

Self-organized criticality in ecology and evolution

In a recent *TREE* perspective, Solé *et al.*¹ argued that (1) multispecies communities display self-similar spatiotemporal patterns, and (2) such patterns are indicative of self-organized criticality (SOC). Although we acknowledge the possible existence of SOC in ecological systems², we feel that the authors failed fully to address problems associated with these two points that potentially undermine their thesis.

On the first point, the apparent power-law patterns might be better described with other functions, in particular an exponential function. Exponential functions can closely approximate a power-law when only a portion of the total distribution is observed. Given that data obtained from natural communities often represent only a small subset of the whole community, it is quite possible that we are looking at part of an exponential curve when we think we find a power-law. Preston's influential work on the log-normal distribution of species abundance³⁻⁵ seems relevant here. He suggested that when sample size is limited, the abundance of rare species can fall below a critical minimum, which he called the 'veil line'. When rare species are veiled, the distribution of species abundance can appear very similar to a power-law on a log-log plot. More recently, G.J. Russell (unpublished) found that a simple probabilistic model of network cascades produces intermediate-type curves that fall between an exponential and power-law function. In short, a rigorous criterion is needed for assessing the aptness of the power-law function. To our knowledge, no convincing arguments exist, so far, in favor of power-laws⁶⁻⁸.

On the second point, it might not always be appropriate to attribute power-law patterns to an SOC process in the system in question. Solé *et al.*¹ briefly acknowledged this problem, but did not address it in depth. SOC is, by definition, a spontaneous emergence of dynamics that arise solely through interactions inherent in the system. It might be difficult in practice, however, to distinguish between patterns that arise from such internal processes and those that arise from the imposition of external forces, especially when external forces are themselves power-law distributed. For example, power-law distributed gaps of tropical rainforests have been attributed to an SOC process in the forest ecosystem⁹. However, if air turbulence assumed a power-law distribution¹⁰ as well, what role do the wind dynamics play in creating the gap pattern? SOC might indeed be operating here, but it is being attributed to the wrong system. In the case of the mass extinction in the fossil record, Newman⁸ showed that external stresses in a model were sufficient to produce power-law patterns without recourse to an SOC process. Similarly, in the case of the extinction in the introduced Hawaiian avifauna¹¹, autecological causes¹², not species interactions, might be responsible for the apparent power-laws exhibited.

SOC has the potential to be a powerful model for natural phenomena across many disciplines. We feel, however, that in future research these problems will require rigorous attention before the SOC model can gain general acceptance among ecologists and evolutionary biologists.

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Reply from R.V. Solé, S.C. Manrubia, M.J. Benton, S. Kauffman and P. Bak

Power-law distributed quantities have been observed in many different communities. Despite the unavoidable presence of noise in real data sets and the sometimes poor sampling, it is often found that a statistical study of the distribution of relevant quantities returns functions spanning up to three decades. When the distribution of gap sizes in a rainforest¹, the life span of marine genera², or the distribution of tree species³, are fitted by a uniparametric function, the presence of an exponentially or a power-law distributed quantity can be unambiguously determined: the previous examples and many others return power-laws. The use of fitting functions with *more than one parameter*, like a log-normal curve [which can also be linked with an SOC (self-organizing criticality) state] might only improve the agreement between the data and the interpolation, but still do not offer any insight into the nontrivial mechanisms producing power-law tails.

Current studies on the organization of biological systems recognize the presence of complex networks of interactions acting at different levels⁴ and of strong self-reinforcing processes among

the hierarchy⁵. This gives rise to invariant properties and to processes acting at different scales⁶. An ecosystem is formed by many interacting parts, the relevant quantities characterizing it are rarely (if ever) independent and, as a result, the response of that system to an external perturbation will be typically nonlinear, in many cases unpredictable, and very often strongly dependent on its internal state. As an example, models of planktonic ecosystems indicate that the outcome of interactions among species in a turbulent ocean (thus showing a power law spectrum for perturbations) does not lead to simple generalizations⁷. If the nonlinear response of a self-organized ecosystem (usually quantified through several dependent variables) distributes according to a power-law, the internal mechanism poising the system to the observed state is termed self-organized criticality (SOC). And, by definition, SOC requires the concomitant action of an external (slow) driving mechanism that maintains the system out of equilibrium: there is no evolution in its absence.

Keitt and Marquet⁸ acknowledged in their work on Hawaiian avifauna the presence of autecological causes that, they argued, could not on its own explain the observed patterns. This is also the case of some stochastic mechanisms that return power-laws when acting on independent units, but only when interactions among elements are considered does one obtain an exponent compatible with the observations⁹. Newman⁹ sustains that external perturbations alone might account for the power-law distribution of extinction events in evolution. Nevertheless, the rightness of his analysis has been questioned (P. Grassberger and H. Flyvbjerg, pers commun.) and, if right, it does not explain the whole spectrum of power-law quantities observed for that system. For instance, the life-time distribution or the correlations in time^{10,11} are not recovered with his simple stochastic model.

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How should cuckoo chicks signal in different host nests?

We welcome Soler and Soler's comments¹ on our paper² in this issue of *TREE*, and agree that only by understanding both links in the chain: chick need–begging signals–host provisioning³ can we fully understand cuckoo chick (*Cuculus canorus*) begging displays. Our *Nature* paper dealt exclusively with the second link, whereas a forthcoming companion paper⁴ focuses on the first link.

In asserting 'the cuckoo chick needs the same provisioning rate as an entire brood of reed warblers' (*Acrocephalus scirpaceus*), Soler and Soler imply that what the cuckoo chick gets is what it wants. But the two are not necessarily the same⁴.

Turning to the behaviour of cuckoo chicks in other host nests, we agree that it would be fascinating to compare their begging displays. However, predictions cannot easily be made simply from our work on reed warbler hosts. We believe that it is impossible to understand how cuckoo chicks should signal to their host parents without understanding: (1) how the needs of a cuckoo chick compare with those of host young, and (2) how host parents integrate begging signals to determine provisioning rates. There are good reasons for supposing that both will differ between hosts, but precisely how they do remains to be determined.

For example, apart from the reed warbler (which weighs ≈12 g), other common British hosts are the dunnock *Prunella modularis* (≈20 g) and the meadow pipit *Anthus pratensis* (≈18 g). The larger the host, the more similar the needs of a cuckoo chick and a single host young will be. In a dunnock nest, therefore, a cuckoo might have to call fast enough to compensate for the visual difference between its own gape and that displayed by two to three dunnock nestlings, rather than four nestlings in a reed warbler nest. This assumes, of course, that its optimal growth rate is the same in both nests. However, predictions about the cuckoo's begging displays are further complicated by the fact that the begging call rate of dunnock nestlings is far more rapid than that of reed warbler nestlings (R.M. Kilner and N.B. Davies, unpublished), which might be because dunnock nestlings typically compete with half-sibs rather than full-sibs⁵. By contrast, meadow pipit young are far less vocal (R.M. Kilner and N.B. Davies, unpublished), perhaps because they occupy ground-nests and so are more vulnerable to predators⁶. All of this suggests that

- 2 Sneppen, K. *et al.* (1995) *Proc. Natl. Acad. Sci. U. S. A.* 92, 5209–5213
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cuckoos will have to tune into different offspring–parent communication systems in the nests of different hosts. This presents a fascinating developmental problem, given that cuckoo host races are restricted to the female line⁷, hinting that either begging is maternally controlled or that cuckoos learn how to beg in different host nests.

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Reply from M. Soler and J.J. Soler

We are grateful to Kilner *et al.*¹ for clarifying the predictions of their *Nature* article² and for the information about begging behaviour in two further cuckoo host species. This will encourage further work and consideration of other hypotheses.

We agree with most of the points raised by Kilner *et al.* with one exception: we did not state that 'what the cuckoo chick gets is what it wants'. The sentence quoted by Kilner *et al.*, in its complete context³, means that if the cuckoo chick fails to get the same food provisioning as an entire brood of reed warblers (*Acrocephalus scirpaceus*), it would starve. Reed warblers would then not be a suitable host species.

Kilner *et al.* suggest that 'cuckoos will have to tune into different offspring–parent communication systems in the nests of different hosts'. As they state, there is a developmental problem with this prediction. We think that this problem is important and that both suggested solutions are unlikely.

First, if begging were maternally controlled, the existence of well defined cuckoo host races would be expected, not only related to egg morph⁴ but also to begging behaviour. This is because cuckoo chicks hatched in nests of another host species with a different offspring–parent communication system would starve. However, 'egg mimicry host races' have only been described for about 15 host species, whereas cuckoo eggs have been found in the nests of about one hundred species⁵. Furthermore, only 44% of the parasitized nests contained cuckoo eggs of the egg-morph corresponding to the host eggs⁵. The other possibility suggested by Kilner *et al.* is that 'cuckoos learn how to beg in different host nests'. This also seems unlikely because cuckoo chicks usually do not coexist with the host chicks in the nest⁶, and are thus not able to learn host nestling begging behaviour.

We consider that the hypothesis of integration of signals explains the exaggerated begging display of common cuckoo chicks in a complex way. We suggested a simpler, but nonexclusive, hypothesis that the begging rate of the cuckoo chick is correlated with its level of need and/or with the feeding capacity of the foster parents³. Our hypothesis has the advantage that it can be applied to other cuckoo species that also have very exaggerated begging displays but in which chicks are reared alongside the host young (i.e. they do not need to compensate for being only one gape in the nest). In one of these species, the great spotted cuckoo (*Clamator glandarius*), chicks beg at a similar call rate (as perceived by the human ear) when parasitizing four different host species that differ considerably in begging intensity (M. Soler and J.J. Soler, unpublished).

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