Emergence of diversity in a biological evolution model

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Abstract. The ecological systems comprise a rich diversity of species, but the minimum requirements to maintain a large species diversity on long time scales are in general unknown. Here we propose one neutral evolution competition mechanism which is identified to ensure successful conservation of the biodiversity in ecosystems. Here we show that, this mechanism can lead the system into a quasistable state regardless of the initial conditions. By changing one parameter \( p \) which represents the probability of introducing one new species, the system can evolve from homogeneous state, the system contains only one species into heterogeneous state, the system contains diversity of species with number of species equal to the system size. This model is simple enough to be analysed theoretically. The theoretical estimation on abundance distribution and the diversity show the same result of simulation. Furthermore, the lifetime of the species is independent of the system size.

1. Introduction

The relationship between biodiversity and ecosystem processes has emerged as a major scientific issue today [1-2]. Multiple species often coexist robustly in natural ecosystems [3]. The interactions between biological species may well be as old as lift itself [4]. The competition, cooperation, or predation are generally considered as major determinants for species diversity [5-7]. However it is not easy to keep an ecosystem with diversity when several species compete for the same resources [8]. It has been found that one way to maintain coexistence of multiple species is to include fitness [9]. Although biologists have offered a staggering number of definitions of fitness, they agree broadly on the essence of the idea. In the crudest terms, fitness involves the ability of organisms or, populations or species to survive and reproduce in the environment. The consequence of this survival and reproduction is that organisms contribute genes to the next generation. Another robust way to maintain high diversity is to include space [10-11]. However, Hubbell proposed Unified Neutral Theory of Biodiversity(UNTB) to explain biodiversity patterns without invoking species differences [12-15]. Neutral theory assumes that each individual prospects of death and reproduction are independent of what species it, or its neighbors, belong to. This assumption, while only an approximation, appears to provide a useful description of an ecological community on some spatial and temporal scales. More significantly, it allows the development of a tractable null theory for testing hypotheses about community assembly rules. Based on the neutral theory, here we present an ecosystem model in which species compete within limited system size, and the model is kept as simple as possible to remain analytically tractable.
This paper is divided into four sections. In Sec.II, we introduce an ecosystem model where species compete for resources. In Sec. III, the creation of ecosystem is both computer simulated and analytical calculated, and finally, in Sec.IV, we provide a discussion of this model.

2. Description of the model

Our model is inspired by the neutral theory, under this assumption, either the species compete with each other equally or being replaced by new species equally within the constant system size. Specifically, we consider a system with fixed population $N$. Initially, there are $M$ species, and each species with $N/M$ individuals. We then study by computer simulation. At each step of the simulation, we either introduce a single new species and replace it with an old randomly chosen individual, or we randomly chose two individuals and replace one by another. The detail computer simulation are, at each step we chose one individual $i$, $(i = 1, 2, ..N)$ despite its species $i_s$, $(s = 1, 2, ...M)$ at random, and do the following(see fig.1).

(1) With probability $p$, we introduce one individual $k$ which belongs to a new species $k_s$, and replace $i$ with $k$.

(2) Otherwise (i.e., with probability $1 - p$) we randomly pick a individual $j$, and replace it by $i$.

Step (1) represents the introduction of new species into teh system. In order to keep the total population as a constant, one old individual must be replaced by the new one. Step (2) represents the neutral competition of the individuals in the system. During this dynamics process, if the last individual of one species is died, this species’ lifetime is the time from its born until the last single one dies. Note that total population of system $N$ is fixed, and each individual can be selected equally regardless of its species.

3. Results

The expected qualitative behavior of the model is clear. Since when $p = 0$, no new species can be introduced, the species in the system exclude each other until all of the individuals belongs to the same type. In this limite, the diversity $D$ (the number of species) is 1. While in the other extreme situation, when $p = 1$, one new species is introduced at each time, the system evolves into the state in which each individual belongs to different species, thus, diversity is equal to
system size $N$. When $p$ is between 0 and 1, the system will reach to a quasistable state with fluctuation as shown in Fig.2. Here we start with constant initial number of species $M = 100$ with different system size $N$.

It is observed from Fig.2 that the system evolves to a quasistable state, in which diversity fluctuates around its average value. In the final stable state, the average diversity increases with increasing system size $N$ and $p$, and thus, species abundance also becomes stable which is due to the conservation of the total population during the evolution.

Due to the neutral replacing and duplicating mechanics, this model can be theoretically analyzed. Considering the birth and replace process in this system, at each time, any species can only increase one or decrease one individual, i.e., the number of species with certain abundance can only increase one or decrease one. In a word, the “species flow”—the number of species which changed their abundance—must be conserved: the total species flow into one andance should be equal to the total species flow out of it (as shown in Fig.3). Let $f_i(i = 1, 2,...N)$ represent the number of species with abundance $i$, we have the simultaneous equations as following when taking into account the conservation of species flow:

\[
\begin{align*}
    f_1 \frac{1}{N}[p + (1-p)(1 - \frac{1}{N})] &= p \\
    f_2 \frac{1}{N}[p + (1-p)(1 - \frac{2}{N})] &= f_1 \frac{1}{N}(1 - \frac{1}{N})(1-p) \\
    \vdots \\
    f_k \frac{1}{N}[p + (1-p)(1 - \frac{k}{N})] &= f_{k-1} \frac{1}{N}(1 - \frac{k-1}{N})(1-p) \\
    \vdots \\
    f_{N-1} \frac{1}{N}[p + (1-p)(1 - \frac{N-1}{N})] &= f_{N-2} \frac{N-2}{N}(1 - \frac{N-2}{N})(1-p) \\
    f_N \frac{1}{N}[p] &= f_{N-1} \frac{N-1}{N}(1 - \frac{N-1}{N})(1-p)
\end{align*}
\]
Figure 3. Computer simulation result (CS) and theoretical estimation (TE) result for abundance distribution when $p = 0.1$, $p = 0.4$ and $p = 0.7$ with system size $N = 1000$.

The first row of Eq(1) represents the conservation of species flow for species with abundance equal to 1. The right hand side is the total inflow, which is the probability $p$ of only one single new species, while the left hand side consists two terms which contribute to the total outflow. The first term corresponds to dynamics step (1) that the species which has only single individual is chosen and its individual is replaced by one new born species. The second term accounts for dynamics step (2) that those single individual composed species is chosen and its individual is replaced by the other species in this system. And so forth for the other rows which corresponds to each species abundance.

The result for abundance $f_k (k = 1, 2, ..., N)$ could express as:

$$ f_k = \frac{N p}{k} \frac{N!}{(N-k)!} \prod_{i=N-k}^{N-1} [N p + i(1-p)] $$

From Eq.(2), it is obvious that the abundance distribution is exponential function under the system size limit ($N \to \infty$):

$$ f_k \sim p (1-p)^{k-1} $$

Both the computer simulation (CS) result and the theoretical estimation (TE) result for abundance distribution are shown in Fig.3. It is found that the system abundance decreases with increasing $p$, which can be explained as following. When $p = 0$, the system will end up with one species, which means abundance is $N$. On the contrary, when $p = 1$, there will be only one sigle individual for each species in the system, which leads to abundance equal to 1. Thus, as $p$ between 0 and 1, the larger $p$, the more new species are introduced into system, the smaller of the species abundance.

From the “species flow” deduced abundance expression Eq.(2), it is easy to calculate the
Figure 4. Computer simulation result (CS) and theoretical estimation (TE) result for diversity as a function of (a) system size $N$ under different $p = 0.1$, $p = 0.4$, $p = 0.7$ and (b) $p$ with different initial species $S_{\text{initial}} = 1000$, $S_{\text{initial}} = 500$, $S_{\text{initial}} = 100$.

Diversity which is the total sum of species with different abundance. It expresses as:

$$D = \sum_{k=1}^{N} f_k = \sum_{k=1}^{N} \frac{Np}{k} \frac{N!}{(N-k)!} \frac{(1-p)^{k-1}}{\prod_{i=N-k}^{N-1} (Np+i(1-p))}$$

The equation (4) is approximately equal to $\frac{Np}{1-p} E_i$ with $E_i = \sum_{k=1}^{N} \frac{(1-p)^k}{k}$. It is found that diversity is a linear function of system size $N$, and nonlinear function of $p$. The result for both computer simulation and theoretical estimation are shown in Fig.4. As stated before, the larger $p$, the larger diversity, and the larger system size $N$ leads to larger diversity. It is found that the final steady state is independent of the initial number of species, it can be understood that for the competitive exclusion process, each individual is equally chosen despite its species, which means all types behave symmetrically, as a result, the initial number of species have no influence on the system steady state.

The dynamics of the population of a given species is governed by generalized birth and death events. Let $p(n,t)$ denote the probability that one species contains $n$ individuals at time $t$. In this simplest scenario, the time evolution of $p(n,t)$ is regulated by the following equation:

$$p(n,t+1) = p(n-1,t) \frac{N-(n-1)}{N} \frac{n-1}{N} (1-p)$$
$$+ p(n,t) \frac{N-n}{N} \left( \frac{N-n}{N} (1-p) + p \right) + \frac{n}{N} \frac{n}{N} (1-p)$$
$$+ p(n+1,t) \frac{n+1}{N} \left( \frac{N-(n+1)}{N} (1-p) + p \right)$$

The right hand side is composed by three terms. The first term is the probability that species increase its individuals from $n-1$ to $n$ by replacing other type of individuals, and the second is...
the probability that the species remain the same number of individuals, either by introduing a
new single species which replaces other types of species or by the duplicated individual replacing
its own type,and the last term is the probability that species decrease one individual from \( n + 1 \)
to \( n \) by either introducing a new single species or duplicating another species. This equation
is the finite difference partial differential equation, which can only be solved numerically. Both
the simulation result and numerical equation results are shown in Fig.5. The lifetime is a log-
normal distribution when \( p = 0 \), and can be rescaled by system size. The Fig.5 (b) shows that
the lifetime can be rescaled by system size \( N \) for \( p > 0 \), and become shorter when \( p \) is larger.
This is easy to understand, the more frequently new species is introduced to this system, the
more individuals will be replaced, which leads to shorter lifetime, and is proportional to system
size \( N \).

4. Discussion
Here we proposed one neutral competition evolution model to explain the biodiversity in
ecological system. This simple model is controlled by one paramater \( p \), which represents the
probability of introducing one new species. Under constant system size, the diversity increases
to systems size \( N \) when \( p = 1 \), or decreases to 1 when \( p = 0 \), or a quasistable state with
fluctuation \( (0 < p < 1) \) when system reaches to steady state. By theoretically analyzing the
“species flow”equations, it is found that the diversity grows linearly with systems size \( N \), and
nonlinear with \( p \). The abundance is exponential distribution and decreases with increasing \( p \).
Finally, the lifetime can be rescaled by system size. It is log-normal distribution when \( p = 0 \)
and decreases with increasing \( p \) when \( p > 0 \). Furthermore, this neutral competition model is
simple enough to make theoretical analysis. The theoretical estimation gives the same results
as the computer simulation, which provide one framework for the more complicated situation
investigation in future work.
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