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Theorems on the invasion process in stage-structured populations with density-dependent dynamics

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Abstract. Several theoretical results on evolution in stage-structured models with density-dependent dynamics are obtained. The first one concerns the invadable condition of mutant types when 'density' is considered as the weighted sum of the population densities at each stage. In the second and third results, it is shown that the invadability is equivalent to the increase of the weighted sum at equilibrium when certain conditions are satisfied. It is also shown that the sensitivity for the dominant eigenvalue is proportional to that for the weighted sum at equilibrium. Finally, a theorem on the coexistence of a wild and the mutant types is obtained and the condition for coexistence is discussed. A part of these results are the extended theorems of what Charlesworth (1971, 1980, 1994) has already obtained.

Key words: Stage-structure – Invasion – Sensitivity – Coexistence – Theorem

1 Introduction

Density-dependence is one of the most important factors affecting the population dynamics. For example, small individuals of perennial plants are usually suppressed by surrounding ones because of their immobility, meaning that their demographic process is basically density-dependent (Yoda et al. 1963; Harper 1977; Schellner et al. 1982; Silvertown and Lovett Doust 1993). The population dynamics of most insects is also regulated strongly by the population density (Pearl and Parker 1922; Utida 1941; Dempster 1975). However, most authors since Fisher have disregarded a density-dependent factor when they obtained the optimal strategies in various models on life history evolution (Fisher 1930; Cole 1954; Lewontin 1965; Gadgil and Bossert 1970; Stearns and Crandall, 1981, 1984; Roff 1984; Kozlowski and Wiegart 1987; Caswell 1989; Stearns 1992). They used either the intrinsic growth rate (r) or Fisher's reproductive value (V_x) as a measure of fitness, i.e. they assumed the

type with the largest r or V_x would be favored under natural selection. However, the optimal strategies under density-independent dynamics must be different from those under density-dependent dynamics. Therefore, some of the above models have been re-examined based on the assumption that density-dependence is important (Charlesworth 1980, 1994; Takada and Nakajima 1992, 1996; Takada 1995).

In parallel with this re-examination, several authors have developed a method of obtaining the optimal strategies in age- or stage-structured models with density-dependent dynamics. Charlesworth and other authors (Charlesworth 1971, 1980, 1994; Roughgarden 1971; Leon and Charlesworth 1978; Kimura 1978; Nagylaki 1979) developed several theorems on the invasion of a mutant type in age-structured populations and demonstrated that the progress of selection is controlled by the carrying capacities. Moreover, Charlesworth (1971, 1980, 1994) showed that selection tends to maximize the number of individuals in the critical equilibrium, i.e. in a restricted sub-group of the population, if the parameters of mortality and fecundity depend negatively on the number of individuals in the critical age-group. Takada and Nakajima (1992, 1996) and Takada (1995) demonstrated that the carrying capacity of a population increases in the course of evolution in stage-structured models with density-dependent dynamics. The theorems obtained by the above authors are useful tools for evaluating the optimal strategies in the density-dependent dynamics. In fact, using those theorems, several central issues related to life history strategies have been analyzed based on the assumptions of densitydependence, e.g. evolution of semelparity and iteroparity, the optimal age of maturation and the optimal allocation between seed and vegetative reproduction (Charlesworth 1980, 1994; Takada and Nakajima 1992, 1996; Takada 1995).

In the present paper, we obtain several theoretical results on evolution in stage-structured models with density-dependent dynamics. The first one concerns the invadable condition of mutant types when 'density' is considered as the weighted sum of the population densities at each stage. In the second and third results, it is shown that the invadability is equivalent to the increase of the weighted sum at equilibrium when certain conditions are satisfied. In the fourth result, it is shown that the sensitivity for the dominant eigenvalue is proportional to that for the weighted sum at equilibrium. We finally obtain a theorem on the coexistence of a wild and the mutant types and speculate the condition for coexistence. A part of these results are the extended theorems of what Charlesworth (1971, 1980, 1994) has already obtained.

2 The invadable condition in stage-structured populations

Takada and Nakajima (1992) obtained the invadable condition of the mutanttype individuals in stage-structured matrix models with density-dependent dynamics and demonstrated the population size at equilibrium (the carrying capacity) continues to increase in the course of evolution if all the elements of the density-dependent projection matrix are monotonically decreasing functions of the population size. As is stated in the Introduction, a similar conclusion had been already derived by Charlesworth and other authors in age-structured matrix models with density-dependent dynamics. We here obtain three extended theorems of the results obtained by Charlesworth (1971) in this section and discuss its meaning.

Let n_{it} and $n_t = (n_{1t}, n_{2t}, \dots, n_{st})^T$ be the population density of stage-class i and the stage-class vector at time t, respectively, where s is the number of stage-classes. The dynamics of a stage-structured population can be written as

$$\mathbf{n}_{t+1} = \mathbf{L}(N_t)\mathbf{n}_t \ . \tag{1}$$

Although the density-dependent dynamics may have oscillatory or chaotic behaviors of the population density (Guckenheimer et al. 1977; Allen 1989), we assume here that the dynamics reaches an equilibrium state. Let $L(N_t)$ and $L'(N_t)$ be the density-dependent projection matrices of wild-type individuals and of mutant-type individuals, respectively, which are irreducible and nonnegative for all N_t . Therefore, as derived from Frobenius theorem, $L(N_t)$ (and $L'(N_t)$) has a positive dominant eigenvalue for each N_t and the positive left and right eigenvectors corresponding to the dominant eigenvalue (Gantmacher 1960, pp. 64–79). The difference between $L(N_t)$ and $L'(N_t)$, $\delta L(N_t) = L'(N_t) - L(N_t)$, is assumed to be sufficiently small because the changes of the elements occur due to mutation. N_t is the weighted sum of the population densities at each stage-class:

$$N_t = \sum_{i=1}^s w_i n_{it} , \qquad (2)$$

where w_i represents the degree of the contribution of n_{it} to the density effect. For example, small individuals have relatively smaller w_i than large individuals. Solbrig et al. (1988) used the weighted sum to represent the density-dependence in the size-structured model, i.e. the survival of seedling depends only on the density of adults (therefore, $w_{\text{adult}} = 1$ and $w_{\text{seedling}} = w_{\text{juvenile}} = 0$). The weighted sum has been employed by several authors in analyzing field data or mathematical models (DeAngelis et al. 1980; Levin and Goodyear 1980; Caswell 1989; Ferriere and Clobert 1992; Nishitani et al. 1995; Takada and Nakashizuka 1996).

We can obtain the invadable condition of mutant-type individuals as follows (the proof can be seen in Appendix A):

Result 1. If the elements of $\delta L(N^*)$ are sufficiently small, the sufficient condition such that a mutant-type population can invade the wild-type population is

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0 , \qquad (3)$$

where N^* is the population density of the wild type at equilibrium, and \mathbf{u} and \mathbf{v}^T are the right and the left eigenvectors of $\mathbf{L}(N^*)$ corresponding to the

eigenvalue 1, respectively, i.e.

$$L(N^*)u = u , (4-1)$$

$$\boldsymbol{v}^T \boldsymbol{L}(N^*) = \boldsymbol{v}^T \ . \tag{4-2}$$

The two eigenvectors satisfy the normalization condition $\mathbf{v}^T \mathbf{u} = 1$.

Eq. (3) means that the sensitivity for the dominant eigenvalue at equilibrium is positive. This result has a form similar to the condition obtained in Takada and Nakajima (1992), where N represents the simple sum of the population densities at each stage. Since N represents the weighted sum in the present paper, this result presented in Eq. (3) is actually the extended theorem of that presented in the earlier papers. When $w_i = 1$ for all i, the weighted sum represents the simple sum of the population densities and its value at equilibrium is the carrying capacity.

We next examine the relationship between the invadability under density-dependent selection and the weighted sum at equilibrium.

Result 2. If the elements of $\delta L(N^*)$ are sufficiently small and $dl_{ij}(N^*)/dN^* \leq 0$ for all i, j and $dl_{ij}(N^*)/dN^* < 0$ for at least one set of (i, j), then the weighted sum of a wild-type population at equilibrium is smaller than that of the mutant-type population at the new equilibrium, where $l_{ij}(N^*)$ is an (i, j) element of $L(N^*)$ (the proof can be seen in Appendix B).

Therefore, if the elements of the projection matrix depend negatively on the weighted sum, its value at equilibrium increases after the successful invasion and establishment of the mutant type. In other words, if the matrix of a mutant type has a larger weighted sum at equilibrium than that of the wild type, then the mutant type is invadable.

The second result is, in two senses, the extended theorem of the result obtained by Charlesworth (1971) in age-structured models. The first one is that the matrices describing the dynamics of age-structured models correspond to a special case of the matrices in stage-structured populations. The other one is that the critical age-group named by Charlesworth (1971) corresponds to a special case of the weighted sum. For example, if $w_1 = 0$, $w_2 = 0, \ldots, w_i = 0, w_{i+1} = 1, \ldots, w_s = 1, N_t$ represents the number of individuals in a restricted sub-group of the population whose size-classes are larger than i.

The key equation in the proof of Result 2 is (see Appendix B):

$$\delta N^* \approx \frac{\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}}{-\mathbf{v}^T \frac{d \mathbf{L}(N^*)}{d N^*} \mathbf{u}}.$$
 (5)

This implies that the increase of the weighted sum at equilibrium $(\delta N^* > 0)$ is equivalent to the invadability of the mutant type $(\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0)$ when $\mathbf{v}^T (d\mathbf{L}(N^*)/dN^*) \mathbf{u}$ is negative. It also implies that N^* increases in the course of evolution as long as $\mathbf{v}^T (d\mathbf{L}(N^*)/dN^*) \mathbf{u}$ is negative, even if some of the

elements of $dL(N^*)/dN^*$ is positive. The next result demonstrates to what extent the positive elements of $dL(N^*)/dN^*$ can be included so that $v^T(dL(N^*)/dN^*)u$ is negative.

Result 3. If the elements of $\delta L(N^*)$ are sufficiently small,

$$\frac{d}{dN^*} \sum_{i \in C_k} l_{ij}(N^*) \leq 0 \quad \text{for all sets of } (k, j)$$
 (6-1)

and

$$\frac{d}{dN^*} \sum_{i \in C_k} l_{ij}(N^*) < 0 \quad \text{for at least one set of } (k,j) \;, \tag{6-2}$$

then the weighted sum of a wild-type population at equilibrium is smaller than that of the mutant-type population at the new equilibrium, where \mathbf{v}_j is the j-th element of the positive left eigenvector and $C_k = \{i | v_i \ge v_k\}$ (the proof is in Appendix C).

Since the positive left eigenvector represents the Fisher's reproductive value in projection matrix models, the condition of the above result means that, for each class, the column sum of the transition probabilities over classes whose reproductive values are equal to or larger than that of the class should be a decreasing function of N_t even if some of the transition probabilities are increasing functions of N_t . Therefore, all the transition probabilities to a class with the largest reproductive value should be decreasing functions of N_t .

For example, suppose that the reproductive values of the following matrix at equilibrium satisfy $v_1 < v_2 < v_3$:

$$L(N) = \begin{bmatrix} \frac{a_1}{2} + b_{11}N & 0 & f - b_{13}N \\ \frac{a_1}{2} - b_{21}N & \frac{a_2}{2} + b_{22}N & \frac{a_3}{2} + b_{23}N \\ 0 & \frac{a_2}{2} - b_{32}N & \frac{a_3}{2} - b_{33}N \end{bmatrix}$$
(7-1)

$$\frac{d\mathbf{L}(N)}{dN} = \begin{bmatrix}
b_{11} & 0 & -b_{13} \\
-b_{21} & b_{22} & b_{23} \\
0 & -b_{32} & -b_{33}
\end{bmatrix},$$
(7-2)

where a_i is the density-independent survival rate of the *i*-th class, f is the density-independent fecundity of the third class and b_{ij} is the coefficient of the density-dependence, respectively. $\sum_{i \in C_k} dl_{ij}(N^*)/dN^*$ for all sets of (k,j) in this example is shown in Table 1. Therefore, if $b_{11} < b_{21}$, $b_{22} < b_{32}$ and $b_{23} < b_{33}$, then the condition of Result 3 is satisfied and the weighted sum at equilibrium increases in the course of evolution.

As shown in this example, even if there are several increasing functions of N_t among the transition probabilities, the weighted sum at equilibrium increases in the course of evolution when the effect of negative density-dependence on classes with higher reproductive value is large. The condition of

Table 1. $\sum_{i \in C_k} dl_{ij}(N^*)/dN^*$ for all sets of (k,j) in the example of Eq. (7-1) when the reproductive value increases monotonically with stage-class

(k,j)	j = 1	j = 2	j = 3
k = 1 $k = 2$ $k = 3$	$ \begin{array}{c} b_{11} - b_{21} \\ - b_{21} \\ 0 \end{array} $	$\begin{array}{c} b_{22} - b_{32} \\ b_{22} - b_{32} \\ - b_{32} \end{array}$	$\begin{array}{c} -b_{13} + b_{23} - b_{33} \\ b_{23} - b_{33} \\ -b_{33} \end{array}$

Result 3 is broader than that of Result 2 which requires that all the matrix elements be decreasing functions.

3 Sensitivity for the weighted sum at equilibrium

From Results 1, 2 and 3 the change in N^* (δN^*), accompanied by the changes in several elements of the density-dependent matrix, is expected to have a relationship with the sensitivity for the dominant eigenvalue. From Eq. (5), we define the sensitivity for the weighted sum at equilibrium as:

$$S_{\text{equilibrium value}} = \begin{cases} e_{ij} | e_{ij} = \frac{v_i u_j}{-v^T \frac{dL(N^*)}{dN^*} u} \end{cases}.$$
(8)

Therefore, we can obtain the following result.

Result 4. The sensitivity for the weighted sum at equilibrium is proportional to the sensitivity for the dominant eigenvalue at equilibrium, i.e.

$$S_{\text{equilibrium value}} = \frac{1}{-v^T \frac{dL(N^*)}{dN^*} u} \times \frac{Sensitivity \ matrix}{for \ the \ dominant \ eigenvalue}. \tag{9}$$

Therefore, if the denomination of the right-hand side of Eq. (9) is positive, the sensitivity for the dominant eigenvalue has the same sign as the sensitivity for the weighted sum at equilibrium. Especially if $L(N^*)$ satisfies the condition of Results 2 and 3, then the invadability of the mutant type (i.e. the sensitivity matrix for the dominant eigenvalue is positive) is equivalent to the positive sensitivity for the weighted sum at equilibrium.

4 The theorem on coexistence of wild and mutant types

The invasion of the mutant type into the wild-type population occurs iteratively in the course of evolution. Although we have already obtained the invadable condition of the mutant type, it is not clear what happens between

the invasion and the establishment of the mutant type. Therefore, in this section, we examine the possibility of coexistence of the wild and mutant types in stage-structured populations.

4.1 The possibility of coexistence of the wild and mutant types

Suppose that the weighted sum (N_t) is represented by

$$N_t = \sum_{i=1}^{s} w_i (n_{it} + n'_{it}) , \qquad (10)$$

when both the wild- and mutant-type individuals exist in the same population. n'_{it} represents the number of the mutant-type individuals with stage i at time t. When $w_i = 1$ for all i, N_t is the total population density including the mutant-type individuals. The dynamics of the wild- and mutant-type populations can be written as:

$$\begin{cases} n_{t+1} = L(N_t)n_t \\ n'_{t+1} = L'(N_t)n'_t, \end{cases}$$
 (11-1)

 $\left(\boldsymbol{n}_{t+1}' = \boldsymbol{L}'(N_t)\boldsymbol{n}_t', \tag{11-2}\right)$

i.e.

$$\begin{bmatrix} \mathbf{n} \\ \mathbf{n}' \end{bmatrix}_{t+1} = \begin{bmatrix} L(N_t) & \mathbf{0} \\ \mathbf{0} & L'(N_t) \end{bmatrix} \begin{bmatrix} \mathbf{n} \\ \mathbf{n}' \end{bmatrix}_t, \tag{12}$$

where n'_t represents the stage-class vector of the mutant type at time t. The following result can be obtained in the dynamical system of Eq. (12).

Result 5. If the elements of $\delta L(N^*)$ are sufficiently small,

$$\sum_{i \in C_k} \frac{dl_{ij}(N^*)}{dN^*} \le 0 \quad \text{for all sets of } (k,j)$$
 (13-1)

and

$$\sum_{i \in C_h} \frac{dl_{ij}(N^*)}{dN^*} < 0 \quad \text{for at least one set of } (k,j) , \qquad (13-2)$$

where v_j is the j-th element of the positive left eigenvector and $C_k = \{i | v_i \ge v_k\}$, then there is no coexistence solution at the equilibrium, i.e. either n^* or n'^* is a zero vector,

$$\begin{cases}
 n^* = L(N^*)n^*, \\
 n'^* = L'(N'^*)n'^*,
\end{cases}$$
(14)

(see Appendix D).

Corollary of Result 5. If $dl_{ij}(N)/dN \leq 0$ for all i, j and $dl_{ij}(N)/dN < 0$ for at least one set of (i, j), then there is no coexistence solution at the equilibrium.

Therefore, if the elements of the projection matrix depend negatively on the weighted sum, there is no coexistence solution at the equilibrium. However, this result does not deny that there could be an oscillatory coexistence solution. It also suggests that if a mutant type has the projection matrix satisfying the invadable condition and if the dynamics is able to reach the equilibrium, the wild-type population is replaced perfectly with the individuals of the mutant type.

Suppose that both a wild and the mutant types have only one stage and that $L(N_t)$ and $L'(N_t)$ are linearly decreasing functions of N_t , i.e. $f - cN_t$ and $f' - c'N_t$. Thus, the dynamical system (11) is a discrete form of the Lotka-Volterra competition equation:

$$\begin{cases} n_{1,t+1} = n_{1,t}(f - cN_t) = n_{1,t}(f - cw_1(n_{1,t} + n'_{1,t})) \\ n'_{1,t+1} = n'_{1,t}(f' - c'N_t) = n'_{1,t}(f' - c'w_1(n_{1,t} + n'_{1,t})) \end{cases}$$
(15)

It is well known that there is a coexistence solution in the Lotka-Volterra competition equation if the parameters used there satisfy a certain condition (Roughgarden 1979, pp. 411–417). However, the parameters used in Eq. (15) do not satisfy the condition, because the isoclines of Eq. (15) do not intersect with each other but are parallel since both the slopes of the isoclines are -1. Therefore, Result 5 implies that a situation similar to this simple example occurs in multi-stage-structured models.

4.2 Numerical examples

As shown in the proof of Result 5, the reason why there is no coexistence solution in this dynamical system is that the density effect is represented in terms of the same weighted sum in both the wild- and mutant-type dynamics. It leads to the same slope of the two isoclines in the one-stage system. A coexistence solution is expected to appear when we use the different weighted sums. To certify the above speculation, we simulate the following dynamical system of the wild and mutant types with two stages each:

$$\begin{bmatrix} n_1 \\ n_2 \\ n'_1 \\ n'_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 2 - cN_t & 0 & 0 \\ 0.5 & 0.7 & 0 & 0 \\ 0 & 0 & 0 & 2.4 - c'N'_t \\ 0 & 0 & 0.5 & 0.7 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n'_1 \\ n'_2 \end{bmatrix}_t,$$
(16)

where the density-independent fecundity of the mutant type is larger than that of the wild-type so that the mutant type can invade the wild-type population when all the other parameters are equal in both types. c and c' are the competition coefficients of each type, respectively. N_t and N_t' are the weighted population densities defined as

$$\begin{cases}
N_t = n_{1,t} + n_{2,t} + wn'_{1,t} + wn'_{2,t} \\
N'_t = n_{1,t} + n_{2,t} + n'_{1,t} + n'_{2,t}
\end{cases}$$
(17)

The definition of N_t means that each individual of the mutant type gives w times density-effect as large as that of the wild type on the individuals of the wild type. If w is smaller than one, the increase of wild-type individuals is less regulated by the mutant-type individuals than by the wild-type individuals.

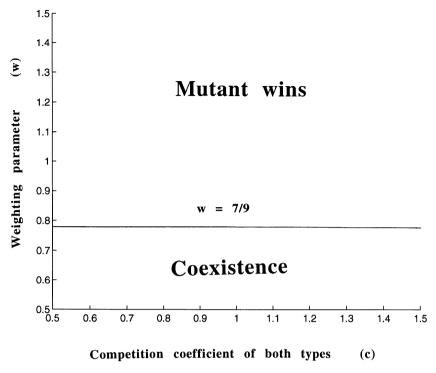


Fig. 1. The result when c = c'. The value of c does not affect whether both types coexist or not. It is only the weighting parameter of the mutant type (w) that affects it. When w < 7/9, there exists a coexistence solution

Figure 1 shows the result of computer calculation in the parameter region of 0.5 < c and w < 1.5 when c = c'. Then, the value of c does not affect whether both types coexist or not. It is only the weighting parameter of the mutant type (w) that affects it. There is no coexistence solution at equilibrium when w = 1 as shown in Result 5. The coexistence appears when w is smaller than 7/9 (see Appendix E) because the regulation of the increase of the wild type is weakened by the relatively smaller weighting of the mutant type. The weaker weighting of the mutant type is balanced with the larger fecundity of the mutant type when the coexistence occurs.

When c'=1, the region of coexistence depends on both the values of w and c (Fig. 2). There is, again, no coexistence solution when w=1. When cw < 7/9 and c < 7/9 (see Appendix E), the wild-type population wins because the competition coefficient of the wild type is small enough to exceed the superior fecundity of the mutant type. When cw > 7/9 and c > 7/9, the mutant type wins because of the superior fecundity of the mutant type. When cw < 7/9 and c > 7/9, there exists a coexistence solution because of the balance between the superior fecundity of the mutant type and the small value of cw. When cw > 7/9 and c < 7/9, either the wild or the mutant type wins,

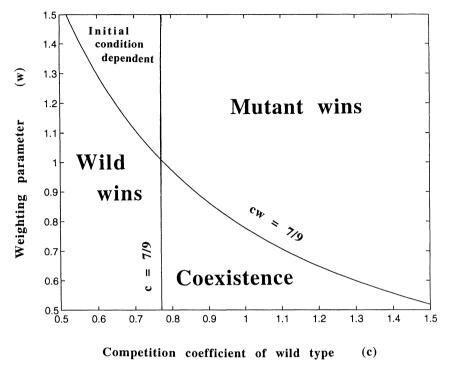


Fig. 2. The result when c' = 1. When cw < 7/9 and c > 7/9, there exists a coexistence solution because of the balance between the superior fecundity of the mutant type and the small value of cw. When cw > 7/9 and c < 7/9, the coexistence solution is not dynamically stable, and thus either the wild or the mutant type wins, depending on the initial values of each type

depending on the initial values of each type. If a small number of mutant-type individuals invade the habitat of the wild type, the wild type wins with high probability in this parameter region.

Since N_t and N_t' are linear combinations of the population densities at each stage of both types, N_t' can be proportional to N_t for a certain set of weighting parameters of both types (see Appendix F). Then, coexistence does not occur because the ratio of N'^* to N^* , which are obtained from the demographic parameters rather than from the weighting parameters, is generally different from the coefficient of the proportional relation. Result 5 is that of a special case where the coefficient of the proportional relation is equal to one. If N_t' is not proportional to N_t , there can be a coexistence for a range of the values of the demographic parameters.

5 Discussion

We obtain several theoretical results on evolution in stage-structured models with density-dependent dynamics, focusing on the density-dependence by

'weighted sum'. The first result concerns the invadable condition of mutant types. In the second result, it is shown that the invadability is equivalent to the increase of the weighted sum at equilibrium when all the elements of the projection matrix are decreasing functions of the weighted sum. These two results are the extended one of what Charlesworth (1971, 1980, 1994) and Takada and Nakajima (1992) have already obtained. These authors employed the simple sum of the population densities at each stage or the sum among the restricted group of stages. They correspond to the cases where w_i has the values of 0 or 1. On the other hand, w_i is an arbitrary positive number in the present paper. The populations of perennial plants, e.g. long-lived herbs and trees, usually have a large variety of sizes. The contribution of the younger adults to density effect could be less than that of the older adults and be not zero, i.e. w_i is not always either 0 or 1. Therefore, the results in earlier papers are not applicable to perennial plant populations or other populations with a large variety of sizes. The first and the second results are useful in such cases

The third result shows that the conclusion of the second result, i.e. the weighted sum at equilibrium increases in the course of evolution, can hold even if the elements of the projection matrix includes several increasing functions of the weighted sum. Although density-dependence usually acts negatively, it does not mean directly that all the elements of the matrix are decreasing functions of the weighted sum. For example, while the probability of the forward transition $(l_{i+1,i})$ is likely to be decreasing function of the weighted sum, the probability of staying the same stage (l_{ii}) has the possibility to be an increasing function. The reason is why the decrease of the growth rate of individuals due to density effect could lead to the increase of the probability of staying the same stage. Although this situation does not occur in the projection matrices of age-structured populations because l_{ii} is equal to zero in the matrices, it would be general in stage-structured projection matrix models. The third result is applicable to the above situation.

If only the large individuals, e.g. individuals belonging to the stage-class larger than 2, depress the other individuals, then $w_1 = 0$, $w_2 = 0$, $w_3 = 1$ and $w_4 = 1 \dots$ and $N_t = n_{3,t+} \dots$. From Result 2, N^* ($= n_3^* + n_{4+}^* \dots$) increases during the course of successful invasions when the elements of the projection matrix depend negatively on N_t . It is common in plant populations that only the larger individuals depress the other individuals. Thus, the number of the depressing individuals, not the total population density, would increase during the course of evolution in plant populations. The increase of the number of the depressing individuals would be realized by the increase of fecundity, or the decrease of mortality or of competition coefficient.

Result 5 shows that, for coexistence, the density effect on the wild type needs to be different from that on the mutant type. There is no coexistence when the common weighted sum is used in the dynamics of both types. Although we only consider the mutation of demographic parameters (e.g. fecundity or transition probability) in the present paper, coexistence will occur

if the mutation of weighting parameters occurs such that a different density effect is caused. Then, these two types would be able to speciate sympatrically.

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Appendices

Appendix A

According to the projection matrix model, the dynamics of population with a stage structure can be written as

$$\boldsymbol{n}_{t+1} = \boldsymbol{L}(N_t)\boldsymbol{n}_t \,. \tag{1}$$

From Eqs. (1) and (2),

$$N^* = \sum_{i=1}^{s} w_i n_i^*$$
 and $n^* = L(N^*)n^*$ (A-1)

at equilibrium. N^* can be obtained from

$$\det[\boldsymbol{L}(N^*) - I] = 0$$

because of Eq. (4-1), where n_i^* is the population density at stage i at equilibrium and n^* is proportional to the right eigenvector, u.

Suppose that a wild-type population within a certain habitat is composed of individuals, whose projection matrix is $L(N_t)$), and that the population is at an equilibrium state. Then, a small number of mutant-type individuals with a different projection matrix ($L'(N_t)$) from that of the wild type invades the habitat.

While $L(N^*)$ has a dominant eigenvalue 1 from Eq. (4), $L'(N^*)$ has a dominant eigenvalue λ' close to one $(\lambda' = 1 + \delta \lambda)$ because the difference between $L'(N^*)$ and $L(N^*)$, $\delta L(N^*)$, is assumed to be small. Let u' be the right eigenvector of $L'(N^*)$ corresponding to λ' and also close to $u(u' = u + \delta u)$. Then,

$$L'(N^*)u' = \lambda'u'. \tag{A-2}$$

From Eq. (A-2),

$$(L(N^*) + \delta L(N^*))(u + \delta u) = (1 + \delta \lambda)(u + \delta u). \tag{A-3}$$

Multiplying Eq. (A-4) by v^T from the left side and substituting Eqs. (4-1) and (4-2) and $v^T u = 1$ into it, we obtain

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} + \mathbf{v}^T \delta \mathbf{L}(N^*) \delta \mathbf{u} = \delta \lambda \mathbf{v}^T \mathbf{u} + \delta \lambda \mathbf{v}^T \delta \mathbf{u} . \tag{A-4}$$

Since u is a positive vector as derived from Frobenius theorem, eliminating the higher-order terms, we obtain

$$\delta \lambda \approx \mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} \ . \tag{A-5}$$

 $\delta \lambda > 0$ (i.e. $v^T \delta L(N^*) u > 0$) means that λ' is greater than 1. Therefore, the mutant-type population satisfying the inequality (3) is invadable.

Appendix B

Suppose that a mutant type can invade the wild-type population and that the mutant type can drive out all of the wild-type individuals. At the new equilibrium, the mutant-type population has the weighted sum, N'^* . Then, the mutant-type population satisfies the following equations:

$$\begin{cases} L'(N^* + \delta N^*)(\boldsymbol{u} + \delta \boldsymbol{u}) = (\boldsymbol{u} + \delta \boldsymbol{u}) \\ (\boldsymbol{v} + \delta \boldsymbol{v})^T L'(N^* + \delta N^*) = (\boldsymbol{v} + \delta \boldsymbol{v})^T \end{cases},$$
 (B-1)

where N'^* , the left and right eigenvectors are represented by $N^* + \delta N^*$, $u + \delta u$ and $v + \delta v$ because the difference between $L(N^*)$ and $L'(N^*)$ is sufficiently small. The left-hand side of Eq. (B-1) can be approximately calculated as

$$L'(N^* + \delta N^*) = L'(N^* + \delta N^*) + \delta L(N^* + \delta N^*)$$

$$\approx L(N^*) + \frac{dL(N^*)}{dN^*} \delta N^* + \delta L(N^*). \tag{B-2}$$

Thus, eliminating the higher order terms and using Eq. (4-1), the first equation of Eq. (B-1) can be rewritten as

$$L(N^*)\delta u + \frac{dL(N^*)}{dN^*} u \delta N^* + \delta L(N^*)u \approx \delta u$$
. (B-3)

Multiplying this by v^T from the left side and substituting Eq. (4-2) gives

$$\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} \approx -\mathbf{v}^T \left\{ \delta N^* \frac{d\mathbf{L}(N^*)}{dN^*} \right\} \mathbf{u}$$
 (B-4)

Therefore,

$$\delta N^* \approx \frac{\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}}{-\mathbf{v}^T \frac{d \mathbf{L}(N^*)}{d N^*} \mathbf{u}}.$$
 (5)

From the assumption of Result 2, the denominator of the right-hand side of (5) is positive and δN^* has the same sign as $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u}$. Thus, if $\mathbf{v}^T \delta \mathbf{L}(N^*) \mathbf{u} > 0$, i.e. the mutant type is invadable, then $\delta N^* > 0$. N^* increases in the course of evolution.

Appendix C

We set the elements of the left eigenvector as $0 < v_1 < v_2 \cdot \cdot \cdot < v_s$ by changing the order of the size classes without the loss of generality. Then, the condition (6-1) can be expressed as

$$\frac{d}{dN^*} \sum_{i=k}^{s} l_{ij}(N^*) \le 0 \quad \text{for all sets of } (k,j) . \tag{C-1}$$

We have

$$\sum_{i=1}^{s} v_i \frac{dl_{ij}}{dN} = v_1 \frac{d}{dN} \sum_{i=1}^{s} l_{ij} + \sum_{k=2}^{s} \left[(v_k - v_{k-1}) \frac{d}{dN} \sum_{i=k}^{s} l_{ij} \right].$$
 (C-2)

From Eqs. (C-1) and (C-2),

$$\sum_{i=1}^{s} v_i \frac{dl_{ij}(N^*)}{dN^*} \le 0$$
 (C-3)

for any j, and from Eq. (6-2), there exists a class j in which the left-hand side of Eq. (C-3) is strictly negative. Thus,

$$\mathbf{v}^T \frac{\mathrm{d}\mathbf{L}(N^*)}{dN^*} \mathbf{u} = \sum_{i,j} \mathbf{v}_i \frac{dl_{ij}(N^*)}{dN^*} \mathbf{u}_j < 0$$
 (C-4)

because $u_j > 0$ for all j. Taking into account Eq. (5), then it is shown that δN^* and $v^T \delta L(N^*) u$ have the same sign. This means that N^* increases in the iteration of the invasions of mutant types.

Appendix D

At the equilibrium,

$$\begin{bmatrix} \mathbf{n}^* \\ \mathbf{n}'^* \end{bmatrix} = \begin{bmatrix} L(N^*) & \mathbf{0} \\ \mathbf{0} & L'(N^*) \end{bmatrix} \begin{bmatrix} \mathbf{n}^* \\ \mathbf{n}'^* \end{bmatrix}. \tag{D-1}$$

 $\det[C - I] = \det[L(N^*) - I] \det[L'(N^*) - I]$ should be zero so that $[n^*, n'^*]^t$ is a non-trivial solution, where

$$C = \begin{bmatrix} L(N^*) & \mathbf{0} \\ \mathbf{0} & L'(N^*) \end{bmatrix}. \tag{D-2}$$

If $\det[L(N^*) - I] = 0$ and $\det[L'(N^*) - I] \neq 0$ at the equilibrium, $n^* \neq 0$ and $n'^* = 0$. If $\det[L(N^*) - I] \neq 0$ and $\det[L'(N^*) - I] = 0$ at the equilibrium, $n^* = 0$ and $n'^* \neq 0$. These two equilibria are not coexistence solutions. If $\det[L(N^*) - I] = 0$ and $\det[L'(N^*) - I] = 0$ at the equilibrium, $n^* \neq 0$ and $n'^* \neq 0$. It is a coexistence solution of the wild and mutant types.

For a given N, the dominant eigenvalue (λ_{\max}) of L(N) satisfies $\det[L(N) - \lambda_{\max}I] = 0$. The first derivative of λ_{\max} with respect to N can be written as

$$\frac{d\lambda_{\text{max}}}{dN} = \boldsymbol{v}^T \frac{d\boldsymbol{L}(N)}{dN} \boldsymbol{u} \tag{D-3}$$

from Eq. (A-5). From Eq. (13), the right-hand side of Eq. (D-3) is always negative (see Appendix C). Since $\lambda_{\max} > 1$ when N = 0 (because if $\lambda_{\max} < 1$, the population would become extinct before the invasion of a mutant type), λ_{\max} decreases monotonically with N and $\lambda_{\max} = 1$ only when $N = N^*$. Similar to the above discussion, the dominant eigenvalue of $L'(N^*)$, λ'_{\max} , decreases monotonically with N and $\lambda'_{\max} = 1$ only when $N = N'^*$. From Result 2, however, N'^* is larger than N^* if the mutant type can invade the wild-type population. Therefore, there is no N^* which satisfies $\det[L(N^*) - I] = 0$ and $\det[L'(N^*) - I] = 0$ at the same time. Either n^* or n'^* is a zero vector.

The corollary of Result 5 can be proved similarly.

Appendix E

When c' = 1, from Eq. (16), N^* and N'^* satisfy the following eigenvalue equations when $\lambda = 1$:

$$\begin{vmatrix} -1 & 2 - cN^* \\ 0.5 & 0.7 - 1 \end{vmatrix} = \begin{vmatrix} -1 & 2.4 - N^* \\ 0.5 & 0.7 - 1 \end{vmatrix} = 0.$$
 (E-1)

The right eigenvector corresponding to the eigenvalue 1 also satisfies

$$\begin{bmatrix} n_1^* \\ n_2^* \\ n_1'^* \\ n_2'^* \end{bmatrix} = \begin{bmatrix} 0 & 2 - cN^* & 0 & 0 \\ 0.5 & 0.7 & 0 & 0 \\ 0 & 0 & 0 & 2.4 - N'^* \\ 0 & 0 & 0.5 & 0.7 \end{bmatrix} \begin{bmatrix} n_1^* \\ n_2^* \\ n_1'^* \\ n_2'^* \end{bmatrix}$$
(E-2)

Using Eqs. (17) and (E-1, 2) we obtain the coexistence solution at equilibrium as:

$$N^* = 7/5c, \qquad N'^* = 9/5$$
 (E-3)

and

$$n_1^* = \frac{3}{5} \frac{7 - 9cw}{8c(1 - w)}, \qquad n_2^* = \frac{7 - 9cw}{8c(1 - w)}, n_1'^* = \frac{3}{5} \frac{9c - 7}{8c(1 - w)}, \qquad n_2'^* = \frac{9c - 7}{8c(1 - w)}.$$
 (E-4)

From Eq. (E-4), there is no positive solution when cw > 7/9, c > 7/9 or cw < 7/9, c < 7/9. The linearization of the dynamical system of Eq. (16) gives

the stability matrix as

$$\begin{bmatrix} -cn_2^* & 2 - cN^* - cn_2^* & -cwn_2^* & -cwn_2^* \\ 0.5 & 0.7 & 0 & 0 \\ -n_2'^* & -n_2'^* & -n_2'^* & 2.4 - N'^* - n_2'^* \\ 0 & 0 & 0.5 & 0.7 \end{bmatrix}.$$
 (E-5)

Calculating the dominant eigenvalues of Eq. (E-5) in the parameter region of 0.5 < c, w < 1.5 by computer, we obtain the result that Eq. (E-4) is dynamically stable when cw < 7/9, c > 7/9, and that it is unstable when cw > 7/9, c < 7/9.

Similarly, we examine the stability of the solutions of $(n_1^*, n_2^*, 0, 0)$ and $(0, 0, n_1^{\prime *}, n_2^{\prime *})$, and obtain the result shown in Fig. 2.

Figure 1 can be obtained by using a procedure similar to the one above.

Appendix F

We define N'_t and N_t as:

$$\begin{cases} N_{t} = \sum_{i=1}^{\infty} w_{i} n_{i}, t + \sum_{i=1}^{\infty} w'_{i} n'_{i,t} \\ N'_{t} = \sum_{i=1}^{\infty} x_{i} n_{i}, t + \sum_{i=1}^{\infty} x'_{i} n'_{i,t} \end{cases}$$
(F-1)

where w_i and x_i are the weighting parameters. Since N_t and N_t' are linear combinations of the population densities at each stage of both types, N_t' is proportional to N_t only when

$$\frac{x_i}{w_i} = \frac{x_i'}{w_i'} = k \text{ (const.)} \quad \text{for all } i.$$
 (F-2)

Then, $N_i' = kN_t$. From the proof of Appendix D, N^* and N'^* are obtained from $\det[L(N^*) - I] = 0$ and $\det[L'(N'^*) - I] = 0$, respectively. Since the elements of $L(N_t)$ and $L'(N_t)$ are independent of the weighting parameters $(w_i$ and $x_i)$, N'^* is not generally equal to kN^* . Therefore, there is no N^* which satisfies $\det[L(N^*) - I] = 0$ and $\det[L'(kN^*) - I] = 0$ at the same time. Either n^* or n'^* is a zero vector.

If N'_t is not proportional to N_t , there can be a coexistence solution for a range of the values of the demographic parameters.

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