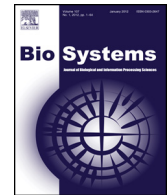




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Punctuated equilibrium based on a locally ambiguous niche

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ABSTRACT

Punctuated equilibrium, recently regarded as the power law distribution of lifespan, is estimated with respect to self-organized criticality. Previous explanations were based on a global property, such as the selection of species depending on their fitness, however a particular entity defined through such global property cannot be relevant to the notion of “self”. Here, we introduce local ambiguity of a niche with respect to function and define a function network by using two types of maps. Due to the local complex structure of the function network, motif and lateral connections, some species are easily replaced by others, and other species have long lives. Punctuated equilibrium can, therefore, be explained by local ambiguous interaction, which suggests the notion of self and supports the idea of self-organized criticality.

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1. Introduction

According to the view of the modern synthesis of evolution, a variant generated by mutants accumulates, leading to the gradual change of phenotype. Eldredge and Gould (1972) and Gould and Eldredge (1977) claimed that the phenotype of a species is not changed in most cases; however, such a silence can be suddenly punctuated, and diverse variants generated in very short time-spans can drive drastic phenotypic change. This idea is called punctuated equilibrium. When they proposed such an idea on evolution, only a few researchers noticed the significance of those evolutionary patterns (e.g., Maynard Smith, 1987). Most researchers thought that evolution results from gradualism in some cases and from punctuated equilibrium in other cases. Since, Bak and Sneppen proposed the model to make a relation between punctuated equilibrium and self-organized criticality (Bak and Sneppen, 1993), the pattern of punctuated equilibrium in evolution is regarded as a scale-free distribution of the lifetimes of species, avalanche size and clade size.

Fossil data that was previously plotted in normal co-ordinates (e.g., Raup and Sepkoski, 1982, 1986) has been re-estimated in a log–log plot (Solé et al., 1997), and the scale-free distribution is regarded as an evolutionary pattern revealing punctuated equilibrium. The scale-free distribution of the lifespans of species,

especially, is characterized by a scale exponent of the power law distribution, 1.5–2.0. The time series of the extinctions of species is also analyzed in terms of power spectrum and is interpreted as a pink noise or $1/f$ noise. This means it has a self-similar structure, which is also relevant for criticality.

While the idea of self-organized criticality sounds reasonable, we claim that the notion of self is doubtful if the mechanism of self-organized criticality is derived from a global definite property. In the Bak–Sneppen model and its variants (Sneppen et al., 1995; Solé and Manrubia, 1996; Head, 1998; Jensen, 2004; Hall et al., 2002), actually, an abstract observer–environment sees all species in an ecosystem and selects a particular species with the least fitness to replace by other species (i.e., extinction of the former species and immigration or generation of new species). In addition, the environment selects two other species, independent of the species with the least fitness, and also replaces these two by other species. On one hand, replacing the species with the least fitness can increase the average fitness of an ecosystem. On the other hand, replacing an additional two species by others can decrease the average fitness. Thus, balancing the increase and decrease can autonomously drive a system toward criticality (other explanations are in Bandt, 2005; Grinfield et al., 2011). In this model, an environment sees all species in an ecosystem, which is nothing but a global property. Because of this global property, the environment can be regarded as a particular entity outside of the ecosystem. That is why the environment is described as the third person rather than the first person. If the description as the first person is not introduced, one cannot use the notion of self and/or self-

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organization. The issue of self-organization, therefore, still remains.

The question of self-organizing criticality can be replaced by the question of how a scale-free distribution (critical phenomenon) generated in a bottom up fashion can have a locally interactive mechanism without a global property. We here find two types of properties in adaptive processes, adaptation and adaptability, and then describe adaptation and adaptability by using two types of maps. A network-like local complex structure driven by two types of maps can give rise to a web of local structures instead of a global property. This can lead to a scale-free distribution showing punctuated equilibrium.

2. Evolution model based on ambiguity in function

An adaptive process that is a basic mechanism for biological evolution could consist of two different parts, adaptation and adaptability (Conrad, 1983). Adaptation reveals the passive mode of biological processes, through which living systems are selected by environments and optimized to some extent for a particular function. Adaptation reveals the passive mode of biological processes. In contrast, adaptability reveals the active mode of biological processes, the ability to thrive in an alternative environment that is hidden within living systems. Adaptability is the ability that can be realized in the future.

Although adaptation and adaptability can correspond to past and future processes, respectively, they can be expressed as two types of maps from niches to functions in environments. Consider a set of niches, S , and a set of functions, P . It is assumed that the primary function of a niche is uniquely determined by a map, $f_p: S \rightarrow P$, while a secondary function of the same niche is also given by another map, $f_s: S \rightarrow P$. For a niche x in S , the primary and secondary function is expressed as $f_p(x)$ and $f_s(x)$, respectively. If adaptation results from a primary function, the secondary function can reveal adaptability, and vice versa. Ambiguity of functions consisting of two maps can implement adaptation and adaptability.

Dynamics of evolution are expressed by time developments of two maps, f_p and f_s . Because the time step is discretely defined, two functions at time t are represented by f_p^t and f_s^t . Initially, f_p^0 and f_s^0 for each niche x in S are determined by one of the elements of P with equal probability. For time step t , the dynamics of evolution are defined by the following: (i) one niche, x , is randomly given. If two functions constitute the motif condition around x , then $f_p^t(x) = f_p^{t-1}(x)$; otherwise, $f_p^t(x)$ is given by one of the elements of P with equal probability. For any other niche y but x in S , $f_p^t(y) = f_p^{t-1}(y)$. (ii) One niche, z , is randomly given. If two functions constitute the relaxation condition around z , $f_s^t(z)$ is given by one of the elements of P with equal probability; otherwise, $f_s^t(z) = f_s^{t-1}(z)$. For any other niche w but z in S , $f_s^t(w) = f_s^{t-1}(w)$. (iii) The motif condition around x is defined by the coincidence of f_p^t and f_s^t for the motif that is a set of niches, M , containing x and that is expressed as $f_p^t(M) = \text{constant}$ and $f_s^t(M) = \text{constant}$, and, i.e., for any m and n in M , $f_p^t(m) = f_p^t(n)$ and $f_s^t(m) = f_s^t(n)$. In general, $f_p^t(m) \neq f_s^t(m)$. Note that M can be a set consisting of just one element m , where $f_p^t(m) = f_s^t(m)$. We call any m in M a member of the motif, and $f_p^t(m)$ and $f_s^t(m)$ a representation of the motif (Fig. 1). (iv) The relaxation condition around z is defined by the existence of the escape root for the motif M such that $f_p^t(M) = \text{constant}$ and $f_s^t(M) = \text{constant}$, where z is contained in M (Fig. 2A). The escape root for the motif M is defined by the probabilistic existence of niche s , which is not a member of the motif (i.e., s is not in M) but has the representation of a motif (i.e., $f_p^t(s) = f_p^t(m)$ or $f_s^t(s) = f_s^t(m)$, where m is in M).

If function $f_s^t(x)$ for a chosen niche x is changed, it implies that the previous species at this niche x is extinct and a new species has been generated or has immigrated to this niche x . It is assumed that

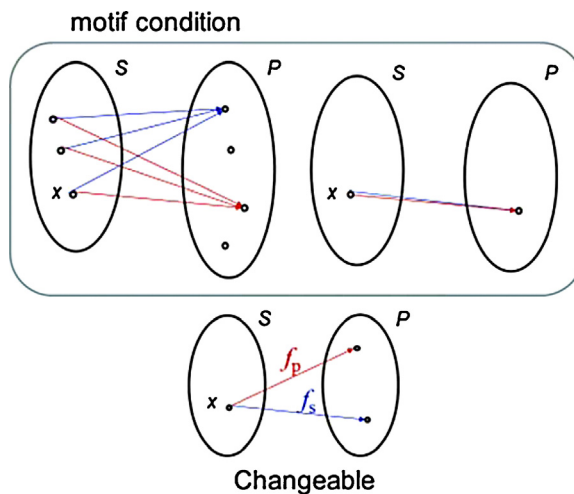


Fig. 1. Examples of the local complex network, i.e., motif. Each niche that is an element of S has two functions, the primary function, f_p , and the secondary function, f_s , where f_p and f_s are defined as a map from S to P . The motif is defined by M , which is a subset of S , such that, for any m in M , $f_p(m) = f_s(m)$. In the upper left, M consists of three niches, and in the upper right, M consists of a single niche.

the change of the function at a niche implies the replacement of the species that occupied this niche.

The probabilistic existence of species s is implemented by using a parameter R , which is the number of random walk steps in the non-directed network involving the motif around x (Fig. 2B). Given a motif around x (Fig. 2A left), the mapping is assumed as a non-directed network (Fig. 2B left). In starting from an element x in the motif, each link is randomly chosen in R steps. In the case of Fig. 2B center, a random walk along the link is chosen in the order, $x, 1-4$. Because the final position at the R th step results in being outside of the motif, there exists an escape root for the motif around x . Because each link in the walk from x is randomly chosen, the

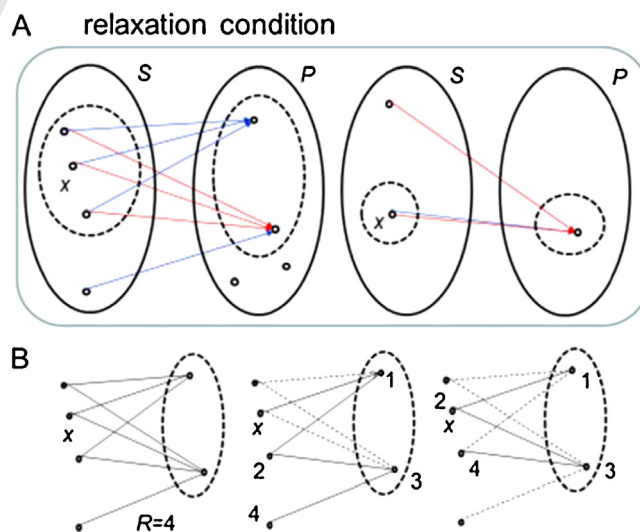


Fig. 2. (A) Examples of networks satisfying the relaxation condition, which allows the destruction of the motif. Niches surrounded by broken lines constitute a motif. If there are some connections between the motif and any other niches outside of the motif, with respect to f_p or f_s , then $f_s(m)$, with m in the motif M , can be replaced with any other function by the random walker algorithm. (B) Random walker algorithm applied to a niche x . First, mappings from S to P are replaced with undirected links (left). Second, in starting from x , the random walker walks along the undirected links in R steps. If the final position of the random walker is outside of the motif (center), $f_s(x)$ can be randomly replaced with other functions. Otherwise (right), nothing happens.

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