BIOLOGICAL ADVECTION AND CROSS-DIFFUSION IN STARVATION DRIVEN DISPERAL

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Abstract. The dispersal of biological organisms

Contents

1. Introduction 1
2. Biological advection for ecology 3
3. Biological advection for chemotaxis 8
4. Biological cross-diffusion 8
4.1. Cross-diffusion theory from SKT model 8
4.2. Cross-diffusion from SDD model 9
4.2.1. Approach #1: cross-diffusion theory with self-diffusion 9
4.2.2. Approach #2: cross diffusion theory without self-diffusion 10
4.3. Numerical Simulation for pattern formation 11
5. Conclusion 11
References 11
5.1. Self-diffusion 12
5.1.1. SKT type self-diffusion 12
5.1.2. SDD type self-diffusion 12
5.2. Cross-diffusion 12
5.2.1. SKT type cross-diffusion 12
5.2.2. SDD type cross-diffusion 12
5.3. Three SDD type diffusions but without advection 12
5.4. SDD type diffusions versus SKT type diffusions 13

1. Introduction

The importance of formulating a realistic dispersal theory for biological species that takes into account interaction between individuals and response to environment has been emphasized by many researchers (see Skellam [15, 16] and Okubo & Levin [14, Chapter 5]). The starvation driven diffusion (or SDD for brevity) includes the both ingredients in a simplest way by increasing random dispersal rate when starvation starts (see [2]). Furthermore, this dispersal includes cross-diffusion and advection phenomena of biological species. The purpose of this paper is to compare the advection and cross-diffusion effect of SDD to the classical ones that appear in mathematical ecology and chemotaxis models.

The choice of your starvation measure depends on the context of your model. For example, if one considers a competition model with a logistic type population reaction, one may take

\[ s = \frac{\text{population}}{\text{amount of resource}}. \]  

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This is the reciprocal of the amount of resource per individuals which actually matters to each of individuals. If the population increases or the resource dwindles, each organism gets less food and this ratio increases. The departing probability \( \gamma \) of a species (or it is also called a mobility) is an increasing function of the starvation measure. We assume that,

\[
\gamma'(s) \geq 0, \quad \gamma(s) \to \ell \text{ as } s \to 0, \quad \text{and} \quad \gamma(x) \to h \text{ as } s \to \infty \text{ for } 0 \leq \ell \leq h. \tag{1.2}
\]

(If \( \ell > 0 \), the problem becomes uniform parabolic. If \( \ell = 0 \), then it is a degenerate case such as the porous medium equation.) It is well known that the corresponding random walk model with the departing probability \( \gamma \) is given by a Fokker–Planck type diffusion law

\[
u_t = \Delta(\gamma(s)u), \tag{1.3}
\]

where \( u \) is the population density (see [14, §5.4]). This diffusion is the starvation driven one that we are going to compare to classical theories.

First consider a single species case with the logistic population dynamics that is given by

\[
u_t = \Delta(\gamma(s)u) + u \left( 1 - \frac{u}{m} \right), \quad x \in \Omega, \ t > 0, \tag{1.4}
\]

where \( m = m(x,t) \) is a non-constant distribution of resources. Here, the starvation measure is taken as

\[
s = \frac{u}{m}, \tag{1.5}
\]

and the diffusion equation (1.3) is written as

\[
u_t = \Delta(\gamma(s)u) = \nabla \cdot \left( \gamma(s)\nabla u + \mu_1(s) \frac{u}{m} \nabla u - \chi(s) \frac{u}{m} \nabla m \right), \tag{1.6}
\]

where \( \mu_1(s) := \gamma'(s) \) is a diffusion coefficient and \( \chi(s) := \gamma'(s)s \) is an advection (or chemotactic) coefficient. In this model we have ordinary diffusion, self-diffusion and advection. In particular, the advection term appears because the diffusion is driven by starvation, but not because the individuals sense the gradient of the resource.

Next consider a Lotka-Volterra type competition model of two species,

\[
u_t = \Delta(\gamma(s)u) + u \left( 1 - \frac{u + av}{m} \right), \quad x \in \Omega, \ t > 0, \tag{1.7}
\]

where \( v = v(x,t) \) is the population density of the competing species. The constant \( a \) measures the competition weight of species \( v \) against \( u \). Here, the starvation measure of the species \( u \) is taken as

\[
s = \frac{u + av}{m}, \tag{1.8}
\]

and the diffusion equation (1.3) is written as

\[
u_t = \Delta(\gamma(s)u) = \nabla \cdot \left( \gamma(s)\nabla u + \mu_1(s) \frac{u}{m} \nabla u + \mu_2(s) \frac{u}{m} \nabla v - \chi(s) \frac{u}{m} \nabla m \right), \tag{1.9}
\]

where \( \mu_2(s) := a\mu_1(s) \) is another diffusion coefficient. This new diffusion term has been introduced to (1.6) and the other three terms are same as the ones in (1.6). However, notice that the definition of the starvation measures for the two cases are different.

The dispersal strategy of biological species is one of the key elements for the survival of the species. There have been intensive studies of biological and ecological dispersals. The most fundamental component is the random dispersal with constant diffusivity and the effect of diffusivity size is understood well. Numerical simulations and analysis show that a smaller dispersal rate is selected if the environment is spatially heterogeneous and that a larger dispersal rate can be selected if there is a temporal fluctuation of the environment (see [1, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 17]). However, this random dispersal is not enough to explain biological dispersal phenomena and other dynamics such as advection, self-diffusion and cross-diffusion have been considered. The starvation driven diffusion written in (1.9) contains all of these dynamics and we will compare them to the classical theories in the following sections.

---

1We don’t really care about the number of employees and the personal expenses of our company. What really important to us is our own salaries and the ratio in (1.1) is the reciprocal of the average of our salaries.
2. Biological advection for ecology

In this section we consider the advection phenomenon in SDD of single species. Take a starvation measure as

\[ s = \frac{u}{m}. \]

Then, the starvation driven diffusion is written as

\[ u_t = \Delta (\gamma(s)u) = \nabla \cdot \left( \gamma(s)\nabla u + \gamma'(s)s\nabla u - \gamma'(s)s\frac{u}{m}\nabla m \right). \] (2.1)

The last term \(-\gamma'(s)s\frac{u}{m}\nabla m\) gives an advection phenomena and is our candidate to model a biological advection. Rewrite the equation as

\[ u_t = \nabla \cdot \left( (\gamma(s) + \gamma'(s)s)\left( \nabla u - \beta(s)\frac{u}{m}\nabla m \right) \right), \quad \beta(s) = \frac{\gamma'(s)s}{\gamma(s) + \gamma'(s)s} < 1. \] (2.2)

Note that the steady state of the equation is independent of the coefficient \(\gamma(s) + \gamma'(s)s\) if the resource distribution \(m(x)\) is independent of the steady state. Hence, we simplify the equation by setting it as a constant, \(d > 0\). We simplify the equation one step further by setting the coefficient \(\beta(s) = \eta\) as a constant and obtain

\[ u_t = \nabla \cdot \left( \nabla u - \eta\frac{u}{m}\nabla m \right), \quad \eta \leq 1, \quad s = \frac{u}{m}. \] (2.3)

Note that the coefficient \(\beta(s)\) is bounded above by one for any choice of the motility function \(\gamma\). Hence one should choose the advection coefficient \(\eta\) less than or equal to 1 if one considers an advection from SDD. This SDD type advection is the one most commonly used in chemotaxis models under the assumption that organisms may sense the gradient of signally chemical such as food. The size of coefficient is not necessarily bounded by one in chemotaxis. In the followings we observe that there is a drastic change if \(\eta\) becomes bigger than one.

**Example 2.1.** Let \(\gamma(s) = s^p\) for \(p \geq 0\). Then, \(\gamma'(s) = ps^{p-1} \geq 0\) and

\[ \beta = \frac{\gamma'(s)s\frac{u}{m}}{\gamma(s) + \gamma'(s)s} = \frac{p}{1 + p} \left( =: \beta_p \right) \to 1 \quad \text{as} \quad p \to \infty. \]

Notice that \(\gamma(s) = s^p\) converges to a jumping discontinuity at \(s = 1\) as \(p \to \infty\). Having a motility function \(\gamma\) that increases sharply at \(s = 1\) gives better fitness \([10]\).

We study the property of advection models using Lotka-Volterra type competition system of dispersal strategies. Consider three competing species with or without advection:

\[
\begin{align*}
  u_1^1 &= d_1 \Delta u_1^1 + u_1^1 (1 - \frac{u_1^1 + u_2^1 + u_3^1}{m}), \\
  u_2^1 &= \Delta u_2^1 + \eta_2 \nabla \cdot (u_2^1 \nabla m) + u_2^1 (1 - \frac{u_1^1 + u_2^1 + u_3^1}{m}), \\
  u_3^1 &= \Delta u_3^1 + \eta_3 \nabla \cdot (u_3^1 \nabla m) + u_3^1 (1 - \frac{u_1^1 + u_2^1 + u_3^1}{m}).
\end{align*}
\] (2.4)

The first one does not have an advection term and the diffusivity parameter \(d_1\) is introduced. The second one has an advection term proportional to \(u\). This is the advection commonly added in ecology models. We will call it a non-SDD type advection. The size of this advection is denoted by the parameter \(\eta_2\) and the diffusivity is fixed at \(d = 1\). The third one has an SDD type advection with a parameter \(\eta_3\). Notice that this advection term is related to SDD only with \(\eta_3 \leq 1\). However, we will also see what happens if \(\eta_3 > 1\).

The semi-trivial steady states of these three equations are given in Figure 1 for several cases. In the computation, we took a one dimensional domain \(\Omega = (0, \pi)\) and a resource distribution \(m(x) = \sin(x)\). The zero flux boundary condition is imposed on the boundary. The shapes of these steady states show the effect of advection clearly. If the steady state fits the resource distribution \(m(x)\) better, then it usually gives a better chance to survive in the competition.

The semi-trivial steady state for the first species without any advection, say \(\theta^1\), has some fitness property to the resource \(m(x)\). Notice that the diffusion makes the steady state flat and only the population reaction gives the fitness. Hence the profile \(\theta^1\) is the state that these two dynamics are balanced. The steady state for the second species, say \(\theta^2_{\eta_2}\), becoming concentrated...
at the maximum point of $m(x)$ as $\eta_2 \to \infty$. This shows that a large advection may give a negative impact. The semi-trivial steady state with the SDD type advection, say $\theta^3_{\eta_3}$, shows the best fitness if $\eta < 1$. In particular, it gives a perfect match to the resource distribution if $\eta_3 = 1$. However, it gives a similar behavior as $\theta^2_{\eta_2}$ when $\eta \to \infty$.

Now we consider the competition of the first two species

$$u^1_t = d_1 \Delta u^1 + u^1(1 - u^2 + u^2 m),$$
$$u^2_t = \Delta u^2 + \eta_2 \nabla \cdot (u^2 \nabla m) + u^2(1 - \frac{u^1 + u^2}{\eta_2}) + u^2(1 - \frac{u^1 + u^2}{m}),$$

(2.5)

where the second species has the non-SDD type advection. This case has been studied by many authors. In particular, a comprehensive picture of the dynamics has been given recently by Lam and Ni. The steady states of this competition model are given in Figure 2 with fixed $d_1 = 1$ and various $\eta_2 > 0$. In the simulation, one may observe that the second species with the advection aggregates near the maximum point of $m(x)$ and the other species takes most of the resources in the other place as $\eta_2 \to \infty$ as shown in Figure 2(e,f). One may also observe that the second species $u^2$ is selected and the first one becomes extinct if $\eta_2 \sim 2$. However, the two species coexist if $\eta_2 \gtrsim 3$. This is because we have fixed $d_1 = 1$ and the diffusivity of the second species is also $d = 1$. Hence, one may ask if the first species may survive with $d_1 \neq 1$.

To obtain a more comprehensive picture of extinction and coexistence of the competition model the total population of steady states for given pairs $(d_1, \eta_2) \in [0, 5]^2$ are computed numerically and their contours maps on $(d_1, \eta_2)$ plane are given in Figure 3 using two different resource distributions. The first row is obtained using the resource distribution $m(x) = \sin(x)$ and the second one using $m(x) = 2 \sin(x)$. One may observe the difference between the two rows and may conclude that the extinction, selection and coexistence of competing species do not depend only of on the parameters $d_1$ and $\eta_2$, but also on the choice of the resource distribution $m(x)$. The figures in the third column are contour maps of product o of the two total populations. If the product is zero, it indicates that one of them is extinguished after the competition. We may observe that this region becomes narrower as $\|m\|_\infty \to \infty$. 
Next we consider the competition between the first and third species, i.e.,

\begin{align*}
u_1^t &= d_1 \Delta u_1^t + \nu_3^t \nabla \cdot \left( \frac{\nu_3^t}{m} \nabla m \right) + u_1^t(1 - u_1^t + u_3^t m), \\
u_3^t &= \Delta u_3^3 + \eta_3 \nabla \cdot \left( \frac{\eta_3}{m} \nabla m \right) + u_3^3(1 - u_1^t + u_3^t m),
\end{align*}

(2.6)

where the third species now has a SDD type advection. The steady states of this competition system are given in Figure 4 with fixed \(d_1 = 1\) and various \(\eta_3 > 0\). If \(\eta_3 \to \infty\), the species with the advection aggregates near the maximum point of \(m(x)\) and the other species takes most of the other resources, which is the same asymptotic behavior the the previous case in Figure
Figure 4. Selection of a SDD-type advection and coexistence. If \( \eta_3 \leq 1 \), then the SDD-type advection is selected. If \( \eta_3 > 1 \), the other species coexists.

Figure 5. Contour maps of total population of steady states of (2.6) on the domain of pairs \((d_1, \eta_3) \in [0, 5]^2\). This contour maps are independent of the choice of \( m(x) \).

2. It seems clear that the condition \( \eta_3 \leq 1 \) for SDD type advection gives the boundary of the selection of SDD type advection and the coexistence of two species. In this simulation, one may observe that the species \( u_3 \) that has the SDD type advection is selected if \( \eta_3 \leq 1 \).

To obtain a comprehensive picture of the competition dynamics, the total population of steady states for given pairs \((d_1, \eta_3) \in [0, 5]^2\) are similarly computed and given in Figure 5. We may observe from Figure 5(c) that two species coexist if \( \eta_3 > 1 \). This is the regime beyond the SDD type advection. This indicates the importance of the SDD regime, \( \eta < 1 \), as an migration strategy of biological organisms. However, even the third species with SDD type advection becomes extinct if \( d_1 < 1 \) and \( \eta_3 \) is small as given in Figure 5(b). It seem that there exists a curve that connects \((\eta_3, d_1) = (1, 0) \) and \((0, 1)\) that separates the region \( \eta_3 < 1 \) in Figure 5(c) into two subregions, one for the extinction of the first species \( u_1 \) and the other of the third species \( u_3 \).

Remark 2.2. The resource distribution \( m(x) = \sin(x) \) has been used in the computation of Figure 5. We also did the same computation with couple of other resource distributions such as \( m(x) = 2 \sin(x) \) and obtained the exactly same contour maps. It seems that the extinction
and coexistence of the competition model (2.6) with SDD-type advection depends only on the parameters $d_1$ and $\eta_3$, but not on $m(x)$. Lastly, we consider a competition between the two advection phenomena,

$$
\begin{align*}
    u_2^t &= \Delta u^2 + \eta_2 \nabla \cdot (u^2 \nabla m) + u^2(1 - \frac{u^2 + u^3}{m}), \\
    u_3^t &= \Delta u^3 + \eta_3 \nabla \cdot (\frac{u^3}{m} \nabla m) + u^3(1 - \frac{u^2 + u^3}{m}).
\end{align*}
$$

The steady states of this system are given in Figure 6. In the simulation six cases are tested for six values of $\eta_3$ with a resource distribution $m(x) = \sin(x)$ and a fixed parameter $\eta_2 = 1.7$. In this example, the selection of the second species $u^2$, the coexistence, selection of the third species $u^3$, coexistence, and selection of $u^2$ are observed in the order as $\eta_3 \to \infty$. Finally, to obtain a comprehensive picture of this complicate dynamics, the total population of steady states for given pairs $(\eta_2, \eta_3) \in [0, 3]^2$ are given in Figure 7. We may observe from Figure 7(c) that two species coexist in two disjoint regimes. These domains are not as simple as the one in Figures 3(c) and 5(c). Furthermore, if we choose a different scale of resource distribution $m(x)$ the picture is changed, which is actually expected from the previous simulation in Figure 3.

Remark 2.3. The extinction, selection and coexistence of the competition systems (2.5) and (2.7) are not decided only by the parameters, but also by the scale of the resource distributions $m(x)$. Definitely, a useful model should give us the same result regardless of the choice of the
scale of population density and this inconsistency indicates the model is invalid. This invalidity comes from the advection term of non-SDD type. Notice that $u$ and $m$ share the same dimension and hence $\frac{u}{m}$ is a dimensionless quantity. One may observe that each term of the equation for $u^3$ has the dimension of the population density. However, the advection term in the equation for $u^2$ has a dimension of the square of the population density. This discrepancy gives the inconsistency of the simulations in Figure 3. However, the competition model (2.6) gives a consistent competition result regardless of the scale of population density.

3. Biological advection for chemotaxis

Keller and Segel’s equations for chemotaxis traveling wave phenomena are usually written as

\[
\begin{align*}
  u_t &= \nabla \cdot (\nabla u - \eta \frac{u}{m} \nabla m), \\
  m_t &= \epsilon \Delta m - ku,
\end{align*}
\]

(3.1)

where $u \geq 0$ is the population density, $m \geq 0$ is concentration of resource of bacteria, $\mu, \epsilon > 0$ are diffusivity coefficients, $\eta > 0$ is the chemo-sensitivity and $k \geq 0$ is the consumption rate. The choice of chemotactic term $-\eta \frac{u}{m} \nabla m$ is called the Weber-Fechner law.

Questions:

(1) What is the range of $\eta$ to have a traveling wave solution.
(2) Is there a relation to the fact that $\beta < 1$ for SDD?

Keller and Segel’s equations for chemotaxis aggregation phenomenon are usually written as

\[
\begin{align*}
  u_t &= \nabla \cdot (\nabla u - \eta \frac{u}{m} \nabla m), \\
  m_t &= \epsilon \Delta m + ku - \alpha m,
\end{align*}
\]

(3.2)

where $m \geq 0$ is concentration of pheromone produced by organisms, $k \geq 0$ is the production rate and $\alpha$ is the degradation rate.

Questions:

(1) What is the range of $\eta$ to have a global solution.
(2) What is the range of $\eta$ to have a aggregation phenomenon.
(3) Is there a relation to the fact that $\beta < 1$ for SDD?
(4) Can we conclude that SDD does not have an aggregation phenomenon? If so, what does it mean?

4. Biological cross-diffusion

A self-diffusion models the a dispersal phenomenon driven by intra-species interaction and a cross-diffusion by inter-species one. In particular, the role of a cross-diffusion in the pattern formation is taking attention of many researchers. One of the well-known cross-diffusion model is the one suggested by Shigesada, Kawasaki and Teramoto, which is simply called SKT model for brevity. On the other hand the starvation driven diffusion also contains cross-diffusion phenomenon. First, we briefly discuss the cross-diffusion theory of the SKT model and then compare it to the cross-diffusion phenomenon in a SDD model.

4.1. Cross-diffusion theory from SKT model. In the context of the Lotka-Volterra competition model of two species, the SKT model is written as

\[
\begin{align*}
  u_i^t &= \Delta((d_i + \sum_j a_{ij} w^j) u^i) + u^i \left(m^i(x) - \sum_j b_{ij} w^j\right), \\
  &= \nabla \cdot (d_i \nabla u^i + (a_{ii} + \sum_j a_{ij} w^j) \nabla u^i + a_{ik} u^i \nabla u^k) + u^i \left(m^i(x) - \sum_j b_{ij} w^j\right),
\end{align*}
\]

(4.1)

where $i = 1, 2$ and $k \neq i$. We may interpret the diffusion process of the model as a random dispersal with a departing probability $\gamma_i = d_i + a_{i1} u^1 + a_{i2} u^2$. Notice that any advection effect or the animal response to the environment is not included in this model.
Remark 4.1. One may easily observe the same discrepancy of dimension in the SKT model (4.1). Some terms are the dimension of population density and others have square of it. If the coefficients $a_{ij}, b_{ij}, d_i$ and $m^i$ are constant, then this discrepancy does not make a trouble. However, if the resource distributions $m^i(x)$ are not homogeneous, then the inconsistency observed in Section 2 may appear. Hence, if one considers a spatial heterogeneity, a model without a dimensional discrepancy should be chosen.

4.2. Cross-diffusion from SDD model. The starvation measure in the context of the Lotka-Volterra competition model in (4.1) for the $i$-th species is given by

\[ s^i = \frac{\sum b_{ij} u^j}{m^i(x)}. \]

We consider two species case with $i = 1, 2$. Let $k \neq i$ be the index of the other species. The starvation driven diffusion is written as

\[ u^i_t = \Delta (\gamma_i(s^i) u^i) = \nabla \cdot \left( \gamma_i(s^i) \nabla u^i + b_{ii} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^i + b_{ik} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^k - \gamma_i'(s^i) s^i \frac{u^i}{m^i} \nabla m^i \right). \]  

This equation is more or less identical to (2.1) except the cross-diffusion term $b_{ik} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^k$. We may consider two ways to develop a cross-diffusion model based on SDD. One is to have the self-diffusion term together and the other is not.

4.2.1. Approach #1: cross-diffusion theory with self-diffusion. We may rewrite (4.2) as

\[ u^i_t = \nabla \cdot \left( \gamma_i(s^i) \left( \nabla u^i + b_{11} \gamma_i(s^i) \frac{u^i}{m^i} \nabla u^i + b_{21} \gamma_i(s^i) \frac{u^i}{m^i} \nabla u^2 - \alpha_i(s^i) s^i \frac{u^i}{m^i} \nabla m^i \right) \right), \]

where the $\alpha_i(s^i)$'s are given by

\[ \alpha_i(s) = \frac{\gamma_i'(s)}{\gamma_i(s)}. \]

To write the equation explicitly we consider a power law $\gamma_i(s) = s^{p^i}$ for $p^i > 0$. Then, we have $\alpha_i(s) = p^i s^{-1}$. Therefore, after dropping the common coefficient $\gamma_i(s^i)$, the starvation driven diffusion is written as

\[ u^i_t = \nabla \cdot \left( \nabla u^i + p^i \frac{b_{11} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^1 + p^i \frac{b_{21} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right), \quad p^i > 0. \]

Notice that each term of this equation has the dimension of population density and hence is consistent on the choice of the scale of density. Now we add an logistic type population dynamics and obtain

\[ u^i_t = \nabla \cdot \left( \nabla u^i + p^i \frac{b_{11} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^1 + p^i \frac{b_{21} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right) + u^i \left( 1 - \frac{\sum b_{ij} u^j}{m^i} \right). \]

If it is expected that $b_{11} u^1 + b_{22} u^2 \equiv m^i$ near the steady state, then we may simplify the equation even further by writing

\[ u^i_t = \nabla \cdot \left( \nabla u^i + p^i \frac{b_{11} u^i}{m^i} \nabla u^1 + p^i \frac{b_{21} u^i}{m^i} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right) + u^i \left( 1 - \frac{\sum b_{ij} u^j}{m^i} \right). \]

For the homogeneous environments that the resource distribution $m^i(x)$ is constant we may obtain a simpler version of diffusion model. For example, if the resource distribution is $m^i = 1$, Eq. (4.12) is written as

\[ u^i_t = \nabla \cdot \left( \nabla u^i + p^i \frac{b_{11} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^1 + p^i \frac{b_{21} u^i}{b_{11} u^1 + b_{22} u^2} \nabla u^2 \right) + u^i \left( 1 - \sum b_{ij} u^j \right), \]

and Eq. (4.13) as

\[ u^i_t = \nabla \cdot \left( \nabla u^i + p^i b_{11} u^1 \nabla u^1 + p^i b_{21} u^1 \nabla u^2 \right) + u^i \left( 1 - \sum b_{ij} u^j \right). \]
The simplest case, Eq. (4.15), is in a similar form as the SKT model (4.1), where the diffusion coefficients are related to the reaction coefficients. Remember that these coefficients are given independently in the SKT model and hence SDD model gives a relation among them. The free variable \( p^i \) represents the value \( \frac{\gamma_i(s)}{\gamma_{(s)}(s)} \) and hence depends on the property of the motility function \( \gamma_i \). If the resource distribution is not constant one need to use (4.12) or (4.13). Each term in these equations has the dimension of population density. We may consider a

4.2.2. Approach #2: cross diffusion theory without self-diffusion. The starvation measure in the context of the Lotka-Volterra competition model in (4.1) for the \( i \)-th species is given by

\[
s^i = \frac{\sum_j b_{ij} u^j}{m^i(x)}.
\]

Then, the starvation driven diffusion is written as

\[
u^i_t = \Delta (\gamma_i(s^i) u^i) = \nabla \cdot \left( \gamma_i(s^i) \nabla u^i + b_{i1} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^i + b_{i2} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^2 - \gamma_i'(s^i) s^i \frac{u^i}{m^i} \nabla m^i \right) \]

(4.9)

\[
u^i = \nabla \cdot \left( \gamma_i(s^i) \left( \nabla u^i + b_{i1} \alpha_i(s^i) \frac{u^i}{m^i} \nabla u^1 + b_{i2} \alpha_i(s^i) \frac{u^i}{m^i} \nabla u^2 - \alpha_i(s^i) s^i \frac{u^i}{m^i} \nabla m^i \right) \right) \]

(4.10)

where the \( \alpha_i(s) \)'s are given by

\[
\alpha_i(s) = \frac{\gamma_i'(s)}{\gamma_i(s)}
\]

Eq. (4.2) is more or less identical to (2.1) except the cross-diffusion term \( b_{ij} \gamma_i'(s^i) \frac{u^i}{m^i} \nabla u^j \) when \( i \neq j \). To write the equation explicitly we consider a power law \( \gamma_i(s) = s^{p^i} \) for \( p^i > 0 \). Then, we have \( \alpha_i(s) = p^i s^{-1} \). Therefore, after dropping the common coefficient \( \gamma_i(s^i) \), the starvation driven diffusion is written as

\[
u^i_t = \nabla \cdot \left( \nabla u^i + p^i b_{i1} \frac{u^i}{m^i} \nabla u^1 + b_{i2} \frac{u^i}{m^i} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right), \quad p^i > 0. \]

(4.11)

Notice that each term of this equation has the dimension of population density and hence is consistent on the choice of the scale of density. Now we add an logistic type population dynamics and obtain

\[
u^i_t = \nabla \cdot \left( \nabla u^i + p^i \frac{b_{i1} u^i}{b_{i1} u^1 + b_{i2} u^2} \nabla u^1 + b_{i2} \frac{u^i}{m^i} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right) + u^i \left( 1 - \frac{\sum_j b_{ij} u^j}{m^i} \right).
\]

(4.12)

If it is expected that \( b_{i1} u^1 + b_{i2} u^2 \cong m^i \) near the steady state, then we may simplify the equation even further by writing

\[
u^i_t = \nabla \cdot \left( \nabla u^i + p^i b_{i1} \frac{u^i}{m^i} \nabla u^1 + p^i b_{i2} \frac{u^i}{m^i} \nabla u^2 - p^i \frac{u^i}{m^i} \nabla m^i \right) + u^i \left( 1 - \frac{\sum_j b_{ij} u^j}{m^i} \right).
\]

(4.13)

For the homogeneous environments that the resource distribution \( m^i(x) \) is constant we may obtain a simpler version of diffusion model. For example, if the resource distribution is \( m^i = 1 \), Eq. (4.12) is written as

\[
u^i_t = \nabla \cdot \left( \nabla u^i + p^i b_{i1} \frac{u^i}{m^i} \nabla u^1 + b_{i2} \frac{u^i}{m^i} \nabla u^2 \right) + u^i \left( 1 - \sum_j b_{ij} u^j \right).
\]

(4.14)

and Eq. (4.13) as

\[
u^i_t = \nabla \cdot \left( \nabla u^i + p^i b_{i1} u^i \nabla u^1 + b_{i2} u^i \nabla u^2 \right) + u^i \left( 1 - \sum_j b_{ij} u^j \right).
\]

(4.15)

The simplest case, Eq. (4.15), is in a similar form as the SKT model (4.1), where the diffusion coefficients are related to the reaction coefficients. Remember that these coefficients are given independently in the SKT model and hence SDD model gives a relation among them. The free variable \( p^i \) represents the value \( \frac{\gamma_i'(s)}{\gamma_{(s)}(s)} \) and hence depends on the property of the motility.
function $\gamma_i$. If the resource distribution is not constant one need to use (4.12) or (4.13). Each terms in these equations has the dimension of population density. We may consider a

4.3. Numerical Simulation for pattern formation.

5. Conclusion

References


Now we simplify (4.2) to obtain an approximated cross-diffusion term. The idea is that one should consider that \( u \) and \( v \) may have a big variation, but not the starvation measure \( s \). For example, the starvation measure is close to 1 near the steady state. Hence we rewrite the equation as

\[
\begin{align*}
    u_t &= \nabla \cdot \left( \gamma(s) \left( \nabla u + a(s) \frac{u}{m} \nabla u \right) \right) + \alpha(s) \frac{u}{m} \nabla \left( \nabla v - s \right), \quad \alpha(s) = \frac{\gamma'(s)}{\gamma(s)}. \n    \end{align*}
\]

Similarly, we eliminate the coefficient \( \gamma(s) \) and write

\[
\begin{align*}
    u_t &= \nabla \cdot \left( \nabla u + \alpha(s) \frac{u}{m} \nabla u + a(s) \frac{u}{m} \nabla v - s \alpha(s) \frac{u}{m} \nabla m \right). \quad (5.1)
\end{align*}
\]

Notice the relation between the coefficients for the self-diffusion and the cross diffusion. Both of them are multiplied by \( \frac{a}{m} \) and the ratio of the other parts is the constant \( a \) given by the Lotka-Volterra equation. To study the effect of this cross-diffusion we consider several competition models in the following subsections.

We will consider cases with \( a = 1 \) and the resource distribution for \( u \) and \( v \) are identical. In other words, the two species \( u \) and \( v \) are identical to each other except diffusion. First, let \( \theta_s \) be the steady state solution of

\[
    u_t = \nabla \cdot \left( \nabla u + \frac{u}{m} \nabla u \right) + u \left( 1 - \frac{u}{m} \right).
\]


5.1.1. SKT type self-diffusion. Consider a competition system

\[
\begin{align*}
    u_t &= \nabla \cdot \left( u \nabla u \right) + u \left( 1 - \frac{u + v}{m} \right), \quad (5.2) \\
    v_t &= \nabla \cdot \left( \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \quad (5.3)
\end{align*}
\]

5.1.2. SDD type self-diffusion. Consider a competition system

\[
\begin{align*}
    u_t &= \nabla \cdot \left( \frac{u}{m} \nabla u \right) + u \left( 1 - \frac{u + v}{m} \right), \quad (5.4) \\
    v_t &= \nabla \cdot \left( \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \quad (5.5)
\end{align*}
\]

5.2. Cross-diffusion.

5.2.1. SKT type cross-diffusion. Consider a competition system

\[
\begin{align*}
    u_t &= \nabla \cdot \left( u \nabla v \right) + u \left( 1 - \frac{u + v}{m} \right), \quad (5.6) \\
    v_t &= \nabla \cdot \left( \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \quad (5.7)
\end{align*}
\]

5.2.2. SDD type cross-diffusion. Consider a competition system

\[
\begin{align*}
    u_t &= \nabla \cdot \left( \frac{u}{m} \nabla v \right) + u \left( 1 - \frac{u + v}{m} \right), \quad (5.8) \\
    v_t &= \nabla \cdot \left( \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \quad (5.9)
\end{align*}
\]

5.3. Three SDD type diffusions but without advection. Consider a competition system

\[
\begin{align*}
    u_t &= \nabla \cdot \left( \nabla u + \frac{u}{m} \nabla u + \frac{u}{m} \nabla v \right) + u \left( 1 - \frac{u + v}{m} \right), \quad (5.10) \\
    v_t &= \nabla \cdot \left( \nabla v + \kappa \frac{v}{m} \nabla u + \frac{v}{m} \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \quad (5.11)
\end{align*}
\]

In this model both species \( u \) and \( v \) have same kind of diffusions. If \( \kappa = 1 \), then the two species are identical. According to previous modeling, \( \kappa = 1 \) seems the best choice. Can we show that \( (u, v) = (\theta, 0) \) is the globally asymptotically stable steady state for all \( \kappa \neq 1 \)?
5.4. SDD type diffusions versus SKT type diffusions. Consider a competition system

\[ u_t = \nabla \cdot \left( \nabla u + \frac{u}{m} \nabla u + \frac{u}{m} \nabla v \right) + u \left( 1 - \frac{u + v}{m} \right), \tag{5.12} \]

\[ v_t = \nabla \cdot \left( \nabla v + v \nabla u + v \nabla v \right) + v \left( 1 - \frac{u + v}{m} \right). \tag{5.13} \]

In this model the species \( u \) has SDD type diffusions and the species \( v \) has SKT type diffusions. Can we show that \((u, v) = (\theta, 0)\) is the globally asymptotically stable steady state?

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