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Proceedings: Biological Sciences, Vol. 260, No. 1358 (May 22, 1995), 119-125.

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Evolution of simple population dynamics

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SUMMARY

We investigated the evolution of demographic parameters determining the dynamics of a mathematical model for populations with discrete generations. In particular, we considered whether the dynamic behaviour will evolve to stability or chaos. Without constraints on the three parameters – equilibrium density, growth rate and dynamic complexity – simple dynamics rapidly evolved. First, selection on the complexity parameter moved the system to the edge of stability, then the complexity parameter evolved into the region associated with stable equilibria by random drift. Most constraints on the parameters changed these conclusions only qualitatively. For example, if the equilibrium density was bounded, drift was slower, and the system spent more time at the edge of stability and did not move as far into the region of stability. If the equilibrium density was positively correlated with the complexity, the opposing selection pressures for increased equilibrium density and for reduced complexity made the edge of stability evolutionarily stable: drift into the stable region was prevented. If, in addition, the growth rate was bounded, complex dynamics could evolve. Nevertheless, this was the only scenario where chaos was a possible evolutionary outcome, and there was a clear overall tendency for the populations to evolve simple dynamics.

1. INTRODUCTION

Do the dynamics of populations evolve towards stability or chaos? Because small density fluctuations imply a low extinction probability, group selection favours populations with stable dynamics (Thomas *et al.* 1980; Berryman & Millstein 1989). But what type of dynamics is favoured by individual selection, which is thought to be a much stronger evolutionary force? If the temporal variation in population size is driven by extrinsic, density-independent factors such as weather, natural selection on individuals will often lead to more stable population dynamics by favouring ‘bet-hedging’ strategies such as dispersal and iteroparity (Stearns 1992). Such strategies lead to a lower fitness variance, which implies a higher mean growth rate (Gillespie 1977). If variation is caused by intrinsic, density-dependent feedback mechanisms, the dynamics can be very complicated (May 1974, 1976). In these situations it is not clear how natural selection changes the demographic parameters determining the dynamics, and in particular whether individual selection on these parameters favours chaos or stability.

In this paper we study the evolution of parameters in the simple models that May (1974, 1976) used to introduce the paradigm of chaos to ecology. We simulated evolution by studying competition between phenotypes in asexual populations. Each phenotype is given by a set of parameters that determine its density-dependent fitness function. Phenotypes go extinct because they are outcompeted by others, and new phenotypes are created by mutation.

We obtained our results by numerically simulating evolution. Analytical insights are generally hard to obtain. The fundamental quantity that determines the course of evolution is the ‘natural invariant measure’ of the underlying dynamic process (Rand *et al.* 1994; Doebeli 1995*a*). This measure reflects the frequency with which various densities are attained over time, i.e. the distribution of the environments (the population densities) that determine fitness. The invariant measure is notoriously hard to compute analytically. However, with Gillespie’s (1977) principle, and with some analytical arguments, our results are intuitively understandable.

When there are no constraints on the parameters, they always evolve to regions in parameter space associated with stable equilibrium dynamics. Thus natural selection moulds the intrinsic feedback mechanisms such that the fluctuations in population size are reduced. Only constraints on the parameters, e.g. through trade-offs, can impede the evolution of stable dynamics.

To some extent, our results are in contrast to previous theoretical work on the evolution of demographic parameters that determine population dynamics (Ferrière & Clobert 1992; Hansen 1992; Gatto 1993; Ferrière & Gatto 1993), which suggests that the evolution of chaos is more likely in more complicated models. On the other hand, our results conform very well with previous empirical work, which showed that complex dynamics should be rare among insect populations in the wild (Hassell *et al.* 1976; Bellows 1981) and in the laboratory (Thomas *et al.* 1980; Mueller & Ayala 1981, Philippi *et al.* 1987).

2. THE MODEL

We used a model for a population with discrete generations of the form

$$N_{t+1} = f(N_t) \cdot N_t, \quad (1)$$

where N_t is the density of the population at time t , and $f(N)$ is the density-dependent fitness function, i.e. $f(N)$ is the reproductive output per individual if the density of the population is N . For the fitness function we used an expression that was introduced by Maynard Smith & Slatkin (1973) and considered by Bellows (1981) to be the most generally applicable one-dimensional ecological model:

$$f(N) = \lambda/[1 + (aN)^b]. \quad (2)$$

Here λ is the intrinsic growth rate of the species, a measures how well the individuals can cope with the environment, and b determines the type of competition that leads to density-dependence (Hassell 1975). When the fitness function is 1, the population is replacing itself, and hence the equilibrium density of the population is the solution N^* of the equation

$$f(N^*) = 1. \quad (3)$$

When perturbed away from this equilibrium, the dynamics of the population are determined by the quantity

$$c = 1 + \frac{df}{dN}(N^*) \cdot N^*. \quad (4)$$

The quantity c is always < 1 , and is typically negative. If $|c| < 1$, N^* is a stable equilibrium, i.e. the population density returns to the value N^* when perturbed away from it. As c decreases below -1 , i.e. as $|c|$ increases above 1, the system exhibits the familiar period doubling route to chaos (May & Oster 1976). Because it is a measure for the complexity of the dynamics, c is called 'dynamic complexity', and we say that the system has a low dynamic complexity if the absolute value $|c|$ is low. The equilibrium density, which can be thought of as the carrying capacity, is given by

$$N^* = [(\lambda - 1)^{1/b}]/a, \quad (5)$$

and the dynamic complexity by

$$c = 1 - b(\lambda - 1)/\lambda. \quad (6)$$

For our purposes it is convenient to replace the parameters a and b in expression (2) by the parameters N^* and c . Then the fitness function has the form

$$f(N) = \frac{\lambda}{1 + (\lambda - 1) \left(\frac{N}{N^*} \right)^{\frac{1-c\lambda}{\lambda-1}}}. \quad (7)$$

To study the evolution of the parameters in this model, we assumed that each set of parameters (λ , N^* , c) corresponds to a phenotype. Thus phenotypes are characterized by their intrinsic growth rate, their equilibrium density and their dynamic complexity, which together determine the phenotypic fitness function. Competition between phenotypes is intro-

duced by assuming that the fitness function of a phenotype depends on the total density of the population, i.e. that the fitness of a phenotype varies with the sum of the densities of all the phenotypes that are present in the population.

To understand evolutionary trends, one has to find the conditions under which a rare mutant will invade a resident population. The dynamics of the resident phenotypes can be very complicated, and according to the fluctuations in their total density, the fitness function of the rare mutant attains different values over time. Whether the mutant is outcompeted and driven to extinction, or whether it can invade, depends on the geometric mean of these fitness values: if the logarithm of this mean is < 0 , the mutant goes extinct, if it is > 0 , the mutant can invade. This leads to the notion of 'invasion exponent' (Metz *et al.* 1992; Rand *et al.* 1994). If N_t , $t = 0, 1, 2, \dots$, is the time series of the densities of the resident phenotypes, and if $f_m(N)$ is the fitness function of the mutant, then the invasion exponent is

$$e = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln f_m(N_t). \quad (8)$$

Depending on whether e is > 0 or < 0 , rare mutants can invade or go extinct. Thus, to determine the fate of a rare mutant one has to know the frequency distribution of the densities in the time series N_t , $t = 0, 1, 2, \dots$: the fitness of the mutant depends mostly on those densities that occur often in the time series generated by all the resident phenotypes.

The basic evolutionary trends in the model can be seen when equation (8) is applied to a situation where the resident population consists of only one phenotype. For example, consider a resident phenotype that exhibits a stable equilibrium, so that $N_t = N^*$ for all times t . Then it is easy to see that a mutant can invade if, and only if, it has a higher equilibrium density than the resident. The general case of a resident with complex dynamics ($|c| > 1$) was studied in Doebeli (1995a). If one considers a mutant with a change in one of the traits, while the other two traits are the same as the resident's, the following selection regimes can be observed:

1. *K*-selection: the strongest selection pressure is for higher equilibrium densities N^* .
2. *r*-selection: higher intrinsic growth rates are favoured. The strength of *r*-selection decreases with decreasing dynamic complexity of the resident.
3. *c*-selection: lower dynamic complexity, i.e. lower values of $|c|$ are favoured. The strength of *c*-selection increases with increasing intrinsic growth rate of the resident.

These are 'local' results in the sense that they only describe when a resident population consisting of only one phenotype can be invaded by a mutant that differs in one trait. Nothing is said about the dynamic consequences of a successful invasion, i.e. whether the mutant drives the resident to extinction, or whether coexistence results. Nor does one generally know the dynamics of coexisting phenotypes, which can be very complicated (Doebeli 1994).

Here we wanted to follow the global dynamics of a system in which there are many resident phenotypes, and new mutants differing in all three traits simultaneously (equilibrium density, intrinsic growth rate and dynamic complexity) are trying to invade at a constant rate. In our simulations, we started with one initial phenotype. In each generation, a new mutant was generated with a certain probability, the mutation rate. The phenotype of the mutant was derived as follows: we averaged the resident phenotypes according to their densities, obtaining a set of parameters $(\bar{\lambda}, \bar{N}^*, \bar{c})$ as the average phenotype of the population. The phenotype of the mutant was then assumed to be drawn from a multivariate normal distribution with means $\bar{\lambda}$, \bar{N}^* and \bar{c} , and with variances that were set at 4% of the mean values. The density of the mutant was set at some (small) fixed initial value. To update our array of phenotypes, phenotypes were assumed extinct if their density dropped below a certain threshold. The fitness functions of the phenotypes were assumed to depend on the total density of all phenotypes present, and the dynamics of these systems were followed for many generations.

3. RESULTS

When all three parameters were free to evolve, the system invariably exhibited stable equilibrium dynamics after some time (figure 1). Thus the mean

dynamic complexity \bar{c} always evolved to values with $|\bar{c}| < 1$. Meanwhile, the mean growth rate $\bar{\lambda}$ increased initially, but the increase got slower and slower as stable dynamics evolved, because the selection pressure for higher growth rates decreased as the complexity decreased. In contrast, the equilibrium density increased without bounds. Once the population exhibited a stable equilibrium, it was dominated by one phenotype, namely the one that currently had the largest equilibrium density.

As the equilibrium density can be thought of as the carrying capacity of a phenotype, it is not realistic that it can increase without bounds. The easiest way to constrain the equilibrium density is to assume that it cannot exceed a certain threshold. If this was done, the same general picture emerged, and the dynamics always evolved to a stable equilibrium (figure 2). However, the period of time until values of $|\bar{c}|$ below 1 were reached was typically much longer, and these values remained close to 1: the population remained at the edge of stability given by $|\bar{c}| = 1$ (figure 2). This happened even though the intrinsic growth rate increased, which should accelerate the evolution to simple dynamics. We explain this result in §4.

More sophisticated constraints on the parameters are obtained by assuming trade-offs between them. This corresponds to assuming that the parameters obey some functional relationship

$$G(\lambda, N^*, c) = 0. \quad (9)$$

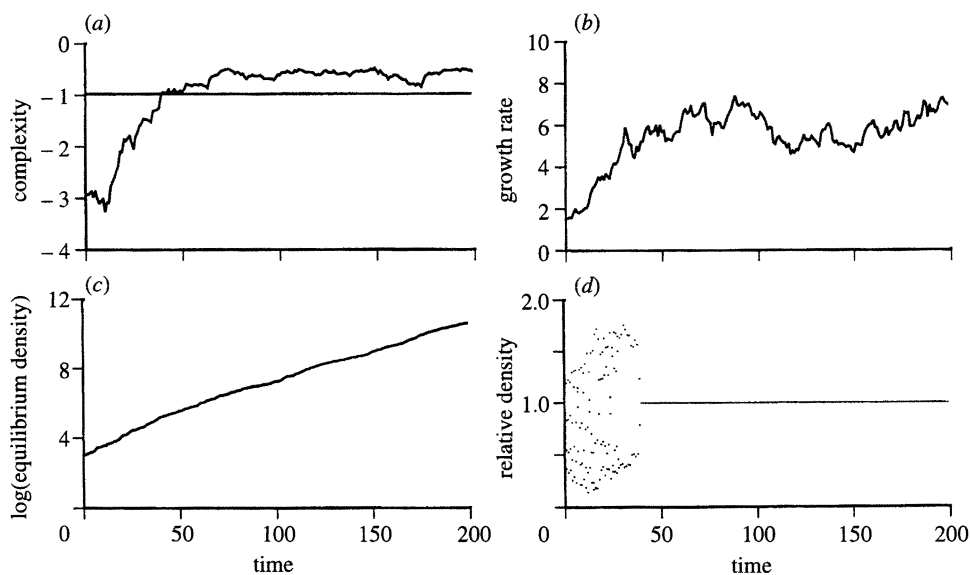


Figure 1. Evolution of demographic parameters and of population dynamics in equation (7). The three parameters – equilibrium density, intrinsic growth rate and dynamic complexity – are free to evolve without any constraints or trade-offs. Evolution was simulated as described in the text. In each panel, a time unit codes for 1000 generations. (a) The dynamic complexity rapidly evolves from values coding for instability ($c < -1$, i.e. $|c| > 1$) to values coding for stable equilibria ($c > -1$, i.e. $|c| < 1$). Although there is no selection pressure for complexity greater than -1 , it can reach values well in the stable region by random drift (see discussion). (b) Growth rate initially increases rapidly, but as the system becomes stable, the selection pressure for higher growth rates decreases until eventually growth rates change only by random drift. (c) Equilibrium density increases without bounds. (d) The relative density of the population, defined as the total density divided by the mean equilibrium density, evolves from chaos through two-cycles to stability. To simulate evolution, we assumed that the probability for a mutation to occur was 0.01 per generation, and that the mutation coded for phenotypic values chosen from Gaussian distributions with the means set to the phenotypic means of the population and the standard deviations set to 4% of the means. New mutants were initialized at a density of 0.01, and we assumed a phenotype to be extinct if its density reached a value of less than 10^{-5} .

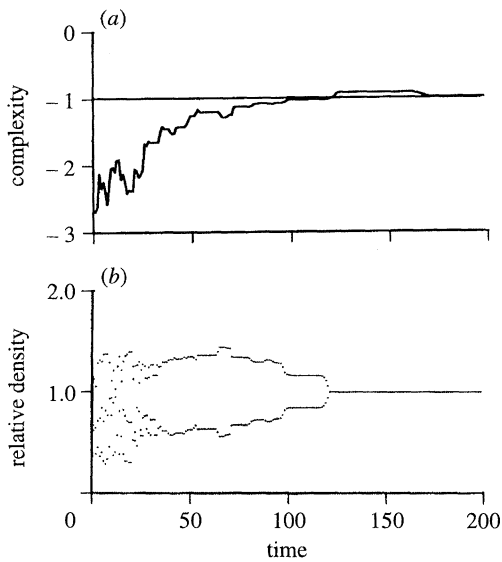


Figure 2. Evolution of dynamic complexity and of population dynamics when the equilibrium density is bounded by 10^5 . All other assumptions are as in figure 1. (a) Complexity evolves to values coding for stability, but the evolution is slower than when equilibrium density is unbounded (figure 1), and the drift into the region coding for stability is smaller. (b) The evolution of the population dynamics reflects the slower evolution of dynamic complexity by extending the time periods where the system is chaotic and where it exhibits a two-cycle. The system reaches a stable equilibrium, but it remains close to the edge of stability given by $c = -1$.

Then the parameters are not free to evolve. Rather, in the three-dimensional parameter space they can only evolve along the surface that is given by equation (9). For example, one could assume that a high equilibrium density can only be attained at the cost of a low intrinsic growth rate, i.e. that these traits are negatively correlated. For instance, the function G in equation (9) could have the form

$$N^* - (k/\lambda) = 0, \tag{10}$$

where k is a constant. Obviously, there are many different ways of assuming trade-offs between the three parameters, and for most of them one could argue biological plausibility. However, keeping in mind the

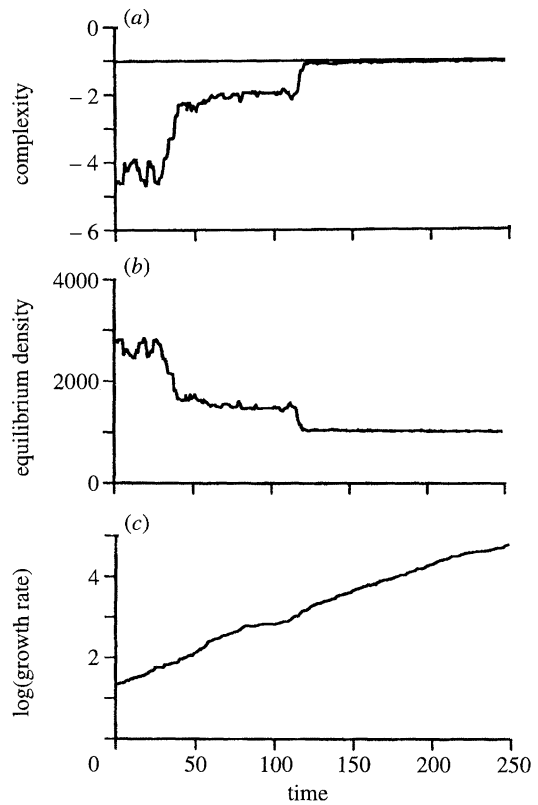


Figure 3. Evolution of demographic parameters when the equilibrium density is positively correlated to the absolute value of the dynamic complexity, i.e. when phenotypes with high equilibrium densities are likely to be unstable. Formally, the correlation is given by $c = 1 - N^*/500$. All other assumptions are as in figure 1. The evolution is driven by the opposing selection pressures to increase equilibrium density and to increase stability. (a) Despite the selection pressure for higher equilibrium density, the dynamic complexity evolves from values coding for chaos to values very close to -1 , i.e. to the edge of stability ($|c| = 1$). In contrast to figures 1 and 2, drift into the stable region is now prevented by selection for higher equilibrium density. (b) Owing to selection for stability, equilibrium density decreases to a value that allows the system to have simple dynamics. (c) Growth rate increases without bounds.

Table 1. *Qualitative effects of correlations between demographic parameters on their evolution*

(The effects are relative to the case with no correlations (figure 1). More details are given in the text.)

correlation	negative	positive
equilibrium density N^* growth rate λ	slower evolution to simple dynamics	more rapid evolution to simple dynamics
growth rate λ dynamic complexity $ c $ (absolute value)	more rapid evolution to simple dynamics	slower evolution to simple dynamics growth rate evolves to lower values
equilibrium density N^* dynamic complexity $ c $ (absolute value)	more rapid evolution to simple dynamics	equilibrium density is limited because opposing selection for simple dynamics if growth rate is unbounded: evolution to the edge of stability if growth rate is bounded: evolution to complex dynamics; the level of complexity depends on the maximum growth rate

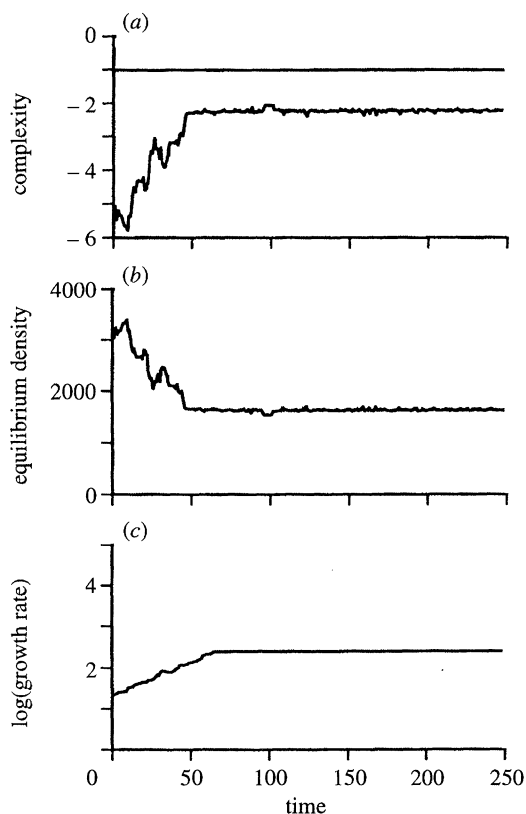


Figure 4. Evolution of demographic parameters as in figure 3, except that the growth rate is bounded by 250. As the growth rate reaches this bound (c), the selection pressure for stability can no longer increase. Therefore, the opposing forces for increased equilibrium density and increased stability equilibrate at a dynamic complexity (a) that codes for instability (chaos in this case), and at a higher equilibrium density (b) than in figure 3.

basic evolutionary trends observed for the invasion of rare mutants, one can infer the effect on the evolution of simple dynamics from the sign of the correlation between traits. For example, a trade-off given by equation (10) will slow down the trend towards simple dynamics, because the strong selection pressure for higher equilibrium density will lead to lower growth rates, at which the selection pressure for lower complexity is weaker.

Table 1 gives an overview of the effects of different trade-offs, given as correlations between traits, on the evolution of simple dynamics. The course of evolution, normally towards simple dynamics, can be reversed towards complex dynamics with a positive correlation between the equilibrium density and the complexity $|c|$. For instance, this could happen if phenotypes with high carrying capacities tend to be regulated by scramble rather than contest competition (i.e. if a high equilibrium density is associated with a high value of b in equation (6)). Then selection for higher equilibrium densities leads to a selection pressure for increased complexity which counteracts the basic trend to simple dynamics. Where these forces equilibrate depends on the constraints on the growth rate. If there are no constraints, the growth rate steadily increases. Hence so does the selection pressure for simple dynamics, so that the system evolves to the edge of stability, i.e. to $|c| = 1$ (figure 3). However, if the growth rate

is bounded, so is the selection pressure for simple dynamics, and the evolutionary forces equilibrate at a complexity $|c| > 1$. Hence natural selection can lead to complex dynamics (figure 4). Even so, this example shows that, depending on the growth rate, c -selection can be stronger than K -selection: selection for stability can lead to lower carrying capacities. This confirms the strong selection pressure for simple dynamics.

4. DISCUSSION

There is a clear evolutionary trend towards simple population dynamics in our model. However, what causes this tendency is not obvious. The selection pressures for higher equilibrium densities and higher growth rates can be understood analytically (Doebeli 1995a). For example, it is clear from equation (7) that, all else being equal, a higher equilibrium density N^* implies a higher fitness at all densities N . Unfortunately, in general only intuitive explanations can be given for the selection of lower complexity, which causes the evolution of simple dynamics. The first step is to determine the selection pressure on c at a given density N , i.e. to calculate the derivative of the fitness function (7) with respect to c :

$$\frac{\partial f}{\partial c}(N) = \frac{\lambda^2 \left(\frac{N}{N^*} \right)^{\frac{(1-c)\lambda}{\lambda-1}}}{\left[1 + (\lambda-1) \left(\frac{N}{N^*} \right)^{\frac{(1-c)\lambda}{\lambda-1}} \right]^2}. \quad (11)$$

This expression is positive for densities above the equilibrium N^* and negative otherwise. Thus lower complexity is favoured at densities above N^* (recall that c is negative, hence an increase in c implies a decrease in $|c|$), and higher complexity at densities below N^* . In the 'local' case, where one mutant tries to invade one resident phenotype, this means that in times of boom, when the density of the resident is below the equilibrium and growing, a mutant with a lower complexity does not do as well as the resident, and does not quite reach the high fitness values of the resident. However, in times of bust, when the density of the resident is above the equilibrium and about to crash, the decrease in fitness is not as severe for the mutant as it is for the resident. Consequently, the mutant tends to have a lower variance in fitness values, which leads to a higher geometric mean growth rate (Gillespie 1977). However, in populations with complicated dynamics higher moments of the distribution of fitness values may play a decisive role (Doebeli 1995b), so that the above is at most a crude intuitive argument why lower complexity is favoured.

A more subtle argument is obtained by noting that a gain in fitness is worth more at low fitness values than it is at high fitness values. Thus the advantage of the mutant at high densities, which lead to low fitness, should be greater than its disadvantage at low densities, where fitness is high. This argument can be made more formal with the 'natural invariant measure' $\mu(N)$ of the dynamic system (Rand *et al.* 1994; Doebeli 1995a). $\mu(N)$ is the probability that the system has density N at any given time. Using it, time averages over a

trajectory of the system can be translated to integrals over phase space. For example, for the invasion exponent (8) we have

$$\lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln f_m(N_t) = \int \ln f_m(N) \mu(N) dN, \quad (12)$$

where f_m is the fitness function of the mutant, $\{N_t\}_{t=0}^{\infty}$ is the time series of the resident, and $\mu(N)$ is the corresponding natural invariant measure. Note that if we denote by f the fitness function of the resident, then the invasion exponent

$$\lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln f(N_t) = \int \ln f(N) \mu(N) dN = 0, \quad (13)$$

because the resident is neither growing nor declining on average, hence the logarithm of its mean fitness is 0. It follows that to determine selection pressures, we just have to calculate the derivative of (13) with respect to the trait variable for which we want to know the course of evolution. If the derivative is positive, an increase in this trait will be favoured. For the complexity, we obtain

$$\frac{\partial}{\partial c} \int \ln f(N) \mu(N) dN = \int \frac{\partial f / \partial c}{f(N)} \mu(N) dN. \quad (14)$$

Thus the derivative of the fitness function with respect to c at a given density has to be weighted with the inverse of the fitness at this density to determine its contribution to the total selection pressure. Unfortunately, the natural invariant measure $\mu(N)$ usually cannot be computed analytically when the resident exhibits complex dynamics. Thus we are stuck with the mere numerical insight that the integral (14) is positive, hence that the complexity $|c|$ of the system decreases. Only as the system approaches stable equilibrium dynamics can one compute expression (14) analytically. For example, if the system moves on a two-cycle, alternating between densities N_1 and N_2 below and above the equilibrium density N^* , equation (14) reduces to

$$\frac{(\partial f / \partial c)(N_1)}{f(N_1)} + \frac{(\partial f / \partial c)(N_2)}{f(N_2)}. \quad (15)$$

When the complexity $|c|$ is near 1, N_1 and N_2 are close to N^* , and one can show analytically that simpler dynamics are favoured. The analysis, which we omit here for the sake of brevity, reveals that, typically, the unweighted selection pressure $\partial f / \partial c$ for higher complexity at the low point of the cycle is stronger than selection for lower complexity at the density of the cycle lying above N^* . But weighting these pressures by dividing them by the corresponding fitness value, which is smaller at the high point of the cycle, tips the balance in favour of simple dynamics.

The derivative $\partial f / \partial c$, equation (11), can also be used to explain why the system tends to spend long periods of time at the edge of stability (figure 2). As the complexity approaches the stable region, the total density of the system approaches the equilibrium N^* . By setting $N = N^*$ in (11), we see that $\partial f / \partial c = 0$ at N^* . Therefore, selection on the complexity ceases as the

system reaches the edge of stability given by $|c| = 1$. Only by random drift does the complexity $|c|$ evolve deeper into the region of stability, i.e. to values $|c| < 1$. When the equilibrium density is free to evolve (figure 1), it increases steadily, and there is a continuous turnover of phenotypes. This enhances drift, and $|c|$ attains values well below 1 (figure 1). In contrast, when the equilibrium density is constrained by some upper bound (figure 2), drift slows down as the phenotypes reach this bound. Even though the system finally reaches stable dynamics, the slow drift leads to values of $|c|$ that are only slightly below 1, and the system remains at the edge of stability. A positive correlation between the equilibrium density and the complexity $|c|$ makes this edge evolutionarily stable (figure 3): as $|c|$ approaches 1, the selection pressure for lower complexity ceases as discussed above, but now selection for higher equilibrium densities prevents drift to values of $|c| < 1$. Instead, the system is poised at the edge of stability. We cannot resist noting the phenomenological analogy of this result to Kauffman's (1993) 'evolution to the edge of chaos'.

That selection should change the feedback mechanisms in simple models such that they cause less variability in population size is in agreement with earlier theoretical work (Turelli & Petry 1980; Mueller & Ayala 1981). These authors also found that simple dynamics are favoured by selection, although in less general settings than ours. Moreover, our results conform with empirical work on insect populations. In an influential study Hassell *et al.* (1976) estimated the parameters of a one-dimensional difference equation for 24 insect populations and found that all but two of these populations had a stable equilibrium. Their results were supported by Bellows (1981). Thomas *et al.* (1980), Mueller & Ayala (1981) and Philippi *et al.* (1987) tested many *Drosophila* populations in the laboratory, of which the overwhelming majority exhibited stable equilibrium dynamics. Our results provide an evolutionary explanation for these findings.

The empirical results lend strong support to the general validity of our results for populations with discrete generations. More theoretical support comes from using different fitness functions. We repeated our simulations with two other fitness functions taken from Bellows (1981), one the model used by Hassell *et al.* (1976), the other entry 4 in Bellows's Table 1. The results were the same: the basic evolutionary trend is towards simple population dynamics.

However, our results are somewhat in contrast to other recent theoretical work (Hansen 1992; Ferrière & Clobert 1992; Gatto 1993; Ferrière & Gatto 1993). One reason is that in some of this work certain trade-offs are implicitly included in the models (e.g. Hansen 1992). For example, if the fitness function is given by the Ricker equation $f(N) = \lambda \exp(-qN)$, then the dynamic complexity $c = 1 - \ln \lambda$, hence c is a function of the growth rate λ . We regard it as a strength of the model we used that it has enough mathematical flexibility for growth rate, carrying capacity and dynamic complexity to appear as independent parameters. This allows us to discern the influence of different selection pressures, and to uncover basic tendencies. That

certain trade-offs can lead to the evolution of complex dynamics follows from table 1. More importantly, Ferrière & Gatto (1993) stress the fact that in their model age-structure, which does not occur here, is crucial for the evolution of chaos. In a similar vein, Turchin & Taylor (1992) argue that if some of the insect populations in Hassell *et al.* (1976) are fitted to a more complicated model that includes two time lags instead of just one, then the whole range from simple to chaotic dynamics occurs. Thus it is not at all clear how far our results generalize to more complicated situations, and the general question remains (Hastings *et al.* 1993): how often should we expect complex dynamics to occur in natural populations? Although many ecologists believe that temporal fluctuations in population size are mainly due to extrinsic stochasticity (Berryman & Millstein 1989), some have argued that in many cases such fluctuations are the result of chaotic dynamics caused by intrinsic density-dependence (Schaffer & Kot 1986; Hastings *et al.* 1993). More work with more complicated models is needed to assess these opposing views with an evolutionary theory of ecosystem dynamics. For such a theory, the concepts of evolutionary stable attractors and phenotype dynamics that were introduced by Rand *et al.* (1994) may prove to be very useful. Our results are a special case of this theory: the coevolutionary dynamics of the phenotypes lead to attractors consisting of single points that represent stable equilibrium dynamics.

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Received 13 December 1994; accepted 21 February 1995