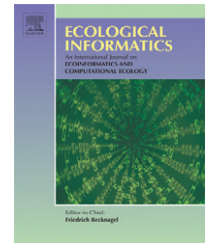


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Statistical mechanics of relative species abundance

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ABSTRACT

Statistical mechanics of relative species abundance (RSA) patterns in biological networks is presented. The theory is based on multispecies replicator dynamics equivalent to the Lotka–Volterra equation, with diverse interspecies interactions. Various RSA patterns observed in nature are derived from a single parameter related to productivity or maturity of a community. The abundance distribution is formed like a widely observed left-skewed lognormal distribution. It is also found that the “canonical hypothesis” is supported in some parameter region where the typical RSA patterns are observed. As the model has a general form, the result can be applied to similar patterns in other complex biological networks, e.g. gene expression.

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1. Macroscopic ecological patterns as eco-information

The most significant feature of large-scale biological networks, such as food webs (Martinez, 1991; <http://userwww.sfsu.edu/~webhead/lrl.html>), metabolic networks in a cell (http://kr.expasy.org/cgi-bin/show_thumbnails.pl) and protein networks (Jeong et al., 2001; <http://www.nd.edu/~networks/gallery.htm>), is overwhelming diversity of components, e.g., species, chemical constituents and proteins, respectively, great complexity of network topology, and homeostatic stability of dynamics on the networks. From a theoretical viewpoint, it is a serious question how living organisms has evolved such a homeostasis because chaotic instability is inherited even in a simple nonlinear system.

As an approach to such a problem, macroscopic patterns observed in various complex networks have been studied (Barabási, 2002). Such studies on *scale-free networks* have been elucidated the characteristics of topology of natural and

artificial complex networks, and the evolutionary conditions which produces such a topology. Unifying approaches to biological and abiological networks have emphasized their similarity and difference. For example, it is pointed out that an infection of computer virus on the internet with scale-free topology is followed by a qualitatively different epidemic dynamics from the one of biological viruses in nature, and, therefore, the computer viruses are hardly eradicated (Pastor-Satorras and Vespignani, 2001).

On the other hand, in a large-scale complex biological networks such as ecosystems, not only a topology of the network links but also a thickness of each link, i.e. the strength of interactions, definitely affect population dynamics and resulting macroscopic patterns. In ecology, classical macroscopic patterns observed and studied for a long time is RSA patterns, in other words, abundance distribution of species, which is one of the most accumulated informations obtained in ecology.

Nevertheless, how to clarify the mechanisms underlying those RSA patterns has been one of the ‘unanswered questions in ecology in the last century (May, 1999)’ even though the knowledge obtained from it would affect vast areas of nature

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conservation. Various models have been applied to ecosystem communities where species compete for niches on a trophic level (Motomura, 1932; Corbet et al., 1943; MacArthur, 1957, 1960; Preston, 1962a,b; Whittaker, 1970; Bazzaz, 1975; May, 1975; Sugihara, 1980; Nee et al., 1991; Tokeshi, 1999; Hubbel, 2001; Hall et al., 2002; Harte, 2003; McGill, 2003; Volkov et al., 2003; Pigolotti et al., 2004; Etienne and Olff, 2004; Chave, 2004; Harte et al., 2005), but these models have left the more complex systems a mystery. Such systems occur on multiple trophic levels and include various types of interspecies interactions, such as prey–predator relationships, mutualism, competition, and detritus food chains. Although RSA patterns are observed universally in nature, their essential parameters have not been fully clarified. In this paper, it is presented that RSA patterns are derived from a statistical mechanical theory (Tokita, 2004), based on a general evolutionary dynamics which is applied in vast area of fields.

We consider here the replicator equation (Hofbauer and Sigmund, 1998) (RE),

$$\begin{aligned} \frac{dx_i}{dt} &= x_i \left(f_i(x) - \frac{1}{N} \bar{f}(x) \right), \\ f_i(x) &= \sum_j J_{ij} x_j, \\ \bar{f}(x) &= \sum_i f_i(x) x_i \end{aligned} \tag{1}$$

where N is the number of species, and $0 \leq x_i(t) \leq N$ denotes i th species' population. The functions $f_i(x)$ and $\bar{f}(x)$ denote fitness of species i and its average, respectively. Interaction between i th species and j is specified by J_{ij} . Note that total population is conserved at any time as $\sum_i x_i = N$ and, that is, the trajectory of the dynamics (1) is bounded in a simplex $\sum_i x_i = N$.

The RE appears in various fields (Hofbauer and Sigmund, 1998). In sociobiology, it is a game dynamical equation for the evolution of behavioral phenotypes; in macromolecular evolution, it is the basis of autocatalytic reaction networks (hypercycles); and in population genetics it is the continuous-time selection equation in the symmetric ($J_{ij} = J_{ji}$) case. The symmetric RE also corresponds to a classical model of competitive community for resources (MacArthur and Levins, 1967). The replicator dynamics, therefore, are often used as a model of complex systems in which many components changes their numbers through complex reaction, replication and reproduction of the components.

Here we assume that (J_{ij}) is a time-independent random symmetric ($J_{ij} = J_{ji}$) matrix whose elements have a normal distribution with mean $m (> 0)$ and variance \bar{j}^2/N as

$$P(J_{ij}) = \sqrt{\frac{N}{2\pi\bar{j}^2}} \exp\left[-\left(\frac{N}{2\bar{j}^2}\right)(J_{ij}-m)^2\right] \quad (i \neq j)$$

Self-interactions are all set to a negative constant as $J_{ii} = -u (< 0)$. Note that the essential parameter is unique as $p = (u+m)/\bar{j}$ because the transformation of the interaction $K_{ij} = (J_{ij}-m)/\bar{j}$ does not change the trajectory of the dynamics (1). Although ecologists do not generally believe in the randomness of interspecies interactions in nature, the discipline has been affected by the random interaction model (May, 1972) as a prototype of complex systems.

Particularly in the context of ecology, the N species RE (Hofbauer and Sigmund, 1998) is equivalent to the $N-1$ species Lotka–Volterra (LV) equation

$$\frac{dy_i}{dt} = y_i \left(r_i - \sum_j^{N-1} b_{ij} y_j \right).$$

That is, the abundance y_i and the parameters in the corresponding LV are described by those in the present RE model as,

$$y_i = x_i/x_M \quad (i = 1, 2, \dots, N), \tag{2}$$

$$r_i = J_{iM} - J_{MM} = J_{iM} + u, \tag{3}$$

$$b_{ij} = J_{ij} - J_{Mj} \tag{4}$$

where the 'resource' species M ($y_M = 1$) can be arbitrarily chosen from N species in the RE. The ecological interspecies interactions (b_{ij}) ($i \neq j$) have a normal distribution with mean 0 and variance \bar{j}^2/N from Eq. (4), and they are no longer symmetric ($b_{ij} \neq b_{ji}$). The present model therefore describes an ecological community with complex prey–predator interactions ($(b_{ij}, b_{ji}) \rightarrow (+, -)$ or $(-, +)$), mutualism $(+, +)$ and competition $(-, -)$. Moreover, a community can have a 'loop' (detritus) food chain $((b_{ij}, b_{ji}) \rightarrow (+, -), (b_{jk}, b_{kj}) \rightarrow (+, -), (b_{ki}, b_{ik}) \rightarrow (+, -))$. The intraspecific interaction b_{ii} turns out to be related to the intrinsic growth rate r_i as $b_{ii} = J_{ii} - J_{Mi} = -u - J_{iM} = -r_i$ and is therefore competitive ($b_{ii} < 0$) for producers ($r_i > 0$) or mutualistic ($b_{ii} > 0$) for consumers ($r_i < 0$).

By Eq. (3), the intrinsic growth rates also have a normal distribution with mean $u+m$ and variance \bar{j}^2/N . The probability at which r_i is positive—that is, that the i th species is a producer—is therefore given by the error function,

$$\text{Prob}(r_i > 0) = \int_{-p\sqrt{N}/2}^{\infty} \frac{dt}{\sqrt{\pi}} \exp(-t^2).$$

Consequently, the parameter p can be termed as the 'productivity' of a community because the larger the p , the greater the number of producers. This can be also understood from the fact that p is connected to the average growth rate:

$$\frac{1}{N} \sum_i r_i = \langle J_{iM} + u \rangle_j = m + u = p\bar{j}. \tag{5}$$

The parameter p is also connected to the maturity of an ecosystem because m increases in time in an evolutionary model (Tokita and Yasutomi, 2003).

Note that the growth rate $(1/x_i)dx_i/dt$ in RE (1) has no ecological meaning because it is defined by the average fitness \bar{f} subtracted from the fitness f_i . We therefore consider the equivalent LV (1) when we discuss the model in the context of ecology as stated above. Why we do not consider LV with random asymmetric interactions from the beginning is that the system we consider here is not general asymmetric LVs but a class of LVs which is corresponded to a symmetric RE whose symmetry is crucial to the present analysis.

While random asymmetric interaction matrix ($J_{ij} \neq J_{ji}$ and, J_{ij} and J_{ji} are independent from each other) was assumed in the classical random population models (Gardner and Ashby, 1970; May, 1972; Tokita and Yasutomi, 1999), here, the symmetric matrix ($J_{ij} = J_{ji}$) enables us to derive RSA patterns and left-skewed (Nee et al., 1991) canonical (Preston, 1962b; May, 1975) lognormal-like distribution, from a single parameter p (Tokita, 2004).

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