Flicker Noise in a Model of Coevolving Biological Populations

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We present long Monte Carlo simulations of a simple model of biological macroevolution in which births, deaths, and mutational changes in the genome take place at the level of individual organisms. The model displays punctuated equilibria and flicker noise with a $1/f$-like power spectrum, consistent with some current theories of evolutionary dynamics.

I. INTRODUCTION

The long-time dynamics of biological evolution have recently attracted considerable interest among statistical physicists, who find in this field new and challenging interacting nonequilibrium systems. An example is the Bak-Sneppen model, in which interacting species are the basic units, and less “fit” species change by “mutations” that trigger avalanches that may lead to a self-organized critical state. However, in reality both mutations and natural selection act on individual organisms, and it is desirable to develop and study models in which this is the case. One such model was recently introduced by Hall, Christensen, and coworkers. To enable very long Monte Carlo (MC) simulations of the evolutionary behavior, we have developed a simplified version of this model, for which we here present preliminary results.

II. MODEL AND NUMERICAL RESULTS

The model consists of a population of individuals with a haploid genome of $L$ binary genes, so that the total number of potential genomes is $2^L$. The short genomes we have been able to study numerically ($L = 13$) should be seen as coarse-grained representations of the full genome. We thus consider each different bit string as a separate “species” in the rather loose sense that this term is used about haploid organisms. In our simplified model the population evolves asexually in discrete, nonoverlapping generations, and the population of species $I$ in generation $t$ is $n_I(t)$. The total population is $N_{\text{tot}}(t) = \sum n_I(t)$. In each generation, the probability that an individual of species $I$ has $F$ offspring before it dies is $P_I\left\{\{n_J(t)\}\right\}$, while it dies without offspring with probability $1 - P_I$. The reproduction probability $P_I$ is given by

$$P_I\left\{\{n_J(t)\}\right\} = \frac{1}{1 + \exp\left[-\sum J M_{IJ} n_J(t)/N_{\text{tot}}(t) + N_{\text{tot}}(t)/N_0\right]}.$$  \hspace{1cm} (1)

The Verhulst factor $N_0$, which prevents $N_{\text{tot}}$ from diverging, represents an environmental “carrying capacity” due to limited shared resources. The time-independent interaction matrix $M$ expresses pair interactions between different species such that the element $M_{IJ}$ gives the effect of the population density of species $J$ on species $I$. Elements $M_{IJ}$ and $M_{JI}$ both positive represent symbiosis or mutualism, $M_{IJ}$ and $M_{JI}$ both negative represent competition, while $M_{IJ}$ and $M_{JI}$ of opposite signs represent predator-prey relationships. To concentrate on the effects of interspecies interactions, we follow in taking $M_{II} = 0$. As in, the offdiagonal elements of $M_{IJ}$ are randomly and uniformly distributed on $[-1, 1]$. In each generation, the genomes of the individual offspring organisms undergo mutation with probability $\mu/L$ per gene and individual.

MC simulations were performed with the following parameters: mutation rate $\mu = 10^{-3}$ per individual, carrying capacity $N_0 = 2000$, fecundity $F = 4$, and genome length $L = 13$. For a system with $M = 0$ or only a single species and $\mu = 0$, the steady-state total population is found by linear stability analysis to be $N_0 \ln(F - 1) \approx 2200$. In

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this regime both the number of populated species and the total population $N_{tot}(t)$ are smaller than the number of possible species, $2^L = 8192$. This appears biologically reasonable in view of the enormous number of different possible genomes in nature.

An important quantity is the diversity of the population, which is defined as the number of species with significant populations. Operationally we define it as $D(t) = \exp[S\left(\{n_I(t)\}\right)]$, where $S$ is the information-theoretical entropy (known in ecology as the Shannon-Weaver index) 

$$S\left(\{n_I(t)\}\right) = -\sum_{\{I|n_I(t)>0\}} \frac{n_I(t)}{N_{tot}(t)} \ln\frac{n_I(t)}{N_{tot}(t)}.$$

Results for a run of $10^6$ generations are shown in Fig. 1. In Fig. 1(a) are shown time series of $D(t)$ and $N_{tot}(t)$. We see relatively quiet periods (quasi-steady states, QSS) punctuated by periods of high activity. During the active periods the diversity fluctuates wildly, while the total population falls below its typical QSS value. A corresponding picture of the species index (the decimal representation of the binary genome) is shown in Fig. 1(b), with grayscale indicating $n_I(t)$. Comparison of the two parts of Fig. 1 show that the QSS correspond to periods during which the population is dominated by a relatively small number of species, while the active periods correspond to transitions during which the system is “searching for” a new QSS.

Closer inspection of Fig. 1 suggests that there are shorter QSS within some of the periods of high activity. This led us to consider the power-spectral densities (PSD) of the diversity and total population, measured in very long simulations of $2^{25} = 33,554,432$ generations. The PSD of the diversity is shown in Fig. 2 and indicates that the model exhibits flicker noise with a spectrum near $1/f$ over at least four to five decades in frequency.

III. RELEVANCE TO EVOLUTIONARY BIOLOGY

It has been much discussed in evolutionary biology whether species evolve gradually or in a succession of QSS, punctuated by periods of rapid change. The latter mode has been termed “punctuated equilibria” by Gould and Eldredge. There is also some indication that flicker noise is found in the fossil record of extinctions, but due to the sparseness of the fossil evidence this is a contested issue. The model discussed here can at best be applied to the evolution of asexual, haploid organisms such as bacteria, and one should also note that no specific, biologically relevant information has been included in the interaction matrix. Nevertheless, we find it encouraging that such a simple model of macroevolution with individual-based births, deaths, and mutations can produce punctuated equilibria and flicker noise reminiscent of current theories of biological macroevolution.

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FIG. 1: Results of a simulation of $10^6$ generations with the parameters given in the text. (a) Time series showing the diversity, $D(t)$ (black), and the normalized total population, $N_{tot}(t)/[N_0 \ln(F-1)]$ (red). (b) Species index $I$ vs time. The symbols indicate $n_I > 1000$ (black), $n_I \in [101, 1000]$ (blue), $n_I \in [11, 100]$ (red), $n_I \in [2, 10]$ (green), and $n_I = 1$ (yellow).

FIG. 2: PSD of the diversity, based on nine independent simulations of $2^{25}$ generations each. The model parameters are those given in the text and used in Fig. 1. The $1/f$ like spectrum is indicative of very long-time correlations and a wide distribution of QSS lifetimes.