortunately, we can make no a priori statement about the direction of change of R for a given change in S . At first sight, it might seem that, as species number S increases, the species

will become more closely packed along the resource axes, and hence a change in one of them will have a greater effect on the others; if so, values of β increase as S increases. However, this argument is fallacious, for the following reason: β_{AB} measures the change in the load of species A for a given change in the load of species B, and not in the phenotype of species B. Hence, although it may be true that, as S increases, the change in the load of species A for a given phenotypic change in species B likewise increases, it does not follow that β_{AB} increases with S . Bearing this in mind, it is hard to predict how the β 's, and hence R , will change with S . We therefore replace (12) by the simplest linear equation,

$$d\bar{L}/dt = (a + b \cdot \bar{L} + c \cdot S) \bar{L}, \quad (14)$$

where $b < 0$ (as in (13)) and a and c are of uncertain sign.

We also need an equation for dS/dt . Rosenzweig (1975a, 1975b) and Stenseth (1979) considered the number of species in an ecosystem as a balance between extinction and speciation (see also Simberloff, 1972; Valentine, 1972; Sepkoski, 1979). This approach is essentially similar to that of MacArthur and Wilson (1967) to island biogeography. Thus

$$dS/dt = \sigma - \epsilon, \quad (15)$$

where σ and ϵ are the rates of speciation and extinction, respectively.

Consider first the effect of \bar{L} on σ and ϵ . The larger \bar{L} , the higher the rates of evolution, and hence the more rapidly will the ecological roles played by different species change, and hence, in turn, the more frequently will it happen that particular species will be faced by ecological deterioration for which evolutionary change can afford no remedy. This is best illustrated by G. C. Williams' (1975) imaginary example of the flea on the passenger pigeon. When the pigeons became extinct, the fleas necessarily became extinct too. Since, when the pigeons become rarer, selection on the flea could only act to make it a better parasite of the pigeon (supposing that no alternative

host was available), no capacity for rapid evolution could save it.

Thus we expect the rate of extinction to increase with lag, because the rapid evolution alters the ecological niches available. Maynard Smith (1976) also assumed that extinction would increase with lag, but for a different reason. He supposed that the extinction of a species was a direct result of the increase in its own lag; in effect, it fell too far behind in the evolutionary race. There is some empirical support for this view: the taxonomic distribution of parthenogens suggests that they are short-lived in evolutionary time, perhaps because they cannot evolve as fast as sexual species (Maynard Smith, 1978). However, we now think this effect is less important in causing extinction rate to rise with \bar{L} than the disappearance of the niches of particular species in a rapidly evolving community.

Rapid evolution may also encourage speciation. Hence

$$d(\sigma - \epsilon)/d\bar{L} = d - e, \quad (16)$$

where d and e are positive constants. Unfortunately, there is no a priori way of deciding the sign of $(d - e)$.

Little need be said about the dependence of σ and ϵ on species number, S . As assumed in island biogeography it seems clear that ϵ will increase with S . The relationship between σ and S is less obvious (for discussions, see Rosenzweig, 1975a, 1975b; Mayr, 1954; Sepkoski, 1979; Stenseth, 1979). What does seem clear, however, is that, close to the equilibrium between speciation and extinction, ϵ increases more rapidly than σ with increasing S (see Stenseth, 1979). That is

$$d(\sigma - \epsilon)/dS = f - g, \quad (17)$$

where $(f - g)$ is negative; f and g are the effects of S on speciation and extinction, respectively.

Hence, combining (15), (16) and (17), we have

$$dS/dt = h + (d - e) \cdot \bar{L} + (f - g) \cdot S. \quad (18)$$

The Behavior of the Model

We can now write down equations for the long-term behavior of the system, in terms of the species number, S and mean lag, \bar{L} . Close to the equilibrium, (S^*, L^*) , we have

$$d\bar{L}/dt = (a + b \cdot \bar{L} + c \cdot S) \cdot \bar{L}, \quad (19a)$$

$$dS/dt = h + (d - e) \cdot \bar{L} + (f - g) \cdot S, \quad (19b)$$

where $b < 0$, but a , c and $(d - e)$ are of uncertain sign.

We first investigate the behavior of the model when $b = 0$ (Fig. 2); that is, we ignore the possible stabilizing effect arising because the β 's may decrease as the lags rise. The results depend on two conditions. i) The sign of $(d - e)$. That is, does the rate of change of species number increase ($d - e > 0$) or decrease ($d - e < 0$) with increasing \bar{L} ? The latter alternative seems more plausible, but we cannot assert that it is true. ii) The sign of c . That is, does R in (8) and (9) increase ($c > 0$) or decrease ($c < 0$) with increasing S ? It is also possible that R is rather insensitive to changes in S , so that $c \approx 0$. (Note that it is not necessary that $c = 0$ for the dynamics to be as shown in the middle row of Figure 2. Thus the $d\bar{L}/dt$ isocline occurs at $S = -a/c$; if c is small and $-a/c$ large and positive, this will lie above the intersection of the dS/dt isocline with the S axis, and diagrams B and E are appropriate.)

One approximation made in analyzing the model needs some justification. It has been assumed that the linear form of equations (19) is appropriate close to the equilibrium, can be used globally. For equation (19a), the $d\bar{L}/dt$ isocline is given by the solution of $a + c \cdot S = 0$ (still assuming $b = 0$); if this is replaced by the more general monotone function of the form $\psi(S) = 0$, the isocline will still be of the form $S = \text{const}$. The nature of the dS/dt isocline depends on the sign of $d - e$. For $d - e < 0$, the isocline has a negative slope at the equilibrium. There must be some maximum value of S . Hence, although the isocline need not be linear, it

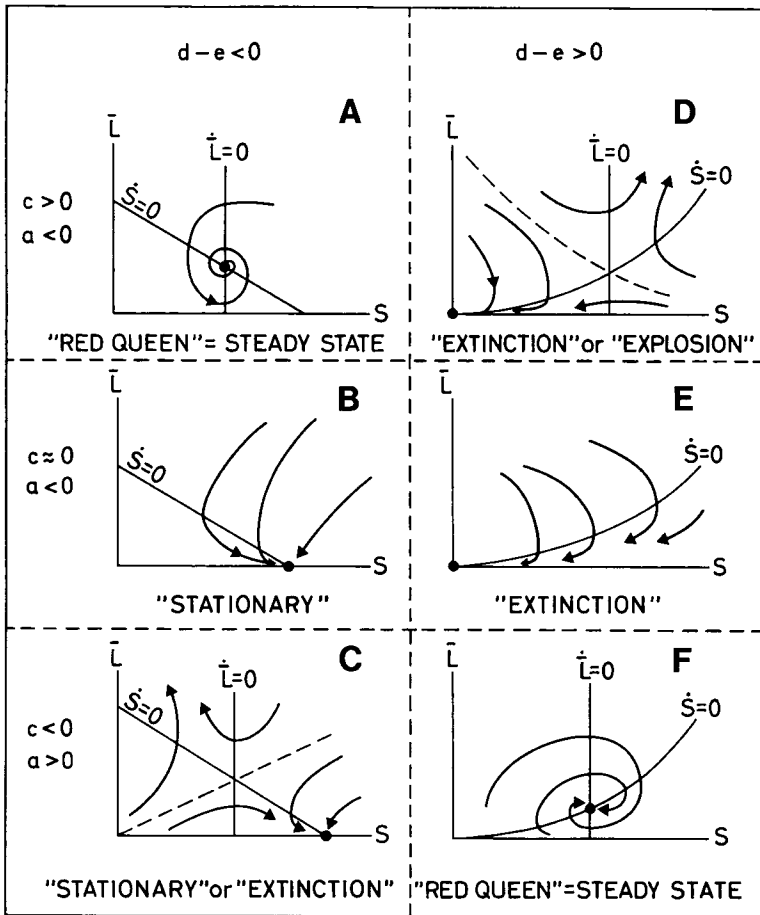


FIG. 2. Dynamics of the evolutionary system for various values of a , c and $d - e$. Notice that the $d\bar{L}/dt$ isocline in Figure E will not intersect the dS/dt isocline since the latter will approach an asymptote far to the left of the $d\bar{L}/dt$ isocline. See the main text for definitions and discussion.

is reasonable to assume that it declines monotonically to meet the S axis. When $d - e > 0$, the isocline has a positive slope which, if continued, would cause it to cut the \bar{L} axis at a negative value of \bar{L} ; since negative lags are impossible, the isocline has been shown curved, to meet the \bar{L} axis at $\bar{L} = 0$.

Assuming $b = 0$, the possible behaviors are as follows: i) "Red Queen," or steady state behavior, characterized by a uniform rate of evolution, speciation and extinction, and a constant number of species. ii) "Stationary": evolutionary change slows down until it stops when

the system contains the maximum number of species. iii) "Extinction": all species are eliminated. iv) "Explosion": an empirically impossible case, in which both S and \bar{L} increase indefinitely.

It is possible, but complicated, to analyze equations (19) when $b \neq 0$; when this is done, no qualitatively new patterns of behavior emerge.

Since we know that ecosystems exist, that they seem to have certain persistent characteristics (see Introduction), and that evolution occurs, the choice really lies between a Red Queen (or steady state) system, and a Stationary one. Since we

cannot, from ecological considerations, be confident about the signs of $d - e$ nor of c , the choice between Red Queen and Stationary models will have to depend primarily on palaeontological evidence.

DISCUSSION

The main question raised in this paper is whether or not evolution will continue at an approximately steady rate, in the absence of changes in the physical environment; if the answer is yes, then Van Valen's (1973) Red Queen picture of evolution is a plausible one. In an earlier paper Maynard Smith (1976) treated the same problem, concluding that the answer was no: he found that the Red Queen picture was structurally unstable, and that any system would either be in a convergent or a divergent mode. Stenseth (1979) pointed out that this conclusion rested on the assumption that the interspecific evolutionary interactions (the β 's) were assumed to be constant, whereas in fact they are functions of the loads and of the number of species in the system. Allowing for this, we have shown that the Red Queen picture is one plausible outcome of our evolutionary model (19).

There are basically two ways of generating a Red Queen solution: i) By taking into account the non-linearities which arise because R increases as loads increase: this can be done while keeping the number of species in the system constant. Essentially, this is a more precise formulation of Maynard Smith's (1976) divergent mode of evolution. Roughgarden (1977, 1979) analyzed an equivalent model with fixed number of species. Although Roughgarden does not say so explicitly, he does not seem to find a Red Queen solution in his model. ii) By treating a dynamical system with both loads and species numbers as variables. Rumel and Roughgarden (1983) and Roughgarden et al. (1983) analyzed a somewhat similar model, but with only three species; they found—as we did—that a Red Queen solution could result.

Referring to Figure 2, it seems that cases A and F (both Red Queen systems) and

B (Stationary) are biologically most plausible. Case C is not particularly plausible, since it implies that an initial high \bar{L} would cause extinction of the entire system. Cases D and E are clearly of no interest. We think that $d - e < 0$ is more plausible than $d - e > 0$; that is, an increase in \bar{L} and in rate of evolution leads to a fall in species number. This is by no means certain, but if it is true, the most plausible alternatives in Figure 2 are A and B.

The Red Queen equilibrium is dominated by biotic interactions: that is, the main feature of the environment of each species consists of the other species in the community. In contrast, if the Stationary picture is correct, evolution is driven by physical changes. It is tempting to suggest that the two pictures correspond respectively to a gradualist and to a stasis plus punctuation interpretation of the fossil record (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1979). We cannot support this interpretation strongly. However, it is relevant that a strictly Darwinian model, in which evolutionary changes occur because of intra-population selection, can lead either to continual change or to stasis depending on the nature of the ecological and evolutionary interactions between species.

We can ask what features of the fossil record would be predicted by the two dynamic patterns. The Red Queen view predicts rather constant rates of extinction (as suggested by Van Valen, 1973), speciation and phyletic evolution together with a constant number of species. There is no necessary connection between changes in the physical environment and evolutionary events. In contrast, on the Stationary view we would expect bursts of evolution, extinction and speciation associated with, and caused by, major changes in the physical environment. Following such bursts, there would be a slowing down of evolutionary change and species turnover, until a new physical catastrophe kicked the system into motion again. The model predicts a constant number of species, but not a constant

(non-zero) extinction rate. Species are expected to remain phenotypically fairly constant for extensive periods. In the former case, phenotypic stasis is not expected; in the latter case, phenotypic stasis is expected.

In practice, it will be hard to distinguish between communities obeying the Red Queen and the Stationary type of dynamics. Hoffman and Kitchell (1984) have, however, attempted to do so, basing their approach on the results reported in the present paper. There are two particular difficulties: i) If there are continuous small changes in physical conditions, this could result in continued evolutionary change which would be indistinguishable from Red Queen dynamics in an unchanging physical environment. It can be shown that a Red Queen system would show oscillations in species number while returning to its steady state after a major disturbance whereas a Stationary system would not show oscillations. However, to distinguish these types of behaviors would require much more detailed palaeobiological data than are at present available, or than we may ever be able to obtain. ii) The assumption that there is, for each species, a local adaptive peak may be untrue. In particular, one species in a community may cross a major selective threshold. For example, at some point the ancestors of the birds reached the stage at which flight was occasionally advantageous. Once past that stage, ancestral birds would have been so far from their adaptive peak that they would continue to evolve for millions of years in the absence of environmental change, and in doing so they would cause evolutionary change in other species in the community. A burst of evolution caused in this way would be hard to distinguish from one caused by a change in the physical environment.

Despite these difficulties, it is important to understand the dynamics of evolving communities over evolutionary time, and the different possible patterns of dynamic behavior. How can our un-

derstanding of long term evolutionary changes be improved? First, it seems necessary to take a community approach to palaeontology (see Bock, 1979; Hoffman, 1979; Hoffman and Kitchell, 1984); that is, to study how many species living together in a community change over time, and to see how species number changes over time. This might, in fact, provide data from which the signs of parameters in model (19) might be determined, and hence enable us to distinguish between the various cases in Figure 2. Second, equivalent—but more reliable—data could be obtained by studying geographical variation in sets of species; this could provide better information on the ecological (α) and evolutionary (β) interactions. This possibility arises because the differences between species in different places at the same time have been caused by selective forces similar to those causing the differences between a species at the same place at different times (see Stenseth, 1984).

In recent years, a number of palaeontologists and developmental biologists have argued that constraints placed by development on the nature of phenotypic change have been important in determining the rates and patterns of evolution (Goodwin et al., 1983). In contrast, our emphasis in this paper has been on the importance of ecology, because, although we accept that developmental constraints limit the directions in which a population can evolve, there is overwhelming evidence that a change in selective pressure does produce evolutionary change in some direction. Hence, if we are to understand the long-term patterns of evolution, we need a theory which says something about selection, and hence, about the environment. Since the major component of the environment of most species consists of other species in the community, it follows that we need a theory of ecosystems in which the component species are evolving by natural selection. The present paper is an attempt in that direction.

SUMMARY

A preliminary attempt is made to develop a theory of the long-term behavior of ecosystems, including changes in the number of species, in their genetic constitutions, and in their relative abundances. The theory is based on the Red Queen hypothesis, on the theory of island biogeography, and on the concepts of species packing and limiting similarity. The main conclusion is that an ecosystem in a physically constant environment may be in one of two evolutionary modes: (i) Red Queen, or steady state of evolutionary change, or (ii) evolutionary stasis. In the latter case, continued evolution necessarily depends on changes in the physical environment. A decision as to which mode has been prevalent in the past will depend on a study of the fossil record. However, it is pointed out that such study of the past necessarily must be accompanied by the study of how organisms interact in current ecosystems.

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