Ideal Free Distribution in Two Patches*

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Abstract In this survey we discuss some recent progress on the ideal free distribution theory in patch models, with the emphasis on two patches. We show that dispersal strategies leading to the ideal free distributions of organisms are generally evolutionarily stable. We will also study the existence of evolutionarily stable dispersal strategies when dispersal strategies do not lead to the ideal free distributions. Applications to some river models are given.

Keywords Ideal free distribution, population dynamics, competition, patch model, evolutionarily stable strategy.

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1. Introduction

Ideal Free Distribution (abbreviated as IFD henceforth) is a theory for habitat choice of organisms, proposed by Fretwell and Lucas [18]. The basic question is: Given possibly heterogeneous environments, how should organisms distribute themselves in space? Two important assumptions, among others, are stated as follows: First, organisms are aware of the distribution of available resources (ideal); Second, there is no cost of movement (free). Under these assumptions, a prediction of Fretwell and Lucas in their theory is that the distribution of organisms should be proportional to the distribution of resources in space, which is termed as the ideal free distribution. The original statement of Fretwell and Lucas was described in terms of the fitness of organisms. As the ratio of the distribution of organisms versus the distribution of resources can be regarded as the fitness of organisms, in this paper we will refer the ratio of the distributions of organisms and resources as the fitness of the population.

The IFD theory has received tremendous interest in the last few decades, both empirically [35, 39] and theoretically [13, 14, 22, 25, 26]; See the references therein. Many biologists have tried to test this theory through experiments. The first experiment is due to Milinski [35], who used sticklebacks in his experiments. In the experiment, he put 6 fishes in a tank, and allocated one pipe at the left end and another at the right end of the fish tank, respectively, to deliver the food. The ratio of the input rate of the pipes at two ends is 5:1, indicating that the resource distributions at two ends are different. The experimental results show that the ratio of the fishes at two ends is also 5:1, which concurs with the prediction from the ideal free distribution theory. In this experiment, each fish can find out the distribution of the resources by swimming between the two ends of the fish tank, so the fishes

have "ideal" knowledge of the resources. Since the fish tank is relatively small, the swimming will not cause significant energy loss for fishes, so the movement can be regarded as relatively "free". In the experiment, Milinski also changed the input rates of the pipes at two ends, and he found that the proportions of the fishes at two ends evolved for a period of time, and the new distribution at the equilibrium still adhered to the ideal free distribution.

Evolutionarily stable strategy (ESS) is one of the important objectives in evolutionary biology. A strategy is said to be evolutionarily stable if any population using it can not be invaded by other population, when rare, using a different strategy. One of the topics in the spatial ecology concerns the evolution of dispersal, i.e., to determine dispersal strategies that are evolutionarily stable. In general, strategies that achieve the ideal free distribution are believed to be evolutionarily stable. Therefore, if one can observe that a species achieves an ideal free distribution across the habitat, it is usually equivalent to discovering an evolutionarily stable dispersal strategy which leads to such ideal free distribution. Of course, most of evolutionarily stable dispersal strategies do not necessarily lead to ideal free distributions.

The goal of this paper is to focus on continuous-time and discrete-space models (patch models) for ideal free distribution and to introduce the relevant theory to readers. We mainly aim to discuss some recent progress in the modeling and analysis of patch models for IFD, with the emphasis on two-patch models. We will propose some open questions for interested researchers. There are a vast of literature on ideal free distributions: For further references, we refer to [5, 6] for multi-patch models, [15, 31] for travels with loss, [7, 24] for discrete-time and discrete-space models, [4, 12] for nonlocal movement models, and [1, 3, 8–11, 19, 27, 30] for PDE models.

This paper is organized as follows: In Sect. 2 we discuss the ideal free distribution in a two-patch model with different carrying capacities. Sect. 3 is an application of the main results from Sect. 2 to a two-species river model. In Sect. 4 we consider river model with other boundary conditions and the main focus is the zero Dirichet boundary conditions. In Sect. 5 we extend some results from Sect. 2 for two patches to n patches. In Sect. 6 we discuss relevant questions in spatially and temporally varying environment.

2. Ideal free distribution and balanced dispersal

To study the evolution of dispersal, McPeek and Holt [34] considered a two-patch model which is discrete in both time and space. To present their idea more transparently, we consider a two-patch model:

$$\begin{cases} \frac{du_1}{dt} = d_{12}u_2 - d_{21}u_1 + u_1(1 - \frac{u_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d_{21}u_1 - d_{12}u_2 + u_2(1 - \frac{u_2}{K_2}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0, \end{cases} \tag{2.1}$$

where $u_i(t)$ denotes the number of individuals in patch i, K_i is the carrying capacity of patch i and is assumed to be a positive constant, $i = 1, 2$. d_{12} is the rate of movement from patch 2 to 1, and d_{21} denotes the rate of movement from patch 1 to patch 2. We also assume that d_{12}, d_{21} are positive constants.

As system (2.1) is monotone and sublinear, one can show that (2.1) has a unique

positive equilibrium, denoted by (u_1^*, u_2^*), which is also globally asymptotically stable among all positive initial data [38].

McPeek and Holt asked: What kind of dispersal strategies would imply the ideal free distribution of populations at equilibrium? If we regard u_i^*/K_i as the fitness of population in patch i, their question can be rephrased as: Find rates of movement d_{12} and d_{21} such that

$$\frac{u_1^*}{K_1} = \frac{u_2^*}{K_2}. \tag{2.2}$$

Note that (u_1^*, u_2^*) satisfies

$$\begin{cases} d_{12}u_2^* - d_{21}u_1^* + u_1^*(1 - \frac{u_1^*}{K_1}) = 0, \\ d_{21}u_1^* - d_{12}u_2^* + u_2^*(1 - \frac{u_2^*}{K_2}) = 0. \end{cases} \tag{2.3}$$

In principle it is not easy to give a closed form of u_1^*, u_2^*, which are functions of parameters d_{12}, d_{21}, K_1, K_2. However, if (2.2) holds, adding two equations of (2.3) we obtain

$$(u_1^* + u_2^*)(1 - \frac{u_1^*}{K_1}) = 0,$$

which implies that $u_i = K_i$ for $i = 1, 2$. Substituting these into (2.3) yields

$$\frac{d_{12}}{d_{21}} = \frac{K_1}{K_2}. \tag{2.4}$$

Hence, (u_1^*, u_2^*) is an IFD if and only if (2.4) holds. In fact, by a similar elementary argument, a more general conclusion holds and we leave the proof of the following result to interested readers:

Lemma 2.1. If $d_{12}K_2 = d_{21}K_1$, then $u_i^* = K_i$ for $i = 1, 2$, and $d_{12}u_2^* - d_{21}u_1^* = 0$; If $d_{12}K_2 > d_{21}K_1$, then $u_1^* > K_1$, $u_2^* < K_2$ and $d_{12}u_2^* - d_{21}u_1^* > 0$; If $d_{12}K_2 < d_{21}K_1$, then $u_1^* < K_1$, $u_2^* > K_2$ and $d_{12}u_2^* - d_{21}u_1^* < 0$.

If we regard $d_{12}u_2^* - d_{21}u_1^*$ as the flux between two patches, the flux is equal to zero if and only if $u_i^* = K_i$ for $i = 1, 2$. That is, the population reaches the ideal free distribution if and only if the flux between patches is zero. McPeek and Holt termed this scenario as the balanced dispersal, and the organisms have no incentive to move in such scenario as the fitness in both patches are the same.

For the rest of the paper, we denote the straight line in $d_{12} - d_{21}$ plane, given by (2.4), as the ideal free line, and we refer to dispersal strategies satisfying (2.4) as ideal free strategies, and strategies not satisfying (2.4) as non-ideal free strategies.

2.1. Ideal free strategy vs non-ideal free strategy

A natural question is: Do ideal free strategies convey competitive advantages over non-ideal free strategies? To address this question, we consider

$$\begin{cases} \frac{du_1}{dt} = d_{12}u_2 - d_{21}u_1 + u_1(1 - \frac{u_1+v_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d_{21}u_1 - d_{12}u_2 + u_2(1 - \frac{u_2+v_2}{K_2}), & t > 0, \\ \frac{dv_1}{dt} = D_{12}v_2 - D_{21}v_1 + v_1(1 - \frac{u_1+v_1}{K_1}), & t > 0, \\ \frac{dv_2}{dt} = D_{21}v_1 - D_{12}v_2 + v_2(1 - \frac{u_2+v_2}{K_2}), & t > 0, \\ u_i(0) > 0, \ v_i(0) > 0, & i = 1, 2, \end{cases} \tag{2.5}$$

where $v_i(t)$ denotes the number of individuals of another species which compete with species u_i, and D_{12}, D_{21} are rates of movement for species v_i. Here we assume that two species are identical except their dispersal strategies, and the underlying biological reasoning is that mutations only occur in dispersal rates; See [16,21,28,29] for further discussions.

System (2.5) has two semi-trivial steady states, denoted by $(u_1^*, u_2^*, 0, 0)$ and $(0, 0, v_1^*, v_2^*)$, respectively, where (v_1^*, v_2^*) is the unique positive equilibrium of (2.1) with d_{ij} being replaced by D_{ij}. The stability of these two semi-trivial steady states are important in determining the dynamics of (2.5). The trivial steady state $(0, 0, 0, 0)$ is always unstable.

Theorem 2.1. *Suppose that*

$$\frac{d_{12}}{d_{21}} = \frac{K_1}{K_2}, \quad \frac{D_{12}}{D_{21}} \neq \frac{K_1}{K_2}.$$

Then $(u_1^*, u_2^*, 0, 0)$ *is globally asymptotically stable.*

Theorem 2.1 is a special case of Theorem 5.1. It implies that the class of ideal free dispersal strategies is evolutionarily stable, as a mutant with a non-ideal free dispersal strategy can not invade when rare. Moreover, any mutant with ideal free dispersal strategies not only can invade a resident with a non-ideal free dispersal strategy but also can eliminate the resident in the long run.

2.2. Non-ideal free strategy vs non-ideal free strategy

If none of the dispersal strategies in (2.5) is ideal free, i.e.

$$\frac{d_{12}}{d_{21}} \neq \frac{K_1}{K_2}, \quad \frac{D_{12}}{D_{21}} \neq \frac{K_1}{K_2},$$

then the dynamics of (2.5) is more complicated. In her Ph.D thesis [37], Noble first established the following result:

Theorem 2.2. *Suppose that*

$$(\frac{d_{12}}{d_{21}} - \frac{K_1}{K_2}) \cdot (\frac{D_{12}}{D_{21}} - \frac{K_1}{K_2}) < 0.$$

Then both semi-trivial steady states are unstable, and (2.5) *has a unique positive equilibrium, denoted by* $(u_1^{**}, u_2^{**}, v_1^{**}, v_2^{**})$*, which is globally asymptotically stable among positive initial data.*

Theorem 2.2 implies that if (d_{12}, d_{21}) and (D_{12}, D_{21}) lie on the opposite sides of the ideal free line, then both species will always coexist. In fact, Noble further showed that

$$u_i^{**} + v_i^{**} = K_i, \quad i = 1, 2.$$

That is, while neither of the distributions of two species at equilibrium is ideal free, their joint distribution is ideal free. This phenomena is termed as the joint ideal free distributions and it has been studied for some PDE models [19]. The joint ideal free distribution may potentially provide an example for the evolution branching and it thus deserves further studies.

Noble then considered the remaining case where (d_{12}, d_{21}) and (D_{12}, D_{21}) lie on the same side of the ideal free line, which turns out to be more complicated. Given any pair of (d_{21}, d_{12}), denote the straight line L in $x - y$ plane by

$$\frac{y - d_{21}}{x - d_{12}} = \frac{u_2^*}{u_1^*}, \tag{2.6}$$

where (u_1^*, u_2^*) is the unique positive solution of (2.3). If (d_{12}, d_{21}) is an ideal free dispersal strategy, as $u_i^* = K_i$ in this case, the line L is reduced to the ideal free line, i.e. $y/x = K_2/K_1$. If (d_{12}, d_{21}) is an non-ideal free dispersal strategy, without loss of generality, we may assume that (d_{12}, d_{21}) lies above the line L, i.e. $d_{12}/d_{21} < K_1/K_2$, then by Lemma 2.1 we have $u_2^*/u_1^* > K_2/K_1$, i.e., the slope of line L is strictly greater than that of the ideal free line and thus line L lies strictly above the ideal free line in the whole closure of the first quadrant.

The second result of Noble in [37] can be stated as follows:

Theorem 2.3. *Given any pair of (d_{21}, d_{12}) satisfying $d_{12}/d_{21} < K_1/K_2$, and let L be the corresponding line given by (2.6).*

(i) *If (D_{21}, D_{12}) lies above line L, then $(u_1^*, u_2^*, 0, 0)$ is globally asymptotically stable;*

(ii) *If (D_{21}, D_{12}) lies between line L and the ideal free line, then $(0, 0, v_1^*, v_2^*)$ is globally asymptotically stable;*

(iii) *If (D_{21}, D_{12}) lies on line L, then there is a continuum of positive equilibria connecting two semi-trivial equilibria; Given any initial data, the solution of (2.5) converges to a positive equilibrium (the limit depends on the initial data).*

Theorems 2.1, 2.2 and 2.3 have some interesting applications, which will be presented in the next few sections.

3. IFD in River models

The two-patch model (2.1) has some interesting biological interpretation in river ecology. If we regard patch 1 as the upper stream end and patch 2 as the downstream end, we may envision that organisms can randomly diffuse between two patches with the same rate, denoted by d, and simultaneously, all individuals in patch 1 are subject to the drift to patch 2 with the rate $q > 0$. The dynamics of the population in two patches can thus be described by

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2}{K_2}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0. \end{cases} \tag{3.1}$$

It is well known that (3.1) has a unique positive equilibrium, denoted also by (u_1^*, u_2^*), which is globally asymptotically stable among positive initial data. If we compare (3.1) with (2.1), we see that the connection is given by

$$d_{21} = d + q, \quad d_{12} = d. \tag{3.2}$$

For such choice of (d_{12}, d_{21}), the unique positive equilibrium (u_1^*, u_2^*) of (3.1) reaches the ideal free distribution if (2.4) holds. It is easy to check that if $K_1 < K_2$, then (2.4) holds if and only if

$$d = \frac{qK_1}{K_2 - K_1}. \tag{3.3}$$

Moreover, if (3.3) holds, then $(u_1^*, u_2^*) = (K_1, K_2)$.

Consider the two-species competition model

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\ \frac{dv_1}{dt} = D(v_2 - v_1) - qv_1 + v_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = D(v_1 - v_2) + qv_1 + v_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\ u_i(0) > 0, \ v_i(0) > 0, & i = 1, 2. \end{cases} \tag{3.4}$$

The following result is a consequence of Theorem 2.1:

Theorem 3.1. *Suppose that $K_1 < K_2$. If*

$$d = \frac{qK_1}{K_2 - K_1}, \quad D \neq \frac{qK_1}{K_2 - K_1},$$

then the semi-trivial equilibrium $(K_1, K_2, 0, 0)$ of (3.4) is globally asymptotically stable.

Theorem 3.1 implies that if the downstream patch has higher carrying capacity than the upperstream, some intermediate dispersal rate is evolutionarily stable; Any single species with such dispersal rate will reach the ideal free distribution at equilibrium. This can also be explained as follows: If the dispersal rate is small, more individuals in the upperstream patch will be drifted to the downstream, which will cause the overcrowding in the downstream patch, and thus small dispersal rate will be selected against. If the dispersal rate is large, the number of individuals in both upperstream and downstream patches are approximately equal to each other, which is not favorable for species as more individuals can move to the upperstream patch which has the lower carrying capacity.

On the other hand, if $K_1 \geq K_2$, then (2.4) never holds for d_{12}, d_{21} satisfying (3.2). In fact, if $K_1 \geq K_2$, for $d_{12} = d$ and $d_{21} = d + q$, $D_{12} = D$ and $D_{21} = D + q$,

$$\frac{d_{12}}{d_{21}} - \frac{K_1}{K_2} < 0, \quad \frac{D_{12}}{D_{21}} - \frac{K_1}{K_2} < 0,$$

so that Theorem 2.3 is applicable. The following result, due to Y. Hamida [20], is a consequence of Theorem 2.3:

Theorem 3.2. *Suppose that $K_1 \geq K_2$.*

(i) *If $0 < q < \frac{K_1 - K_2}{K_1 + K_2}$ and $d < D$, then $(u_1^*, u_2^*, 0, 0)$ is globally asymptotically stable;*

(ii) *If $q > \frac{K_1 - K_2}{K_1 + K_2}$ and $d < D$, then $(0, 0, v_1^*, v_2^*)$ is globally asymptotically stable.*

For the case $K_1 > K_2$, it is easy to check that

$$\begin{cases} u_1^* > u_2^* & \text{if} \quad q < \frac{K_1 - K_2}{K_1 + K_2}; \\ u_1^* = u_2^* & \text{if} \quad q = \frac{K_1 - K_2}{K_1 + K_2}; \\ u_1^* < u_2^* & \text{if} \quad q > \frac{K_1 - K_2}{K_1 + K_2}. \end{cases}$$

This implies that if $q < \frac{K_1 - K_2}{K_1 + K_2}$ and $D > d$, then the point $(D_{21}, D_{12}) = (D, D + q)$ lies above the ideal free line L passing through $(d_{21}, d_{12}) = (d, d + q)$ with the slope u_2^*/u_1^*, i.e.

$$\frac{D_{21} - d_{21}}{D_{12} - d_{12}} = \frac{D - d}{D - d} = 1 > \frac{u_2^*}{u_1^*}. \tag{3.5}$$

Therefore, part (i) of Theorem 3.2 follows from (i) of Theorem 2.3. Similarly, (ii) of Theorem 3.2 is a consequence of (ii) of Theorem 2.3. We refer to [20] for further discussions. When $q = \frac{K_1 - K_2}{K_1 + K_2}$, it is easy to check that for any d, D, system (3.4) has a continuum of equilibria, which is given by

$$\left(\frac{2sK_1K_2}{K_1 + K_2}, \ \frac{2sK_1K_2}{K_1 + K_2}, \ \frac{2(1-s)K_1K_2}{K_1 + K_2}, \ \frac{2(1-s)K_1K_2}{K_1 + K_2} \right), \qquad s \in (0, 1),$$

and two species will coexist in this case.

For the case $K_1 = K_2$, part (i) of Theorem 3.2 is void, and part (ii) implies that the species with the larger diffusion rate has the competitive advantage over the species with the smaller dispersal rate, i.e. large diffusion rate will evolve in this case. An underlying reason is that as $d \to \infty$, $(u_1^*, u_2^*) \to (K_1, K_2)$; i.e. the spatial distribution of the single species is close to the ideal free distribution for sufficiently large d. See [32, 33] for similar conclusions for PDE models.

Finally, we mention that similarly as in this section, Theorems 2.1, 2.2 and 2.3 are also applicable to the two-patch model in [36] to yield a complete understanding of the evolutionarily stable dispersal strategy found there.

4. River model with different boundary conditions

In this section we derive several patch models with various "boundary" conditions under proper biological assumptions. We hope such formal derivations will help readers understand the underlying biological assumptions for these different models. We envision that organisms reside within four patches, denoted by patch i, $i = 0, 1, 2, 3$, respectively. We assume that, for $i = 0, 1, 2$, organisms can move between patches i and $i + 1$ with the same rate d, and organisms in patch i are subject to drift and they are transported from patch i to patch $i + 1$ with the same rate q. Let u_i denote the number of individuals in patch i, $i = 0, 1, 2, 3$. The changes of u_i for $i = 1, 2$ can be described by

$$\begin{cases} \frac{du_1}{dt} = d(u_2 + u_0 - 2u_1) + qu_0 - qu_1 + u_1(1 - \frac{u_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d(u_1 + u_3 - 2u_2) + qu_1 - qu_2 + u_2(1 - \frac{u_2}{K_2}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0. \end{cases} \tag{4.1}$$

No-flux boundary conditions: The flux from patch 0 to patch 1 is given by $d(u_0 - u_1) + qu_0$, and the flux from patch 2 to patch 3 is $d(u_2 - u_3) + qu_2$. If we

assume that these two fluxes are zero, i.e.

$$d(u_0 - u_1) + qu_0 = d(u_2 - u_3) + qu_2 = 0,$$

then (4.1) is reduced to (3.1). This means that in model (3.1), we assume that there are no flux at both upperstream and downstream patches, i.e., the system is closed.

Free flow condition at the downstream: If we assume that $d(u_0 - u_1) + qu_0 = 0$ and $u_2 = u_3$ (which is equivalent to $d(u_2 - u_3) + qu_2 = qu_2$), then (4.1) is reduced to the following model:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 - qu_2 + u_2(1 - \frac{u_2}{K_2}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0. \end{cases} \tag{4.2}$$

For this case, the upperstream end is closed, but at the downstream end, individuals can diffuse between patches 2 and 3, but those individuals drifted from patch 2 to 3 are not returning to patch 2. This means that a portion of individuals in patch 2 are "washed" out to patch 3, so suffering a lose there. We refer to [30] for further references of the corresponding PDE models.

For (4.2), it has at most one positive equilibrium, denoted by (u_1^*, u_2^*), which is globally asymptotically stable whenever it exists. If $K_1 = K_2$, we expect that the higher dispersal rate will be selected. More precisely, consider the two-spices competition model

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0 \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 - qu_2 + u_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\ \frac{dv_1}{dt} = D(v_2 - v_1) - qv_1 + v_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0, \\ \frac{dv_2}{dt} = D(v_1 - v_2) + qv_1 - qv_2 + v_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\ u_i(0) > 0, \ v_i(0) > 0, \quad i = 1, 2. \end{cases} \tag{4.3}$$

Suppose that $K_1 = K_2$ and $d > D > 0$. We conjecture that the semi-trivial equilibrium $(u_1^*, u_2^*, 0, 0)$ of (4.3), whenever it exists, is globally asymptotically stable; If $(u_1^*, u_2^*, 0, 0)$ does not exist, then the trivial equilibrium $(0, 0, 0, 0)$ is globally asymptotically stable; See [30] for similar results for PDE models. If $K_1 \neq K_2$, the dynamics of (4.3) is more complicated and it deserves further studies.

Dirichlet boundary conditions at the downstream: If we assume that $d(u_0 - u_1) + qu_0 = 0$ and $u_3 = 0$, then (4.1) is reduced to the following model:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1}{K_1}), & t > 0, \\ \frac{du_2}{dt} = d(u_1 - 2u_2) + qu_1 - qu_2 + u_2(1 - \frac{u_2}{K_2}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0. \end{cases} \tag{4.4}$$

For this model, the upperstream end remains closed, but at the downstream end, individuals can diffuse between patches 2 and 3, but no individuals can survive in patch 3. This is the worst scenario for the population.

If $d \geq 1$, (4.4) does not have positive equilibrium for any $q \geq 0$; For any $d \in (0, 1)$, (4.4) has a positive equilibrium if and only if $0 \leq q < 1 - d + \sqrt{d}$; See [40]. Furthermore, (4.4) has at most one positive equilibrium, and whenever it exists, it is globally asymptotically stable.

Consider the two-species competition model

$$
\begin{cases}
\frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0, \\
\frac{du_2}{dt} = d(u_1 - 2u_2) + q(u_1 - u_2) + u_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\
\frac{dv_1}{dt} = D(v_2 - v_1) - qv_1 + v_1(1 - \frac{u_1 + v_1}{K_1}), & t > 0, \\
\frac{dv_2}{dt} = D(v_1 - 2v_2) + q(v_1 - v_2) + v_2(1 - \frac{u_2 + v_2}{K_2}), & t > 0, \\
u_i(0) > 0, \ v_i(0) > 0, & i = 1, 2.
\end{cases}
\tag{4.5}
$$

The main result of [40] can be stated as follows:

Theorem 4.1. *Suppose that $K_1 = K_2$. For any $q \in (0, \frac{5}{4})$, there exists a unique $d^* > 0$ such that if $d = d^*$ and $D \neq d^*$, then $(u_1^*, u_2^*, 0, 0)$ is always locally asymptotically stable.*

Theorem 4.1 shows that in homogeneous environment, some intermediate dispersal rate is evolutionarily stable and is thus selected. There are a number of unsolved problems here. First, under the same condition as in Theorem 4.1, is $(u_1^*, u_2^*, 0, 0)$ globally asymptotically stable? If $(d - d^*)(D - d^*) < 0$, is there at most one positive (coexistence) equilibrium, and whenever it exists, is it globally asymptotically stable? If $D < d < d^*$ or $d^* < d < D$, is $(u_1^*, u_2^*, 0, 0)$ always globally asymptotically stable? Furthermore, how to extend these results to river models with more than two patches? What about the $K_1 \neq K_2$ case?

5. IFD in n patches

In this section we extend models (2.1) and (2.5) to n patches, $n \geq 2$. Let u_i denote the number of individuals in patch i, $1 \leq i \leq n$, where n is the total number of patches. Let d_{ij} denote the proportion of individuals which move from patch j to patch i, where $d_{ij} \geq 0$ and $d_{ii} = 0$. We say that a matrix is irreducible if it is not similar to a block upper triangular matrix with two blocks via a permutation.

Suppose that u_i satisfies

$$
\frac{du_i}{dt} = \sum_{j=1}^{n} (d_{ij} u_j - d_{ji} u_i) + u_i \left(1 - \frac{u_i}{K_i} \right), \quad t > 0,
\tag{5.1}
$$

and $u_i(0) > 0$ and $K_i > 0$ for every $1 \leq i \leq n$.

Following Cantrell et al. [5], we give the following definitions:

Definition 5.1. Given $K_1, ..., K_n$, (d_{ij}) is an ideal free dispersal strategy if

$$
\sum_{j=1}^{n} d_{ij} K_j = \left(\sum_{j=1}^{n} d_{ji} \right) K_i
\tag{5.2}
$$

holds for every $1 \leq i \leq n$. We say that (d_{ij}) is not an ideal free dispersal strategy if (5.2) fails to hold for some i.

If (d_{ij}) is an ideal free dispersal strategy, then (5.1) has a unique positive equilibrium, given by $(K_1, ..., K_n)$, which is globally asymptotically stable for any initial data $u_i(0) > 0$, $1 \leq i \leq n$.

Consider the two-species model in n-patch:

$$
\begin{cases}
\dfrac{du_i}{dt} = \displaystyle\sum_{j=1}^{n} (d_{ij}u_j - d_{ji}u_i) + u_i\left(1 - \dfrac{u_i + v_i}{K_i}\right), & t > 0, \\[3ex]
\dfrac{dv_i}{dt} = \displaystyle\sum_{j=1}^{n} (D_{ij}v_j - D_{ji}v_i) + v_i\left(1 - \dfrac{u_i + v_i}{K_i}\right), & t > 0,
\end{cases}
\tag{5.3}
$$

where $u_i(0), v_i(0) > 0$ for $1 \le i \le n$. We also assume that $D_{ij} \ge 0$ and $D_{ii} = 0$ for $1 \le i, j \le n$.

The following result was established in [6] and it is an extension of Theorem 2.1:

Theorem 5.1. *Suppose that both matrices (d_{ij}) and (D_{ij}) are irreducible. If (d_{ij}) is an ideal free dispersal strategy and (D_{ij}) is not an ideal free dispersal strategy, then $(K_1, ..., K_n, 0, ..., 0)$ is an equilibrium of* (5.3) *which is stable, and*

$$
\lim_{t \to \infty} (u_1, ..., u_n, v_1, ..., v_n) = (K_1, ..., K_n, 0, ..., 0).
$$

To prove Theorem 5.1, we say that an $n \times n$ matrix A is line-sum-symmetric if for every $1 \le i \le n$, the sum of the elements in the i-th row of A equals the sum of the elements in the i-th column of A. The following result gives a classification of line-sum-symmetric matrices (Corollary 3, [17]).

Theorem 5.2. *Let $A = (a_{ij})$ be an $n \times n$ non-negative matrix. Then A is line-sum-symmetric if and only if*

$$
\sum_{i,j=1}^{n} a_{ij} \frac{x_i}{x_j} \ge \sum_{i,j=1}^{n} a_{ij}
\tag{5.4}
$$

for all $x_i > 0$, $1 \le i \le n$. Moreover, if A is irreducible and line-sum-symmetric, equality in (5.4) *holds if and only if $x_i = x_j$ for any $1 \le i, j \le n$.*

For the reader's convenience, we illustrate an idea of Z. Shuai to establish inequality (5.4). Recall the well known inequality

$$
y \ge 1 + \ln y, \qquad y > 0.
$$

Hence, given any $x_i > 0$, $1 \le i \le n$, we have

$$
\frac{x_i}{x_j} \ge 1 + \ln \frac{x_i}{x_j}, \qquad 1 \le i, j \le n.
\tag{5.5}
$$

Multiplying (5.5) by a_{ij} and summing over i, j we obtain

$$
\sum_{i,j=1}^{n} a_{ij} \frac{x_i}{x_j} \ge \sum_{i,j=1}^{n} a_{ij} + \sum_{i,j=1}^{n} a_{ij} \ln \frac{x_i}{x_j} = \sum_{i,j=1}^{n} a_{ij},
\tag{5.6}
$$

where the last inequality follows from

$$\sum_{i,j=1}^{n} a_{ij} \ln \frac{x_i}{x_j} = \sum_{i,j=1}^{n} a_{ij} \ln x_i - \sum_{i,j=1}^{n} a_{ij} \ln x_j$$

$$= \sum_{i,j=1}^{n} a_{ij} \ln x_i - \sum_{i,j=1}^{n} a_{ji} \ln x_i$$

$$= \sum_{i,j=1}^{n} a_{ij} \ln x_i - \sum_{i=1}^{n} \ln x_i \left(\sum_{j=1}^{n} a_{ji} \right)$$

$$= \sum_{i,j=1}^{n} a_{ij} \ln x_i - \sum_{i=1}^{n} \ln x_i \left(\sum_{j=1}^{n} a_{ij} \right) \quad \text{(line sum symmetric property)}$$

$$= 0.$$

(5.7)

For the converse part in Theorem 5.2, we refer to [17]. For a partial extension of Theorem 5.2, see Cantrell et al. [4].

The key point in the proof of Theorem 5.1 is to show that the following functional V is a Lyapunov functional:

$$V(u_1, ..., u_n, v_1, ..., v_n) = \sum_{i=1}^{n} (u_i + v_i) - \sum_{i=1}^{n} K_i \ln(u_i).$$

We show that if $\sum_j (d_{ij} K_j - d_{ji} K_i) = 0$ for every $1 \leq i \leq n$, then $\dot{V}(u) \leq 0$ as follows:

$$\dot{V}(u) = -\sum_{i=1}^{n} \frac{(u_i + v_i - K_i)^2}{K_i} - \left[\sum_{i,j=1}^{n} \frac{K_i}{u_i} d_{ij} u_j - \sum_{i,j=1}^{n} K_i d_{ji} \right].$$

Set $a_{ij} = d_{ij} K_j$. By assumption on matrix (d_{ij}), (a_{ij}) is line-sum-symmetric, non-negative and irreducible. Set $x_i := K_i/u_i > 0$. Then by Theorem 5.2,

$$\sum_{i,j=1}^{n} \frac{K_i}{u_i} d_{ij} u_j - \sum_{i,j=1}^{n} K_i d_{ji} = \sum_{i,j=1}^{n} a_{ij} \frac{x_i}{x_j} - \sum_{i,j=1}^{n} a_{ij} \geq 0.$$

Hence, $\dot{V}(u) \leq 0$. For detailed proof of Theorem 5.1, we refer to [6].

Theorem 5.1 concerns the case when (d_{ij}) is an ideal free dispersal strategy but (D_{ij}) is not. When neither (d_{ij}) and (D_{ij}) is an ideal free dispersal strategy, the dynamics of (5.3) appears rather complicated, and it is challenging to extend Theorem 2.3 to n patches with $n \geq 3$.

6. IFD in time-periodic environment

We first consider a two-patch model in spatially and temporally varying environment:

$$\begin{cases} \frac{du_1}{dt} = d_{12}(t) u_2 - d_{21}(t) u_1 + u_1 (1 - \frac{u_1}{K_1(t)}), & t > 0, \\ \frac{du_2}{dt} = d_{21}(t) u_1 - d_{12}(t) u_2 + u_2 (1 - \frac{u_2}{K_2(t)}), & t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0, \end{cases}$$

(6.1)

where $u_i(t)$ denotes the number of individuals in patch i, $K_i(t)$ is the carrying capacity of patch i and is assumed to be positive, non-constant, continuously differentiable, and periodic in time with period T, $i = 1, 2$. We also assume that diffusion rates d_{12}, d_{21} are positive, continuous and periodic in time with period T.

It can be shown that (6.1) has a unique positive periodic solution, still denoted as $(u_1(t), u_2(t))$ for the sake of simplicity, which is globally asymptotically stable for all positive initial data. A natural question for (6.1) is whether there exist dispersal strategies $(d_{12}(t), d_{21}(t))$ such that $u_i = K_i$ for $i = 1, 2$ and $t \in [0, T]$. To this end, substituting $u_i = K_i$ into (6.1) we obtain

$$\begin{cases} \frac{dK_1}{dt} = d_{12}(t)K_2 - d_{21}(t)K_1, & t > 0, \\ \frac{dK_2}{dt} = d_{21}(t)K_1 - d_{12}(t)K_2, & t > 0. \end{cases} \tag{6.2}$$

Hence, a necessary condition for $(u_1(t), u_2(t)) = (K_1, K_2)$ is that $(K_1 + K_2)' = 0$, i.e. $K_1(t) + K_2(t) = K$ for some positive constant K. This was first observed by Cantrell and Cosner in [2] for PDE models.

Next we illustrate that if $K_1 + K_2$ is a positive constant, then there exist dispersal strategies $(d_{12}(t), d_{21}(t))$ such that $u_i = K_i$ for $i = 1, 2$ and $t \in [0, T]$. By the above reasoning, it suffices to show that there exist $(d_{12}(t), d_{21}(t))$ satisfying (6.2). By $K_1 + K_2 = K$, it suffices to find $(d_{12}(t), d_{21}(t))$ satisfying

$$d_{12} = \frac{d_{21}K_1 + K_1'}{K_2}, \quad t > 0. \tag{6.3}$$

Given K_1 and K_2, choose $d_{21}(t)$ to be positive and $T-$periodic such that $d_{21}(t) > -K_1'(t)/K_1(t)$ for $t \in [0, T]$. Then choose d_{12} by (6.3). For such choice, both d_{12} and d_{21} are positive and $T-$periodic, and the corresponding unique positive T-periodic solution of (6.3) satisfies $u_i = K_i$ for $i = 1, 2$ and $t \in [0, T]$.

Similarly as in previous sections, we may enquire whether ideal free strategies convey competitive advantages over non-ideal free strategies. To this end we may consider

$$\begin{cases} \frac{du_1}{dt} = d_{12}(t)u_2 - d_{21}(t)u_1 + u_1(1 - \frac{u_1 + v_1}{K_1(t)}), & t > 0, \\ \frac{du_2}{dt} = d_{21}(t)u_1 - d_{12}(t)u_2 + u_2(1 - \frac{u_2 + v_2}{K_2(t)}), & t > 0, \\ \frac{dv_1}{dt} = D_{12}(t)v_2 - D_{21}(t)v_1 + v_1(1 - \frac{u_1 + v_1}{K_1(t)}), & t > 0, \\ \frac{dv_2}{dt} = D_{21}(t)v_1 - D_{12}(t)v_2 + v_2(1 - \frac{u_2 + v_2}{K_2(t)}), & t > 0, \\ u_i(0) > 0, \; v_i(0) > 0, \quad i = 1, 2. \end{cases} \tag{6.4}$$

If $K_1 + K_2$ is a positive constant, d_{ij} and D_{ij} are positive and $T-$periodic functions satisfying

$$d_{12} \equiv \frac{d_{21}K_1 + K_1'}{K_2}, \quad D_{12} \not\equiv \frac{D_{21}K_1 + K_1'}{K_2}, \qquad t \in [0, T], \tag{6.5}$$

we may ask whether $(K_1, K_2, 0, 0)$ is globally asymptotically stable in (6.4); For the case

$$d_{12} \not\equiv \frac{d_{21}K_1 + K_1'}{K_2}, \quad D_{12} \not\equiv \frac{D_{21}K_1 + K_1'}{K_2}, \qquad t \in [0, T], \tag{6.6}$$

the dynamics of (6.4) will be more complex. In fact, if both d_{12} and d_{21} are positive constants, there is no ideal free distribution, i.e. $u_i \equiv K_i$ for $i = 1, 2$. To see

this, it suffices to show that when $K_1 + K_2 = K$, (6.3) can not hold. We argue by contradiction: If not, suppose that d_{12} and d_{21} are positive constants, $K_1 + K_2 = K$ for some positive constant K and (6.3) holds, i.e.

$$\frac{dK_1}{dt} + (d_{12} + d_{21})K_1 = d_{21}K,$$

from which it follows that

$$K_1(t) = \frac{d_{21}K}{d_{12} + d_{21}} + Ce^{-(d_{12}+d_{21})t}$$

for some constant C. As K_1 is periodic, $C = 0$, which implies that K_1 is a constant function, contradicting the assumption that K_1 is non-constant.

It would be of interest to consider the dynamics of (6.4) for constant functions d_{ij} and D_{ij}. A special but interesting case is to consider $d_{12} = d_{21} = d$ and $D_{12} = D_{21} = D$ for some positive constants d and D, that is,

$$
\begin{cases}
\frac{du_1}{dt} = d(u_2 - u_1) + u_1(1 - \frac{u_1+v_1}{K_1(t)}), & t > 0, \\
\frac{du_2}{dt} = d(u_1 - u_2) + u_2(1 - \frac{u_2+v_2}{K_2(t)}), & t > 0, \\
\frac{dv_1}{dt} = D(v_2 - v_1) + v_1(1 - \frac{u_1+v_1}{K_1(t)}), & t > 0, \\
\frac{dv_2}{dt} = D(v_1 - v_2) + v_2(1 - \frac{u_2+v_2}{K_2(t)}), & t > 0, \\
u_i(0) > 0, \ v_i(0) > 0, & i = 1, 2.
\end{cases}
\tag{6.7}
$$

The dynamics of (6.7) is not fully understood when K_1 and K_2 are two positive, time periodic functions. For example, the slower diffusing species may not have competitive advantage in model (6.7), which is different from the spatially heterogeneous but temporally constant case, i.e. K_1, K_2 are positive, distinct constants. See Hutson et al. [23] for such results for PDE models.

Another interesting case is to study the following two-species river model in spatially heterogeneous and temporally varying environment:

$$
\begin{cases}
\frac{du_1}{dt} = d(u_2 - u_1) - q(t)u_1 + u_1(1 - \frac{u_1+v_1}{K_1(t)}), & t > 0, \\
\frac{du_2}{dt} = d(u_1 - u_2) + q(t)u_1 + u_2(1 - \frac{u_2+v_2}{K_2(t)}), & t > 0, \\
\frac{dv_1}{dt} = D(v_2 - v_1) - q(t)v_1 + v_1(1 - \frac{u_1+v_1}{K_1(t)}), & t > 0, \\
\frac{dv_2}{dt} = D(v_1 - v_2) + q(t)v_1 + v_2(1 - \frac{u_2+v_2}{K_2(t)}), & t > 0, \\
u_i(0) > 0, \ v_i(0) > 0, & i = 1, 2,
\end{cases}
\tag{6.8}
$$

where K_i is positive, time-periodic functions, $i = 1, 2$. Here q could also be a positive and time-periodic function, reflecting the variability of seasonal changes of the river flow.

Acknowledgements

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