

# Diffusion-Driven Instability in Reaction–Diffusion Systems

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For a stable matrix  $A$  with real entries, sufficient and necessary conditions for  $A - D$  to be stable for all non-negative diagonal matrices  $D$  are obtained. Implications of these conditions for the stability and instability of constant steady-state solutions to reaction–diffusion systems are discussed and an example is given to show applications. © 2001 Academic Press

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## 1. INTRODUCTION

Let  $f: \mathbf{R}^n \rightarrow \mathbf{R}^n$  be a  $C^1$  function and assume that  $f(0) = 0$ . Then  $u = 0$  is an equilibrium solution to the system of ordinary differential equations

$$\frac{du}{dt} = f(u). \quad (1.1)$$

The equilibrium is locally asymptotically stable if the Jacobian matrix  $A = f'(0)$  is stable; namely, all the eigenvalues of  $A$  have negative real parts (see [7]). Let  $\Omega \subset \mathbf{R}^m$  be a bounded domain with smooth boundary and  $D = \text{diag}(d_1, \dots, d_n)$  with  $d_i \geq 0$ . Then  $u = 0$  is also a spatially homogeneous steady-state solution to the following reaction–diffusion



system with Neumann boundary condition

$$\begin{aligned} u_t &= D \Delta u + f(u) && \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial \nu} &= 0 && \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) &= u_0(x) && \text{in } \Omega, \end{aligned} \tag{1.2}$$

where  $u = (u_1, \dots, u_n) \in \mathbf{R}^n$ ,  $\Delta$  is the Laplacian in the variable  $x \in \Omega \subset \mathbf{R}^m$ , and  $\nu$  is the unit outward normal to  $\partial\Omega$ . System (1.1) is the *kinetic* system of (1.2). It is well known that, if the diffusion coefficients  $d_i$  are the same, an asymptotically stable equilibrium  $u = 0$  of (1.1) remains asymptotically stable for the reaction–diffusion system (1.2) (see [1, 19]). Turing [20] is the first to demonstrate that different diffusion coefficients can cause  $u = 0$  to cease to be stable for (1.2). Turing’s idea has since been further explored by many authors (see [2, 16–18] and references therein), and diffusion-driven instability has become an important mechanism for the emergence of interesting patterns in many model systems.

The stability of  $u = 0$  for (1.2) is customarily studied by the method of linear approximation. Let

$$\begin{aligned} v_t &= D \Delta v + Av && \text{in } \Omega \times (0, \infty), \\ \frac{\partial v}{\partial \nu} &= 0 && \text{on } \partial\Omega \times (0, \infty), \\ v(x, 0) &= v_0(x) && \text{in } \Omega \end{aligned} \tag{1.3}$$

be the linearization of (1.2) at  $u = 0$ , where  $A = f'(0)$ , the Jacobian matrix of  $f$  at 0. Then  $u = 0$  is asymptotically stable for (1.2) if  $v = 0$  is asymptotically stable for (1.3); namely,  $\|v(x, t)\| \leq K \exp(-\alpha t)\|v_0(x)\|$  for some  $K, \alpha > 0$  and all  $t > 0$ .  $u = 0$  is unstable if there exists  $k$  such that  $A - \lambda_k D$  has an eigenvalue with positive real part, where  $0 = \lambda_0 \leq \lambda_1 \leq \dots \leq \lambda_k \leq \dots$  are the eigenvalues of the negative Laplacian in  $\Omega$  with Neumann boundary condition (see [1, 19]). At the core of the stability analysis are the following matrix problems. Assume that  $A$  is stable. (1) Find necessary and sufficient conditions that  $A - D$  is stable for all  $D = \text{diag}(d_1, \dots, d_n)$  with  $d_i \geq 0$ . (2) Let such a  $D$  be given; find necessary and sufficient conditions such that  $s(A - \lambda D) \leq -\delta$  for some  $\delta > 0$  that is uniform for all  $\lambda \geq 0$ . Here  $s(B)$  denotes the largest real part of all eigenvalues of a matrix  $B$ . Answers to problem (1) will give rise to conditions for the diffusion-driven instability to occur, whereas solutions to problem (2) will provide a way to prove the stability of constant steady-state for reaction–diffusion systems.

In this paper, we derive a set of conditions, which we call the *minors condition*, that seem to be at the heart of both problems (1) and (2). We prove in Theorem 3.1 that, for a stable matrix  $A$ , the minors condition is necessary for  $A - D$  to be stable for all non-negative diagonal  $D$ . This allows a systematic way of detecting the occurrence of diffusion-driven instability by checking the signs of principal minors of  $A = f'(0)$ . For  $n \leq 3$  or if  $A$  satisfies a stronger stability property, we prove in Theorem 3.8 that the strict minors condition is sufficient and necessary for  $s(A - \lambda D) \leq -\delta$  to hold for some  $\delta > 0$  that is uniform for all  $\lambda \geq 0$  and all non-negative diagonal  $D$ . This in turn implies that  $u = 0$  is asymptotically stable for (1.2) with respect to all non-negative diagonal diffusion matrices. Furthermore, under a similar assumption, we prove in Theorem 3.9 that the strict minors condition is sufficient and necessary for all the principal submatrices of  $A$  to be stable. From a matrix theoretical viewpoint, this last result is interesting on its own right. Casten and Holland [1] have considered similar problems. For a positive diagonal matrix  $D$ , they prove the asymptotical stability of  $u = 0$  for (1.2) under the assumption that  $A - \lambda D$  is stable for all  $\lambda \geq 0$ . For  $n \leq 3$ , they prove that a sufficient condition for this assumption to hold is that all the principal submatrices of  $A$ , together with  $A$  itself, are stable.

Cross-diffusion is not considered in our paper; the diffusion matrix  $D$  will be assumed to be diagonal throughout the paper. It is known that cross-diffusion can induce instability [12, 13, 17]. It is also known that diffusion and cross-diffusion can induce other types of instability such as finite time blowup of solutions (see [14]) or extinction of solutions (see [9]).

The paper is organized as follows. In the next section, we provide necessary preliminary results. In Section 3, we study various matrix properties related to the problems (1) and (2) stated above. Implications of these matrix properties for the instability and stability of a steady-state  $u = 0$  of (1.2) are studied in Section 4. The paper ends with an example in Section 5.

## 2. PRELIMINARIES

Let  $\mathbf{M}_n(\mathbf{R})$  be the linear space of  $n \times n$  matrices with entries in  $\mathbf{R}$ , the field of real numbers, and let  $A = (a_{ij})_{n \times n} \in \mathbf{M}_n(\mathbf{R})$ . For  $1 \leq k \leq n$ , let  $I_k$  denote the set

$$I_k = \{(i_1, i_2, \dots, i_k) \mid 1 \leq i_1 < i_2 < \dots < i_k \leq n\}.$$

Set  $I_0 = \phi$ . For any  $J = (i_1, i_2, \dots, i_k) \in I_k$ , let  $P_J(A)$  denote the  $k \times k$  principal submatrix of  $A$

$$\begin{bmatrix} a_{i_1 i_1} & a_{i_1 i_2} & \cdots & a_{i_1 i_k} \\ a_{i_2 i_1} & a_{i_2 i_2} & \cdots & a_{i_2 i_k} \\ \vdots & \vdots & \ddots & \vdots \\ a_{i_k i_1} & a_{i_k i_2} & \cdots & a_{i_k i_k} \end{bmatrix},$$

and define  $P_\phi(A) = 1$ . If  $D$  is a diagonal matrix with non-negative diagonal entries  $d_1, d_2, \dots, d_n$ , and let  $d_J = \prod_{j \in J} d_j$  for  $J \in I_k$  and  $d_\phi = 1$ . Let  $J' = \{1, 2, \dots, n\} \setminus J$  for  $J \in I_k$ . The determinant  $\det(A - D)$  can be expressed as a polynomial of  $d_j$  as follows:

$$\begin{aligned} \det(A - D) &= \sum_{k=0}^n (-1)^k \sum_{J \in I_k} \det(P_{J'}(A)) d_J \\ &= \det(A) + \sum_{k=1}^{n-1} (-1)^k \sum_{J \in I_k} \det(P_{J'}(A)) d_J + (-1)^n \prod_{j=1}^n d_j. \end{aligned} \tag{2.1}$$

If  $D = \lambda I_{n \times n}$  then (2.1) is the characteristic polynomial of  $A$ .

Let  $\sigma(A)$  be the *spectrum* of  $A$ , and  $s(A) = \max\{\text{Re } \lambda \mid \lambda \in \sigma(A)\}$ . A matrix  $A$  is said to be *stable* if  $s(A) < 0$  and *unstable* if  $s(A) > 0$ .

Let “ $\wedge$ ” denote the exterior product in  $\mathbf{R}^n$ . With respect to the canonical basis in the second exterior product space  $\wedge^2 \mathbf{R}^n$ , the *second additive compound matrix*  $A^{[2]}$  of  $A$  represents a linear operator on  $\wedge^2 \mathbf{R}^n$  defined by

$$A^{[2]}(u_1 \wedge u_2) = Au_1 \wedge u_2 + u_1 \wedge Au_2$$

for decomposable elements  $u_1 \wedge u_2$ . Definition over the whole  $\wedge^2 \mathbf{R}^n$  is done by linear extension. It is clear that  $A^{[2]}$  is an  $\binom{n}{2} \times \binom{n}{2}$  matrix. The second additive compound matrices are given in the Appendix for  $n = 2, 3$ , and 4. For a detailed discussion on compound matrices, the reader is referred to [4, 15]. Pertinent to the present paper is the following spectral property of  $A^{[2]}$ : if  $\sigma(A) = \{\lambda_i \mid i = 1, \dots, n\}$ , then  $\sigma(A^{[2]}) = \{\lambda_{i_1} + \lambda_{i_2} \mid 1 \leq i_1 < i_2 \leq n\}$ .

Let  $|\cdot|$  denote a vector norm in  $\mathbf{R}^n$  and the operator norm it induces in  $\mathbf{M}_n(\mathbf{R})$ . The *Lozinskii measure*  $\mu$  on  $\mathbf{M}_n(\mathbf{R})$  with respect to  $|\cdot|$  is defined by (see [3, p. 41])

$$\mu(A) = \lim_{h \rightarrow 0^+} \frac{|I + hA| - 1}{h},$$

for  $A \in \mathbf{M}_n(\mathbf{R})$ . Lozinskii measures satisfy the standard properties of a measure. In particular,  $\mu(A + B) \leq \mu(A) + \mu(B)$ . The Lozinskii measures of  $A = (a_{ij})$  with respect to the three common norms  $|x|_\infty = \sup_i |x_i|$ ,  $|x|_1 = \sum_i |x_i|$ , and  $|x|_2 = (\sum_i |x_i|^2)^{1/2}$  are, respectively,

$$\mu_\infty(A) = \sup_i \left( \operatorname{Re} a_{ii} + \sum_{k, k \neq i} |a_{ik}| \right), \quad (2.2)$$

$$\mu_1(A) = \sup_k \left( \operatorname{Re} a_{kk} + \sum_{i, i \neq k} |a_{ik}| \right), \quad \text{and} \quad (2.3)$$

$$\mu_2(A) = s \left( \frac{A + A^*}{2} \right). \quad (2.4)$$

A Lozinskii measure  $\mu(A)$  dominates  $s(A)$  as the following lemma states; see [3] for a proof.

LEMMA 2.1. *Let  $\mu$  be a Lozinskii measure. Then  $s(A) \leq \mu(A) \leq |A|$ .*

Let  $P \in \mathbf{M}_n(\mathbf{R})$  be invertible and let  $|\cdot|$  be a given norm in  $\mathbf{R}^n$ . Define a new norm  $|\cdot|_P$  in  $\mathbf{R}^n$  by  $|x|_P = |Px|$  and denote the Lozinskii measures with respect to  $|\cdot|$  and  $|\cdot|_P$  by  $\mu$  and  $\mu_P$ , respectively. The following result is standard (see [3]).

LEMMA 2.2. *Let  $P \in \mathbf{M}_n(\mathbf{R})$  be invertible. Then*

$$\mu_P(A) = \mu(PAP^{-1}).$$

The following stability criterion is proved in [10, Theorem 3.2].

THEOREM 2.3. *For  $A$  to be stable, it is sufficient and necessary that  $(-1)^n \det(A) > 0$  and  $\mu(A^{[2]}) < 0$  for some Lozinskii measure  $\mu$  on  $\mathbf{M}_N(\mathbf{R})$ ,  $N = \binom{n}{2}$ .*

The proof for the sufficiency in Theorem 2.3 is an easy application of the spectral properties of  $A^{[2]}$ . In fact,  $\mu(A^{[2]}) < 0$  implies that the eigenvalues of  $A$  satisfy  $\operatorname{Re} \lambda_i + \operatorname{Re} \lambda_j < 0$ ,  $i \neq j$ , and thus can have at most one non-negative real part. The condition  $(-1)^n \det(A) > 0$  then implies that all the real parts are negative and hence  $A$  is stable. See [10] for the proof of necessity and for an application in epidemic models.

### 3. STABILITY AND INSTABILITY RESULTS FOR MATRICES

Let  $D = \operatorname{diag}(d_1, \dots, d_n)$ . We say  $D \geq 0$  if  $d_i \geq 0$  for all  $1 \leq i \leq n$ , and  $D > 0$  if  $d_i > 0$  for all  $1 \leq i \leq n$ . In this and the remaining sections,  $D$  always denotes a diagonal matrix.

**THEOREM 3.1.** *Assume that  $A$  is stable and that  $A$  satisfies  $(-1)^k \det(P_J(A)) < 0$  for some  $1 \leq k \leq n$  and  $J \in I_k$ . Then there exists  $D \geq 0$  such that  $A - D$  is unstable.*

*Proof.* It suffices to show the existence of  $D \geq 0$  such that

$$(-1)^n \det(A - D) < 0.$$

Choose  $D$  such that  $d_i = 0$  for  $i \in J$  and  $d_i = d > 0$  for  $i \in J'$ . Then  $(-1)^n \det(A - D) = (-1)^n \det(A) + (-1)^k \det(P_J(A))d^{n-k}$  by (2.1). Since  $(-1)^k \det(P_J(A)) < 0$ ,  $(-1)^n \det(A - D) < 0$  if  $d$  is sufficiently large. ■

In the light of Theorem 3.1, the following question is natural. Suppose  $(-1)^k \det(P_J(A)) \geq 0$  for all  $J \in I_k$  and  $1 \leq k \leq n$ . Does the stability of  $A$  imply that of  $A - D$  for all  $D \geq 0$ ? If  $A$  is symmetric or if  $A$  is an  $M$ -matrix [5, 6], it is easy to see that the answer to the question is affirmative. For a general matrix  $A$ , we provide an answer in the next two theorems.

A matrix  $A$  is said to satisfy the *minors condition* if  $(-1)^k \det(P_J(A)) \geq 0$  for all  $J \in I_k$  and  $1 \leq k \leq n$ . The minors condition is said to be *strict* if the inequalities in the above definition are strict.

**THEOREM 3.2.** *Assume that  $n \leq 3$  and  $A$  is stable. Then  $A - D$  is stable for all  $D \geq 0$  if and only if  $A$  satisfies the minors condition.*

*Proof.* The necessity follows from Theorem 3.1. To show the sufficiency, we use the Routh–Hurwitz conditions for the stability of matrices [3]. In the cases  $n = 1$  or  $n = 2$ , the proof is straightforward. For  $n = 3$ , let  $A = (a_{ij})_{3 \times 3}$ . The Routh–Hurwitz conditions state that  $A$  is stable if and only if

$$\operatorname{tr}(A) < 0, \quad \det(A) < 0, \quad \text{and} \quad \operatorname{tr}(A)a_2 < \det(A), \quad (3.1)$$

where  $a_2$  is the sum of all  $2 \times 2$  principal minors of  $A$ . Assume that  $A$  satisfies the minors condition. We want to show that  $A - D$  also satisfies the Routh–Hurwitz conditions for an arbitrary  $D \geq 0$ . First,  $\operatorname{tr}(A - D) = \operatorname{tr}(A) - \operatorname{tr}(D) < 0$  since  $\operatorname{tr}(A) < 0$  and  $D \geq 0$ . It follows from (2.1) and the minors condition that  $\det(A - D) < 0$ . It remains to verify the condition  $\operatorname{tr}(A - D)\bar{a}_2 < \det(A - D)$ , where  $\bar{a}_2$  is the sum of all  $2 \times 2$  principal minors of  $A - D$ . More specifically,

$$A - D = \begin{bmatrix} a_{11} - d_1 & a_{12} & a_{13} \\ a_{21} & a_{22} - d_2 & a_{23} \\ a_{31} & a_{32} & a_{33} - d_3 \end{bmatrix}$$

and

$$\begin{aligned}
 \bar{a}_2 &= \begin{vmatrix} a_{11} - d_1 & a_{12} \\ a_{21} & a_{22} - d_2 \end{vmatrix} + \begin{vmatrix} a_{11} - d_1 & a_{13} \\ a_{31} & a_{33} - d_3 \end{vmatrix} + \begin{vmatrix} a_{22} - d_2 & a_{23} \\ a_{32} & a_{33} - d_3 \end{vmatrix} \\
 &= \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} - a_{11}d_2 - a_{22}d_1 + d_1d_2 \\
 &\quad + \begin{vmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{vmatrix} - a_{11}d_3 - a_{33}d_1 + d_1d_3 \\
 &\quad + \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{22}d_3 - a_{33}d_2 + d_2d_3. \tag{3.2}
 \end{aligned}$$

Thus

$$\begin{aligned}
 \operatorname{tr}(A - D)\bar{a}_2 &= (a_{11} + a_{22} + a_{33} - d_1 - d_2 - d_3)\bar{a}_2 \\
 &= (\operatorname{tr}(A) - d_1 - d_2 - d_3)(a_2 - a_{11}d_2 - a_{22}d_1 + d_1d_2 \\
 &\quad - a_{11}d_3 - a_{33}d_1 + d_1d_3 - a_{22}d_3 - a_{33}d_2 + d_2d_3) \tag{3.3}
 \end{aligned}$$

and

$$\begin{aligned}
 \det(A - D) &= \det(A) - \left( \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} d_1 + \begin{vmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{vmatrix} d_2 + \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} d_3 \right) \\
 &\quad + a_{33}d_1d_2 + a_{22}d_1d_3 + a_{11}d_2d_3 - d_1d_2d_3. \tag{3.4}
 \end{aligned}$$

Note that  $\det(A)$  dominates  $\operatorname{tr}(A)a_2$  by (3.1), and that all the remaining terms in (3.4) appear in (3.3). It can be verified, using the minors condition, that all the terms in (3.3) are non-positive. Therefore  $\operatorname{tr}(A - D)\bar{a}_2 < \det(A - D)$ , and thus  $A - D$  is stable, completing the proof. ■

For  $n \geq 3$ , Casten and Holland [1] prove that  $A - D$  is stable for all  $D > 0$  if  $A$  and all its principal submatrices are stable. This result now follows from Theorem 3.2. Furthermore, our minors condition is both sufficient and necessary. For a general  $n \times n$  matrix  $A$ , Theorem 3.1 shows that the minors condition is necessary for  $A - D$  to be stable for all  $D \geq 0$ . We conjecture that it is also sufficient.

*Conjecture.* Assume that  $A$  is stable. Then  $A - D$  is stable for all  $D \geq 0$  if and only if  $A$  satisfies the minors condition.

A Lozinskiĭ measure  $\mu$  is said to be *admissible* if  $\mu(-D) \leq 0$  for all diagonal  $D \geq 0$ . It is easy to verify that  $\mu_\infty$ ,  $\mu_1$ , and  $\mu_2$  are admissible. Let  $P = \begin{bmatrix} 1 & 2 \\ 1 & 3 \end{bmatrix}$  and  $D = \operatorname{diag}(1, 2)$ . Then  $\mu_P$  is not admissible since, by Lemma 2.2,  $\mu_P(-D) = \mu_\infty(-PDP^{-1}) = 3 > 0$ .

DEFINITION. An  $n \times n$  matrix is said to be *strongly stable* if

$$(-1)^n \det(A) > 0 \quad \text{and} \quad \mu(A^{[2]}) < 0$$

for some admissible Lozinskiĭ measure  $\mu$  on  $M_N(\mathbf{R})$ ,  $N = \binom{n}{2}$ .

It follows from Theorem 2.3 that every strongly stable matrix is stable.

THEOREM 3.3. *Assume that  $A$  is strongly stable. Then  $A - D$  is strongly stable for all  $D \geq 0$  if and only if  $A$  satisfies the minors condition.*

*Proof.* The necessity follows from Theorem 3.1. For the sufficiency,  $(-1)^n \det(A) > 0$  and the minors condition imply  $(-1)^n \det(A - D) > 0$  by (2.1). Also,  $\mu((A - D)^{[2]}) = \mu(A^{[2]} - D^{[2]}) \leq \mu(A^{[2]}) + \mu(-D^{[2]}) \leq \mu(A^{[2]}) < 0$ , by the admissibility of  $\mu$ . Therefore  $A - D$  is also strongly stable. ■

A matrix  $B = (b_{ij})$  is said to be *diagonally dominant* in rows or in columns if  $|b_{ii}| > \sum_{j \neq i} |b_{ij}|$  or  $|b_{ii}| > \sum_{j \neq i} |b_{ji}|$  for all  $i$ , respectively. If, in addition,  $b_{ii} < 0$  for  $1 \leq i \leq n$ , we say  $B$  is *negatively diagonally dominant*. By (2.2) and (2.3),  $B$  is negatively diagonally dominant in rows if  $\mu_\infty(B) < 0$  and in columns if  $\mu_1(B) < 0$ . Choosing the  $\mu$  in Theorem 3.3 as  $\mu_\infty$ ,  $\mu_1$ , or  $\mu_2$ , we arrive at the following corollaries.

COROLLARY 3.4. *Assume that  $(-1)^n \det(A) > 0$  and that  $A^{[2]}$  is negatively diagonally dominant in rows or in columns. Then  $A - D$  is strongly stable for all  $D \geq 0$  if and only if  $A$  satisfies the minors condition.*

COROLLARY 3.5. *Let  $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_n$  be the eigenvalues of  $(A + A^*)/2$ . Assume that  $\lambda_1 + \lambda_2 < 0$  and  $(-1)^n \det(A) > 0$ . Then  $A - D$  is strongly stable for all  $D \geq 0$  if and only if  $A$  satisfies the minors condition.*

Next, for a given diagonal  $D \geq 0$ , we study conditions that ensure  $s(A - \lambda D) \leq -\delta < 0$  for some  $\delta > 0$  that is uniform for all  $\lambda \geq 0$ . When  $D > 0$ , as shown in Casten and Holland [1], this property is equivalent to  $A - \lambda D$  being stable for all  $\lambda \geq 0$ .

THEOREM 3.6. *Let  $D > 0$  be given. Then  $s(A - \lambda D) \leq -\delta < 0$  for all  $\lambda \geq 0$  if and only if  $A - \lambda D$  is stable for all  $\lambda \geq 0$ .*

*Proof.* See [1, proof of Theorem 1]. ■

The assumption  $D > 0$  is crucial in Theorem 3.6. The uniform upper bound  $-\delta$  may not exist if  $D$  is only non-negative as the following example shows. Let  $A = \begin{bmatrix} -4 & 2 \\ -2 & 0 \end{bmatrix}$ . It has eigenvalue  $-2$  with multiplicity 2, so  $A$  is stable. Furthermore, by Theorem 3.2,  $A - D$  is stable for all  $D \geq 0$  since  $A$  satisfies the minors condition. Let  $D = \text{diag}(1, 0)$ . Simple



calculation gives  $s(A - \lambda D) = -2 + (\sqrt{\lambda^2 + 8\lambda} - \lambda)/2 < 0$  for all  $\lambda \geq 0$ . However,  $s(A - \lambda D) \rightarrow 0$  as  $\lambda \rightarrow \infty$ .

Let  $D \geq 0$  be given; without loss of generality, assume that

$$D = \begin{bmatrix} \bar{D} & 0 \\ 0 & 0 \end{bmatrix}, \quad (3.5)$$

where  $\bar{D}$  is diagonal with positive entries. Write  $A$  in the corresponding block-form

$$A = \begin{bmatrix} A_1 & A_2 \\ A_3 & A_4 \end{bmatrix}, \quad (3.6)$$

where  $A_1$  has the same dimensions as  $\bar{D}$ . The following is a generalization of Theorem 3.6.

**THEOREM 3.7.** *Let  $D \geq 0$  be given as in (3.5). Then  $s(A - \lambda D) \leq -\delta < 0$  for all  $\lambda \geq 0$  if and only if  $A - \lambda D$  is stable for all  $\lambda \geq 0$  and  $A_4$  is stable.*

*Proof.* The sufficiency is proved in [1]. To show the necessity, we need only to verify that  $A_4$  is stable. Observe that, if  $\lambda > 0$ ,

$$\begin{aligned} A - \lambda D &= \begin{bmatrix} A_1 - \lambda \bar{D} & A_2 \\ A_3 & A_4 \end{bmatrix} \approx \begin{bmatrix} A_1 - \lambda \bar{D} & \lambda A_2 \\ \frac{A_3}{\lambda} & A_4 \end{bmatrix} \\ &= \begin{bmatrix} A_1 - \lambda \bar{D} & \lambda A_2 \\ 0 & A_4 \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ \frac{A_3}{\lambda} & 0 \end{bmatrix}, \end{aligned} \quad (3.7)$$

where “ $\approx$ ” denotes similarity of matrices. Since the eigenvalues of a matrix depend continuously on its entries, the relations (3.7) and  $s(A - \lambda D) \leq -\delta < 0$  imply the stability of

$$\begin{bmatrix} A_1 - \lambda \bar{D} & \lambda A_2 \\ 0 & A_4 \end{bmatrix}$$

when  $\lambda$  is sufficiently large, and hence that of  $A_4$ . ■

*Remark.* Even under the conditions of Theorem 3.7, the relation  $s(A - \lambda D) \leq s(A)$  may not hold for all  $\lambda \geq 0$ . For example, let  $A = \begin{bmatrix} -4 & 2 \\ -2 & -1 \end{bmatrix}$  and  $D = \text{diag}(1, 0)$ . Then  $s(A) = -3$  and  $s(A - \lambda D) = -3 + (\sqrt{\lambda^2 + 8\lambda} - \lambda)/2 \rightarrow -1 > s(A)$  as  $\lambda \rightarrow \infty$ .

THEOREM 3.8. *Assume that one of the following conditions holds.*

- (a)  $n \leq 3$  and  $A$  is stable.
- (b)  $A$  is strongly stable.

*Then  $s(A - \lambda D) \leq -\delta$  for some  $\delta > 0$  that is uniform for all  $D \geq 0$ ,  $\lambda \geq 0$  if and only if  $A$  satisfies the strict minors condition.*

*Proof.* Assume that  $A$  satisfies the strict minors condition. Then, by continuity,  $A + \delta I_{n \times n}$  also satisfies the strict minors condition for sufficiently small  $\delta > 0$ . If  $A$  is strongly stable, then  $\mu(A^{[2]}) < 0$  for an admissible  $\mu$ , and thus  $\mu((A + \delta I_{n \times n})^{[2]}) = \mu(A^{[2]} + \delta I_{n \times n}^{[2]}) \leq \mu(A^{[2]}) + 2\delta < 0$  if  $\delta$  is sufficiently small; namely,  $A + \delta I_{n \times n}$  is also strongly stable. Therefore, under either assumption (a) or (b) of Theorem 3.8, and by Theorem 3.2 or Theorem 3.3, respectively,  $A + \delta I_{n \times n} - D$  is stable for all  $D \geq 0$ . Hence  $s(A - \lambda D) \leq -\delta$  for some  $\delta > 0$  that is uniform for all  $D \geq 0$  and  $\lambda \geq 0$ . ■

Suppose that either condition (a) or (b) in Theorem 3.8 holds. If in addition  $A$  satisfies the strict minors condition, then there exists  $\delta > 0$  such that  $s(A - \lambda D) \leq -\delta$  for all  $D \geq 0$ ,  $\lambda \geq 0$  by Theorem 3.8. Furthermore, by Theorem 3.7, all the principal submatrices of  $A$  must be stable. On the other hand, if  $A$  and all its principal submatrices are stable, then  $A$  satisfies the strict minors conditions. We thus have the following result.

THEOREM 3.9. *Suppose that either condition (a) or (b) of Theorem 3.8 holds. Then all the principal submatrices of  $A$  are stable if and only if  $A$  satisfies the strict minors condition.*

#### 4. STABILITY AND INSTABILITY IN REACTION-DIFFUSION SYSTEMS

Let  $\|\cdot\|$  denote the supreme norm in the space  $C(\Omega \rightarrow \mathbf{R}^n)$  of continuous functions. A steady-state solution  $\bar{u}(x)$  to the reaction-diffusion system (1.2) is *stable* if, for any  $\epsilon > 0$ , there exists  $\delta > 0$  such that  $\|u(0, x) - \bar{u}(x)\| < \delta$  implies  $\|u(t, x) - \bar{u}(x)\| < \epsilon$  for all  $t \geq 0$ . The solution  $\bar{u}(x)$  is said to be *asymptotically stable* if it is stable and there exists  $\delta > 0$  such that  $\|u(0, x) - \bar{u}(x)\| < \delta$  implies  $\|u(t, x) - \bar{u}(x)\| \rightarrow 0$  as  $t \rightarrow \infty$ . We say that  $\bar{u}(x)$  is *unstable* if it is not stable (see [1, 19]). Suppose the Jacobian matrix  $A = f'(0)$  is stable. Then  $u = 0$  is a locally asymptotically stable equilibrium for the kinetic system (1.1). We study the stability of the constant steady-state  $u = 0$  of the diffusive system (1.2) via the linearized system (1.3).

Let  $\{\phi_k(x)\}$  be the orthonormal basis of  $C(\Omega \rightarrow \mathbf{R})$  formed by all the eigenfunctions of

$$\begin{aligned} -\Delta w &= \lambda w && \text{in } \Omega, \\ \frac{\partial w}{\partial \nu} &= 0 && \text{on } \partial\Omega, \end{aligned} \quad (4.1)$$

Let  $0 = \lambda_0 \leq \lambda_1 \leq \dots \leq \lambda_k \leq \dots$  be the corresponding eigenvalues (see [19]). A function  $v_0 \in C(\Omega \rightarrow \mathbf{R}^n)$  has the Fourier expansion

$$v_0(x) = \sum_{k=0}^{\infty} \psi_k \phi_k(x), \quad (4.2)$$

where  $\psi_k \in \mathbf{R}^n$  are the Fourier coefficients. Let  $T_k(t)$  be the solution to the initial value problem of the linear system of ordinary differential equations in  $\mathbf{R}^n$ ,

$$\begin{aligned} T'_k(t) &= (A - \lambda_k D)T_k(t) && t > 0, \\ T_k(0) &= \psi_k. \end{aligned} \quad (4.3)$$

Then the solution  $v(t, x)$  to the linear diffusive system (1.3) can be expressed as

$$v(t, x) = \sum_{k=0}^{\infty} T_k(t) \phi_k(x). \quad (4.4)$$

Using (4.4) and Theorem 3.1, we first prove the following instability result.

**THEOREM 4.1.** *Suppose that  $A = f'(0)$  is stable. Then the steady-state  $u = 0$  of (1.2) is unstable for some diffusion matrix  $D \geq 0$  if  $A$  does not satisfy the minors condition.*

*Proof.* Suppose that  $A$  does not satisfy the minors condition. Then  $A - \lambda_k D$  is unstable for some  $D \geq 0$  and eigenvalue  $\lambda_k > 0$  of (4.1), by Theorem 3.1. Let  $v_0(x) = \psi_k \phi_k(x)$ , where  $\psi_k$  and  $\phi_k$  are given as in (4.1)–(4.4). Then  $v(t, x) = T_k(t) \phi_k(x)$  is a solution to the linearized system (1.3) and it blows up exponentially as  $t \rightarrow \infty$ . Therefore,  $u = 0$  is unstable by linear approximation (see [1, 19]). ■

From an application viewpoint, Theorem 4.1 provides a simple and systematic way of detecting the occurrence of diffusion-driven instability in a general diffusive system (1.2). The regions for diffusion matrices that give rise to instability can be so found that  $A - \lambda_k D$ , for some  $\lambda_k$ , has an

eigenvalue with positive real part. We refer the readers to [8, 16] for discussions on instability regions.

Expansion (4.4) and results derived in Section 3 can also be used to prove the stability of a steady-state. Let  $D \geq 0$  be given. Assume that  $D$  is written as in (3.5). Also decompose  $A = f'(0)$  as in (3.6).

**THEOREM 4.2.** *Assume that*

- (a)  $n \leq 3$  and  $A = f'(0)$  is stable, or
- (b)  $A$  is strongly stable.

*Then the steady-state solution  $u = 0$  to (1.2) is asymptotically stable if  $A$  satisfies the minors condition and  $A_4$  is stable, where  $A_4$  is given in (3.6).*

*Proof.* Assume that either assumption (a) or (b) holds. Then by Theorem 3.2 or Theorem 3.3, respectively,  $A - \lambda D$  is stable for all  $\lambda \geq 0$ . This, together with the stability of  $A_4$ , implies that  $s(A - \lambda_k D) \leq -\delta < 0$  for all the eigenvalues  $\lambda_k$  of (4.1) by Theorem 3.7. Therefore,  $\|v(t, x)\| \leq K \exp(-\delta t)\|v(0, x)\|$  for some  $K, \delta > 0$  and for all  $t > 0$ . This implies the asymptotic stability of the zero solution to (1.3), and thus that of the steady-state  $u = 0$  of (1.2). ■

In many applications, it is necessary to investigate whether  $u = 0$  remains stable with respect to all diagonal diffusion matrices  $D$ . Suppose that only positive  $D$  are considered. Then, by Theorem 4.2,  $u = 0$  is asymptotically stable with respect to all  $D > 0$  if  $A$  satisfies the minors condition. On the other hand, if non-negative  $D$  are allowed, a stronger condition is required to ensure the stability of  $u = 0$ . We have the following result.

**THEOREM 4.3.** *Suppose that either assumption (a) or (b) of Theorem 4.2 holds.*

- (1) *If  $A$  satisfies the minors condition, then the steady-state  $u = 0$  of (1.2) is asymptotically stable for all diffusion matrices  $D > 0$ .*
- (2) *If  $A$  satisfies the strict minors condition, then  $u = 0$  is asymptotically stable for all  $D \geq 0$ .*

*Proof.* The claim (1) follows directly from Theorem 4.2. From the proof of Theorem 4.2,  $u = 0$  is asymptotically stable if  $A - \lambda D \leq -\delta$  for some  $\delta > 0$  that is uniform for all  $\lambda \geq 0$ . By Theorem 3.8, such a  $\delta$  can be chosen independent of  $D \geq 0$  if the strict minors condition holds. This proves the claim (2), and hence Theorem 4.3. ■

COROLLARY 4.4. *Let  $A = f'(0)$ . Then the conclusions of Theorem 4.3 hold if any of the following is satisfied.*

- (a)  $A^{[2]}$  is negatively diagonally dominant in rows.
- (b)  $A^{[2]}$  is negatively diagonally dominant in columns.
- (c)  $\lambda_1 + \lambda_2 < 0$ , where  $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_n$  are eigenvalues of  $(A + A^*)/2$ .

## 5. AN EXAMPLE FROM EPIDEMIOLOGY

Consider a mathematical model in epidemiology,

$$\begin{aligned} S' &= b - bS - \lambda IS + \alpha IS, \\ E' &= \lambda IS - (\epsilon + b)E + \alpha IE, \\ I' &= \epsilon E - (\gamma + \alpha + b)I + \alpha I^2, \\ R' &= \gamma I - bR + \alpha IR, \end{aligned} \tag{5.1}$$

where  $S$ ,  $E$ ,  $I$ , and  $R$  denote the fractions of susceptible, exposed (infected but not yet infectious), infectious, and recovered individuals in a population and  $S + E + I + R = 1$ . The model describes the population dynamics for an infectious disease that spreads in the host population through direct contact of hosts. The parameter  $b$  is the birth rate,  $\alpha$  the disease-caused death rate,  $\gamma$  the recovery rate, and  $\epsilon$  the rate at which the exposed individuals become infectious. The parameter  $\lambda$  is the effective per capita contact rate among individuals. For the derivation and a detailed analysis of the model, we refer the reader to [11]. Note that  $R$  does not appear in the first three equations; this allows us to study the system

$$\begin{aligned} S' &= b - bS - \lambda IS + \alpha IS, \\ E' &= \lambda IS - (\epsilon + b)E + \alpha IE, \\ I' &= \epsilon E - (\gamma + \alpha + b)I + \alpha I^2, \end{aligned} \tag{5.2}$$

and determine  $R$  from  $R = 1 - S - E - I$ .

It is shown in [11] that the global dynamics of (5.2) is controlled by the basic reproduction number

$$\sigma = \frac{\lambda \epsilon}{(\epsilon + b)(\gamma + \alpha + b)}.$$

More specifically, if  $\sigma \leq 1$ , the disease-free equilibrium  $P_0 = (1, 0, 0)$  is globally asymptotically stable in the feasible region. If  $\sigma > 1$ , the disease becomes endemic and a unique endemic equilibrium  $P^* = (S^*, E^*, I^*)$  with  $S^* > 0, E^* > 0, I^* > 0$  is globally asymptotically stable (see [11]).

The population in model (5.2) is assumed to be spatially homogeneous. It is important to investigate whether and how the spatial heterogeneity will affect the disease dynamics in (5.2). If the movement of individual hosts is approximated by diffusion, one arrives at the diffusive model

$$\begin{aligned} S' &= d_1 \Delta S + b - bS - \lambda IS + \alpha IS, \\ E' &= d_2 \Delta E + \lambda IS - (\epsilon + b)E + \alpha IE, \\ I' &= d_3 \Delta I + \epsilon E - (\gamma + \alpha + b)I + \alpha I^2, \end{aligned} \tag{5.3}$$

with the homogeneous Neumann boundary condition on a bounded domain in  $\mathbf{R}^2$ . The constant solution  $(S(t, x), E(t, x), I(t, x)) = (S^*, E^*, I^*)$  is a constant steady-state solution to (5.3). A question of both biological and mathematical interest is whether this steady-state, also denoted by  $P^*$ , remains asymptotically stable with respect to the diffusive system (5.3) for all possible diffusion coefficients,  $d_i \geq 0$ . Note that the Jacobian matrix  $J(P^*)$  of (5.2) at  $P^*$  is

$$J(P^*) = \begin{bmatrix} -b - \lambda I^* + \alpha I^* & 0 & -\lambda S^* + \alpha S^* \\ \lambda I^* & -(\epsilon + b) + \alpha I^* & \lambda S^* + \alpha E^* \\ 0 & \epsilon & -(\gamma + \alpha + b) + 2\alpha I^* \end{bmatrix}, \tag{5.4}$$

and that  $S^*, E^*$ , and  $I^*$  satisfy

$$\begin{aligned} b - bS^* - \lambda I^* S^* + \alpha I^* S^* &= 0, \\ \lambda I^* S^* - (\epsilon + b)E^* + \alpha I^* E^* &= 0, \\ \epsilon E^* - (\gamma + \alpha + \beta)I^* + \alpha I^{*2} &= 0. \end{aligned} \tag{5.5}$$

Applying the theory developed in the previous sections, we prove that diffusion-driven instability will not occur when the disease-caused death rate  $\alpha = 0$ , and it can occur if  $\alpha > 0$ .

**THEOREM 5.1.** *Assume  $\alpha = 0$ . Then the endemic steady-state  $P^*$  of (5.3) is locally asymptotically stable for all diffusion coefficients  $d_i > 0, i = 1, 2, 3$ .*

*Proof.* By Theorem 4.3 (1), it suffices to show that the Jacobian matrix  $J(P^*)$  of (5.2) at  $P^*$  in (5.4) satisfies the minors condition when  $\alpha = 0$ . In fact, using (5.5), it is straightforward to verify that all the diagonal entries

of  $J(P^*)$  are negative, and all the  $2 \times 2$  principal minors are non-negative. The relation  $\det(J(P^*)) < 0$  follows from the local stability of  $P^*$  with respect to (5.2). ■

**THEOREM 5.2.** *Assume  $\alpha > 0$ . Then the endemic steady-state  $P^*$  of (5.3) is unstable for some  $d_i \geq 0$ ,  $i = 1, 2, 3$ .*

*Proof.* By Theorem 4.1, it suffices to show that the Jacobian matrix  $J(P^*)$  of (5.2) at  $P^*$  in (5.4) does not satisfy the minors condition when  $\alpha > 0$ . In fact, using (5.5), we can show that the  $2 \times 2$  principal minor

$$\begin{aligned} & \begin{vmatrix} -(\epsilon + b) + \alpha I^* & \lambda S^* + \alpha E^* \\ \epsilon & -(\gamma + \alpha + b) + 2\alpha I^* \end{vmatrix} \\ &= \begin{vmatrix} -\frac{\lambda I^* S^*}{E^*} & \lambda S^* + \alpha E^* \\ \epsilon & -\frac{\epsilon E^*}{I^*} + \alpha I^* \end{vmatrix} = -\frac{\lambda \alpha (I^*)^2 S^*}{E^*} - \alpha \epsilon E^* < 0. \end{aligned}$$

■

## APPENDIX

For  $n = 2, 3$ , and 4, the second additive compound matrix of an  $n \times n$  matrix  $A = (a_{ij})$  is, respectively,

$$n = 2: \quad a_{11} + a_{22}$$

$$n = 3: \quad \begin{bmatrix} a_{11} + a_{22} & a_{23} & -a_{13} \\ a_{32} & a_{11} + a_{33} & a_{12} \\ -a_{31} & a_{21} & a_{22} + a_{33} \end{bmatrix}$$

$$n = 4:$$

$$\begin{bmatrix} a_{11} + a_{22} & a_{23} & a_{24} & -a_{13} & -a_{14} & 0 \\ a_{32} & a_{11} + a_{33} & a_{34} & a_{12} & 0 & -a_{14} \\ a_{42} & a_{43} & a_{11} + a_{44} & 0 & a_{12} & a_{13} \\ -a_{31} & a_{21} & 0 & a_{22} + a_{33} & a_{34} & -a_{24} \\ -a_{41} & 0 & a_{21} & a_{43} & a_{22} + a_{44} & a_{23} \\ 0 & -a_{41} & a_{31} & -a_{42} & a_{32} & a_{33} + a_{44} \end{bmatrix}.$$

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