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Appendix A

The mathematical justification of the reduction from a reaction-diffusion model to a compartment model

In the text, we reduced the 2-species Lotka-Volterra reaction-diffusion competition model to the compartment models by using the results and arguments (Fang 1990, Mimura et al. 1991). Naturally, we need several assumptions to state the mathematical results. Actually, there are at least two gaps between the assumptions in those papers and in our statements: One is that we always used the only compartment model with the dispersal rate defined by the width and length of the corridor region, the area of the habitats, and the diffusive coefficients. Note that we need three types of the reduced equations depending on the diffusive coefficients when we state our mathematical results in the following. Another is in the range of the width W where the arguments (Fang 1990, Mimura et al. 1991) are applicable to our situation. The corridor region was supposed to have to be narrow in these papers, while we often took a relatively large value of W in the text. Due to these gaps, we cannot directly derive our results from those (Fang 1990, Mimura et al. 1991). Hence it is important to clarify the conditions where the reduction holds true mathematically and point out what statements in the text are obtained by only formal analysis.

In the next section, we first describe the mathematically precise conditions and results obtained by the arguments (Fang 1990, Mimura et al. 1991) (see Theorem 1). From this, the readers know what conditions are needed when using our reduction formula. After that, we explain the mathematical gaps more specifically and discuss about the possibility to extend the mathematical results. We finally state that our statements in the text are correct formally. In the last part of this section, we introduce further mathematical results obtained (Fang 1990, Mimura et al. 1991), which has the information about the dynamics and bifurcation point in the reaction-diffusion equations.

Mathematical result for the reduction

The 2-species Lotka-Volterra reaction-diffusion competition model is precisely represented by

$$\begin{cases} \dfrac{\partial N_1}{\partial t} = (r_1 - \alpha_1 N_1 - \beta_1 N_2)N_1 + D_1 \left(\dfrac{\partial^2 N_1}{\partial x^2} + \dfrac{\partial^2 N_1}{\partial y^2} \right), \\ \dfrac{\partial N_2}{\partial t} = (r_2 - \beta_2 N_1 - \alpha_2 N_2)N_2 + D_2 \left(\dfrac{\partial^2 N_2}{\partial x^2} + \dfrac{\partial^2 N_2}{\partial y^2} \right) \end{cases} \tag{A.1}$$

in $R \times (0, \infty)$ with the zero-flux boundary conditions on $\Gamma \times (0, \infty)$

$$\frac{\partial N_1}{\partial n} = \frac{\partial N_2}{\partial n} = 0$$

and the initial functions

$$N_1(x, y, 0) = N_{10}(x, y) \geq 0, \quad N_2(x, y, 0) = N_{20}(x, y) \geq 0,$$

where $r_1, r_2, \alpha_1, \alpha_2, \beta_1, \beta_2, D_1, D_2$ are positive constants, and a 2-dimensional habitat configuration R consists of three parts R_1, R_2, R_C like Figure 1 and has a smooth boundary Γ. Here two habitats R_1, R_2 are convex with the smooth boundaries and the corridor region R_C is given by

$$R_C = \{(x, y) \mid |x| \leq L/2,\ |y| \leq W/2\}.$$

We define R_C^L and R_C^R by

$$R_C^L = \{(x, y) \mid |x + L| \leq L/2,\ |y| \leq W/2\},$$

$$R_C^R = \{(x, y) \mid |x - L| \leq L/2,\ |y| \leq W/2\}$$

and suppose that R_C^L and R_C^R are included in R_1 and R_2. Under these settings, we derive the following mathematical results from the arguments (Fang 1990, Mimura et al. 1991).

Theorem 1. *Let* $(N_1(x, y, t), N_2(x, y, t))$ *be a solution of (A.1). Suppose that only* D_1 *and* D_2 *depends on* W *and satisfies* $0 < \lim_{W \to 0} D_1 W^{\theta} < \infty$ *and* $0 < \lim_{W \to 0} D_2 W^{\theta} < \infty$ *for some* *positive constant* θ*, and other parameters are fixed independently of* W*. For* $\delta, T > 0$ *arbitrarily fixed, it holds that*

$$\int\int_{R_1} |N_1(x,y,t) - N_{11}(t)|^2 dxdy = O(\sqrt{W}),$$
$$\int\int_{R_1} |N_2(x,y,t) - N_{21}(t)|^2 dxdy = O(\sqrt{W}),$$
$$\int\int_{R_2} |N_1(x,y,t) - N_{12}(t)|^2 dxdy = O(\sqrt{W}),$$
$$\int\int_{R_2} |N_2(x,y,t) - N_{22}(t)|^2 dxdy = O(\sqrt{W})$$

as $W \to 0$ *uniformly in* $t \in (\delta, T)$*, where* $N_{11}(t), N_{12}(t), N_{21}(t), N_{22}(t)$ *is a solution of the compartment model either (A.2) in the case of* $\theta > 1$ *or (A.3) in the case of* $0 < \theta \leq 1$ *with an initial values uniquely determined by the initial function of* $(N_{10}(x,y), N_{20}(x,y))$*. The symbol* $O(\sqrt{W})$ *means that if a function* $h(W)$ *satisfies* $h(W) = O(\sqrt{W})$*, there are* $A, W_0 > 0$ *such that* $|h(W)| \leq A\sqrt{W}$ *for any* $0 < W < W_0$*.*

The compartment models described in the statement above have different forms for $\theta > 1$ and $0 < \theta \leq 1$;

(i) Case of $\theta > 1$

$$\begin{cases} \dfrac{dN_1}{dt} = (r_1 - \alpha_1 N_1 - \beta_1 N_2)N_1, \\ \dfrac{dN_2}{dt} = (r_2 - \beta_2 N_1 - \alpha_2 N_2)N_2, \\ (N_1, N_2) = (N_{11}, N_{21}) = (N_{12}, N_{22}). \end{cases} \tag{A.2}$$

(ii) Case of $0 < \theta \leq 1$

$$\begin{cases} \dfrac{dN_{11}}{dt} = (r_1 - \alpha_1 N_{11} - \beta_1 N_{21})N_{11} - d_{11}(\theta)(N_{11} - N_{12}), \\ \dfrac{dN_{21}}{dt} = (r_2 - \beta_2 N_{11} - \alpha_2 N_{21})N_{21} - d_{21}(\theta)(N_{21} - N_{22}), \end{cases}$$
$$\begin{cases} \dfrac{dN_{12}}{dt} = (r_1 - \alpha_1 N_{12} - \beta_1 N_{22})N_{12} + d_{12}(\theta)(N_{11} - N_{12}), \\ \dfrac{dN_{22}}{dt} = (r_2 - \beta_2 N_{12} - \alpha_2 N_{22})N_{22} + d_{22}(\theta)(N_{21} - N_{22}), \end{cases} \tag{A.3}$$

where $d_{ij}(\theta)$ for $i, j = 1, 2$ is defined by

$$d_{ij}(\theta) = \begin{cases} 0 & \text{in the case of } 0 < \theta < 1, \\ \lim\limits_{W \to 0} \dfrac{W}{L} \dfrac{D_i}{S_j} & \text{in the case of } \theta = 1. \end{cases} \tag{A.4}$$

In the habitats 1 and 2, the densities of two species are denoted by (N_{11}, N_{21}), (N_{12}, N_{22}), respectively.

Theorem 1 states that the behavior of the solution of (A.1) in the habitats is governed by that of the compartment models with a suitable initial value. The initial functions N_{10}, N_{20} can have spatially inhomogeneous states over the habitat configuration. In order to use Theorem 1, we need the conditions that the corridor region must be narrow and the diffusive coefficients are large dependently on the width of the corridor region.

Under these conditions, the reduced compartment models have different forms depending on θ. In the case of $\theta > 1$, both diffusion coefficients of two species are quite large. Then both species spread rapidly in R so that the densities of the species in the two habitats tend to the same homogeneous states. In the case of $\theta = 1$, the most important case in the text, the compartment model (A.4) has the dispersal rate explicitly defined by the width and length of the corridor region, the area of the two habitats, and the diffusive coefficients. Apparently, since the corridor region is very narrow, two species in the patch 1 seem to behave independently of those in the patch

2. However, two species can migrate through the narrow corridor region because the diffusive coefficients are large dependently on W. In the case of $\theta = 1$, this diffusive effect exactly balance with the narrowness of the corridor region so that the dispersal rates appear in the compartment model. In the case of $0 < \theta < 1$, the diffusion coefficients are relatively small so that two species can hardly migrate between two patches through the narrow corridor region. As a result, the behavior of two species in the patch 1 is almost independent of one in the patch 2.

Mathematical gaps

As described previously, there are two mathematical gaps between the results (Fang 1990, Mimura et al. 1991) and our statement in the text. The first gap is related to the type of the compartment models. When we reduce the reaction-diffusion model in the text, we always focus on the compartment model with the dispersal rates. Other two models, (A.2) and (A.3) for the case $0 \leq \theta < 1$, were not used. Actually, these two models can be included in the compartment model for $\theta = 1$ in some sense. Roughly speaking, if the diffusive coefficients D_1, D_2 are large, the densities of two species correspond to homogeneous states, and if D_1, D_2 are relatively small, the behavior of two species in the habitat 1 is independent of that in the habitat 2. On the other hand, in the compartment model with the dispersal rate, the similar facts hold true (Levin 1974). Hence we no longer need to pay attention to three types of the compartment models. We can simply understand the dynamics of the reaction-diffusion model by (A.1) for the case of $\theta = 1$.

The second gap is in the range of the width W. If we would like to apply Theorem 1, we should let D_1, D_2 larger and larger as W become small. On the other hand, in the text, the only width of the corridor region W is a parameter and other factors, constants, the length of the corridor region, and the area of the habitats, are fixed. In fact, the following conjecture holds true.

Suppose that the diffusive coefficients, the area of two habitats, and the square of the length of the corridor region have the same order as each other. Then, there is a critical width of the corridor region W_* such that (A.1) has a stable inhomogeneous state for $W < W_*$, while (A.1) does not have any stable inhomogeneous states for $W > W_*$.

As is well-known, under the conditions

$$r_1 = r_2, \alpha_1 = \alpha_2, \beta_1 = \beta_2, d_{ij}(1) = d \tag{A.5}$$

for a constant $d > 0$ in (A.4), it was rigorously proved that there is a critical value d_* such that for $d < d_*$, (A.4) has a stable inhomogeneous state, while for $d > d_*$, any inhomogeneous equilibrium solution is unstable in (A.4) (Levin 1974). However there is no mathematical evidence that such a threshold W_1 exists in the compartment model with the parameters which do not satisfy (A.5) or in the reaction-diffusion model. The numerical results seem to support our statement. Hence the reduction still works when we can change W with other factors fixed (see Figure 4 (a)).

In the conjecture above, we supposed that the diffusive coefficients has the same order as the area of two habitats and the square of the length of the corridor region. This assumption is crucial. (A.1) was considered under the conditions that D_1, D_2 are small and obtained an interfacial equation reduced from (A.1) (Ei and Yanagida 1994). By this result, it can be shown that under (A.5), one species occupy both two habitats while another does the corridor region. This solution can never be approximated by any solution in the compartment models, and our approximation formula does not work in this case. Therefore we need the condition that D_1, D_2 are not much smaller than the area of two habitats and the square of the length of the corridor if we would like to use the reduction formula.

Remarks and further mathematical results

Theorem 1 indicates the possibility to reduce the reaction-diffusion system to the compartment model for any finite time. However it does not imply in a rigorous sense that steady states of the reaction-diffusion system can be approximated by those of the compartment model. In other words, we do not know from Theorem 1 whether the reaction-diffusion system has a bifurcation point predicted by using the compartment model. In fact, the two papers (Fang 1990, Mimura et al. 1991) introduced previously have further mathematical results about the approximation of steady states and bifurcation points. In this section we describe these results. After that, we state that we can extend all results to the case of $\theta = 0$, that is, the diffusive coefficients are independent of the width of the corridor regions.

First we consider the case of $\theta > 1$ and the dynamics of solutions in the reaction-diffusion model can be approximated by (A.2) for all time $t > 0$.

Theorem 2. *Let* $(N_1(x, y, t), N_2(x, y, t))$ *be a solution of (A.1). Suppose that only* D_1 *and* D_2 *depends on* W *and satisfies* $0 < \lim_{W \to 0} D_1 W^\theta < \infty$ *and* $0 < \lim_{W \to 0} D_2 W^\theta < \infty$ *for some positive constant* θ*, and other parameters are fixed independently of* W*. In the case of* $\theta > 1$*, there are positive constants* c, m, W_0 *independent of* W *such that for any* $0 < W < W_0$*,*

$$\int_{R_1 \cup R_2} |N_1(x, y, t) - \bar{N}_1(t)|^2 dxdy \leq ce^{-mt}, \quad t \geq 0,$$

$$\int_{R_1 \cup R_2} |N_2(x, y, t) - \bar{N}_2(t)|^2 dxdy \leq ce^{-mt}, \quad t \geq 0,$$

where $\bar{N}_1, \bar{N}_2$ *are the spatial average of* N_1 *and* N_2 *as defined in Theorem 1.*

As described previously, in the case of $\theta > 1$, (A.1) is reduced to the compartment model without dispersal rates. More precisely, any solution of (A.1) can be approximated by a solution of (A.2) with an appropriate initial value for any finite time. Theorem 2 states that this approximation can be extended to the whole time. Note that the difference between solutions of (A.1) and (A.2) decreases exponentially as $t \to \infty$.

The next theorem states the equivalence of *nondegenerate* stationary solutions in (A.1) and (A.3) in the case of $0 < \theta \leq 1$. It is well-known that bifurcation phenomena occurs at some parameter in the compartment model in the case of $\theta = 1$. Then, at least one zero eigenvalue exists in the associated linearized matrix with respect to the stationary solution for the parameter, which is called a *degenerate equilibrium.* In general, complicated phenomena happen near the bifurcation point, which is difficult to treat mathematically. Then we only consider the nondegenerate case in the theorem below.

Theorem 3. *Set* $0 < \theta \leq 1$. *Let* $(N_1(x,y), N_2(x,y))$ *be a stationary solution of (A.1). Then there are stationary solutions of (A.3) denoted by* (N_{11}, N_{21}) *and* (N_{12}, N_{22}) *such that*

$$\begin{aligned} &\lim_{W \to 0} \int_{R_1} (|N_1(x,y) - N_{11}|^2 + |N_2(x,y) - N_{21}|^2) dxdy = 0, \\ &\lim_{W \to 0} \int_{R_2} (|N_1(x,y) - N_{12}|^2 + |N_2(x,y) - N_{22}|^2) dxdy = 0. \end{aligned} \tag{A.6}$$

Conversely, for any pair of nondegenerate equilibria (N_{11}, N_{21}) *and* (N_{12}, N_{22})*, there is a positive constant* W_0 *such that a stationary solution* $(N_1(x,y), N_2(x,y))$ *of (LV) exists for* $0 < W < W_0$ *which satisfies (A.6).*

Since (A.1) is reduced to the compartment model, all steady states are also approximated by those of the compartment model because only nondegenerate stationary solutions are treated in Theorem 3. On the other hand, it is difficult to study degenerate equilibria, in particular, bifurcation points so that Theorem 3 describes nothing about degenerate equilibria. In the previous work, the only simple case was considered as

$$d_1 = d_2 (= d), \quad R_1 = R_2 (= R), \quad \alpha_1 = \alpha_2 (= a), \quad \beta_2 = \beta_2 (= b)$$

with the bistable condition $a < b$, and the dependency of d, α on steady states of (A.3) was studied (Mimura et al. 1991). Note that the dispersal rates are not equal to each other even in the conditions for parameters because the measure of the patch 1 are different from that of the measure of the patch 2. In the end, it was shown that the bifurcation (more precisely, pitchfork bifurcation) of (A.3) inherited to (A.1).

Finally, we explain that our result holds true in the case of $\theta = 0$. Almost the same settings as in Theorem 1 was considered and it was assumed that the diffusive coefficients are large independently of the width of the corridor region (Morita 1990). In other words, the case that D_1, D_2 are large and fixed, and $\theta = 0$ was studied. Then, the same result as Theorem 1 was proved rigorously (see Theorems 4.1, 5.1 (Morita 1990)), which implies that our statements can be extended to the case of $\theta = 0$ although we need the condition that D_1, D_2 are large.

Appendix B

The details of general models and Figure 5

Generalized Model

When k species interact each other, the reaction-diffusion model is denoted by

$$\frac{\partial}{\partial t}N_i(x,y,t) = f_i(N_1,N_2,\ldots,N_k,x) + D_i\left(\frac{\partial^2 N_i}{\partial x^2} + \frac{\partial^2 N_i}{\partial y^2}\right) \qquad \text{for } i = 1, 2, \ldots, k \qquad \text{(B.1)}$$

where a function f_i represents the effects of intra- and inter-specific interaction on the growth rate of sp.i's population. When environment is spatially heterogeneous, the function also depends explicitly on the spatial coordinates. We consider a case where only horizontal variation exists in environment (i.e., f_i does not depend on y).

One-species metapopulation dynamics

A simple example of spatially heterogeneous model is given by the following one-species reaction-diffusion equation

$$\frac{\partial}{\partial t}N_1(x,y,t) = f(N_1,x) + D_1\left(\frac{\partial^2 N_1}{\partial x^2} + \frac{\partial^2 N_1}{\partial y^2}\right)$$

where

$$f(N_1,x) = \left(1 - \frac{N_1}{K(x)}\right)N_1$$

represents logistic growth with carrying capacity depending on the position x. The carrying capacity is given by

$$K(x) = K_1(1-p(x)) + K_2 p(x)$$

where

$$p(x)=\begin{cases}0 & \text{if } x<-L/2\\ \dfrac{x}{L}+\dfrac{1}{2} & \text{if } \text{-L/2}\le x\le L/2\\ 1 & \text{if } x>L/2\end{cases}$$

The equation means that the carrying capacity is K_1 in a region R_1 and K_2 in a region R_2. In the corridor region R_C, the carrying capacity is spatially smoothed linearly. The corresponding two-patch compartment model is given by

$$\frac{dN_{11}}{dt}=(1-\frac{N_{11}}{K_1})N_{11}-d_{11}(N_{11}-N_{12})$$
$$\frac{dN_{12}}{dt}=(1-\frac{N_{12}}{K_2})N_{12}+d_{12}(N_{11}-N_{12})$$

where the effective dispersal rate d_{ij} is given by our formula (Eqn. 3). The numerical solution of the reaction-diffusion model and that of the compartment model are shown in Figure 5a. ($K_1=1, K_2=0.2, D_1=1$, $L=2, S_1=S_2=4, W=0.12$). The dynamics of the reaction-diffusion model is well approximated by the compartment model.

Two-species metacommunity dynamics

We consider a case where intra-specific competition coefficients of Lotka-Volterra competition are spatially heterogeneous. Using (B.1), the model for k = 2 species is given by

$$f_1(N_1,N_2,x)=(1-N_1-\beta_1(x)N_2)N_1$$
$$f_2(N_1,N_2,x)=(1-\beta_2(x)N_1-N_2)N_2$$

where

$$\beta_1(x)=g(1-p(x))+Gp(x)$$
$$\beta_2(x)=G(1-p(x))+gp(x)$$

The numerical results show good agreement between the reaction-diffusion model and the reduced compartment model (Figure 5b; $G=2.0, g=1.5, D_1=D_2=1$, $L=2, S_1=S_2=4, W=0.12$).

One-resource-two-consumer dynamics

As another example, we consider the competition between sp.1 (N_1) and sp.2 (N_2) for common resource (N_3). The model is denoted by

$$\begin{aligned} f_i(N_1,N_2,N_3,x) &= \left(\gamma_i(x)N_3 - 1\right)N_i \qquad \text{for} \quad i=1,2 \\ f_3(N_1,N_2,N_3,x) &= \left(1-N_3\right)N_3 - \left(\gamma_1(x)N_1 + \gamma_2(x)N_2\right)N_3 \end{aligned}$$

where resource consumption rate for sp.i is given by

$$\begin{aligned} \gamma_1(x) &= H(1-p(x)) + hp(x) \\ \gamma_2(x) &= Hp(x) + h(1-p(x)) \end{aligned}$$

which means sp.1 is the superior consumer in R_1 and sp.2 in R_2. The numerical results show good agreement between the reaction-diffusion model and the reduced compartment model (Figure 5c; $H=3, h=1, D_1=D_2=D_3=1$, $L=2, S_1=S_2=4, W=0.12$).

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Figure Caption in Appendix

Figure A1 The spatio-temporal dynamics of the reaction-diffusion model (coexistence or competitive exclusion). (a) Coexistence of sp. 1 and sp. 2 is realized. Initially, sp. 1 and sp. 2 partly inhabit regions R_1 and R_2, respectively. The system quickly reaches a simple distribution where distribution within each region is almost homogeneous. The linear gradient of both species is formed in a corridor region, which is the front of competition between the two species. In this movie, the corridor width is narrow and the front does not move (stable coexistence). Parameters: W = 0.08, L = 2.0, $S_1 = S_2 = 4.0$, β_1 = 1.5, β_2 = 2.0. (b) Sp. 1 competitively excludes sp. 2. Settings are the same as for (a) except that the corridor width is wider (W = 0.32). After reaching a simple distribution, the front slowly moves and finally sp. 1 invades and dominates the whole region.

Figure A1