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SPECIES-ABUNDANCE RELATION AND DIVERSITY

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SPECIES-ABUNDANCE RELATION AND DIVERSITY

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1. Introduction

The scenic affluence of nature is attributable to the fact that most ecological communities contain a wide variety of species of organisms with widely different abundance. Many ecologists have been interested in the distribution of the abundance of different species found in a chosen area. Commonly the "species-abundance" curves obtained from the observed data for a some taxonomic group, have been studied. They tried to find an optimum form of frequency distribution with a small number of parameters that fits the data from the majority of observed communities only by adjusting the parameter values. Then, we can use these parameters as the significant measures to characterize the type of communities. Thus several types of frequency distribution laws have been proposed by Fisher, Corbet and Williams (1943), Preston (1948), Brian (1953) and others; for examples, logarithmic series distribution, lognormal distribution, negative binomial distribution. Sometimes we encounter such cases that some of the distribution give better fit to one community but other distributions fit to another community and one cannot easily answer the question: which is the optimum distribution as a general law?

However, roughly speaking, it is a common qualitative feature of species-abundance relation found in the majority of natural communities that only a few species have large population sizes and many other rare species have small numbers of individuals, that is, singleton species are numerous, and doubletons and tripleton and so on are successively less numerous. Thus, if we plot the number of species as a function of the population size, it always gives a monotone decreasing concave curve. Here a question will immediately arizes: why the natural communities have such a common qualitative feature of "species-abundance" relations? MacArthur(1957) proposed the well known "broken stick model". by assuming random occupation of nonoverlapping niches and population size of species proportional to the size of species'niche, and obtained a result which gives a reasonable distribution pattern. As we shall state in the next section, Utida (1943) derived a geometric series distribution by using a very simple inter-species competition model.

On the other hand, a similar distribution law has been also discussed on quite different items and is known by the name of "Zipf law". It states that, in a collection of many subject of the same item, if we give the rank x (integer) to each subject just in the order of its size, y, then, in many cases, we have a rank-size relation $xy = \text{const}$. For examples, English words ranked by the frequency of usage (the first rank "the", the second rank "and" and so on), urban communities ranked by the population size (the first rank "Tokyo", the second rank "Osaka" and so on), and rivers ranked by their length show approximately the Zipf relation $xy = \text{const}$. If we consider the frequency distribution of size, $f(y)$, it is easily shown that the rank x of a subject with size y is given by $x = \int_y^\infty f(y')dy'$. Therefore, in terms of frequency distribution, Zipf's rank-size relation can be expressed by $f(y) = c/y^2$. Yule(1924) also discussed the size (number of species) distribution of the genera and derived a hyper-geometric series distribution by taking into account the "specific mutation" and the "generic mutation" as a stochastic birth process. He showed that the frequency distribution has a form $f(y) \propto y^{-(1+1/\rho)}$ (where $\rho<1$) for large value of y. The result was compared with the observed data which was used by Willis(1922) in his discussion on the evolution. As has been discussed by Rapaport(1978), if this type of the distribution is commonly found in a wide variety of objects, there may be a possibility that the distribution can be commonly characterized by some special probabilistic model, just as in the case of normal distribution for the sum of independent random variables. The studies on the species-abundance relation of ecological communities, which is also characterized by similar monotone decreasing concave curves, arouse theoretical interest also from this point of view.

2. Geometric Series Distribution and Competition Model

In Japan, Motomura (1932) proposed the geometric series distribution to fit the data of the bottom fauna of Japanese lakes obtained by Miyadi. He found good fit to the data by introducing the rank-size relation

$$\log y + ax = b,$$

where y is the population size of the species of rank x. Here all species are ranked in the order of their population sizes. Obviously this expresses a geometric progression with the ratio $\exp(-a)$ and gives the size distribution $f(y) \propto 1/y$, instead of $1/y^2$ (Zipf law). Typical examples are shown in Figs. 1 and 2. In order to explain the geometiric series distribution, Utida (1943) considered a very simple competition model. Consider an area which consists of M compartments and n individuals of each species A,B,... randomly occupying these compartments. Here we assume that more than two individuals of the same species cannot occupy the same compartment simultaneously (this assumption was removed later by Motomura). Then we have the compartments with different species like (A,D), (A,B,D), (B,C) and so on. Furthermore, we suppose that these species have a relative superiority of strengths for interspecies competition just in the order of A,B,... and only one individual of the strongest species can survive in each compartment. Then the above example is reduced to (A),(A),(B)... Under these assumptions, all n individuals of species A can obviously survive occupying n compartments, and among n individuals of species B, in the average, $n(1-n/M)$ individuals which entered the A-absent compartments can have the chance of survival. Similarly $n\{1-n/M - \frac{n}{M}(1-n/M)\} = n(1-n/M)^2$ individuals of the species C can survive. In this way, it is easily shown that the population size distribution becomes a geometric series with the ratio $(1-n/M)$. There may be critical opinions on the assumptions underlying this simple model. However, the effect of the competition seems to be a possible key of rationale of common type of species-abundance relation in the ecological communities. Thus, in the following sections, we shall discuss this problem based on a polulation dynamical standpoint.

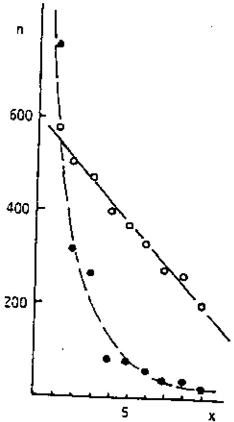

Fig.1. Bottom fauna of Lake Aoki (Miyadi,1931)

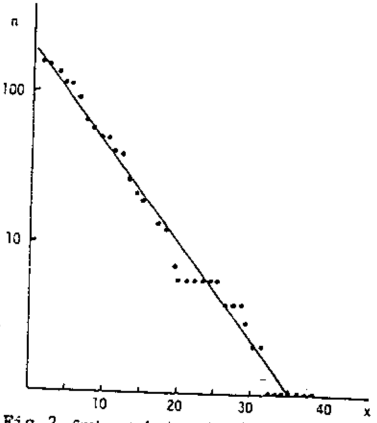

Fig.2. Crabs at Amakusa Bay (Ono,1961)

3. Competitive Multi-Species Model

Consider the Lotka-Volterra model of competitive multi-species system

$$\frac{d}{dt} x_i = (\varepsilon_i - \sum_j \mu_{ij} x_j) x_i, \qquad i=1,2,\ldots,N \qquad (1)$$

where x_i is the population density of the ith species, ε_i is its intrinsic growth rate. μ_{ii} and μ_{ij} $(i \neq j)$ are the coefficients of intra- and inter-species competition, respectively. Here we introduce a conceptual assumption that the competitive interaction consists of two factors, the intrinsic power of interference (or attack) to other individuals and the intrinsic ability of defense against the attack of other individuals. Thus we assume that the competition coefficients can be written in the form

$$\begin{aligned} \mu_{ij} &= \beta_i \gamma_j && \text{for } i \neq j, \\ &= \beta_i \alpha_i && \text{for } i = j, \end{aligned} \qquad (2)$$

where γ_j is an intrinsic factor of intereference of an individuals of the jth species and its effect on the ith species is reduced, due to the defense ability of the ith species, by a factor β_i ($\beta_i < 1$), and intra-species competition is distinguished by using a different factor of interference α_i. Hereafter in our discussion we assume that

$$\alpha_i > \gamma_i \ . \qquad i = 1, 2, \ldots, N \qquad (3)$$

This assumption is not so unrealistic, because intra-species interference in the same ecological niche seems to be severer, as they are depending on the same resource.

Rewriting Eq.(1), we have

$$\frac{d}{dt} x_i = (\varepsilon_i - \beta_i\alpha_i x_i - \sum_{j\neq i} \beta_i\gamma_j x_j) x_i \qquad (4)$$

$$\equiv f_i(x) x_i \ , \qquad i = 1,2,\ldots,N$$

where x denotes a set of variables $x_1, x_2, \ldots, x_N$, $\alpha_i > \gamma_i$ for all i, and the number is assigned to each species in the order as

$$\frac{\varepsilon_1}{\beta_1} > \frac{\varepsilon_2}{\beta_2} > \quad \cdots \quad > \frac{\varepsilon_N}{\beta_N} \ . \qquad (5)$$

4. Dynamical Properties

Here we shall study the final state of the system given by the solution of (4) when it starts with some initial state x^0 with all positive x_i^0. Eq.(4) have generally 2^s critical points in the whole state space ($-\infty < x_i < \infty$ for all i), including degenerated ones. First of all we shall consider the condition of the existence of a positive critical point x^* ($x_i^* > 0$ for all i). The critical point $x^* = (x_1^*, x_2^*, \ldots, x_N^*)$ which satisfies the equations

$$f_i(x) = \varepsilon_i - \beta_i\alpha_i x_i - \beta_i \sum_{j\neq i} \gamma_j x_j = 0 \ , \quad i=1,2,\ldots,N \qquad (6)$$

can be obtained as

$$x_i^* = \frac{\xi_i}{\gamma_i} \left\{ \frac{-\sum_k \frac{\varepsilon_k}{\beta_k} \xi_k}{1 + \sum_k \xi_k} + \frac{\varepsilon_i}{\beta_i} \right\} , \qquad i=1,2,\ldots,N \qquad (7)$$

where

$$\xi_i = \frac{\gamma_i}{\alpha_i - \gamma_i} \ (> 0) \ .$$

Thus, using the assumptions (3) and (5), we can easily derive the following Lemma:

<u>Lemma</u>

The values of x_i^* ($i=1,2,\ldots,N$) at the critical point (7) satisfy the relation

$$(\alpha_1 - \gamma_1)x_1^* > (\alpha_2 - \gamma_2)x_2^* > \cdots \quad > (\alpha_N - \gamma_N)x_N^* \ , \qquad (8)$$

and this gives the positive critical point ($x_i^* > 0$ for all i) if and only if the parameters satisfy the condition

$$-\sum_k \left(\frac{\varepsilon_k}{\beta_k} - \frac{\varepsilon_N}{\beta_N}\right)\xi_k + \frac{\varepsilon_N}{\beta_N} > 0 \ . \qquad (9)$$

As we can see in the next section, this positive critical point is globally stable. However, the relation (9) may be a very severe condition especially for a many species system (large N). Actually the condition (9) scarcely holds, except for such special cases that

(i) $\quad \frac{\varepsilon_k}{\beta_k} - \frac{\varepsilon_N}{\beta_N} \ll 1 \ ,$ for all k, or

(ii) $\quad \xi_i \ll 1 \quad (\alpha_i \gg \gamma_i) \ .$

Thus it has been shown that the competitive multi-species populations can not be usually expected to realize the coexistence, as known by the name of "Gause's competitive exclusion". Therefore, as the next step, we shall study more natural cases.

In order to proceed with our discussion, here we shall introduce the concept "sector stability" defined by Goh(1980).

Definition

Suppose a dynamical model of multi-species system

$$\frac{d}{dt} x_i = f_i(x) x_i , \qquad i=1,2,\ldots,N \qquad (10)$$

where all $f_i(x)$ have continuous partial derivatives. Considering a nonnegative critical point $x^* = (x_1^*, x_2^*, \ldots, x_N^*)$, we define the subsets P and Q of $I = \{1,2,\ldots,N\}$ by

$$P = \{i \mid x_i^* > 0\} , \quad Q = \{j \mid x_j^* = 0\} , \qquad (11)$$

and let Ω be the subspace

$$\Omega = \{x \mid x_i > 0 \text{ for } i \in P;\ x_j \geq 0 \text{ for } j \in Q\}.$$

The nonnegative critical point x^* is *globally sector stable*, if every solution of (10) which starts from Ω remains in Ω for all finite time t and converges to x^* as $t \to \infty$.

If we use this prescription in our model (4), we can prove the following theorem (Proof in Appendix).

Theorem

In the system (4), by choosing an arbitrary number $n \in \{1,2,\ldots,N\}$, we consider a set of equations

$$\begin{aligned} f_i(x) &= 0 \quad \text{for} \quad i = 1,2,\ldots,n \\ x_j &= 0 \quad \text{for} \quad j = n+1,\ n+2,\ldots,N . \end{aligned} \qquad (12)$$

Let

$$x^*(n) = (x_1^*(n),\ x_2^*(n),\ldots,\ x_n^*(n),\ 0,\ 0,\ldots,0) ,$$

be the critical point given by (12) for each $n = 1,2,\ldots,N$ and let s be the maximum of n which satisfies the condition

$$x_1^*(n) > 0,\ x_2^*(n) > 0,\ \ldots,\ x_n^*(n) > 0.$$

Then $x^*(s) = (x_1^*(s), x_2^*(s), \ldots, x_s^*(s), 0, \ldots, 0)$, where

$$x_i^* = \frac{\beta_i}{\gamma_i}\left\{ \frac{-\sum_{k=1}^{s} \frac{\varepsilon_k}{\beta_k} \xi_k}{1 + \sum_k \xi_k} + \frac{\varepsilon_i}{\beta_i} \right\} , \qquad i = 1,2,\ldots,s \qquad (13)$$

is a globally sector stable critical point of the system (4) and they satisfy the relations

$$(\alpha_1 - \beta_1)\, x_1^*(s) > (\alpha_2 - \beta_2)\, x_2^*(s) > \cdots\cdots > (\alpha_s - \beta_s)\, x^*(s) > 0 . \quad (14)$$

This theorem presents the criterion of the survival of species in competitive multispecies communities. Among N species ranked in the order of values ε_i/β_i, starting from arbitrary initial population densities $x_i^0 > 0$ $(i = 1,2,\ldots,N)$, only the species of rank up to s can survive asymptotically approaching the finite stationary population densities $x_i^*(s)$ $(i = 1,2,\ldots,s)$ and other species of ranks from s+1 to N go out of existence. Here it should be noted that the poplation sizes realized at the final state do not necessarily follow the order of ranks, but satisfy the relation (14).

Here we shall consider the invasion of new species in some chosen area where already several former occupant species are living with the stationary poplation densities. At the stage of invasion, we can apply our theorem to the system of the community including the invader species. Then it is clear that if the rank of the invader species in terms of ε_i/β_i is higher than that of the former occupant species with the lowest rank, the invasion will succeed and some of the former occupant species with the rank lower than the invader species become extinct unless the criterion of survival given by the theorem is fulfilled again for this new system.

Therefore, if N species considered in our theorem invade the given area one after another in random order, the final stable community will be established with the s surviving species satisfying the condition of theorem and other species will fail to invade or become extinct on some occasion. Therefore, it is concluded that the theorem can represent also the result of succession of the ecological community caused by the successive invasion of new species.

5. Environmental Heterogeneity and Species-Abundance Relation

Generally any area where we are interested in the ecological community does not have uniform environmental conditions, but it has a complex heterogeneous structure consisting of many different ecological niches. The structure of ecological niche may continuously change from place to place in the given area. However, in order to take into account this complexity in a similar way, here we shall assume that the niche space can be divided into M patches and in each patch there are intra- and inter-species competitions among the invader species but no competition between those of different patches.

It seems to be natural to assume that the parameters in Eq.(4) for a given species i have different values ε_i^μ, α_i^μ, β_i^μ, γ_i^μ $(\alpha_i^\mu > \gamma_i^\mu)$ depending on the patches $\mu = 1,2,\ldots,M$. Then we have the equations

$$\begin{aligned} \frac{d}{dt} x_i = (\varepsilon_i^\mu - \beta_i^\mu \alpha_i^\mu x_i^\mu - \beta_i^\mu \sum_{j \neq i} \gamma_j^\mu x_j^\mu) \, x_i^\mu & \qquad \mu = 1,2,\ldots,M \\ - D_i^\mu x_i^\mu + \sum_{\mu' \neq \mu} D_i^{\mu\mu'} x_i^{\mu'} \, , & \qquad i = 1,2,\ldots,N \end{aligned} \qquad (15)$$

where the migration is taken into consideration by introducing the rate of migration $D_i^{\mu\mu'}$ from the patch μ' to μ and $D_i^\mu = \sum_{\mu \neq \mu'} D^{\mu\mu'}$.

When the migration scarcely occur and all patches can be regarded as isolated systems, we can apply our theorem directly to each set of equations for patch $\mu = 1,2,\ldots,M$. Then we have the set of globally sector stable solutions

$$x^{*\mu} = (x_1^{*\mu}, \; x_2^{*\mu}, \; \ldots, \; x_{s_\mu}^{*\mu}, \; 0, \ldots, \; 0), \quad \mu = 1,2,\ldots,M \qquad (16)$$

where at the final stable state, the patches obviously have different number of species s_μ. As for the problem how this stable solution is affected by the presence of migration terms, S. Levin(1976) and B.S. Goh (1980) already discussed the same problem for more general systems. By using the theorem given by Levin, we can show that if all migration rates are sufficiently small, there exists a sector stable solution $\{x^{*\mu}(D)\}$, and it continuously approaches the solution (16) as the migration rates tend to zero. Therefore, we can say that, so far as the migration rates are sufficiently small, the number of species and their population sizes can be approximately given by the stable solution (16). Thus the species-abundance relation as the result of our competition model can be obtained by calculating the populations of surviving species in the whole area

$$x_i^* = \sum_\mu x_i^{*\mu} \, , \qquad i = 1,2,\ldots,N \qquad (17)$$

where obviously $x_i^{*\mu} = 0$ for $i > s_\mu$.

6. Numerical Simulation of Results

In order to see the qualitative feature of species-abundamce relation, we assumed, in our computer calculations, that the parameters except ε_i^μ $(\mu = 1,2,\ldots,M)$ have the same values independently of the patch and used the values $\mu_{ii} = \beta_i \alpha_i = 1$ and $\mu_{ij} = \beta_i \gamma_j = 0.5$ for all i and j. For values of parameters ε_i^μ, we considered a frequency distribution of the values of ε_i^μ $(\mu = 1,2,\ldots,M)$,

$$\mathrm{Prof}(\varepsilon < \varepsilon_i^\mu < \varepsilon + d\varepsilon) = \rho_i(\varepsilon) d\varepsilon, \qquad i = 1,2,\ldots,N$$

and actually used a box type distribution

$$\begin{aligned} \rho_i(\varepsilon) &= 1/\sigma \qquad \text{for } E_i - \sigma/2 < \varepsilon < E_i + \sigma/2, \\ &= 0 \qquad \text{otherwise} \, . \end{aligned} \qquad (18)$$

N real numbers randomly chosen from the interval (5 10) were assigned to the mean values E_i in the order of their magnitude. Then the values ε_i ($\mu = 1, 2, \ldots, M$) were randomly selected according to the frequency distribution (18) for each species, respectively. Using these parameter values and $N = 200$, $\sigma = 2.5$, stable populations at every patch were calculated by the procedure stated in our theorem. Fig.3 shows our result of the species-abundance relation which expresses the population sizes of surviving species given by (17) as a function of their ranks. Here all surviving species are ranked in the order of their population sizes, so it should be noticed that the rank r does not necessarily coincide with the suffix i which specifies the species.

We can conclude from the result shown in these figures that when the area consists of many patches ($M > 10$), the logarithm of the population size shows the linear relation with the species rank, namely the geometric series distribution becomes a plausible approximation in a wide range of rank. This qualitative feature of the distribution was not altered by different choice of parameter values.

In conclusion, we can say that the common qualitative feature of species-abundance relation of the ecological community that it usually consists of a few species with large population sizes and many rare species with small population sizes can be expected wherever the niche space of given area has a complex patchy structure.

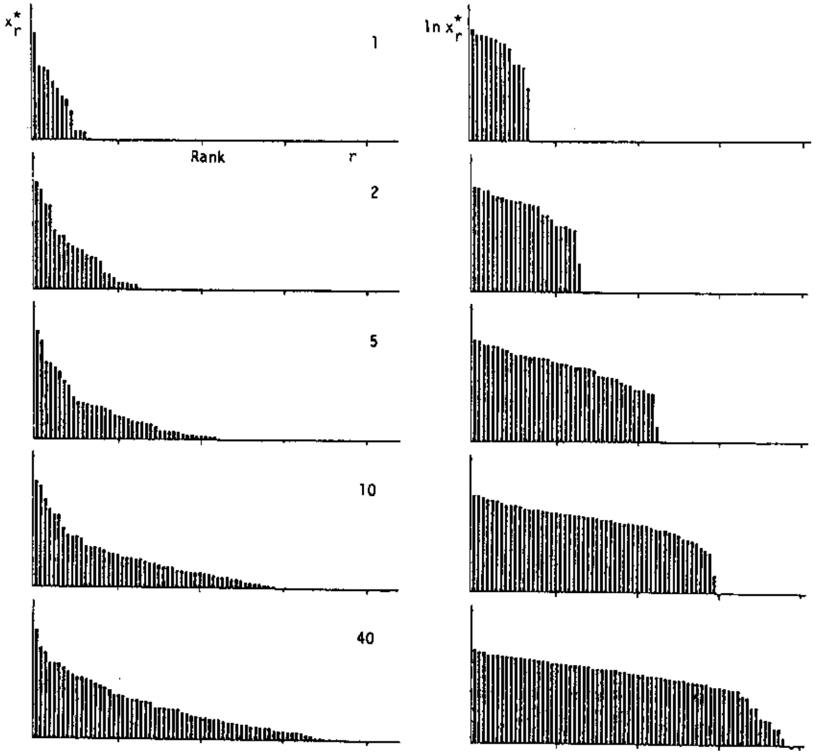

Fig.3. Species-abundance relations for the cases M=1, 2, 5, 10 and 40.

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Appendix (Proof of Theorem)

Let $P=\{1,2,..,s\}$ and $Q=\{s+,s+2,..,N\}$ where s is the number defined in Theorem, and consider a domain defined as $\Omega=\{x|x_i>0 \text{ for } i\varepsilon P;\ x_j\geq 0 \text{ for } j\varepsilon Q\}$. It is evident that the solution of Eq.(4) which begins in the set Ω remains in Ω for all finite values of t, since $\frac{d}{dt}x_i=0$ at $x_i=0$ for $i=1,2,\ldots,N$.

In order to prove the stability of the solution of Eq.(4) confined in Ω, we will show that any solution of Eq.(4) starting from Ω converges to $x^*(s)$ as $t\to\infty$. To this end, we propose the following Lyapunov function,

$$V(x)=\sum_{i\varepsilon P}\frac{\gamma_i}{2\beta_i}\{x_i-x_i^*(s)-x_i^*(s)\ln x_i/x_i^*(s)\}+\sum_{j\varepsilon Q}\frac{\gamma_j}{2\beta_j}|x_j|\geq 0, \qquad \text{(A-1)}$$

where equality sign holds only at the point $x=x^*(s)\equiv(x_1^*(s),x_2^*(s),\ldots,x^*(s),0,\ldots,0)$ in Ω, which is given by

$$x_i^*(s)=\frac{\frac{\xi_i}{\gamma_i}\{\frac{\varepsilon_i}{\beta_i}+\sum_{k\varepsilon P}(\frac{\varepsilon_i}{\beta_i}-\frac{\varepsilon_k}{\beta_k})\xi_k\}}{1+\sum_{k\varepsilon P}\xi_k} \qquad \text{for } i=1,2,\ldots,s. \qquad \text{(A-2)}$$

The time derivative of Eq.(A-1) is calculated as

$$\frac{d}{dt}V(x)=-\frac{1}{2}\{\sum_{i\varepsilon I}\gamma_i(x_i-x_i^*(s))\}^2-\frac{1}{2}\sum_{i\varepsilon I}(\alpha_i-\gamma_i)\gamma_i(x_i-x_i^*(s))^2$$
$$+\sum_{j\varepsilon Q}\frac{\gamma_j}{2\beta_j}\{\varepsilon_j-\beta_j\sum_{i\varepsilon P}\gamma_i x_i^*(s)\}x_i(s), \qquad \text{(A-3)}$$

where $I=P+Q\equiv\{1,2,\ldots,N\}$. Thus if

$$f_l(x^*(s))\equiv\varepsilon_l-\beta_l\sum_{i\varepsilon P}\gamma_i x_i^*(s)\geq 0 \qquad \text{for all } l\varepsilon Q, \qquad \text{(A-4)}$$

then

$$\frac{d}{dt}V(x)\leq 0,$$

where equality sign holds only at $x=x^*(s)$, and hence $x^*(s)$ becomes globally sector stable.

Hereafter we will prove the relation (A-4). Substituting (A-2) into (A-4), we obtain

$$f_\ell(x^*(s)) = \varepsilon_\ell - \beta_\ell \frac{\sum_{k\varepsilon P} \frac{\varepsilon_k}{\beta_k}\xi_k}{1+\sum_{k\varepsilon P}\xi_k}$$

$$= \frac{\beta_\ell\{-\sum_{k\varepsilon\{P,\ell\}}(\frac{\varepsilon_k}{\beta_k}-\frac{\varepsilon_\ell}{\beta_\ell})\,\xi_k+\frac{\varepsilon_\ell}{\beta_\ell}\}}{1+\sum_{k\varepsilon P}\xi_k} \qquad \text{for } \ell\,\varepsilon\,Q\ . \qquad \text{(A-5)}$$

To describe this equation more concisely, let us introduce the following set of equations for $\ell\,\varepsilon\,Q$,

$$\begin{aligned} f_i(x) &\equiv \varepsilon_i - \beta_i\alpha_i x_i - \sum_{j\neq i}\beta_i\gamma_j x_j = 0 \quad \text{for } i=1,2,\dots,s \text{ and } \ell, \\ x_j &= 0 \qquad\qquad \text{for } j=s+1,s+2,\dots,N \ \text{ except } \ell. \end{aligned} \qquad \text{(A-6)}$$

The solution of (A-6), $x^*(s|\ell) = (x_1^*(s|\ell), x_2^*(s|\ell), \dots, x_s^*(s|\ell), 0, \dots, 0, x_\ell^*(s|\ell), 0, \dots, 0)$, is given by

$$x_i^*(s|\ell) = \frac{\frac{\xi_i}{\gamma_i}\{-\sum_{k\varepsilon\{P,\ell\}}(\frac{\varepsilon_k}{\beta_k}-\frac{\varepsilon_i}{\beta_i})\,\xi_k+\frac{\varepsilon_i}{\beta_i}\}}{1+\sum_{k\varepsilon\{P,\ell\}}\xi_k} \qquad \text{for } i\,\varepsilon\,\{P,\ell\}. \qquad \text{(A-7)}$$

Especially, the ℓ-th element $x_\ell^*(s|\ell)$ is written as

$$x_\ell^*(s|\ell) = \frac{\frac{\xi_\ell}{\gamma_\ell}\{-\sum_{k\varepsilon\{P,\ell\}}(\frac{\varepsilon_k}{\beta_k}-\frac{\varepsilon_\ell}{\beta_\ell})\,\xi_k+\frac{\varepsilon_\ell}{\beta_\ell}\}}{1+\sum_{k\varepsilon\{P,\ell\}}\xi_k}\ . \qquad \text{(A-8)}$$

Note that the parenthesized term in the numerator of (A-8) is exactly the same as that of (A-5). Thus $f_\ell(x^*(s))$ can be rewritten as

$$f_\ell(x^*(s)) = \frac{\gamma_\ell\beta_\ell(1+\sum_{k\varepsilon\{P,\ell\}}\xi_k)}{\xi_\ell\,(1+\sum_{k\varepsilon P}\xi_k)}\,x_\ell^*(s|\ell) \qquad \text{for } \ell\,\varepsilon\,Q\ . \qquad \text{(A-9)}$$

Now we will show that

$$x_\ell^*(s|\ell) \le 0 \qquad\qquad \text{for all } \ell\,\varepsilon\,Q,$$

which assure $f_\ell(x^*(s)) \le 0$ for all $\ell\,\varepsilon\,Q$. By using Eq.(A-6) and the relation (5), we find the following equation,

$$x_{s+1}^*(s|s+1)\times\frac{\gamma_{s+1}}{\xi_{s+1}}\times(1+\sum_{k\varepsilon\{P,s+1\}}\xi_k) - x_\ell^*(s|\ell)\times\frac{\gamma_\ell}{\xi_\ell}\times(1+\sum_{k\varepsilon\{P,\ell\}}\xi_k)$$

$$= (\frac{\varepsilon_{s+1}}{\beta_{s+1}} - \frac{\varepsilon_\ell}{\beta_\ell})\,(1+\sum_{k\varepsilon P}\xi_k) \ge 0 \qquad \text{for } \ell\,\varepsilon\,Q\ . \qquad \text{(A-10)}$$

Comparing the set of equations of (A-6) with that of (12) in the text, we find that (A-6) for the case of $\ell = s+1$ is idential to (12) for the case of $n = s+1$. Thus we have the following equation

$$x_{s+1}^*(s|s+1) = x_{s+1}^*(s+1)\ .$$

Furtheremore, recalling the definition of s in Theorem and the relation (8) in Lemma in the text, we have

$$x_{s+1}^*(s+1) \le 0,$$

and hence from (A-10), we can conclude

$$x_\ell^*(s|\ell) \le 0 \qquad\qquad \text{for all } \ell\,\varepsilon\,Q\ .$$