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H. Nakajima, K. Yonejima, T. Matsuoka and H. Seno

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LOTKA–VOLTERRA TWO-SPECIES SYSTEM WITH PERIODIC INTERRUPTION OF COMPETITION

H. NAKAJIMA

*Department of Physics, Ritsumeikan University
Kusatsu 525-8577, Japan*

K. YONEJIMA

*Department of Information and Computer Sciences
Faculty of Science, Nara Women's University
Nara 630-8506, Japan*

T. MATSUOKA and H. SENO*

*Department of Mathematical and Life Sciences
Graduate School of Science, Hiroshima University
Kagamiyama 1-3-1, Higashi-hiroshima, Hiroshima, 739-8526, Japan
seno@math.sci.hiroshima-u.ac.jp

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We consider the two-species Lotka–Volterra competition system with a temporally periodic interruption of competition coefficient. We assume that the competition coefficient is constant in a time interval of fixed length τ_+ , while it is zero in the other time interval of length τ_- . The temporal variation of the competition coefficient is rigorously periodic with period $\tau_+ + \tau_-$, in which the competition coefficient becomes a given positive constant and zero by turns, the other parameters being constant in time. We analyze the system analytically and numerically, and derive the condition for the permanence of the whole system, the coexistence of two competing species, and the change of the species-dominance in terms of the competition. We discuss some interesting natures of our system, distinguished from the original two-species Lotka–Volterra competition system with constant competition coefficients. The temporal interruption of competition could cause the change of the destiny of competing species.

Keywords: Lotka–Volterra System; Competition; Temporal Heterogeneity; Permanence; Mathematical Model.

1. Introduction

The Gause's competitive exclusion hypothesis says that two species depending on a common niche for their persistence cannot coexist, so that one of them eventually goes extinct.¹ However, not a few empirical and theoretical researches in ecology have indicated that, if some environmental factor has heterogeneity to regulate their

*Corresponding author.

competitive relationship, two competing species can coexist, even depending on a common niche for their persistence. In short, some environmental heterogeneity could allow the coexistence of two species competing about a common niche (for a review, see Begon *et al.*²). In such a case, the environmental "heterogeneity" is spatial and/or temporal. Indeed, in nature, any inter-specific relationship is neither temporally nor spatially homogeneous. Especially as for the temporal heterogeneity, a seasonal niche change could cause a temporal variation of some natures about the inter-specific relationship.²⁻⁴ What is the effect of such a temporal heterogeneity of the inter-specific relationship on the nature of population dynamics?

Hutchinson^{3,4} discussed the effect of a temporal heterogeneity of niche on the competitive relationship, and argued that the temporal heterogeneity allows the coexistence of competing species. As for theoretical and mathematical researches about the effect of a temporally environmental heterogeneity on the competition system, the Lotka-Volterra competition system with temporally periodic coefficients has been studied by some mathematical researchers in the last century.⁵⁻⁸ In those researches, the temporally periodic coefficients are assumed to always have positive values, and the model involved a seasonal change of the strength of competition. They have shown that a temporally periodic variation of coefficients in the Lotka-Volterra competition system causes a variety of dynamical natures which do not appear with constant coefficients.

In this paper, we consider the two-species Lotka-Volterra system with temporally periodic interruption of the inter-specific competitive relationship. We assume that the competition coefficient is constant in a time interval of fixed length τ_+ , while it is zero in the other time interval of length τ_- . The temporal variation of the competition coefficient is rigorously periodic with period $T = \tau_+ + \tau_-$, in which the competition coefficient becomes a given positive constant and zero by turns, the other parameters being constant in time. We analyze the system analytically and numerically, and consider how the coexistence of two competing species occurs with the interruption of competition, especially in the bistable case for the population dynamics without such interruption of competition.

Not only for the competitive relationship but also for any other type of inter-specific relationships, such a temporal interruption of inter-specific relationship would occur in nature, for example, due to a seasonal separation of niches (habitat, homerange, food, etc.) of two species. From a mathematical viewpoint, this type of inter-specific relationship can be modeled by introducing a temporally interruptive vanishment of terms which represent the inter-specific relationship.

In a sense, such a system with temporally discontinuous change of terms governing the dynamics may be regarded as an *impulsive system*.⁹⁻¹¹ However, as in most papers dealing with such impulsive systems about the Lotka-Volterra competition model (for example, Struk and Tkachenko¹² and Liu and Chen¹³), the impulsive system generally involves the temporally discontinuous change of the state variables (i.e. the population sizes) themselves. In contrast, our model involves the temporally discontinuous change of parameters, and does not that of population size. So in the more conventional sense our system is not of the impulsive system.

We discuss some interesting natures of our system, distinguished from the original two-species Lotka-Volterra competition system with constant competition coefficients, and show that the temporal interruption of competition could cause the change of the destiny of competing species, although some of them provide some open mathematical problems.

2. Modeling

2.1. Two-species Lotka-Volterra competition system

We consider the following Lotka-Volterra competition system of two species:

$$(2.1) \quad \begin{aligned} \frac{dn_1(t)}{dt} &= \{r_1 - \beta_{11}n_1(t) - \mu_{12}(t)n_2(t)\}n_1(t); \\ \frac{dn_2(t)}{dt} &= \{r_2 - \mu_{21}(t)n_1(t) - \beta_{22}n_2(t)\}n_2(t), \end{aligned}$$

where $n_i(t)$ ($i = 1, 2$) is the population size of species i at time t . Parameters r_i and β_i ($i = 1, 2$) are all positive, respectively the intrinsic growth rate to give the maximal reproductive capacity, and the intra-specific competition coefficient to indicate the strength of density effect from the other individuals of same species. Functions $\mu_{ij}(t)$ ($i, j = 1, 2; i \neq j$) of time introduce the inter-specific competitive interaction between populations of species 1 and 2. These functions are now defined as rigorously periodic in time: $\mu_{ij}(t + T) = \mu_{ij}(t)$ for any $t (\geq 0)$ with a given positive constant T , which gives the species-independent period of temporal variation in the strength of inter-specific competition. We assume that the competitive relationship temporally changes in a rigorously periodic manner, for instance, because of a seasonal environmental change to cause a seasonal niche change of each species.

2.2. Temporally interruptive competition coefficient

In this paper, we consider the two competing-species system with temporal interruption of inter-specific competitive relationships. We assume that the competition coefficient μ_{ij} ($i, j = 1, 2; i \neq j$) is a positive constant in a time interval of fixed length τ_+ , while it is zero in the other time interval of length τ_- , and that the temporal variation of competition coefficient is rigorously periodic with period $T = \tau_+ + \tau_-$, in which the competition coefficient becomes a given positive constant and zero by turns. Mathematically in short, we assume

$$(2.2) \quad \mu_{ij} = \begin{cases} \mu_{ij} & (kT \leq t < kT + \tau_+) \\ 0 & (kT + \tau_+ \leq t < (k+1)T) \end{cases} \quad (i, j = 1, 2; i \neq j),$$

for $k = 0, 1, 2, \dots$. Parameter μ_{ij} ($i, j = 1, 2; i \neq j$) is a given positive constant independent of competitive season. The temporal average of the competition coefficient $\langle \mu_{ij} \rangle$ is defined by $\langle \mu_{ij} \rangle = \mu_{ij} \tau_+ / T$.

2.3. Non-dimensionalized system

Making use of the following non-dimensionalized transformation of variables and parameters, we can reduce the number of parameters to be considered in our mathematical analysis ($i, j = 1, 2; i \neq j$):

$$t = \frac{T}{r_i} N_i; \quad N_i = \frac{r_i}{\beta_i} n_i; \quad \rho_i = r_i T; \quad m_{ij} = \frac{r_j \beta_{ij}}{r_i \beta_j}$$

With these transformations, we get the following system that is mathematically equivalent to (2.1):

$$\begin{aligned} \frac{dN_1(t)}{dt} &= \rho_1 \{1 - N_1(t) - m_{12} N_2(t)\} N_1(t); \\ \frac{dN_2(t)}{dt} &= \rho_2 \{1 - m_{21} N_1(t) - N_2(t)\} N_2(t). \end{aligned} \tag{2.3}$$

Temporally interruptive competition coefficient m_{ij} ($i, j = 1, 2; i \neq j$) is now given by

$$m_{ij}(t) = \begin{cases} m_{ij} & (k \leq t < k + \tau_+); \\ 0 & (k + \tau_+ \leq t < k + 1), \end{cases}$$

where $k = 0, 1, 2, \dots$, and $m_{ij} = (r_j/r_i)\beta_{ij}/\beta_j$ ($i, j = 1, 2; i \neq j$). The interval with competition $\tau_+ = \tau_+/T$ satisfies now that $0 < \tau_+ < 1$, because the period of temporally repetitive change of competitive relationship is now normalized into 1 (see Fig. 1).

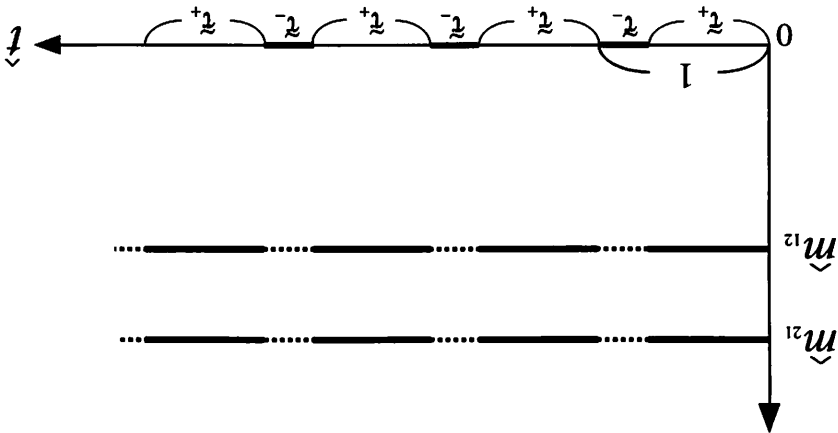


Fig. 1. Temporally interruptive competition coefficients. Illustratively drawn with non-dimensionalized parameters, $m_{ij} = r_j \beta_{ij} / (r_i \beta_j)$ ($i, j = 1, 2; i \neq j$), $\tau_+ = \tau_+ / T$ ($0 < \tau_+ < 1$) and $\tau_- = 1 - \tau_+$. In the other season, m_{12} and m_{21} are positive constant, and in another season, $m_{12} = m_{21} = 0$. In our mathematical modeling, these two seasons repetitively occur one after another in an exactly periodic manner.

3. Analysis

In the case when $m_{12} > 1$ and $m_{21} < 1$ without any interruption of competition, two species coexist. In this case, it is trivial that two species can coexist with or without the interruption of competition. In this reason, we do not consider any more the case when $m_{12} > 1$ and $m_{21} < 1$, and we analyze only case when $m_{12} > 1$ or $m_{21} < 1$.

3.1. Local stability of the competitive exclusion equilibrium state

As for the local stability of the competitive exclusion equilibrium state $(N_i, N_j) = (0, 1)$, we can carry out the local stability analysis about the time-discrete dynamical system of $\{(N_1(k), N_2(k)) | k = 0, 1, 2, \dots\}$ for the linearized system derived from (2.3), and get the following result:

If the temporal average of m_{ij} :

$$\langle m_{ij} \rangle = m_{ij} \cdot \tau_+ = \frac{r_i h_{ij}}{r_j h_{ij}} \cdot \frac{J}{\tau_+} = \frac{r_i \beta_j}{r_j \langle h_{ij} \rangle}$$

is less than 1, the equilibrium state $(N_i, N_j) = (0, 1)$ is unstable. If $\langle m_{ij} \rangle > 1$, it is asymptotically stable.

This result shows that the survival of the competitively inferior species can be realized by the interruption of competition. The first half of this result indicates that, even when $m_{ij} < 1$ and the species i eventually goes extinct due to the inter-specific competition in the case without the interruption of competition, it is possible that the species i does not go extinct with an interruption of competition such that $\langle m_{ij} \rangle > 1$. Moreover, if $\langle m_{12} \rangle > 1$ and $\langle m_{21} \rangle < 1$, neither of species 1 and 2 tends to zero as $t \rightarrow \infty$, so that both species persist. The second half of the above result indicates that, if $\langle m_{ij} \rangle > 1$ even with an interruption of competition, there is a set of initial states with which the species i goes extinct. Such a set of initial states eventually includes a neighborhood of the equilibrium state $(N_i, N_j) = (0, 1)$. Finally, this result indicates that the local stability of the competitive exclusion equilibrium state coincides with that for the corresponding system which has the constant inter-specific competition coefficient equivalent to the temporally averaged competition coefficient $\langle h_{ij} \rangle$:

$$\frac{dn_1(t)}{dt} = \{r_1 - \beta_1 n_1(t) - \langle h_{12} \rangle n_2(t)\} n_1(t);$$

$$\frac{dn_2(t)}{dt} = \{r_2 - \langle h_{21} \rangle n_1(t) - \beta_2 n_2(t)\} n_2(t).$$

3.2. Permanent coexistence with the interruption of competition

In the bistable case when $m_{12} > 1$ and $m_{21} < 1$, we can numerically find the appearance of coexistence with the interruption of competition, even though the

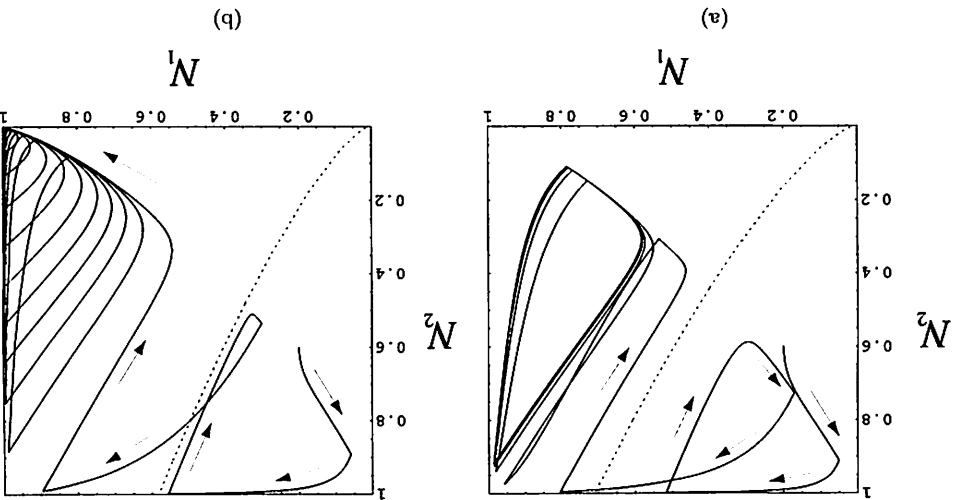


Fig. 2. Numerical examples of trajectory in the phase plane of (N_1, N_2) in a bistable case. Dashed curve is the numerically drawn separatrix in the case without the interruption of competition. With the periodic interruption of competition, (a) a trajectory converges to a coexistent state with $m_{21} = 1.4$; (b) a trajectory converges to the state $(1, 0)$ with $m_{21} = 1.5$. In both cases, $(N_1(0), N_2(0)) = (0.2, 0.6)$; $\rho_1 = 10.0$; $\rho_2 = 15.0$; $m_{12} = 1.36$; $\tau_- = 0.3$. Without the interruption, the trajectory would converge to the state $(0, 1)$, because the initial point is above the separatrix in the case when the competition is kept without the interruption.

coexistence would be impossible without it. In Fig. 2a, we show a numerical example of the coexistent state realized by an interruption of competition. Also for the case when one species forces another go extinct independently of the initial condition, that is, when $m_{12} > 1$ and $m_{21} < 1$ or when $m_{12} < 1$ and $m_{21} > 1$, we can find the appearance of coexistence with an interruption of competition. In such case, the corresponding coexistent periodic orbit is similar to that shown in Fig. 2a. If the system is mathematically *permanent*, then two species coexist independently of the initial state. Now we can obtain the following result about the *permanence* of the system (2.3), which can be realized by the interruption of competition (the outline of proof is given in Appendix):

The system (2.3) is permanent if and only if $\langle m_{12} \rangle < 1$ and $\langle m_{21} \rangle < 1$.

Therefore, if $\max[\langle m_{12} \rangle, \langle m_{21} \rangle] < 1$, the system (2.3) is not permanent. In such case, there exists a set of initial states to cause the extinction of one species. If the interruption of competition makes the temporal average of competition coefficients less than 1, that is, if the interruption of competition is sufficiently long, the coexistence of two competing species is established independently of the initial state.

3.3. Inversion of the competitive dominance

With the interruption of competition, we can find the *inversion of the competitive dominance*: Species i is eventually eliminated and species j persists with the

interruption of competition, whereas species j is eventually eliminated and species i persists without it. The trajectory is shown in Fig. 2b is a numerical example for the inversion of the competitive dominance.

Let us consider the case when $\hat{m}_{12} > \hat{m}_{21} > 1$, which is a bistable case. In this case, we can choose the value of $\tilde{\tau}_-$ such that $\langle m_{12} \rangle > 1 > \langle m_{21} \rangle$. Then, the result about the local stability of the competitive exclusion equilibrium state given in Sec. 3.1 indicates that the extinction of species 2 never occurs, whereas species 2 could go extinct depending on the initial state without the interruption of competition. This is a case of the inversion of the competitive dominance.

From the viewpoint of the invasion of a species, as far as $\langle m_{12} \rangle > \langle m_{21} \rangle > 1$, the invasion of the other species fails at the equilibrium state $(1, 0)$ or $(0, 1)$. However, if $\langle m_{12} \rangle > 1 > \langle m_{21} \rangle$ with an intermediately long length of the competition interruption, species 2 can invade at the equilibrium state $(1, 0)$, while species 1 cannot at $(0, 1)$. This argument implies that the interruption of competition could control the invasion success of a species.

Moreover, when $\hat{m}_{12} > 1 > \hat{m}_{21}$, that is, when species 1 goes extinct independently of the initial state without the interruption of competition, we can choose the value of $\tilde{\tau}_-$ such that $\langle m_{12} \rangle > 1 > \langle m_{21} \rangle$, again. In such case, the result about the local stability of the competitive exclusion equilibrium state given in Sec. 3.1 indicates that the interruption of competition cannot change the destiny of species in terms of their extinction or survival.

3.4. Dependence on the interruption length

We analyze the dependence of equilibrium states mentioned in the previous sections on the *length* of the interruption of competition, that is, $\tilde{\tau}_-$, making use of numerical calculations.

For convenience, we define the following two critical lengths of the interruption of competition:

$$\begin{aligned} \min[\langle m_{12} \rangle, \langle m_{21} \rangle] &= 1 & \text{with } \tilde{\tau}_- &= \tilde{\tau}_-^*; \\ \max[\langle m_{12} \rangle, \langle m_{21} \rangle] &= 1 & \text{with } \tilde{\tau}_- &= \tilde{\tau}_-^{**}. \end{aligned}$$

Always $\tilde{\tau}_-^* \leq \tilde{\tau}_-^{**}$. The results in the previous sections show that, for $\tilde{\tau}_- < \tilde{\tau}_-^*$, the local stability of equilibrium states $(1, 0)$ and $(0, 1)$ is unchanged even with the interruption of competition. For $\tilde{\tau}_- > \tilde{\tau}_-^*$, one of two species never goes extinct independently of the initial state. For $\tilde{\tau}_- > \tilde{\tau}_-^{**}$, both of two species never goes extinct independently of the initial state, and their coexistence occurs. In the following analysis, we can see the further detail about the effect of the interruption of competition on the equilibrium state, making use of numerical calculations.

3.4.1. Inversion of the competitive dominance

According to the inversion of the competitive dominance, we numerically investigated the area of the initial state $(N_1(0), N_2(0))$ in $(0, 1) \times (0, 1)$ as shown by the

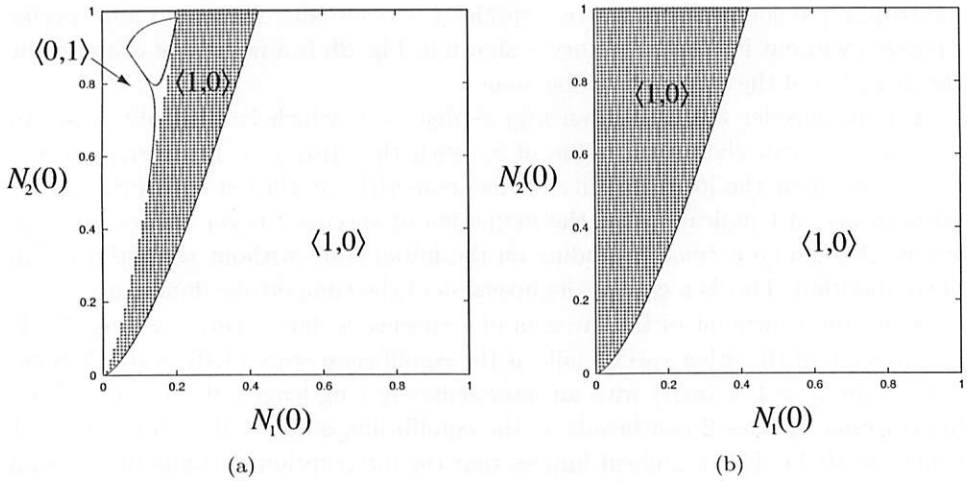


Fig. 3. Dependence of the equilibrium state on the initial state. Numerically obtained result. The solid curve indicates the separatrix in the case when the competition always exists without the interruption. For the initial condition $(N_1(0), N_2(0))$ in the region $\langle 0,1 \rangle$, species 1 goes extinct while species 2 persists. For that in the region $\langle 1,0 \rangle$, species 2 goes extinct while species 1 persists. Dotted region indicates the initial state with which the extinction of species 1 occurs without the interruption of competition, whereas that of species 2 occurs with the interruption. (a) $\tilde{\tau}_- = 0.125$; (b) $\tilde{\tau}_- = 0.176$. In both cases, $\rho_1 = 10.0$; $\rho_2 = 15.0$; $\hat{m}_{12} = 1.2$; $\hat{m}_{21} = 1.4$; $\tilde{\tau}_+^* = 0.167$; $\tilde{\tau}_+^{**} = 0.286$. In (a), a numerical trajectory from the initial state $(N_1(0), N_2(0)) = (0.123931, 0.50)$ is shown, which appears converging to an unstable periodic orbit.

dotted region in Fig. 3. For the initial state in the region indicated by the dotted region in Fig. 3, the extinction of species 1 occurs without the interruption of competition, whereas that of species 2 occurs with the interruption. Comparing Fig. 3a with Fig. 3b, we can see that the difference of $\tilde{\tau}_-$ is significantly reflected to the area of the initial state for the inversion of the competitive dominance.

The boundary between the regions of $\langle 0,1 \rangle$ and $\langle 1,0 \rangle$ in Fig. 3 may be regarded as the separatrix essential for our system with the interruption of competition, depending on which species goes extinct. As shown in Fig. 3a, our numerical calculation implies that the trajectory from the initial state on the boundary converges to an unstable periodic orbit. Our numerical calculations imply that the unstable periodic orbit which can be reached from the initial state on the boundary would uniquely exist. Moreover, the trajectory from any initial state on the boundary keeps every point $(N_1(k), N_2(k))$ at $\tilde{t} = k$ on the boundary for any integer $k > 0$.

3.4.2. Coexistence

According to the coexistence, we numerically checked the area of the initial states $(N_1(0), N_2(0))$ in $(0,1) \times (0,1)$ as shown by the dark dotted region in Fig. 4. For the initial state in the region indicated by the dark dotted region in Fig. 4, two species coexist converging to a periodic orbit (see Fig. 1a). As already shown in Sec. 3.2,

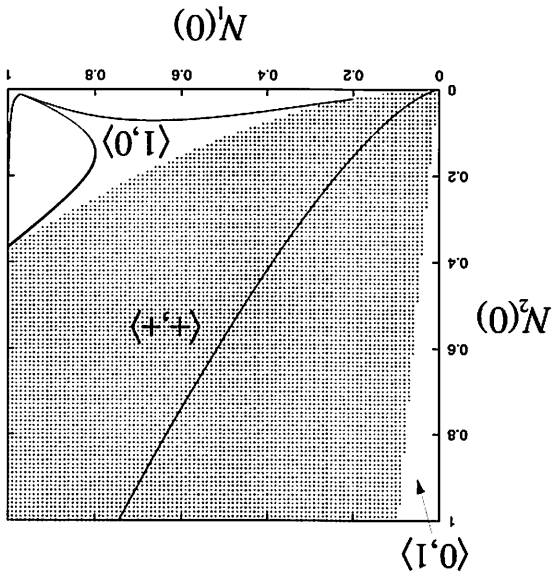


Fig. 4. Dependence of the equilibrium state on the initial state. A numerically obtained result. $p_1 = 10.0$; $p_2 = 15.0$; $m_{12} = 1.38$; $m_{21} = 1.4$; $\tau_- = 0.263$; $\tau_+^* = 0.275$; $\tau_-^{**} = 0.286$. With the initial state in the dark dotted region $(+, +)$, two species can coexist with the interruption of competition, converging to a stable periodic orbit. A numerical trajectory from the initial state $(N_1(0), N_2(0)) = (0.20, 0.02050361)$ is shown, which converges to an unstable periodic orbit. Without the interruption of competition, the system is in a bistable situation, so that one of two species goes extinct depending on the initial state. The solid curve form the origin shows the numerically obtained separatrix in the case without the interruption of competition.

the dark dotted region covers everywhere in $(0, 1) \times (0, 1)$ for $\tau_- > \tau_-^{**}$, since then $(m_{12} > 1$ and $m_{21} > 1$.

As shown in Fig. 4, for the trajectory from the initial state on the boundary between the region of $(+, +)$ and that of $(1, 0)$, our numerical calculations imply again that it converges to a unique unstable periodic orbit.

Fig. 5a-2 demonstrates the τ_- -dependence of the occurrence of the inversion of the competitive dominance which we can numerically observe for the equilibrium state approached from the initial state $(0.01, 0.99)$ with $m_{12} = 1.2$ and $m_{21} = 1.4$. We cannot observe it from the same initial point with $m_{12} = 1.38$ and $m_{21} = 1.4$. The convergence to the coexisting state depends on the initial point as seen from Figs. 5a-1 and a-2. Moreover, the largest amplitude of the periodic variation in case of the coexistence would be realized for a unique value of τ_- .

Figure 6 shows the numerical result about the τ_- -dependence of the inversion of the competitive dominance and the occurrence of the coexistence, measuring the area of the initial state $(N_1(0), N_2(0))$ causing the extinction of one species in $(0, 1) \times (0, 1)$, and the area causing the coexistence. The area of the initial state causing the coexistence appears for τ_- beyond a critical value less than τ_-^{**} beyond which any initial point is attracted to a periodic orbit, that is, a stationary coexistent state.

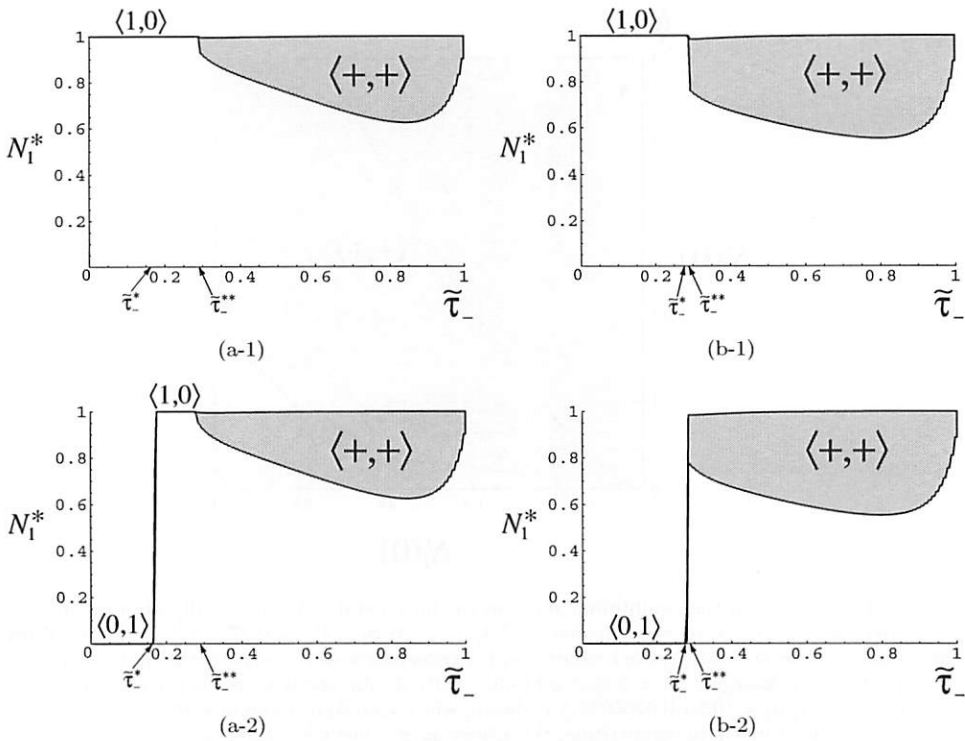


Fig. 5. Dependence of the equilibrium state on the length of the competition interruption. Numerically obtained results. (a-1, 2) $\hat{m}_{12} = 1.2$; $\hat{\tau}_-^* = 0.167$; (b-1, 2) $\hat{m}_{12} = 1.38$; $\hat{\tau}_-^* = 0.275$. Commonly $\hat{m}_{21} = 1.4$ and $\hat{\tau}_-^{**} = 0.286$. (a-1) and (b-1) are for the initial state (0.99, 0.01); (a-2) and (b-2) are for the initial state (0.01, 0.99).

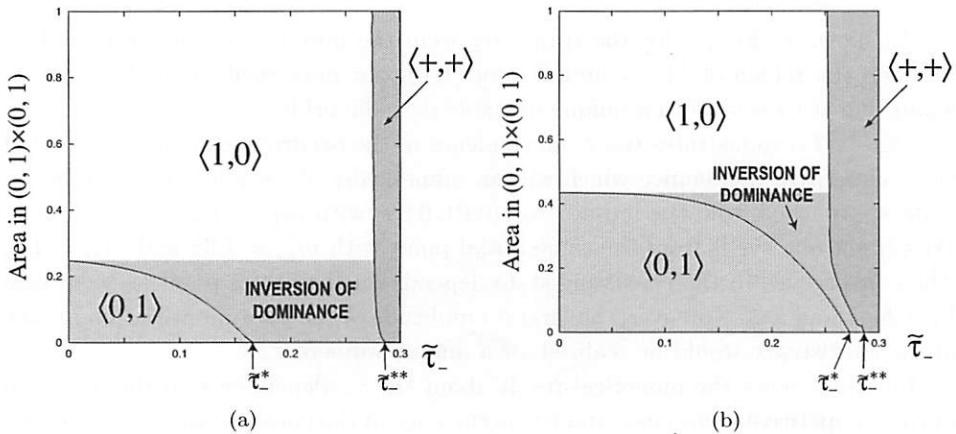


Fig. 6. $\tilde{\tau}_-$ -dependence of the inversion of the competitive dominance and the occurrence of the coexistence. Areas of $\langle 0, 1 \rangle$, $\langle 1, 0 \rangle$ and $\langle +, + \rangle$ in $(0, 1) \times (0, 1)$ are numerically calculated for each value of $\tilde{\tau}_-$. (a) $\hat{m}_{12} = 1.2$; $\hat{\tau}_-^* = 0.167$; (b) $\hat{m}_{12} = 1.38$; $\hat{\tau}_-^* = 0.275$. Commonly $\hat{m}_{21} = 1.4$ and $\hat{\tau}_-^{**} = 0.286$.

As numerically indicated, a set of initial states going to a stationary coexistent state appears even when the extinction state $(0, 1)$ or $(1, 0)$ is locally stable. Especially as shown in Figs. 4 and 6b, for a range of $\tilde{\tau}_-$, we can find that there could exist a tristable situation with locally stable extinction states $(0, 1)$, $(1, 0)$, and locally stable coexistent state.

3.5. Dependence on the competition coefficient

Figure 7 shows a numerical result about the $(\tilde{\tau}_-, \hat{m}_{12})$ -dependence of the extinction and the coexistence. We can see that the inversion of the competitive dominance and the occurrence of the coexistence significantly depend not only on the length of competition interruption, $\tilde{\tau}_-$, but also on the difference between two coefficients \hat{m}_{12} and \hat{m}_{21} . Especially when $\hat{m}_{12} < 1$, that is, when species 1 never extinct, there exists a critical value for $\tilde{\tau}_-$ such that, if $\tilde{\tau}_-$ is below the critical value, species 2 goes extinct from any initial state in $(0, 1) \times (0, 1)$, and if beyond it, the coexistence occurs from any initial state in $(0, 1) \times (0, 1)$. The critical value is given by $\tilde{\tau}_-^{**}$ ($= 0.286$ in case of Fig. 7 with $\hat{m}_{21} = 1.4$). Furthermore, from Fig. 7, even when $\hat{m}_{12} \geq 1$, we can see some other cases with such a critical dependence of the destiny for competing species on the length of competition interruption.

With the numerical result shown in Fig. 7 and theoretical ones obtained in the previous sections, we can finally obtain the result about the $(\tilde{\tau}_-, \hat{m}_{12})$ -dependence of the extinction and the coexistence of species as shown in Fig. 8. We can see that the interruption of competition could make the coexistence occur even when an extinction equilibrium state is locally stable. This could hold in the bistable situation with two extinction equilibrium states $(0, 1)$ and $(1, 0)$ both of which are locally stable. The interruption of competition could change the destiny of competing species.

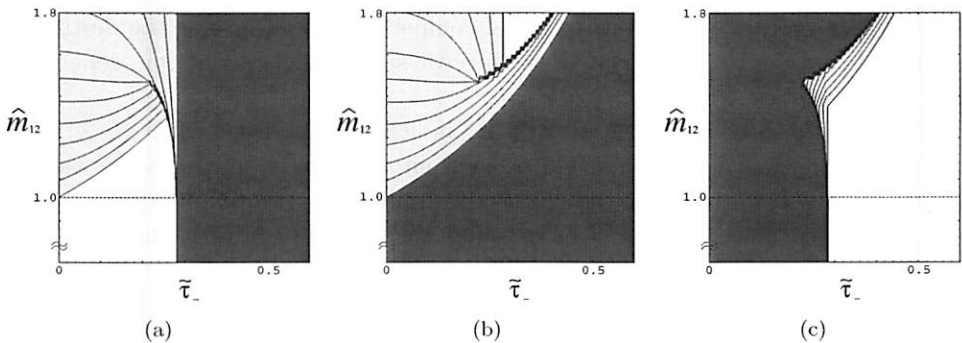


Fig. 7. $(\tilde{\tau}_-, \hat{m}_{12})$ -dependence of the extinction and the coexistence of species with $\hat{m}_{21} = 1.4$, when $\langle m_{21} \rangle = 1$ with $\tilde{\tau}_- = 0.286$. Solid curves give some isopleths numerically obtained for the area of (a) $\langle 1, 0 \rangle$; (b) $\langle 0, 1 \rangle$; (c) $\langle +, + \rangle$. The white (blank) region in each figure indicates when the area covers everywhere in $(0, 1) \times (0, 1)$, and the heavy dark region does when the area does not exist. The light dark region does when the area covers only a part of $(0, 1) \times (0, 1)$. In (b), the boundary curve of the heavy dark region is given by $\langle m_{12} \rangle = \tilde{\tau}_+ \hat{m}_{12} = 1$.

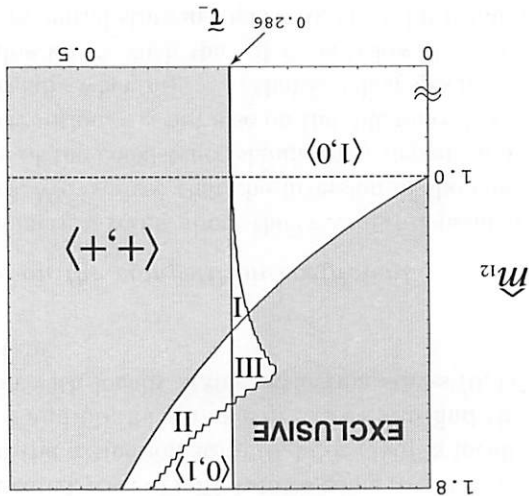


Fig. 8. (τ_-, m_{12}) -dependence of the extinction and the coexistence of species for $m_{21} = 1.4$, when $\langle m_{21} \rangle = 1$ with $\tau_- = 0.286$. For the region EXCLUSIVE, only one species goes extinct, depending on the initial state; For the regions $\langle +,+ \rangle$, $\langle 0,1 \rangle$, and $\langle 1,0 \rangle$, the coexistence, the extinction of species 1, and the extinction of species 2, respectively, occur from any initial state; For the regions I, II, and III, two species coexist from some initial states, while the extinction of species 2, species 1, and one of two, respectively, occurs from the other initial state. Boundary curve between regions II and $\langle +,+ \rangle$, III and I, EXCLUSIVE and $\langle 1,0 \rangle$ is commonly given by $\langle m_{12} \rangle = \tau_+ m_{12} = 1$. Boundaries between regions $\langle 0,1 \rangle$ and II, EXCLUSIVE and III, $\langle 1,0 \rangle$ and I are numerically drawn.

In a bistable case indicated by the region I or II in Fig. 8, the coexistence or the inversion of the competitive dominance occurs, depending on the initial state (see also Figs. 3 and 4). Moreover, we found the tristable case indicated by Figs. 4 and 6b, and by the region III in Fig. 8. In such a case, depending on the initial state, one of two species goes extinct or the coexistence occurs. Further, as indicated by the region $\langle 1,0 \rangle$ or $\langle 0,1 \rangle$, the interruption of competition could inverse the destiny of the extinct species to its survival, or the survival species to its extinction, depending on the initial state.

The existence of regions I, II, and III indicates that, even when $\langle m_{12} \rangle > 1$ or $\langle m_{21} \rangle < 1$, the coexistence could occur from some initial states. So we cannot determine the occurrence of the coexistence only from the temporally averaged competition coefficients. This is the nature of the system (2.1) with the temporally periodic interruption of competition, different from the system without it.

4. Concluding Remarks

Our results indicates that, with a temporally interruptive competition, it could change which species goes extinct, or whether the coexistence occurs even if two competing species cannot coexist without the interruption of competition. The

interruption of competition could change the destiny of competing species, and then the Gause's competitive exclusion principle cannot necessarily hold. Furthermore the possibility of the coexistence between competing species cannot be estimated only from the temporally averaged competition coefficients.

A temporal interruption of the competition could happen, for instance, because of the existence of a period without the niche overlapping which causes the inter-specific competition. A season-dependent change of food or habitat may cause such a non-competitive period. Our results imply that the consequence of a competition may be changed by such an interruption of the competition: the inverse of competitive dominance or the coexistence (also see Seno¹⁴). In a certain long time scale, such an effect of the interruption of competition would drive the exchange of species in a habitat or work to maintain the species diversity.

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Appendix

The *permanence* means that there exists a compact set K in the positive cone of phase space for (N_1, N_2) such that all trajectories in the interior do not exit K . This can be mathematically expressed by the following equivalent condition (for instance, see Hofbauer and Sigmund¹⁵):

There exists a $\delta > 0$ such that

$$\delta > \liminf_{t \rightarrow \infty} N_i^*(t) \quad \text{for } i = 1, 2,$$

whenever $N_i^*(0) < 0$ ($i = 1, 2$).

For the proof of the result about the permanence shown in the main text we use the invariance of $(0, 1) \times (0, 1)$ in the phase plane of (N_1, N_2) without its proof. For the initial state belonging to $(0, 1) \times (0, 1)$, $(N_1(t), N_2(t))$ belongs to $(0, 1) \times (0, 1)$ for any time $t \geq 0$. Since the carrying capacity for each population is now given by 1 for the system (2.3), we consider only the initial state within $(0, 1) \times (0, 1)$, from the viewpoint of mathematical modeling. In this appendix, we show the outline of the proof of the permanence of the system (2.3).

At first, we can prove that the condition $\max\langle m_{12} \rangle, \langle m_{21} \rangle > 1$ is necessary for the permanence. That is, we prove that, if $\max\langle m_{12} \rangle, \langle m_{21} \rangle < 1$, the system (2.3) is not permanent. To prove this, it is necessary and sufficient to show that, if $\langle m_{12} \rangle > 1$, then there exists a solution of $N_1(t)$ with $N_1(0) < 0$ which converges to 0 as $t \rightarrow \infty$.

Next, we can prove the following two features of the system (2.3):

Feature 1. If $\max\langle m_{12} \rangle, \langle m_{21} \rangle > 1$, then the solution with the initial state in

$$R_c = \{(N_1, N_2) \in (0, 1) \times (0, 1) \mid \Phi(N_1, N_2) = N_1^{\rho_2} N_2^{\rho_1} \leq c^{\rho_1 \rho_2}\}$$

goes out of R_c in a finite time, where c is a positive number independent of the initial state.

Feature 2. If $\max\langle m_{12} \rangle, \langle m_{21} \rangle > 1$, then for the solution which passes through a point on $\Phi(N_1, N_2) = N_1^{\rho_2} N_2^{\rho_1} = c^{\rho_1 \rho_2}$ of R_c at $t = t_0 \geq 0$, there exists a positive number γ such that the solution cannot enter a region

$$R_\gamma = \{(N_1, N_2) \in R_c \mid \Phi(N_1, N_2) \leq \gamma \leq c^{\rho_1 \rho_2}\}$$

for any $t > t_0$.

The positive number c in these features can be chosen commonly. Feature 1 shows that the solution goes away from the neighborhood of axes, and Feature 2 does that the solution never goes near the neighborhood of axes once it goes away from it. Therefore, these two features prove the permanence of the system (2.3).