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Coexistence and chaos in complex ecologies

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Abstract

Many complex dynamical systems in ecology, economics, neurology, and elsewhere, in which agents compete for limited resources, exhibit apparently chaotic fluctuations. This Letter proposes a purely deterministic mechanism for evolving robustly but weakly chaotic systems that exhibit adaptation, self-organization, sporadic volatility, and punctuated equilibria.

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An ongoing debate [1,2] among ecologists centers on the fact that while most theoretical models predict instability and extinction of most species [3–5], observations in nature suggest that complex and diverse ecologies are relatively stable [6–8]. While laboratory experiments with flour beetles suggest chaos [9,10], there is scant evidence of chaos in nature perhaps because of the dynamical complexity and measurement limitations [11,12]. Our work suggests that erratic fluctuations, which are common and are usually attributed to random external influences, may be evidence of chaos.

Many different mathematical models [13] have been used to study the dynamics of interacting species or agents in a variety of different contexts and systems. The parameters in such models can be determined in several ways, including using values taken from real ecologies [14], using random values [15], or building up the values by choosing species randomly from some large pool containing species of various types [16]. In addition, the parameters can be changed in time to model evolution, mutation, extinction, etc. [17–19]. The majority of these models use random or stochastic terms, which can give rise to aperiodic or chaotic type behavior. In contrast, most

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non-evolutionary models produce chaos over a relatively narrow range of parameters, bounded on one side by stable behaviour and on the other by extinction.

Here we show that a simple model with realistic and purely deterministic adaptation can produce highly complex systems in which most species coexist with weakly chaotic fluctuations independent of the initial conditions. The proposed mechanism offers a possible explanation for the observed biodiversity and at least some of the fluctuations and unpredictability in nature, and it suggests why it may be difficult to stabilize such systems by human intervention.

Our model is a variant of the generalized Lotka–Volterra equations [20,21]. This model was chosen because of its simplicity and the fact that it can be viewed as the first approximation in a Taylor series expansion for a much wider class of models [22]. We consider N competing species with population x_i for $i = 1$ to N satisfying

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

where the vector of growth rates r_i and the matrix of interactions a_{ij}, are the parameters which model the biology (economics, sociology, etc.). The elements a_{ij}, which are positive to indicate competition, describe the average extent to which members of species j compete with members of species i. A key point that is often overlooked in these models is that as any given species approaches extinction, the averaging of the a_{ij} elements for this species will occur over smaller and smaller populations, and hence more variability becomes possible, causing the model to fail.

In a general ecology, one expects the linear growth rates r_i to be different for each species as well as the species interactions a_{ij}, to be both positive and negative, especially if the species are animals rather than plants. However, Coste et al. [23] have shown that any such N-dimensional Lotka–Volterra system can be extended to an equivalent $(N + 1)$-dimensional system with positive a_{ij} and equal growth rates. Since we are concerned with high-dimensional systems, in the interest of simplicity, we take $a_{ij} \geqslant 0$ and $r_i = 1$ for $1 \leqslant i, j \leqslant N$. Taking all the a_{ij} positive, i.e. looking at competitive systems, also guarantees that the solutions remain bounded in the range 0 to 1, but it ignores mutualism and the effect of varying individual prey populations on the predators. However, the results are not substantially altered if some of the a_{ij} are allowed to be negative. Finally, without further loss of generality, we can take the self-interaction terms a_{ii} equal to unity, which is equivalent to measuring x_i in units of its carrying capacity in the absence of the other species.

For competitive systems, chaos is not possible with fewer than four species because the dynamics occur on an $(N - 1)$-dimensional carrying simplex. For larger ecologies, a sense of the rarity of parameter values that lead to chaotic solutions follows from the observation that choosing a_{ij} from a random exponential distribution (so as to have a broad spectrum of positive values) with mean 1.0, with $N = 4$ leads to chaotic solutions with all species coexisting in only about 1 in 10^5 cases for a sample of 10^6 cases, and for $N = 5$ in only 1 in 4×10^5 cases. Coexisting chaotic systems for realistically large N ($\geqslant 100$) are vanishingly rare and almost impossible to find in such a random search, although work of Smale [24] guarantees their existence. The conditions for coexistence (an equilibrium with all x_i positive) and for chaos (the equilibrium being locally unstable) are somewhat mutually exclusive and occur in very small regions of this vast space of parameters.

Nature probably does not choose randomly from all possible ecologies, but instead individual species adapt to their environment so as to enhance their survival. Many models have attempted to include such adaptation, as mention earlier. These models often assume extinction when a species drops below a critical level [25,26] or modify the basic equations to prevent such extinction [27], but we believe there is considerable justification to instead consider models in which adaptation occurs primarily at these points. The individuals in a nearly extinct species are presumably the most fit and are those best able to survive by finding alternate resources and by evading their predators. Thus, as a species approaches extinction, the increased variability of the a_{ij} coefficients in Eq. (1) along with the effects of directional selection may lead to a shift in the a_{ij} coefficients. Also, when the population of a species becomes too small, its predators may find it too inefficient to prey upon, and it is thus better able to compete for resources. Finally, the model could be interpreted as species becoming extinct and then being replaced with new similar (perhaps mutated) species