STATIONARY RANK-SIZE RELATION FOR COMMUNITY OF LOGISTICALLY GROWING GROUPS

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ABSTRACT

Rank-size relation derived from the size distribution for a number of growing groups is considered with a mathematical model described by a type of von Foerster equation. Size of each group grows in the logistic manner with the common intrinsic growth rate and carrying capacity. New groups are produced from present groups with a reproduction rate, which depends on the size of the mother group. Each group undergoes the extinction probability which depends on the group size. We discuss how the characteristics of some typical rank-size relations of the community of groups depend on the dynamical factors governing the community. It is shown that the typical rank-size relation requires specific form of the size-dependence of extinction rate, and we discuss how the observed typical rank-size relation could really reflect the dynamical factor governing the community.

Keywords: Rank-size relation, size distribution, group size, logistic growth, von Foerster equation.

1. Introduction

Stability of the ecological community of a number of species is affected by the community structure which corresponds to how the inter-specific relations among them are. It has been attracting lots of theoretical researchers. One of the problems related to it is the community structure constructed by a number of groups. As a characteristic factor, the size distribution of such community appears important to consider the community dynamics. It is expected that a rank-size relation among groups may characterize the dynamics which governs the growth of community. We can assign the rank $k = 1, 2, \ldots$ of sampled groups from the largest to the smallest with respect to its size X_k . Then, a rank-size relation can be obtained: $X_k = S(k)$. Theoretically, given the size frequency distribution function f(x)dx for

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the size range between x and x + dx, the rank-size relation is formally defined as

$$K(x) = W \int_{x}^{+\infty} f(x)dx, \qquad (1)$$

where W is the total number of groups, and the rank K(x) for the size x is defined as real number. Note that, as easily seen from (1), if the rank K(x) and the size frequency distribution function f(x) are sufficiently smooth, they have the following relation, too:

$$f(x) = -\frac{1}{W} \frac{dK(x)}{dx} \,. \tag{2}$$

Some particular types of rank-size relation were observed for samples of various contexts, and have been theoretically discussed [14,20-22,27]. Auerbach [2] 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 observed in such range that $1 < q \le 2$. The same type of rank-size relation has been observed also for some data in the other contexts: personal incomes [13], occurrence of words in a book or in a number of issues of a newspaper [4], number of biological species in genera [8, 24] (also see the references in [14,25]). For real value of k, the corresponding size distribution function f(x) can be calculated from (2) as follows:

$$f(x) \propto x^{-q}$$
.

Motomura [12] and Corbet [5] fit another relation, the geometric law, to the data of populations of multi-species communities:

$$X_k \propto r^k$$
,

where r is a positive constant less than 1. The corresponding size distribution function f(x) is

$$f(x) \propto x^{-1}$$
.

It is remarked that, for both of these two typical rank-size relations, the theoretically corresponding size distribution function is inversely proportional to a power of the size. These special types of size distribution can be considered to have made use of mathematical models [15,17,20,26].

Further, some other theoretical models on the observed rank-size relations are considered, of which the broken-stick model and the niche overlapping model, proposed by MacArthur [9], 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 groups. The corresponding size distribution function f(x) is of the negative exponential distribution [14]:

$$f(x) \propto \exp[-wx]$$
.

The latter rank-size relation is:

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

where Γ is the gamma function, and the corresponding size distribution function f(x) is linear [14]:

 $f(x) \propto 1 - \frac{x}{x_{\text{max}}}$.

 x_{max} is the possible maximum size of group.

In this paper, some ecological characteristics of the rank-size relation for a number of growing groups are discussed with a mathematical model described by a type of von Foerster equation. As for the corresponding general mathematical system, VanSickle [23] has carried out the detail mathematical analysis. In our fundamental multi-group system, population of every group grows in the logistic manner with the common intrinsic growth rate and carrying capacity. New group is reproduced from one of present groups with a reproduction rate, which depends on the population size of the mother group. Besides, each group undergoes the extinction probability which depends on the group size. We discuss how the characteristics of some typical rank-size relations of the community of groups reflect the dynamical factors (e.g. the reproduction rate, the extinction rate, etc.), which govern the community structure. It will be shown that the above specific rank-size relations can also be realized for our model with some constraints, and it will be discussed how the observed typical rank-size relation could really reflect the dynamical factor governing the community.

2. Dynamical Factors Within Community

We consider a single-species population that constructs a community consisting of growing number of groups. For example, we can consider the community which consists of self-growing colonies, towns, or firms. The total number of groups in the community and the size of each group are assumed to change temporally with the following dynamics (for the scheme of our model, see Fig. 1):

Growth of group size: Each of the groups grows in a logistic manner, that is, the group size n = n(t) is obeyed to the differential equation

$$\frac{dn}{dt} = r\left(1 - \frac{n}{K}\right)n\,, (3)$$

where r and K are positive constants and respectively mean the intrinsic growth rate and the carrying capacity for the group size growth (see Fig. 2). Logistic growth

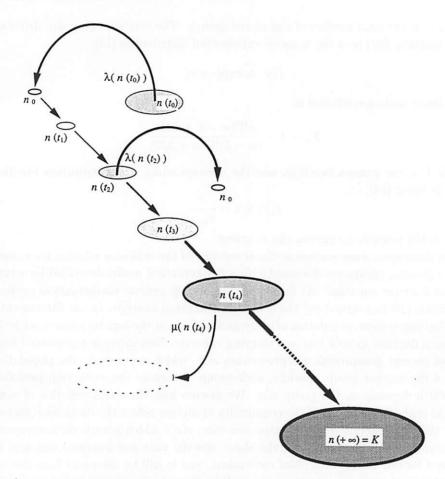


Fig. 1. Dynamics of growing group in the community. Each group grows in size from n_0 up to K in a logistic manner. Present group reproduces the new group with size n_0 at rate λ which in general depends on the size of the mother group. The group becomes extinct at rate μ which in general depends on the group size. As for the more detailed explanation, see the text.

has been observed for a variety of animal populations including human population (for example, see [1, 3]). It was reported in [16] that the growth of plant size would be in the logistic manner. Provided that the total number of individuals of a species, or that of species per plant is proportional to the plant size, we could apply (3) for the number n per plant. In such cases, the number of groups corresponds to that of plants.

Now, we take the following non-dimensionalizing changes of variables:

$$N \equiv \frac{n}{K}; \quad \tau \equiv rt. \tag{4}$$

Then, Eq. (3) becomes

$$\frac{dN}{dt} = (1 - N)N \equiv G(N).$$

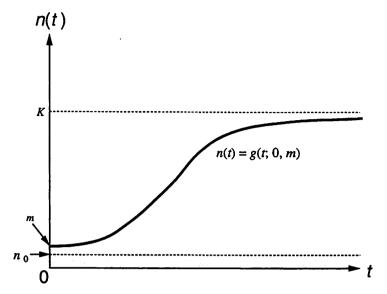


Fig. 2. Group size growing curve in a logistic manner, given by (3).

This equation can be solved as follows:

$$N(\tau) = \left\{ 1 + \left(\frac{1}{m} - 1 \right) e^{-(\tau - \tau_0)} \right\}^{-1} \equiv g(\tau; \ \tau_0, \ m), \tag{5}$$

where $N(\tau_0) = m > 0$. The group with size m < 1 at time τ_0 asymptotically grows toward size 1.

Reproduction rate of new groups: Present groups reproduce new groups in a community. A new group is born from one of the present groups, and the reproduction rate λ is assumed to depend in general on the size of the mother group: $\lambda = \lambda(N)$. A new born group is assumed to have the size N_0 independent of which group is the mother. In our model, the minimum size of the group is given by $N_0 < 1$. The new born group is assumed not to reproduce: $\lambda(N_0) = 0$. Every new born group grows independent of the present groups. This means that new groups are located isolatedly. Any migrations among present groups are ignored. In the above-mentioned case when the group size corresponds to the total number of individuals of a species, or that of species per plant (provided that the number would be proportional to the plant size), the reproduction of groups might be regarded as that of plants.

Extinction rate of a group: Each of the present groups has its extinction rate μ that depends in general on the group size: $\mu = \mu(N) \geq 0$ for any $N \geq N_0$. The extinction of a group occurs due to, for example, some ecologically drastic disturbance. In other words, groups which are unable to reproduce can be regarded to become extinct. In this sense, the considered group size distribution would be for those active groups that could reproduce some new groups. For the model considered in this paper, only such active groups are considered, indeed as clearly shown in the next section for

3. Dynamics of Group Size Distribution

Our present interest is in the group size distribution for the community, which is given by the number of groups $u(N,\tau)$ with size N at time τ . Supposing those dynamical factors within the community as given in the previous section, we can derive the partial differential equation that describes the temporal variation of the group size distribution $u(N,\tau)$ as follows:

$$\frac{\partial}{\partial \tau} u(N,\tau) + \frac{\partial}{\partial N} \left\{ G(N)u(N,\tau) \right\} = -\mu(N)u(N,\tau). \tag{6}$$

The derivation is given in Appendix A.

The number of new born groups, $u(N_0, \tau)$ at time $\tau(>0)$ is given by

$$G(N_0)u(N_0,\tau) = \int_{N_0}^1 \lambda(\nu)u(\nu,\tau)d\nu\,, (7)$$

which means that the flux at the size N_0 is equal to the number of new born groups accumulated over the reproductions by the present groups at each moment τ . A family of systems including that of (6) and (7) has been mathematically studied in a variety of contexts [6,7,10,11,19,23]. Takada and Iwasa [18] discussed the size distribution of plants with interaction by shading, making use of a mathematical model of Eq. (6). In their work, $u(x,\tau)dx$ denotes the density of individual plants with weights ranged between x and x+dx, which is in part corresponding to the example mentioned in the previous section, which is the case when the group size corresponds to the total number of individuals of a species, or that of species per plant, provided that the number would be proportional to the plant size.

As the initial size distribution u(N,0), we consider such situation that there exists only one group with size N_0 at the initial time $\tau = 0$. According to our mathematical modelling, therefore, we put

$$u(N,0) = \delta(N - N_0), \tag{8}$$

where $\delta(x)$ is the Dirac's delta function.

4. Solution Along Characteristic Curve

We can formally solve Eq. (6) with (7), making use of the method of characteristic curve [23]. The characteristic curve with the initial size m corresponds to the trail of temporal variation of the group size of the subpopulation which has the size m at the initial time $\tau = \tau_0$. It is the function of time and the initial size m. For our

model, it is $N = g(\tau; \tau_0, m)$ given by (5), where $N_0 \le m \le 1$ and $\tau_0 \ge 0$, and the solution for (6) with (7) along the characteristic curve can be obtained as follows (as for the details of derivation, see Appendix B):

$$u(N,\tau) = \begin{cases} u(N_0, \tau - g^{-1}(N; 0, N_0)) \cdot k_-(N) & \text{when } N < g(\tau; 0, N_0); \\ u(g(0; \tau, N), 0) \cdot k_+(N, \tau) & \text{when } N \ge g(\tau; 0, N_0), \end{cases}$$
(9)

where $k_{-}(N)$ and $k_{+}(N,\tau)$ are functions given by

$$k_{-}(N) = \exp\left[-\int_{\tau-g^{-1}(N;0,N_0)}^{\tau} \left[\mu(M) + \frac{dG(M)}{dM}\right]_{M=g(z;\tau-g^{-1}(N;0,N_0),N_0)} dz\right]$$

$$= \exp\left[-\int_{0}^{g^{-1}(N;0,N_0)} \left[\mu(M) + \frac{dG(M)}{dM}\right]_{M=g(z;0,N_0)} dz\right]; \tag{10a}$$

$$k_{+}(N,\tau) = \exp\left[-\int_{0}^{\tau} \left[\mu(M) + \frac{dG(M)}{dM}\right]_{M=g(z;0,g(0;\tau,N))} dz\right]. \tag{10b}$$

However, the solution (9) when $N < g(\tau; 0, N_0)$ is not definitely determined because the expression $u(N_0, \tau - g^{-1}(N; 0, N_0))$ is not yet determined, while the solution (9) when $N \geq g(\tau; 0, N_0)$ gives the explicit expression with the initial distribution $u(g(0; \tau, N), 0)$ given a priori. This means that the solution (9) is not sufficient as the complete solution for (6). Now, we consider the reproduction process given by (7), which gives the following renewal equation, substituting (9) into it:

$$G(N_0)u(N_0,\tau) = \int_{N_0}^{g(\tau;0,N_0)} \lambda(\nu)k_-(\nu)u(N_0,\tau - g^{-1}(\nu;0,N_0))d\nu + \int_{g(\tau;0,N_0)}^{1} \lambda(\nu)k_+(\nu,\tau)u(g(0;\tau,\nu),0)d\nu = \int_0^{\tau} K(\tau - z)u(N_0,z)dz + h(\tau),$$
(11)

where $K(\tau)$ and $h(\tau)$ are

$$K(\tau) \equiv \lambda(g(\tau; 0, N_0)) k_-(g(\tau; 0, N_0)) \frac{dg(\tau; 0, N_0)}{d\tau};$$

$$h(\tau) \equiv \int_{g(\tau; 0, N_0)}^{1} \lambda(\nu) k_+(\nu, \tau) u(g(0; \tau, \nu), 0) d\nu$$

$$= \int_{N_0}^{1} \lambda(g(\tau; 0, z)) k_+(g(\tau; 0, z), \tau) \{g(\tau; 0, z)\}^2 u(z, 0) \frac{e^{-\tau}}{z^2} dz,$$
(13)

where both of $K(\tau)$ and $h(\tau)$ can be calculated from given functions and initial distribution. The renewal Eq. (11) is of the type of the third kind of Volterra's integral equation.

By means of Laplace transformation, the renewal Eq. (11) can be formally solved in terms of $u(N_0, \tau)$, and then, the solution (9) with it gives the complete solution for (6) (see Appendix C). Especially when the reproduction and the extinction rates λ and μ are both constants independent of the group size, we can directly solve the renewal Eq. (11) by means of Laplace transformation, and explicitly get

$$u(N_0, \tau) = \frac{\lambda}{N_0(1 - N_0)} \cdot e^{-\sigma_0 \tau} \qquad (\tau > 0),$$
 (14)

where

$$\sigma_0 \equiv \mu - \lambda \,. \tag{15}$$

5. Stationary Group Size Distribution

We consider the stationary size distribution $u^*(N,\tau)$ given by the form

$$u^*(N,\tau) = \nu(N)w(\tau). \tag{16}$$

Substituting (16) into (6), we obtain the following equation:

$$-\frac{1}{w(\tau)} \cdot \frac{d}{d\tau} w(\tau) = \frac{1}{\nu(N)} \cdot \frac{d}{dN} \left\{ G(N)\nu(N) \right\} + \mu(N). \tag{17}$$

The left-hand side of (17) is only of time τ , whereas the right-hand side is only of size N. Therefore, each side must be equal to a constant σ independent of both τ and N:

$$-\frac{1}{w(\tau)} \cdot \frac{d}{d\tau} w(\tau) = \sigma; \qquad (18a)$$

$$\frac{1}{\nu(N)} \cdot \frac{d}{dN} \left\{ G(N)\nu(N) \right\} + \mu(N) = \sigma. \tag{18b}$$

At first, (18a) can be easily solved as follows:

$$w(\tau) \propto e^{-\sigma \tau}$$
 (19)

Next, (18b) gives the following formal solution:

$$\nu(N) \propto \frac{G(N_0)}{G(N)} \cdot \exp\left[\int_{N_0}^N \frac{\sigma - \mu(\nu)}{G(\nu)} d\nu\right].$$
 (20)

Hence, we obtain

$$u^*(N,\tau) \propto \frac{G(N_0)}{G(N)} \cdot \exp\left[-\sigma\tau + \int_{N_0}^N \frac{\sigma - \mu(\nu)}{G(\nu)} d\nu\right].$$
 (21)

Now, we substitute (21) into (7) and get

$$1 = \int_{N_0}^{1} \frac{\lambda(N)}{G(N)} \cdot \exp\left[\int_{N_0}^{N} \frac{\sigma - \mu(\nu)}{G(\nu)} d\nu\right] dN.$$
 (22)

For the existence of the stable size distribution $u^*(N,\tau)$, it is necessary that there exists a σ satisfying (22).

VanSickle [23] studied a family of systems including ours and showed that the birth rate becomes exponential as $t \to \infty$. This means that the size distribution asymptotically approaches the stationary one given in the above, that is, the above stationary distribution is asymptotically stable, and the value of σ is uniquely determined (also see [10]). As a specific case, when the reproduction and the extinction rates λ and μ are both constant, independent of the group size, we can directly calculate the integral of (22) and solve it. Then, we get the result that $\sigma = \sigma_0$ given by (15).

As for the total group population $U^*(\tau)$ for the group population (21):

$$U^*(\tau) \equiv \int_{N_0}^1 u^*(N, \tau) dN \,, \tag{23}$$

its temporal growth is determined by the signature of σ : If σ is positive, the total group population decreases to zero, and the extinction of the community results, while, if σ is negative, it diverges to infinite. In the specific case when the reproduction and the extinction rates λ and μ are both constant independent of the group size, since $\sigma = \sigma_0$ given by (15), the total group population asymptotically decreases to zero only when $\mu > \lambda$.

The stationary group size frequency distribution $f^*(N,\tau)$ is, on the other hand, defined by $u^*(N,\tau)/U^*(\tau)$, where $U^*(\tau)$ is the total group population given by (23):

$$f^*(N, \tau) = f^*(N) = \frac{1}{v} \cdot \frac{G(N_0)}{G(N)} \cdot \exp\left[\int_{N_0}^N \frac{\sigma - \mu(\nu)}{G(\nu)} d\nu\right], \tag{24}$$

where

$$v \equiv \int_{N_0}^1 \frac{G(N_0)}{G(m)} \cdot \exp\left[\int_{N_0}^m \frac{\sigma - \mu(\nu)}{G(\nu)} d\nu\right] dm, \qquad (25)$$

and v corresponds to $1/f^*(N_0)$ as easily seen from (24). It is remarked that the obtained stationary group size frequency distribution is independent of time. This means that, independently of whether the total number of groups in the community tends to grow infinitely or become extinct, the size frequency distribution asymptotically approaches the stationary one given above.

Now, from (22), (24), and (25), the following relations useful for our subsequent argument can be obtained:

$$G(N_0)f^*(N_0) = \int_{N_0}^1 \lambda(N)f^*(N)dN;$$
 (26)

$$\mu(N) = \sigma - \frac{d}{dN} G(N) - G(N) \frac{d}{dN} \ln f^*(N). \tag{27}$$

The relation (27) can be derived by differentiating (24) by N.

6. Extinction Rate Function for Typical Rank-Size Relations

In this section, we consider how the typical rank-size relation for the considered group community depends on the dynamical factors within the community.

Provided that the stationary size frequency distribution $f^*(N)$ would be for some typical rank-size relations, what constraints should be required for the size-dependency of the reproduction rate $\lambda(N)$ or the extinction rate $\mu(N)$? In the following argument, we see that the relation (27) gives specific form of the extinction rate function $\mu(N)$ for the given size frequency distribution $f^*(N)$.

Power-law size frequency distribution: This case corresponds to the case when the rank is proportional to a power of the size or to the logarithm of the size:

$$f^*(N) = CN^{-q} \,, \tag{28}$$

where q is a positive constant and the normalization constant C can be calculated by integrating (28) on $[N_0, 1]$:

$$C = \begin{cases} \frac{q-1}{1/N_0^{q-1} - 1} & \text{for } q \neq 1; \\ -\frac{1}{\ln N_0} & \text{for } q = 1. \end{cases}$$
 (29)

From (27), we can obtain the concrete form of $\mu(N)$ as follows:

$$\mu(N) = (2 - q)N + q - 1 + \sigma. \tag{30}$$

We note that the extinction rate linearly depends on the group size, and especially when q=2, the extinction rate is constant, independent of the group size. For q<2, the extinction rate is linearly increasing as the size gets larger, while, for 2< q, it is linearly decreasing. As for the observed rank-size relations in this case, the parameter q takes such range that $1 \le q \le 2$. Especially, when q=1, the corresponding rank-size relation is of the geometric law. Hence, it is remarked that the result (30) indicates that the extinction rate is required to be monotonically increasing in terms of group size for almost all those observed distributions. Each group of such community would be regarded as to have characteristics of instability increasing as the size grows.

Since it requires that $\mu(N_0) \ge 0$ and $\mu(1) \ge 0$ from the definition of the extinction rate, the following conditions should be satisfied:

$$q \ge 2 - \frac{1+\sigma}{1-N_0};\tag{31a}$$

$$1 + \sigma \ge 0. \tag{31b}$$

Linear size frequency distribution: Corresponding to the niche overlapping rank-size relation [9,14], the following size frequency distribution can be considered:

$$f^*(N) = \frac{2}{(1 - N_0)^2} (1 - N). \tag{32}$$

In this case, from (27), the extinction rate becomes

$$\mu(N) = 3N - 1 + \sigma. {(33)}$$

The required extinction rate is monotonically increasing in terms of group size. In order that $\mu(N_0) \geq 0$ and $\mu(1) \geq 0$, the following is required:

$$\sigma \ge 1 - 3N_0. \tag{34}$$

Negative exponential size frequency distribution: This corresponds to the brokenstick rank-size relation [9,14]:

$$f^*(N) = \frac{se^{sN_0}}{1 - e^{-s(1 - N_0)}} \cdot e^{-sN}, \qquad (35)$$

where s is a positive constant. In this case, the relation (27) gives the following extinction rate:

$$\mu(N) = -s\left(\frac{2}{s} - N\right)(1 - N) + 1 + \sigma. \tag{36}$$

In order to satisfy the definition as the extinction rate, it requires that $\mu(N_0) \ge 0$ and $\mu(1) \ge 0$, therefore,

$$s \ge \frac{2}{N_0} - \frac{1+\sigma}{N_0(1-N_0)};\tag{37a}$$

$$1 + \sigma \ge 0. \tag{37b}$$

Especially when 2 < s, the extinction rate takes its maximal value at a size between N_0 and 1. Otherwise, when $s \le 2$, it is monotonically increasing.

7. Linearly Size-Dependent Reproduction and Extinction Rates

As shown in the previous section, the typical rank-size relations require some specific forms of the extinction rate function $\mu(N)$, while the form of the reproduction rate function $\lambda(N)$ would not seem to undergo any constraint from the form of rank-size relation. However, the characteristics of the reproduction rate function $\lambda(N)$ is implicitly reflected in the value σ via the renewal relation (26). In this section, we argue the relation between the rank-size relation and the reproduction rate function, analyzing our model with the linearly size-dependent reproduction rate $\lambda(N)$ (see Fig. 3):

$$\lambda = \lambda(N) = b + \alpha \frac{N - N_0}{1 - N_0}, \qquad (38)$$

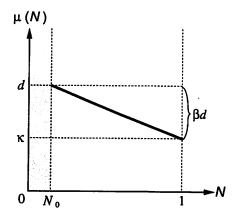


Fig. 3. Linearly size-dependent reproduction and extinction rates, λ and μ .

where b gives the reproduction rate for the group with size N_0 , and α is a constant. In the case when $\alpha = 0$, the reproduction rate is constant, independent of the size of mother group. From the relation (26) with (38), we can get the following relation:

$$G(N_0)f^*(N_0) = b + \alpha \frac{\langle N \rangle - N_0}{1 - N_0},$$
 (39)

where

$$\langle N \rangle = \int_{N_0}^1 N f^*(N) dN \,.$$

This relation (39) gives the constraint for those parameters α and b, which means that the relation (26) does the constraint for the form of the reproduction rate function $\lambda(N)$. Indeed, in the specific case when the reproduction rate is constant, that is, when $\alpha = 0$, the relation (39) gives the following:

$$b = G(N_0)f^*(N_0). (40)$$

This means that the stationary frequency of the group with size N_0 uniquely determines the constant reproduction rate in the considered community. And, if b=0, which is a rather reasonable case when the reproduction rate is linearly depending on the group size because it is natural that the reproduction rate is assumed to be zero for the group with the minimum size N_0 (just after the birth!),

$$\alpha = \frac{1 - N_0}{\langle N \rangle - N_0} \cdot G(N_0) f^*(N_0) \,. \tag{41}$$

This means that the stationary frequency size distribution uniquely determines the size-proportional ratio of the reproduction rate in the considered community. In the following argument, we focus on those two cases when $\alpha = 0$ and when b = 0. As shown in Appendix D, from (39) with (28), we can obtain the concrete relation between parameters for distribution functions for three specific cases and α or b.

As shown in the previous section, except for the case of the broken-stick rank-size relation, we got the linear size-dependency of the extinction rate. In this section, we analyze some characteristics of the stationary size frequency distribution for the community with both the linearly size-dependent reproduction rate (38) and the following linearly size-dependent extinction rate (see Fig. 3):

$$\mu = \mu(N) = d\left(1 - \beta \frac{N - N_0}{1 - N_0}\right), \tag{42}$$

where d gives the extinction rate for the group with size N_0 , and β is a constant equal to or less than 1. In the case when $\beta = 0$, the extinction rate is constant independent of the group size.

In this case, we can directly calculate those functions $k_{-}(N)$, $k_{+}(N,\tau)$, $K(\tau)$, and $h(\tau)$, given by (10), (12), and (13), as follows:

$$k_{-}(N) = \left(\frac{N_0}{N}\right)^{\kappa+\omega+1} \left(\frac{1-N}{1-N_0}\right)^{\kappa-1};$$
 (43)

$$k_{+}(N,\tau) = (1 - N + Ne^{-\tau})^{-(\omega+2)} e^{-(\kappa+\omega+1)\tau};$$
 (44)

$$h(\tau) = \left(\frac{N_0}{g(\tau; 0, N_0)}\right)^{\omega} \cdot \left(b + \alpha \frac{g(\tau; 0, N_0) - N_0}{1 - N_0}\right) \cdot e^{-\kappa \tau}; \tag{45}$$

$$K(\tau) = N_0(1 - N_0) \cdot h(\tau) \,, \tag{46}$$

where

$$\kappa \equiv (1 - \beta)d > 0; \tag{47a}$$

$$\omega \equiv \frac{\beta d}{1 - N_0} \,. \tag{47b}$$

The renewal Eq. (22) has the following form:

$$N_0 = \int_0^1 \frac{b + \alpha m}{(1 - m)^{\omega + 2}} \cdot \left(\frac{1 - m}{1 + (1/N_0 - 1)m}\right)^{\kappa + \omega - \sigma + 1} dm, \qquad (48)$$

where ω is as before, and the variable transformation $m = (N - N_0)/(1 - N_0)$ was used. It is proved in Appendix E that (48) has the unique root σ such that

$$\sigma < (1 - \beta)d = \kappa. \tag{49}$$

Therefore, the existence of the stationary size frequency distribution is proved, which has the asymptotic stability as proved by VanSickle [23]. The stationary size frequency distribution (24) becomes

$$f^{*}(N) = \frac{1}{v} \cdot \left(\frac{N_0}{N}\right)^{\kappa + \omega - \sigma + 1} \left(\frac{1 - N}{1 - N_0}\right)^{\kappa - \sigma - 1} , \tag{50}$$

where the constant v is correspondingly given by (25). The shape of the graph of f^* depends on those parameters, $\kappa - \sigma$ and ω as shown in Fig. 4. Besides, by the relation (1), we can get the corresponding rank-size relation function $K^*(N)$ for the stationary community, though the right-hand side integral of (1) in general cannot be expressed by any fundamental analytical functions. From the result (50), we can analytically examine the shape of the corresponding rank-size relation function $K^*(N)/W$ defined by (1), which depends on those parameters, $\kappa - \sigma$ and ω as shown in Fig. 5.

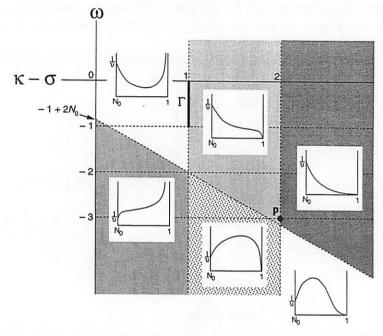


Fig. 4. $(\omega, \kappa - \sigma)$ -dependence of the shape of the stationary size frequency distribution $f^*(N)$ given by (50), assumed that $N_0 \ll 1$. The segment Γ and the point P indicate the parameter regions corresponding respectively to the observed geometric power-law rank-size relation and to the niche overlapping model.

As already seen in the previous section, in cases of the power-law size frequency distribution and the linear size frequency distribution, which are respectively related to the geometric power-law rank-size relation and to the niche overlapping model, the corresponding *linearly* size-dependent extinction rate functions are required within the framework of our modelling. Now, in addition, comparing (30) and (33) to (42), we can derive the following correspondences for parameters of our model:

Power-law size frequency distribution:

$$\omega = q - 2\,, (51a)$$

$$\kappa - \sigma = 1. \tag{51b}$$

Linear size frequency distribution:

$$\omega = -3 \tag{52a}$$

$$\kappa - \sigma = 2. \tag{52b}$$

In the former case, for the observed range of q such that $1 < q \le 2$, the parameter ω must be restricted to the following range: $-1 < \omega \leq 0$. The corresponding parameter regions for both cases of (51) and (52) are indicated as the segment Γ and the point P in Fig. 4 and Fig. 5. This result shows that both of the geometric power-law rank-size relation and the niche overlapping model are specific cases with some rigid parameter constraints within the framework of our modelling.

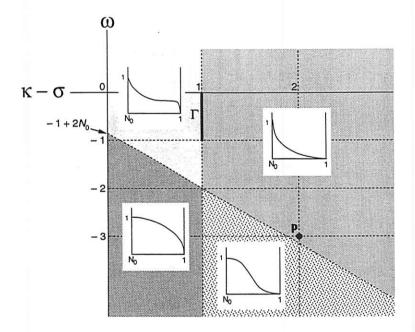


Fig. 5. $(\omega, \kappa - \sigma)$ -dependence of the shape of the corresponding rank-size relation function $K^*(N)/W$ defined by (1) for $f^*(N)$ given by (50), assumed that $N_0 \ll 1$. The segment Γ and the point P indicate the parameter regions corresponding respectively to the observed geometric power-law rank-size relation and to the niche overlapping model.

The renewal Eq. (48) corresponds to the 4-dimensional hyper surface in the $(b,\alpha,\omega,\kappa-\sigma)$ -parameter space with given N_0 . Now, let us focus on the case when b=0, which is, as already mentioned, the reasonable case since it is natural that the reproduction rate is assumed to be zero for the group with the minimum size N_0 (just after the birth!). Then, the renewal Eq. (48) gives the 3-dimensional surface Ω in the $(\alpha, \omega, \kappa - \sigma)$ -parameter space with given N_0 as shown in Fig. 6. These parameters $(\alpha, \omega, \kappa - \sigma)$ are restricted on the surface Ω . If and only if the parameter σ is negative, the community continues to grow, otherwise, it declines

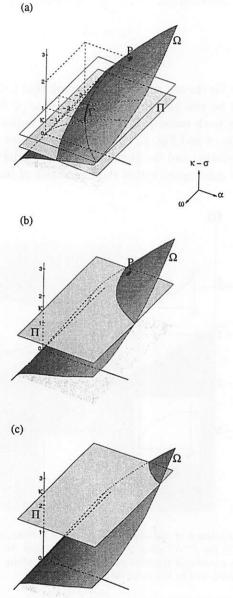


Fig. 6. Parameter region Ω for $(\alpha, \omega, \kappa - \sigma)$, given by the renewal Eq. (48) with b = 0, and the plane Π corresponding to $\sigma = 0$. (a) $\kappa < 1$; (b) $1 < \kappa < 2$; (c) $2 < \kappa$. The segment Γ and the point P indicate the parameter regions corresponding respectively to the observed geometric power-law rank-size relation and to the niche overlapping model. Also see Figs. 4 and 5. For detailed explanation, see the text.

to its extinction. In the $(\alpha, \omega, \kappa - \sigma)$ -parameter space with given N_0 , the growing community with negative σ should have the parameters on Ω over the plane Π given by $\kappa - \sigma = \kappa$, which is the plane corresponding to $\sigma = 0$ (see Fig. 6a). As

exemplified in Fig. 6, only when $\kappa < 1$, both of the curve Γ and the point P are located over the plane Π . This means that both rank-size relations for the geometric power-law and the niche overlapping model would be for the growing community with $\kappa < 1$. When $1 < \kappa < 2$ (Fig. 6b), since the curve Γ is located below Π , the community in which the geometric power-law rank-size relation would be applicable tends to decline. Further, when $2 < \kappa$ (Fig. 6c), both Γ and P are below Π , which means that neither rank-size relations for the geometric power-law and the niche overlapping model would be observable for any growing community in this case.

8. Discussion

For our model for the community structure of groups which are growing their size in the logistic manner, we have analyzed the characteristics of the stationary size distribution, related to the rank-size relation which could be regarded as to reflect the dynamical structure within the community.

Especially, for three types of specific rank-size relation: geometric power-law, broken-stick model, and niche overlapping model, we considered the corresponding size frequency distributions, and examined how these specific cases are identified within the framework of our model. It is shown that, except for the case of brokenstick model, the group extinction rate is required to depend linearly on the group size: The larger group has the higher extinction rate. In examples mentioned in the main text such as when the group size corresponds to the total number of individuals of a species, or that of species per plant, provided that the number would be proportional to the logistically growing plant size, the extinction of groups might be regarded as that of plants, that is, habitats due to predation or harvest, etc. In such a case, the harvest or the predation might be more likely to occur for the larger plant. In contrast, in a case of the broken-stick model, shown as (36), the required corresponding extinction rate parabolically depends on the group size. Thus, it is likely that the extinction rate might have the maximum at an intermediate group size in the case of the broken-stick model. In the above-mentioned example for the groups whose habitats are plants, such situation would correspond to size-restricted harvest or predation, that is, to the case when plants with intermediate size would be more likely to suffer from harvest or predation.

In a reasonable case when the extinction rate linearly depends on the group size and when the reproduction rate is linearly dependent on the group size and is zero for the group with the minimum size N_0 just after birth, that is, b=0 for (38), the renewal Eq. (48) gives the 3-dimensional surface Ω in the $(\alpha, \omega, \kappa - \sigma)$ -parameter space with given N_0 as shown in Fig. 6. Those parameters $(\alpha, \omega, \kappa - \sigma)$ are restricted on the surface Ω . The parameter regions Γ and P corresponding to the geometric power-law rank-size relation and the niche overlapping model appear in the curve and the point on Ω (see Fig. 6a). Now, it should be noted that the rank-size relations following the geometric power-law or the niche overlapping model have

been observed for some data sampled for the real world. We consider that this might mean the community which gives such rank-size relation was stationarily growing, because it would be hard to observe any declining community in the real world. In our model, this corresponds to the community with the negative value of σ : if and only if the parameter σ is negative, the community continues to grow, otherwise, it declines to its extinction. In the $(\alpha, \omega, \kappa - \sigma)$ -parameter space with given N_0 , the growing community with negative σ should have the parameters on Ω over the plane Π given by $\kappa - \sigma = \kappa$, which is the plane corresponding to $\sigma = 0$ (see Fig. 6). As already argued for Fig. 6 in the previous section, the observability of rank-size relations for the geometric power-law and the niche overlapping model strongly depends on the parameter κ . As defined by (47a), the parameter κ represents the extinction rate for the group with the maximal size 1. The larger value of κ means that the extinction rate rapidly changes as the group size gets larger. Analysis on our mathematical model concludes that the typical rank-size relation such as for the geometric power-law or the niche overlapping model might be the more observable one for the community in which the extinction rate changes more slowly as the group size gets larger.

However, in the case when the extinction rate in our model linearly depends on the group size, those two specific cases of the geometric power-law and the niche overlapping model are identified within the framework of our model as cases with some rigid parameter constraints given by (51) and (52). Indicated as the segment Γ and the point P in Figs. 4 and 5, these two specific cases are located at or near the boundary for the parameter region of monotonically decreasing frequency distribution function and the whole concave shape of rank-size relation function. This implies that, even if the monotonicity of frequency distribution or the concavity of rank-size relation would be vulnerable for some sampling data, the result of statistical treatment could apply one of the two specific rank-size relations for the data. In this sense, although the two specific rank-size relations could be realized with some restricted conditions, they could be expected to be observable for a little wider range of sampled data. Much of the rank-size relation estimated for sampled data is derived from a rather rough statistical estimation.

Within the framework of our model, three typical rank-size relations are clearly distinguished: the rank-size relations for the geometric power-law and the niche overlapping model are respectively corresponding to the distinct parameter regions for the community with the linearly size-dependent reproduction and extinction rates for the group in it. The rank-size relation for the broken-stick model appears for the community with the parabolically size-dependent extinction rate. Therefore, indeed, it is shown that the rank-size relation can represent the nature of a community.

Our work is on the community structure with an ideal dynamics of logistic growth of group size, linearly density-dependent extinction and reproduction rates. Such modelling might seem to be oversimplified. There must be some effects of individual migration among groups, nonlinear extinction or reproduction rates. It

is expected that our work will be referred as a metaphor to consider the structure of more realistic and complex community.

Appendix A

In this appendix, referring to Fig. A, we show the outline of the derivation of Eq. (6) for the group size distribution $u(N,\tau)$, which is the number of groups with size N at time τ (for more mathematically detailed explanation, see for instance [10]). The number of groups with the size in the range $[N, N + \delta N]$ at time τ with a size

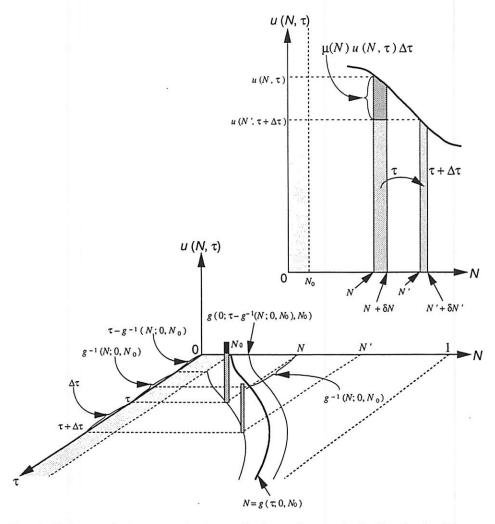


Fig. A. Each group in the community temporally changes its state in the time-size-density space. Groups with a labeled size change their state along the corresponding characteristic curve. For detailed explanation, see the text.

interval δN is now given by

$$\int_{N}^{N+\delta N} u(\nu,\tau) d\nu \,. \tag{A.1}$$

After a time interval $\Delta \tau$, this subpopulation (A.1) of groups becomes

$$\int_{N'}^{N'+\delta N'} u(\nu, \tau + \Delta \tau) d\nu . \tag{A.2}$$

Note that, in the interval $\Delta \tau$, the subpopulation with size N becomes N', while that with $N + \delta N$ becomes $N' + \delta N'$. The difference between (A.1) and (A.2) corresponds to the extinction of groups of the focused subpopulation in the time interval $\Delta \tau$. Therefore, we obtain the following equation:

$$\int_{N'}^{N'+\delta N'} u(\nu,\tau+\Delta\tau)d\nu - \int_{N}^{N+\delta N} u(\nu,\tau)d\nu = -\int_{\tau}^{\tau+\Delta\tau} \int_{N}^{N+\delta N} \mu(\nu)u(\nu,\tau)d\nu d\tau.$$
(A.3)

With Taylor expansion around N and N', (A.3) becomes

$$\{u(N', \tau + \Delta \tau)\delta N' + o(\delta N')\} - \{u(N, \tau)\delta N + o(\delta N)\}$$

$$= -\int_{\tau}^{\tau + \Delta \tau} [\mu(N)u(N, \tau)\delta N + o(\delta N)]d\tau. \tag{A.4}$$

Moreover, with Taylor expansion around τ , it further becomes

$$\left\{ u(N',\tau)\delta N' + \frac{\partial u(N',\tau)}{\partial \tau} \Delta \tau \delta N' + o(\delta \tau \delta N') + o(\delta N') \right\}
- \left\{ u(N,\tau)\delta N + o(\delta N) \right\}
= -\mu(N)u(N,\tau)\Delta \tau \delta N + o(\Delta \tau \delta N).$$
(A.5)

On the other hand, since the growth of group size is governed by (5), that is, since $N' = g(\tau + \Delta \tau; \tau_0, m)$ for $N = g(\tau; \tau_0, m)$, we can obtain the following with Taylor expansion around τ :

$$N' = g(\tau + \Delta \tau; \tau_0, m) = N + G(N)\Delta \tau + o(\Delta \tau), \qquad (A.6)$$

where we used the fact that $g(\tau; \tau_0, m)$ satisfies (3) with (4). In the same way, we can obtain

$$N' + \delta N' = N + \delta N + G(N + \delta N)\Delta \tau + o(\Delta \tau)$$

$$= N + \delta N + G(N)\Delta \tau + \frac{dG(N)}{dN}\delta N\Delta \tau + o(\delta N\Delta \tau) + o(\Delta \tau),$$
(A.7)

where we used the fact that the subpopulation with size N at time τ grows to that with size N' at time $\tau + \Delta \tau$, while that with size $N + \delta N$ grows to that with size $N' + \delta N'$. Substituting (A.6) into (A.7), we can obtain the relation between δN and $\delta N'$:

 $\delta N' = \delta N + \frac{dG(N)}{dN} \delta N \Delta \tau + o(\delta N \Delta \tau) + o(\Delta \tau). \tag{A.8}$

Now, substituting (A.6) and (A.8) into (A.5) and ignoring those terms of higher order, we arrive at the following equation:

$$u(N + G(N)\Delta\tau, \tau) \left(\delta N + \frac{dG(N)}{dN} \delta N \Delta\tau\right)$$

$$+ \frac{\partial u(N + G(N)\Delta\tau, \tau)}{\partial \tau} \Delta\tau \left(\delta N + \frac{dG(N)}{dN} \delta N \Delta\tau\right)$$

$$- u(N, \tau)\delta N = -\mu(N)u(N, \tau)\delta N \Delta\tau.$$
(A.9)

Further, making use of Taylor expansion and ignoring those terms of higher order, (A.9) finally becomes

$$\frac{\partial u(N,\tau)}{\partial N} G(N)\delta N \Delta \tau + \frac{dG(N)}{dN} u(N,\tau)\delta N \Delta \tau + \frac{\partial u(N,\tau)}{\partial \tau} \delta N \Delta \tau
= -\mu(N)u(N,\tau)\delta N \Delta \tau.$$
(A.10)

Canceling out $\delta N \Delta \tau$ in both sides of (A.10), we can obtain Eq. (6).

Appendix B

In this appendix, we give the route to the solution of (6) with (7) along the characteristic curve. Refer to Fig. A again. As seen from (5), the function g can be regarded as of $\tau - \tau_0$, m, that is, $g(\tau; \tau_0, m) = g(\tau - \tau_0, m)$. Thus, it can be additionally assured for g that $g(\tau + a; \tau_0 + a, m) = g(\tau; \tau_0, m)$ for any value a. It is remarked that, since g is the monotonically increasing one-to-one continuous function of τ for a fixed m, it has the inverse function g^{-1} such that $\tau = g^{-1}(N; \tau_0, m)$. Moreover, it can be proved easily from the nature of the function g that $m = g(\tau_0; \tau, N)$ when $N = g(\tau; \tau_0, m)$.

Along the characteristic curve $N=g(\tau;\tau_0,m)$, the function $u(N,\tau)$ can be regarded as only of the time τ with parameters m and τ_0 which are uniquely determined for each of the characteristic curves. Since

$$\frac{du(N,\tau)}{d\tau} = \frac{\partial u(N,\tau)}{\partial \tau} + G(N) \cdot \frac{\partial u(N,\tau)}{\partial N},$$
 (B.1)

we can obtain the following equation from (6) along the characteristic curve $N = g(\tau; \tau_0, m)$:

$$\frac{du(g(\tau;\tau_0,m),\tau)}{d\tau} = -\left[\mu(N) + \frac{dG(N)}{dN}\right]_{N=g(\tau;\tau_0,m)} u(g(\tau;\tau_0,m),\tau). \tag{B.2}$$

The effective characteristic curve which gives the value of u(M,T) for the size M at time T is determined as follows:

$$N = g(\tau; \tau_0, N_0) \quad (0 < \tau_0 \le \tau)$$
 when $M < g(T; 0, N_0)$; (B.3a)

$$N = g(\tau; 0, m)$$
 $(0 \le \tau, N_0 \le m \le 1)$ when $M \ge g(T; 0, N_0)$, (B.3b)

where τ_0 and m are given as the following functions of M and T:

$$\tau_0 = T - g^{-1}(M; 0, N_0), \tag{B.4}$$

$$m = g(0; T, M). \tag{B.5}$$

The subpopulation u(M,T) with $M \geq g(T;0,N_0)$ originates from the initially distributed population u(m,0) at time 0, while the subpopulation u(M,T) with $M < g(T;0,N_0)$ does from the new born population $u(N_0,\tau_0)$ at a time $\tau_0 > 0$.

The characteristic curve (B.3a) starts from the point (N_0, τ_0) to (M, T), therefore,

$$M = g(T; \tau_0, N_0). \tag{B.6}$$

Since the new born population $u(N_0, \tau_0)$ at a time τ_0 grows in size from N_0 to M during $T - \tau_0$, we can give another equation which determines τ_0 :

$$M = g(T - \tau_0; 0, N_0). \tag{B.7}$$

that is,

$$\tau_0 = T - g^{-1}(M; 0, N_0).$$
 (B.7')

The coincidence between (B.6) and (B.7) is easily proved by such nature of the function $g(\tau; \tau_0, N_0)$ that it can be regarded as the function of $\tau - \tau_0$ with a parameter N_0 because the growth of the group size depends not on the time itself but on the period from its birth.

From the functional nature of g, we can trace back the characteristic curve (B.3b) from the point (M,T) to (m,0), which means that

$$m = g(0; T, M). \tag{B.8}$$

Now, we can easily solve (B.2) along the characteristic curve and get the resulting solution (9).

Appendix C

In this appendix, we show that, by means of Laplace transformation, the renewal Eq. (11) can be formally solved in terms of $u(N_0, \tau)$. Let us denote the Laplace transformed function for F with L[F]. Making Laplace transformation for both sides of (11) in terms of τ , we can obtain the following equation with transformed functions:

$$G(N_0) \cdot L[u] = L[K] \cdot L[u] + L[h],$$
 (C.1)

where we used the following nature of Laplace transformation for the convolution integral:

$$L\left[\int_0^t F_1(z)\cdot F_2(t-z)dz\right] = L[F_1]\cdot L[F_2].$$

Since (C.1) can be easily solved in terms of L[u], we can obtain the formal expression of $u(N_0, \tau)$ with the Laplace inverse transformation L^{-1} :

$$u(N_0, \tau) = L^{-1} \left[\frac{L[h]}{G(N_0) - L[K]} \right] (N_0, \tau).$$
 (C.2)

Appendix D

In this appendix, using relations (40) and (41) for linearly size-dependent reproduction rate function $\lambda(N)$ given by (38), we show the concrete form of the relation between parameters for distribution functions for three specific cases and α or b.

Power-law size frequency distribution:

(i) When $\alpha = 0$,

$$\dot{b} = \begin{cases} \frac{1 - N_0}{-\ln N_0} & \text{for } q = 1; \\ 1 & \text{for } q = 2; \\ (q - 1) \frac{1 - N_0}{1 - N_0^{q - 1}} & \text{for } q \neq 1, 2. \end{cases}$$
 (D.1)

(ii) When b=0,

$$\alpha = \begin{cases} \frac{1 - N_0}{1 + \frac{N_0}{1 - N_0} \ln N_0} & \text{for } q = 1; \\ -\frac{1}{N_0 + \frac{N_0}{1 - N_0} \ln N_0} & \text{for } q = 2; \\ (q - 1) \frac{1 - N_0}{N_0^{q - 1} \left(\frac{1}{2 - q} \frac{1 - N_0^{2 - q}}{1 - N_0} - 1\right)} & \text{for } q \neq 1, 2. \end{cases}$$
(D.2)

Linear size frequency distribution:

(i) When $\alpha = 0$,

$$b = 2N_0. (D.3)$$

(ii) When b = 0,

$$\alpha = 6N_0. \tag{D.4}$$

Negative exponential size frequency distribution:

(i) When $\alpha = 0$,

$$b = \frac{sN_0(1 - N_0)}{1 - e^{-s(1 - N_0)}}.$$
 (D.5)

(ii) When b = 0,

$$\alpha = \frac{sN_0(1-N_0)^2}{\frac{1}{s}(1-e^{-s(1-N_0)})-(1-N_0)e^{-s(1-N_0)}}.$$
 (D.6)

Appendix E

In this appendix, we show the unique existence of σ which determines the nature of the stationary size distribution $u^*(N,\tau)$. Equation (17) — to determine σ — can be rewritten as follows:

$$N_{0} = b \int_{0}^{1} \frac{1}{(1-m)^{\omega+2}} \cdot \left(\frac{1-m}{1+(1/N_{0}-1)m}\right)^{\theta} dm$$

$$+ \alpha \int_{0}^{1} \frac{m}{(1-m)^{\omega+2}} \cdot \left(\frac{1-m}{1+(1/N_{0}-1)m}\right)^{\theta} dm$$

$$\equiv bJ_{0}(\theta) + \alpha J_{1}(\theta) \equiv I(\theta), \tag{E.1}$$

where $\theta = \kappa + \omega - \sigma + 1$. Each integral of (E.1) is regarded as function of $\theta \in \mathbf{R}$. If $\theta \leq 0$, since the integrand is positive on [0, 1],

$$\int_0^1 \frac{1}{(1-m)^{\omega+2-\theta}} \, dm \equiv R_0(\theta) \le J_0(\theta) \,; \tag{E.2a}$$

$$\int_{0}^{1} \frac{m}{(1-m)^{\omega+2-\theta}} dm \equiv R_{1}(\theta) \le J_{1}(\theta).$$
 (E.2b)

We can calculate the integrals $R_0(\theta)$ and $R_1(\theta)$ in the left-hand sides of (E.2a) and (E.2b), and show that they positively diverge when $\theta \leq 0$. Therefore, the integral $I(\theta)$ will also positively diverge when $\theta \leq 0$.

When $\theta > 0$, the following inequalities are easily obtained by the positiveness of the integrands of $J_0(\theta)$ and $J_1(\theta)$:

$$N_0^{\theta} \cdot R_i(\theta) < J_i(\theta) < R_i(\theta) \qquad (i = 0, 1), \qquad (E.3)$$

where we used the trivial inequality that $1 < 1 + (1/N_0 - 1)m < 1/N_0$ for m on (0, 1). By direct calculation, we can obtain the following natures of the integrals $R_0(\theta)$ and $R_1(\theta)$:

$$R_0(\theta) = \begin{cases} +\infty & \text{when } \theta \le \omega + 1; \\ \frac{1}{\theta - \omega - 1} & \text{when } \theta > \omega + 1; \end{cases}$$
 (E.4a)

$$R_1(\theta) = \begin{cases} +\infty & \text{when } \theta \le \omega + 1; \\ \frac{1}{(\theta - \omega)(\theta - \omega - 1)} & \text{when } \theta > \omega + 1. \end{cases}$$
 (E.4b)

Thus, from (E.3), it is shown that $I(\theta)$ positively diverges when $\theta \leq \omega + 1$. In contrast, when $\theta > \omega + 1$, since both $R_0(\theta)$ and $R_1(\theta)$ take finite positive values, $I(\theta)$ is a continuous function of θ , which takes a finite positive value. Further, from (E.3) and (E.4), since both $R_0(\theta)$ and $R_1(\theta)$ converge to zero as $\theta \to \infty$, it is shown that $J_i(\theta) \to 0$ (i = 0, 1), that is, $I(\theta) \to 0$ as $\theta \to \infty$. Lastly, since

$$\frac{1-m}{1+(1/N_0-1)m}<1\,,$$

 $I(\theta)$ is continuously and monotonically decreasing from positively infinite to zero for θ on $(\omega+1,+\infty)$. This means that (E.1) has a unique root θ such that $\theta > \omega+1$.

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