Temporally Interruptive Interaction Allows Mutual Invasion of Two Competing Species Dispersing in Space

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Abstract. With a reaction-diffusion system, we consider the dispersing two-species Lotka-Volterra model with a temporally periodic interruption of the interspecific competitive relationship. We assume that the competition coefficient becomes a given positive constant and zero by turns periodically in time. We investigate the condition for the coexistence of two competing species in space, especially in the bistable case for the population dynamics without dispersion. We could find that the spatial coexistence, that is, the spatially mutual invasion of two competing species appears with two opposite-directed travelling waves if a condition for the temporal interruption of the interspecific relationship is satisfied. Further, we give a suggested mathematical expression of the velocity of travelling waves.

1 Introduction

The spatial distribution of organisms has been attracting empirical/theoretical ecological researches (for review, see [11, 22, 25] and references therein). The spread of an invader species in space could be characterized by some natures of the temporally variable spatial distribution, which is naturally affected by the interaction with the other species: competition,

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predation/parasitism, mutualism, etc.

Gause's competitive exclusion hypothesis says that two species utilizing a common niche for their persistence cannot coexist, so that one of them eventually goes extinct [9]. However, not a few empirical and theoretical researches have indicated that two competing species can coexist even when they utilize a common niche for their persistence, if some environmental factor has a heterogeneity to regulate their competitive relationship: The environmental heterogeneity could allow the coexistence of two species competing for a common niche (for a review, see Chapter 7 of [3]). In such a case, the environmental 'heterogeneity' could be spatial and/or temporal. Indeed, in nature, any interspecific relationship is neither temporally nor spatially homogeneous in time and/or in space. Especially as for the temporal heterogeneity, a seasonal change of niche could cause a temporal variation of the interspecific relationship [3, 14, 15]. What effect does the temporal heterogeneity of an interspecific relationship have on the nature of population dynamics?

Hutchinson [14, 15] discussed the effect of temporal heterogeneity of niche on the competitive relationship, and argued that the temporal heterogeneity allows the coexistence of competing species. Hutchinson's ideas have been elaborated on by many researchers, and discussed the effect of environmental seasonal change, for example, about the food availability on the competing species coexistence (for a review, see [10]). As for theoretical and mathematical researches about the effect of 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, 6, 19, 20, 21]. In those researches, the temporally periodic coefficients are assumed to have positive value, so that the model involves a seasonal change of the strength of competition. Those works showed that such 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, including not only the coexistence but also a tristable situation depending on the initial state (frequently mentioned as the state at which a new species invades).

On the other hand, the temporal variation of spatial distribution of competing species has been studied theoretically with some mathematical models, for example, of the reaction-diffusion system, the cellular automaton, or the integro-difference/differential equations (for a review, see [11]). Specifically with respect to the travelling wave emerging for the Lotka-Volterra type of reaction-diffusion model of two competing species in one-dimensional space, some mathematical analyses have discussed the critical velocity [8, 13, 16, 17, 18]. They analyzed the Lotka-Volterra competition system in the homogeneous space, and presented the mathematical estimation of the velocity of travelling wave. However, some mathematical open problems have been left, especially about the velocity of travelling wave.

In this paper, we consider the dispersing two-species Lotka-Volterra system with a temporally periodic interruption of the interspecific competitive relationship. Two competing populations diffuse in one-dimensional space. We assume that the competition coefficient is constant in a fixed time interval of 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. In the same framework of mathematical model without diffusion, Nakajima *et al.* [19] discussed the condition for the coexistence of two competing species and that for the permanence of the system. In this paper, we discuss the spatial coexistence of two competing species, that is, the mutual invasion to cause a coexisting zone in space, especially in the bistable case for the population dynamics without dispersion. Such a coexisting zone is expanding by two opposite-directed travelling wave fronts at the boundary layers. Their velocities are different from each other, about which we give the suggested mathematical expression of the velocity, making use of numerical results.

Not only for the competitive relationship but also for any other type of interspecific relationship, such a temporal interruption of the interspecific relationship would occur in nature, for example, due to a seasonal separation of niches (habitat, home range, food, etc.) for two species. From a mathematical viewpoint, such a type of temporally variable interspecific relationship can be modelled by introducing a temporally interruptive vanishment of terms which represent the interspecific relationship in the model equations.

We find some interesting natures of such a competition system, distinguished from the Lotka-Volterra competition system with the temporally constant interspecific competitive relationship, although some of them are still mathematically open problems. The spatial coexistence, that is, the spatially mutual invasion of two competing species can occur if a condition for the temporal interruption of the interspecific relationship is satisfied. We demonstrate the possibility of the coexistence between competing species in a common spatial region without the segregation of habitats, which could be realized by a temporal heterogeneity of the interspecific relationship, even for two competing species that cannot coexist in a temporally and spatially stationary/homogeneous environment.

2   Model

2.1   Two Competing Species with Diffusion

We consider the following Lotka-Volterra competition system of two species in one dimensional space:

$$\begin{cases} \dfrac{\partial n_1(x,t)}{\partial t} &= D_1 \dfrac{\partial^2 n_1(x,t)}{\partial x^2} + \left\{ r_1 - \beta_1 n_1(x,t) - \mu_{12}(t) n_2(x,t) \right\} n_1(x,t) \\[2mm] \dfrac{\partial n_2(x,t)}{\partial t} &= D_2 \dfrac{\partial^2 n_2(x,t)}{\partial x^2} + \left\{ r_2 - \beta_2 n_2(x,t) - \mu_{21}(t) n_1(x,t) \right\} n_2(x,t), \end{cases} \tag{2.1}$$

where $n_i(x,t)$ $(i = 1, 2)$ is the population density of species i at position x and time t. Parameters D_i, r_i and β_i $(i = 1, 2)$ are all positive, which respectively mean the diffusion coefficient to indicate the mobility, the intrinsic growth rate to give the maximal reproductive capacity, and the intraspecific competition coefficient to indicate the strength of the density effect on each individual from the others of the same species.

The function of time $\mu_{ij}(t)$ $(i, j = 1, 2; \ i \neq j)$ introduces the interspecific competition between populations of species 1 and 2. In this paper, this function is assumed to be rigorously periodic in time: $\mu_{ij}(t + T) = \mu_{ij}(t)$ for any t (≥ 0) with a given positive constant T. Constant T gives the species-independent period of the temporal variation in the strength of interspecific competition. We assume that the competitive relationship temporally changes in a rigorously periodic manner, because of a seasonal environmental change to cause consequently a seasonal change of the niche utilized by each species.

2.2   Boundary Condition

We consider the system (2.1) on the infinite one dimensional space, $x \in \mathbb{R}$, with the following boundary condition:

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{x \to -\infty} = \begin{pmatrix} \frac{r_1}{\beta_1} \\ 0 \end{pmatrix} \ \text{and} \ \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{x \to +\infty} = \begin{pmatrix} 0 \\ \frac{r_2}{\beta_2} \end{pmatrix} \ \text{for any } t \ (\geq 0),$$

where r_i/β_i $(i = 1, 2)$ is the carrying capacity for species i, that is, the stationary population size of species i without the competing species.

2.3   Initial Condition

We consider our model (2.1) with the following initial condition:

$$n_1(x, 0) = \begin{cases} r_1/\beta_1 & \text{for } x \in (-\infty, 0] \\ 0 & \text{for } x \in (0, +\infty) \end{cases}$$

$$n_2(x, 0) = \begin{cases} 0 & \text{for } x \in (-\infty, 0] \\ r_2/\beta_2 & \text{for } x \in (0, +\infty). \end{cases}$$

Hence, we consider the case of a spatial collapse of two competing populations. In back of the front to the counter population, each population asymptotically has the saturated population density following the carrying capacity, as introduced by the boundary condition given in the previous section.

2.4   Temporally Interruptive Competition Coefficient

In this paper, we consider the two competing species system with a temporal interruption of the interspecific competitive relationship (see Fig. 1). We assume that the competition coefficient μ_{ij} $(i, j = 1, 2; i \neq j)$ is a positive constant in a time interval of length τ_+, while it is zero in another time interval of length τ_-. Besides, we assume that 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. Mathematically
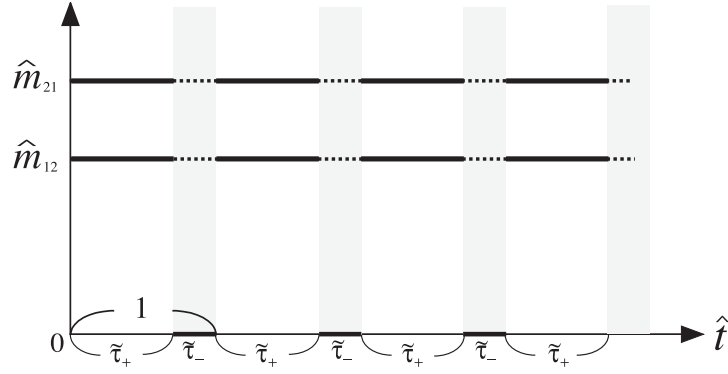
Figure 1: Temporally interruptive competitive relationship for (2.3) with non-dimensionalized parameters, $\hat{m}_{ij} = r_j \hat{\mu}_{ij}/(r_i \beta_j)$ $(i, j = 1, 2; i \neq j)$, $\tilde{\tau}_+ = \tau_+/T$ $(0 < \tilde{\tau}_+ < 1)$ and $\tilde{\tau}_- = 1 - \tilde{\tau}_+$.

in short, we assume the following:

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

where $k = 0, 1, 2, \ldots$, and $\hat{\mu}_{ij}$ $(i, j = 1, 2; i \neq j)$ is a given positive constant.

2.5   Non-dimensionalized System

Making use of the following transformation of variables and parameters, we can reduce the number of parameters to be considered in our mathematical analysis:

$$\tilde{t} = \frac{t}{T}; \quad \tilde{x} = \frac{x}{\sqrt{D_1 T}}; \quad N_i = \frac{\beta_i}{r_i} n_i \quad (i = 1, 2);$$

$$\rho_i = r_i T \quad (i = 1, 2); \quad m_{ij} = \frac{r_j \mu_{ij}}{r_i \beta_j} \quad (i, j = 1, 2; i \neq j); \quad d_{21} = \frac{D_2}{D_1}.$$

With these transformations, we get the following non-dimensionalized system mathematically equivalent to (2.1):

$$\begin{cases} \dfrac{\partial N_1(\tilde{x}, \tilde{t})}{\partial \tilde{t}} = \dfrac{\partial^2 N_1(\tilde{x}, \tilde{t})}{\partial \tilde{x}^2} + \rho_1 \left\{ 1 - N_1(\tilde{x}, \tilde{t}) - m_{12}(\tilde{t}) N_2(\tilde{x}, \tilde{t}) \right\} N_1(\tilde{x}, \tilde{t}) \\ \dfrac{\partial N_2(\tilde{x}, \tilde{t})}{\partial \tilde{t}} = d_{21} \dfrac{\partial^2 N_2(\tilde{x}, \tilde{t})}{\partial \tilde{x}^2} + \rho_2 \left\{ 1 - N_2(\tilde{x}, \tilde{t}) - m_{21}(\tilde{t}) N_1(\tilde{x}, \tilde{t}) \right\} N_2(\tilde{x}, \tilde{t}), \end{cases} \tag{2.3}$$

with the boundary condition

$$\begin{pmatrix} N_1 \\ N_2 \end{pmatrix}_{\tilde{x} \to -\infty} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} \text{ and } \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}_{\tilde{x} \to +\infty} = \begin{pmatrix} 0 \\ 1 \end{pmatrix} \quad \text{for any } \tilde{t} \; (\geq 0),$$
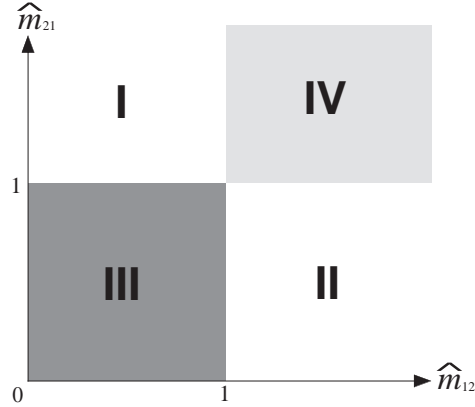
Figure 2: In case of temporally continuous competition without diffusion. For the system given by (2.3), when the diffusion terms are omitted and when $\tilde{\tau}_+ = 1$ with $\tilde{\tau}_- = 0$, the stationary state (N_1^*, N_2^*) is determined only by those constant competitive coefficients $\hat{m}_{ij}$ $(i,j=1,2; i \neq j)$. Region I: Species 2 goes extinct, $(N_1^*, N_2^*) = (1,0)$; Region II: Species 1 goes extinct, $(N_1^*, N_2^*) = (0,1)$; Region III: Two species coexist, $(N_1^*, N_2^*) = ((1 - \hat{m}_{12})/(1 - \hat{m}_{12}\hat{m}_{21}), (1 - \hat{m}_{21})/(1 - \hat{m}_{12}\hat{m}_{21}))$; Region IV: One species goes extinct, while another survives, depending on the initial state. This is the bistable case.

and the initial condition

$$N_1(\tilde{x}, 0) = \begin{cases} 1 & \text{for } \tilde{x} \in (-\infty, 0] \\ 0 & \text{for } \tilde{x} \in (0, +\infty) \end{cases}$$

$$N_2(\tilde{x}, 0) = \begin{cases} 0 & \text{for } \tilde{x} \in (-\infty, 0] \\ 1 & \text{for } \tilde{x} \in (0, +\infty). \end{cases}$$

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

$$m_{ij}(\tilde{t}) = \begin{cases} \hat{m}_{ij} & (k \leq \tilde{t} < k + \tilde{\tau}_+) \\ 0 & (k + \tilde{\tau}_+ \leq \tilde{t} < k + 1) \end{cases} \quad (i,j=1,2; i \neq j),$$

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

3   Analysis

3.1   The Case Without Diffusion

Lotka-Volterra two species competition system (2.1) without diffusion (i.e. $D_1 = D_2 = 0$) and with a temporally interruptive competitive relationship same as (2.2) was studied by

Nakajima *et al.* [19] according to the species coexistence and the permanence. Especially, they analyzed the effect of interruption of competitive relationship in case that, if the competition is temporally kept constant without any temporal interruption, the system is in the bistable situation, that is, one of two species goes extinct and another persists depending on the initial state (see Fig. 2). With numerical calculations and some analytical arguments, they showed the following dynamical natures brought by the interruption of competitive relationship:

- For sufficiently large $\tilde{\tau}_-$, there appears a set of initial states with which the coexistence occurs in a periodic oscillation (Fig. 3(a)).

- For an intermediate range of $\tilde{\tau}_-$, there appears a set of initial states with which one species goes extinct although it is persistent if the competition is temporally kept constant (see Fig. 3(b)). In short, the inversion of which species goes extinction occurs.

- For sufficiently small $\tilde{\tau}_-$, for any initial state, the equilibrium state is identical to that in case with temporally constant competitive relationship.

- The *permanence* of system can be realized by the interruption of competitive relationship, where the *permanence* means that there exists such a compact set K in the positive cone of phase space for (N_1, N_2) that all trajectories in the interior do not exit K. This is equivalently expressed by the following condition (for instance, see [12]):

  There exists a $\delta > 0$ such that

  $$\delta < \liminf_{t \to \infty} N_i(t) < \infty \quad \text{for } i = 1, 2,$$

  whenever $N_i(0) > 0$ $(i = 1, 2)$.

In our case, the permanence is determined by $\tilde{\tau}_-$ and the competition coefficients ($\hat{m}_{12}$ and $\hat{m}_{21}$). Nakajima *et al.* [19] proved the following theorem:

> *If and only if the following condition is satisfied, the system is permanent, so that two species coexist independently of the initial state,*

$$\max\left[\langle m_{12}\rangle, \langle m_{21}\rangle\right] < 1. \tag{3.4}$$

The left side of inequality (3.4) means that both of the time-averaged competition coefficients $\langle m_{ij}\rangle$ $(i, j = 1, 2; \ i \neq j)$ is less than 1. This condition for the permanence (3.4) gives the following critical value $\tilde{\tau}_-^{\dagger}$ for $\tilde{\tau}_-$ in terms of the permanence:

$$\tilde{\tau}_-^{\dagger} = 1 - \frac{1}{\max\left[\hat{m}_{12}, \hat{m}_{21}\right]}. \tag{3.5}$$

When and only when $\tilde{\tau}_- > \tilde{\tau}_-^{\dagger}$, the permanence can hold.
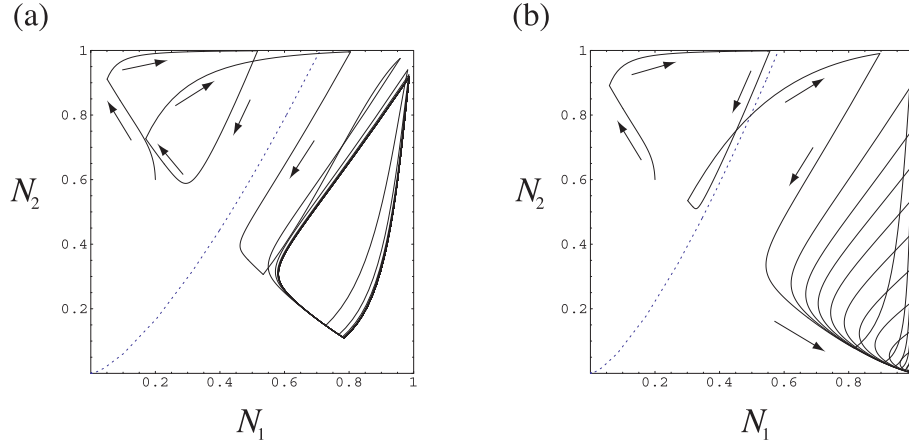
Figure 3: Numerical examples of the trajectory in the phase plane of (N_1, N_2) in a bistable case for the Lotka-Volterra two species competition system without diffusion and with temporally interruptive competitive relationship. Dashed curve is the numerically drawn separatrix in the case without the interruption of competition. With the periodic interruption of competition, (a) a trajectory converges to a coexistent state with $\hat{m}_{21} = 1.4$; (b) a trajectory converges to the state $(1, 0)$ with $\hat{m}_{21} = 1.5$. In both cases, $(N_1(0), N_2(0)) = (0.2, 0.6)$; $\rho_1 = 10.0$; $\rho_2 = 15.0$; $\hat{m}_{12} = 1.36$; $\tilde{\tau}_- = 0.3$. Without the interruption of competition, the trajectory would converge to the state $(0, 1)$, because the initial point is above the separatrix in the corresponding case.

3.2   Spatial Dynamics

Numerical calculations

In this paper, we show some interesting results given by numerical calculations for (2.3) in which we commonly used parameter values $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$. Parameter values except for d_{21} correspond to the bistable case for the population dynamics with temporally continuous competition without diffusion, that is, when $\hat{m}_{12} > 1$ and $\hat{m}_{21} > 1$ (see Fig. 2). The value of the diffusion coefficient d_{21} is chosen to realize the standing distribution when the competition coefficients are temporally constant, making use of the mathematical result by Rodrigo and Mimura [23, 24].

Profile of travelling wave

Numerical calculations show the existence of some travelling wave solutions which have a temporally periodic change of the profile (see Fig. 4). After a transition state affected by the initial distribution, the spatial distribution of each population density appears to converge asymptotically a travelling wave which has a temporally periodic change of its shape.

    In case of relatively small $\tilde{\tau}_-$ $(= 1 - \tilde{\tau}_+)$, when the period with no competition is relatively short, the wave shape oscillates due to the temporal change of competitive coefficients. In case of Fig. 4(a), the spatial distribution of population density shows a temporal shift to
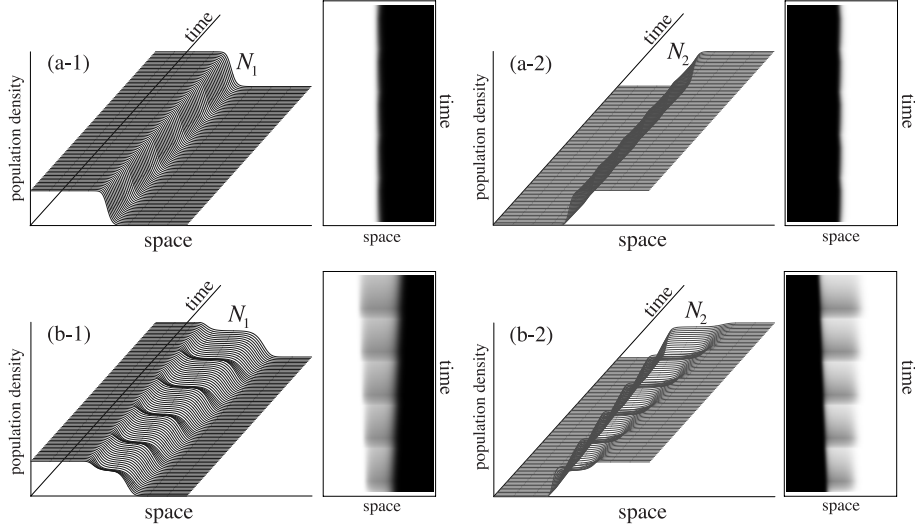
Figure 4: Profile of travelling waves after sufficient transient period from the initial distribution. The 3D drawings and the corresponding density plots by numerical calculations. In the density plot, the darker plot indicates the lower population density. (a-1, a-2) In case of $\tilde{\tau}_- = 0.3$. Both fronts appear to oscillate back and forth and eventually go to left with a common time-averaged velocity. The spatial distribution of species 1 expands while that of species 2 shrinks. (b-1, b-2) In case of $\tilde{\tau}_- = 0.75$. The wave front for species 1 goes to right while that for species 2 does to left. Spatial distributions of both species expand. In case of (b-1, b-2), population densities in the middle region between two fronts appear plateau (spatially constant) distribution. For both calculations, $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$.

left. This means the spatial invasion of species 2 into the habitat of species 1, while species 1 shrinks its spatial distribution due to the competitor's spatial invasion. As illustrated by Fig. 5(a), after a transition state, each travelling wave at time $t + T$ appears to have a shape approximatedly identical to that at time t, that is, the ultimate wave shape temporally changes and periodically repeats the same with period T. In case of Fig. 5(a), it seems that two wave fronts move parallel in terms of the time-averaged location. About this point, we will consider in detail the temporal variation of the location of wave front in the next section.

In case of sufficiently large $\tilde{\tau}_-$ larger than a certain critical value $\tilde{\tau}_-^*$, when the temporal break of the competition is relatively long, two wave fronts go in direction opposite to each other in terms of the time-averaged location after a transient period (see Fig. 4(b)). In this case, we can say that the mutual invasion of the competitive species occurs. In such a case as indicated by Fig. 4(b), the population density in the region between two wave fronts appears to have a quasi-plateau (spatially almost constant) distribution, which shows a temporally periodic oscillation. The movement of two wave fronts expands such a zone of the quasi-plateau distribution. This means that the coexistent zone temporally expands. Also in this case, after a transition state, each spatial distribution of the population density appears to converge asymptotically a travelling wave which has a temporally periodic change
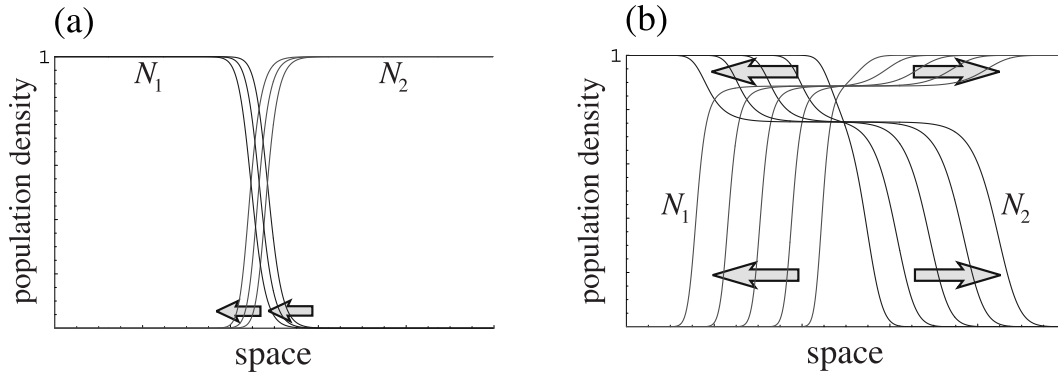
Figure 5: Temporal snapshots of the profile of travelling waves. Comparison at different temporal moments by period T. Numerically drawn. It is demonstrated that the shape of travelling front is identical between two moments different by period T, that is, the shape has a temporally periodic nature with period T. (a) In case of $\tilde{\tau}_- = 0.3$. Both fronts appear to go to left with a common time-averaged velocity. Spatial distribution of species 1 expands while that of species 2 shrinks. (b) In case of $\tilde{\tau}_- = 0.75$. The wave front for species 1 goes to right while that for species 2 does to left. Spatial distributions of both species expand. In case of (b), it is clear that population densities in the middle region between two fronts appear plateau (spatially constant) distribution. For both calculations, $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$.

of the shape, as illustrated by Fig. 5(b).

Location of wave fronts

To examine the direction and the velocity of the wave front movement, which is affected by the nature of temporally variable competitive relationship, we temporally trace the location of wave front at a given (low) value of the population density N_i ($i = 1, 2$), making use of numerical calculations. The result is illustrated in Fig. 6.

From numerical calculations with $\tilde{\tau}_- = 0.0$, when every competition coefficient is temporally constant so that the competition relationship always exists, we see that the front stops moving and realizes the standing distribution after a transient period affected by the initial distribution, as shown in Fig. 6(a). This is the expected result due to our choice of the parameter values as mentioned in the first part of this section.

In case of relatively small $\tilde{\tau}_-$, when the period with no competition is relatively short, the wave front oscillates due to the temporal change of competitive coefficient. Further, the time-averaged location of wave front moves as shown in Fig. 6(b) (see also Figs. 4(a) and 5(a)). We note that the time-averaged locations of two wave fronts become parallel after a transient state. This means that the time-averaged velocities of two wave fronts asymptotically approach a common constant. This type of the time-averaged parallel movement of wave fronts appears for $\tilde{\tau}_-$ less than a certain critical value $\tilde{\tau}_-^*$, although the time-averaged velocity depends on the value of $\tilde{\tau}_-$.
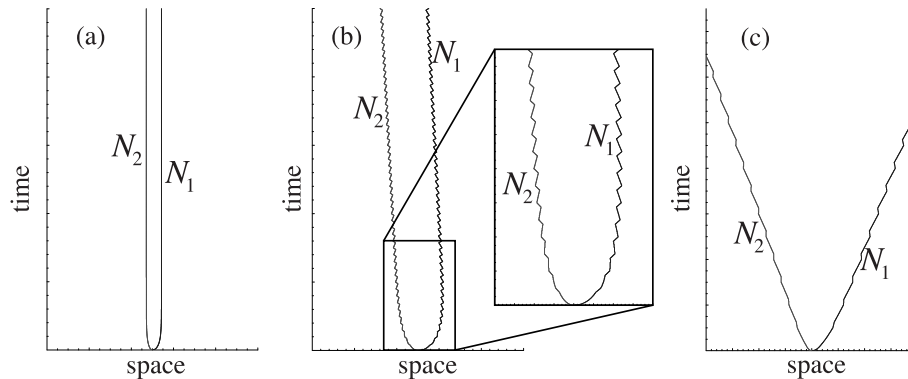
Figure 6: Temporal variation of the location of wave fronts. Numerically drawn. (a) In case of $\tilde{\tau}_- = 0.0$, when the competition coefficients are temporally constant, so that the competition relationship always exists. After a transient period affected by the initial distribution, the front stops moving and realizes the standing distribution. (b) In case of $\tilde{\tau}_- = 0.3$. Early transient variation is shown magnified. Both fronts appear to oscillate and eventually go to left with a common time-averaged velocity. The spatial distribution of species 1 expands while that of species 2 shrinks. (c) In case of $\tilde{\tau}_- = 0.75$. The wave front for species 1 goes to right while that for species 2 does to left. Spatial distributions of both species expand. For all calculations, $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$.

For $\tilde{\tau}_-$ larger than a certain critical value $\tilde{\tau}_-^*$, when the period with no competition is sufficiently long, the time-averaged locations of two wave fronts go in direction opposite to each other after a transient state (Fig. 6(c), Figs. 4(b) and 5(b)). In this case, we can say that the mutual invasion of competing species occurs. The time-averaged velocity asymptotically approaches a constant, although the magnitude depends on the species. In such a case, as illustrated in Fig. 5(b), the population densities in the zone between two wave fronts appear a quasi-plateau (spatially almost constant) distribution, and show a temporally periodic oscillation. The movement of two wave fronts expand such a zone of the quasi-plateau distribution. Since the time-averaged velocity asymptotically approaches a constant, the expansion of such a zone has a time-averaged constant speed after a transient state.

Time-averaged velocity

As indicated in Fig. 6, the wave front appears to have a time-averaged *constant* velocity of its movement after a transient state from the initial distribution. So we numerically examined the time-averaged velocity of the wave fronts of two competing populations after a sufficiently long initial period. As shown in Fig. 7, it is clearly indicated that there exists a critical value $\tilde{\tau}_-^*$ for $\tilde{\tau}_-$, below which the temporally interruptive competition causes a time-averaged movement of the wave fronts in a common direction which velocity would depend also on the difference of diffusion coefficients for two populations (i.e. the value of d_{21} in the non-dimensionalized system (2.3)). Numerical calculations indicate that, in such a case,
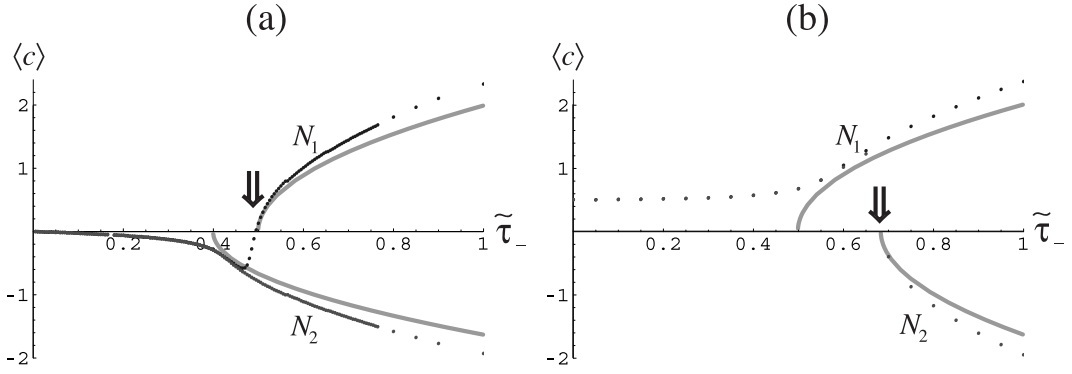
Figure 7: $\tilde{\tau}_-$-dependence of the time-averaged velocity $\langle c \rangle$ of wave fronts. Numerical plots for different $\hat{m}_{21}$: (a) $\hat{m}_{21} = 5.0/3.0$; (b) $\hat{m}_{21} = 19.0/6.0$. Commonly for both cases, $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, and $\hat{m}_{12} = 2.0$. The arrow indicates the critical value $\tilde{\tau}_-^*$ of $\tilde{\tau}_-$ with respect to the mutually spatial invasion of competing species. The thick gray curves indicate the theoretically suggested time-averaged velocities $\langle c_1 \rangle$ and $\langle c_2 \rangle$ given by (3.6) and (3.7) with the time-averaged competition coefficient $\langle m_{ij} \rangle = \hat{m}_{ij}(1 - \tilde{\tau}_-)$ $(i, j = 1, 2;\ i \neq j)$.

the time-averaged velocities of the wave fronts equal to each other, which means a parallel movement of the two wave fronts in the same direction as illustrated in Fig. 6(b).

With $\tilde{\tau}_-$ beyond the critical value $\tilde{\tau}_-^*$, the mutual invasion occurs in space, and the two wave fronts go in direction opposite to each other in terms of time-averaged location after a transient period from the initial distribution (see also Figs. 4(b), 5(b) and 6(c)), that is, the two wave fronts have time-averaged velocities different in sign.

This type of "bifurcation" in the time-averaged velocity appears even with another set of parameter values as illustrated in Fig. 7(b). This is a case when the spatial distribution of species 2 expands while that of species 1 shrinks if the competition always exists between two species (i.e. $\tilde{\tau}_- = 0$). In contrast, in case of Fig. 7(a), if the competition always exists, an immobile (i.e. standing) spatial distribution fronts appear (see also Fig. 6(a)).

Theoretical implications

In case of $\tilde{\tau}_- = 1.0$, two populations are independent of each other because of no interspecific relationship between them. Each wave front asymptotically approaches a temporally constant shape of the travelling wave with a constant velocity, which is so-called the Fisher type of travelling wave solution. The asymptotic velocity is $2\sqrt{\rho_1}$ and $-2\sqrt{d_{21}\rho_2}$ respectively for N_1 and N_2 [7] (for review, see [22] and its references). The competition could reduce the time-averaged velocity compared to that for the Fisher type of travelling wave, as indicated in Fig. 7 with $2\sqrt{\rho_1} = 2.0$ and $-2\sqrt{d_{21}\rho_2} = -1.63$. Although the numerically estimated time-averaged velocity in Fig. 7 appears beyond that for the Fisher type, it may occur due to some numerical artifacts to estimate the time-averaged velocity.

Further, for the case of $\tilde{\tau}_- < 1.0$, we have a theoretical cue to discuss the numerical

results more detail. When $\tilde{\tau}_- = 0$, that is, when the competitive reaction always exists, making use of the marginal stability analysis [1], we have the following critical velocities below which no travelling wave solution exists [8]:

$$c_1 = 2\sqrt{\rho_1(1 - \hat{m}_{21})} \qquad \text{for species 1;}$$

$$c_2 = -2\sqrt{\rho_2 d_{21}(1 - \hat{m}_{12})} \qquad \text{for species 2,}$$

only if $\hat{m}_{21} < 1$ and $\hat{m}_{12} < 1$ respectively. Hence, in our case, let us consider the following theoretically suggested time-averaged critical velocities to compare with the numerical results:

$$\langle c_1 \rangle = 2\sqrt{\rho_1(1 - \langle m_{21} \rangle)} \qquad \text{for species 1;} \tag{3.6}$$

$$\langle c_2 \rangle = -2\sqrt{\rho_2 d_{21}(1 - \langle m_{12} \rangle)} \qquad \text{for species 2,} \tag{3.7}$$

where $\langle m_{ij} \rangle = \hat{m}_{ij}(1 - \tilde{\tau}_-)$ $(i, j = 1, 2; \ i \neq j)$ is the time-averaged competition coefficient. As a result, shown in Fig. 7, numerical calculations give well-matched results compared to these theoretically suggested time-averaged critical velocities, although the numerically obtained time-averaged velocities appear beyond them in magnitude. These numerical results may include some numerical artifacts already mentioned above.

As for the case when $\hat{m}_{21} > 1$ and $\hat{m}_{12} > 1$ for $\tilde{\tau}_- = 0$, that is, when $\langle m_{21} \rangle > 1$ and $\langle m_{12} \rangle > 1$ in our model, we could not find any theoretical cue applicable for our numerical results. As implied by [13], when the interspecific competition is stronger than the intraspecific competition, that is, when $\hat{m}_{21}\hat{m}_{12} > 1$ for $\tilde{\tau}_- = 0$ or when $\langle m_{21} \rangle \langle m_{12} \rangle > 1$ in our model, these theoretically obtained critical velocities would not be attainable and some other velocity would be realized. Indeed, travelling waves emerge with a constant time-averaged velocity even when $\langle m_{21} \rangle \langle m_{12} \rangle > 1$ in our model, as indicated by Fig. 7.

Comparison to the case without diffusion

From numerical calculations for the diffusion system (2.3), as shown in Fig. 7, we note that the critical value $\tilde{\tau}_-^\dagger$ given by (3.5) would correspond to the critical value $\tilde{\tau}_-^*$ for the diffusion system (2.3), since the corresponding numerical value of $\tilde{\tau}_-^*$ in numerical calculations appeared to coincide with the critical value $\tilde{\tau}_-^\dagger$: $\tilde{\tau}_-^* = \tilde{\tau}_-^\dagger$. This is just a conjecture at present, and hence is an open mathematical problem to be considered in the next step of this research. Indeed, as shown in Fig. 8, numerical calculations showed a d_{21}-dependence of the time-averaged velocity of the travelling wave and subsequently the possibility of the mutually spatial invasion, although we cannot deny at present the possibility that it may be caused by some numerical artifacts.

In case of the mutual invasion for the diffusion system (2.3), as shown in Fig. 9, we found that the population densities in the middle region between two travelling fronts appear plateau (spatially constant) distribution, and show a temporally periodic oscillation. Since the spatially constant distribution indicates that the contribution of the diffusion to
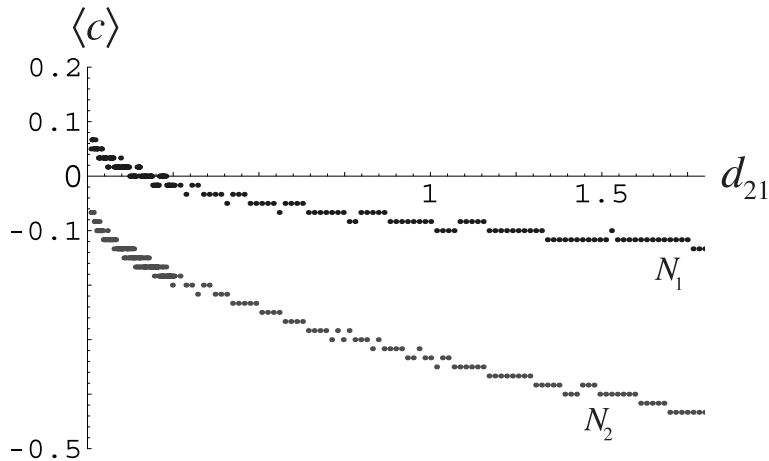
Figure 8: d_{21}-dependence of the time-averaged velocity of travelling wave, numerically calculated with $\tilde{\tau}_- = 0.35$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$. The time-averaged competition coefficient $\langle m_{ij} \rangle = \hat{m}_{ij}(1 - \tilde{\tau}_-)$ $(i, j = 1, 2; \ i \neq j)$ is beyond 1 for both species.

the temporally periodic oscillation of population density would be negligible, such a temporally periodic oscillation in the middle region between travelling fronts could be regarded to correspond to the periodic oscillation in the case without diffusion (i.e. the periodic orbit in the phase space. See Fig. 3(a)). In this sense, we could imply that at least $\tilde{\tau}_-^* \geq \tilde{\tau}_-^\dagger$, because the mutually spatial invasion occurs with such a zone of the plateau distribution of population density.

4 Concluding Remarks

Analyzing the dispersing two-species Lotka-Volterra system with temporally periodic interruption of interspecific competitive relationship, we demonstrate that temporally interruptive competition can allow a mutual invasion of two competing species dispersing in space, so as to establish a zone of coexistence.

For a snapshot of the spatial distribution in case of the mutual invasion, we can classify the spatial distribution into three zones (Fig. 9, also see Figs. 4(b), 5(b) and 6(c)): species 1 dominant zone (resident region of species 1), species 2 dominant zone (resident region of species 2), and coexistent zone (interspecific reaction-elicited region). Especially in our model, population densities appear a temporally periodic oscillation within the coexistent zone, due to the temporally periodic variation of competitive relationship. Since such a temporally periodic variation is involved only in the competitive relationship, the temporally periodic oscillation of population density could be observed only in the coexistent zone. If a seasonal change of the environment or the animal behavior affects only some features of an interspecific relationship, this type of spatially restricted seasonal variation of population density would be observed.
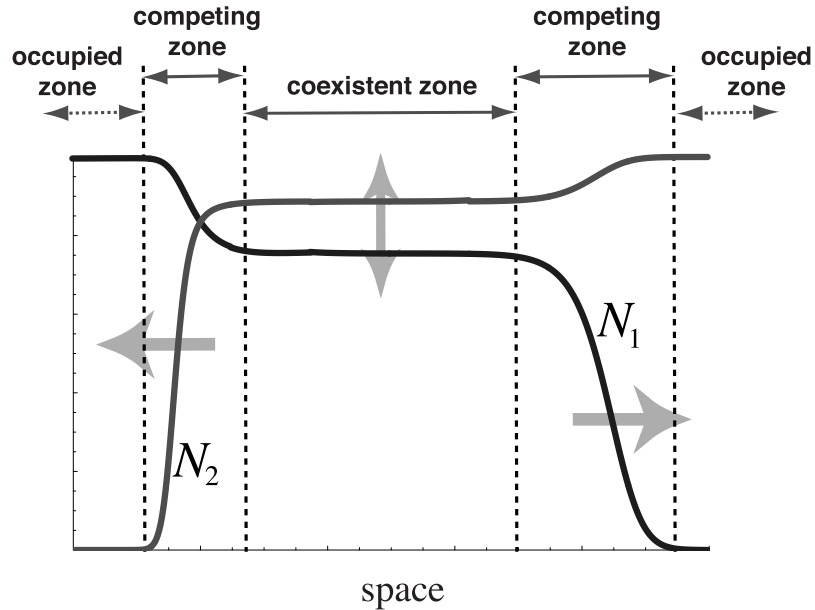
Figure 9: A snapshot of the travelling wave profile. Numerically drawn in case of the mutually spatial invasion, with $\tilde{\tau}_- = 0.75$, $d_{21} = 1.0/3.0$, $\rho_1 = 1.0$, $\rho_2 = 2.0$, $\hat{m}_{12} = 2.0$ and $\hat{m}_{21} = 5.0/3.0$.

Species coexistence in space was frequently discussed from the viewpoint of the spatial heterogeneity: shelter, buffer, or reserver etc [3]. Alternatively it was discussed also from a niche separation/differentiation [2, 4]: a subsequent segregation of habitats after an inter-specific reaction. In this paper, we demonstrated the possibility of the coexistence between competing species in a common spatial region without the segregation of habitats, which could be realized by a temporal heterogeneity of the interspecific relationship, even for two competing species that cannot coexist in a temporally and spatially stationary/homogeneous environment (e.g. in an experimental setting). In some cases, the spatial heterogeneity and/or the niche separation would not be essential for the competing species' coexistence in nature. In our model, the condition for the occurrence of such a coexistence in space is determined by the time-averaged strength of competition, although the time-averaged velocity of the subsequently emerging travelling wave, that is, the time-averaged velocity of the expanding/shrinking resident-occupied region significantly depends on the detail of parameter values. So a temporal expansion/shrink of a species habitat could not be dis-cussed only from the time-averaged nature of population dynamics, while the possibility of the coexistence would be determined only from it.

   We examined the time-averaged velocity with numerical calculations for our dispersing two-species Lotka-Volterra system with a temporally periodic interruption of the interspecific competitive relationship. Dependence of the time-averaged velocity on parameters in our model suggests some mathematically open problems. In fact, even in case of the two-species Lotka-Volterra competition system with constant parameters, the velocity of travelling wave

solution is still a mathematically open problem (for instance, see [18]).

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