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Competition with evolution in ecology and finance

J.C. Sprott

Department of Physics, University of Wisconsin-Madison, Madison, WI 53706, USA

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Abstract

A variant of the multi-species Lotka–Volterra model is studied in which species competing for fixed finite resources are replaced by new randomly chosen species whenever they become extinct. The model exhibits chaos, punctuated equilibria, leptokurtosis, and self-organized criticality. It has application to ecology, finance, and possibly other diverse systems.
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Variants of the Lotka–Volterra model [1,2] have been widely used as the starting point for understanding nonlinear dynamical systems in which two or more species or agents interact through competition for resources, especially in ecology [3]. Such models often predict that only a few of the fittest species survive (the principle of competitive exclusion) [4]. This Letter describes a model in which species that become extinct are replaced by new randomly chosen species in an attempt to evolve an ecology with high diversity and fitness. Surprisingly, the diversity remains low but exhibits temporal fluctuations that suggest chaos (sensitive dependence on initial conditions), punctuated equilibria (sporadic volatility), leptokurtosis (fat tails), and self-organized criticality (scale invariance), which are characteristics of many complex nonlinear dynamical systems such as those in ecology and finance.

Consider an ecology in which N species with population x_i for $i = 1$ to N compete for a finite set of resources according to

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \sum_{j=1}^{N} a_{ij} x_j \right), \tag{1}$$

where r_i is the growth rate of the ith species, and a_{ij} is the extent to which species j competes for the resources of species i. Without loss of generality, we can set the diagonal terms (self-interactions) a_{ii} to 1, which amounts to measuring the population of each species in units of its carrying capacity in the absence of the other species. Also, one of the growth rates r_1 can be set to 1, which amounts to measuring time in units of the inverse growth rate of the species $i = 1$. Eq. (1) is a form of the Lotka–Volterra model, which is a system in which $\dot{x}_i/x_i$ is a linear function of the x_i's, and it is quite general because it can be viewed

E-mail address: sprott@physics.wisc.edu (J.C. Sprott).

as the first approximation in a Taylor series expansion for a wide class of models [5].

All the biology is contained in the vector of growth rates r_i and the matrix of interactions a_{ij}, which are chosen randomly from an exponential distribution $P(a) = \exp(-a)$ with mean 1, so that all the growths are positive and there is only competition rather than mutualism (symbiosis) and predation, which are less common in real ecosystems [6]. Actually, predation is common, but if the predators have many species upon which to prey, the prey behave somewhat like a fixed resource, and the effect on the prey is equivalent to competition. In fact, the results are not substantially changed if some of the r_i's and a_{ij}'s are moderately negative, although unbounded solutions are then possible in what May [7] calls 'an orgy of mutual benefaction'. An exponential distribution of random a values can be produced using $a = -\ln \eta$ where η is uniform random in the interval $(0, 1)$. The parameters are held constant throughout the calculation, but the calculation is repeated for many choices of parameters to ensure that the results are typical.

The solutions of Eq. (1) for arbitrary initial conditions typically exhibit a chaotic transient, which can last for a very long time for large N, after which the system approaches a static equilibrium with a small number (typically less than ten) of species surviving [8]. This result is not surprising given that the system has 2^N equilibria (each of the N species can be either present or absent), only one of which corresponds to coexistence of all species. Oscillatory solutions (limit cycles) are possible [9] for $N > 2$, and chaotic solutions (strange attractors) can occur for $N > 3$, but they require careful tuning of the parameters [10]. Chaos can also occur for $N = 3$ if some of the elements of a_{ij} are negative [11] or if the a_{ij} depend on the densities of the species [12]. A typical example of a chaotic transient for $N = 48$ and $x_i(0) = 0.1$ for all i is shown in Fig. 1. In this case all but five species become extinct after about $t = 200$, and the system approaches a stable equilibrium. Such solutions are the most common.

To produce sustained, aperiodic fluctuations for arbitrary parameters, any species $i = m$ whose population falls below 10^{-3} and is decreasing is replaced by a new species with the same population but with r_m, a_{mj}, and a_{jm} for $j = 1$ to N chosen from a ran-
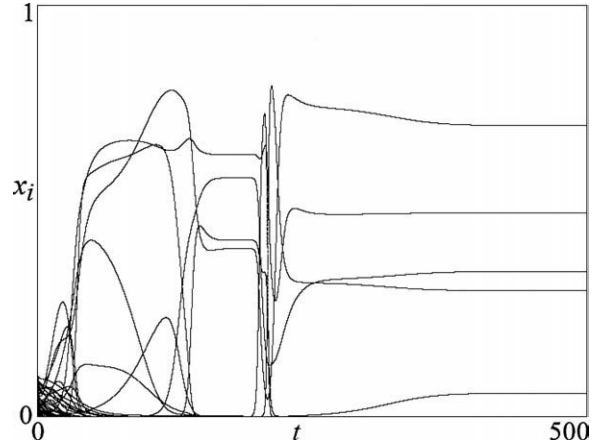

Fig. 1. Typical temporal variation of 48 species without evolution.

dom exponential distribution. This procedure crudely models evolution (or speciation) in an ecology with a fixed maximum number of species. When the number of species is small, a stable steady state is eventually reached with all species present, but for N large, the required time is enormously long. When new species come into existence faster than the chaotic transient decays, the chaos persists. Surprisingly, there is no evidence that the solution evolves toward a state of increased fitness, but rather various species dominate for a time and then become extinct and are replaced by others. The behavior seen in first half of Fig. 1 then persists indefinitely, and offers a sobering message for humanity.

To illustrate the dynamics, define the total biomass M as

$$M = \frac{1}{N} \sum_{i=1}^{N} x_i, \tag{2}$$

which is normalized to a maximum value of 1.0, and the biodiversity D as

$$D = 1 - \frac{1}{2(N-1)} \sum_{i=1}^{N} \left| \frac{x_i}{M} - 1 \right|, \tag{3}$$

which is zero if there is a single existing species and 1.0 if all species are present in equal amounts. A typical result for 48 species is shown in Fig. 2.

To demonstrate that the model is chaotic [13], Fig. 3 shows the same biomass data as in Fig. 2 superimposed on a similar plot in which one of
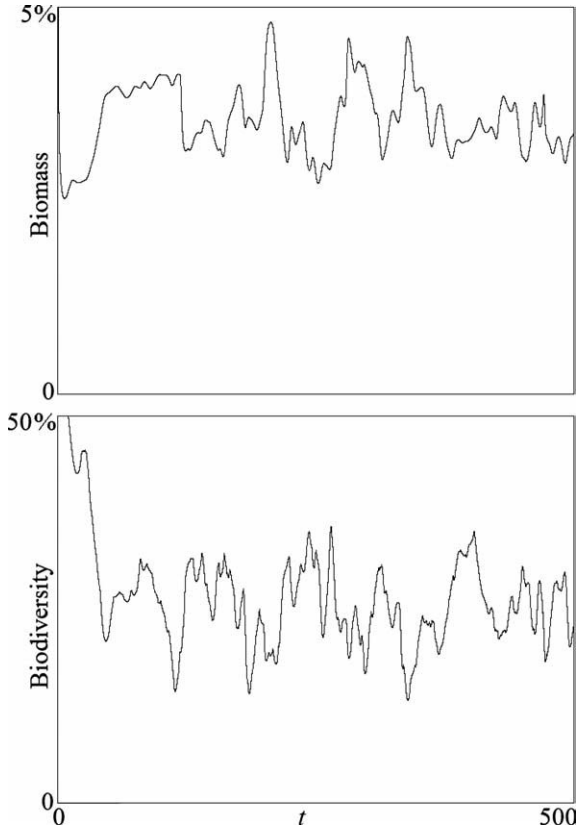
Fig. 2. Fluctuations in average biomass and biodiversity for 48 species with evolution.

Fig. 3. Fluctuations in biomass for two initial conditions that differ by 10^{-9}.

the 48 species has its initial condition different by one part in 10^9. The two plots track each other closely until about $t = 200$, whereupon they begin to exhibit very different trajectories, showing an alternate realization of the model for the same parameters. A plot of biodiversity (not shown) is similar. Although the species are chosen from a random exponential distribution, the same seed is used for the random number generator for the two cases so that the same species are brought into each population in the same order, although at different times.

Analysis of a thousand-times-longer record shows that the largest Lyapunov exponent [14] (base-e) is approximately 0.0656, which is consistent with the perturbation growing by a factor of 10^9 in a time of $t = 316$. After a sufficiently long time, the model has essentially sampled all possible ecologies drawn from the prescribed distribution, since the parameters
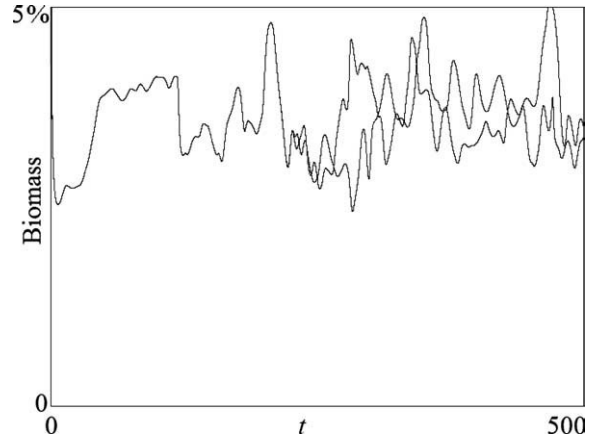
are continually changing. Although ecologists have yet to document an unequivocal example of chaos in nature [15], laboratory experiments with flour beetles do indicate chaos [16,17]. Ecological data certainly fluctuate erratically, and a prediction time of $1/0.065 \cong 15$ growth times as suggested by the model is plausible and interesting.

One feature of the model is periods of quiescence separated by intervals of rapid change, reminiscent of the 'punctuated equilibrium' postulated by Gould and Eldridge [18] based on paleobiological records. The reason may be that in passing through different ecologies some combinations of parameters produce larger fluctuations than others. Similar behavior is observed in financial data such as market averages and exchange rates, where the phenomenon is called 'volatility'. Indeed, the stock market can be viewed as group of traders competing for resources, which are the values of the companies being traded, or as a collection of stocks competing for the wealth of the investors. Traders drop in and out of the market and occasionally change strategies, and stocks disappear from market indices and are replaced by new stocks.

To compare the model with stock movements, define a measurement function

$$y(t) = \frac{1}{M(t)} \frac{dM(t)}{dt}, \tag{4}$$

which is the fractional rate of change of the biomass, corresponding to a market average, and calculate the
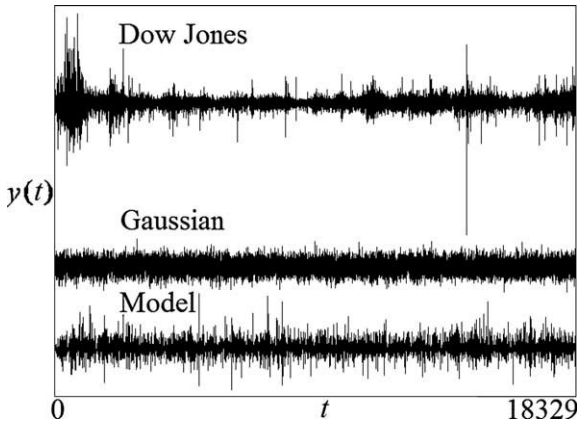
Fig. 4. Fluctuations of the stock market (1930–2002), a Gaussian distribution, and the model, all normalized to the same standard deviation.

Fig. 5. Probability distribution function of volatility showing a power-law scaling.

kurtosis

$$K = \frac{1}{T} \int_0^T \left[(y(t) - \bar{y})/\sigma \right]^4 dt - 3, \qquad (5)$$

which is zero for a normal distribution, where $\bar{y}$ is the time average of $y(t)$ and σ is its standard deviation. The quantity $y(t)$ is plotted in Fig. 4 for the daily Dow Jones Industrials average for the period 1930–2002, for a Gaussian random distribution, and for the model biomass with $N = 48$, all scaled to the same standard deviation. The model with $N = 48$ gives $K = 4.00$ for biomass and $K = 3.24$ for biodiversity, which is strongly leptokurtic (fat-tailed), much like the Dow Jones Industrials average, which has $K = 21.8$, mostly due to the single event on October 17, 1987. Over the more typical period 1944–1986, the kurtosis is $K = 3.73$. Other financial time series have similarly large kurtosis [19,20]. For example, the daily Standards and Poor index of common stocks over the period 1975–1987 (up to the October crash) has $K = 2.13$. The daily Pound/\$ exchange rate for 1971–2003 has $K = 2.35$, the Yen/\$ exchange rate for 1973–2003 has $K = 4.77$, and the DM/\$ exchange rate for 1973–1987 has $K = 6.51$.

A signature of self-organized criticality is a power-law variation of various quantities, implying scale invariance [21]. Consider the volatility defined as $v(t) = y^2(t)$, which is large when the biomass is rapidly changing, and small otherwise. A plot of the probability distribution function $dP(v)/dv$ versus v in Fig. 5
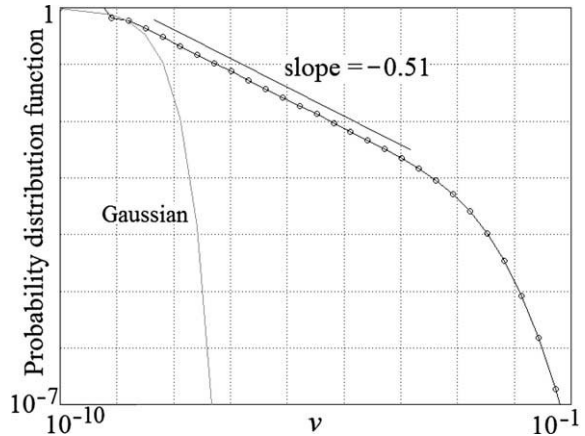
shows a range of five decades of v over which the slope on a log–log scale is nearly constant at a value of -0.51, although changes greater than about 1% per unit time ($v > 10^{-4}$) are relatively underrepresented. A Gaussian probability distribution function $\exp(-y^2)$ is plotted on the same scale to illustrate the extent to which the tail of the distribution is enhanced. A similar plot (not shown) of the probability distribution function for the volatility of the biodiversity has a slope of -0.50 over the same five decades. Other quantities also show a power law, although typically over a more narrow range. For example, the power spectral density of $y(t)$ has a slope of about -2.0 over a range of about two decades of frequency from $0.1 < f < 10$. Such power-law fluctuations have been observed in stock market data and models [22–26].

In summary, a variant of the Lotka–Volterra equations has been proposed that exhibits chaos (sensitive dependence on initial conditions), punctuated equilibria (sporadic volatility), leptokurtosis (fat tails), and self-organized criticality (scale invariance). The fact that the model is chaotic means that in principle it can be stabilized by relatively small perturbations [27,28]. While it is intriguing that a purely deterministic model can produce erratic fluctuations, natural systems almost certainly have random exogenous shocks that are not adequately described by such a model. Obvious extensions of the model include stochastic or periodic forcing and relaxation of the requirement that all parameters be positive. Although originally developed to simulate ecology, the model may also have applica-

tion to financial markets and other systems in which agents compete for finite resources and are occasionally replaced by new agents when they compete unsuccessfully.

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