



Transition matrix model for persistence of monocarpic perennial plant population under periodically ecological disturbance

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Abstract

We consider the disturbance-controlled persistence of monocarpic perennial plant population with a transition matrix modeling and discuss the contribution of perennation to the population persistence under the ecological disturbance that periodically occurs. The considered population is fundamentally subordinate in terms of the persistence at the habitat. Our mathematical results indicate that the ecological disturbance with an appropriate period assures the persistence of such subordinate species of plant. Further, we demonstrate that, under some ecological disturbances that periodically occur, the perennation could work better for the population persistence. In some cases, the perennial population could be persistent, while the annual becomes extinct in the environment with the ecological disturbance. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

In some cases of specifically subordinate species of monocarpic annual plants, the persistence of population considerably depends on some kinds of ecological disturbance, for example, by the

typhoon (for instance, see Silvertown and Doust, 1993). An aster *A. kantoensis* is such a species of plant, which is now of rare species going extinct (Takenaka et al., 1996; Wasitani et al., 1997). It inhabits in the zone of riverside and has survived with the spatial disturbance by the flood. For its population persistence, it is essential to utilize the gap space to grow the seeds which are considered not to have the capacity of dormancy so that they simultaneously germinates. Recent reconstruc-

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tions of riverbank are eliminating chance of flood, that is, possibility of ecological disturbance, so as to reduce the persistent possibility for such subordinate species of plants. In some cases of the subordinate species, without some appropriate ecological disturbance, the population goes extinct due to inter-specific and intra-specific competitions and the other environmental changes to decrease the favorability of habitat, for example, the fertility (for instance, see Pickett and White, 1985).

For plant population, the *transition matrix* modeling is well-known to describe the structured population, for example, with seed, rosette and flower classes (Charlesworth, 1980). A variety of mathematical models with the transition matrix, introduced some biologically considerable factors, for instance, density effects or temporally environmental variation, have been studied (Leslie, 1945, 1948; Pielou, 1969; Charlesworth, 1980; Caswell, 1990; Tuljapurkar, 1990; Silvertown and Doust, 1993).

Giho and Seno (1997) considered the disturbance-controlled persistence of monocarpic annual plant population with a basic transition matrix modeling and discussed the contribution of ecological disturbance, which periodically occurs, to the population persistence. Like an aster *A. kantoensis*, the considered population was assumed fundamentally subordinate in terms of the persistence in the habitat. Their mathematical results indicate that the ecological disturbance with an appropriately intermediate period assures the persistence of such subordinate species of plant.

In this paper, along the similar line of mathematical modeling with that in Giho and Seno (1997), we consider the mathematical modeling with the transition matrix for the population dynamics of perennial plant under the ecological disturbance that periodically occurs. In our mathematical model consideration, we focus on the contribution of perennation to the monocarpic plant population persistence. By analyzing our mathematical model, we will demonstrate that, under some ecological disturbances that periodically occur, the perennation could work better for the monocarpic plant population persistence and in some cases, the monocarpic perennial popula-

tion could be persistent, while the monocarpic annual becomes extinct in the environment with the ecological disturbance.

2. Model

We consider a monocarpic plant population structured with three classes: seed; juvenile; and flowering. In our model, the transition among these classes is assumed as shown in Fig. 1, in which: σ_i , survival rate of individual of juvenile class $R(i = 1, 2, 3)$; r , probability of successful germination; S , seed production by individual of flowering class F ; a , rate for juvenile individual not to flowering in a season; δ_j , time interval characterizing stages of individual growth ($j = 1, 2$).

Both of σ_i and r are positive not beyond 1. Parameters σ_i , r and S are in general assumed to be monotonically decreasing functions of generation t . This assumption means the decrease of environmental favorability for the considered plant population. In this paper, we especially consider the case when such a decreasing favorability of environment tends to make the plant population go to extinction. Parameters a and δ_i are assumed to be positive constants not beyond 1. Value $1 - a$ corresponds to the flowering rate for juvenile.

In the transition scheme for our model as shown in Fig. 1, we can focus two classes of seed and juvenile, which are expressed by the following 2-dimensional vector \mathbf{V}_t of seed population S_t and juvenile one R_t :

$$\mathbf{V}_t = \begin{pmatrix} S_t \\ R_t \end{pmatrix}. \quad (1)$$

We define the transition matrix \mathbf{A}_t at generation t , as follows:

$$\begin{aligned} \mathbf{A}_t &= \begin{pmatrix} S(t) \cdot (1 - a) \sigma_2(t) \\ \sigma_3(t) \cdot a \sigma_2(t) \end{pmatrix} \begin{pmatrix} r(t) & \sigma_1(t) \end{pmatrix} \\ &= \begin{pmatrix} S(t) \cdot (1 - a) \sigma_2(t) \cdot r(t) & S(t) \cdot (1 - a) \sigma_2(t) \cdot \sigma_1(t) \\ \sigma_3(t) \cdot a \sigma_2(t) \cdot r(t) & (\sigma_3(t) \cdot a \sigma_2(t) \cdot \sigma_1(t)) \end{pmatrix}. \end{aligned} \quad (2)$$

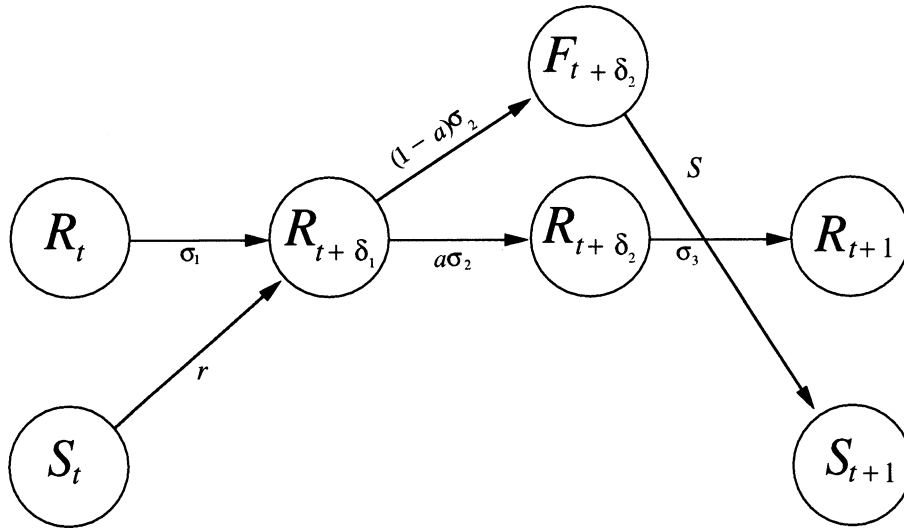


Fig. 1. Population transition from the seed class S_t and the juvenile class R_t to the flowering $F_{t+\delta_2}$ and the juvenile $R_{t+\delta_2}$ via the juvenile $R_{t+\delta_1}$ in the t -th generation (or year). The flowering class $F_{t+\delta_2}$ succeeds in making the seed class S_{t+1} at the $t+1$ -th generation and disappears from the population. The juvenile class $R_{t+\delta_2}$, turns up to the juvenile R_{t+1} at the $t+1$ -th generation with a probability σ_3 . For explanation of parameters, see the main text.

With the vector \mathbf{V}_t and the matrix \mathbf{A}_t , the population dynamics between subsequent generations is given by

$$\mathbf{V}_{t+1} = \mathbf{A}_t \mathbf{V}_t. \tag{3}$$

This leads to the general form for \mathbf{V}_t :

$$\mathbf{V}_t = \left\{ \prod_{k=0}^{t-1} \mathbf{A}_k \right\} \mathbf{V}_0. \tag{4}$$

Further, from Eq. (2), we obtain the following:

$$\prod_{k=0}^{t-1} \mathbf{A}_k = \left\{ \prod_{k=0}^{t-1} \sigma_2(k) \right\} \left\{ \prod_{k=0}^{t-2} [r(k+1)(1-a)S(k) + \sigma_1(k+1)a\sigma_3(k)] \right\} \times \begin{pmatrix} r(0)(1-a)S(t-1) & \sigma_1(0)(1-a)S(t-1) \\ r(0)a\sigma_3(t-1) & \sigma_1(0)a\sigma_3(t-1) \end{pmatrix}. \tag{5}$$

In our model, the ecological disturbance is introduced by multiplication of the following matrix \mathbf{Q} :

$$\mathbf{Q} = \begin{pmatrix} q_s & 0 \\ 0 & q_r \end{pmatrix}, \tag{6}$$

where q_s and q_r are, respectively, the survival rates of seed and juvenile to the disturbance. The above parameters are positive constants not beyond 1. The disturbance is assumed to occur just after the seed production. When the disturbance occurs at generation $T > 1$, the population state \mathbf{V}_T before the disturbance becomes $\mathbf{Q}\mathbf{V}_T$ after it.

Moreover, it is assumed that the environment for the considered plant population is renewed to the initial condition after the disturbance, that is, monotonically decreasing functions σ_i , r and S of generation t are reset to the initial values, $\sigma_i(0)$, $r(0)$ and $S(0)$. With this assumption, under the periodical disturbance of period T , the transition matrix \mathbf{A}_t is assumed to be subjected to the following periodically generational variation:

$$\mathbf{A}_0 \rightarrow \mathbf{A}_1 \rightarrow \mathbf{A}_2 \rightarrow \dots \rightarrow \mathbf{A}_{T-1} \Rightarrow \mathbf{A}_0 \rightarrow \dots \rightarrow \mathbf{A}_{T-1} \Rightarrow \mathbf{A}_0 \rightarrow \dots$$

Therefore, under the periodical disturbance of period T , the population \mathbf{V}_t is subjected to the generational variation as follows:

$$\begin{aligned} \mathbf{V}_0 \rightarrow \mathbf{V}_1 \rightarrow \mathbf{V}_2 \rightarrow \cdots \rightarrow \mathbf{V}_{T-1} \Rightarrow \mathbf{QV}_T \rightarrow \mathbf{A}_0 \mathbf{QV}_T \\ \rightarrow \mathbf{A}_1 \mathbf{A}_0 \mathbf{QV}_T \rightarrow \cdots \end{aligned}$$

Now, we consider the population just after the disturbance. Let \mathbf{W}_n be the population just after the n -th disturbance. Then, the above argument indicates that \mathbf{W}_n is governed by the following recurrence relation:

$$\mathbf{W}_{n+1} = \mathbf{\Gamma} \mathbf{W}_n, \quad (7)$$

where $\mathbf{W}_0 = \mathbf{V}_0$ and the matrix $\mathbf{\Gamma}$ is now defined by

$$\mathbf{\Gamma} \equiv \mathbf{Q} \prod_{k=0}^{T-1} \mathbf{A}_k. \quad (8)$$

Since the population becomes extinct if and only if $\mathbf{W}_n \rightarrow 0$ as $n \rightarrow \infty$, we hereafter focus \mathbf{W}_n to consider the persistence of considered population.

3. Criterion for population persistence

If and only if the absolute values of every eigenvalues for matrix $\mathbf{\Gamma}$ are less than 1, $\mathbf{W}_n \rightarrow 0$ for any \mathbf{W}_0 as $n \rightarrow \infty$, that is, the extinction necessarily occurs for any initial population \mathbf{V}_0 . From Eqs. (5), (6) and (8), we can directly calculate the eigenvalue for $\mathbf{\Gamma}$ and immediately find that both of two eigenvalues are real, of which one is zero and another positive. This indicates that \mathbf{W}_n changes monotonically as n increases. Positive eigenvalue $\lambda_+(T, a)$ is corresponding to the intrinsic growth rate for the considered population under the disturbance. It is obtained as follows:

$$\begin{aligned} \lambda_+(T, a) \equiv \lambda_+(T, 0) \left\{ \prod_{t=0}^{T-2} [1 - \{1 - z(t)\}a] \right\} \\ \times [1 - \{1 - \mu z^*(T)\}a] \end{aligned} \quad (9)$$

where

$$\lambda_+(T, 0) \equiv q_s \prod_{t=0}^{T-1} \{r(t)\sigma_2(t)S(t)\} \quad (10)$$

$$z(t) \equiv \frac{\sigma_1(t+1)\sigma_3(t)}{r(t+1)S(t)} \quad (11)$$

$$z^*(T) \equiv \frac{\sigma_1(0)\sigma_3(T-1)}{r(0)S(T-1)} \quad (12)$$

$$\mu \equiv \frac{q_r}{q_s}. \quad (13)$$

$\lambda_+(T, 0)$ determines the persistence of annual population with $a = 0$. If and only if $\lambda_+(T, 0) > 1$, the annual population can persist independent of the initial state. This is exactly corresponding to the result obtained by Giho and Seno (1997). In addition, it can be easily shown that always $\lambda_+(T, 1) < 1$. Because $q_r \leq 1$ and $\sigma_i(t) \leq 1$ for any i and t and from Eqs. (9)–(13), we obtain

$$\lambda_+(T, 1) \equiv q_r \prod_{t=0}^{T-1} \{\sigma_1(t)\sigma_2(t)\sigma_3(t)\}. \quad (14)$$

Therefore, when $a = 1$, that is, when no flowering occurs, the population necessarily becomes extinct. This implies that the population extinction could occur when the flowering rate $1 - a$ is sufficiently small.

The criterion for the persistence of population with the perennation parameter a under the periodical disturbance of period T is now given by $\lambda_+(T, a) > 1$. We note that, even if $\lambda_+(T, 0) > 1$, the persistence criterion could not be assured since the other factors of Eq. (9) may become less than 1. Similarly, even if $\lambda_+(T, 0) < 1$, the population extinction could not occur since the other factors of Eq. (9) may become more than 1. These arguments present one question about the population persistence: Is there such case that the population with an intermediate perennation parameter a is the most persistent under a periodical disturbance? This corresponds to the mathematical question what value of a makes the eigenvalue $\lambda_+(T, a)$ maximum more than 1.

4. Perennation rate to maximize population persistence

To consider the perennation rate a to maximize the population persistence, we at first consider the value of a which maximizes the eigenvalue $\lambda_+(T, a)$ for fixed other parameters. By direct calculations of $\partial^2 \{\ln \lambda_+(T, a)\} / \partial a^2$ and $\partial \{\ln \lambda_+(T, a)\} / \partial a$ for Eq. (9), the following result is obtained about the maximal value of $\lambda_+(T, a)$ in terms of a (Appendix A):

$\max_a \lambda_+(T, a) = \lambda_+(T, 0)$ if and only if

$$\frac{1}{T} \left\{ \sum_{t=0}^{T-2} z(t) + \mu z^*(T) \right\} \leq 1;$$

$\max_a \lambda_+(T, a) = \lambda_+(T, 1)$ if and only if

$$\left[\frac{1}{T} \left\{ \sum_{t=0}^{T-2} \frac{1}{z(t)} + \frac{1}{\mu z^*(T)} \right\} \right]^{-1} \geq 1;$$

$\max_a \lambda_+(T, a) = \lambda_+(T, a^*)$ ($0 < \exists a^* < 1$) otherwise. (15)

The second condition of Eq. (15) is sufficient for the extinction of population with any a , since $\lambda_+(T, 1) < 1$, as mentioned in the previous section. In case of the first of Eq. (15), since the intrinsic growth rate is maximized at $a = 0$, the population persistence can be regarded as to be the highest when the population is annual. When $\lambda_+(T, a)$ takes its maximum for an intermediate value of a , the intrinsic rate is higher for the perennial population than for the annual.

5. Exponentially decreasing environmental favorability

In this section, we consider the case where generationally variable parameters are exponentially decreasing functions as follows:

$$r(t) = c_r^t r(0); \tag{16}$$

$$S(t) = c_s^t S(0); \tag{17}$$

$$\sigma_i(t) = c_i^t \sigma_i(0) \quad (i = 1, 2, 3), \tag{18}$$

where $r(0)$, $\sigma_i(0)$ and c_k ($k = 1, 2, 3, r, s$) are positive and not beyond 1. Initial value $S(0)$ is positive. With these parameters, Eqs. (10)–(12) are expressed as follows:

$$\lambda_+(T, 0) = q_s \bar{c}_*^{T(T-1)/2} w^T; \tag{19}$$

$$z(t) = \frac{\bar{\sigma}}{w} \cdot \frac{c_1}{c_r} \cdot \left(\frac{\bar{c}}{\bar{c}_*} \right)^t; \tag{20}$$

$$z^*(T) = \frac{\bar{\sigma}}{w} \cdot \left(\frac{c_3}{c_s} \right)^{T-1}, \tag{21}$$

where we define the following parameters for convenience:

$$w \equiv r(0) \sigma_2(0) S(0);$$

$$\bar{c}_* \equiv c_r c_2 c_s;$$

$$\bar{c} \equiv c_1 c_2 c_3;$$

$$\bar{\sigma} \equiv \sigma_1(0) \sigma_2(0) \sigma_3(0).$$

The parameter w corresponds to the initial and maximal reproductive rate in the case where the population is annual ($a = 0$). In case of perennial plant ($a > 0$), the parameter w can be translated as the intrinsic maximal reproductive potential.

5.1. Persistence of monocarpic annual population

The persistent parameter region for monocarpic annual population is given by $\lambda_+(T, 0) > 1$ and shown in Fig. 2. The region has the distinct feature depending on the value $T_c \equiv \sqrt{2 \ln q_s / \ln \bar{c}_*}$. It has the feature shown in Fig. 2(a) if $T_c < 1$, that is, if $q_s^2 \geq \bar{c}_*$. In contrast, if $\bar{c}_* > q_s^2$, its feature is shown by Fig. 2(b). In the case where $\bar{c}_* = 1$, that is, when $c_r = c_s = c_2 = 1$, we can consider it as a limit $T_c \rightarrow \infty$, as shown in Fig. 2(c).

As the result by Giho and Seno (1997), we obtain the result that, in some cases corresponding to Fig. 2(a,b), the annual population could be persistent only when the period of disturbance is in an intermediate range. In such case, the annual population becomes extinct under such an ecological disturbance as with the shorter or the longer period. For our model, this result is obtained for the case when and only when $q_s^2 < \bar{c}_* < 1$. This condition means that the decrease of environmental favorability is sufficiently slow in generations, or the survival probability of seed regarding the disturbance is sufficiently small. Under the condition with the more rapid decrease of environmental favorability, the extinction of annual population occurs if the period of disturbance is sufficiently long. The annual population could persist if the period is sufficiently short.

Without such decrease of environmental favorability, when the environmental favorability is constant independently of generation, the contribution of environmental factor to the persistence of annual population is just by the ecological disturbance. As indicated by Fig. 2(c), the annual population could persist if the period of distur-

bance is sufficiently long. Since $\lambda_+(T, 0)$ is related not to q_r but just to q_s , the population persistence depends only on the disturbance effect upon the seed stage.

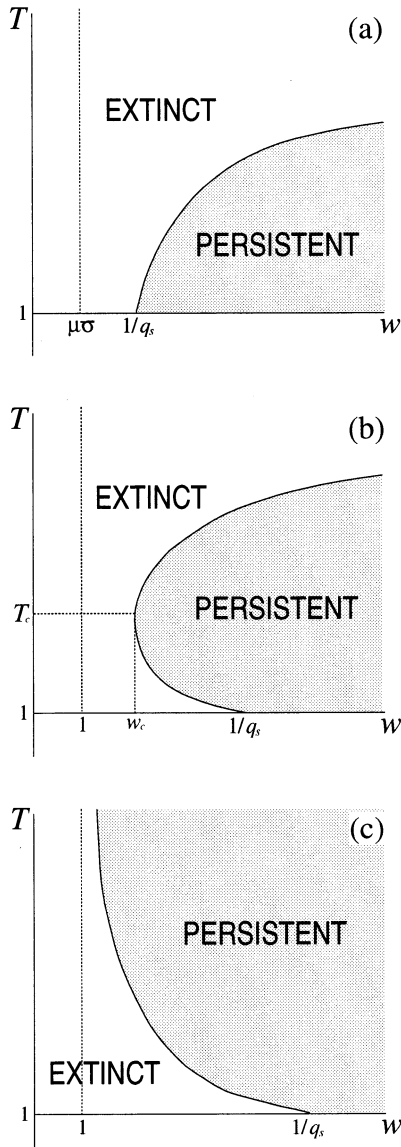


Fig. 2. Parameter region for the monocarpic annual population ($a = 0$) in (w, T) -parameter space. Exponentially decreasing environmental favorability. (a) $\bar{c}_* < 1$ and $T_c \equiv \sqrt{2 \ln q_s / \ln \bar{c}_*} \leq 1$, that is, $\bar{c}_* \leq q_s^2$; (b) $\bar{c}_* < 1$ and $T_c \equiv \sqrt{2 \ln q_s / \ln \bar{c}_*} > 1$, that is, $q_s^2 < \bar{c}_* < 1$; (c) $\bar{c}_* = 1$. $w_c \equiv \sqrt{\bar{c}_*} \cdot \exp[\sqrt{2 \ln q_s / \ln \bar{c}_*}]$.

5.2. Season-dependent decreasing environmental favorability

At first, for mathematical simplicity in case of monocarpic perennial population, we analyze the case when $c_r = c_1$, $c_s = c_3$ and $\bar{c}_* = \bar{c}$. This is the case where the decreasing favorability of environment affects to each stage with a common strength as long as concerned the same season (see Fig. 1). The decreasing rate depends not on the stage of growth but on the season. In this case, as easily seen from Eqs. (20) and (21), both $z(t)$ and $z^*(T)$ becomes a common generation-independent constant z given by

$$z(t) = z^*(T) = z \equiv \frac{\bar{\sigma}}{w}, \tag{22}$$

and then the expression for $\lambda_+(T, a)$ appears in the following simpler form:

$$\lambda_+(T, a) = \lambda_+(T, 0)[1 - (1 - z)a]^{T-1} \times [1 - (1 - \mu z)a]. \tag{23}$$

From Eq. (15), we can immediately obtain the following:

$$\begin{aligned} \max_a \lambda_+(T, a) &= \lambda_+(T, 0) \quad \text{if and only if } w \geq w_H; \\ \max_a \lambda_+(T, a) &= \lambda_+(T, 1) \quad \text{if and only if } w \leq w_L; \\ \max_a \lambda_+(T, a) &= \lambda_+(T, a^*) \quad (0 < \exists a^* < 1) \\ &\text{otherwise,} \end{aligned} \tag{24}$$

where

$$w_L \equiv \left\{ 1 + \frac{\mu - 1}{\mu T - (\mu - 1)} \right\} \bar{\sigma}; \tag{25}$$

$$w_H \equiv \left(1 + \frac{\mu - 1}{T} \right) \bar{\sigma}. \tag{26}$$

So, eventually, if and only if $w_L < w < w_H$, $\lambda_+(T, a)$ takes its maximum for an intermediate value of a , $a = a^*$ such that $0 < a^* < 1$. From the equation $\partial \lambda_+(T, a) / \partial a = 0$, a^* can be explicitly obtained as follows:

$$a^* = 1 - \frac{\bar{\sigma}}{T} \left\{ \frac{1}{\bar{\sigma} - w} + \frac{\mu(T - 1)}{\mu \bar{\sigma} - w} \right\}. \tag{27}$$

We can easily show that $a^* = 0$ when $w = w_H$, while $a^* = 1$ when $w = w_L$. Lastly,

$$\lambda_+(T, a^*) = q_s \bar{c}^{T(T-1)/2} \frac{(T-1)^{T-1} \{(\mu-1)\bar{\sigma}w\}^T}{T^T (w-\bar{\sigma})(\mu\bar{\sigma}-w)^{T-1}} \quad (28)$$

We can find that $\lambda_+(T, 0)|_{w=w_H} > 1$ is the necessary and sufficient condition for the existence of persistent monocarpic perennial population under the disturbance period T (Appendix B). It can be also shown in Appendix B that, in terms of the intrinsic growth rate represented by λ_+ , when the persistent perennial population exists, it is more favored by the environment than the annual with the common (w, T) , since the intrinsic growth rate is larger for the perennial than for the annual.

For $\mu \leq 1$, we can prove that the perennial population eventually becomes extinct for $w_L < w < w_H$ (Appendix B). This means that, if $\mu \leq 1$, the perennial population cannot persist and the population persistence requires the annual.

For $\mu > 1$, the perennial population could be persistent. In this case, we can derive the following necessary condition for the persistence of the perennial population (Appendix C):

$$\sqrt{\frac{1}{2} \ln \frac{1}{\bar{c}}} < \sqrt{\ln \frac{1}{q_s}} - \sqrt{\ln \frac{1}{q_i \bar{\sigma}}} \quad (29)$$

This necessary condition implies that the existence of persistent monocarpic perennial population under disturbance that periodically occurs requires a sufficiently slow decrease of environmental favorability in the interval between subsequent disturbances, a sufficiently small survival probability for the seed under the disturbance, a sufficiently large survival probability for the juvenile under the disturbance and a relatively large survival probability for the juvenile in the interval between subsequent disturbances.

When there exist some points (w_H, T) satisfying $\lambda_+(T, 0)|_{w=w_H} > 1$ in (w, T) -parameter space, we have such a parameter region shown in Fig. 4(a) for $\bar{c} < 1$ and Fig. 4(b) for $\bar{c} = 1$ (the dark greyed region) that the monocarpic perennial is persistent while the monocarpic annual becomes extinct. In both Fig. 4(a,b), the parameter region is classified into four distinct regions: Both the monocarpic annual and perennial populations are persistent and the annual is more adaptive than the perennial (the light greyed region); Both are persistent

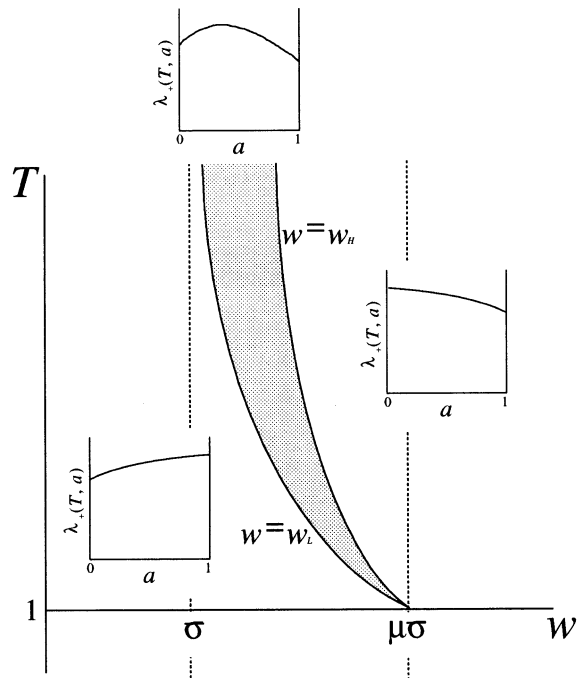


Fig. 3. Parameter region (grey) for $w_L < w < w_H$ in (w, T) -parameter space when $\mu > 1$. For the definitions of w, w_L and w_H , see the main text. The parameter space is divided into three by the curves $w = w_L$ and $w = w_H$. For these regions, the a -dependence of $\lambda_+(T, a)$ is different from each other.

and the perennial is more adaptive (the striped region); Only the perennial is persistent (the dark greyed region); Both become extinct (the blank region). The boundary between the first and the fourth or between the first and the second is respectively given by that in Fig. 2(b or c). The boundary between the third and the fourth is defined by $\lambda_+(T, a^*) = 1$. From Eq. (28), we can prove that the boundary shape is always unimodal in the region $w_L < w < w_H$ as shown in Fig. 4 (see Appendix D).

In Fig. 5, we show a numerical result about the parameter region for the population persistence in (w, T) -parameter space when $\mu > 1$ and there exists the parameter region for the persistent perennial population. Numerical calculations as in Fig. 5 demonstrate that there could actually exist such some parameter pairs (w, T) even for the integer value of T that only the monocarpic perennial is persistent (triangle symbols in Fig. 5).

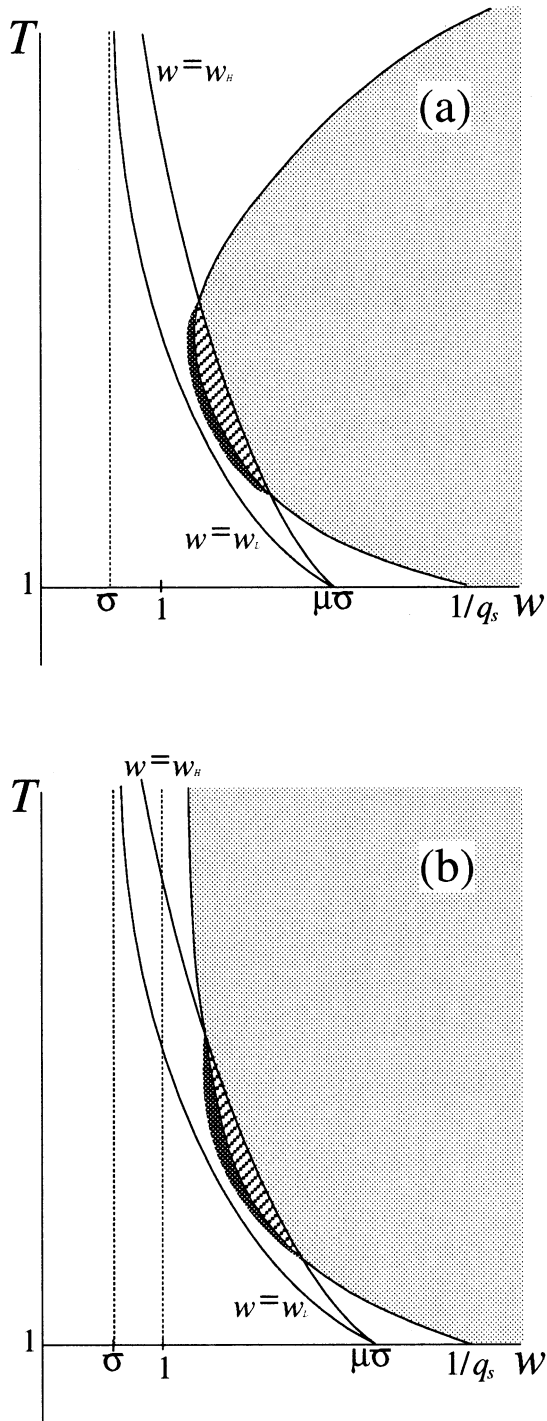


Fig. 4.

Note that these results are valid also in case of $c_k = 1$ ($k = 1, 2, 3, r, s$) when the parameters are all constant independently of generation and the environmental favorability is constant throughout generations. Especially when $c_r = c_1$, $c_s = c_3$ and $\bar{c}_* = \bar{c}$, the \bar{c} -dependence is only for $\lambda_+(T, 0)$ in Eq. (23), so that the constant parameter case with $\bar{c} = 1$ affects only $\lambda_+(T, 0)$ in Eq. (23).

5.3. Decreasing successful germination rate

As in case of aster *A. Kantoensis*, the persistence under an ecological disturbance could fundamentally depend on the survival and the successful germination of seeds in not few cases (Silvertown and Doust, 1993). In this section of analysis, we focus the adaptivity of seed population in the environment with an ecological disturbance that periodically occurs.

We consider our model of the exponentially decreasing parameters given by Eqs. (16)–(18) with $c_1 = c_2 = c_3 = c_s = 1$ and $c_r < 1$. This is the case when only the successful germination rate is exponentially decreasing in generation, for instance, due to the interspecific competition or the degradation of soil fertility. In this case, differently from the previous case of season-dependent decreasing environmental favorability, numerical calculations with Eqs. (9), (15) and (19)–(21) give the essential nature of $\lambda_+(T, a)$ and we get the result represented by Fig. 6 at last.

As shown by Fig. 6, the parameter region for the population persistence in (w, T) -parameter space has some specific features different from those for the previous case. Numerical calcula-

Fig. 4. Parameter region for the population persistence in (w, T) -parameter space when $\mu > 1$, in case of season-dependent exponentially decreasing environmental favorability. (a) $q_s^2 < \bar{c}_* < 1$; (b) $\bar{c}_* = 1$. For the light grey region, both the annual and the perennial populations are persistent and the annual is more adaptive than the perennial. For the striped region, both the annual and the perennial populations are persistent and the perennial is more adaptive than the annual. For the dark grey region, the perennial population is persistent, while the annual becomes extinct. In the blank region, both become extinct.

tions indicate that there could always exist such a significantly large parameter region that both annual and perennial populations are persistent and the perennial is more adaptive than the annual (the striped region in Fig. 6). Further, they indicate also that there could *always* exist such another significantly large parameter region that only the monocarpic perennial population is persistent (the dark greyed region in Fig. 6). We can give the *mathematical proof* for both of these two numerically obtained results (see Appendices E and F), too. Therefore, in this case when only the successful germination rate is significantly affected by the decreasing environmental favorability, there always exist one parameter region with which the monocarpic perennial population is persistent and more adaptive than the monocarpic

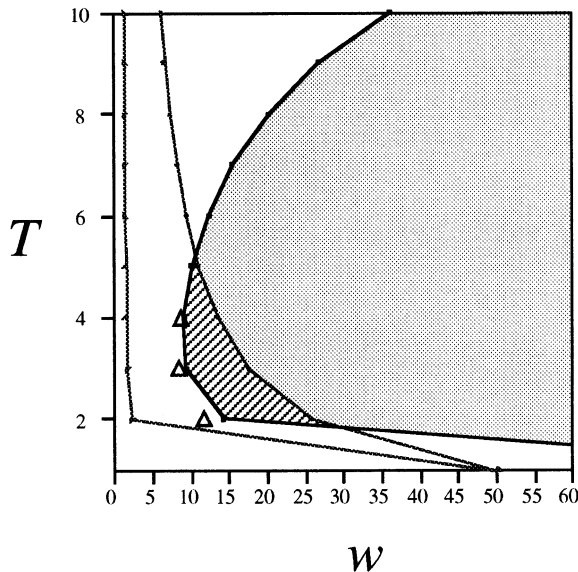


Fig. 5. Parameter region for the population persistence in (w, T) -parameter space when $\mu > 1$, in case of season-dependent exponentially decreasing environmental favorability. Numerical result with Eqs. (23) and (24). $c_1 = c_r = 0.5$; $c_2 = c_3 = c_s = 1.0$; $q_r = 0.5$; $q_s = 0.01$; $\sigma_i(0) = 1.0$ ($i = 1, 2, 3$). For the light greyed region, both the annual and the perennial populations are persistent and the annual is more adaptive than the perennial. For the striped region, both the annual and the perennial populations are persistent and the perennial is more adaptive than the annual. The triangle symbols indicate such parameter points (w, T) obtained by numerical calculations for some integer values of T that the perennial population is persistent, while the annual becomes extinct. In the blank region, both become extinct.

annual one and another parameter region with which only the perennial is persistent under the ecological disturbance that periodically occurs.

Numerical calculations indicate that the arrangement of those regions in (w, T) -parameter space is always topologically equivalent to that shown by Fig. 6, although the actual place and the size depends on the other parameters. Therefore, as shown in Fig. 6, for sufficiently short period of disturbance, both the monocarpic annual and perennial populations are persistent and the annual is more adaptive than the perennial (the light greyed region in Fig. 6); For the appropriately longer period of disturbance, only the perennial is persistent (the dark greyed region in Fig. 6); For some intermediate period of disturbance, both are persistent and the perennial is more adaptive (the striped region in Fig. 6); For sufficiently long period of disturbance, both become extinct (the blank region in Fig. 6). This feature is held for any fixed appropriately large w as shown in Fig. 6. It is implied that the annual population is favored only for sufficiently short periods of ecological disturbance and the perennial population is favored for relatively long periods. This is the feature different from that for the previous case in which the annual is favored for the longer period of disturbance.

Numerical results imply also that, for any fixed relatively long period T of disturbance, the reproductive potentiality w is required larger than a critical value for the population persistence and the persistent *perennial* requires the less reproductive potential than the persistent annual does. In other words, for any fixed relatively long period T of disturbance, the perennial population is persistent with the smaller w , so that the perennial would be more easily persistent than the annual. This tendency could be seen in the previous case.

6. Conclusion

With a transition matrix modeling, we consider the disturbance-controlled persistence of monocarpic perennial plant population, focusing the contribution of perennation to the population persistence under ecological disturbance that peri-

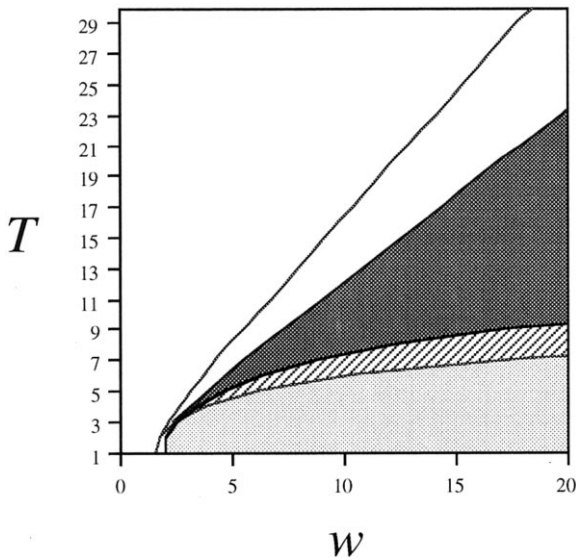


Fig. 6. Parameter region for the population persistence in (w, T) -parameter space, in case of decreasing successful germination rate. Numerical result with Eqs. (9), (15) and (19)–(21). $c_r = 0.5$; $c_1 = c_2 = c_3 = c_s = 1.0$; $q_r = 0.8$; $q_s = 0.5$; $\sigma_i(0) = 1.0$ ($i = 1, 2, 3$). For the light greyed region, both the annual and the perennial populations are persistent and the annual is more adaptive than the perennial. For the striped region, both the annual and the perennial populations are persistent and the perennial is more adaptive than the annual. For the dark greyed region, the perennial population is persistent, while the annual becomes extinct. In the blank region, both become extinct.

odically occurs. The considered population is fundamentally subordinate in terms of the persistence at the habitat. This means that the population eventually goes extinct without the ecological disturbance, due to the decreasing environmental favorability which includes the inter-specific competition or the degradation of soil fertility. Our mathematical results indicates that the ecological disturbance with an appropriately intermediate period assures the persistence of such subordinate species of plant. Further, we demonstrate that, under some ecological disturbances that periodically occur, the perennation could work better for the population persistence. When the perennial population could be persistent, the perennial is more adaptive than the annual. In some cases, the perennial population is persistent, while the annual becomes extinct.

Even under the condition that the considered monocarpic plant is a subordinate species in terms of the persistence at the habitat, if the plant could evolve its life history adaptive to utilize the ecological disturbance occurring at the habitat in order to persist, it could be persistent in such environment. Our modeling considerations demonstrate that such a persistence would be closely connected to the characteristics of ecological disturbance. Thus, if some characteristics of ecological disturbance would change, the persistent potentiality of inhabiting plant species might be violated so that such species is endangered to become extinct. An aster *A. kantoensis* is considered as such a species of plant, which is now of rare species going extinct, because of the decrease of disturbance frequency by the artificial reconstruction of riverbank (Takenaka et al., 1996; Wasitani et al., 1997).

It is also demonstrated that the adaptivity of perennation is closely related to the characteristics of ecological disturbance and the plant reproductive potentiality. Especially in case of decreasing successful germination rate, in which only the successful germination rate is exponentially decreasing in generation due to the decreasing environmental favorability, it is resulted for our model that, if the period of ecological disturbance becomes relatively longer, that is, if the frequency of disturbance is reduced, the monocarpic annual plant becomes extinct and the persistence of monocarpic population requires the perennation. In the case, the monocarpic annual plant could persist just under the relatively short period of disturbance. This means that, if the frequency of disturbance is increased, the annual population could be favored in the environment. In our model, since the considered monocarpic population is assumed to be subordinate in terms of the persistence at the habitat, the population eventually goes extinct without the disturbance.

Our results also imply that the change of disturbance frequency could have some contribution to the exchange of species in the disturbance-affected habitat. In a specific case when only the successful germination rate is exponentially decreasing in generation due to the decreasing environmental favorability, it is apparently demonstrated by the

result given by Fig. 6 that the decrease of the disturbance frequency would cause the extinction of an annual plant, following a prevalence of some other perennial plants.

Although our modeling is one of the most basic and simplified ones, we expect that our modeling considerations will give some intuitive or perspective views to consider the contribution of ecological disturbance to the persistence of some subordinate plant species.

Appendix A

In this appendix, we describe how the a -dependence of $\lambda_+(T, a)$ is. From Eq. (9), by direct calculations of a -derivative of $\ln \lambda_+(T, a)$, the following can be obtained:

$$\frac{\partial^2 \{\ln \lambda_+(T, a)\}}{\partial a^2} = - \left[\frac{1 - \mu z^*(T)}{1 - \{1 - \mu z^*(T)\}a} \right]^2 - \sum_{t=0}^{T-2} \left[\frac{1 - z(t)}{1 - \{1 - z(t)\}a} \right]^2 \leq 0$$

Thus, $\ln \lambda_+(T, a)$ is a convex function of a . This indicates that the maximal of $\ln \lambda_+(T, a)$ uniquely exists for $0 \leq a \leq 1$. Therefore, $\lambda_+(T, a)$ has unique maximum for $0 \leq a \leq 1$.

Next, we consider the signs of following a -derivatives of $\ln \lambda_+(T, a)$ at $a = 0$ and $a = 1$:

$$\begin{aligned} \left. \frac{\partial \{\ln \lambda_+(T, a)\}}{\partial a} \right|_{a=0} &= \mu z^*(T) - T + \sum_{t=0}^{T-2} z(t) \quad (30) \\ \left. \frac{\partial \{\ln \lambda_+(T, a)\}}{\partial a} \right|_{a=1} &= -\frac{1}{\mu z^*(T)} + T - \sum_{t=0}^{T-2} \frac{1}{z(t)} \quad (31) \end{aligned}$$

If both of them are non-positive, since $\ln \lambda_+(T, a)$ is convex, $\ln \lambda_+(T, a)$ and also $\lambda_+(T, a)$ are monotonically decreasing for $0 \leq a \leq 1$, so that the maximum of $\lambda_+(T, a)$ is at $a = 0$. If they are both non-negative, $\lambda_+(T, a)$ is monotonically increasing for $0 \leq a \leq 1$, so that the maximum is at $a = 1$. In this case, the population necessarily becomes extinct for any a , because the maximal $\lambda_+(T, 1)$ is always less than 1 as shown in the analysis of main text. If the a -derivatives of $\lambda_+(T, a)$ is non-negative at $a = 0$ and non-positive at $a = 1$, $\lambda_+(T, a)$ has a unique maximal peak at

an intermediate a such that $0 < a < 1$. This last case corresponds to the possible case when an intermediate perennation might work best for the population persistence. This argument with Eqs. (30) and (31) derives the result given by Eq. (15).

Appendix B

In this appendix, we show that the condition $\lambda_+(T, 0)|_{w=w_H} > 1$ is the necessary and sufficient condition for the existence of persistent monocarpic perennial population under the ecological disturbance and is also necessary and sufficient for the existence of such (w, T) in (w, T) -parameter space (where T is now extended to real value) that the monocarpic perennial population is persistent while the monocarpic annual becomes extinct under the ecological disturbance. Besides, it will be also shown that, in terms of the intrinsic growth rate represented by λ_+ , when the persistent monocarpic perennial population exists, it is more favored by the environment than the corresponding annual with the common (w, T) . Further, we prove that, if $\mu \leq 1$, always $\lambda_+(T, 0)|_{w=w_H} < 1$.

From direct calculations about Eqs. (27) and (28), we can easily find that $\partial a^*/\partial w < 0$ and $\partial \lambda_+(T, a^*)/\partial w > 0$ for $w_L < w < w_H$, so that a^* is monotonically decreasing and $\lambda_+(T, a^*)$ is monotonically increasing as w gets larger for $w_L < w < w_H$. Therefore, since $a^* = 0$ for $w = w_H$ and $a^* = 1$ for $w = w_L$:

$$\begin{aligned} \lambda_+(T, a^*)|_{w=w_L} &= \lambda_+(T, 1)|_{w=w_L} \leq \lambda_+(T, a^*) \\ &\leq \lambda_+(T, a^*)|_{w=w_H} \\ &= \lambda_+(T, 0)|_{w=w_H}. \end{aligned} \quad (32)$$

Note that $\lambda_+(T, 1)|_{w=w_L} < 1$ from the argument for Eq. (14).

So, it is necessary that $\lambda_+(T, 0)|_{w=w_H} > 1$, in order that we could expect the persistent monocarpic perennial population with $a > 0$ such that $\lambda_+(T, a) \geq 1$. Inversely, if $\lambda_+(T, 0)|_{w=w_H} > 1$, we can say that $\lambda_+(T, a^*) > 1$ for some w sufficiently large and less than w_H , because of the continuously increasing monotonicity of $\lambda_+(T, a^*)$ in terms of such w that $w_L < w < w_H$. For such w ,

since $\lambda_+(T, a^*) > \lambda_+(T, 0)$, the monocarpic perennial population is more adaptive to the environment than the annual.

Furthermore, such point (w_H, T) as $\lambda_+(T, 0)|_{w=w_H} > 1$ in (w, T) -parameter space must be in the region for $\lambda_+(T, 0) > 1$. Thus, the existence of such a point means that the curve $w = w_H$ intersects with the region for $\lambda_+(T, 0) > 1$ in (w, T) -parameter space. Inversely, if the curve $w = w_H$ intersects with the region for $\lambda_+(T, 0) > 1$ in (w, T) -parameter space, we could find some w_H satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$ for some T .

If $\lambda_+(T, 0)|_{w=w_H} < 1$, then $\max_a \lambda_+(T, a) = \lambda_+(T, a^*) < 1$ so that the population eventually becomes extinct for $w_L < w < w_H$. In this case, such point (w_H, T) as satisfying $\lambda_+(T, 0)|_{w=w_H} < 1$ in (w, T) -parameter space must be out of the region for $\lambda_+(T, 0) > 1$.

We remark that the curve $w = w_L$ does not have any intersection with the region for $\lambda_+(T, 0) > 1$ in (w, T) -parameter space. This is because any point on the curve $w = w_L$ must be out of the region for $\lambda_+(T, 0) > 1$ in (w, T) -parameter space, since:

$$\lambda_+(T, 0)|_{w=w_L} \leq \lambda_+(T, 1)|_{w=w_L} < 1. \quad (33)$$

The first inequality of Eq. (33) can be easily proven by the fact that $\lambda_+(T, a)|_{w=w_L}$ is monotonically increasing in terms of a .

The condition that $\lambda_+(T, 0)|_{w=w_H} > 1$ is expressed as:

$$q_s \bar{c}^{\pi(T-1)/2} \left(\frac{T-1+\mu\bar{\sigma}}{T} \right)^T > 1. \quad (34)$$

It is easily seen from Eq. (34) that, if $\mu \leq 1$, the condition Eq. (34) can be never satisfied because q_s , \bar{c} and $\bar{\sigma}$ are all not beyond 1.

Appendix C

In this appendix, we can derive the necessary condition Eq. (29) for the persistence of the perennial population. When $\mu > 1$, the parameter region for $w_L < w < w_H$ in (w, T) -parameter space is obtained as in Fig. 3. With the argument given in Appendix B, for the existence of such a point

(w_H, T) as $\lambda_+(T, 0)|_{w=w_H} > 1$ in (w, T) -parameter space, that is, for the existence of persistent perennial population, the parameter region for $w_L < w < w_H$, given by Fig. 3, must intersect with the region for $\lambda_+(T, 0) > 1$, given by Fig. 2. From this argument, we can derive such a necessary condition for the persistence of the perennial population that $\bar{c} = 1$ or $T_c \equiv \sqrt{2 \ln q_s / \ln \bar{c}} > 1$. This necessary condition for the existence of persistent perennial population can be alternatively represented by such condition for \bar{c} that $q_s^2 < \bar{c} \leq 1$.

When $\bar{c} > q_s^2$, we can obtain another necessary condition for the existence of persistent perennial population such that $w_c \equiv \sqrt{\bar{c}} \cdot \exp[\sqrt{2 \ln q_s \ln \bar{c}}]$ in Fig. 2(b) is less than $\mu\bar{\sigma}$, that is, $\mu > w_c/\bar{\sigma}$. Since $w_c > 1$ and $\bar{\sigma} < 1$, this condition is stronger than $\mu > 1$.

Now, we will prove that these two necessary conditions turn out to be simultaneously satisfied if and only if the condition Eq. (29) is satisfied. The condition that $w_c < \mu\bar{\sigma}$ and $1 < T_c$ can be rewritten as follows:

$$\begin{aligned} \sqrt{\bar{c}} \cdot \exp[\sqrt{2 \ln q_s \ln \bar{c}}] &< \mu\bar{\sigma}, \\ \sqrt{2 \ln q_s \ln \bar{c}} &> 1. \end{aligned} \quad (35)$$

Since \bar{c} , $\bar{\sigma}$, q_s and q_r are all less than 1, we define the following positive parameters ξ , θ , η for convenience: $\xi^2 \equiv -\ln \sqrt{\bar{c}}$; $\theta^2 \equiv -\ln q_s$; $\eta^2 \equiv -\ln(q_r \bar{\sigma})$. Then, the condition Eq. (35) can be rewritten as follows:

$$\begin{aligned} (\xi - \theta - \eta)(\xi - \theta + \eta) &> 0, \\ \xi &< \theta. \end{aligned} \quad (36)$$

The condition Eq. (36) indicates that $\xi < \theta - \eta$. The derived condition results in Eq. (29).

Also in case of $\bar{c} = 1$, we can separately consider and obtain a necessary condition for the intersection between the persistent parameter region of Fig. 2(c) and the parameter region for $w_L < w < w_H$ of Fig. 3 in (w, T) -parameter space: $\mu\bar{\sigma} > 1$, which is a specific condition involved in Eq. (29) with $\bar{c} = 1$.

Appendix D

In this appendix, from Eq. (28), we prove that the boundary between the parameter regions in

Fig. 4 for the case when only the monocarpic perennial population is persistent (the dark greyed region) and for the case when both the monocarpic annual and perennial populations become extinct (the blank region) is always unimodal, connecting two intersections between $\lambda_+(T, 0) = 1$ and $w = w_H$. Further, it is proved that the boundary curve is located in the region where $\lambda_+(T, 0) < 1$ and $w_L < w < w_H$.

From the argument in Appendix B, the (w, T) -parameter region satisfying the condition that $\lambda_+(T, a^*) > 1$ and $0 < a^* < 1$ can exist when and only when $\lambda_+(T, 0)|_{w=w_H} > 1$. This means the following:

Lemma. The corresponding (w, T) -parameter region is located in and only in the range of T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$.

As for the existence of such (w, T) -parameter region that $\lambda_+(T, 0)|_{w=w_H} > 1$, as shown in Appendix B, it is necessary and sufficient that the curve $w = w_H$ and $\lambda_+(T, 0) = 1$ have two different intersections. With the parameter (w, T) at each intersection, $\lambda_+(T, 0) = 1$ and $a^* = 0$. Therefore, as indicated in Fig. 4, the curve $\lambda_+(T, a^*) = 1$ in the (w, T) -parameter space must pass the intersection between $\lambda_+(T, 0) = 1$ and $w = w_H$, because $\lambda_+(T, a^*)|_{w=w_H} = \lambda_+(T, 0)|_{w=w_H} = 1$ at the intersection.

From Eq. (32) in Appendix B, the boundary of the region $\lambda_+(T, a^*) \geq 1$ in (w, T) -parameter space lies in the region $w_L < w$, because $\lambda_+(T, a^*)|_{w=w_L} = \lambda_+(T, 1)|_{w=w_L} < 1$.

From the direct w -derivative of Eq. (28), we obtain $\partial\lambda_+(T, a^*)/\partial w > 0$ for any w such that $w_L < w < w_H$. Therefore, we can obtain the following:

Lemma. $\lambda_+(T, a^*)$ is a monotonically increasing function of w in the range of w such that $w_L < w < w_H$.

Since $\lambda_+(T, a^*)|_{w=w_L} < 1$ and $\lambda_+(T, a^*)|_{w=w_H} = \lambda_+(T, 0)|_{w=w_H} > 1$ in the range of T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$, the following result is obtained:

Lemma. For each T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$, there exists the value w^* of w such that:

$$\lambda_+(T, a^*) < 1 \text{ for } w < w^*;$$

$$\lambda_+(T, a^*) > 1 \text{ for } w > w^*,$$

where $w^* = w^*(T)$ satisfies the condition that $w_L < w^* < w_H$ and is uniquely given for each T by the following: $\lambda_+(T, a^*)|_{w=w^*} = 1$.

With these arguments, we can conclude the following:

Lemma. The boundary curve $\lambda_+(T, a^*) = 1$ ($0 < a^* < 1$) in the (w, T) -parameter space is a continuous curve in the region such that $w_L < w < w_H$ and connects two intersections between $\lambda_+(T, 0) = 1$ and $w = w_H$. Further, for $w_L < w < w_H$, since $\lambda_+(T, a^*) > \lambda_+(T, 0)$, the boundary curve is located in the region where $\lambda_+(T, 0) < 1$.

Now, we consider $\ln \lambda_+(T, a^*)$ as a function of T . We have:

$$\left. \frac{\partial \{\ln \lambda_+(T, a^*)\}}{\partial T} \right|_{T=T_L} = \left(T_L - \frac{1}{2} \right) \ln \bar{c} + \ln \bar{\sigma} < 0, \tag{37}$$

where T_L is a value of T satisfying $w_L = w_L(T) = w$ for each w . Since the curve $w_L = w_L(T)$ is a monotonically decreasing function of T as indicated in Fig. 4, it has the unique inverse function $T = T_L(w)$, which is monotonically decreasing in terms of w , from Eq. (25) with:

$$\lim_{w \downarrow \bar{\sigma}} T_L(w) = +\infty$$

$$\lim_{w \uparrow \mu\bar{\sigma}} T_L(w) = 1.$$

Hence, for each w such that $\bar{\sigma} < w < \mu\bar{\sigma}$, the equation $w_L(T) = w$ in terms of T has a unique solution $T = T_L$ such that $T_L > 1$.

The above-mentioned range of T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$ exists in the region where $T > T_L$, because the curve $T = T_L(w)$ is the same as $w = w_L(T)$ and the (w, T) -parameter region satisfying the condition that $\lambda_+(T, a^*) > 1$ and $0 < a^* < 1$ exists in the region where $w > w_L$.

Moreover, we obtain:

$$\frac{\partial^2 \{\ln \lambda_+(T, a^*)\}}{\partial T^2} = \frac{\ln \bar{c}}{T(T-1)} \left(T^2 - T + \frac{1}{\ln \bar{c}} \right),$$

and then:

$$\frac{\partial^2 \{\ln \lambda_+(T, a^*)\}}{\partial T^2} > 0 \text{ for } 1 \leq T < T^*;$$

$$\frac{\partial^2 \{\ln \lambda_+(T, a^*)\}}{\partial T^2} < 0 \text{ for } T > T^*,$$

where:

$$T^* \equiv \frac{1 + \sqrt{1 - \frac{4}{\ln \bar{c}}}}{2} (> 1).$$

We remark that the critical value T^* depends only on the parameter c . Therefore, $\partial \{\ln \lambda_+(T, a^*)\} / \partial T$ is a unimodal function of T . Taking Eq. (37) into account, we can conclude the following:

Lemma. $\ln \lambda_+(T, a^*)$ is a monotonically decreasing function without extremum or has one minimal and another maximal extremum with respect to $T > T_L$. The latter case occurs if $\partial \{\ln \lambda_+(T, a^*)\} / \partial T$ takes positive value in a certain range of $T > T_L$.

If $T^* \leq T_L$, $\ln \lambda_+(T, a^*)$ is monotonically decreasing for $T > T_L$. Only if $T^* > T_L$, it is possible that $\ln \lambda_+(T, a^*)$ could have one minimal and another maximal extremum for $T > T_L$. Since, from the above arguments, T_L is monotonically decreasing from $+\infty$ to 1 as w gets larger from $\bar{\sigma}$ to $\mu\bar{\sigma}$ and since T^* is independent of w and is larger than 1, the condition that $T^* > T_L$ can be satisfied for w less than $\mu\bar{\sigma}$ and larger than a certain critical value determined only by the parameter \bar{c} . Further, since:

$$\frac{\partial}{\partial w} \cdot \frac{\partial \{\ln \lambda_+(T, a^*)\}}{\partial T} = \frac{1}{w} + \frac{1}{\mu\bar{\sigma} - w} > 0 \text{ for } 0 < w < \mu\bar{\sigma};$$

$$\lim_{w \uparrow \mu\bar{\sigma}} \frac{\partial \{\ln \lambda_+(T, a^*)\}}{\partial T} = +\infty,$$

the T -derivative $\partial \{\ln \lambda_+(T, a^*)\} / \partial T$ could take positive values for sufficiently large w less than $\mu\bar{\sigma}$. Lastly, we conclude the following:

Lemma. For w larger than a critical value and less than $\mu\bar{\sigma}$, $\ln \lambda_+(T, a^*)$ has one minimal and another maximal extremum with respect to $T > T_L$.

Now, since $\ln \lambda_+(T, a^*)|_{T=T_L} = \ln \lambda_+(T, a^*)|_{w=w_L} = \ln \lambda_+(T, 1)|_{w=w_L} < 0$, the equation $\ln \lambda_+(T, a^*) = 0$, that is, $\lambda_+(T, a^*) = 1$ has no solution with respect to $T(> T_L)$ if $\ln \lambda_+(T, a^*)$ is monotonically decreasing in terms of

$T(> T_L)$. Moreover, from Eq. (37), even though $\ln \lambda_+(T, a^*)$ has one minimal and another maximal extremum with respect to $T > T_L$, the equation has no solution if the maximal extremum is negative.

On the other hand, we have already shown in the above that, for each T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$, there exists a point (w^*, T) such that $\lambda_+(T, a^*)|_{w=w^*} = 1$ and $w_L < w^* < w_H$. This result indicates that there must exist the case in which the equation $\lambda_+(T, a^*) = 1$ has its solution with respect to $T(> T_L)$. Since $\ln \lambda_+(T, a^*)$ is monotonically increasing in terms of w such that $w_L < w < w_H$, if the equation $\lambda_+(T, a^*) = 1$ has its solution with respect to $T(> T_L)$ for a value of $w (< w_H)$, then the equation does for any w less than w_H and larger than the value of w , too. There are two different solutions, if exist, because then $\ln \lambda_+(T, a^*)$ must have one minimal and another *positive* maximal extremum and

$$\lim_{T \rightarrow +\infty} \ln \lambda_+(T, a^*) = -\infty.$$

With this argument, we can conclude that, in the range of T satisfying the condition that $\lambda_+(T, 0)|_{w=w_H} > 1$, there exists w_c such that the equation $\lambda_+(T, a^*) = 1$ has no solution with respect to $T(> T_L)$ for $w < w_c$ and has two solutions $T_1(w)$ and $T_2(w)$ for $w_c < w$, where $\lambda_+(T, a^*) > 1$ if $T_1(w) < T < T_2(w)$. This indicates the unimodality of the boundary curve $\lambda_+(T, a^*) = 1$. Functions $T_1(w)$ and $T_2(w)$ are, respectively, increasing and decreasing one with respect to w , because $\lambda_+(T, a^*)$ is an increasing function of w .

Appendix E

In this appendix, we prove that, in the case when only the successful germination rate is significantly affected by the decreasing environmental favorability, that is, in case of the successful germination rate decreasing in generation with fixed other generation-independent parameters, there exist such parameters (w, T) that, under the ecological disturbance that periodically occurs, both annual and perennial populations are persis-

tent and the perennial is more adaptive than the annual.

In this case, $z(t) = (\bar{\sigma}/w)c_r^{-t-1}$. From Eqs. (9) and (19), it is easily shown that if inequalities

$$q_s w^T c_r^{T(T-1)/2} > 1 \tag{38}$$

and

$$\frac{\bar{\sigma} (1/c_r)^{T-1} - 1}{w (1 - c_r)} - T > 0 \tag{39}$$

are satisfied, then $\lambda_+(T, 0) > 1$ and $\partial\lambda_+(T, a)/\partial a|_{a=0} > 0$ and so $\lambda_+(T, a)$ has a maximum at $a = a^*$ where $0 < a^* < 1$, because always $\lambda_+(T, 1) < 1$.

If inequality

$$\left(\frac{1}{q_s}\right)^{1/T} \left(\frac{1}{c_r}\right)^{(T-1)/2} < \frac{\bar{\sigma} (1/c_r)^{T-1} - 1}{T (1 - c_r)} \tag{40}$$

holds, there exists a value of w such that

$$\left(\frac{1}{q_s}\right)^{1/T} \left(\frac{1}{c_r}\right)^{(T-1)/2} < w < \frac{\bar{\sigma} (1/c_r)^{T-1} - 1}{T (1 - c_r)} \tag{41}$$

is satisfied, therefore Eqs. (38) and (39) are simultaneously satisfied for the value of w . From Eq. (40), we have its equivalent inequality

$$T \leq T \left(\frac{1}{q_s}\right)^{1/T} < \frac{2\bar{\sigma}}{1 - c_r} \sinh\left(\frac{T-1}{2} \ln \frac{1}{c_r}\right). \tag{42}$$

When $T=1$, the condition Eq. (42) cannot be satisfied. As T becomes larger, the left hand side of Eq. (42) monotonically approaches T , while the right hand side does const. $\times (1/c_r)^{T/2}$.

So, for a sufficiently large T , the condition Eq. (42) is satisfied. In detail, there is a value T_* of T such that the condition Eq. (42) is satisfied for $T > T_*$. Lastly, for $T > T_*$, there exists w satisfying the condition Eq. (41). With this argument, we prove that there exist such parameters (w, T) that both annual and perennial populations are persistent and the perennial is more adaptive than the annual.

Appendix F

In this appendix, we prove that, in the case when only the successful germination rate is sig-

nificantly affected by the decreasing environmental favorability, that is, in case of the successful germination rate decreasing in generation with fixed other generation-independent parameters, there exist a parameter region with which only the monocarpic perennial population is persistent under the ecological disturbance that periodically occurs.

Suppose $T > T_*$, where T_* is given in Appendix E. For $T > T_*$, the condition Eq. (40) is satisfied. Now, we consider such value of $w = w^*(T)$ that

$$w^*(T) = \left(\frac{1}{q_s}\right)^{1/T} \left(\frac{1}{c_r}\right)^{(T-1)/2}. \tag{43}$$

From Eq. (19), it is held that $\lambda_+(T, 0) = 1$ when $w = w^*(T)$. From the argument in Appendix E, for $T > T_*$, it is held that there exists such an intermediate value of $a = a^*$ that $0 < a^* < 1$ and $\max_a \lambda_+(T, a) = \lambda_+(T, a^*) > \lambda_+(T, 0)$ and necessarily $\partial\lambda_+(T, a)/\partial a|_{a=0} > 0$. Besides, we can easily see from Eq. (19) that $\lambda_+(T, 0)$ is monotonically increasing in terms of w . Therefore, because of the continuity of $\lambda_+(T, a)$ in terms of w and T , there exists such a certain $\epsilon(T) (> 0)$ that, for some $T > T_*$ and $w = w^*(T) - \epsilon(T)$, $\lambda_+(T, 0) < 1$ and $\max_a \lambda_+(T, a) = \lambda_+(T, a^*) > 1$ with $0 < a^* < 1$. This argument proves that there exists a parameter region with which only the monocarpic perennial population is persistent.

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