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 systems[2], 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 abundance[3-5] 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 More recently, G.J. Russell (unpublished) found that a simple probabilistic model of network cascades produces intermediate-type curves that fall between an exponential and power-law function.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-laws[6-8].

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 ecosystem[9]. However, if air turbulence assumed a power-law distribution[10] 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, Newman[8] 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 avifauna[11], autecological causes[12], 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 rainforest[1], the life span of marine genera[2], or the distribution of tree species[3], are fitted by an 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 levels[4] and of strong self-reinforcing processes among the hierarchy[5]. This gives rise to invariant properties and to processes acting at different scales[6]. 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 generalizations[7]. 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 Marquet[8] 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 observations[3]. Newman[9] 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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