Coexistence and chaos in complex ecologies

J.C. Sprott [*], J.A. Vano, J.C. Wildenberg, M.B. Anderson, J.K. Noel

Departments of Physics and Mathematics, University of Wisconsin, Madison, WI 53706, USA

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. © 2004 Elsevier B.V. All rights reserved.

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

[*] Corresponding author.
E-mail address: sprott@physics.wisc.edu (J.C. Sprott).

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

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

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
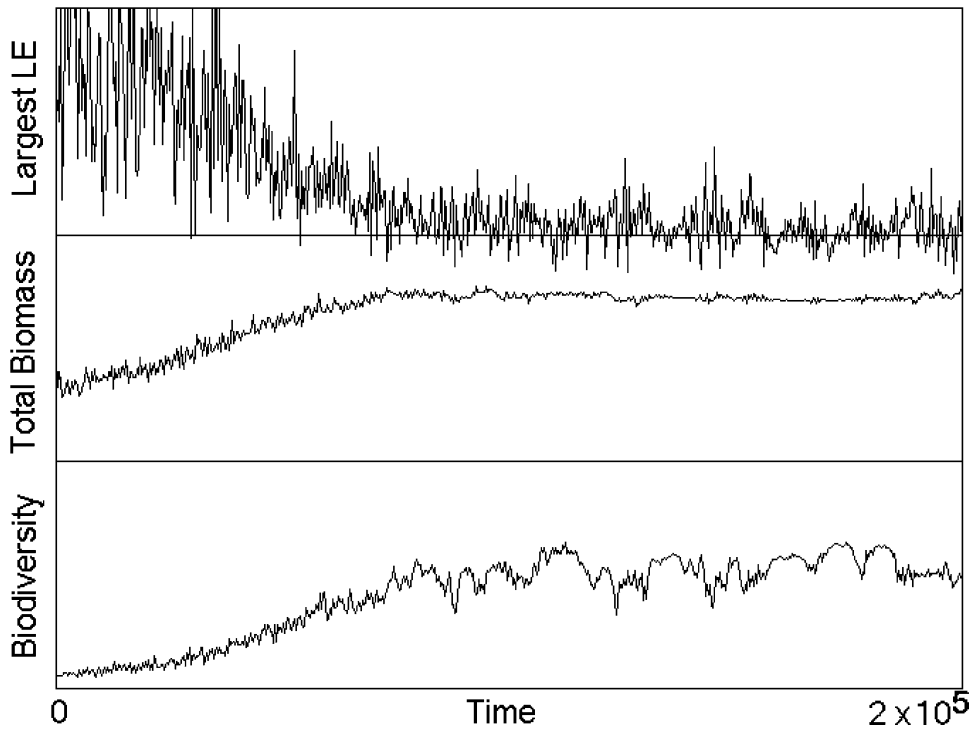
Fig. 1. Evolution of the largest Lyapunov exponent (0.02 full scale), total biomass (0.05 full scale), and biodiversity (1 full scale) showing how a typical system with 100 species slowly evolves toward a weakly chaotic state with high diversity and then remains there with fluctuations in the biodiversity suggestive of sporadic volatility and punctuated equilibria.

that are less susceptible to the prevailing competition [28,29]. We model this process as follows: initially the elements a_{ij} are taken from an exponential distribution with mean 1, although any distribution of positive values will suffice. The system converges fastest to the weakly chaotic state if the mean a_{ij} is close to the desired final value, which is typically on the order of $\sqrt{10/N}$. A time on the order of $t = 10^6$ is usually required to reach a state that is chaotic in the absence of adaptation. Initial x_i values are not critical, and they can be either random in the range 0 to 1 or purely deterministic. At each iteration for which any x_i falls below 10^{-6}, x_i is clamped at 10^{-6} and its matrix elements a_{ij} are replaced with $a_{ij}(1 - \varepsilon_1 x_j)$ for $j = 1$ to N and $j \neq i$ until the decline is arrested. In addition to this species-specific adaptation, all the off-diagonal elements of the matrix are increased by the factor $(1 + \varepsilon_2)$ every 20 iterations to model general adaptation of the entire ecosystem over time toward enhanced competition or to model a slowly increasing environmental stress (e.g., climate change or human encroachment [30]). The values are not critical, but they should be small and are here taken as $\varepsilon_1 = 10^{-4}$ and $\varepsilon_2 = 10^{-6}$. There may be some advantage to starting with relatively large ε values and slowly reducing them in the spirit of simulated annealing.

In this way, the system is guaranteed to have all N species coexisting with near optimal fitness. Note that this model is purely deterministic (no stochastic component) even while it is adapting, and thus any persistent aperiodic fluctuations are evidence of deterministic chaos. In addition to its ecological plausibility, the method provides a powerful numerical algorithm for finding the rare chaotic solutions for large N.

Such a system slowly evolves into one that is weakly chaotic with a typical largest Lyapunov exponent of 0.001 ± 0.001, whereupon it remains chaotic with all or most of the species coexisting even if the adaptation mechanism described above is turned off. The Lyapunov exponent [31,32] is a measure of the sensitivity to initial conditions, with a positive value signifying chaos. Abrupt or premature termination of
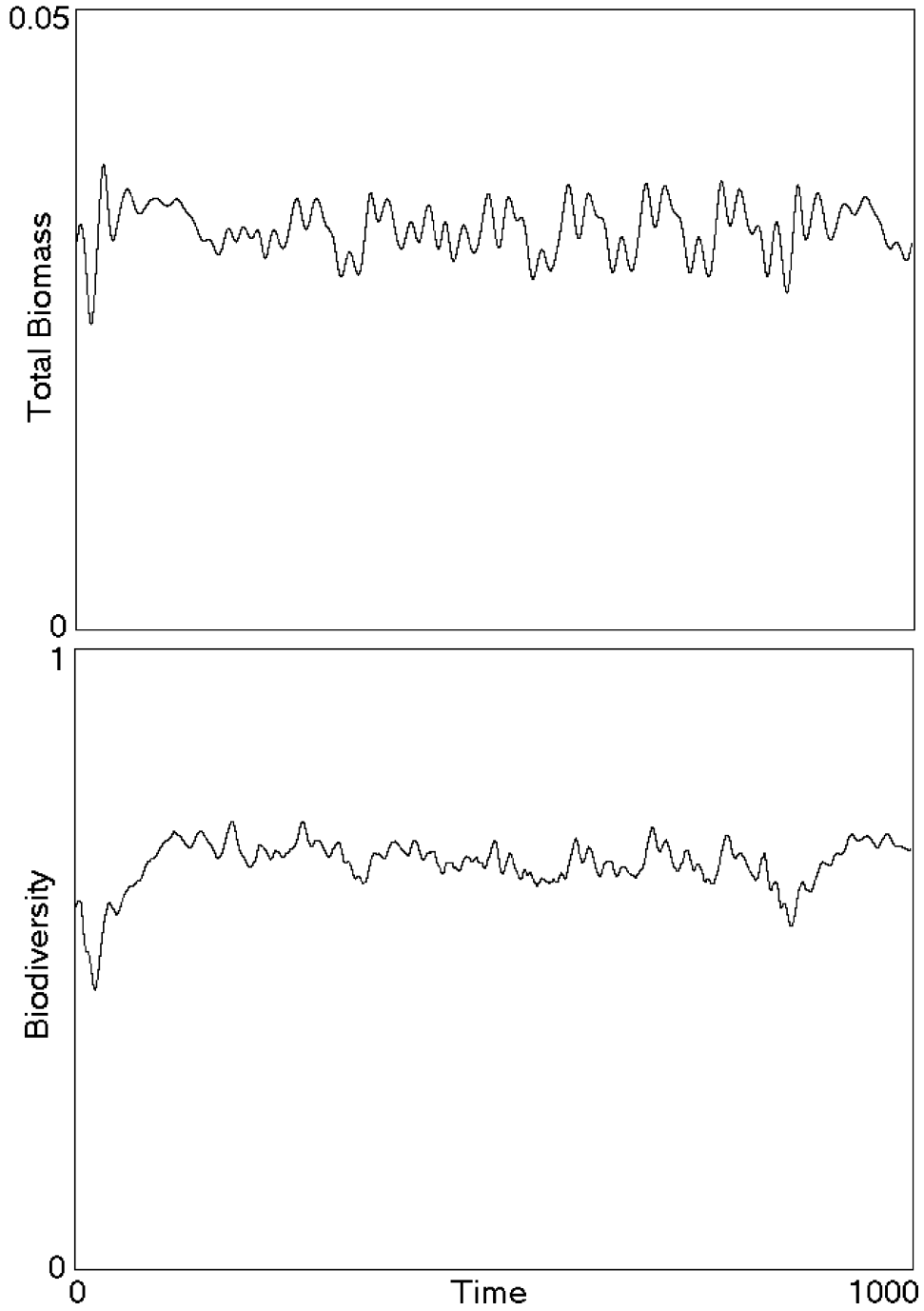
Fig. 2. Typical chaotic fluctuations in the total biomass and biodiversity for a system with 100 species after adaptation has been turned off.
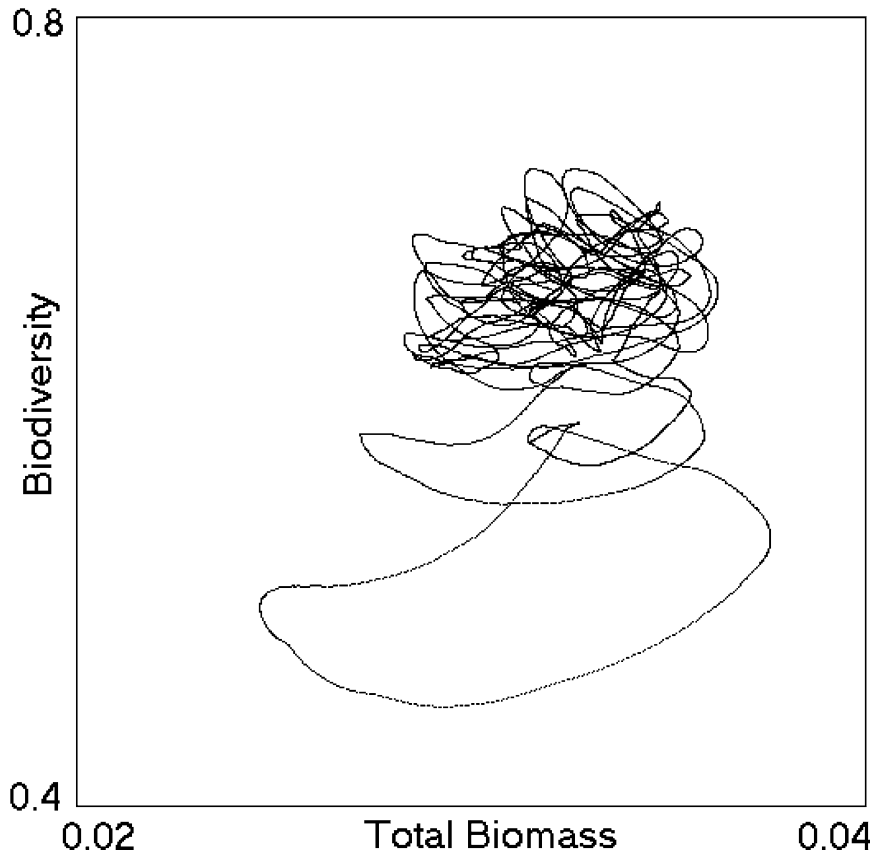
Fig. 3. A portion of the strange attractor for the same typical system as in Fig. 2 with 100 species after adaptation has been turned off.

the adaptation mechanism, however, may result in the extinction of some species and the suppression of the chaos.

Fig. 1 shows the evolution of the largest Lyapunov exponent along with the total biomass

$$M = \frac{1}{N} \sum_{i=1}^{N} x_i \qquad (2)$$

and biodiversity

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

for a typical highly competitive case that starts with most of the 100 species on the verge of extinction and strongly chaotic dynamics. As it evolves, the largest Lyapunov exponent generally decreases but remains mostly positive, while the biomass and biodiversity increase. Fluctuations in the biodiversity are suggestive

of sporadic volatility and punctuated equilibria [33]. A similar final state is reached if the initial a_{ij} values are small, giving a high initial degree of coexistence and stability with a temporally increasing Lyapunov exponent.

Fig. 2 shows the chaotic fluctuations in the total biomass and biodiversity for a typical such system with $N = 100$ after adaptation has been turned off. Note the very different time scales for the adaptation in Fig. 1 and the fluctuations in Fig. 2. Fig. 2 can be viewed as a slice of the dynamics in Fig. 1 over a short time scale where adaptation is negligible. Fluctuations in the population of individual species are much larger than in the total biomass.

Fig. 3 shows a portion of the strange attractor for the same system projected onto the space of total biomass and biodiversity. The Kaplan–Yorke dimension [34] of the attractor is about 6.3 with two positive Lyapunov exponents, making it hyperchaotic, although

only weakly so with a largest Lyapunov exponent of about 0.0021. This value implies that the system has memory and predictability on the time scale of 500 growth times for a typical species.

There does not appear to be a unique distribution of a_{ij} toward which the model evolves, suggesting that a wide variety of weakly chaotic ecologies is possible, although the mean value of the matrix elements for the case in Figs. 2 and 3 is about 0.38, which is typical of cases with $N = 100$. We have generated model ecologies with up to 400 surviving species by this method. Since these systems are fully connected with relatively large connection strengths, they violate the May–Wigner stability condition [35], which states that a network whose stability matrix contains elements from a normal random distribution with mean zero and variance σ^2 is almost certainly stable (and hence non-chaotic) if $NC\sigma^2 < 1$, where the connectivity C is the probability that a matrix element is non-zero.

In conclusion, we expect that the evolution method would work for almost any network model characterized by a matrix of interactions between its agents, and it is not restricted to models of ecology. Other networks that involve competition for resources and that are subject to crashes include financial markets, the electrical power grid, the Internet, traffic flow, and the brain. It is possible that all these systems are pushed toward a weakly chaotic dynamic by a mechanism similar to the one described here, and that such a state is relatively robust to modest disturbances, either intentional or unintentional. This state has been called "the edge of chaos" [36], and it provides the condition under which complex systems exhibit adaptation, self-organization, scale invariance, self-organized criticality, and similar features that characterize dissipative systems that are driven far from equilibrium by the throughput of energy or some equivalent quantity. Thus models of this type are ripe for further study and detailed comparison with the corresponding natural systems.

Acknowledgements

References

[1] S.L. Pimm, The Balance of Nature?, University of Chicago Press, Chicago, 1991.
[2] K.S. McCann, Nature 405 (2000) 228.
[3] M.R. Gardner, W.R. Ashby, Nature 228 (1970) 784.
[4] R.M. May, Stability and Complexity in Model Ecosystems, Princeton Univ. Press, Princeton, 1973.
[5] S.L. Pimm, J.H. Lawton, Nature 275 (1978) 542.
[6] E.P. Odum, Fundamentals of Ecology, Saunders, Philadelphia, 1953.
[7] R.H. MacArthur, Ecology 36 (1955) 533.
[8] C.S. Elton, Ecology of Invasions by Animals and Plants, Chapman & Hall, London, 1958.
[9] C. Godfray, M. Hassell, Science 275 (1997) 323.
[10] R.F. Constantino, R.A. Desharnais, J.M. Cushing, B. Dennis, Science 275 (1997) 389.
[11] C. Zimmer, Science 284 (1999) 83.
[12] S.P. Ellner, P. Turchin, Am. Nat. 145 (1995) 343.
[13] J.D. Murray, Mathematical Biology, Springer, Berlin, 1993.
[14] P. Yodzis, Nature 289 (1981) 674.
[15] J.C. Sprott, Phys. Lett. A 325 (2004) 329.
[16] R. Law, in: J. McGlade (Ed.), Advanced Ecological Theory: Principles and Applications, Blackwell, Oxford, 1999, pp. 143–171.
[17] K. Tokita, A. Yasutomi, Theor. Popul. Biol. 63 (2003) 131.
[18] K. Yoshida, Ecol. Model. 163 (2003) 131.
[19] B. Drossel, A.J. McKane, C. Quince, J. Theor. Biol. 229 (2004) 539.
[20] A.J. Lotka, Elements of Physical Biology, Williams and Wilkins, Baltimore, MD, 1925.
[21] V. Volterra, Memorie dell'Academia dei Lincei 2 (1926) 31.
[22] R.H. MacArthur, Theor. Popul. Biol. 1 (1970) 1.
[23] J. Coste, J. Peyraud, P. Coullet, SIAM J. Appl. Math. 36 (1979) 516.
[24] S. Smale, J. Math. Biol. 3 (1976) 5.
[25] C.S. Holling, Adaptive Environmental Assessment and Management, Wiley, London, 1978.
[26] K. Tokita, A. Yasutomi, Theor. Popul. Biol. 63 (2003) 131.
[27] Z.I. Dimitrova, N.K. Vitanov, Physica A 300 (2001) 91.
[28] L.R. Ginzburg, H.R. Akçakaya, J. Kim, J. Theor. Biol. 133 (1988) 513.
[29] R. Happel, P.F. Stadler, J. Theor. Biol. 195 (1998) 329.
[30] P.M. Vitousek, H.A. Mooney, J. Lubchenco, J.M. Melillo, Science 277 (1977) 494.
[31] J.C. Sprott, Chaos and Time-Series Analysis, Oxford Univ. Press, Oxford, 2003, pp. 116–117.
[32] L. Barreira, Y.B. Pesin, Lyapunov Exponents and Smooth Ergodic Theory, American Mathematical Society, Providence, RI, 2002.
[33] S.J. Gould, N. Eldridge, Paleobiology 3 (1977) 115.
[34] J. Kaplan, J. Yorke, in: H.-O. Peitgen, H.-O. Walther (Eds.), Functional Differential Equations and Approximation of Fixed Points, in: Lecture Notes in Mathematics, vol. 730, Springer, Berlin, 1979, pp. 228–237.
[35] H.M. Hastings, J. Theor. Biol. 97 (1982) 155.
[36] M. Waldrop, Complexity: The Emerging Science at the Edge of Order and Chaos, Simon and Schuster, New York, 1992.