

**Persistence of Two-species System**  
**with**  
**Temporal Intermittence of Competitive Interaction**

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Kaori YONEJIMA

95251853

*Department of Information and Computer Sciences, Faculty of Science*  
*Nara Women's University*  
*Kita-uoya-nishi-machi, Nara, 630-8506*  
*JAPAN*

## 論文概要

# 間欠的時間変動を伴う種間競争関係下にある 2種系の絶滅と存続

奈良女子大学理学部情報科学科  
95251853 米島香織

生物はひとつの個体で生活しているわけではない。集団をつくって生活しているのが普通である。植物は、光を求め互いに重なり合わないよう葉や根を張るが、隣の個体の陰になってしまったものは成長しにくくなる。動物の場合にも、同じ種類の食物を利用したり、限られた地域を住み場所として生息しているときは、ある種が生息することで他の種の成長や繁殖などを妨げることになる。このように、生物が互いに迷惑をかけあう、つまり成長速度や増殖率に悪影響を及ぼし合うことは、競争 (competition) と呼ばれ、同種個体間だけでなく異なる種の間でも生じる [1]。

また、生態学にはニッチ (niche) という概念がある。この言葉に対しては生態的地位という日本語訳が使われているが、これはある種の生活の場とか、ある種の適応の全体をあらわす概念で、その種がどの種類の食物を食べるか、どこに住むかなどで特徴づけられる [2, 3, 4]。このニッチの概念から、「完全に同じニッチ関係をもつ2種の生物は、共存し続けることはできず、どちらか一方が絶滅する」という競争排除則 (ガウゼの法則) が生まれた。この法則については、競争種について、1925, 1926年、ロトカとボルテッラによる理論 (後述) が出た後、1932年、ガウゼによる酵母菌を用いた詳細な実験によってこの排他性の予測が確かめられた [2, 5]。このように、生物のニッチと種間競争関係の間には密接な関係がある。

そこで、互いに競争関係にある2種の個体群密度の変動を考えよう。まず、一方の種が存在しない場合、それぞれの種は種内での密度効果のみに依存して個体群の増殖率が決まると、個体群密度の時間的変化が式 (1) のロジスティック方程式 (logistic equation) [2] に従うものと仮定する。

ここに、生息に必要な資源をめぐる種間競争を導入するためには、一方の種の存在によりもう一方の種の増殖率が下がるような効果を考えなければいけない。本論文では、2種の生物の増殖率が互いに競争相手の個体群密度にも比例して低下すると仮定する [2, 6]。すなわち、それぞれの個体群密度の時間的変化を式 (2) もしくは式 (3) によって数理モデリングする。式 (2) や (3) によるモデルはロトカ・ボルテッラの競争モデル (Lotka–Volterra competition model) と呼ばれている。

競争の方程式 (3) による個体群密度時間変動の挙動はパラメータ  $\theta$ ,  $m_{12}$ ,  $m_{21}$  に依存して次の4つの場合に分類されることが分かっており、2種が共存、もしくは、どちらかの種だけが生き残るという解析結果が導かれる (Figs. 1, 2 参照)。

本論文では、種間競争の時間的間欠性が種の絶滅と存続に及ぼす影響についての数理生物学的考察を行う。2種間に種間競争関係が存在するシーズン (競争シ-

ズン)と種間競争関係がないシーズン(非競争シーズン)があるものとする。2種が種間競争を伴うかどうかは、ニッチがオーバーラップするかしないかに依存し、非競争シーズンは、ニッチが異なり、それぞれの種が独立して生息していると考えることができる。また、数理モデリングにおいては、この二つのシーズンは、交互に永続的に訪れるものと仮定し、このような時間変動を伴う競争を、間欠的種間競争と呼ぶことにする。

2種の個体群密度の時間的変化が式(3)で与えられているとすると、間欠的種間競争は、種間競争係数 $m_{12}$ と $m_{21}$ に関する時間的変動を与えることによって数理モデリングに導入することができる。競争シーズンの間は、種間競争係数 $m_{12}$ と $m_{21}$ は正の定数とし、非競争シーズンの間は、種間競争係数 $m_{12}$ と $m_{21}$ はゼロとする。

特に、種間競争が永続的である場合に関する式(3)の解析結果において、種1が絶滅するか種2が絶滅するかが初期状態に依存して決定されているという場合、すなわち、2つの平衡状態が双安定に存在する場合に着目する。数値計算のパラメータをこの場合に相当するように与え、間欠的種間競争が十分続いた後の種の絶滅と存続に関する数値計算による解析を行った。この解析から、間欠的種間競争関係下においては、2種の個体群密度の初期状態に依存して、永続的競争関係下における存続性の逆転が起こるとということが分かった。言い換えれば、競争関係に間欠性があることによって、永続的な競争関係下では、種 $i$ が生き残り種 $j$ が絶滅するという状態が、競争関係に間欠性があることによって種 $j$ が生き残り種 $i$ が絶滅する状態に入れ替わるということである。さらに、ある間欠的種間競争下においては、2種の個体群密度初期状態に依存して、2種の共存も起こり得るとということが分かった(Fig. 4参照)。

非競争シーズンの長さへの存続性の依存性についての数値計算による解析の結果、存続性の逆転は、非競争シーズンの長さが長くなるほど起こり易くなるが、その起こり易さには上限があることが分かった。また、競争係数 $m_{12}$ と $m_{21}$ の差がより小さい場合には、存続性の逆転が起こるために必要な非競争シーズンの長さの最小値が大きくなることも示唆された(Figs. 5, 6)。

非競争シーズンの長さの2種共存への依存性についての数値計算による解析の結果、2種の共存は、非競争シーズンの長さがある臨界の長さを越えると起こることが分かった。また、競争係数 $m_{12}$ と $m_{21}$ の差がより小さい場合には、2種共存が起こるために必要な非競争シーズンの長さの最小値が小さくなることも示唆された。さらに、初期値への依存性はあるが、存続性の逆転と2種共存は、非競争シーズンの長さについてある狭い値域でしか同時には起こらないことも分かった(Figs. 7, 8参照)。

さらに、2種の競争係数 $m_{12}$ と $m_{21}$ の差への依存性についての数値計算による解析も行った。この解析の結果から、種間競争が永続的である場合の式(3)において、種1が絶滅するか種2が絶滅するかが初期状態に依存して決定されている場合は、2種の競争係数 $m_{12}$ と $m_{21}$ の差が大きければ大きいほど、存続性の逆転が起こり得る非競争シーズンの範囲が広がることが分かり、それに伴い、2種の共存は、ある程度、間欠性が強まらなければ起こらないということが分かった。また、種間競争が永続的である場合の式(3)において、種1が絶滅するか種2が絶滅するかが初期値に依存せずに定まる場合は、非競争シーズンの長さがある臨界の長さを越えると2種の共存が起こり得るとということが分かった。さらに、競

争シーズンの長さとは非競争シーズンの長さの差によって、存続性の逆転のみが起こる場合と、存続性の逆転と共存が起こり得るという場合があることがわかった (Fig. 9 参照)。競争シーズンの長さとは非競争シーズンの長さによって、ある間欠的種間競争関係下においては、存続性の逆転と共存が起こる 2 種の個体群密度初期状態の範囲がかわることも分かった (Fig. 10 参照)。

本論文では、間欠的種間競争は 2 種のニッチがオーバーラップするかしないかに依存して起こると仮定した。これは例えば、季節変動によって種が食べる餌の種類が変わるとか、棲む場所が変わるなどと考えることができる。2 種の個体群の間の競争関係の間欠性は、渡り鳥がある一定の期間ある湖にきて、定住している鳥と同じ湖内で暮らしているとする、渡り鳥がその場所を離れる期間の長さによって測ることができると考えられる。たとえば、永続的に渡り鳥がその湖にいると渡り鳥の方が絶滅してしまうという場合、渡り鳥がその湖を離れる期間が長い、つまり、渡りをする場所までが遠ければ、渡り鳥は定住している鳥と共存できる可能性がある。また、渡り鳥がその湖を離れる期間が中程度の長さ、つまり、渡りをする場所がある程度近ければ、渡り鳥と定住している鳥との競争の強弱関係が逆転して、渡り鳥が生き残り、定住している鳥が絶滅するという生き残る種の逆転が起こり得る。つまり、競争関係にある渡り鳥の渡りの特性に依存してその湖に定住している鳥の種が減ることがあり得る。一方、永続的に渡り鳥がいると定住している種の方が絶滅してしまうという場合、渡り鳥がその湖を離れる期間が長い、つまり、渡りをする場所までが遠ければ、定住している鳥は渡り鳥と共存できる可能性がある。また、渡り鳥がその湖を離れる期間が中程度の長さ、つまり、渡りをする場所がある程度近ければ、定住している鳥と渡り鳥の競争の強弱関係が逆転して、定住している鳥が生き残り、渡り鳥が絶滅するという定住種の強い存続性が現われ得る。

本来の競争の強弱とどちらの種が絶滅するかという結果に基づく競争関係の強弱というのは、2 種間の競争関係の間欠性によって異なり得ることが示唆された。間欠性によるこのような存続性の逆転は長いスパンでみた種の間入れ替わり関わり得ると考えることができるかもしれない。

# 1 Modeling

## 1.1 Lotka-Volterra Two-species Competition System

We consider two populations which inhabit in the common habitat region. Without any inter-specific interaction between them, we now assume that the *intra*-specific competition regulates each population independent of each other. We introduce such density-dependent regulation of population by the following logistic type of growth:

$$\frac{dN_i(t)}{dt} = \varepsilon_i N_i(t) - \lambda_i \{N_i(t)\}^2 \quad (i = 1, 2), \quad (1)$$

where  $N_i(t)$  is the population density of species  $i$  at time  $t$ .  $\varepsilon_i$  is the intrinsic growth rate for the population growth of species  $i$ .  $\lambda_i$  is the coefficient of intra-specific competition for the population growth of species  $i$ .

Now, let us consider the *inter*-specific interaction between these two species in terms of a common niche. We assume such competitive interaction that the net growth rate of population size of one species becomes lower when another species coexists in the same niche than when it does not. We consider the following Lotka-Volterra competition system, which can be regarded as a fundamental extension of the logistic growth (1) with such inter-specific interaction:

$$\begin{cases} \frac{dN_1(t)}{dt} = \varepsilon_1 N_1(t) - \lambda_1 \{N_1(t)\}^2 - \mu_{12} N_2(t) N_1(t) \\ \frac{dN_2(t)}{dt} = \varepsilon_2 N_2(t) - \lambda_2 \{N_2(t)\}^2 - \mu_{21} N_1(t) N_2(t), \end{cases} \quad (2)$$

where  $\mu_{ij}$  is the coefficient of competitive interaction, which reflects the strength of inter-specific effect from species  $j$  to  $i$ .

For mathematical convention, we consider the following non-dimensionalized variable system of (2) without any loss of generality:

$$\begin{cases} \frac{dn_1(\tau)}{d\tau} = n_1(\tau) - \{n_1(\tau)\}^2 - \theta m_{12} n_2(\tau) n_1(\tau) \\ \frac{dn_2(\tau)}{d\tau} = \theta n_2(\tau) - \theta \{n_2(\tau)\}^2 - m_{21} n_1(\tau) n_2(\tau), \end{cases} \quad (3)$$

where the following transformations of variables are applied for (2):

$$\varepsilon_1 t \equiv \tau;$$

$$\frac{N_i(t)}{\varepsilon_i / \lambda_i} \equiv n_i(\tau) \quad (i = 1, 2);$$

$$\frac{\mu_{lk}}{\lambda_l} \equiv m_{lk} \quad (l, k = 1, 2; l \neq k);$$

$$\frac{\varepsilon_2}{\varepsilon_1} \equiv \theta.$$

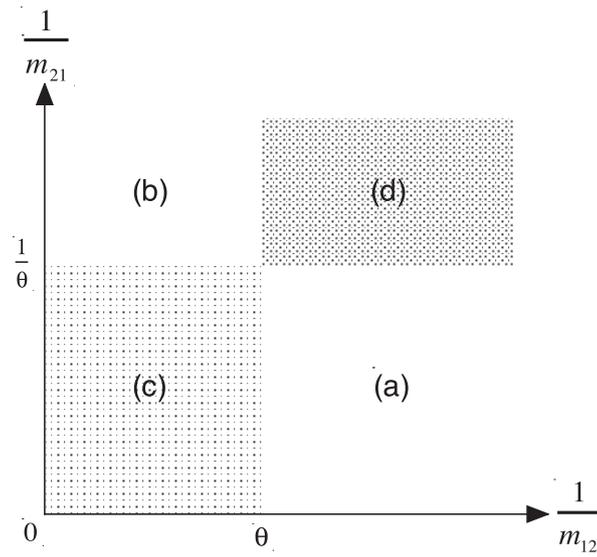


Figure 1: Parameter dependence of the equilibrium state for (3). For the parameter region (a), when  $m_{12} < 1$  and  $m_{21} > 1$ , species 2 is eventually eliminated and species 1 persists. For (b), when  $m_{12} > 1$  and  $m_{21} < 1$ , species 1 is eventually eliminated and species 2 persists. In contrast, for (c), when  $m_{12} > 1$  and  $m_{21} > 1$ , one of two species is eliminated and another persists, depending on the initial condition. For (d), when  $m_{12} < 1$  and  $m_{21} < 1$ , both species ultimately coexist.

As well-known for the Lotka-Volterra competition system (2) (for instance, see [8]), the solution of (3) has the following natures depending on the parameter  $\theta$ ,  $m_{12}$  and  $m_{21}$  (Fig. 1):

- (a) if  $m_{12} < 1/\theta$  and  $m_{21} > \theta$ ,  
species 2 is eventually eliminated and only species 1 persists;
- (b) if  $m_{12} > 1/\theta$  and  $m_{21} < \theta$ ,  
species 1 is eventually eliminated and only species 2 persists;
- (c) if  $m_{12} > 1/\theta$  and  $m_{21} > \theta$ ,  
one of two species is eliminated and another persists, depending on the initial condition;
- (d) if  $m_{12} < 1/\theta$  and  $m_{21} < \theta$ ,  
both species ultimately coexist.

For each of these cases, some trajectories in the phase plane of  $(n_1, n_2)$  are for example shown in Fig. 2.

## 1.2 Temporally Intermittent Competition

We now assume that there is a season in which two species lose their inter-specific interaction. For example, in such a season, they would inhabit independently with niches different from each other. In another season, they have a competitive inter-specific interaction, for instance, due to their overlapping niches. We assume that these seasons with and without the competitive interaction repetitively occur one after another (see Fig. 3). In this paper, we call this type of inter-specific relationship *the temporally intermittent competition*. We denote by  $T_+$  the duration of season with the competitive interaction, by  $T_-$  that without it. In our modelling, we assume that both  $T_+$  and  $T_-$  are constant as indicated in Fig. 3.

For the competitive two-species dynamical system (2) or (3), in the competitive season mentioned above, two species have the competitive interaction between them with the constant coefficients of competitive interaction,  $\mu_{12}$  and  $\mu_{21}$ , that is,  $m_{12}$  and  $m_{21}$ . In contrast, in the non-competitive season with the intermittency of competition, since two species have no inter-specific relationship, we consider the system (2) or (3) with  $\mu_{12} = \mu_{21} = 0$  or with  $m_{12} = m_{21} = 0$ , which is the case corresponding to (1).

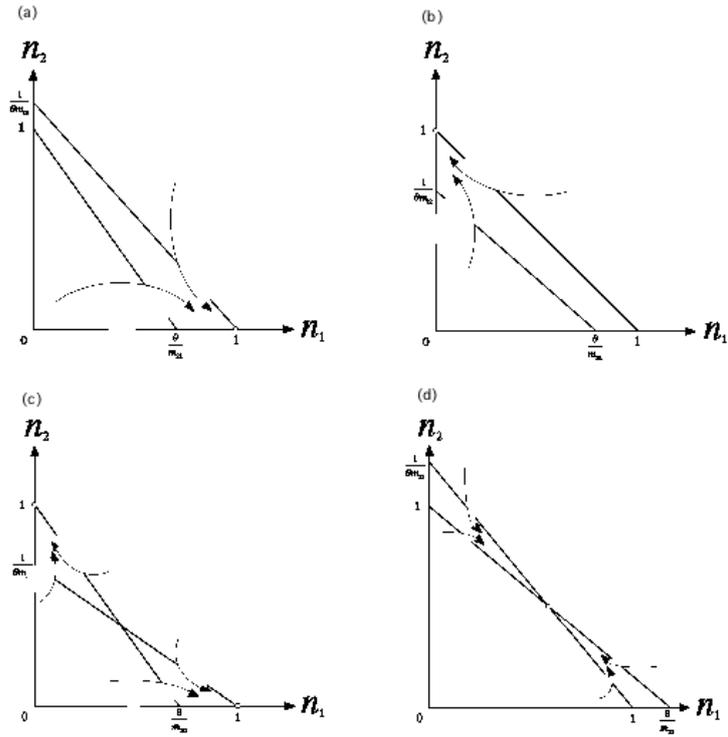


Figure 2: Phase planes of  $(n_1, n_2)$  for Lotka-Volterra competition system (3). Some trajectories are schematically given. For the parameter region (a), when  $m_{12} < 1$  and  $m_{21} > 1$ , species 2 is eventually eliminated and species 1 persists. For (b), when  $m_{12} > 1$  and  $m_{21} < 1$ , species 1 is eventually eliminated and species 2 persists. In contrast, for (c), when  $m_{12} > 1$  and  $m_{21} > 1$ , one of two species is eliminated and another persists, depending on the initial condition. For (d), when  $m_{12} < 1$  and  $m_{21} < 1$ , both species ultimately coexist.

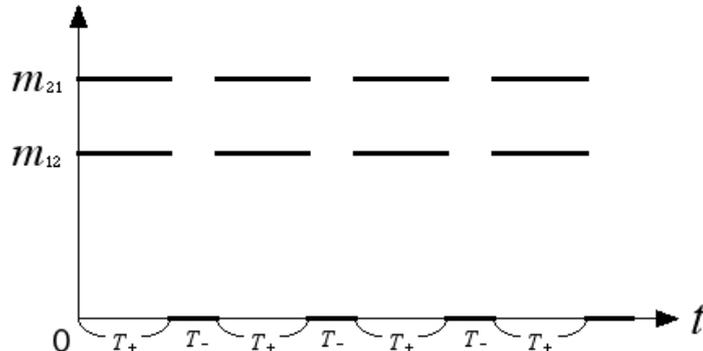


Figure 3: Temporally intermittent competition. In a season,  $m_{12}$  and  $m_{21}$  are positive constant, and in another season,  $m_{12} = m_{21} = 0$ . In our mathematical modelling, these two seasons repetitively occur one after another in an exactly periodical manner. The competitive season with positive  $m_{12}$  and  $m_{21}$  has the duration  $T_+$ , while the non-competitive one with zero  $m_{12}$  and  $m_{21}$  does  $T_-$ . Each of competition coefficients  $m_{12}$  and  $m_{21}$  is assumed to be the same value in any competitive season.

## 2 Analysis

As the first step of our mathematical study, we analyze the case when  $\theta = 1$ , so that the population dynamics of two species are governed by the identical logistic equation in the non-competitive season. As indicated by Fig. 1 and Fig. 2, in the case when  $m_{12} < 1$  and  $m_{21} < 1$  without any intermittency of competition, two species eventually coexist. Since each population grows toward a positive equilibrium during the non-competitive season, it is trivial that two species can coexist with or without the intermittency of competition when  $m_{12} < 1$  and  $m_{21} < 1$ . In this reason, in our analysis, we do not consider any more the case when  $m_{12} < 1$  and  $m_{21} < 1$ . We consider only the case when  $1 < m_{12}$  or  $1 < m_{21}$ . Since  $\theta = 1$ , the population has the nature symmetric with respect to two species. Thus, without any loss of generality, we hereafter focus the case when  $m_{21} > 1$ . Hence, in any of our numerical calculations, we use the value  $m_{21} = 1.4$ .

### 2.1 Inversion of Persistence

To consider the effect of temporal intermittency of inter-specific competitive interaction, we analyze at first the case of Fig. 1(c) or Fig. 2(c), when the extinction of one species occurs depending on the initial condition, that is, the bistable case if the inter-specific competitive interaction would stationarily exist with no intermittency.

Now, with the intermittency of competition, we can find *the inversion of*

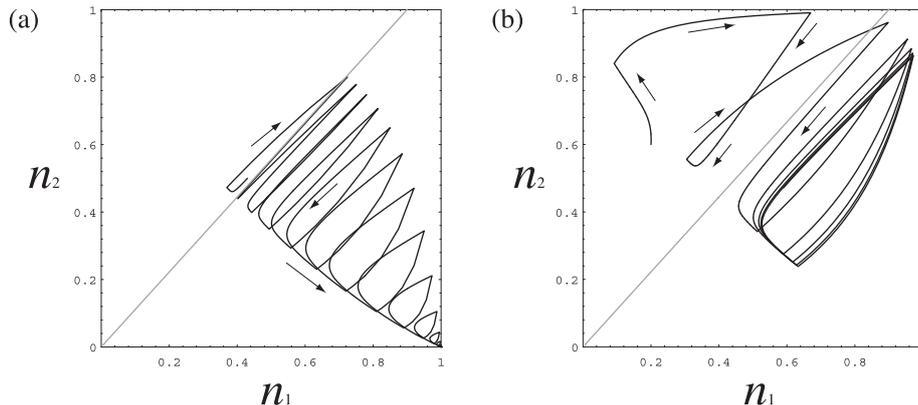


Figure 4: Numerical examples of trajectory in the phase plane of  $(n_1, n_2)$ . (a) a trajectory converging to the state  $(1, 0)$  with the periodical with intermittency of competition. Without the intermittency, the trajectory would converge to the state  $(0,1)$ , because the initial point  $(n_1(0), n_2(0)) = (0.43, 0.5)$  is above the separatrix in the case when the competition is kept without the intermittency; (b) a trajectory converging to a coexistent state. The initial point is  $(n_1(0), n_2(0)) = (0.2, 0.6)$ . In both cases,  $m_{12} = 1.36$ ,  $m_{21} = 1.4$ ,  $T_+ = 7.0$ ,  $T_- = 3.0$ . The gray curve indicates the separatrix in the case without the intermittency of competition.

*persistence* only in the case of Fig. 1(c) or Fig. 2(c): Species  $i$  is eventually eliminated and species  $j$  persists with the intermittency of competition, whereas species  $j$  is eventually eliminated and species  $i$  persists without it. A trajectory for the inversion of persistence is shown in Fig. 4(a).

## 2.2 Coexistence by Intermittency of Competition

As in the previous section, to consider the effect of the temporal intermittency of inter-specific competitive interaction, we analyze the case of the Fig. 1(c) or Fig. 2(c), and can find the appearance of coexistence by the intermittency of competition, even though the coexistence could not be realized without it. In Fig. 4(b), we show an example of coexistent state realized by the intermittency of competition.

Also for the case of Fig. 1(a) or Fig. 2(a) and that of Fig. 1(b) or Fig. 2(b), we can find the appearance of coexistence. The corresponding coexistent trajectory is similar to that shown in Fig. 4(b).

## 2.3 Dependence on The Strength of Intermittency

We analyze the dependence of equilibrium states mentioned in the previous sections on the *strength* of intermittency of competition. Now we measure the strength of intermittency by the duration  $T_-$  for fixed  $T_+$ . When  $T_- = 0$ , no

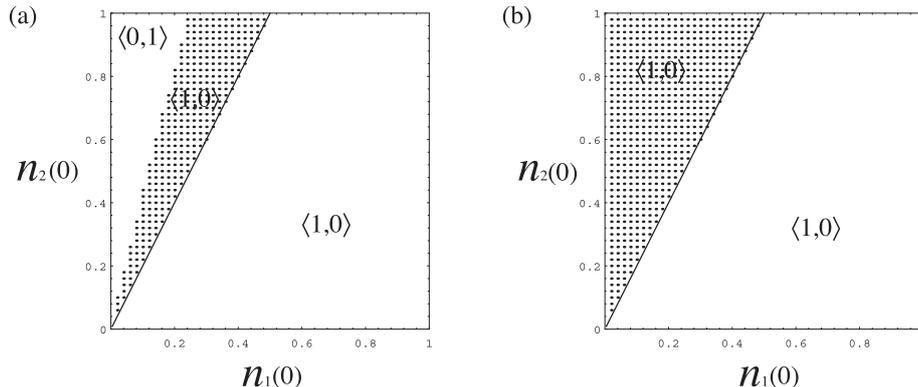


Figure 5: Dependence of equilibrium state on the initial condition. Numerically obtained result. The solid curve indicates the separatrix in the case when the competition stationarily exists without the intermittency. For the region  $\langle 0, 1 \rangle$  of initial condition  $(n_1(0), n_2(0))$ , species 1 goes extinct while species 2 persists, and inverse for the region  $\langle 1, 0 \rangle$ . Dotted region indicates the initial condition with which species 1 going extinct without the intermittency of competition can persist with the intermittency, whereas species 2 changes from persistent to extinct. (a)  $T_- = 1.0$ ; (b)  $T_- = 1.5$ . In both cases,  $m_{12} = 1.2$ ,  $m_{21} = 1.4$ ,  $T_+ = 7.0$ .

intermittency occurs. This can be formally regarded as the case of the weakest intermittency. For fixed  $T_+$ , we regard the intermittency as stronger if the duration of non-competitive season  $T_-$  gets longer.

### 2.3.1 Inversion of Persistence

At first, we consider the inversion of persistence. Since we can identify the area  $S$  of the region of initial condition  $(n_1(0), n_2(0))$  in  $(0, 1) \times (0, 1)$  as shown in Fig. 5 in terms of the inversion of persistence, we regard the area  $S$  as the degree of *occurrence* of the inversion of persistence. Hence, we numerically analyze the dependence of the area  $S$  on the parameter  $T_-$  with the other fixed parameters including  $T_+$ . Indeed, comparing Fig. 5(a) to (b), we can see that the difference of the value of  $T_-$  could be significantly reflected to the area for the inversion of persistence, which is indicated by the dotted region in Figs. 5(a) and (b).

Fig. 6 shows the numerical results about the  $T_-$ -dependence of the occurrence of the inversion of persistence. Fig. 6(a) shows the result for the smaller  $m_{12}$  than Fig. 6(b) does. The region of initial condition for the inversion of persistence appears for the relatively weaker intermittency. The area  $S$  for the inversion of persistence increases as the intermittency gets stronger till a critical value. From the numerical results, if the strength of intermittency is beyond the critical value, the inversion of persistence suddenly shrinks to disappear, and instead the coexistence occurs. Inversely, if the strength of intermittency is below it, there exist some initial conditions for the inversion of persistence.

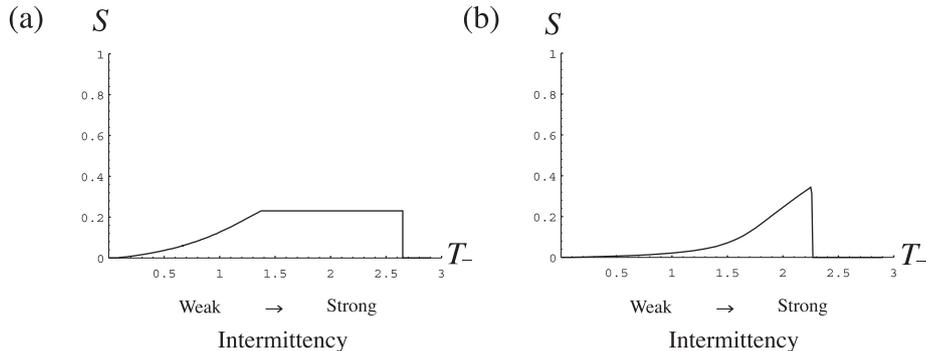


Figure 6: Dependence of the occurrence of the inversion of persistent species on the intermittency of competition. Numerically obtained results. The strength of intermittency is measured by the duration  $T_-$ , and the occurrence of the inversion of extinct species is done by the area  $S$  of the region of initial condition  $(n_1(0), n_2(0))$  in  $(0, 1) \times (0, 1)$ , indicated for instance by the dotted region  $\langle 1, 0 \rangle$  in Fig. 5. (a)  $m_{12} = 1.2$ ; (b)  $m_{12} = 1.36$ . In both cases,  $m_{21} = 1.4$ ,  $T_+ = 7.0$ .

### 2.3.2 Coexistence by Intermittency of Competition

Next, we consider the coexistence. Since we can again identify the area  $W$  of the region of initial condition  $(n_1(0), n_2(0))$  in  $(0, 1) \times (0, 1)$  as shown in Fig. 7 in terms of the coexistence, similarly we regard the area  $W$  as the occurrence of the coexistence. We numerically analyze the dependence of the area  $W$  on the parameter  $T_-$  with the other fixed parameters including  $T_+$ . Indeed, comparing Fig. 7(a) to (b), we can see that the difference of the parameter value  $T_-$  could be significantly reflected to the area for the coexistence, which is indicated by the light dotted region in Figs. 7(a) and (b).

Fig. 8 shows the numerical results about the  $T_-$ -dependence of the occurrence of the coexistence. Figs. 8(a-1, 2) show the results for the smaller  $m_{12}$  than Figs. 8(b-1, 2) do. The region of initial condition for the coexistence appears for the relatively stronger intermittency. The area  $W$  for the coexistence increases suddenly as the intermittency gets stronger beyond a critical value. If the strength of intermittency is above a critical value, there exist some initial conditions for the coexistence. As shown in Figs. 8(a-2) and (b-2), the regions for the inversion of persistence and for the coexistence could simultaneously exist just for a relatively narrow range of  $T_-$ .

### 2.3.3 Dependence on The Coefficient of Competition

Fig. 9 shows the numerical results about the  $(m_{12}, T_-)$ -dependence of the inversion of persistent species and the coexistence. As shown in Fig. 9, we can see that the occurrence of the inversion of persistence and the coexistence are significantly depending not only on the strength of intermittency of competition,  $T_-$ ,

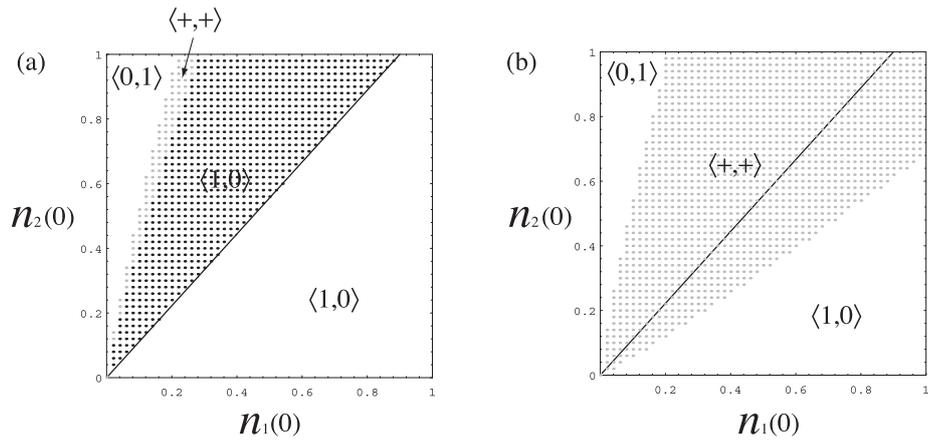


Figure 7: Dependence of equilibrium state on the initial condition. Numerically obtained results. The solid curve indicates the separatrix in the case when the competition stationarily exists without the intermittency. For the region  $\langle 0, 1 \rangle$  of initial condition  $(n_1(0), n_2(0))$ , species 1 goes extinct while species 2 persists, and inverse for the region  $\langle 1, 0 \rangle$ . Light dotted region  $\langle +, + \rangle$  indicates the initial condition with which two species can coexist in the case with the intermittency of competition. Dark dotted region  $\langle 1, 0 \rangle$  indicates the initial condition with which one species going extinct without the intermittency of competition can persist with the intermittency, whereas another changes from persistent to extinct. (a)  $T_- = 2.26$ ; (b)  $T_- = 2.27$ . In both cases,  $m_{12} = 1.36$ ,  $m_{21} = 1.4$ ,  $T_+ = 7.0$ .

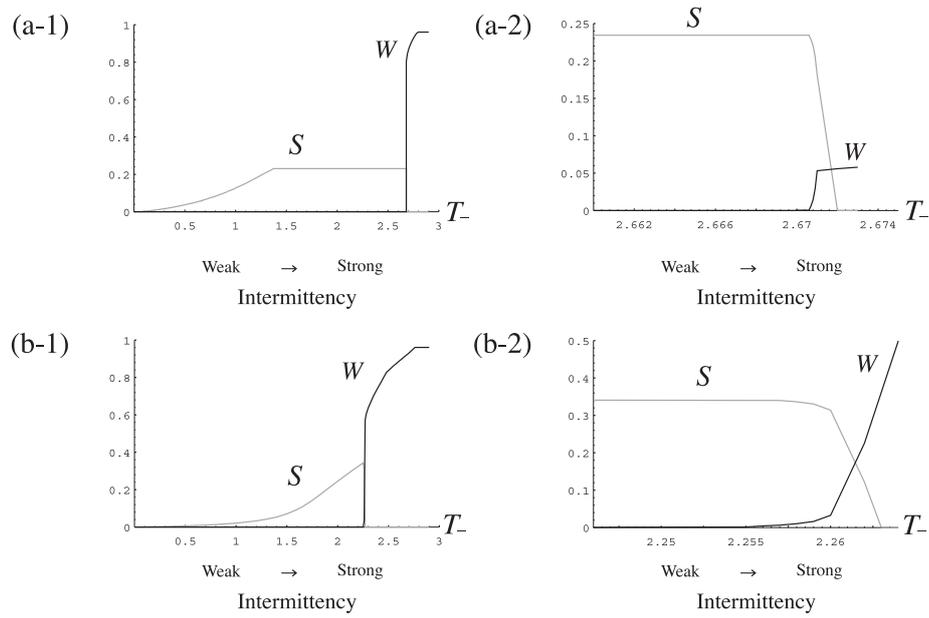


Figure 8: Dependence of the occurrence of coexistence on the intermittency of competition. Numerically obtained results. The strength of intermittency is measured by the duration  $T_-$ , and the occurrence of coexistence is done by the area  $W$  of the region of initial condition  $(n_1(0), n_2(0))$  in  $(0, 1) \times (0, 1)$ , indicated by the dotted region  $(+, +)$  in Fig. 7. (a-1, 2)  $m_{12} = 1.2$ ; (b-1, 2)  $m_{21} = 1.36$ . In both cases,  $m_{21} = 1.4$ ,  $T_+ = 7.0$ . The black curve shows  $W$ , and the gray one does  $S$ . In both cases of (a) and (b), there exists a narrow range of  $T_-$  in which these two simultaneously exist.

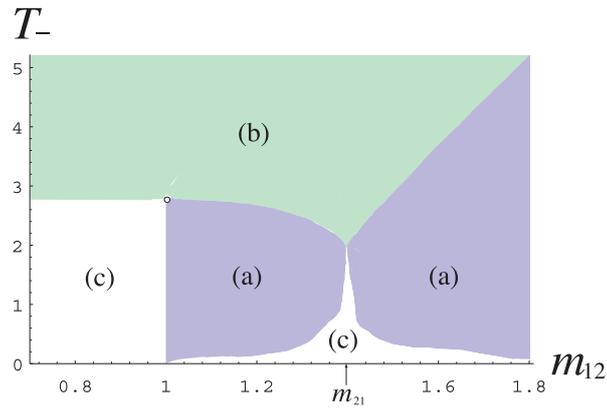


Figure 9:  $(m_{12}, T_-)$ -dependence of the occurrence of the inversion of persistence species and the coexistence. Numerically obtained result. (a) only the inversion of persistence occurs; (b) the coexistence occurs; (c) Neither of the inversion of persistence nor the coexistence occur, that is, the intermittency of competition causes no difference in terms of the equilibrium state.

but also on the difference between two coefficients of competitive interaction, that is, between  $m_{12}$  and  $m_{21}$ .

Fig. 10 shows the dependence of the location and the area of  $S$  and  $W$  on the coefficient  $m_{12}$  of competitive interaction. Fig. 10(a) shows the result for the larger  $T_- (= 2.66)$  than Fig. 10(b) does  $(= 1.33)$ . Indeed, comparing Fig. 10(a) to (b), we can see that the value of  $T_-$  could be significantly reflected to the location and the area of  $S$  and  $W$ , which is indicated by the grayed region in Figs. 10(a) and (b).

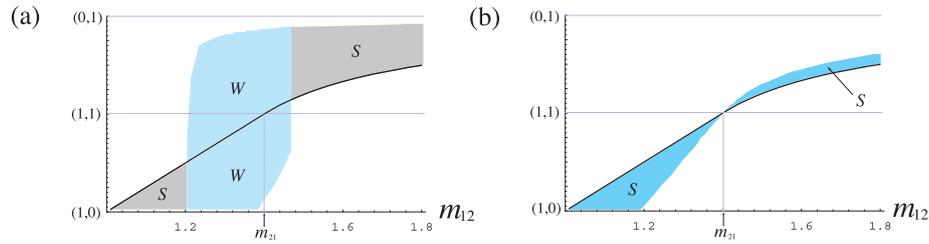


Figure 10: Dependence of the occurrences of the inversion of persistence and the coexistence on the coefficient  $m_{12}$  of competitive interaction. Numerically obtained results. (a)  $T_- = 2.66$ ; (b)  $T_- = 1.33$ . In both cases,  $T_+ = 7.0$ . Vertical axis corresponds to the location and the area of region of  $S$  or  $W$  in  $(0, 1) \times (0, 1)$  of the phase plane of  $(n_1, n_2)$ . The solid curve indicates the location of separatrix in the case without intermittency of competition. The upper side of the solid curve corresponds to the region below the separatrix in  $(0, 1) \times (0, 1)$ , and the lower side of the solid curve does to the region beyond it.

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