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

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Abstract

We consider the disturbance-controlled persistence of perennial plant population with a transition matrix modelling, and discuss the contribution of perennation to the population persistence under the periodically occured ecological disturbance. Our mathematical results indicates that the ecological disturbance with an appropriate period assures the persistence of a subordinate species of plant. Further, we demonstrate that, under some periodically occurred ecological disturbance, 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.

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 [1]). 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 [2]).

For plant population, the *transition matrix* modelling is well-known to describe the structured population, for example, with seed, rosette, and flower classes (Charlesworth [3]). A variety of mathematical models with the transition matrix, introduced some biologically cosiderable factors, for instance, density effects or temporally environmental variation, have been studied (for review, see Caswell [4]).

In this paper, along the similar line of mathematical modelling with that in Giho and Seno [5], we consider the mathematical modelling with the transition matrix for the population dynamics of perennial plant under the periodically occured ecological disturbance. In our mathematical modelling consideration, we focus on the contribution of perennation to the population persistence. We demonstrate that, under some periodically occurred ecological disturbance, 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.

2 Model

We consider a monocarpic plant population structured with three classes: seed, juvenile, and flower. In our modelling, 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 flower in a season;
δ_j : time interval characterizing stages of individual growth $(j = 1, 2)$.

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

From the transition sheme for our model shown in Fig. 1, we can focus two classes of seed and juvenile, utilizing the following 2-dimensional vector $\mathbf{V}_t$ of seed population S_t and juvenile one R_t, and 2×2 matrix $\mathbf{A}_t$ at

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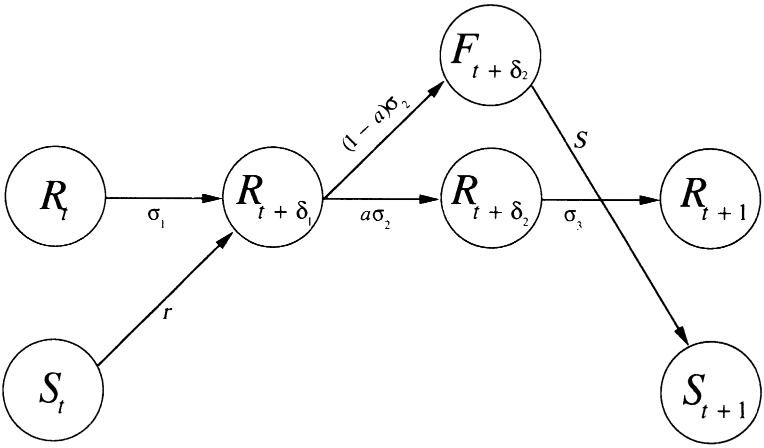

Fig. 1. Population transition from the seed class S_t and the juvenile class R_t to the flowering $F_{t+\delta_2}$ and the juvenile $R_{t+\delta_2}$ via the juvenile $R_{t+\delta_1}$ in the t th year. The flowering class $F_{t+\delta_2}$ succeeds in making the seed class S_{t+1} at the $t+1$ th year,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

generation t:

$$\mathbf{V}_t = \begin{pmatrix} S_t \\ R_t \end{pmatrix} \tag{1}$$

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

With the vector $\mathbf{V}_t$ and the matrix $\mathbf{A}_t$, the population dynamics between subsequent generations is given by $\mathbf{V}_{t+1} = \mathbf{A}_t\mathbf{V}_t$. Therefore,

$$\mathbf{V}_t = \left\{\prod_{k=0}^{t-1} \mathbf{A}_k\right\} \mathbf{V}_0. \tag{3}$$

The ecological disturbance is introduced by the following matrix $\mathbf{Q}$:

$$\mathbf{Q} = \begin{pmatrix} q_s & 0 \\ 0 & q_r \end{pmatrix}, \tag{4}$$

where q_s and q_r are respectively the survival rates of seed and juvenile with respect to the disturbance. They are positive constants less than 1. The disturbance is assumed to occur just after the seed production. When the disturbance occurs at generation $T > 1$, the population $\mathbf{V}_T$ before the disturbance becomes $\mathbf{QV}_T$ 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 modelling 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:

$$\mathbf{A}_0 \to \mathbf{A}_1 \to \mathbf{A}_2 \to \cdots \to \mathbf{A}_{T-1} \Rightarrow \mathbf{A}_0 \to \cdots \to \mathbf{A}_{T-1} \Rightarrow \mathbf{A}_0 \to \cdots$$

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

$$\mathbf{V}_0 \to \mathbf{V}_1 \to \cdots \to \mathbf{V}_{T-1} \Rightarrow \mathbf{QV}_T \to \mathbf{A}_0\mathbf{QV}_T \to \mathbf{A}_1\mathbf{A}_0\mathbf{QV}_T \to \cdots$$

Now, we consider the population just after the disturbance. Under the periodical disturbance of period T, with the initial population $\mathbf{V}_0$, let $\mathbf{W}_n$ the population just after the n th disturbance. Then, the above argument indicates that $\mathbf{W}_n$ is governed by the following recurrence relation: $\mathbf{W}_{n+1} = \mathbf{\Gamma W}_n$, where $\mathbf{W}_0 = \mathbf{V}_0$ and the matrix $\mathbf{\Gamma}$ is now defined by

$$\mathbf{\Gamma} \equiv \mathbf{Q}\prod_{k=0}^{T-1} \mathbf{A}_k. \tag{5}$$

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

3 Criterion for population persistence

When and only when the absolute values of every eigenvalues for matrix $\mathbf{\Gamma}$ are less than 1, $\mathbf{W}_n \to 0$ for any $\mathbf{W}_0$ as $n \to \infty$, that is, the extinction necessarily occurs for any initial population $\mathbf{V}_0$. From (2), (4) and (5), we can directly calculate the eigenvalue for $\mathbf{\Gamma}$ and immediately find that both of two eigenvalues are real and they are zero and 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, obtained as follows:

$$\lambda_+(T,a) \equiv \lambda_+(T,0)\left\{\prod_{t=0}^{T-2}[1-\{1-z(t)\}a]\right\}[1-\{1-\mu z^*(T)\}a], \quad (6)$$

where

$$\lambda_+(T,0) \equiv q_s \prod_{t=0}^{T-1}\{r(t)\sigma_2(t)S(t)\} \quad (7)$$

$$z(t) \equiv \frac{\sigma_1(t+1)\sigma_3(t)}{r(t+1)S(t)} \quad (8)$$

$$z^*(T) \equiv \frac{\sigma_1(0)\sigma_3(T-1)}{r(0)S(T-1)} \quad (9)$$

$$\mu \equiv \frac{q_r}{q_s}. \quad (10)$$

$\lambda_+(T, 0)$ determines the persistence of *annual* population with $a = 0$. When and only when $\lambda_+(T, 0) > 1$, the annual population can persist independently of the initial population. This is exactly corresponding to the modelling result obtained in Giho and Seno [5]. In addition, it can be easily shown that always $\lambda_+(T, 1) < 1$. The criterion for the persistence of population with the perennation parameter a under the periodical disturbance of period T is now given by $\lambda_+(T, a) > 1$.

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. The following result can be obtained about the maximal value of $\lambda_+(T,a)$ in terms of a:

$$\max_a \lambda_+(T,a) = \begin{cases} \lambda_+(T,0) \\ \quad \text{if and only if} \quad \frac{1}{T}\left\{\sum_{t=0}^{T-2} z(t) + \mu z^*(T)\right\} \leq 1 \\ \lambda_+(T,1) \\ \quad \text{if and only if} \quad \left[\frac{1}{T}\left\{\sum_{t=0}^{T-2} \frac{1}{z(t)} + \frac{1}{\mu z^*(T)}\right\}\right]^{-1} \geq 1 \\ \lambda_+(T,a^*) \quad (0 < \exists a^* < 1) \\ \quad \text{otherwise.} \end{cases} \tag{11}$$

The second condition of (11) is sufficient for the extinction of population with any a, since $\lambda_+(T,1) < 1$ for any a, as mentioned in the previous section. In case of the first of (11), since the intrinsic growth rate is maximized for $a = 0$, 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 paper, we specifically consider the exponentially decreasing functions for those generationally variable parameters as follows:

$$r(t) = c_r^t r(0); \tag{12}$$
$$S(t) = c_s^t S(0); \tag{13}$$
$$\sigma_i(t) = c_i^t \sigma_i(0) \quad (i = 1,2,3), \tag{14}$$

where $r(0)$, $\sigma_i(0)$, and c_k ($k = 1,2,3,r,s$) are positive and not beyond 1. $S(0)$ is positive. Then, (7), (8) and (9) are expressed as follows:

$$\lambda_+(T,0) = q_s \bar{c}_*^{T(T-1)/2} w^T; \tag{15}$$
$$z(t) = \frac{\bar{\sigma}}{w} \cdot \frac{c_1}{c_r} \cdot \left(\frac{\bar{c}}{\bar{c}_*}\right)^t; \tag{16}$$
$$z^*(T) = \frac{\bar{\sigma}}{w} \cdot \left(\frac{c_3}{c_s}\right)^{T-1}, \tag{17}$$

where we defined the following parameters for convenience:

$$\begin{aligned} w &\equiv r(0)\sigma_2(0)S(0); \\ \bar{c}_* &\equiv c_r c_2 c_s; \\ \bar{c} &\equiv c_1 c_2 c_3; \\ \bar{\sigma} &\equiv \sigma_1(0)\sigma_2(0)\sigma_3(0). \end{aligned}$$

The parameter w corresponds to the initial reproductive rate in the case when the population is annual ($a = 0$).

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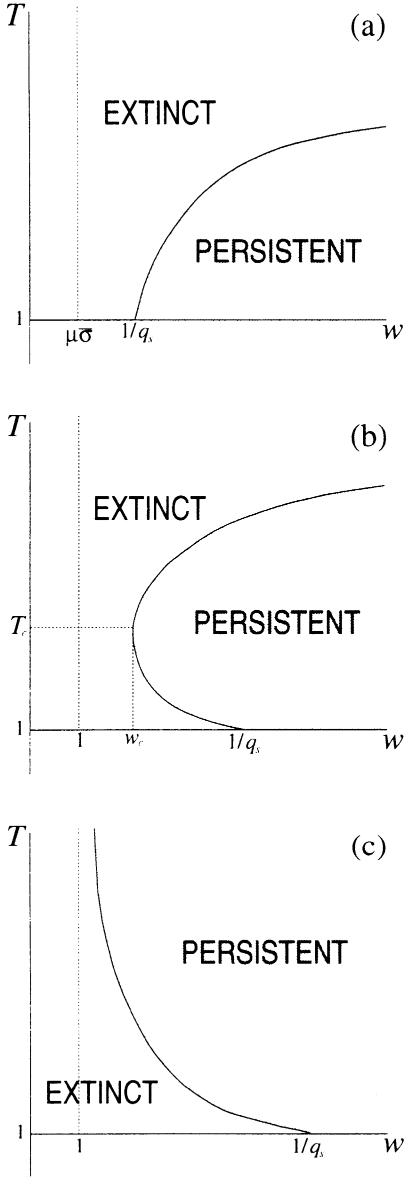

Fig. 2. Parameter region for the annual population (a = 0) in the (w, T)-parameter space. Exponentially decreasing environmental favorability. (a) $\bar{c}_* < 1$ and $T_c \equiv \sqrt{2\ln q_s / \ln \bar{c}_*} \leq 1$, that is, $\bar{c}_* \leq q_s^2$; (b) $\bar{c}_* < 1$ and $T_c > 1$, that is, $q_s^2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

5.1 Persistence of annual population

The persistent parameter region for the *annual* population is given by $\lambda_+(T,0) > 1$ and shown in Fig. 2. The region has the different feature depending on the value $T_c \equiv \sqrt{2\ln q_s/\ln \bar{c}_*}$. That is, the region has the feature shown in Fig. 2(a) if $T_c \leq 1$, that is, if $q_s^2 \geq \bar{c}_*$. If $\bar{c}_* > q_s^2$, its feature is shown by Fig. 2(b). For the case when $\bar{c}_* = 1$, that is, when $c_r = c_s = c_2 = 1$, as shown in Fig. 2(c), we can see that the feature of $\lambda_+(T,0)$ is significantly different from that in case of $\bar{c}_* < 1$.

5.2 Season-dependent decreasing environmental favorability

For mathematical simplicity in case of perennial population, we analyze the case when $c_r = c_1$, $c_s = c_3$, and $\bar{c}_* = \bar{c}$. This is the case when the decreasing favorability of environment affects to each stage with a common strength as long as considered 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 (16) and (17), both $z(t)$ and $z^*(T)$ becomes a generation-independent constant z given by

$$z(t) = z^*(T) = z \equiv \frac{\bar{\sigma}}{w}, \tag{18}$$

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

$$\lambda_+(T,a) \equiv \lambda_+(T,0)\left[1-(1-z)a\right]^{T-1}\left[1-(1-\mu z)a\right]. \tag{19}$$

From (11), we can immediately obtain the following:

$$\max_a \lambda_+(T,a) = \begin{cases} \lambda_+(T,0) & \text{if and only if } \; w \geq w_H \\ \lambda_+(T,1) & \text{if and only if } \; w \leq w_L \\ \lambda_+(T,a^*) & (0 < \exists a^* < 1) \;\; \text{otherwise,} \end{cases} \tag{20}$$

where

$$\begin{aligned} w_L &\equiv \left\{1 + \frac{\mu - 1}{\mu T - (\mu - 1)}\right\}\bar{\sigma}; \\ w_H &\equiv \left(1 + \frac{\mu - 1}{T}\right)\bar{\sigma}. \end{aligned}$$

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

We can find that $\lambda_+(T,0)|_{w=w_H} > 1$ is the necessary and sufficient condition for the existence of persistent perennial population under the ecological disturbance. Then it is easily proved that, if $\mu \leq 1$, the condition

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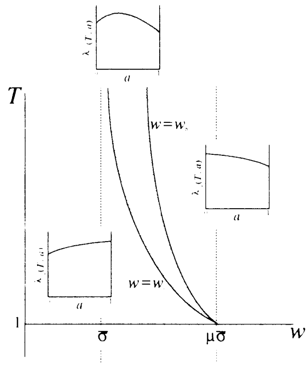

Fig. 3. Parameter region (grey) for $w_L < w < w_H$ in the (w, T)-parameter space when $\mu > 1$. For the definition of w_L and w_H, see the main text. The parameter space is devided into three by the curves $w = w_L$ and $w = w_H$. For these regions, the a-dependence of $\lambda_+(T, a)$ is different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

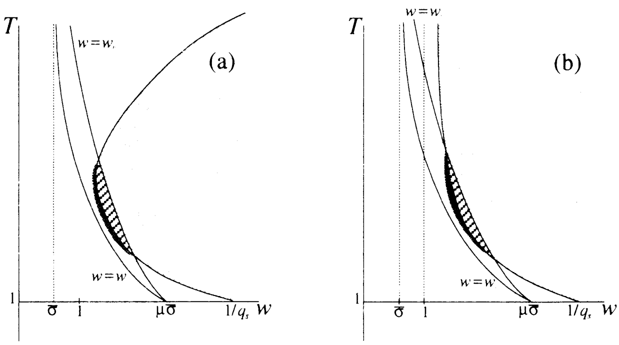

Fig. 4. Parameter region for the population persistence in the (w, T)-parameter space when $\mu > 1$ and there exists the parameter region for the persistent perennial population. Season-dependent exponentially decreasing environmental favorability. (a) $q_s^2 < \bar{c}_* < 1$; (b) $\bar{c}_* = 1$. For 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 other region, both become extinct.

$\lambda_+(T,0)|_{w=w_H} > 1$ cannot be satisfied. Thus, if $\mu \leq 1$, the perennial population eventually becomes extinct for $w_L < w < w_H$. This means that, if $\mu \leq 1$, the population persistence requires the annual. When $\mu > 1$, the parameter region for $w_L < w < w_H$ in the (w, T)-parameter space is obtained as in Fig. 3. Then, if and only if the curve $w = w_H$ intersects with the region for $\lambda_+(T,0) > 1$ in the (w, T)-parameter space, there could exist some w_H satisfying the condition that $\lambda_+(T,0)|_{w=w_H} > 1$ for some T. When there exists some point (w_H, T) satisfying $\lambda_+(T,0)|_{w=w_H} > 1$ in the (w, T)-parameter space, we have such a parameter region shown in Fig. 4 that the perennial is persistent while the annual becomes extinct.

Summary

We considered the disturbance-controlled persistence of perennial plant population with a transition matrix modelling, and analyzed the model with regard to the contribution of perennation to the population persistence under the periodically occured ecological disturbance. The considered population is fundamentally subordinate in terms of the persistence at the habitat. Our mathematical results indicates that the ecological disturbance with an appropriate period assures the persistence of such subordinate species of plant. Further, we demonstrate that, under some periodically occurred ecological disturbance, 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.

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