

# Order and Chaos in the Evolution of Diversity

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## Abstract

We propose a family of measures of population diversity—total diversity  $D$  and its within-gene  $W_g$  and between-gene  $B_g$  components. We observe the dynamics of these quantities in the context of a particular model—a two-dimensional world with organisms competing for resources and evolving by changes in their movement strategy—measuring diversity as a function of selection and mutation.

Punctuated equilibria in diversity appear at appropriately tuned mutation rates, whether or not selection is present. More generally, systematic exploration of mutation rates reveals two qualitatively different regions in the space of evolving systems captured by our model: static “ordered” populations of genetically similar individuals, and rapidly changing “chaotic” populations of random varying individuals. The relationships among diversity  $D$  and its components  $W_g$  and  $B_g$  capture the typical features of these ordered and chaotic systems.

## 1 To Study the Evolution of Diversity

Complex adaptive systems are embodied in many settings, ranging from ecological populations of organisms, through immune systems of antigens and antibodies, even to networks of neurons in the brain. By abstracting away the diverse details, one can model complex adaptive systems at a level of generality sufficient to hope to reveal fundamental principles governing broad classes of such systems—this we take to be the working hypothesis of artificial life [1].

One reason for the impressive results of many artificial life models is their “emergent” architecture: The system’s global adaptive behavior emerges implicitly from an explicitly modeled population of low-level individuals. We have been studying a class of models consisting of a population of computation agents (basically, individual computer programs) that interact with each other and with their

environment in a way that allows natural selection implicitly to shape their strategies for achieving various global computational goals. Our approach starts with the attempt to formulate definitions of statistical “macrovariables”—loosely akin to thermodynamic macrovariables like pressure or temperature—that reflect fundamental aspects of a system’s adaptive behavior (e.g., see [3]). Then we try to identify simple laws relating these macrovariables to other fundamental system parameters (e.g., see [2]), and we try to use these macrovariables to identify and explain basic classifications of systems.

An obvious but striking feature of complex adaptive systems is change (and stasis) in population diversity. One fundamental task for artificial life is to describe and explain the evolutionary dynamics of population diversity. How can population diversity be defined and measured? How does diversity change as a population evolves? How do diversity dynamics vary as a function of other fundamental system parameters, such as mutation rate and selection pressure? Does population diversity define qualitatively different kinds of evolving systems? The present study addresses these questions (see also [4, 5]).

## 2 A Simple Model of Evolution

The model used here is designed to be simple yet able to capture the essential features of an evolutionary process [8, 3]. The model consists of organisms (sometimes called “bugs”) moving about in a two dimensional world. The only thing that exists in the world besides the organisms is food. Food is put into the world in heaps that are concentrated at particular locations, with levels decreasing with distance from a central location. Food is refreshed periodically in time and randomly in space. The frequency and size of the heaps are variable parameters in the simulation.

The food represents energy for the organisms. Organisms interact with the food field by eating it at their current site at each time step, decrementing the food value in the environment and incrementing their internal food supply. Organisms must continually replenish their internal food supply to survive. Surviving and moving expend energy. Organisms pay a tax just for living and a movement tax proportional to the distance traveled. If a organism’s internal food supply drops to zero, it dies and disappears from the world. On the other hand, an organism can remain alive indefinitely if it can continue to find enough food. Any evolutionary learning that occurs in the model is the effect of the one stress of continually finding enough food to remain alive. A good strategy for flourishing in this model would be to efficiently acquire and manage vital energetic resources.

It is important to note that selection and adaptation in the model are “intrinsic” or “indirect” in the sense that survival and reproduction is determined solely by the contingencies involved in each organisms finding and expending food. No externally-specified fitness function governs the evolutionary dynamics [8, 3].

The organisms in this model follow individually different strategies for finding food (and hence are sometimes called “strategic bugs” [3]). The behavioral disposition of bugs is genetically hardwired. A behavioral strategy is simply a map taking

sensory data from a local neighborhood (the five site von Neumann neighborhood) to a vector indicating a magnitude and direction for movement:

$$S : (s_1, \dots, s_5) \rightarrow \vec{v} = (r, \theta). \quad (1)$$

A bug's sensory data has two bits of resolution for each site, allowing the bugs to recognize four food levels (least food, somewhat more food, much more food, most food). Its behavioral repertoire is also finite, with four bits of resolution for magnitude  $r$  (zero, one, ..., fifteen steps), and three bits for direction  $\theta$  (north, northeast, east, ...). A unit step in the NE, SE, SW, or NW direction is defined as movement to the next diagonal site, so its magnitude is  $\sqrt{2}$  times greater than a unit step in the N, E, S, or W direction. Each movement vector  $\vec{v}$  thus produces a displacement  $(x, y)$  in a square space of possible spatial destinations from a bug's current location.

The graph of the strategy map  $S$  may be thought of as a look-up table with  $2^{10}$  entries, each entry taking one of  $2^7$  possible values. This look-up table represents an organism's overall behavioral strategy. The entries are input-output pairs that link a specific behavior (output) with each sensory state (input) that an organism could possibly encounter. The input entries in the look-up table represent genes or loci, and the movement vectors assigned to them represent alleles. Since bugs have 1024 genes or loci, each containing one out of a possible 128 alleles or behaviors, the total number of different genomes is  $128^{1024}$ . Although finite, this space of genomes allows for evolution in a huge space of genetic possibilities, which simulates the much larger number of possibilities in the biological world.

Bugs reproduce both asexually and sexually. When an organism's internal food supply crosses a threshold, it reproduces. If it finds itself adjacent to another bug with sufficient internal food, the pair flip a biased coin to decide whether to reproduce sexually. If the original bug does not reproduce sexually, it produces some number of offspring by asexual budding. In either case, after reproduction, the parental food supply is divided equally among the new children and the parent(s).

Parental genes are inherited with some probability of mutation. Analogous to the exchange of genetic material during crossover, each child contains a mix of genetic material randomly chosen from the two parents (sometimes called "uniform" crossover). There is no gender distinction so sexual reproduction simply involves offspring that are produced with a mixture of parental genetic material. Point mutations of the genes change the output values of entries in a child's look-up table. The mutation rate  $\mu$  determines the probability with which individual loci mutate during reproduction. At the limit of  $\mu = 1$ , every allele has probability one of mutating and thus each child's alleles are chosen completely randomly.

While mutation rate is an explicit parameter of the model, selection pressure is controlled indirectly by adjusting other explicit parameters. The parameter called "output noise" is defined as the probability that the behavior *actually* performed by a bug on a given occasion in a given local environment will be chosen *randomly* from the  $2^7$  possible behaviors, rather than determined by the bug's genes. If the probability of noise is one, then natural selection never has an opportunity to "test" the usefulness of the behavioral traits encoded in a bug's genome. So, the

alleles or traits transmitted in reproduction reflect chance only. There is heritable genetic variation but no heritable *phenotypic* variation, so no natural selection. In simulations reported in this paper, noise was set to either zero or one, thus creating pairs of simulations identical except with respect to selection.

This model is a very abstract and idealized representation of a population of evolving organisms, and has many biologically unrealistic respects. Nevertheless, our working hypothesis is that this model captures many fundamental aspects of evolving systems, and is thus a useful way to investigate the essential aspects of more complex evolving systems [8, 3, 1].

### 3 Measures of the Components of Diversity

How might population diversity be measured? Our proposal, very roughly, is to plot the population as a cloud of points in an abstract genetic space, and then define the population's diversity as the spread of that cloud. In the present model, an allele is a movement vector, a spatial displacement, and an individual's genotype is a set of spatial displacements. To capture the total population diversity,  $D$ , then, collect all the displacements of all bugs in all environments into a cloud, and measure the spread of that cloud. (In what follows "diversity" always means *population* diversity.)

We can divide this total diversity  $D$  into two components. First, collect the spatial displacements of each bug in the population in a given environment, i.e., the traits encoded at a given gene across the population, and calculate the spread of this environment-gene cloud. The average spread of *all* such environment-gene distributions is a population's within-gene diversity  $W_g$ . Now, form another, second-order collection of the centers of gravity of each environment-gene cloud, i.e., a cloud of each "average" displacement across the population in a given environment-gene. The spread of this second cloud is the population's between-gene diversity  $B_g$ , which measures the diversity of the average population response across all environments, i.e., genes.

It turns out that the total diversity is the sum of the within- and between-gene components,  $D = W_g + B_g$ . The relative proportions of these components reflects a population's genetic structure. Consider a population consisting of "random individuals," in the sense that each bug's alleles are chosen randomly from the set of possible alleles, different bug's genes being chosen independently. In this case, the distribution across the population at any given environment-gene will be a huge cloud covering the whole set of possible spatial displacements, so the population's within-gene diversity  $W_g$  will be quite large. Since the center of gravity of each of these huge clouds will be virtually the same point—the center of the space of possible behavioral displacements—the distribution of these centers of gravity will be quite tight, and so the between-gene diversity will be nearly zero,  $B_g \approx 0$ . The population's total diversity will approximately equal the within-gene diversity,  $D \approx W_g$ .

Another extreme case is a population consisting of genetically identical bugs

that have "tuned" their behavior in such a way that what they do in one environment differs significantly from what they do in another. In this case, the within-gene diversity is zero,  $W_g = 0$ , since the average spread of the cloud of behavioral displacements at each environment-gene is nil. On the other hand, since the average behaviors in different environments are quite different, the between-gene diversity is large and equal to the total diversity,  $D = B_g$ .

More formally, we define total diversity as the mean squared deviation between the average movement of the whole population, averaged over all individuals and over all environmental conditions, and the individual movements of particular individuals subject to particular conditions, i.e.,

$$D = \frac{1}{IJ} \sum_{i=1}^I \sum_{j=1}^J [(x_{ij} - \bar{x}^{IJ})^2 + (y_{ij} - \bar{y}^{IJ})^2] \quad (2)$$

where  $I$  is the number of individuals  $i$ ,  $J$  is the number of environmental conditions (or, in the present model, genes)  $j$ ,  $(x_{ij}, y_{ij})$  is the movement vector of individual  $i$  subject to input  $j$ , and  $\bar{x}^{IJ} = \frac{1}{IJ} \sum_{i=1}^I \sum_{j=1}^J x_{ij}$  (similarly for  $\bar{y}^{IJ}$ ). So,  $(\bar{x}^{IJ}, \bar{y}^{IJ})$  is the  $(x, y)$  displacement of the population averaged over all individuals  $i$  and genes (environments)  $j$ . Then, the within- and between-gene components of the total diversity are defined as follows:

$$W_g = \frac{1}{IJ} \sum_{i=1}^I \sum_{j=1}^J [(x_{ij} - \bar{x}_j^I)^2 + (y_{ij} - \bar{y}_j^I)^2] \quad (3)$$

$$B_g = \frac{1}{J} \sum_{j=1}^J [(\bar{x}_j^I - \bar{x}^{IJ})^2 + (\bar{y}_j^I - \bar{y}^{IJ})^2] \quad (4)$$

where  $\bar{x}_j^I = \frac{1}{I} \sum_{i=1}^I x_{ij}$  (and similarly for  $\bar{y}_j^I$ ). So,  $(\bar{x}_j^I, \bar{y}_j^I)$  is the  $(x, y)$  displacement of the population in gene (environment)  $j$  averaged over all individuals  $i$ . (Further formal analysis of diversity and its components is developed elsewhere [4, 5].)

Absolute diversity values presented here reflect the size of the model's output space. (To compare diversity measurements across different size output spaces, measurements could be normalized by the size of output space; since all our simulations have the same size output space, we have not done this.) The maximum possible diversity value corresponds to the distribution in output space that is peaked at the four corners; in this case, each point is maximally distant from the mean (in this case, the center of output space). In the present context in which the maximum displacement is fifteen squares, the diversity value of this "corner post" distribution is the sum of the  $x$  and  $y$  displacements from the mean, i.e.,  $15^2 + 15^2 = 450$ . In a flat random distribution in our modified polar coordinate system of 128 possible movements, since movements in the NE, SE, SW, or NW directions are  $\sqrt{2}$  times larger than movements in the N, E, S, or W directions, the diversity value of the flat distribution is  $\frac{4[(1^2 + \sqrt{2}^2) + (2^2 + (2\sqrt{2})^2) + \dots + (15^2 + (15\sqrt{2})^2)]}{128} = 116.25$ .

Intuitively, the "corner post" distribution is *not* maximally diverse, while the flat distribution *is*, but the diversity measures defined here are much higher for the

“corner post” than for the flat distribution. However, recall that food is placed in the simulated world in heaps that slope away from the center and that the bugs pay a movement tax proportional to distance traveled. So, it is not surprising that observed diversity values exceed 116 only in special circumstances when selection is absent.

## 4 Observations of the Evolution of Diversity

Diversity was measured in a series of simulations in which mutation rate and the presence or absence of selection were varied, while all other parameters of the model, including the size of the world and the food environment, were held constant. We simultaneously measured two crude aspects of the “performance” of the population—the population level and the amount of uningested food in the environment—on the assumption that higher population level and lower uningested food reflects better evolutionary learning on the part of the population.

In all simulations reported here, traits were assigned to the founder population randomly, with displacement direction chosen from the eight compass directions and distance in steps chosen from zero, one and two. Thus, in the founder population, the total diversity was relatively low,  $D = 2.5$ , and virtually all of the total diversity was in the within-gene component,  $D \approx W_g$  and  $B_g \approx 0$ .

Typical results from the first 10,000 time steps of simulations with mutation rate  $\mu = 0$  are shown in figure 1. Notice that the within-gene diversity  $W_g$  drops over time and eventually reaches zero when the entire population becomes genetically identical (this effect typically takes more than 10,000 time steps if selection is absent, as in figure 1 right). Furthermore, notice that the between-gene diversity  $B_g$  increases over time until it eventually equals the total diversity  $D$  (again, typically more than 10,000 time steps are required when selection is absent).

This crossing of the  $W_g$  and  $B_g$  components is to be expected under selection:  $W_g$  will drop as selection progressively weeds out traits at given loci, and  $B_g$  will rise as traits at different loci become specialized in different directions. Pure genetic drift will produce similar component crossing:  $W_g$  will drop as stochastic sampling fixes more loci, and  $B_g$  will rise as different traits become fixed. What can differentiate whether or not component crossing is due to selection is its timing; selection should make crossing faster, as indicated in figure 1 (left vs. right). Population performance data corroborate this explanation, since selection supports larger populations that extract much more food from the environment.

### 4.1 Punctuated Equilibria

Artificial life systems commonly display punctuated equilibria in quantities like species concentration [7] and average fitness [6]. Yet the causes of these punctuated dynamics remain uncertain. Ecological complications such as host-parasite interactions or genetic complications such as extensive epistasis are typically thought to be implicated, and it is almost universally assumed that selection plays an essential role. Our observations question both these presumptions.

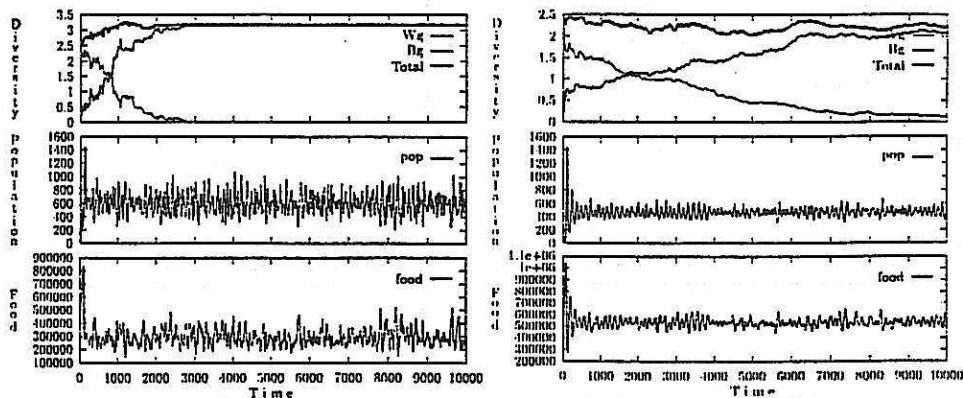


Figure 1: Diversity, population level, and uningested food in the first 10,000 time steps of two typical simulations with mutation rate  $\mu = 0$ ; normal selection on the left (output noise = 0), no selection on the right (output noise = 1).

Diversity in the present model displays clear punctuated equilibria. Figure 2 shows the typical dynamics of diversity for simulations with very low mutation rates; in these cases,  $0.00001 \leq \mu \leq 0.00003$ . The total diversity  $D$  remains largely static for significant periods of time, but every now and then diversity is punctuated by very rapid changes. The resulting picture is characterized by relatively flat plateaus separated by abrupt cliffs. (In these punctuated equilibria  $D$  is comprised almost totally of between-gene diversity  $B_g$ ; diversity components are discussed further in the next section.)

It is striking that these punctuated equilibria occur in such a simple model. None of the ecological or genetical complications usually thought to play a role are explicitly present in the model. For example, the population has no explicit division into anything like host and parasite and the genetic structure has no epistasis. It is true that the model could support the emergence of implicit sub-populations following competing or cooperating food-finding strategies. Such sub-populations would produce a substantial within-gene diversity  $W_g$ , since the average trait at given loci must then differ between the sub-populations.  $W_g$  values in the two simulations with selection (figure 2, left) are consistent with the presence of slightly different sub-populations for some periods, but the simulations without selection (figure 2, right) show no signs of sub-populations. Thus, implicit sub-populations might sometimes contribute to punctuations in some of the simulations, but they clearly play no fundamental role in punctuated equilibria generally.

The most striking aspect of these punctuations is their presence even when natural selection is absent. Although punctuated equilibria in the absence of selection occur only when the mutation rate  $\mu$  is appropriately poised near 0, the effect is quite robust. The presumption that punctuated equilibria reflect certain aspects of selection is simply wrong. Therefore, even when punctuated equilibria occur *with* selection, we cannot assume that selection plays any important role in its genesis. Evidently, there is an intrinsic tendency for evolving systems absent selection—that is, stochastically branching, trait-transmitting processes—to produce punctuated diversity dynamics, provided the branching rate is suitably poised. How to explain

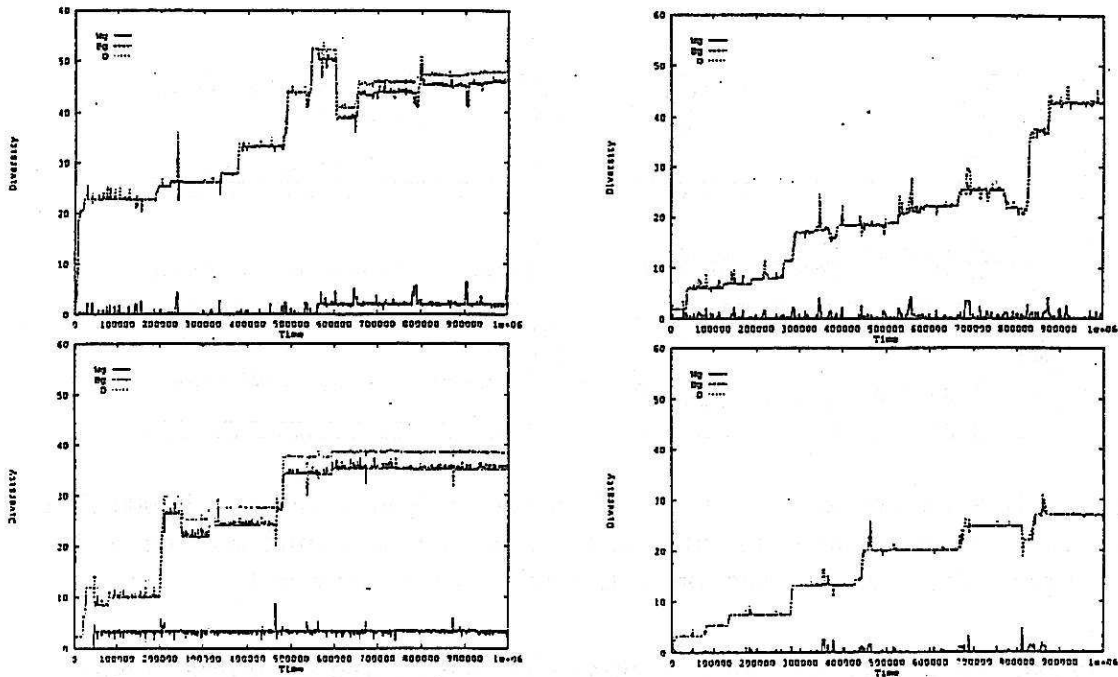


Figure 2: Diversity data from the first 1,000,000 time steps of four typical low mutation simulations with low initial diversity. Selection operates normally in the simulations on the left (output noise = 0) and there is no selection on the right (output noise = 1); mutation rate  $\mu = 0.00003$  in the simulations on the top and  $\mu = 0.00001$  on the bottom.

this effect remains an open question.

## 4.2 Structure in the Space of Evolving Systems

Punctuated diversity dynamics fit into a broader pattern suggesting a fundamental classification of qualitatively different kinds of evolving systems, at least in the space of systems akin to those defined by the parameter space of the present model. We measured total diversity  $D$  and its within-gene  $W_g$  and between-gene  $B_g$  components in a series of pairs of selection/no-selection simulations, smoothly varying the mutation rate  $\mu$  (on a log scale). Figure 2 shows two typical pairs of simulations with  $\mu$  near 0, and figure 3 shows two typical pairs of simulations with  $\mu$  near 1.

The diversity data reveal two qualitatively different kinds of evolutionary dynamics. When  $\mu$  is quite low (figure 2), the total diversity is well approximated by the between-gene diversity,  $D \approx B_g$ , and the dynamics of  $D$  consists of periods of stasis punctuated by rapid shifts in diversity (as discussed in the previous section). Furthermore, the frequency of the punctuations increases with  $\mu$ . On the other hand, when  $\mu$  is toward the high end of the spectrum, the total diversity is well approximated by the within-gene diversity,  $D \approx W_g$ , and the total diversity  $D$  exhibits noisy fluctuations around an equilibrium value. As the mutation rate drops, the amplitude of the fluctuations increases. When  $\mu = 1$  the equilibrium diversity value equals the theoretically calculated value of a totally random, "flat" distribution of alleles. As  $\mu$  falls off from 1, so does the equilibrium diversity value, but this



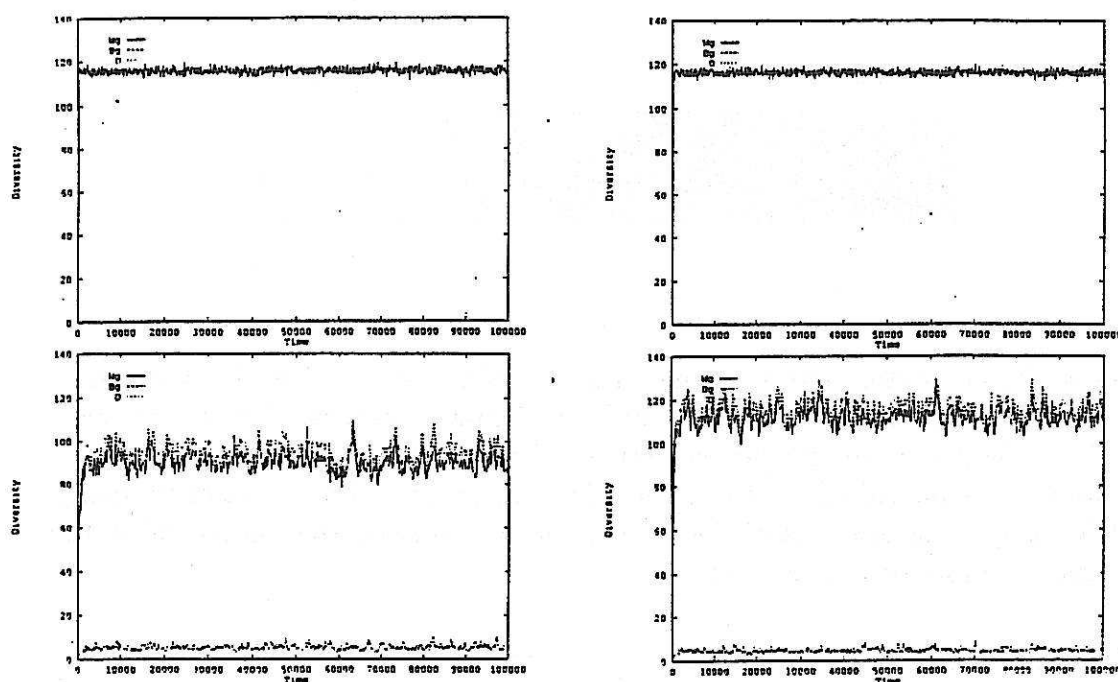


Figure 3: Diversity data from the first 100,000 time steps of four typical high mutation simulations with low initial diversity: normal selection in the simulations on the left (output noise = 0) and no selection on the right (output noise = 1); mutation rate  $\mu = 1$  in the simulations on the top and  $\mu = 0.1$  on the bottom.

drop in equilibrium diversity value is greater when selection is present (compare figure 3, bottom left and right). Although selection does have some subtle effect of the details of these diversity dynamics, the broad qualitative classification applies whether or not selection is present. (Further details of the effects of mutation and selection are described elsewhere [4, 5].)

Figure 4 summarizes these observations. The abstract space of evolving systems (at least those akin to the present model) has two qualitatively distinct regions, at the respective ends of the mutation spectrum (figure 4). Low mutation systems are “ordered,” consisting of a population of genetically identical (or, nearly identical) individuals—in effect, a population of near “clones.” Different loci encode different traits, and this distribution of traits across loci abruptly shifts from time to time. By contrast, high mutation systems are “chaotic,” consisting of a population of genetically distinct individuals, each of which has a random collection of alleles. The gene pool is a furiously boiling random distribution. Finally, the ordered and chaotic regions surround a broad gray area, perhaps hiding additional structure.

The diversity components can be used to define the border separating the ordered and the chaotic regions from the intervening gray area. As  $\mu$  increases from 1 in the ordered region, the frequency of  $D \approx B_g$  punctuations increases and the average duration of the periods of stasis decreases (as is to be expected). The ordered region dissolves away when the duration of the periods of diversity stasis drops to zero. On the other hand, as  $\mu$  falls off from 1 in the chaotic region, the amplitude of the fluctuations around the equilibrium  $D$  value increases (as could be expected). The chaotic region dissolves away when the amplitude of these fluctuations diverges to its maximum value.

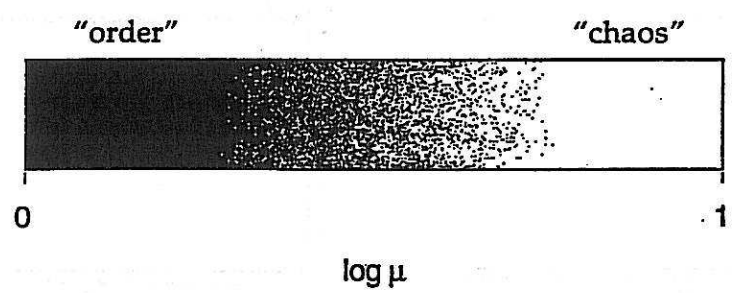


Figure 4: A schematic picture of the structure of the space of evolving systems, indicating two regions of qualitatively different behavior separated by a large gray area that might contain further structure. Systems with low mutation rate  $\mu$  are "ordered"—individuals in the population are more or less genetically identical. High  $\mu$  systems are "chaotic"—the genetic structure of each individual in the population is more or less random.

This structure in the space of evolving systems has an interesting connection with optimal population performance, measured by how much food the population can extract from the environment. Three robust patterns in uningested food emerge (figure 5). First, as could be expected, when selection is absent uningested food is flat across the mutation scale and is significantly higher than in simulations with selection. Second, when selection is present, uningested food rises as  $\mu$  approaches 1 (as could be expected), as well as when  $\mu$  is extremely close to 0 (again, as could be expected). Finally, food extraction is maximized when  $\mu$  is broadly in the vicinity of the boundary between the ordered region and intervening gray area.

This effect might reflect a balance between two competing demands of evolutionary learning. On the one hand, the need to remember what has been learned argues for a low enough mutation rate; on the other hand, the need to explore novel possibilities argues for a high enough mutation rate. Optimal evolutionary learning, then, requires the mutation rate to balance these competing needs appropriately. This optimally poised mutation rate evidently coincides with the region around the edge of order.

## 5 Towards a Science of Artificial Life

We are aiming to achieve two goals simultaneously: first, to develop plausible and useful measures of population diversity and, second, to use those measures to discern fundamental features of the evolution of diversity. Progress towards these goals is related. One reason for finding our observations plausible and interesting is that our measures of diversity seem appropriate, and one sign that our measures of diversity are appropriate is that they reveal apparently plausible and interesting effects.

To confirm the extent of our progress toward these goals requires further work. Many analytical details remain to be settled, of course, and extensive simulations are required to construct a more precise statistical analysis of our effects. But the most important task is to replicate our results in other models. Seeking similar di-

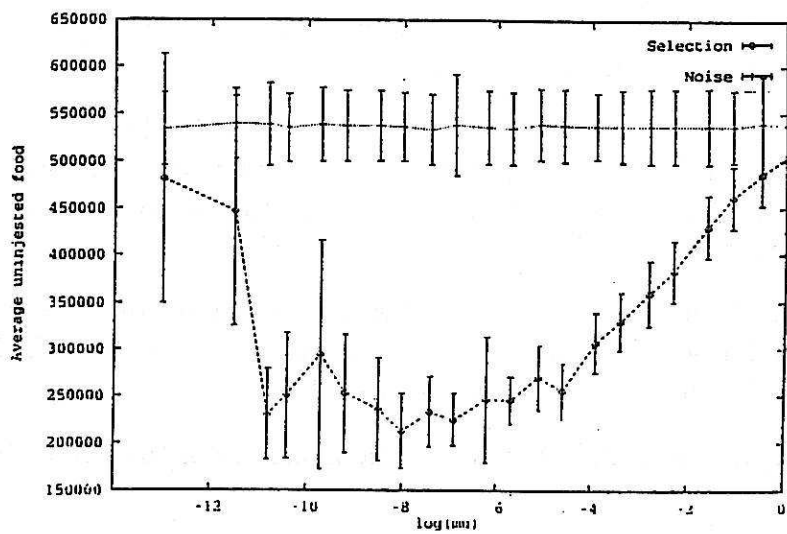


Figure 5: Time averages of uningested food across typical simulations as mutation rate  $\mu$  is varied (on a log scale). One set of simulations has normal selection; the other has no selection (output noise = 1). The “bars” surrounding each point indicate the standard deviation of the time series of food values. The leftmost selection and noise points represent  $\mu = 0$ .

iversity effects across models is feasible only if our measures of diversity can be suitably generalized. Although some formal details do depend on some idiosyncrasies of our model, the basic thrust of our approach is quite general. Furthermore, all of the present results pertain to one model; so, simple and general as the model may be, the generality and robustness of our results remains conjectural. Final confirmation of the importance of our measures and the universality of our effects—and vindication of artificial life’s fundamental working hypothesis—can come only from comparing quantitative results across a host of complex adaptive systems.

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