

Phase diagram and stability of ecosystems

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Abstract

The relation between the diversity and the interspecies interactions in ecosystems is studied using a simple population dynamics model. The interaction terms have the characteristic form of $x_i^\lambda x_j^{1-\lambda}$. Simple rules for addition and elimination of species is also included. This model is called the “scale-invariant” model and known to reproduce various statistical properties in real ecosystems. It is found that this model system has two phases depending on the parameter λ . When λ is smaller than a certain value λ_c , the number of species fluctuates in finite range. As λ approaches λ_c , the average number of species diverges as $(\lambda_c - \lambda)^{-1}$. When $\lambda > \lambda_c$, the number of species grows to infinite. Further it is found that larger λ yields both stabilization of the system and enforcement of interactions at the same time.

1 Introduction

What is the difference between ecosystems in which many species can coexist and those in which only few species can survive? How does the interaction among species (preying, competition, cooperation, parasitism and so on) affect the stability of whole ecosystems? Understanding the relations between diversification of whole ecosystems and underlying dynamics of each species has been one of the most challenging problems in science of complex systems [1, 2, 3, 4, 5, 6].

Since real ecosystems are organized through Darwinian processes, it is natural to construct model ecosystems through trial and error schemes: the model should include some kind of rules of invasions, mutations or extinctions. In this paper, we study a simple population dynamical model in which the ecosystem self-organize to diverse structure through invasions and extinctions.

The authors have proposed a simple population dynamics model called the “scale invariant” model in

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which the interaction term are given as follows:

$$a_{ij} \left(\frac{x_i}{x_j}\right)^\lambda x_j = a_{ij} x_i^\lambda x_j^{1-\lambda}, \quad (1)$$

where $0 < \lambda < \frac{1}{2}$. The model succeeded in organizing diversifying ecosystems [7]. Furthermore, it was found that the model reproduces statistical characteristics of real ecosystems. For example, life span of species obtained from the simulation shows good agreement with fossil data and is well fitted by a q-exponential function[8]. Topological feature of food web structures is also reproduced by the model [9].

Those facts implies the simple model still captures some essential features of the real ecosystem. Therefore it is natural to expect that some features are universally shared in systems in which many species make interactions with each other. In this paper, the relationship between the interspecies interactions and diversity and the stability of the system is systematically studied using the scale-invariant model.

2 Model

2.1 population dynamics

The population dynamics of species is described as follows:

$$\dot{x}_i = -c_i x_i + \sum_{a_{ij} < 0} a_{ij} x_i^\lambda x_j^{(1-\lambda)} + \sum_{a_{ij} > 0} a_{ij} x_i^{(1-\lambda)} x_j^\lambda, \quad (2)$$

where x_i is the population density and c_i is the metabolization rate of i -th species. The equation consists of the metabolization term and the scale-invariant interaction terms with the characteristic exponent $0 < \lambda < \frac{1}{2}$.

We focus on energy transport in the food web and only assumes prey-predator interaction for simplicity. Hence interaction coefficients are assumed to be anti-symmetric form : $a_{ij} = -a_{ji}$. All metabolization rate c_i are set to be 1 in the following. Without any interaction terms, x decays exponentially according to the metabolization term.

For simplicity, λ is set to be uniform for all species in each simulation. Preying term is limited to be convex as a function of prey and predator. This corresponds that preying rate per predator saturates under the condition when prey and predator are abundant. These saturation is not so unrealistic and will be common in nature.

Since species mentioned above do not have growth term, we need some autotrophic species which have growth term. Hence we introduce a unique producer, which is called “plant” species in the following. And we call the heterotrophic species mentioned above “animal” species. The role of the plant species is to supply energy to animal species. The population dynamics of the plant species consists of a logistic growth term and interaction terms. The equation is as follows:

$$\dot{x}_0 = Gx_0(1 - x_0) + \sum_j a_{0j}x_0^\lambda x_j^{(1-\lambda)}, \quad (3)$$

where G is the growth rate.

In our model, only the logistic growth term have the scale dependent form and, therefore, this term determines the scale of x of the whole system. Energy generated by plant species are distributed to animal species by preying interactions. Animal species dissipate energy gained directly or indirectly from plant species. Hence animal species can not survive without energy supplied by plant. We consider the system to be organized by one plant and many animal species. In the following, growth rate is set to be large (100) in order to avoid the whole extinction caused by the extinction of the plant species.

2.2 addition of new species and extinction

To see the dynamics of species richness, the rules of invasions of new species and extinctions are introduced in this model.

If the population of i -th species (x_i) becomes 0, the species is regarded as being extinct and eliminated from the system. Animal species which become to have no prey also go extinct.

Invasions of new species are applied when all the populations of the system become stable. Only one species invades at a time. The initial population density of new comer is chosen to be very low (10^{-8}). The number of interaction of new comer is selected randomly from $\{1, 2, 3, \dots, m\}$. The interaction coefficients are also selected randomly from uniform distribution ranging $[-\alpha, \alpha]$. Therefore m and α are the parameters which determines the strength of interaction. In the beginning of each simulation, there exists only plant species in the system.

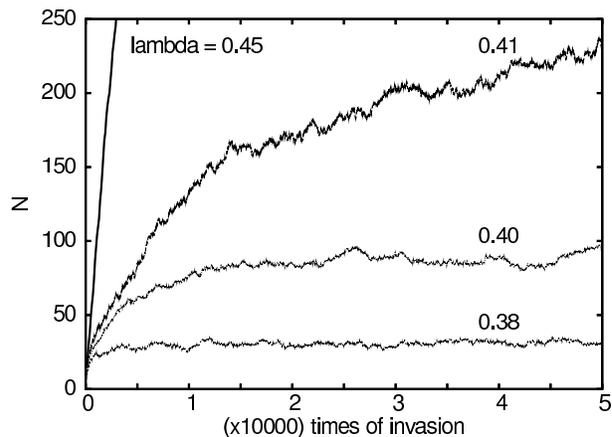


Figure 1: Temporal behavior of N when λ changes. Four lines corresponds to the case when $\lambda = 0.45$ (diversifying phase), 0.41 (near critical value), 0.40 (steady phase) and 0.38 (steady phase) from top to bottom respectively. The lines are averaged over 10 samples($\lambda = 0.45$) or 100 samples($\lambda = 0.41, 0.40, 0.38$). The diversity saturates when $\lambda < \lambda_c$, on the other hand, it continues to increase when $\lambda \geq \lambda_c$.

3 Results

3.1 diversifying behavior

First we investigated the dependence of temporal behavior of the number of species, N , on the interaction exponent λ . The parameters were set to $\alpha = 1.0, m = 5$.

Temporal behavior of N shows two phases as λ changes. Fig. 1 shows typical dynamics of diversity in both two phases. The first phase is observed when λ is smaller than some characteristic value λ_c . In this phase, the ecosystem tend to collapse and N do not increase. The system remains to be a simple structure. We call this phase “steady phase”. The other phase is “diversifying phase”. This phase is found when λ is larger than λ_c . In this phase, N begin to increase with time and large scale community of species can be organized. Diversity spontaneously emerges and the system can maintain the diversity in this phase. Near the boundary of these two phases ($\lambda \approx \lambda_c$), N fluctuates with neither trend to grow nor to collapse. Sample average of N grows as $\propto \sqrt{t'}$ approximately, here t' is number of invasions.

The system has tendency to have more species with larger λ in both two phases. Enlargement of λ enables the system to have more coexisting species. The average number of species, $\langle N \rangle$, in steady phase are plotted

as a function of λ in Fig. 2. We define the diversifying phase as the phase in which N tend to increase after 40 thousands invasion times. Critical value λ_c is 0.41 and the $\langle N \rangle$ in steady phase diverges as $(\lambda_c - \lambda)^{-\mu}$. The exponent μ is about 1.

The critical behavior can be understood as an asymmetric random walk in diversity space. If the probability that N increases (p_+) and the probability that it decreases (p_-) are independent of N , the temporal change in N should be described by asymmetric random walk. When $\lambda < \lambda_c$, p_+ is considered to be smaller than p_- . Hence N remains in certain range. When $\lambda = \lambda_c$, two probabilities are considered to become the same ($p_+ = p_-$). When $\lambda > \lambda_c$, p_+ becomes larger than p_- . Hence N diverges to infinite as time when $\lambda \geq \lambda_c$. N corresponds to distance of random walker from its starting point because N is bounded to be positive. Therefore the sample average of the N diverges as $\propto \sqrt{t}$ when $\lambda = \lambda_c$, which is qualitatively consistent with the simulation result. If $\Delta p \equiv (p_- - p_+)$ are proportional to $(\lambda_c - \lambda)$, $\langle N \rangle$ diverges as $(\lambda_c - \lambda)^{-1}$, which is also consistent with the simulation result.

Behavior of N is also depend on m and α . Larger m or α makes the system harder to organize diverse structure. Therefore the observed phase is depend on m, α and λ . Fig. 3 shows the phase boundary between two phases and λ_c monotonously increase with m and α . This can be explained that λ must be large enough that the ecosystem can diversify when m or α is larger. The result seems to be consistent with the “paradox of ecology”: higher connectance and higher magnitude of interactions make species prone to extinct.

3.2 stability of emerged ecosystems

Since the dynamics of populations is asymptotically stable in almost all the case, we can estimate the stability of the whole ecosystem by calculating the eigenvalues of linear stability matrix ($S_{ij} = \frac{\partial x_i}{\partial x_j}$) around its fixed point. Although temporal behavior of N depends not only on stability but also on feasibility, stability is considered to be a key factor to diversification. In addition, comparison with May’s argument will be also important.

We calculated the linear stability matrix and evaluated the stability using eigenvalues of linear stability matrix. Since surviving species are selected through extinctions, the linear stability can not be evaluated directly from λ , m and α . They must be calculated from the simulation results. We executed simulations till N become 50 for each parameters and then calculated the eigenvalues of the linear stability matrix.

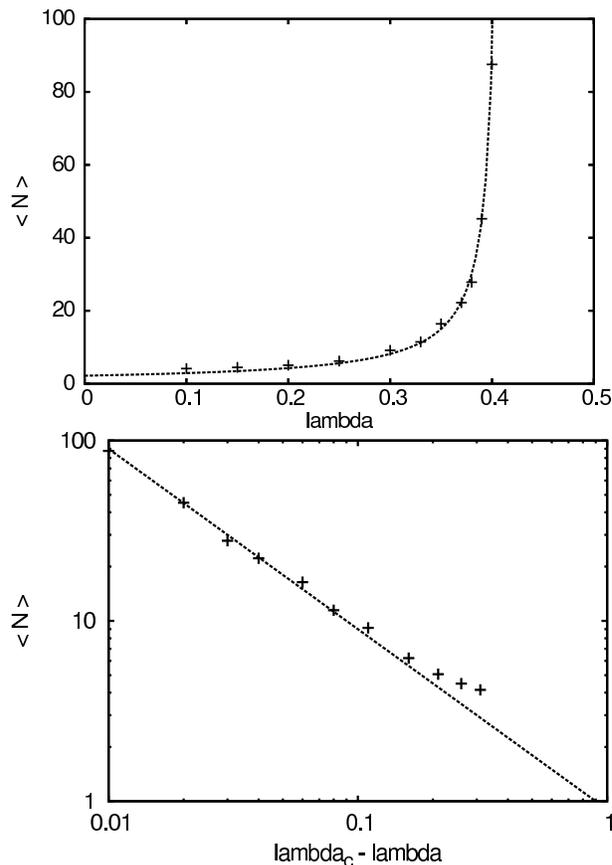


Figure 2: Average number of species in steady phase is shown as a function of λ (left) and $\lambda - \lambda_c$ (right). The dotted line corresponds to a function proportional to $(\lambda_c - \lambda)^{-1}$. The critical value λ_c is 0.41.

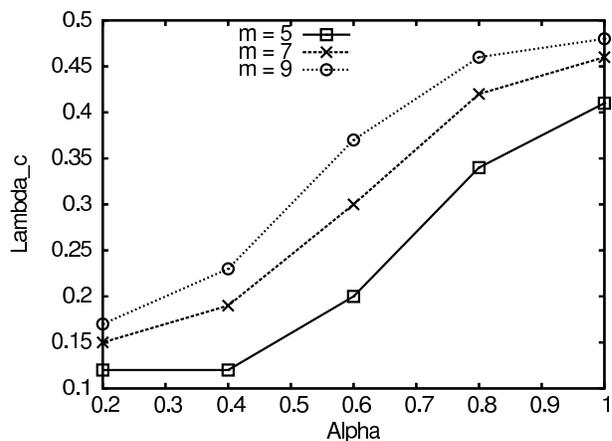


Figure 3: Critical values λ_c as a function of α . Three lines corresponds to the case $m = 9, 7$ and 5 from top to bottom.

Fig. 4 shows the distributions of the real part of the eigenvalues. The distributions moves to smaller side (left side in Fig. 4) and becomes more sharp around their peak as λ becomes larger. This means that the whole ecosystem becomes more stable when λ becomes larger. Fig. 5 shows the distributions of off-diagonal elements of the linear stability matrix. This graph shows that the off-diagonal elements of the linear stability matrix are widely distributed when λ is large. the variance of the off-diagonal part become larger as λ increases. According to May's argument, large variance of off-diagonal part of the matrix destabilize the system when elements are completely random. However this plot shows inverse results and seems to conflicting with May's results. The reason why large λ stabilize the system even though variance of the elements increases is that the matrix become more close to anti-symmetric form from random matrix as λ increases. Since we assume a_{ij} to be anti-symmetric form, the matrix becomes closer to anti-symmetric form when λ increases. The distribution in Fig. 5 certainly become more symmetric around 0 when λ is large.

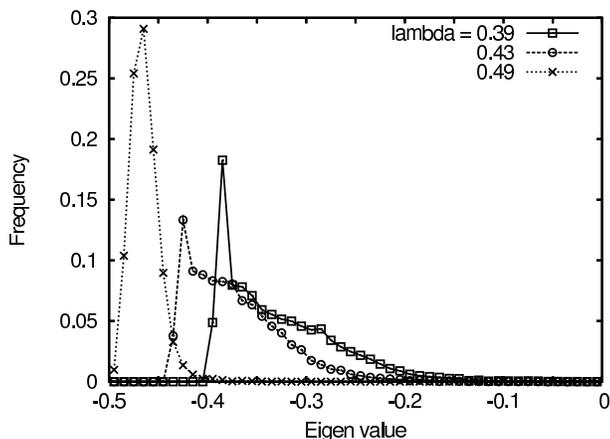


Figure 4: Distributions of eigenvalues when 50 species coexist with each λ . The data are averaged over 500 samples.

4 Conclusion

We have found that the diversity of the system in the scale invariant model shows a kind transition from poor states to diversifying states as changing the characteristic exponent λ . We could find a similarity between the transition and the ordinal second-order phase transition. The linear stability analysis illus-

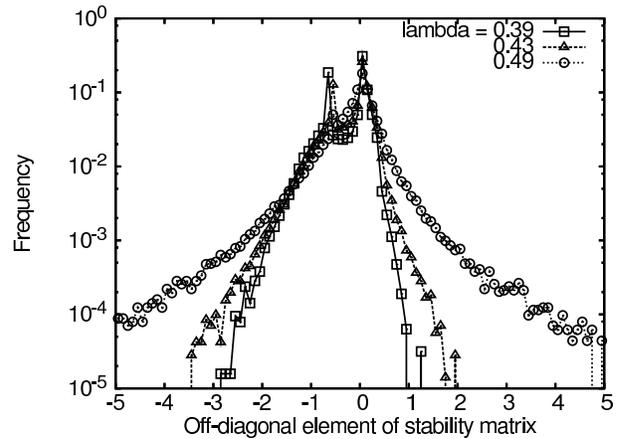


Figure 5: Distributions of off diagonal part element of the stability matrix when 50 species coexist with each λ . The data are averaged over 500 samples.

trated that the larger λ brings both stronger interactions and stabilizing of the system together.

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