# Limits of Chaos and Progress in Evolutionary Dynamics

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**Abstract**

There are a number of standard models for the evolutionary process of mutation and selection as a mathematical dynamical system on a fitness space. We apply basic topology and dynamical systems results to prove that every such evolutionary dynamical system with a finite spatial domain is asymptotic to a recurrent orbit; to an observer the system will appear to repeat a known state infinitely often. In a mathematical evolutionary dynamical system driven by increasing fitness, the system will reach a point after which there is not observable increase in fitness.

**Key words:** population dynamics, evolutionary dynamics, evolutionary network, evolutionary equilibrium, fitness space, fitness network

## 1. Introduction

### 1.1 *Goals and Perspective.*

The goal of this paper is to apply standard mathematical theorems from topology and dynamical systems to mathematical models of evolution. Mathematical topology is the logical study of the shape of objects without using specific measurements such as angles and curvature — for example an oval, a square and a circle are all topological the same — and mathematical dynamical systems involves the application of topology to processes that change over time, often without precise formulation of the process.

Like most cross-disciplinary research, this paper requires the difficult task of attempting to speak across the language and style of two disparate technical fields. To those trained in one field or another, exposition in their own field will appear trivial and work presented from the other takes time to digest. The author is an applied mathematician and the tools of this paper are mathematical, and so despite the author's best efforts the style will inevitably tend toward that field, especially when dealing with theorems and proofs.

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Historically, when the apparent chasm between fields is breeched results can be profound. Mathematics offers tools — rigorous ways to understand things that can be rigorously described — and science offers objects and processes to be understood. Over the past century, applications of topology have been central to progress in several scientific fields, and to understand the work in this paper it will be helpful to review how topology has been applied in the past.

We should make an important distinction regarding terminology. A dynamical system most generally is anything that changes over time governed by a set of rules. A *mathematical dynamical system* is one that is defined in mathematical logic — it consists of a state space X and a function which, for a given initial state, will determine the state of the system at future times. (This definition will be made in more detail and more broadly involving the possibility of randomness later in this paper.) A *biological dynamical system* consists of organisms that reproduce and grow. We will use the terms mathematical dynamical systems and biological dynamical system to distinguish between the two when not clear from the context. We will also use the term *model* to refer to a mathematical dynamical system that is designed to model a biological one.

Accordingly, we can prove theorems about mathematical dynamical systems and these theorems would only be applicable to biological dynamical systems to the extent to which the mathematics accurately models the biology. In physics, where dynamical systems originated, the distinction is not usually made because the process involved are the result of physical laws such as Newtonian or Relativistic mechanics; conclusions proven about mathematical systems are taken as automatically pertinent to physical ones. Biological organisms are not subject to the same types of laws; individuals are assumed to have probabilities regarding specific behavior and the ability to model the behavior of system as a whole results from averaging the probabilities across a large number of organisms, for example as with the quasispecies equation (See [1]). This is analogous to statistical mechanics and thermodynamics, where the predictability of the collective whole is assumed by averaging out over many individual components.

It is broadly accepted that the process of evolution can be effectively modeled using mathematics. The study of mathematical dynamical systems modeling evolution is called *evolutionary dynamics* and the interested reader is referred to Novak's excellent introduction *Evolutionary Dynamics, Exploring the Equations of Life* [1]. Mathematical dynamical systems modeling evolution are the topic of study in this paper and using the proper tools we prove restrictive behavior about very broad classes of such models. Determining which models are accurate or appropriate for evolution is beyond the scope of this paper.

Mathematical models are developed by formulating some assumed governing scientific principles into mathematics and the resulting behavior of the model is

taken to be the logical consequence of the assumed principles. Models can be used in a predictive manner (ie what will happen to a certain species if the harvesting rate is increased) or in an explanatory manner (ie why did the codfish population decrease) and we are concerned with the latter in this paper.

Using mathematical models to explore underlying causes requires a proper understanding of what the models can and cannot tell. In models where the governing principles are derived from laws (ie physics and chemistry), the behavior of the model is taken as the behavior of the physical system in the ideal case. In models where the governing principles are not derived directly from scientific laws (ie economics and ecology), the behavior of the system is only understood to match the behavior of the physical system *if* the assumed governing principles where the most important factors in the process. Thus, it is impossible to prove that certain principles result (or resulted) in observed behavior, but it is possible to prove that certain behavior is impossible as a consequence of certain governing principles. In short, mathematical models cannot demonstrate what is *true* about a physical system, but they can demonstrate what is *false* by way of a hypothesis test; if the behavior in a mathematical model does not match observed phenomena, then original assumed principles cannot be the cause of the observation.

The main results of this paper are for a mathematical dynamical system modeling evolution: 1) If the state space is compact (ie the physical system exists in a finite area) and the genotype has a bounded finite length then the change in phenotype with either stop or appear to repeat some state and the amount of increase in fitness is bounded, stated formally in Theorem 3; and 2) If the system is chaotic (and the fitness is a continuous function that is nondecreasing on orbits) then there is no increase in fitness, stated formally in Theorem 4. The first might not be surprising, although by way of this result we suggest a focus on the bounds of evolution in mathematical models, for example using information theory to quantify the bounds. The second result seems contrary to the prevailing understanding of evolutionary dynamics.

## 1.2 *History and Application of Topology and Dynamical Systems*

To bridge the gap between mathematical definitions and theorems of topology and their role of in science, we discuss the history of applied topology over the past century. Topology began as a theory in the late 1800s out of attempts to answer two seemingly separate questions — one abstract mathematical question and one applied scientific.

In the late 1800s, German mathematician Gregor Cantor was attempting to define dimension as part of his quest to develop a rigorous theory of points and

sets, things that had been taken for granted since the investigations of Greek mathematicians (See [2]). A by-product of this re-development of the foundations of mathematics was the discovery that some sets have a dimension greater than a line but less than a plane — that is some sets have a fractional dimension — the most famous of these sets being the Cantor Set. These sets are what we now call *fractals* (a term coined by Benoît Mandelbrot in 1975). The tools required to study them is not the lines, angles and curves of geometry and calculus, but a more general class of definitions and theorems that make up topology.

Also in the late 1800s, French mathematician Henri Poincaré was studying planetary motion using calculus and differential equations. In his attempt to solve the equations of motion for multiple heavenly bodies, Poincaré wrote his *Les méthods nouvelles de la mécanique Célest*; New Methods in Celestial Mechanics (See [3]). The first printed version of this manuscript contained an error, and in correcting the error Poincaré discovered that equations for planetary motion have solutions that are too complex to be explicitly written in the usual formulas from calculus. Having shown that the solutions are too complex to be solved via calculus, Poincaré developed a new set of tools which we now call topology. Having discovered that the solution to some problems lies not in the formulas but in the general shape and behavior, Poincaré developed a new approach to understanding motion without reference to exact formula, which we now call *dynamical systems*. The type of behavior that Poincaré encountered in his solutions is what we now call *chaos*, a term coined by Jim York in 1975 [4]. The tools of topology have been applied to dynamical systems continually since the time of Poincaré. (See Strogatz [5] for an excellent applied introduction.)

The utility of applied topology comes from the ability to prove mathematical properties of very general classes of objects and phenomena. Since Poincaré's pioneering work, this has been exploited in a number of disparate fields.

In 1950-51, John Nash used topology (in particular the Brower Fixed Point Theorem) to demonstrate the existence of Nash Equilibrium in a very broad class of non-cooperative games. (See [6] and [7, Chapter 4.7]). This result revolutionized game theory with applications in economics, politics and biology. Topology enables the proof of existence of Nash Equilibria in mathematical games even when the exact formulation of the player's strategies are not known, and has application to human conflicts where no precisely defined game or strategy exists. Because of the applicability of topology to a very broad class of games, this result is assumed to apply even to real games where the strategies are not mathematical but are derived from the psychology of the players.

In condensed matter physics, states of matter other than solids liquids and gases can occur as the result of collective behavior of interactions between molecules. Symmetries of forces result in behavior more structured then that of a liquid but

less rigid than a crystal or solid. A familiar example is the liquid crystals in a computer display. Pressing on the display creates outward swirls of rotation resulting from the local pressure. The patterns are studied with topology; the twists and singularities, or defects, exist to maintain a consistent global topology even when the exact local positions are not known. This has proven important for understanding states and collective behavior of matter such as superconductors. (See [7-10]).

One of the grand questions in cosmology has been the shape of the universe. Since Aristotle conjectured that the universe is a great sphere, cosmologists have been attempting to infer the structure from observations. Inferring this topological and geometric structure has been one of the main purposes of the NASA WMAP (Wilkenson Microwave Anisotropy Probe) — patterns in the anisotropic cosmic microwave background radiation could be used to determine the topology of the universe. The role of topology is beyond the scope of this paper, but the interested reader is referred to Weeks [11] for an excellent exposition or to Basener [7].

The goal of this paper is to apply some basic theory from the mathematical field of dynamical systems to mathematical models of evolution. The reason we employ the mathematical theory from topology is twofold. First, as with the examples cited in this section, we are then able to prove theorems for broad classes of models; the machinery of topology and dynamical systems allows us to prove theorems about mathematical models of evolution without an exact formulation of the models. Second, in addressing chaotic dynamical systems we are required to use topology (or some equivalent machinery, for example geometry if we assume a suitable state space) as even the definition of chaos requires some level of topology.

The mathematics is basic topology and the theorems we prove are quite simple; they could be basic homework exercises in an upper level undergraduate course in dynamical systems. However, the insights resulting from the application do not seem to be generally known or understood in the study of evolutionary dynamics, either in theory or application. The remainder of this paper consists of a series of expository examples of evolutionary dynamics with application of dynamical systems theory, building up to the main results in Theorems 3 and 4.

## 1.3  *General Questions in Evolutionary Models*

Every living organism has a genotype, its genetic sequence, and phenotype, the phenomenological manifestation of the genotype. The standard model of evolution is that the genotype determines the phenotype, and combined with other factors this determines the fitness level of the organism in its environment, and this fitness level determines the probability of survival of the organism in competition with other organisms. Reproduction and random mutations create organisms with new

genotypes, and the fitness of the new genotypes determines their subsequent survival rates. Consequently, the genotypes of organisms dynamically migrate to those with generally higher fitness levels.

A sort of evolution can be observed experimentally [12] using a series of test tubes each of which contains the four nucleotides ATP, GTP, UTP, and CTP as well as the enzyme $Q\beta$ replicase. An RNA template is added to the first test tube, left for 30 minutes, then a fraction of the solution from the first is added to the second, and the process is repeated. The $Q\beta$ replicase creates almost prefect copies of the RNA molecules in each test tube, and after a series of transfers the RNA will consist of a modified variant that is replicated more quickly than the original. While this biological process is not actual evolution of living organisms, the 'genotype' in this experiment corresponds to the RNA sequence and the 'phenotype' is the resulting replicating performance. The resulting rate of replication by $Q\beta$ replicase determines the 'fitness' of the RNA molecules. The type of RNA sequence in the final equilibrium state is determined by the environment of the solution.

Observe that the dynamic behavior of the $Q\beta$ RNA system is very simple; the RNA 'genotype' goes to an equilibrium which is determined by the parameters of the system. This is the typical behavior of evolutionary dynamical systems based on evolutionary genetics. This raises the question of whether the genetic processes are sufficient to account for macroevolution; quoting John Maynard Smith [12, p.273]: "This book has been concerned with processes that can be studied in contemporary populations over short periods of time. Our picture of evolution on a larger scale — macroevolution — comes from comparative anatomy and embryology, from taxonomy and geographical distribution. The question naturally arises whether the processes of population genetics are sufficient to account for macroevolution. Very different views can be held on this..."

The goal of this paper is to apply basic structure theorems from topological dynamics to answer, at least in part, Maynard's question. We investigate conditions on evolutionary models that guarantee behavior observed in the $Q\beta$ RNA system — evolution progressing for period of time and then ceasing. We show in a very general class of evolutionary models, which includes the standard continuous (differential equations), discrete (iterations of maps), deterministic, stochastic, and spatial evolutionary genetics — based models, this is the only possible behavior.

This is really not surprising. In evolutionary progression that can be studied in contemporary populations over short periods of time, we observe a process that does a finite amount of increase in fitness and then ceases; we do not directly observe evolutionary progress of a species through continually higher, more complex, more fit, genotypes-phenotypes. It is also the behavior observed in standard dynamic models for evolution.

Perhaps the only potentially surprising result is that no evolution takes place within chaotic dynamics, Theorem 4. Chaotic behavior is sometimes offered as an explanation of how complex systems might come from simple governing laws. For example, Novak [1, p.6] writes "Chapter 9 gives an account of evolutionary dynamics on spatial grids. ... We will observe evolutionary kaleidoscopes, dynamic fractals, and spatial chaos. There is all the complexity one could wish for — making it unnecessary for God to play dice." The suggestion seems to be that complex features of nature, implicitly complex organisms resulting from evolution, can result from chaotic dynamics. Theorem 4 shows that, to the contrary, no sustained increase in complexity or fitness is possible within a chaotic dynamical system. Specifically, to within any small amount of observational error, a chaotic system repeats each given state infinitely often. Subsequently, an evolution trajectory that is asymptotic to a chaotic set receives no more increase in fitness than one that is asymptotic to an equilibrium.

Our conclusion stresses again the question of whether the population genetic process of mutation — selection is by itself sufficient to account for macroevolution. As before, this seems not so surprising, as even speciation, the divergence of a single species into different species, seems to require external environmental factors. Again, quoting Smith [12, p.275], "It is widely agreed that the differences between species usually originate during geographical isolation." The isolation can be physical geographic isolation or any factor that inhibits reproduction between two groups of organisms. In terms of evolutionary genetics dynamics models, creating of a new species (let alone new anatomy) seems to require an external dialing of the fitness parameters by a changing external environment. We discuss additional conclusions in Section 4.

## 2. Evolutionary Models and Dynamical Systems

The primary laws governing the interactions between genotype, phenotype, fitness, and the resulting variation over time can be described by mathematical dynamical systems [1]. A mathematical dynamical system is any system that changes over time with governing rules for change that depend on previous states of the system, possibly including external factors that may be deterministic or stochastic.

The two primary classes of mathematical models for evolutionary dynamics are discrete systems (iterated maps) and continuous systems (differential equations). In either case we have a state space, $X$, which is the space of all possible states of the system. In evolutionary dynamics, the state space usually incorporates the number of organisms of each genotype. That is, if we are considering a system with $n$ different possible genotypes then $X$ is $n$-dimensional Euclidean space,

points (or states) $\vec{x} = (x_0, x_1, \ldots, x_n)$ are vectors of length $n$ with $x_i$ being the number (or proportion) of organisms with genotype $i$ and $n$ being the number of genotypes being considered. We use $\vec{x}$ when we want to emphasize the vector nature of this variable or just $x$ otherwise.

For discrete systems we have a function (or map) $f$ such that if $x$ is the state of the system at a given time then $f(x)$ is the state one unit of time later. Thus, in discrete systems time passes in discrete steps — that is in jumps. If our units of time are say years, then state of the system two years later will be $f(f(x)) = f^2(x)$, and $n$ years later it will be $f(f(\ldots f(x) \ldots)) = f^n(x)$.

Continuous dynamical systems typically arise as solutions to differential equations. The state space $X$ still constitutes the space of all possible states. For a state $x$, the state that will occur $t$ time units later will be written as either $\varphi(t, x)$ or $x(t)$. If the system is governed by a differential equation, we begin an equation $x' = f(x)$ and then $\varphi(t, x)$ is the solution with initial condition $x$ (that is, $\dfrac{d\varphi}{dt}(t,x) = f(x)$ and $\varphi(0, x) = x$.)

There is an efficient mathematical framework for simultaneously treating continuous and discrete dynamical systems. A *mathematical dynamical system* is a state space $X$ together with a time space $T$ ($T$ is either the real numbers or integers) and a continuous group action (or semi-group action) $\varphi: T \times X \to X$. For a differential equation, $\varphi(t, x)$ is the solution with initial condition x. For a discrete dynamical systems defined by iteration of a map $f: X \to X$ the group action is $\varphi(n, x) = f^n(x)$. In either case, the system inputs a state (given by $x$) and a time (given by either $t$ or $n$ in $T$) and outputs that state after the allotted time has passed. Treating dynamical systems in such general terms enables us to focus on the topological and geometric phenomena that are true in general instead of what is only true for a given formulation.

The class of dynamical systems described above includes all deterministic dynamical systems (ie differential equations and iterated maps), those systems where the future is determined by the current state and time. Non-deterministic systems will be treated separately, although these often 'average out' to deterministic ones when many organisms are involved as with the quasi-species equation. (See Basener [7] for a treatment of topology in general; see Strogatz [5], Devaney [13] and Robinson [14] for dynamical systems; and see Novak [1] for dynamical systems as models of evolution). Like all mathematical models, the system can be simple or complex, depending on the number of simplifying assumptions.

## 2.1. *Simple Population Models*

Some simple models incorporate only the competition between populations, and thus focus on the competition-selection portion of evolution. Such models include

the Malthusian logistic single species $y' = ay(1 - y)$ and competing species model $x' = r_1 x(1 - bc - cy)$, $y' = r_2 y(1 - fx - gy)$ which can lead to survival of one or both species. Nonlinear systems model more complex interactions, and can result in finite time extinction of one or more of the species.

The theory of mathematical dynamical systems can be applied to general formulations of these types of equations. In 1936 A. N. Kolmogorov gave conditions under which equations of the form

$$x' = xF(x, y)$$
$$y' = yG(x, y)$$

has either a stable limit cycle or equilibrium. This has broad implications for biological systems — see May [15]. (A *limit cycle* is either a periodic orbit or a sequence of equilibria, $p_1, p_2, \ldots, p_n$ with heteroclinic trajectories connecting $p_i$ to $(p_{i+1 \ mod \ n}.)$ More generally, the Poincare-Bendixson Theorem says that any bounded solution to a 2-dimensional system of differential equations is asymptotic to either an equilibrium or a limit cycle [16]. These examples illustrate the power of the dynamical systems approach; geometric or topological theorems restrict the potential behavior of a system even if the governing laws/equations are only partially known.

Discrete systems in any dimension and continuous systems in more than 2-dimensions can exhibit more complex behavior. For example, an orbit in the discrete 2-dimensional system for a simple ecosystem with two organisms

$$P_{n+1} = P_n + aP_n(1 - P_n/R_n)$$
$$R_{n+1} = R_n + cR_n(1 - R_n/M) - hP_n$$

is shown in Figure 1 for three sets of parameters. This system was used in Basener *et al.* [17] to model the rise and fall of the civilization on Rapa Nui (Easter Island). The mathematics of chaotic and recurrent behavior is discussed in Section 3.

## 2.2. *Simple Mutation-Selection Models*

Simple models may also focus solely on the genetic aspect of evolution. The METHINKSITISAWEASEL system, created by Dawkins in 1989, is commonly used to illustrate evolution by mutation and natural selection as in Smith [12]. The state space $X$ is the space of all strings of 19 letters. Topologically, $X$ is a discrete space with $26^{19} \approx 7.66 \times 10^{26}$ points. Iteration of the system involves making ten copies of a parent state $x$ in which each letter of the copy has a 0.99 probability of being the same as the corresponding letter in the parent. The fitness of a state is equal to the hamming distance from the sequence METHINKSITISAWEASEL;
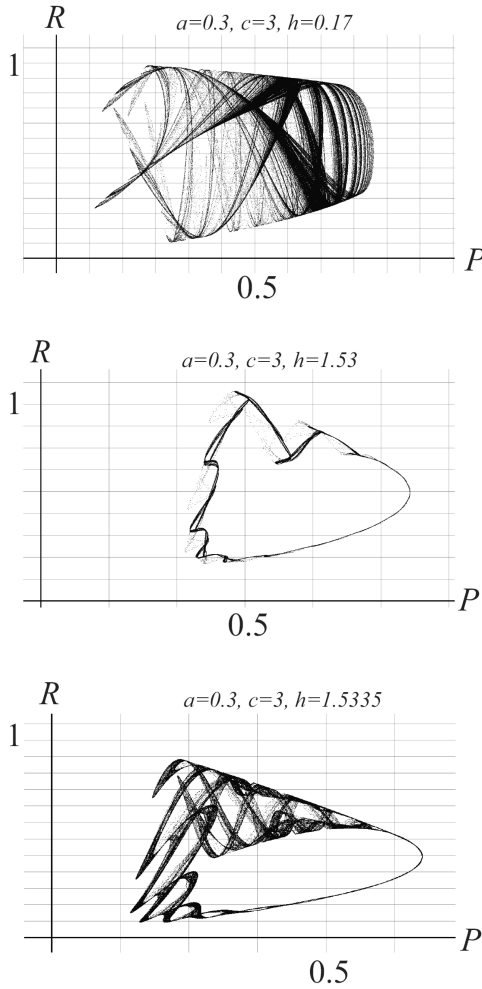
**Fig. 1.**   Three chaotic attractors for discrete dynamical system modeling a simple two species ecosystem.

that is, the number of letters in the correct location with this goal sequence. The child with the highest fitness level is chosen as the new parent in the next generation. Although the system is not deterministic, for any initial condition the probability that the resulting sequence of iterations will reach the goal sequence is equal to 1.

   This system is not an accurate model of evolution (see [12]), but it is useful to illustrate the simple description of evolution with mutation and natural selection. It also has typical evolutionary behavior; the 'genotype' undergoes modification over generations and then stabilizes at an equilibrium. This is the same behavior

as with the RNA molecules in the Q$\beta$ replicase. It is worth considering more general systems of this variety. In Theorem 1 we show that if the state space is finite with a simple model of evolution, then evolution will run its process and then cease. Once maximal fitness is achieved, all subsequent mutations are irrelevant for fitness.

To describe a general situation of an evolutionary process, we will use *X* to denote a state space which could in general be any topological space. We assume that there are some laws governing the process of evolution on *X*, although they may in general be continuous differential equations, a discrete map, stochastic, or nondeterministic. If the system is discrete, the process of evolution will result in a sequence of points

$$x_0 = x, \ x_1 = f(x), \ x_2 = f(f(x)) = f^2(x), \ \ldots, \ x_n = f^n(x)$$

according to the governing laws. If it is continuous, the process of evolution will result in a path $x(t)$ in X. In the first case, we call $x_0, x_1, \ldots$ a (discrete) evolutionary trajectory and in the second we call $x(t)$ a (continuous) evolutionary trajectory. By a fitness function on *X* we mean a continuous function $F: X \rightarrow R$ (the domain is X and the range is R, the real numbers) that is nondecreasing on evolutionary trajectories. (Either $F(x_i) \leq F(x_j)$ for $i < j$ in the first case, or $F(x(s)) \leq F(x(t))$ for $s < t$ in the second.). Our first theorem, Theorem 1, shows that the behavior of the METHINKSITISAWEASEL system is the only possible behavior for a system with only finitely many states.

**THEOREM 1.** *Let X be any finite state space with a fitness function F: X → R. Suppose $x_0, x_1, \ldots$ is a discrete evolutionary trajectory. Then there exists an N such that $F(x_n) = F(x_N)$ for all n > N.*

The proof is very simple; the set $F(\{x_0, x_1, \ldots\})$ is finite, being a subset of the finite space *X*, and therefore attains a maximum at some $x_N$. Since this is the maximum on the sequence $F(x_n) \leq F(x_N)$ for all $(x_n)$ and *F* is nondecreasing $F(x_N) \leq F(x_n)$ for $(N < n)$, we have $F(x_n) = F(x_N)$ for all $n > N$.

It is clear from Theorem 1 that this type of a system — either a deterministic or nondeterministic progression of increasing fitness of a genotype in a sequence space — by itself does not result in an ongoing increase in fitness of organisms.

Related models can be constructed incorporating multiple organisms as well as spatial distributions. As long as the state space is compact (such as any a closed and bounded subset of Euclidean space, as is the case for any system with a finite area in which the organisms live), a similar theorem holds for systems with a fitness function that does not decrease over time. To work with continuous and

discrete dynamical systems, with stochastic and deterministic ones, and with cases where the system is chaotic, we make some general terminology. If $X$ is a state space, F is a fitness function on $X$ and $x_0, x_1, \ldots$ is a sequence of points in $X$ resulting from a model of evolution on $X$ for which $F$ is nondecreasing, we will refer to $x_0, x_1, \ldots$ as a *discrete evolutionary trajectory* in $X$. Similarly, a path $x(t)$ in $X$ on which $F$ is nondecreasing will be called an *continuous evolutionary trajectory* in $X$.

**THEOREM 2.** *Let X be any compact state space with a fitness function $F: X \rightarrow R$. If $x_0, x_1, \ldots$ is a discrete evolutionary trajectory, then there exists an $F_*$ such that $F(x_n) \rightarrow F_*$ as $n \rightarrow \infty$. If $x(t)$ is a continuous evolutionary trajectory, then there exists an F\* such that $F(x(t)) \rightarrow F_*$ as $t \rightarrow \infty$.*

*Proof.* Since $X$ is compact, $F$ is bounded on $X$. In the first case, $F(\{x_0, x_1, \ldots\})$ is a bounded subset of $R$, and thus has a supremum $F^*$. Since $F(x_n)$ is nondecreasing, it goes monotonically to $F^*$. In the second case, $F(\{x(t) \,|\, t \,\varepsilon\, R\})$ is a bounded subset of $R$, and thus has a supremum $F^*$. As before, $F(x(t))$ is nondecreasing, and so it goes monotonically to $F^*$.

The sequence $x_0, x_1, \ldots$ in Theorem 2 can be the solution to either a stochastic or deterministic discrete system on $X$, and the path $x(t)$ can be the solution to either a stochastic or deterministic continuous system on $X$. Observe that this theorem states that evolution will run its course until some point after which increase in fitness is inconsequential. (Specifically, for any small positive number $\varepsilon$ there is a time after which the increase in fitness is less than $\varepsilon$.)

It may seem counterintuitive that Theorem 2 would apply to systems with chaos; for chaos has often been suggested as a mechanism for producing very complex structures. We address chaotic dynamics in Section 3, where it is proven that fitness never increases on chaotic sets.

## 2.3. *Population Models with Mutation-Selection*

To construct a more accurate model of evolution, we need to consider more aspects of genetics, mutations, populations and ecology. In this section we consider quasispecies, which is are ensemble of similar genomic sequences generated by a mutation-selection process, a notion developed by Manfred Eigen and Paul Schuster [18].

As before, we take our genotype information in a sequence space, say $X = \{A,T,C,G\}^N$ which is the set of all sequences in the letters A, T, C and G of length $N$. There are $4^N$ different organisms that can have their genotype in this

space. Imagine a large population of such organisms. We denote the fraction of the total population consisting of genotype $i$ by $x_i$, for $i = 1, \ldots, N$. So each $x_i$ is in $[0, 1]$ and $\Sigma_i x_i = 1$. Our state space $X$ is the set of all $\vec{x} = (x_0, x_1, \ldots, x_N)$ satisfying $\Sigma_i x_i = 1$, which is the unit simplex in $R^{N+1}$. Observe that the state space $X$ is compact.

Let $f_i > 0$ be the fitness of species $i$. For now, assume that the fitness corresponds to the growth rate. (It is common practice to equate fitness with growth rate. This seems sufficient in the short-term. However, organisms with a high fitness, resulting in a high reproduction rate, can overpopulate their ecosystem, destroying their food source and subsequently themselves as a population. This behavior is the main topic in the study of the collapse of ancient human civilizations in Basener and Ross [19] and Basener *et al.* [20].) The state space $X$ together with the fitness function $\vec{f} = (f_0, f_1, \ldots, f_N)$ is called a *fitness landscape*.

Let $Q$ be the matrix such that $q_{ij}$ is the probability of mutation from genotype $i$ to genotype $j$. (The rows of the square matrix sum to 1.) The *quasispecies equation* is then the differential equation

$$\vec{x}' = \sum_{j=0}^{N} x_j f_j q_{ij} - \phi x_i$$

where $\phi = \Sigma_i f_i x_i$ is the average fitness. The first term provides for reproduction and mutation, while the second term maintains $\Sigma_i x_i = 1$. If we let $\vec{W} = \vec{f}Q$, then the equation becomes

$$\vec{x} = W\vec{x} - \phi\vec{x}$$

which has a (generically stable) equilibrium at the solution to the eigenvector equation $W\vec{x} = \phi\vec{x}$.

For quasispecies, the fitness function determines the fitness of each genomic sequence, not the fitness of the quasispecies. Because individuals with more fit genomic sequences continually produce mutations with lower fitness, the quasispecies equation does not maximize an overall fitness. For modest mutation rates, quasispecies will appear as a peak centered on the genomic sequence with the greatest fitness. For this reason, we cannot apply Theorem 2 directly using the given fitness function. However, generically the conclusion still holds — evolution runs its course to the equilibrium.

Stochastic systems — systems in which mutations occur from each genotype to other genotypes at prescribed mutations rates and with some approximately deterministic rules governing population change over time for various genotypes — can all be modeled as a dynamical system on the same state space as the quasispecies equation. The following theorem says that even though fitness is not strictly increasing in these systems, regardless of the rules governing the population

change the net effect of evolution over time is not much different than in previous theorems. Instead of going to an equilibrium, the system has a point which it will get close to, then may move away and will come back to again even closer, and then repeat the process of closer and closer approaches, infinitely often. To an observer, the system will continue to repeat (or return to) some state infinitely often.

**THEOREM 3.** *Let X be any compact state space. Then for any trajectory of a (discrete or continuous) dynamical system on X, there is a state $x_*$ such that the orbit comes repeatedly close to $x_*$ as time goes to $\infty$, as follows. If $x_0$, $x_1$, … is a discrete evolutionary trajectory, then there exists a state $x^* \varepsilon X$ and a subsequence $x_{i(1)}$, $x_{i(2)}$, … such that $x_{i(k)} \to x_*$ as $k \to \infty$ . If $\varphi(t, x)$ is a continuous evolutionary trajectory, then there exists an $x_*$ and a sequence of times $t_1$, $t_2$, … such that $\varphi(t_k, x) \to x_*$ as $k \to \infty$.*

*Proof.* If $x_0$, $x_1$, … is a sequence of points, since $X$ is compact the collection of sets $\overline{\{x_i\}_{i=1}^\infty} \supseteq \overline{\{x_i\}_{i=2}^\infty} \supseteq \overline{\{x_i\}_{i=3}^\infty}$ … is a nested sequence of compact sets. Thus the intersection $\bigcap_{n=1}^\infty \overline{\{x_i\}_{i=n}^\infty}$ is nonempty. Then let $x_*$ be any point in $\bigcap_{n=1}^\infty \overline{\{x_i\}_{i=n}^\infty}$ and $x_*$ is the desired point.

If $\varphi(t, x)$ is a path in $X$, since $X$ is compact the collection of sets $\overline{\{\varphi(t,x)\}_{t>\alpha}}$ is a nested sequence of compact sets. Thus the intersection $\bigcap_{\alpha \in R} \overline{\{\varphi(t,x)\}_{t>\alpha}}$ is nonempty. Then let $x_*$ be any point in $\bigcap_{\alpha \in R} \overline{\{\varphi(t,x)\}_{t>\alpha}}$ and $x_*$ is the desired point.

## 3. Chaos and Recurrent Behavior

A dynamical system $\varphi:T \times X \to X$ is said to be *chaotic* on an infinite subset $A \subseteq X$ if

(i) Periodic orbits are dense in $A$.

(ii) There exists one orbit in $A$ which is dense.

(iii) If $X$ is a metric space then the system has *sensitive dependence of initial conditions*: There exists an $\varepsilon > 0$ such that for any point $x \varepsilon A$ and any neighborhood $N$ of $x$, there exists a $y \varepsilon N$ and a $t > 0$ such that $d(\varphi(t, x), \varphi(t, x)) > \varepsilon$.

(See Basener [7] for mathematical terms, Robinson [14] for details on the dynamical systems in this section and Strogatz [5] for applications). Note that chaotic subsets are necessarily compact and in variant. It has been shown that the first two conditions are sufficient to imply the third (See Banks et al. [21] and Basener [7]),

although in practice sensitive dependence is often taken alone as a definition of chaos because it is easy to compute experimentally.

For real-life systems, the periodic orbits in chaotic sets are less observable that the tendency to wander around the set; the small perturbations that occur in any real system will prevent it from actually being periodic. However, the behavior both in theory and practice has periodic-like aspects. Specifically, for any point $x \varepsilon A$, there is a sequence of times $t_0, t_1, \ldots$ with $t_i \rightarrow \infty$ such that $\varphi(t_i, x) \rightarrow x$ as $i \rightarrow \infty$. To an observer, the system appears to repeatedly return to its initial state forever. Hence, whether there is a fitness function that is nondecreasing on trajectories as with mutation-selection models, or if there is a fitness function that is defined on species but is not optimized in general as with the quasispecies model, on a chaotic set the system will continue to repeat a given state, and thus a given level of fitness, repeatedly.

More can be said if we assume that the fitness is nondecreasing with time; in this case, the fitness level is constant on a chaotic set.

**THEOREM 4.** *Let $\varphi: T \times X \rightarrow X$ be any dynamical system with a fitness function $F: X \rightarrow R$ such that $F(\varphi(s, x)) < F(\varphi(t, x))$ for any $s < t$. If $A$ is a subset of $X$ upon which $\varphi$ is chaotic then $F$ is constant on $A$. That is, there is no increase in fitness for orbits in $A$.*

*Proof.* Since $\varphi$ is chaotic on $A$, there is a sequence of times $t_0, t_1, \ldots$ with $t_i \rightarrow \infty$ such that $\varphi(t_i, x) \rightarrow x$. Then, since $F$ is continuous, $F(\varphi(t_i, x)) \rightarrow F(x)$. Since $F$ is nondecreasing on orbits, $F$ is constant.

## 4. Conclusions

Our first conclusion is that chaos and nonlinear dynamical systems contribute nothing to the ongoing increase in complexity or evolutionary fitness of biological systems. Statements such as that quoted earlier from Novak [1, p.9], suggesting that complexity of life results from nonlinear chaotic systems, are contrary to mathematics.

Second, the evolutionary process driven by mutation-selection, in both mathematical models and directly observed behavior, is that of a system going to an equilibrium and staying there. It seems the discussion of evolution in biology is that of an ongoing process but the study of mathematical models of evolution is that of equilibrium dynamics. There is nothing inherent in the fitness-driven mathematical system that leads to ongoing progress; to the contrary, mathematical systems, both those which are specific models such as the quasispecies equation

and very general classes of models, have limits on the amount of increase in fitness that occurs. This is really well-known, as speciation is believed to occur only when driven by geographical isolation [12, p.275].

We have determined certain means of evolutionary progress to be impossible, and some of these means, for example the idea that chaos can lead to extreme evolutionary progress, have in the past been used as hypothetical possibilities for evolutionary dynamics. This leads us to ask what is left?

The space of all possible genotypes, while a compact space (assuming we disallow genotypes of unbounded length), is still enormous. The potential fitness, while bounded, is still extremely high. We can imagine this space as an enormous dimensional space, and imagine every viable species as a point in this space. We can image a line segment connecting every pair of viable genotypes if there is a reasonable probability that mutation from one to the other, as suggested in Figure 2. The result is an enormous network amenable to analysis by mathematical
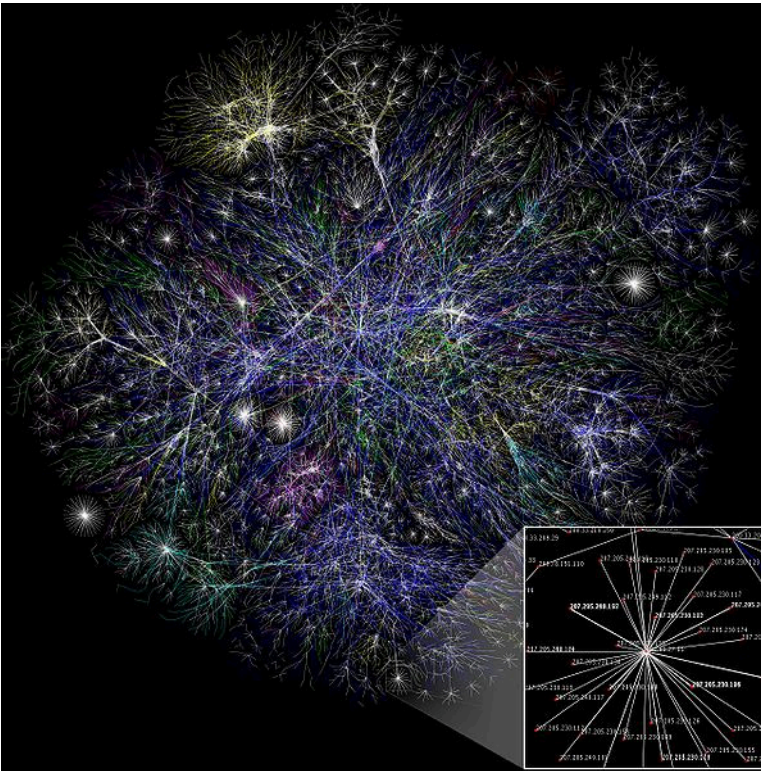


**Fig. 2.**   A large network with sparsely connected groups. The question we pose is whether the genotype network is connected like this, or if there are many disconnected islands. This image shows a partial map of the internet based on the January 15, 2005 data found on opte.org. Each line is drawn between two nodes, representing two IP addresses. The length of each line are indicates the delay between its endpoint nodes. See [22].

network theory. The quasispecies equation provides the local equilibrium dynamics in this space, and there is no mathematical reason to expect generally other than the equilibrium state naturally from the system; stability is what we observe experimentally and from well-supported equations.

In the genotype network described above, each quasispecies lives within a group of highly interconnected points, called a community or clique in social network theory. If environmental conditions change, the quasispecies shifts within this group. In most cases, if the environment shifts to far (or at least too quickly) then the quasispecies is pushed to the edge of its local group, to points with low fitness, and then goes extinct. This decrease in fitness near the boundary of a local group can be observed in selective breeding; if too many desired properties in an animal or vegetation are attempted to be optimized through selective breeding, the simultaneous optimization becomes difficult and the species becomes less fit as a whole.

A question for evolution is to determine the structure of this genotype network. Are there bridges between groups of interconnected genotypes? How can we tell? What is the density of the network? How populated must a group be in order to support a quasispecies? Can the dimension of a local group be inferred, for example as the number of properties of a species that can be simultaneously optimized through selective breeding?

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