Optimality at the Edge of Chaos?

Rinaldi and De Feo (1999) have recently presented a paper in which they reviewed the dynamics of three food chain models and concluded that ‘top-predator mean abundance is maximum at the edge of chaos’. This result was then used to propose ‘effective guidelines for the sustainability of complex ecosystems ...’. The patterns reported by the authors are certainly interesting, however, we find three key areas of disagreement with their interpretation.

1 The Edge of Chaos

Rinaldi & De Feo inappropriately use the term the ”edge of chaos”; specifically, they use it as a synonym of the term ”onset of chaos”. Although these terms sound very similar, they have quite different (mathematical) definitions and dynamical properties. It is important to explain these differences since there is a danger that this confusion of terms may become widespread and generally accepted in ecology.

The term ”onset of chaos” (OOC) was used in the 1970s when the early theory of chaos started to develop. It refers to the transition point where a dynamical system suddenly passes from a state of regularity (constant, periodic or quasiperiodic motion) to chaotic behaviour (sensu Devaney, 1989) as some control parameter is modified (Eckmann, 1981). At the onset of chaos, the Lyapunov exponent – which measures the rate at which initially close trajectories converge or diverge – changes from negative (ordered state) to positive (chaos). The patterns that Rinaldi and De Feo reported in their paper is, clearly, a typical OOC scenario.

The Edge of Chaos (EOC) concept was popularised by Langton (1990), Kauffammn (1991) and others in the early 1990s but in fact refers to a much older idea. Simply put, it refers to a region where a dynamical system is poised between order and disorder, exhibiting its most complex behaviour (Grassberger, 1986). Those interested in complex systems are excited about EOC because they consider it ‘plausible that the most complex, most integrated, and most evolvable behavior might occur in this boundary region’ (Kauffman 1993, p219). Strictly, this region is at a smooth phase transition (in the thermodynamical sense) and disorder is not necessarily related to chaos (in Devaney’s sense) but to the idea of a disordered field distribution (Afraimovich et al., 1992). It is then essential not to confuse ”chaos”, that in the OOC involves determinism, with ”disorder”, that in the EOC may even involve probabilistic events.

The EOC is conveniently described by a number of established complexity measures such as S-K entropy, mutual information, power-law scaling, correlation distances, etc. (Solé & Miramontes 1995). Rinaldi & De Feo do not use any of these measures, and so provide no firm evidence for EOC in any of the models they study. Nor is there
any intuitive way to speculate about the existence of EOC in their models in the absence of such measures since EOC is not necessarily observed in all dynamical systems. Moreover, there is a profound error when the authors claim that they can effectively derive their results “without invoking evolutionary theories or thermodynamic principles”. The EOC involves the notion of order-disorder that in turn strongly suggest an entropic concept coming out from the laws of thermodynamics. This misunderstanding can only be satisfactorily repaired after the realization that the scenario in question is an OOC where thermodynamic-like arguments may be comfortably relegated (if wanted so).

There is an extensive catalogue of population models where the OOC scenario has been demonstrated, ranging from May’s (1976) work on the period-doubling cascades in the logistic equation to more elaborate models where quasiperiodic and intermittent chaos have been shown (Rohani et al., 1994; Doebeli 1994). There are also a number of studies that explore the potential ecological and evolutionary benefits of different population dynamics (Allen et al., 1993; Ferrière & Gatto, 1993; Ruxton, 1994; Rohani & Miramontes 1995; Holt & McPeek 1996; Savill et al. 1997). In contrast, the EOC in the context of ecosystems is an attractive idea but remains a matter of conjecture and controversy. There are just a few examples where this scenario has been claimed to exist, such as in models of ant populations where the information capacity of the colony has been claimed to be at its maximum at an order-disorder transition (Solé & Miramontes, 1995; Miramontes, 1995). For all these reasons, it is essential that we do not equate the terms OOC and EOC, as Rinaldi & De Feo have done.

2 Optimality

Rinaldi & De Feo ask whether “ecosystems enjoy special properties at the edge of chaos”? We have already established that they mean "onset of chaos" rather than "edge of chaos". This point aside, they argue that the answer to their question is ‘yes’ since – as stated above – at the onset of chaos, mean top predator density is maximum (in their models). This is certainly very interesting from a modelling perspective. It would be interesting from a dynamical viewpoint to explore the generality of this result, and the mechanisms responsible for it. However, it is not clear to us that this result has any evolutionary significance. Rinaldi & De Feo provide no explanation for why natural selection might be expected to drive the dynamics of an ecosystem to a region where top predator mean abundance is highest? It is extremely unlikely that the authors are dealing with an appropriate evolutionary currency.

Support for this optimality argument is sought in the work of Ellner & Turchin (1995), who estimated Lyapunov exponents from time-series data for a number of field and laboratory populations and showed that many lie very close to zero. Thus, it is argued by Rinaldi & De Feo that many natural populations are at the edge of chaos (or rather onset of chaos), as predicted by their study. There are problems with this conclusion:
(i) estimating Lyapunov exponents from noisy data is universally acknowledged to be extremely difficult and whilst Ellner & Turchin’s study was novel and important, their results are far from unequivocal, (ii) many of the populations in Ellner & Turchin’s study were not top predators (or at the top of their food chain), (iii) there are a range of dynamical behaviour that may give rise to a zero Lyapunov exponent, such as quasiperiodic motion and a system near a bifurcation.

3 Management Implications

If it is generally true that systems near the OOC have maximal mean top predator density, what are the applied implications of this work? The authors suggest that their simple “rule” may be used in the management of populations, be it for economic or conservation purposes. This too is a problematic conclusion. Neither companies involved in resource harvesting nor those attempting to preserve biological diversity would be interested in maintaining a population in regions near the OOC, where population numbers generally would fluctuate significantly (the former for economic reasons and the latter for risk reasons). Those seeking to harvest or preserve species would rather have a system where the oscillations are bounded within narrow margins.

In conclusion, it is interesting that the three general food chain models of Rinaldi & De Feo all show that top predator population numbers are, on average, highest at the onset of chaos. Further study of the generality and underlying mechanism of this effect should be of interest to population dynamicists. However, we feel Rinaldi & De Feo need to reconsider their interpretation of these observations.

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5 References


