RANK-SIZE RELATION FOR A MULTI-SPECIES SYSTEM WITH AN EXCLUSIVE INTERFERENCE

HIROMI SENO

Department of Mathematics, Faculty of Science, Hiroshima University,
Kagamiyama 1-3-1, Higashi-hiroshima, 724 Japan

ABSTRACT

A rank-size relation for a stationary distribution of a multi-species diffusion system is considered. Each species in the community is characterized by the population size in an isolated region. It is easily able to be assigned the rank $k(= 1, 2, \ldots)$ of species from the largest to the smallest with respect to the population size. We discuss the rank-size relation of a stationary community, making use of a stationary solution for a multi-species system of diffusion equations with an exclusive interference among species.

Keywords : Rank-size relation, diffusion system, exclusive interference, niche-preemption model.

1. Introduction

In a multi-species community, it is expected that a rank-size relation among species may characterize interspecific competitions among them for resources: foods, light, space, etc. Now, focusing on a bounded region where populations are afforded to habit, we can assigned the rank $k(= 1, 2, \ldots)$ of sampled species from the largest to the smallest with respect to its population size X_k. Then, a rank-size relation can be obtained: $X_k = S(k)$. Some particular types of rank-size relation were observed for samples of various contexts, and have been theoretically discussed [9,13,14,19] (Fig. 1). Auerbach [1] found the following type of rank-size relation fit for data of urban populations:

$$X_k \propto k^{-1/(q-1)} \, ,$$

where q is a positive constant such that $1 < q \leq 2$. The same type of rank-size relation has been observed also for some data in other contexts: personal incomes [8], occurrence of words in a book or in a number of issues of a newspaper [2], number of biological species in genera ([4,16], and also see the references in [9,17]). Motomura [6] and Corbet [3] fit another relation, the geometric law, to the data of populations of multi-species communities:
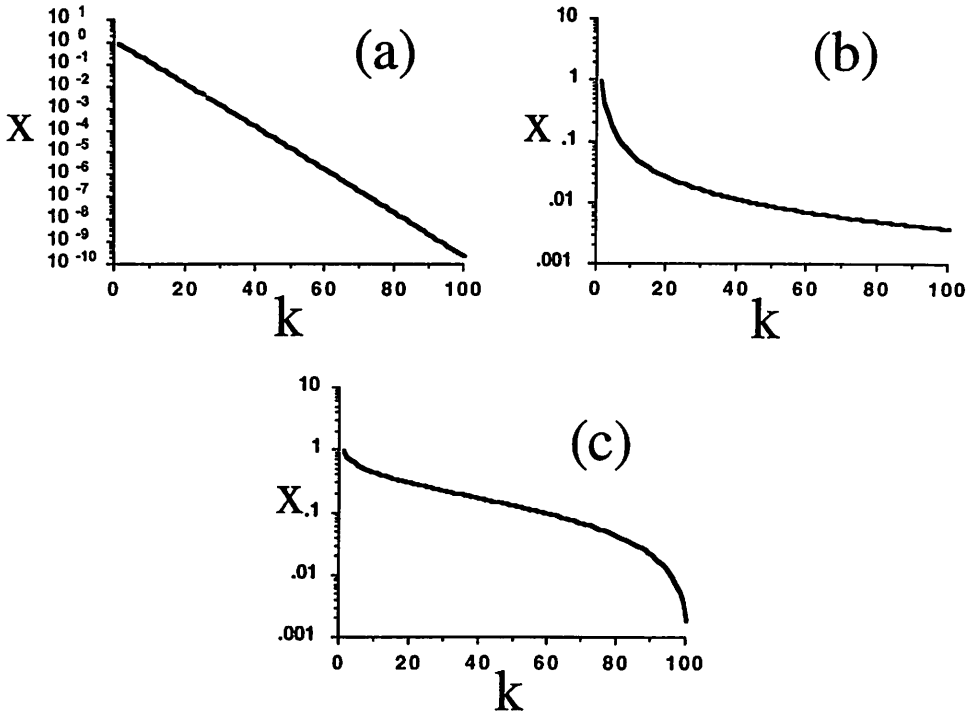
$$X_k \propto r^k \, ,$$

Fig. 1. Rank-size relation for well-known models. (a) $X_k = c'r^k$ $(0 < c', 0 < r < 1)$; (b) $X_k = ck^{-1/(q-1)}$ $(0 < c, 1 < q \le 2)$; (c) Broken-stick model, $X_k = (1/w) \sum_{j=k}^{w} (1/j)$.

where r is a positive constant less than 1. These special types of size distribution can be considered made use of mathematical models [11,13,18]. Especially, with *the niche preemption hypothesis* [7,15], the geometric law is well-knownly explained. Suppose that the dominant species in a w-species community preempts as its share a fraction $1 - r$ of the limiting resource, the second strongest species preempts a fraction $1 - r$ of what remains, and so on. Suppose also that the frequency of each species is proportional to the resource fraction it has preempted. Then, the rank-frequency list is $1 - r$, $(1 - r)r$, $(1 - r)r^2$, ..., $(1 - r)r^{w-2}$, $(1 - r)r^{w-1}$. Further, some other theoretical models on the rank-size relation are well-known, of which the broken-stick model and the niche overlapping model [5] are very famous. The former brings the following rank-size relation:

$$X_k = \frac{1}{w} \sum_{j=k}^{w} \frac{1}{j} ,$$

where w is the total number of considered species. As seen from its naming, the limiting resource divided up is likened to a "stick", or line, of unit length that is

broken into w disjunct segments by breaks at $w-1$ points located at random along its length. The length of the segments represents the "size" of each species. With this assumption, the above rank-size relation can be derived [10]. Next, the latter's rank-size relation is:

$$X_k = 1 - \frac{w!\Gamma(w-k+3/2)}{(w-k)!\Gamma(w+3/2)} .$$

Γ is the gamma function [9]. In this case, the environment is likened to a unit "stick". It is supposed that the frequency of each species is proportional to the distance between two points located at random upon it. The species are assumed to be independent of one another and the model differs from the niche preemption and the broken stick models in not assuming that some limiting resource must be shared among competitors but rather that each species takes what it needs. These models belong to the class of "resource apportioning models" [9,14]; such models are constructed by postulating the way in which coexisting species subdivide among themselves some necessary resource which is assumed to be the limiting factor that sets a limit to each species' population size.

In this paper, we investigate a rank-size relation deduced by a model of diffusing multi-species community, which was constructed by Teramoto and Seno [12]. In the model, an interspecific competition is embodied by an exclusive interference among species, which can be regarded as a competition for the space. Increasing density of a species population has such effect as to cause to decrease that of another species' population. Making use of a system of diffusion equations which describes the model, only a stationary solution will be under consideration in this paper. Differently from some previous models, our approach begins with some dynamical assumptions which define the dynamical structure among species and the enhanced stationary distribution is considered as the result from the interspecific dynamics. Our model does not belong to the "resource apportioning models", because the population size of each species is assumed to be determined not by the resource share but by the interference strength with the other dominant species. The population size of a species exposed to the strong exclusive interference effect from some dominant species is surpressed smaller than that of another species exposed to the weaker exclusive effect from any dominant species. By the way, since our discussion is focused only on the stationary state, it may be vulnerable for a multi-species community whose structure is unstably variable.

2. Statement of Model

By Teramoto and Seno [12], the following type of a system of density-dependent diffusion equations was investigated with respect only to its stationary solution up to two-species system:

$$\frac{\partial \mathbf{n}}{\partial t} = -\frac{\partial \mathbf{J}}{\partial x} \tag{2.1}$$

$$\mathbf{n} = (n_1, n_2, \ldots, n_w)^{\mathrm{T}}$$

$$\mathbf{J} = (J_1, J_2, \ldots, J_w)^{\mathrm{T}}$$

$$J_i = -n_i \frac{\partial}{\partial x}(\mathbf{U} + 2\mathbf{Bn} + \mathbf{\Gamma n})_i \quad (i = 1, 2, \ldots, w) \tag{2.2}$$

$$\mathbf{U} = (U_1(x), U_2(x), \ldots, U_w(x))^{\mathrm{T}}$$

$$\mathbf{B} = \begin{pmatrix} \beta_1 & & & & 0 \\ & \beta_2 & & & \\ & & \ddots & & \\ & & & \beta_{w-1} & \\ 0 & & & & \beta_w \end{pmatrix}$$

$$\mathbf{\Gamma} = \begin{pmatrix} 0 & & & & \\ \gamma_{12} & 0 & & & 0 \\ \gamma_{13} & \gamma_{23} & 0 & & \\ \vdots & & & & \\ \vdots & & & 0 & \\ \gamma_{1w} & \gamma_{2w} & \cdots & \cdots & \gamma_{w-1,w} & 0 \end{pmatrix}$$

n_i is the ith species' population density at position x and time t. w is the number of species considered now.

U_i is a system potential function for the ith species, satisfying the following conditions for any i:

(P1) U_i is smooth on $\Omega - \{0\}$

(P2) $\left[\dfrac{dU_i}{dx}\right]_{0 \le x} \ge 0 \qquad$ on Ω

(P3) $U_i(-x) = U_i(x)$

(P4) $U_i(x) < +\infty \qquad$ on $\partial\Omega$,

where Ω is a considered region, that is a connected interval which contains the origin $x = 0$. $\partial\Omega$ is the boundary of Ω. Following these assumptions for the system potential, each population has a tendency to aggregate in the direction to the origin $x = 0$. This tendency can counterbalance to the exclusive interference effect.

In this paper, we consider only the following type of system potential $\mathbf{U}$:

$$\mathbf{U}(x) = \Psi(x)\mathbf{K} ,$$

where $\mathbf{K} = (\kappa_1, \kappa_2, \ldots, \kappa_w)^{\mathrm{T}}$ and κ_i is a positive constant which represents the ith species' sensitivity to a system potential function, $\Psi(x)$, which is a species-independent scholar function independent of the community structure. $\Psi(x)$ can

be regarded as the expression of the combined system potential over the considered species. This type of system potential was assumed also by Teramoto and Seno [12], in which it is called "environmental potential".

$\beta_i n_i$ corresponds to the density dependent diffusion coefficient for the ith species, which depends only on its own density and is independent of any other species' densities.

A positive value γ_{ij} introduces an effect of exclusive interference for the jth species from the ith. A repulsive force originated to the population density of the species from 1 to $i - 1$th is assumed to work to the ith species. Therefore, we can regard the species' order i as indicating a dominancy in terms of the exclusive interference effect.

Boundary Condition: We consider an interval $\Omega = (-L/2, L/2)$ which has a length L. At the boundary $\partial\Omega$, that is at $x = \pm L/2$, the following condition is assumed:

$$\mathbf{n}\left(\pm\frac{L}{2}, t\right) = 0 . \tag{2.3}$$

This means that the population never returns back into Ω once it gets out of Ω. If the flux (2.2) of population density is density-independent with a constant diffusion coefficient, any species' population must become extinct at $t \to \infty$ because (2.1) does not have any term of population growth and population only leaks out from the boundary. But, in the case of density-dependent diffusion, this is not always true. In the following section, we see that there can exist a non-zero stationary distribution for (2.1).

3. Analysis

3.1. *Stationary Distribution*

The stationary distribution of (2.1) is given by the solution of $\mathbf{J} = 0$. As easily seen from (2.2), $\mathbf{J} = 0$ has 2^w varieties of its solution depending on which n_i is zero or positive on Ω. In this paper, let us focus on the stationary state satisfying the following (Fig. 2):

$$(\text{H}) \qquad n_i^* > 0 (i = 1, 2, \ldots, w) \text{ on } \Omega - \partial\Omega .$$

At $t \to \infty$, the reached stationary state may depend on the initial distribution. Besides, it is likely that an species disappearing at $t \to \infty$ may have an effect to the existence of another species through the exclusive interference when $t < \infty$. But, let us assume that the observed community is at the stationary state and that what we can do is to sample present species in it. The numbering i of those species is assumed to follow the species' dominancy with respect to the exclusive interference affected by the other species, ordered from the species minimally affected to maximally affected. Note that the first dominant species is now assumed not to be
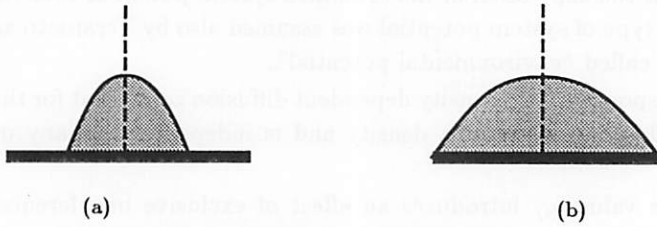
(a)   (b)

Fig. 2. The possible stationary distribution for (2.1). (a) shows a truncated distribution in Ω, which is the case excluded in this paper. Only the case of (b), in which the distribution is positive everywhere within the patch and zero at the boundary of Ω, is considered in this paper.

affected by the exclusive interference from any other species. In the other words, the first dominant species is not exposed to competitions with any other species, while the distribution of the first dominant species affects that of the other species. As showed by Teramoto and Seno [12], it is possible that, depending on the initial distribution and the strength of interference, our system may have a stationary state at which a species has a distribution disconnected and its density is zero in an interval containing the origin $x = 0$. Moreover, it is also possible that the support of a species' distribution has a length less than that of Ω (Fig. 2). In this paper, we do not consider these cases and focus on the stationary state satisfying (H). This means the following requirement for our model: *The initial total population of each species is large enough not to cause any disconnected stationary distribution, and enough to satisfy* (H). In the other words, each population has the size maximally allowed in Ω. Thus, the considered stationary distribution of every species is assumed to be connected in Ω and has the length L.

Now, the stationary distribution is obtained from:

$$\mathbf{U} + 2\mathbf{B}\mathbf{n}^* + \Gamma\mathbf{n}^* = \mathbf{C} ,$$

where $\mathbf{C} = (C_1, C_2, \ldots, C_w)^{\mathrm{T}}$. C_i is a constant determined by the boundary condition (2.3): $\mathbf{C} = \mathbf{U}(L/2)$. Lastly, we obtain

$$(2\mathbf{B} + \Gamma)\mathbf{n}^* = \mathbf{U}\left(\frac{L}{2}\right) - \mathbf{U}(x) . \tag{3.1}$$

Since the matrix $2\mathbf{B} + \Gamma$ is regular, eventually

$$\mathbf{n}^* = (2\mathbf{B} + \Gamma)^{-1}\left\{\mathbf{U}\left(\frac{L}{2}\right) - \mathbf{U}(x)\right\} . \tag{3.2}$$

Especially,
$$n_1^* = \frac{1}{2\beta_1}\left\{U_1\left(\frac{L}{2}\right) - U_1(x)\right\} . \tag{3.3}$$

3.2. *Weighted Relative Frequency*

For the potential $U(x) = \Psi(x)K$, we can reduce the number of considered parameters, using the following variable transformation:

$$\mu_i \equiv \frac{\kappa_i}{2\beta_i} \; ; \quad \sigma_{ij} \equiv \frac{\mu_i \gamma_{ij}}{\kappa_j} \; ; \quad \hat{n}_i \equiv \frac{n_i^*/\mu_i}{n_1^*/\mu_1} \; , \tag{3.4}$$

where $i = 1, 2, \ldots, w$; $j = i+1, i+2, \ldots, w$. $\hat{n}_i$ can be called the ith species' *weighted relative frequency* of population density. Then, we obtain (Appendix A):

$$\hat{n} = (E + S)^{-1} e \; , \tag{3.5}$$

where we define the following vectors and matrices:

$$\hat{n} = (1, \hat{n}_2, \ldots, \hat{n}_w)^T$$

$$e = (1, 1, \ldots, 1)^T$$

$$S = \begin{pmatrix} 0 & & & & \\ \sigma_{12} & 0 & & 0 & \\ \sigma_{13} & \sigma_{23} & & & \\ \vdots & & & & \\ \vdots & & & 0 & \\ \sigma_{1w} & \sigma_{2w} & \cdots & \cdots & \sigma_{w-1,w} & 0 \end{pmatrix}$$

$$E = \begin{pmatrix} 1 & & 0 \\ & \ddots & \\ 0 & & 1 \end{pmatrix} \; .$$

Lastly, the weighted relative frequency $\hat{n}$ is characterized only by the matrix S, independently of $\Psi(x)$.

Up to now, we have focused on the population density n^*. But, those arguments are valid also for the total population N_ω^* in any sub-region $\omega \subseteq \Omega$, which is defined by:

$$N_\omega^* \equiv \int_\omega n^* dx \; . \tag{3.6}$$

Indeed, integrating both sides of (3.1) on ω and using (3.6), we can easily reach the result corresponding to (3.7). Thus, the following can be shown:

Result 1: *For the stationary multi-species community satisfying (H) for the diffusion system (2.1), the relative frequency of total population on any sub-region $\omega \subseteq \Omega$ is the same with that of population density at any position x on Ω.*

This result can be translated as follows: The relative population frequency among species is *independent of the sample region* in Ω. Thus, the rank-size relation is independent of the sample region, too. Hereafter, we consider only $\hat{n}$.

By the way, in order that $\hat{n}$ given by (3.5) consists with (H), there must be some constraints for S. We can easily obtain the following sufficient condition for it (Appendix B):

Result 2: *If* $\underset{i}{\text{Max}} \sum_{k=1}^{i-1} \sigma_{ki} < 1$, *then* $\hat{n}$ *given by (3.5) consists with (H).*

Further, we can obtain the following necessary condition for it, too (Appendix C):

Result 3: *If* $\hat{n}$ *given by (3.5) consists with (H), then* $\underset{j}{\text{Max}} \underset{i}{\text{Min}} \sigma_{ij} < 1$.

In this paper, we consider four specific cases for $\{\sigma_{ij}\}$:

(i) *Even-interference case:* $\sigma_{ij} = \sigma = $ const. for any i, j. Every species cannot distinguish the species of dominant order. In other words, the exclusive interference effect is determined by the population density summed up through all the dominant species.

(ii) *Dominant species-dependent case:* $\sigma_{ij} = \sigma_i$ for any i, j. The strength of exclusive interference depends only on which species of dominant order undergoes the effect. For example, it is the case when the strength is determined only by the body size characterizing each of dominant species population.

(iii) *Subordinant species-dependent case:* $\sigma_{ij} = \sigma_j$ for any i, j. Each species cannot distinguish any species of dominant order. The population density summed up over the dominant species contributes to the exclusive interference. Differently from the even-interference case, the exclusive interference effect is determined by multiplying subordinant species-specific weight to the population density summed up over the dominant species. The weight, that is, the strength of the effect depends on which subordinant species is affected. For example, it is the case when the strength is determined only by the strength of the subordinant species' tendency to avoid the dominant species.

(iv) *Completely random variation* of $\{\sigma_{ij}\}$: Each σ_{ij} is assumed to be independent of the others and follow the uniform distribution whose mean value is $\langle\sigma\rangle$ and variance is $\delta\langle\sigma\rangle$ $(0 \le \delta \le 1)$. δ is the coefficient of variance of $\{\sigma_{ij}\}$. Then, the possible maximal value of $\{\sigma_{ij}\}$ is $(1+\delta)\langle\sigma\rangle$ and the minimal is $(1-\delta)\langle\sigma\rangle \ge 0$.

For the former three special cases, the form of $\hat{n}$ can be explicitly obtained as the function of $\{\sigma_{ij}\}$.

(i) *Even-interference case:*

$$\hat{n}_i = (1-\sigma)^{i-1} \quad (i = 1, 2, \ldots, w) . \tag{3.7}$$

Clearly, $\sigma < 1$ is sufficient and necessary in order of the consistence between $\hat{n}$ and (H).

(ii) *Dominant species-dependent case:*

$$\hat{n}_i = \prod_{k=1}^{i-1}(1 - \sigma_k) \quad (i = 2, 3, \ldots, w) \,. \tag{3.8}$$

As easily seen, $\sigma_i < 1$ for any i is sufficient and necessary for this case in order of the consistence between $\hat{n}$ and (H).

(iii) *Subordinant species-dependent case:*

$$\hat{n}_i = 1 - \sigma_i \cdot \left\{ 1 + \sum_{j=2}^{i-1} \prod_{k=j}^{i-1}(1 - \sigma_k) \right\} \quad (i = 2, 3, \ldots, w) \,. \tag{3.9}$$

In order of the consistence between $\hat{n}$ and (H), the righthand size of (3.9) must be positive. Making use of numerical calculation, we obtain the critical value of such satisfactory $\{\sigma_{ij}\}$ (Fig. 3). If σ_j for a j is *below* the critical value, the consistence is violated and the stationary distribution is different from that considered now.
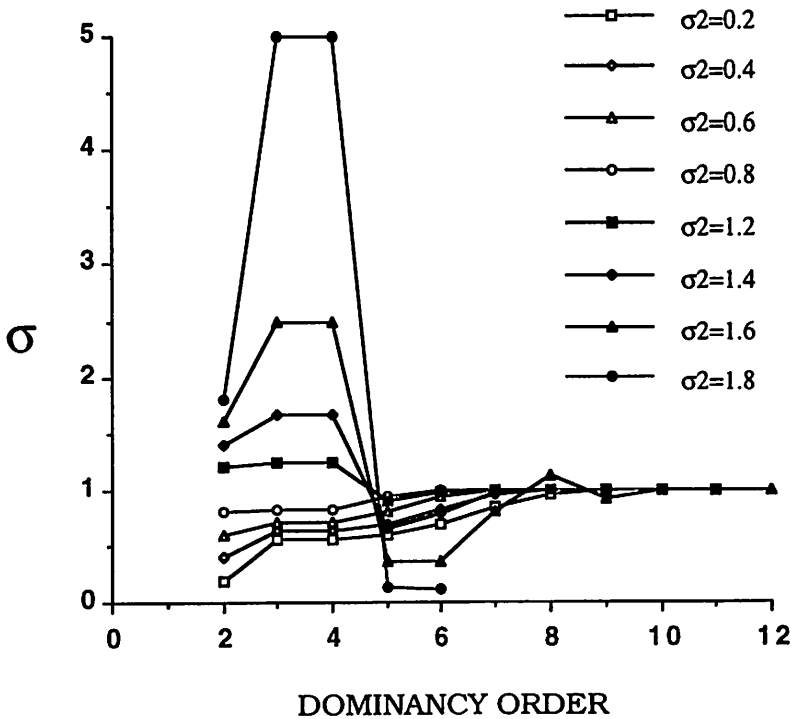
Fig. 3. Critical values of $\{\sigma_{ij}\}$ for the positiveness of the righthand side of (3.9) in case of the subordinant species-dependent case. Numerical calculations give the result for each given value of σ_2. If σ_j for some j is *below* the critical value, the stationary distribution is different from that considered in this paper.

In the following analysis, we investigate the relative frequency n̂ in these specific cases, including those with randomly given $\{\sigma_{ij}\}$. We focus on and investigate the effect of the randomness of $\{\sigma_{ij}\}$ to the relative frequency, using computer simulations explained in Appendix D.

3.3. *Fugitive Species*

(i) *Even-interference case:* As easily seen from (3.7), when $\sigma < 1$, the number of fugitive species w is infinite. On the other hand, when $1 \leq \sigma$, only the first dominant species can be fugitive and survive in Ω.

(ii) *Dominant species-dependent case:* Through numerical calculations for this case, the number of fugitive species w depends on given $\langle \sigma \rangle$ and δ. When $\langle \sigma \rangle \leq 0.5$, since $(1 + \delta)\langle \sigma \rangle \leq 1$ for any δ, the number is infinite, as easily seen from (3.8). The mean number of fugitive species $\langle w \rangle$ decreases as δ becomes larger when $0.5 < \langle \sigma \rangle < 1$, while it increases when $1 < \langle \sigma \rangle$ (Fig. 4(a)). On the other hand, the mean for $\{\sigma_{ij}\}$ averaged over the fugitive species almost coincides with the given $\langle \sigma \rangle$ when $\delta < 1$, while it decreases when $1 \leq \delta$. The mean is always less than 1, and so be should the maximum of $\{\sigma_{ij}\}$ for fugitive species, as easily seen from (3.8).

(iii) *Subordinant species-dependent case:* Also in this case, some numerical calculations show that the number of fugitive species w is significantly influenced by given $\langle \sigma \rangle$ and δ. Differently from the previous cases, the number of fugitive species appears finite for any positive $\langle \sigma \rangle$ and δ. The δ-dependency is clearly different between cases for small $\langle \sigma \rangle$ and for large $\langle \sigma \rangle$. For sufficiently small $\langle \sigma \rangle$ less than 0.5, the mean number of fugitive species $\langle w \rangle$ decreases as δ gets larger (Fig. 4(b)). Otherwise, it increases as δ gets larger. Also as for the mean for $\{\sigma_{ij}\}$ averaged
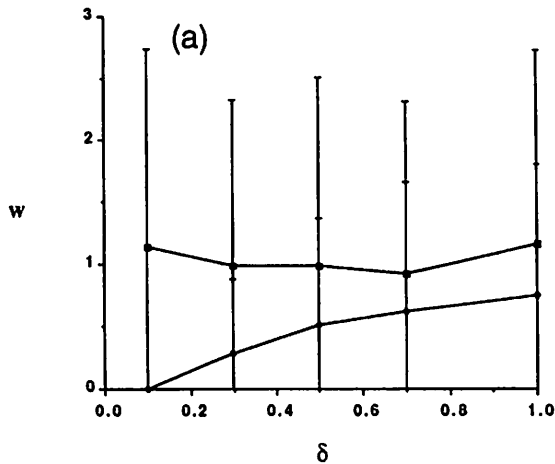
Fig. 4. Mean number of fugitive species, numerically calculated for (a) the dominant-species dependent case; (b) the subordinant-species dependent case; (c) the completely random $\{\sigma_{ij}\}$ case. The error bars are of S.D. Cases for four given values of $\langle \sigma \rangle$ are drawn.
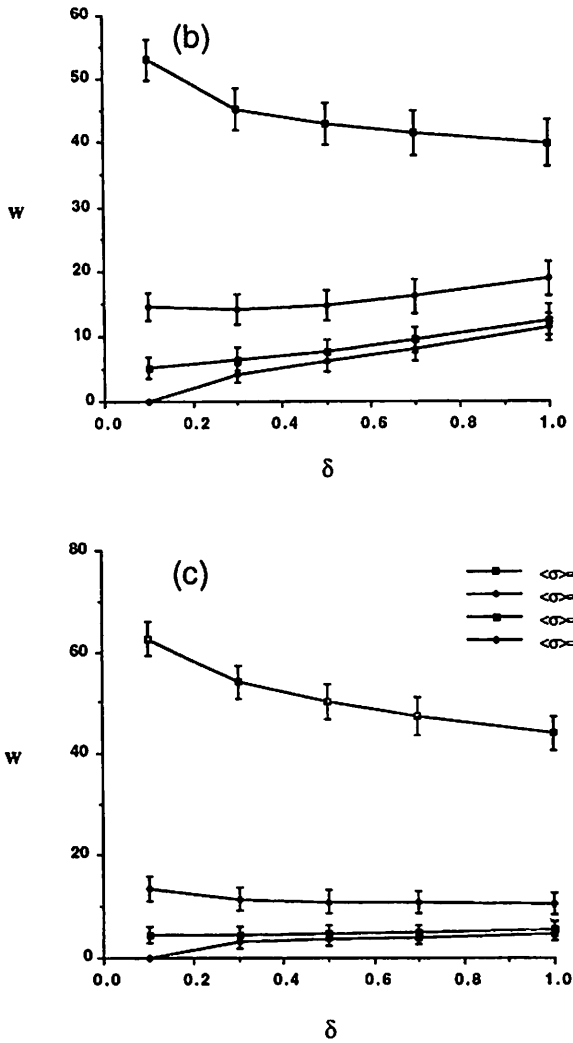
Fig. 4. (*Continued*)

over the fugitive species, some characteristics appears different from those in the previous cases. In this case, the mean decreases from given $\langle \sigma \rangle$ as δ gets larger for any δ. Besides, the maximum of $\{\sigma_{ij}\}$ in terms of fugitive species simultaneously decreases from less than or equal to 1, too.

(iv) *Completely random variation of* $\{\sigma_{ij}\}$: The number of fugitive species w is significantly affected by the randomness of $\{\sigma_{ij}\}$. By a number of numerical trials to obtain the number w, it is shown that w has δ-dependency similar to but different from that for the subordinant species-dependent case (Fig. 4(c)). When $\langle \sigma \rangle < 1$, the larger δ leads the less number of fugitive species. Besides, the mean value

of $\{\sigma_{ij}\}$ averaged over the fugitive species becomes smaller as the given possible variance of $\{\sigma_{ij}\}$ gets larger. In contrast, when $\langle\sigma\rangle > 1$, the larger δ appears to allow the larger number of fugitive species. For assuring this result, we made such computer simulations as to sample values of variance for some fixed $\langle\sigma\rangle$, below which no population but for the first dominant species is sampled. Hereafter, we call such a value of variance the "critical variance". The result is given in Fig. 5. The hypothesized tendency obviously appears. The critical variance becomes larger as $\langle\sigma\rangle$ gets larger. To consider this tendency of critical variance, we can easily obtain the following from Result 3:

Corollary: *If* $\hat{n}$ *given by (3.5) consists with (H), then* $\langle\sigma\rangle - \delta\langle\sigma\rangle < 1$.

The last inequality shows a relation between the mean $\langle\sigma\rangle$ and the coefficient of variance δ. It is overlaid in Fig. 5. Although the sampled critical variance has its own variance, its tendency is very similar to that derived in the above corollary. Note that some values of $\{\sigma_{ij}\}$ of the fugitive species possibly take the given maximal $(1+\delta)\langle\sigma\rangle$ or the given minimal $(1-\delta)\langle\sigma\rangle$, which is shown by some numerical trials.
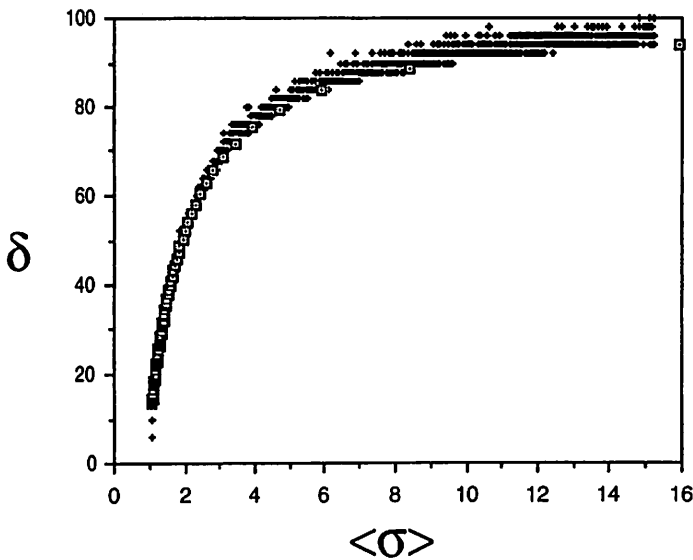
Fig. 5. The critical variance below which no population is sampled. "+" shows the numerical results, "□" is the critical point analytically obtained, mentioned as the corollary in the text.

3.4. Rank-Size Relation

(i) *Even-interference case:* From (3.7), we can obtain the following (Appendix E):

Result 4: *The weighted relative frequency* $\hat{n}$ *follows a geometric law in the order i of the dominancy, if and only if* $\sigma_{ij} = \sigma = const. < 1$ *for any i, j.*

Since the relative frequency (3.7) is monotonically decreasing with respect to i, i can be regarded as the rank of ith species' population size. If not only σ but all parameters are common among species, the exclusive interference effect is simply an exclusive effect of population density summed up in terms of species which have the higher dominancy. In this sense, the result (3.7) corresponds to that by the niche preemption model [7,15]. But, since (3.7) is derived only with the assumption $\sigma_{ij} = \sigma$, this result still has a degree of parameters' freedom, even though we might add another assumption $\mu_i = \mu$. Therefore, this result may be regarded as a kind expanding the result of the niche preemption model. It is very interesting that, differently from the niche preemption model, this result can be obtained for a stationary state reached by a dynamical process.

(ii) *Dominant species-dependent case:* For the random $\{\sigma_i\}$, it is concluded that, independently of the values of $\langle\sigma\rangle$ and δ, the rank-size relation follows a quasi-geometric law (see Fig. 6).
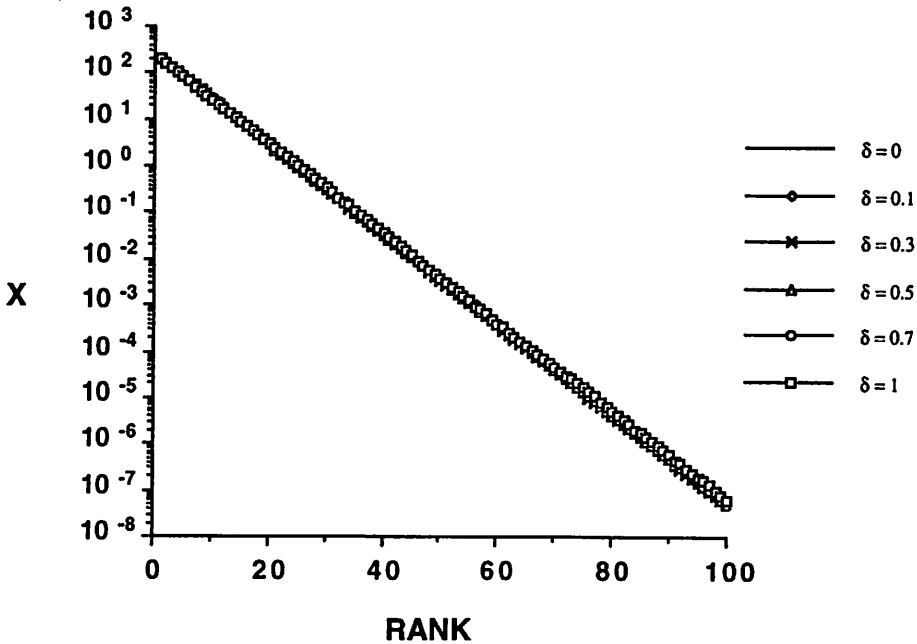
Fig. 6. Numerically sampled rank-size relation for the dominant-species dependent case. $\langle\sigma\rangle =$ 0.2. The δ-dependence is very little, and graphs for different values of δ are almost overlapped.

(iii) *Subordinant species-dependent case:* Contrarily to the previous case, the randomness of $\{\sigma_j\}$ significantly distorts the rank-size relation, compared to the geometric law (Fig. 7). Positive δ tends to shift up the population size of the lower rank and to shift down that of the higher rank. Especially, in case of large δ, the
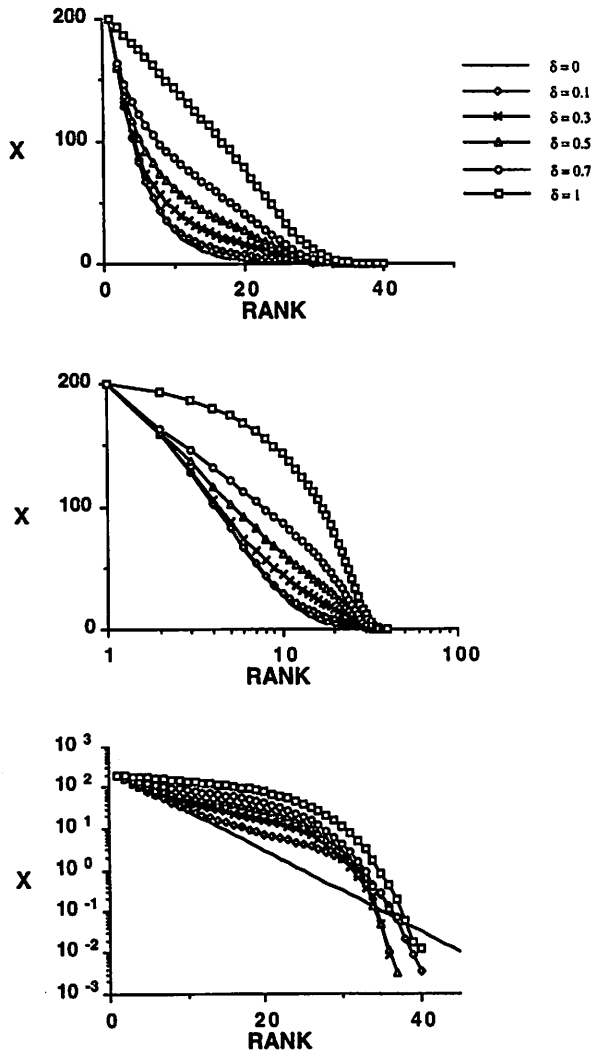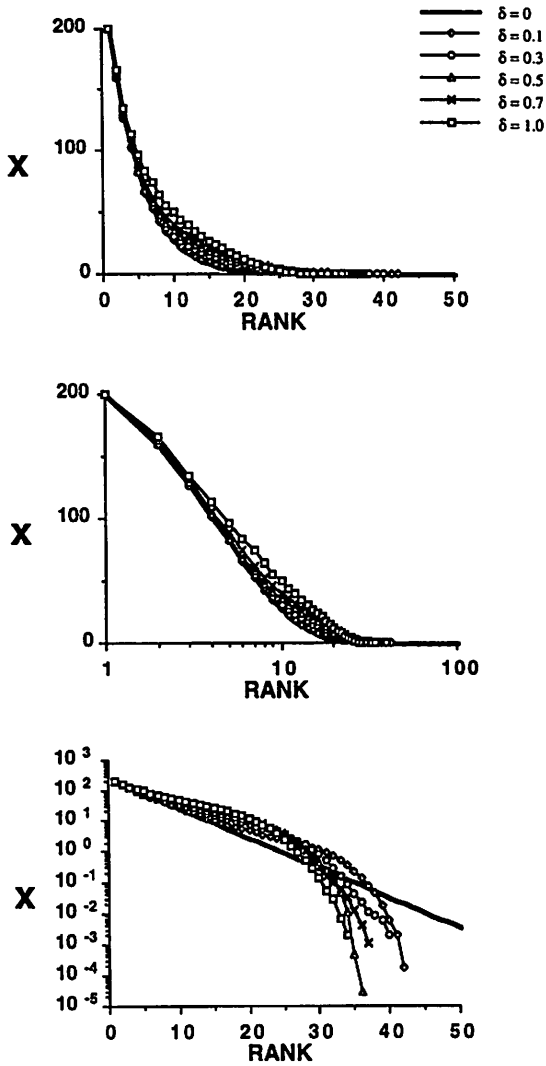
Fig. 7. Numerically sampled rank-size relation for the subordinant-species dependent case. $\langle \sigma \rangle = 0.2$. The rank-size relation is shown respectively in normal-normal, log-normal and normal-log axes.

rank-size relation distorts to an approximatedly linear one. On the other hand, the intermediate δ brings the rank-size relation to an approximatedly logarithmic one.

(iv) *Completely random variation of* $\{\sigma_{ij}\}$: Distortion of the rank-size relation is clearly shown in Fig. 8. Positive value of δ clearly distorts the rank-size relation from the geometric law. It seems that positive δ shifts up the population size in the lower ranks while shifts it down in the higher ranks. This tendency is the same

Fig. 8. Numerically sampled rank-size relation for the dominant-species dependent case. $\langle \sigma \rangle =$ 0.2. The rank-size relation is shown respectively in normal-normal, log-normal, and normal-log axes.

as in the subordinant-species case. However, the degree of distortion is smaller in this case than in the subordinant-species dependent case. Large δ brings the rank-size relation to an approximatedly logarithmic one. The rank-size relation for any δ cannot be approximated by any linear relation as in the subordinant-species dependent case.

As a consequence, the rank-size relation appears nonlinear even in normal-log axis, while the geometric relation in case of $\delta = 0$ shows a linear relation in it. Referring to Fig. 1 in which the other well-known models are shown, we can say that this distortion tends to lead the rank-size relation from the geometric toward another.

4. Discussion

We analyzed a relative population frequency embodied as a stationary state for a multi-species density-dependent diffusion system. Although the system is very simple, it is expected that it may contribute to the mathematical consideration on the species-abundance relation. Our model includes an interspecific exclusive interference, which can be regarded as a competition for space or as a specific population pressure effect among species. A typical species-abundance relation, the geometric law, can be derived from our model in a special case. This result indicates that the geometric law may have a close relation with the competition for space, as explained with the niche preemption hypothesis [7,15]. In this reason, our model can be regarded as extended from the niche preemption model, too.

Our model involves a hierarchy of dominancy among species, which is related to how many species' densities have effect on the distribution of each species: how many species have the exclusive effect on the considered one species determines the dominancy rank of the species in the multi-species system. The rank among species in terms of the population size can correspond to the order of dominancy. In such cases, the strength of exclusive effect among species is required to satisfy a specific relation. Thus, in general, such a typical rank-size relation may be difficult to be realized, whereas a relation distorted more or less from typical one can be sampled. Indeed, in our model, it is shown that the randomness of the strength of exclusive effect among species distorts the relation. On the other hand, however, even when the order of dominancy and the rank of population size are not coincident each other, some typical rank-size relations may be realized (Appendix F). Consequently, some typical rank-size relations can be sampled in nature with a positive probability. On the other hand, there is positive probability with which another rank-size relation is realized by the same dynamics that can realize a typical rank-size relation in the other cases. It depends on the realized interspecific relation whether a typical rank-size relation is sampled or not.

As already mentioned, the randomness of the strength of exclusive interference effect among species deforms the rank-size relation from the typical one. Rigorously speaking in our model, since each $\{\sigma_{ij}\}$ is independently subjected to the uniform distribution on $[(1 - \delta)\langle\sigma\rangle, (1 + \delta)\langle\sigma\rangle]$ with the common mean $\langle\sigma\rangle$, the mathematically expected value of $\hat{n}$ follows the geometric law which can be realized in the case when $\sigma_{ij} = \sigma = $ const. for any i, j. However, the expected value mentioned here could be embodied only with an infinite number of samples for n. In the other words, 'the expected value' is just regarded as ideal and in mathematical sense. In

reality, there must be some effect of 'chance' and of finiteness of samples. Therefore, the realized rank-size relation is possibly different from the ideally expected one. With a finite number of numerical sampling, it is analyzed and shown in this paper.

By the way, in some cases, the randomness seems to reduce the species diversity in the system. As shown in Fig. 4, the species diversity decreases as the randomness, i.e., the variance of exclusive interference parameter gets large when the mean is less than 1. In contrast, it seems that the randomness increases the diversity, when the mean of exclusive effect parameter is more than 1 and then no population except for the first species can exist at $t \to \infty$ if the variance is zero so that the randomness does not exist. Indeed, as seen in Fig. 4, the randomness can give the system a multi-species diversity even if the mean of exclusive interference parameter does not permit the existence of any population except for the first species. Consequently, when the exclusive interference effect is strong, the randomness works to increase the species diversity, while the randomness tends to reduce the diversity when the effect is relatively weak.

Our model includes no population growth term. In this reason, rank-size relation in our model may be regarded as for the time scale shorter than for that of population growth process. If a population growth was introduced in the model, some other features might appear. The model of density-dependent diffusion system with a growth term should be analyzed in the next step, but it is still an open problem. Our results may be acceptable when the growth is sufficiently slow compared to the diffusion speed.

Another speciality of our model is the system potential, which makes every populations have a tendency to aggregate to a common place. This tendency counterbalances to the interspecific exclusive interference effect and the density-dependent diffusion. Such situation may be embodied when there would be a place which has a favorable and attractive environment for several species.

Simple models may be sometimes too simple to consider the real phenomenon sampled in nature. But some may give useful cues to consider the phenomena in biological sense. We expect that the same will occur to our analysis.

Appendix A

In this appendix, we show the way how the variable transformation (3.4) brings the relation (3.5). We begin with introducing the following *relative frequency* of population density: $\tilde{n} = n^*/n_1^*$, which is given by

$$\tilde{n} = 2\beta_1(2B + \Gamma)^{-1} \frac{U\left(\frac{L}{2}\right) - U(x)}{U_1\left(\frac{L}{2}\right) - U_1(x)}, \tag{A1}$$

where (3.2) and (3.3) are used.

For the potential $U(x) = \Psi(x)K$, the relative frequency (A1) becomes:

$$\tilde{n} = \frac{2\beta_1}{\kappa_1}(2B + \Gamma)^{-1}K .$$ (A2)

Note that this equation is independent of $\Psi(x)$.

From (A2), we can easily get the following equation for the ith species:

$$2\beta_i \frac{n_i}{n_1} + \sum_{k=1}^{i-1} \gamma_{ki} \frac{n_k}{n_1} = 2\beta_1 \frac{\kappa_i}{\kappa_1} .$$

This equation can be rewritten with variables (3.4) as follows:

$$\frac{\mu_1}{\mu_i} \frac{n_i}{n_1} + \sum_{k=1}^{i-1} \frac{\mu_k \gamma_{ki}}{\kappa_i} \frac{\mu_1}{\mu_k} \frac{n_k}{n_1} = 1 .$$

This means $\hat{n} + S\hat{n} = e$, and brings (3.5).

Appendix B

We prove Result 2 for the consistency between (3.5) and (H). From (3.5), we can obtain

$$\hat{n}_i = 1 - \sum_{k=1}^{i-1} \sigma_{ki}\hat{n}_k \quad (i = 2, 3, \ldots, w) .$$ (B1)

Then,

$$\hat{n}_i > 1 - \left(\sum_{k=1}^{i-1} \sigma_{ki}\right) \cdot \underset{j}{\text{Max }} \hat{n}_j .$$ (B2)

Now, from (B1), $\hat{n}_i \leq 1$ for any i. Thus, (B2) brings us:

$$\hat{n}_i > 1 - \sum_{k=1}^{i-1} \sigma_{ki} .$$ (B3)

If the righthand size of (B3) is positive for any i, (H) is sufficiently satisfied. This means

$$1 - \underset{i}{\text{Max }} \sum_{k=1}^{i-1} \sigma_{ki} > 0 .$$

The result is proved.

Appendix C

We prove Result 3. From (B1),

$$\hat{n}_i \leq 1 - P_{i-1} \cdot \underset{k}{\text{Min }} \sigma_{ki} ,$$ (C1)

where $P_i = \sum_{k=1}^{i} \hat{n}_k$ ($i = 2, 3, \ldots, w$). If (H) is satisfied, the righthand side of (C1) must be positive for any i. This means

$$0 \le 1 - \underset{i}{\mathrm{Max}} \left\{ P_{i-1} \cdot \underset{k}{\mathrm{Min}} \, \sigma_{ki} \right\} . \tag{C2}$$

Making use of the trivial fact that $\hat{n}_1 = 1 < P_{i-1} \le P_i$ ($i = 3, 4, \ldots, w$), if (C2) is satisfied, then

$$0 < 1 - \underset{i}{\mathrm{Max}} \left\{ \underset{k}{\mathrm{Min}} \, \sigma_{ki} \right\} .$$

This proves the result.

Appendix D

In this appendix, the explanation of our computer calculation is given. $\{\sigma_{ij}\}$ is assumed to follow the uniform distribution whose mean value is $\langle \sigma \rangle$ and variance is $\delta^2/3$ ($0 \le \delta \le 1$). We used the following scheme in our computer calculation:

(A) Population densities $\hat{n}_i$ are calculated from $i = 2$ to 100, made use of (3.5) with randomly selected $\{\sigma_{ij}\}$.
(B) For obtained $\hat{n}_i$ ($i = 2, 3, \ldots, m$), if $\hat{n}_{m+1}$ becomes negative following (3.5), then $\hat{n}_{m+1}$ is put zero because it is against the assumption (H).
(C) By repeating (B) for 100 populations, remained populations are re-ordered from 1 to w, where w is regarded as the number of species fugitive in the considered region.

Appendix E

We prove Result 4. Suppose that $\hat{n}_i = \eta^{i-1}$ ($0 < \eta < 1$; $i = 2, 3, \ldots, w$). Then, from (3.5), we can obtain:

$$\eta^{i-1} = 1 - \sum_{k=1}^{i-1} \sigma_{ki} \eta^{k-1}$$

This can be rewritten as follows:

$$\sum_{k=1}^{i-1} \left\{ \sigma_{ki} - (1 - \eta) \right\} \eta^{k-1} = 0 ,$$

using the equation

$$1 - \eta^{i-1} = (1 - \eta) \sum_{k=1}^{i-1} \eta^{k-1} .$$

This equation must be valid for any i ($i = 2, 3, \ldots, w$). Thus, consequently $\sigma_{ki} = 1 - \eta$ for any k and i. This means that (3.5) gives a geometric law only when

$\sigma_{ij} = \sigma = $ const. for any i, j. Inversely, when $\sigma_{ij} = \sigma$ for any i, j for (3.5), we can explicitly obtain $\hat{n}$ as (3.7), which shows a geometric law.

Appendix F

In this appendix, for three typical rank-size relations, the geometric law, the Zipf's law, and the broken-stick law, we numerically calculate and exemplify distributions of $\{\sigma_{ij}\}$ which realize the typical rank-size relations.

Geometric law: Although Result 4 is valid only for the geometric law *in the order* i of the dominancy among species, it is likely that another geometric law may be realized from (3.5), whose rank-size order does not corresponds to that of the dominancy i. Such a geometric relation for (3.5) can be embodied with a special balance among $\{\sigma_{ij}\}$. In Fig. 9, an example distribution of $\{\sigma_{ij}\}$ is shown for 200-species system in the case when $\sigma_{ij} = \sigma_j$ for any i and j. In the case when $\sigma_{ij} = \sigma_i$, by a number of numerical calculations, a balance among $\{\sigma_{ij}\}$ does not seem to be easily realized for a large multi-species system.
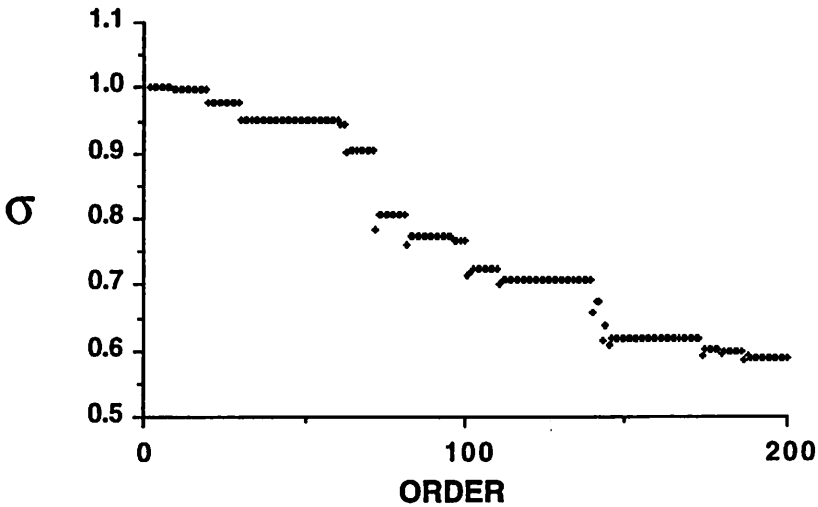

Fig. 9. An example distribution of $\{\sigma_{ij}\}$ for 200-species system in the case when $\sigma_{ij} = \sigma_j$ for any i and j. The rank-size relation follows a geometric law.

Zipf's Law: We consider the Zipf's law derived from (3.5). Only the case when the rank-size order corresponds to that of the dominancy i is investigated. Moreover, for simplicity, we consider only two special cases: (i) dominant species-dependent case; $\sigma_{ij} = \sigma_i$, (ii) subordinant species-dependent case; $\sigma_{ij} = \sigma_j$. In each case, the necessary distribution of $\{\sigma_{ij}\}$ can be uniquely derived for a Zipf's law:

$$\sigma_i = 1 - \left(\frac{i}{i+1} \right)^{\rho} \quad \text{in the dominant species-dependent case;}$$

$$\sigma_j = \frac{1 - j^{-\rho}}{\displaystyle\sum_{k=1}^{j-1} k^{-\rho}} \quad \text{in the subordinant species-dependent case,}$$

where ρ is a positive constant. Examples of $\{\sigma_{ij}\}$ are shown in Fig. 10.
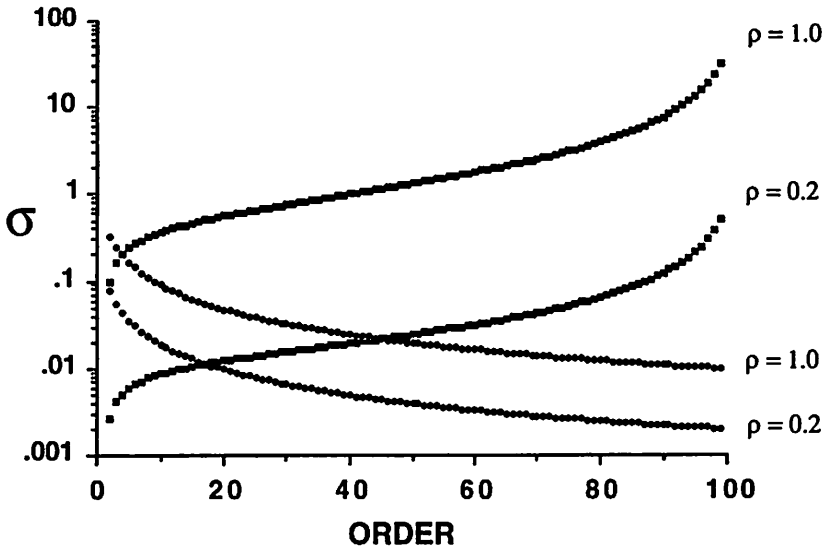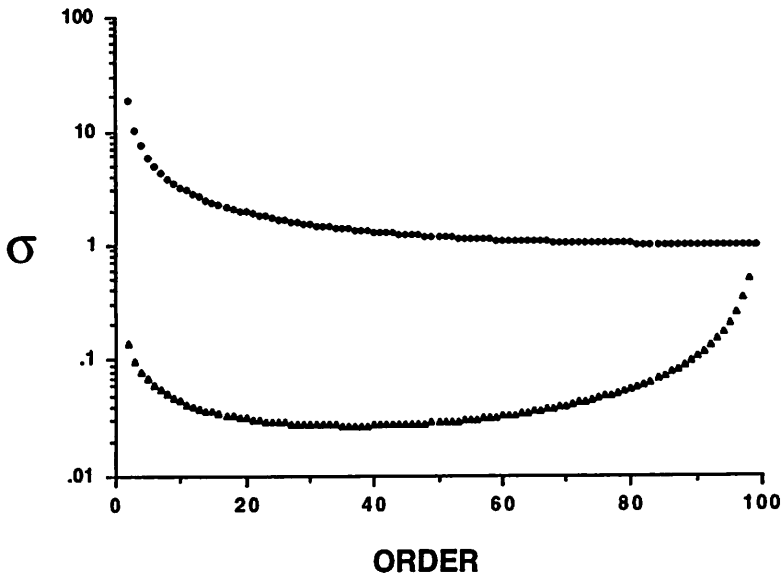

Fig. 10. Example distributions of $\{\sigma_{ij}\}$ for 100-species system in two special cases: the dominant species-dependent case (∘) when $\sigma_{ij} = \sigma_i$ for any i and j; the subordinant species-dependent case (■) when $\sigma_{ij} = \sigma_j$ for any i and j. The rank-size relation is of $X_k = ck^{-\rho}$.

Broken-stick Law: Also in this case, we consider only the case when the rank-size order corresponds to that of the dominancy i for two special cases as before. In each special case, the necessary distribution of $\{\sigma_{ij}\}$ can be uniquely derived for a broken-stick law with the total number w of species:

$$\sigma_i = \left(\sum_{j=i+1}^{w} \frac{i}{j} \right)^{-1} \quad \text{in the dominant species-dependent case}$$

$$\sigma_j = \frac{w}{j-1} \cdot \frac{1 - \dfrac{1}{w} \displaystyle\sum_{k=j}^{w} [1/k]}{1 + \displaystyle\sum_{k=j}^{w} [1/k]} \quad \text{in the subordinant species-dependent case.}$$

The example distribution $\{\sigma_{ij}\}$ for $w = 100$ is shown in Fig. 11.

Fig. 11. Example distributions of $\{\sigma_{ij}\}$ for 100-species system in two special cases: the dominant species-dependent case (o) when $\sigma_{ij} = \sigma_i$ for any i and j; the subordinant species-dependent case (▲) when $\sigma_{ij} = \sigma_j$ for any i and j. The rank-size relation is of the broken-stick model.

5. Acknowledgements

References

[1] Auerbach F., Das Gesetz der Bevölkerungskonzentration, *Petermanns Geographische Mitteilungen* **59** (1913) pp. 74–76.
[2] Condon E. U., Statistics of vocabulary, *Science* **67** (1928) pp. 300.
[3] Corbet A. S., The distribution of butterflies in the Malay Peninsula (Lepid.), *Proc. Roy. Ent. Soc. London* **A16** (1942) pp. 101–116.
[4] Fisher R. A., Corbet A. S. and Williams C. B., The relation between the number of species and the number of individuals in a random sample of an animal population, *J. Anim. Ecol.* **12** (1943) pp. 42–48.
[5] MacArthur R. H., On the relative abundance of bird species, *Proc. Nat. Acad. Sci. U.S.A.* **43** (1957) pp. 293–295.
[6] Motomura I., *Research Reports on Ecology* **1** (1935) pp. 195–199.
[7] Motomura I., *Physiol. Ecol. Japan* **1** (1947) pp. 55–60.

[8] Pareto V., *Cours d' 'Economie Politique*, Lausanne and Paris (1897).

[9] Pielou E. C., *Ecological Diversity* (Wiley, New York, 1975).

[10] Pielou E. C. and Arnason A. N., Correction to one of MacArthur's species-abundance formulas, *Science* **151** (1965) pp, 592.

[11] Simon H. A., On a class of skew distributions, *Biometrika* **42** (1955) pp. 425–440.

[12] Teramoto E. and Seno H., Modelling of biological aggregation patterns, in *Biomathematics and Related Computational Problems*, ed. by Ricciardi L. M. (Kluwer Academic Publishers, Dordrecht, 1988) pp. 409–419.

[13] Teramoto E., Shigesada N. and Kawasaki K., Species-abundance relation and diversity, in *Lecture Notes in Biomathematics*, ed. by Levin S. A. and Hallam T. G. (Springer-Verlag, 1984) pp. 163–177.

[14] Tokeshi M., Niche apportionment or random assortment: species abundance patterns revisited, *J. Anim. Ecol.* **59** (1990) pp. 1129–1146.

[15] Uchida T., A theoretical consideration on Motomura's geometric series law of species-abundance relation in animal communities, *Research Reports on Ecology* **9** (1943) pp. 173–178.

[16] Willis C. J., *Age and Area* (Cambridge Univ. Press, 1922).

[17] Winiwarter P. and Cempel C., Life symptoms: the behaviour of open systems with limited energy dissipation capacity and evolution, *Systems Research* **9** (1992) pp. 9–34.

[18] Yule G. U., A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S., *Phil. Trans. Roy. Soc.* **B213** (1924) pp. 21–81.

[19] Zipf G. K., *Human Behavior and the Principle of Least Effort* (Addison-Wesley Press, Cambridge, 1949).