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EFFECTS OF SPATIAL VARIATIONS AND DISPERSAL STRATEGIES ON PRINCIPAL EIGENVALUES OF DISPERSAL OPERATORS AND SPREADING SPEEDS OF MONOSTABLE EQUATIONS

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ABSTRACT. The current paper is concerned with the following two separate, but related, dynamical problems: the effects of spatial variations on the principal eigenvalues of dispersal operators with random or discrete or nonlocal dispersal and periodic boundary condition, and the effects of spatial variations and dispersal strategies on the spreading speeds of monostable equations in periodic environments. It first shows that spatial variation cannot reduce the principal eigenvalue (if it exists) of a dispersal operator with random, discrete or nonlocal dispersal and periodic boundary condition, and indeed it is increased except for degenerate cases. It then shows that spatial variation enhances the spatial spreading in a non-degenerate spatially periodic monostable equation with random or discrete or nonlocal dispersal. It also shows that, for two monostable equations with the same population dynamics, but different dispersal strategies, one of which is random and the other is nonlocal, the spatial spreading speed of the equation with random dispersal is greater (respectively, smaller) than the spreading speed of the equation with nonlocal dispersal if the dispersal distance is small (respectively, large). The results obtained in the paper reveal the importance of spatial variation and dispersal strategies in population dynamics.

1. Introduction.

In this paper we study the effect of spatial variability on the propagation of organisms in a spatially periodic habitat. In particular, we are interested in how spatial variations affect the spreading speed and how the spreading speed depends upon the dispersal strategies.

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Classically, one assumes random dispersal which leads to the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = \nu_1 \Delta u + u f_1(x,u), \quad x \in \mathbf{R}^N, \tag{1.1}$$

where ν_1 is the diffusion rate and f_1 is the specific growth rate. We assume that $f_1(x,u)$ is periodic in x with period vector $\mathbf{p}_1 = (p_{11}, p_{12}, \dots, p_{1N}) \in (0,\infty)^N$, i.e., $f_1(\cdot + p_{1i}\mathbf{e_i}, \cdot) = f_1(\cdot,\cdot)$, where $\mathbf{e}_i = (\delta_{i1}, \delta_{i2}, \dots, \delta_{iN})$, $\delta_{ij} = 1$ if $i = j$ and 0 if $i \neq j$. Moreover, $f_1(\cdot, u)$ is negative for u large, $\partial f_1/\partial u < 0$, and $u \equiv 0$ is an unstable stationary solution of (1.1) under periodic perturbation (see (H1) below for details). Of concern are nonnegative solutions, only, since population densities are nonnegative quantities.

One of the central problems is to understand how fast a population (bacteria, e.g.) spreads. To this end, fix a direction $\xi \in S^{N-1} := \{\widetilde{\xi} \in \mathbf{R}^N \mid \|\widetilde{\xi}\| = 1\}$ ($\|\cdot\|$ denotes the norm in $\mathbf{R}^N$) and assume that the initial population density u^0 is greater than some positive constant σ_0 in the region $x \cdot \xi \ll -1$ and identically 0 in the region $x \cdot \xi \gg 1$ ($x \cdot \xi$ denotes the inner product of x and ξ). How fast does the population invade into the latter region?

The spatial spreading dynamics for (1.1) has been widely studied since the pioneering works by Fisher [**16**] and Kolmogorov, Petrowsky, Piscunov [**29**] (see [**1, 2, 4–6, 15, 17, 19, 21, 22, 27, 30–32, 34–37, 39–42, 49–51**] and the references therein). Let u_1^+ be the stable positive periodic stationary solution of (1.1) with period vector $\mathbf{p}_1$ ($\mathbf{p}_1$-periodic for short in the following) (see the remark after (H1) in Section 2 for the existence and uniqueness of u_1^+). It has been established that, for any $\xi \in S^{N-1}$, there is a $c_1^*(\xi) \in \mathbf{R}$, the so-called minimal wave speed, characterized by the following feature. For any $c \geq c_1^*(\xi)$, there exists a traveling wave solution connecting u_1^+ and 0 and propagating in the direction of ξ with speed c, and there is no such traveling wave solution of speed slower than $c_1^*(\xi)$ in the direction of ξ. The minimal wave speed is an important spreading property and equals the *spreading speed* in the direction of ξ (see [**4–6, 30, 36, 37, 51**] and the references therein). More precisely, let $\xi \in S^{N-1}$; then the minimal wave speed $c_1^*(\xi) \in \mathbf{R}$ of (1.1) in the direction of ξ satisfies

$$\liminf_{\substack{x\cdot\xi \leq ct \\ t\to\infty}} (u^1(t,x;u^0) - u_1^+(x)) = 0 \quad \text{for all } c < c_1^*(\xi)$$

and

$$\limsup_{\substack{x\cdot\xi \geq ct\\ t\to\infty}} u^1(t,x;u^0) = 0 \quad \text{for all } c > c_1^*(\xi),$$

provided that $u^0 \in C(\mathbf{R}^N, \mathbf{R}^+)$, $u^0(x) \geq \sigma_0$ for some $\sigma_0 > 0$ and all $x \cdot \xi \ll -1$, and $u^0(x) = 0$ for $x \cdot \xi \gg 1$. Here $u^1(t,x;u^0)$ is the solution of (1.1) with $u^1(0,x;u^0) = u^0$ (see [**50, 51**]).

A second dispersal strategy is nearest neighbor interaction in a patchy environment modeled by the lattice $\mathbf{Z}^N$. This leads to the lattice system of ordinary differential equations:

$$\dot{u}_j = \nu_2 \sum_{k=(k_1,k_2,\dots,k_N)\in K} (u_{j+k} - u_j) + u_j f_2(j, u_j), \quad j \in \mathbf{Z}^N \tag{1.2}$$

where $K = \{(k_1, k_2, \dots, k_N) \in \mathbf{Z}^N \mid k_1^2 + \cdots + k_N^2 = 1\}$, ν_2 is the interaction coefficient, $f_2(j,u)$ is periodic in j with period vector $\mathbf{p}_2 = (p_{21}, p_{22}, \dots, p_{2N}) \in \mathbf{N}^N$, and exhibits the same features as f_1 with respect to u (see (H1) below). Again, one finds a minimal wave speed $c_2^*(\xi) \in \mathbf{R}$ which is equal to the spreading speed of (1.2) in direction ξ. We refer to [**9, 18, 23, 43, 47, 48, 50–53**], etc., for the study of spatial spreading dynamics of (1.2). As for the relationship between random dispersal and nearest point interaction, one notes that (1.2) can be viewed as a spatial discretization of (1.1).

The third dispersal strategy of concern in this paper is nonlocal dispersal, which leads, following [**25**], to

$$\frac{\partial u}{\partial t} = \nu_3 \left[\int_{\mathbf{R}^N} k_\delta(y-x) u(t,y)\, dy - u(t,x) \right] + u(t,x) f_3(x, u(t,x)), \quad x \in \mathbf{R}^N \tag{1.3}$$

where $\nu_3 > 0$ is a dispersal rate, $\delta > 0$ represents the nonlocal dispersal distance, and $k_\delta(\cdot)$ is given by $k_\delta(z) = 1/\delta^N k(z/\delta)$ for all $z \in \mathbf{R}^N$ and some C^1 function $k(\cdot) : \mathbf{R}^N \to \mathbf{R}^+$ which satisfies $k(z) = k(z')$ for $z, z' \in \mathbf{R}^N$ with $\|z\| = \|z'\|$, $k(z) > 0$ if $\|z\| < 1$, $k(z) = 0$ if $\|z\| \geq 1$, and $\int_{\mathbf{R}^N} k(z)\, dz = 1$. A standard example is

$$k(z) = \begin{cases} C \exp\left(\frac{1}{\|z\|^2 - 1}\right) & \text{for } \|z\| < 1, \\ 0 & \text{for } \|z\| \geq 1, \end{cases} \tag{1.4}$$

where the constant $C > 0$ is chosen such that $\int_{\mathbf{R}^N} k(z)\,dz = 1$. We assume that $f_3(x,u)$ is periodic in x with period vector $\mathbf{p}_3 = (p_{31}, p_{32}, \dots, p_{3N}) \in (0,\infty)^N$, and exhibits the same features as f_1 with respect to u (see (H1) below).

In order to indicate the relationship between nonlocal and random dispersal define K_δ and I as

$$(K_\delta u)(x) = \int_{\mathbf{R}^N} k_\delta(y-x)u(y)\,dy$$

and

$$(Iu)(x) = u(x),$$

respectively, for $u \in C(\mathbf{R}^N, \mathbf{R})$ $\mathbf{p}_3$-periodic. One has for $k(\cdot)$ being as in (1.4), $\delta \ll 1$ and a smooth function $u(x)$,

$$\begin{aligned}\big((K_\delta - I)u\big)(x) &= \int_{\mathbf{R}^N} k_\delta(y-x)u(y)\,dy - u(x)\\ &= \int_{\mathbf{R}^N} k(z)\bigg[u(x) + \delta(\nabla u(x)\cdot z)\\ &\qquad\qquad + \frac{\delta^2}{2}\sum_{i,j=1}^{n} u_{x_i x_j}(x) z_i z_j + O(\delta^3)\bigg]\,dz\\ &\quad - u(x)\\ &= \frac{\delta^2}{2N}\int_{\mathbf{R}^N} k(z)\|z\|^2\,dz\Delta u(x) + O(\delta^3).\end{aligned}$$

Hence, the operator $K_\delta - I$ with $k(\cdot)$ being as in (1.4) "behaves" the same as the operator $\delta^2/2N\int_{\mathbf{R}^N} k(z)\|z\|^2\,dz\Delta$ for $\delta \ll 1$, and δ basically plays the role of a dispersal rate. Consequently, equations (1.1), (1.2) and (1.3) are, on the one hand, all related to each other, but deserve, on the other hand, great interest on their own.

Recently, the nonlocal dispersal equation (1.3) has found quite some interest, and we refer to [**3, 7, 12, 24–26, 28, 44**] for the study of the spectral theory for nonlocal dispersal operators and the existence, uniqueness and stability of nontrivial positive stationary solutions and to [**11, 13, 14, 50, 51**] for the study of the existence of spreading speeds and traveling wave solutions connecting the trivial solution $u = 0$ and a nontrivial positive stationary solution. Most existing works, though, deal with spatially homogeneous equations (i.e., $f_3(x, u)$ in (1.3) is independent of x). In that case the existence and characterization of the spreading speed can be obtained by results of Weinberger in [**50**] which deals with spatial spreading dynamics for biological models in spatially homogeneous habitats. It should be pointed out that Weinberger in [**51**] deals with the spatial spreading dynamics for very general population dispersal models in periodic habitats. However, these results do not cover general nonlocal dispersal equations of the form (1.3), since there are no suitable choices of phases spaces where the solution operator of (1.3) exhibits the required compactness properties. The second and third authors of the current paper have investigated the existence of spreading speed $c_3^*(\delta, \xi)$ of (1.3) in direction $\xi \in S^{N-1}$ in a very recent work [**45**]. They define a real number $c_3^*(\delta, \xi)$ to be the *spreading speed* of (1.3) in the direction of ξ if one has

$$\liminf_{\substack{x\cdot\xi \le ct \\ t\to\infty}} (u^3(t, x; u^0) - u_3^+(x)) = 0 \quad \text{for all } c < c_3^*(\delta, \xi)$$

and

$$\limsup_{\substack{x\cdot\xi \ge ct \\ t\to\infty}} u^3(t, x; u^0) = 0 \quad \text{for all } c > c_3^*(\delta, \xi),$$

provided that $u^0 \in C(\mathbf{R}^N, \mathbf{R}^+)$, $u^0(x) \ge \sigma_0$ for some $\sigma_0 > 0$ and all $x \cdot \xi \ll -1$, and $u^0(x) = 0$ for $x \cdot \xi \gg 1$. Here u_3^+ denotes the positive periodic stationary solution of (1.3) with period vector $\mathbf{p}_3$ (see the remark after (H1) in Section 2 for the existence and uniqueness of u_3^+), and $u^3(t, x; u^0)$ is the solution of (1.3) with $u^3(0, \cdot; u^0) = u^0$. Observe that this natural definition does not guarantee the existence of spreading speeds. Existence of $c_3^*(\delta, \xi)$ for all $\delta > 0$ and $\xi \in S^{N-1}$ is proved in [**45**] in the following cases: the periodic habitat is *nearly globally homogeneous* in the sense that $\max_{x\in\mathbf{R}^N} f_3(x, 0) - \min_{x\in\mathbf{R}^N} f_3(x, 0) < \nu_3$ or it is *nearly homogeneous in a region where it is most conducive to population growth in the zero-limit population* in the sense that $f_3(x, 0)$ is C^N and the partial derivatives of $f_3(x, 0)$ up to order $N - 1$ are zero at some $x_0 \in \mathbf{R}^N$ with $f_3(x_0, 0) = \max_{x\in\mathbf{R}^N} f_3(x, 0)$. Note that, if $1 \le N \le 2$, then the periodic habitat is always nearly homogeneous in a region where it is most conducive to population growth in the zero-limit population. It is also shown in [**45**] that, in general, there is a $\delta_0 > 0$ such that $c_3^*(\delta, \xi)$ exists for any $0 < \delta < \delta_0$ and any $\xi \in S^{N-1}$. In the paper [**46**], the existence of traveling wave solutions of (1.3) connecting u_3^+ and 0 with propagating speed $c \geq c_3^*(\delta, \xi)$ in the direction of ξ is studied.

One of the objectives of the current paper is to explore the effects of spatial variations and dispersal strategies on the spreading speeds of (1.1)–(1.3). To this end, consider the following eigenvalue problems

$$(1.5) \qquad \begin{cases} \nu_1 \Delta u - 2\mu\nu_1 \xi \cdot \nabla u + (a_1(x) + \nu_1 \mu^2) u = \lambda u, & x \in \mathbf{R}^N \\ u(x + p_{1i}\mathbf{e_i}) = u(x), & x \in \mathbf{R}^N, \end{cases}$$

$$(1.6) \qquad \begin{cases} \nu_2 \sum_{k \in K} (e^{-\mu k \cdot \xi} u_{j+k} - u_j) + a_2(j) u_j = \lambda u_j, & j \in \mathbf{Z}^N \\ u_{j+p_{2i}\mathbf{e_i}} = u_j \end{cases}$$

and

$$(1.7) \qquad \begin{cases} \nu_3 [\int_{\mathbf{R}^N} e^{-\mu(y-x)\cdot\xi} k_\delta(y - x) u(y) dy - u(x)] & \\ \quad + a_3(x) u(x) = \lambda u, & x \in \mathbf{R}^N \\ u(x + p_{3i}\mathbf{e_i}) = u(x), & x \in \mathbf{R}^N, \end{cases}$$

where $a_j(x) = f_j(x, 0)$, $j = 1, 2, 3$, $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$. Assume that the principal eigenvalues of (1.5)–(1.7) exist; then, we characterize the spreading speeds of (1.1)–(1.3) (see Proposition 4.1) by the corresponding principal eigenvalues. Note that, for $\mu = 0$, (1.5)–(1.7) are independent of $\xi \in S^{N-1}$ and are the associated eigenvalue problems of the linearizations of (1.1)–(1.3) at 0.

Our other objective is to study the effect of spatial variations on the principal eigenvalues of (1.5)–(1.7). Such findings are important for investigating the effects of spatial variations and dispersal strategies on the spreading speeds of (1.1)–(1.3), but are also of great interest on their own.

The main results of the paper can be roughly stated as follows.

• If the principal eigenvalues of (1.6) and (1.7) exist, they are greater than those of the associated spatially homogeneous problem unless a_j

is a constant (see Theorem 2.1) (it is known that the statement holds for the principal eigenvalue of (1.5)).

• Spatial variation enhances the spatial spreading in (1.1)–(1.3) (see Theorem 2.2).

• Assume that $\nu_1 = \nu_3$ and $f_1(x,u) = f_3(x,u)$. The spatial spreading speed of (1.1) is greater (respectively, smaller) than the spreading speed of (1.3) if the dispersal distance δ is small (respectively, large) (see Theorem 2.3).

These results reveal important features of the effects of spatial variation and of dispersal strategies in population dynamics.

The rest of the paper is organized as follows. In Section 2, we state the main results, i.e., Theorems 2.1–2.3, of the paper. We investigate the effects of spatial variations on the principal eigenvalues of (1.2) and (1.3) and prove Theorem 2.1 in Section 3. In Section 4, we explore the effects of spatial variations and dispersal strategies on the spreading speeds of (1.1)–(1.3) and prove Theorems 2.2 and 2.3.

2. Main results. In this section, we state the main results of the paper.

Let $N \in \mathbf{N}$, $\mathbf{p}_j = (p_{j1}, \dots, p_{jN})$ be in $(0,\infty)^N$ for $j = 1,3$ and in $\mathbf{N}^N$ for $j = 2$. Set

$$X_1 = \{u \in C(\mathbf{R}^N, \mathbf{R}) \mid u(x + p_{1i}\mathbf{e_i}) = u(x)\},$$
$$X_2 = \{\{u_j\}_{j\in\mathbf{Z}^N} \mid u_{j+p_{2i}\mathbf{e_i}} = u_j\}$$

and

$$X_3 = \{u \in C(\mathbf{R}^N, \mathbf{R}) \mid u(x + p_{3i}\mathbf{e_i}) = u(x)\}.$$

Let

$$\widetilde{X}_1 = \{u \in C(\mathbf{R}^N, \mathbf{R}) \mid \sup_{x\in\mathbf{R}^N} |u(x)| < \infty\},$$
$$\widetilde{X}_2 = \{u \in C(\mathbf{Z}^N, \mathbf{R}) \mid \sup_{j\in\mathbf{Z}^N} |u(j)| < \infty\},$$

and

$$\widetilde{X}_3 = \widetilde{X}_1.$$

For $u \in \widetilde{X}_1$ ($\widetilde{X}_2$, $\widetilde{X}_3$), we write $u \geq 0$ if $u(x) \geq 0$ ($u_j \geq 0$, $u(x) \geq 0$) for $x \in \mathbf{R}^N$ ($j \in \mathbf{Z}^N$, $x \in \mathbf{R}^N$). For $u \in X_1$ (X_2, X_3), we write $u \gg 0$ if $u(x) > 0$ ($u_j > 0$, $u(x) > 0$) for $x \in \mathbf{R}^N$ ($j \in \mathbf{Z}^N$, $x \in \mathbf{R}^N$).

Observe that, if f_1 (f_2, f_3) is a C^1 function, then for every $u^0 \in \widetilde{X}_1$ ($u^0 \in \widetilde{X}_2$, $u^0 \in \widetilde{X}_3$), (1.1) ((1.2), (1.3)) has a unique (local) solution $u^1(t, \cdot; u^0)$ ($u^2(t, \cdot; u^0)$, $u^3(t, \cdot; u^0)$) with $u^1(0, \cdot; u^0) = u^0$ ($u^2(0, \cdot; u^0) = u^0$, $u^3(0, \cdot; u^0) = u^0$) (see [**20, 38**]). Moreover, if $u^0(\cdot) \geq 0$, then $u^i(t, \cdot; u^0) \geq 0$ for t in the existence interval of the solution. For biological reasons, we are mainly interested in solutions of (1.1) ((1.2), (1.3)) with nonnegative initial data. Observe that, if $u^0 \in X_i$, then $u^i(t, \cdot; u^0) \in X_i$ for t in the existence interval of the solution ($i = 1, 2, 3$).

Throughout this paper, we assume

(H1) *$f_i(\cdot, \cdot)$ are C^2 and are monostable in their second variables. More precisely, $f_i(\cdot, u) < 0$ for $u \gg 1$ and $i = 1, 2, 3$; $\partial_2 f_i(\cdot, \cdot) < 0$ for $i = 1, 2, 3$, where ∂_2 denotes the partial derivative of a function with respect to its second variable; and the trivial solutions $u \equiv 0$ of* (1.1)–(1.3) *are unstable with respect to periodic perturbations in the sense that there is a $\delta_0 > 0$ such that, for any $u^0 \in X_i^+ \setminus \{0\}$, $u^i(t, \cdot; u^0) \geq \delta_0$ for $t \gg 1$ ($i = 1, 2, 3$).*

Remark. Assumption (H1) implies the existence of $u^i(t, \cdot; u^0)$ for all $t \geq 0$, if $0 \leq u^0 \in X_i$. Moreover, there exists a $u_1^+(x)$ ($u_2^+(j)$, $u_3^+(x)$) satisfying that $u_1^+(x)$ ($u_2^+(j)$, $u_3^+(x)$) is periodic in x (in j, in x) with period vector $\mathbf{p}_1$ ($\mathbf{p}_2$, $\mathbf{p}_3$). Furthermore, $0 < u_1^+(x)$ ($0 < u_2^+(j)$, $0 < u_3^+(x)$), $u = u_1^+(x)$ ($u = \{u_j\} = \{u_2^+(j)\}$, $u = u_3^+(x)$) is a stable solution of (1.1) ((1.2), (1.3)) under $\mathbf{p}_1$ ($\mathbf{p}_2$, $\mathbf{p}_3$) periodic perturbations, and there are no other stationary solutions of (1.1) ((1.2), (1.3)) which are periodic in x (in j, in x) with period vector $\mathbf{p}_1$ ($\mathbf{p}_2$, $\mathbf{p}_3$), and lie between 0 and $u_1^+(x)$ (0 and $u_2^+(j)$, 0 and $u_3^+(x)$).

Let $a_1(x) = f_1(x, 0)$, $a_2(j) = f_2(j, 0)$ and $a_3(x) = f_3(x, 0)$.

We first state our main results on the effect of spatial variations on the principal eigenvalues of (1.2) and (1.3). For given $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$, we define $A_i(\mu,\xi):\mathcal{D}(A_i(\mu,\xi))\subset X_i\to X_i$ $(i=1,2,3)$ by

$$\begin{aligned}(A_1(\mu,\xi)u)(x)&=\nu_1\Delta u-2\mu\nu_1\xi\cdot\nabla u+(a_1(x)+\nu_1\mu^2)u(x),\\(A_2(\mu,\xi)u)_j&=\nu_2\sum_{k\in K}(e^{-\mu k\cdot\xi}u_{j+k}-u_j)+a_2(j)u_j,\end{aligned}$$

and

$$\begin{aligned}(A_3(\mu,\xi)u)(x)=\nu_3\left[\int_{\mathbf{R}^N}e^{-\mu(y-x)\cdot\xi}k_\delta(y-x)u(y)\,dy-u(x)\right]\\+a_3(x)u(x).\end{aligned}$$

Let $\sigma(A_i(\mu,\xi))$ be the spectrum of $A_i(\mu,\xi)$ $(i=1,2,3)$ and

$$\lambda_i(\mu,\xi)=\sup\{\operatorname{Re}\lambda\mid\lambda\in\sigma(A_i)\}.$$

We call $\lambda\in\sigma(A_i(\mu,\xi))\cap\mathbf{R}$ the *principal eigenvalue* of $A_i(\mu,\xi)$ if it is an algebraically simple eigenvalue with an eigenfunction $\phi^i\in X_i$, $\phi^i\gg 0$ (called *principal eigenfunction*), and for any $\mu\in\sigma(A_i(\mu,\xi))\setminus\{\lambda\}$, $\operatorname{Re}(\mu)<\lambda$. To indicate the dependence of $A_3(\mu,\xi)$ on δ, we may write $A_3(\delta,\mu,\xi)$.

Observe that the existence of principal eigenvalues, denoted by $\lambda_1(\mu,\xi)$ and $\lambda_2(\mu,\xi)$, of $A_1(\mu,\xi)$ and $A_2(\mu,\xi)$ follows from the Krein-Rutman theorem. Moreover,

$$\lambda_i(\mu,\xi)=\sup\{\operatorname{Re}\lambda\mid\lambda\in\sigma(A_i(\mu,\xi))\},\quad i=1,2.$$

If $A_3(\mu,\xi)$ has a principal eigenvalue, denoted by $\lambda_3(\delta,\mu,\xi)$, then

$$\lambda_3(\delta,\mu,\xi)=\sup\{\operatorname{Re}\lambda\mid\lambda\in\sigma(A_3(\delta,\mu,\xi))\}.$$

However, the principal eigenvalue of $A_3(\delta,\mu,\xi)$ may not exists when $N\geq 3$ and δ is not small (see example in [**45**]). Hence, there is some essential difference between random dispersal and nonlocal dispersal. For convenience, we introduce the following standing assumption.

(H2) (i) $0<\delta\ll 1$.

(ii) $\max_{x\in\mathbf{R}^N}a_3(x)-\min_{x\in\mathbf{R}^N}a_3(x)<\nu_3$.

(iii) $a_3(\cdot)$ is C^N and the partial derivatives of $a_3(x)$ up to order $N-1$ are zero at some $x_0 \in \mathbf{R}^N$ with $a_3(x_0) = \max_{x\in\mathbf{R}^N} a_3(x)$.

The following proposition is proved in [**45**].

Proposition 2.1. *If* (H2) (i), (H2) (ii) *or* (H2) (iii) *holds, then* $\lambda_3(\delta,\mu,\xi)$ *exists for any* $\mu \in \mathbf{R}$ *and* $\xi \in S^{N-1}$.

Note that (H2) (i) indicates the nonlocal dispersal is nearly local. The periodic habitat satisfying (H2) (ii) is called *nearly globally homogeneous.* If (H2) (iii) is satisfied, the periodic habitat is said to be *nearly homogeneous in a region where it is most conducive to population growth in the zero-limit population.* When $1 \le N \le 2$, (H2) (iii) always holds. If $N \ge 3$ and δ is not small, $\lambda_3(\delta,\mu,\xi)$ may not exist (see example in [**45**]).

Let $\overline{\lambda}_1(\mu,\xi)$, $\overline{\lambda}_2(\mu,\xi)$, and $\overline{\lambda}_3(\delta,\mu,\xi)$ be the principal eigenvalues of (1.5)–(1.7) with $a_1(x)$, $a_2(j)$ and $a_3(x)$ being replaced by $\overline{a}_1$, $\overline{a}_2$ and $\overline{a}_3$, respectively, where

$$\overline{a}_1 = \frac{1}{|D_1|}\int_{D_1} a_1(x)\,dx,$$
$$\overline{a}_2 = \frac{1}{\#(D_2)}\sum_{j\in D_2} a_2(j),$$
$$\overline{a}_3 = \frac{1}{|D_3|}\int_{D_3} a_3(x)\,dx,$$

$$D_1 = \{x \in \mathbf{R}^N \mid 0 \le x \le \mathbf{p_1}\},$$
$$D_2 = \{j \in \mathbf{Z}^N \mid 0 \le j \le \mathbf{p_2}\},$$
$$D_3 = \{x \in \mathbf{R}^N \mid 0 \le x \le \mathbf{p_3}\},$$

and $|D_1|$ and $|D_3|$ are the Lebesgue measures of D_1 and D_3, respectively, $\#(D_3)$ is the total number of elements in D_3. Observe that $\overline{\lambda}_1(\mu,\xi)$, $\overline{\lambda}_2(\mu,\xi)$ and $\overline{\lambda}_3(\delta,\mu,\xi)$ exist for any $\mu \in \mathbf{R}$, $\xi \in S^{N-1}$ and $\delta > 0$, and

$$\overline{\lambda}_1(\mu,\xi) = \nu_1\mu^2 + \overline{a}_1, \tag{2.1}$$

$$\overline{\lambda}_2(\mu,\xi) = \nu_2\Big[\sum_{k\in K}(e^{-\mu k\cdot\xi} - 1)\Big] + \overline{a}_2, \tag{2.2}$$

and

$$\overline{\lambda}_3(\delta,\mu,\xi) = \nu_3\left[\int_{\mathbf{R}^N} e^{-\mu z\cdot\xi} k_\delta(z)\,dz - 1\right] + \overline{a}_3 \tag{2.3}$$

(see Proposition 3.2). The following well-known proposition addresses the effect of spatial variations on the principal eigenvalue of $A_1(\mu,\xi)$.

Proposition 2.2. *$\lambda_1(\mu,\xi) \geq \overline{\lambda}_1(\mu,\xi)$ for any $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$, and equality holds for some $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$ if and only if $a_1(x) \equiv \overline{a}_1$.*

In this paper, we prove

Theorem 2.1. (1) *For any $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$, $\lambda_2(\mu,\xi) \geq \overline{\lambda}_2(\mu,\xi)$. $\lambda_2(\mu,\xi) = \overline{\lambda}_2(\mu,\xi)$ for some $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$ if and only if $a_2(j) \equiv \overline{a}_2$.*

(2) *Given $\delta > 0$, assume that $\lambda_3(\delta,\mu,\xi)$ exists for any $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$. Then $\lambda_3(\delta,\mu,\xi) \geq \overline{\lambda}_3(\delta,\mu,\xi)$ for any $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$. $\lambda_3(\delta,\mu,\xi) = \overline{\lambda}_3(\delta,\mu,\xi)$ for some $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$ if and only if $a_3(x) \equiv \overline{a}_3$.*

Theorem 2.1 reveals the important fact that spatial variations cannot reduce the principal eigenvalues of $A_2(\mu,\xi)$ and $A_3(\delta,\mu,\xi)$, and they are indeed increased except for degenerate cases. Hence, discrete dispersal and nonlocal dispersal share similar properties with random dispersal. Note that the condition in Theorem 2.1 (2) is satisfied if (H2) (i), (H2) (ii) or (H2) (iii) holds.

Next we state our main results on the effects of spatial variations and dispersal strategies on the spreading speeds of (1.1)–(1.3). Let

$$\overline{f}_1(u) = \frac{1}{|D_1|}\int_{D_1} f_1(x,u)\,dx,$$
$$\overline{f}_2(u) = \frac{1}{\#(D_2)}\sum_{j\in D_2} f_2(j,u),$$

and

$$\overline{f}_3(u) = \frac{1}{|D_3|} \int_{D_3} f_3(x,u)\, dx.$$

By (H1), $\overline{f}_j(u) < 0$ for $u \gg 1$ and $\overline{f}_j'(u) < 0$. We assume that $\overline{f}_j$ $(j = 1, 2, 3)$ satisfy

(H3) $\overline{f}_j(0) > 0$ for $j = 1, 2, 3$.

Then $\overline{f}_i$ $(i = 1, 2, 3)$ are also monostable type functions. Let $\overline{c}_1^*(\xi)$, $\overline{c}_2^*(\xi)$ and $\overline{c}_3^*(\delta, \xi)$ be the spreading speeds of the following averaged equations of (1.1)–(1.3),

$$\frac{\partial u}{\partial t} = \nu_1 \Delta u + u\overline{f}_1(u), \tag{2.4}$$

$$\dot{u}_j = \nu_2 \sum_{k \in K} (u_{j+k} - u_j) + u_j \overline{f}_2(u_j), \tag{2.5}$$

and

$$\frac{\partial u}{\partial t} = \nu_3 \left[\int_{\mathbf{R}^N} k_\delta(y-x) u(t,y)\, dy - u(t,x) \right] + u\overline{f}_3(u), \tag{2.6}$$

respectively.

Observe that $\overline{c}_3^*(\delta, \xi)$ always exists. The following proposition is proved in [**6**] (also see [**42**]).

Proposition 2.3. *$c_1^*(\xi) \geq \overline{c}_1^*(\xi)$ for any $\xi \in S^{N-1}$ and $c_1^*(\xi) = \overline{c}_1^*(\xi)$ for some $\xi \in S^{N-1}$ if and only if $a_1(x) \equiv f_1(x, 0)$ is independent of x.*

In this paper, we prove

Theorem 2.2. (1) *$c_2^*(\xi) \geq \overline{c}_2^*(\xi)$ for any $\xi \in S^{N-1}$, and $c_2^*(\xi) = \overline{c}_2^*(\xi)$ for some $\xi \in S^{N-1}$ if and only if $a_2(j) \equiv f_2(j, 0)$ is independent of j.*

(2) *Given $\delta > 0$, assume that $\lambda_3(\delta, \mu, \xi)$ exists for any $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$. Then $c_3^*(\xi)$ exists for any $\xi \in S^{N-1}$, and $c_3^*(\delta, \xi) \geq \overline{c}_3^*(\delta, \xi)$*

for any $\xi \in S^{N-1}$. *Moreover,* $c_3^*(\delta,\xi) = \overline{c}_3^*(\delta,\xi)$ *for some* $\xi \in S^{N-1}$ *if and only if* $a_3(x) \equiv f_3(x,0)$ *is independent of* x.

Theorem 2.2 shows that it is a generic scenario that spatial variation increases the spreading speed. The condition in Theorem 2.2 is satisfied if (H2) (i), (H2) (ii) or (H2) (iii) holds.

While all three types of monostable equations under consideration have been used to model population dispersal, it is natural to ask how the spreading speeds depend on the dispersal strategies. In [**18**], some relation between (1.1) and (1.2) is obtained.

In this paper, we prove

Theorem 2.3. (1) *If* $f_1(x,u) = f_1(u) = f_3(x,u) = f_3(u) := f(u)$ *and* $\nu_1 = \nu_3$, *then* $c_3^*(\delta,\xi)$ *exists for any* $\delta > 0$ *and* $\xi \in S^{N-1}$, *and for any* $\xi \in S^{N-1}$, *there is a* $\delta_0^*(\xi) > 0$ *such that*

$$c_1^*(\xi)\begin{cases} > c_3^*(\delta,\xi) & \text{for } 0 < \delta < \delta_0^*(\xi) \\ < c_3^*(\delta,\xi) & \text{for } \delta > \delta_0^*(\xi). \end{cases}$$

(2) *In general, assume that* $\lambda_3(\delta,\mu,\xi)$ *exists for any* $\delta > 0$, $\mu \in \mathbf{R}$ *and* $\xi \in S^{N-1}$. *Then* $c_3^*(\delta,\xi)$ *exists for any* $\delta > 0$ *and* $\xi \in S^{N-1}$. *If* $f_1(x,u) = f_3(x,u)$ *and* $\nu_1 = \nu_3$, *then for any* $\xi \in S^{N-1}$, *there are* $0 < \delta_1^*(\xi) \le \delta_2^*(\xi) < \infty$ *such that*

$$c_1^*(\xi)\begin{cases} > c_3^*(\delta,\xi) & \text{for } 0 < \delta < \delta_1^*(\xi) \\ < c_3^*(\delta,\xi) & \text{for } \delta > \delta_2^*(\xi). \end{cases}$$

Theorem 2.3 reveals the following interesting biological scenario: nonlocal dispersal with small dispersal distance spreads slower than random and nonlocal dispersal and large dispersal distance spreads faster than the random dispersal. The condition in Theorem 2.3 is satisfied if (H2) (ii) or (H2) (iii) holds. It remains open whether $\delta_1^*(\xi) = \delta_2^*(\xi)$ in Theorem 2.3 (2).

3. Principal eigenvalues. In this section, we explore the effect of spatial variations on the principal eigenvalues of (1.5)–(1.7) and prove Theorem 2.1.

Recall that $\lambda_1(\mu,\xi)$ and $\lambda_2(\mu,\xi)$ exist for any $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$. $\lambda_3(\delta,\mu,\xi)$ exists for any $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$ if (H2) (i), (H2) (ii) or (H2)(iii) holds.

Recall also that, for any $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$, $\lambda_1(\mu,\xi) \geq \overline{\lambda}_1(\mu,\xi)$. $\lambda_1(\mu,\xi) = \overline{\lambda}_1(\mu,\xi)$ for some $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$ if and only if $a_1(x) \equiv \overline{a}_1$.

The proof of Theorem 2.1 employs the inequality between the arithmetic and geometric mean:

$$\left(\prod_{j=1}^{n} x_j\right)^{1/n} \leq \frac{1}{n}\sum_{j=1}^{n} x_j \tag{3.1}$$

for $n \in \mathbf{N}$, $x_1,\dots,x_n \geq 0$ with equality occurring, if and only if $x_1 = \cdots = x_n$, and the Jensen's inequality (see [**33**, Theorem 2.2])

$$F\left(\frac{1}{|D_3|}\int_{D_3} g(x)\,dx\right) \leq \frac{1}{|D_3|}\int_{D_3} F(g(x))\,dx \tag{3.2}$$

for any continuous function $g : D_3 \to (c,d)$ and strictly convex function $F : (c,d) \to \mathbf{R}$ with equality occurring, if and only if $g(x)$ is a constant function.

Proof of Theorem 2.1 (1). Suppose that $\phi = \{\phi_j\}_{j\in\mathbf{Z}^N}$ is a positive principal eigenvector and therefore strictly positive, that is, $\phi_j > 0$, $j \in \mathbf{Z}^N$, satisfies (1.6). First we divide both sides of (1.6) by ϕ_j and obtain

$$\nu_2 \sum_{k\in K}\left(e^{-\mu k\cdot\xi}\frac{\phi_{j+k}}{\phi_j} - 1\right) + a_2(j) = \lambda_2(\mu,\xi). \tag{3.3}$$

Take the sum over all $j \in D_2$,

$$\begin{aligned}\sum_{j\in D_2}\left(\nu_2 \sum_{k\in K}\left(e^{-\mu k\cdot\xi}\frac{\phi_{j+k}}{\phi_j} - 1\right) + a_2(j)\right) &= \sum_{j\in D_2}\lambda_2(\mu,\xi)\\ &= \#(D_2)\lambda_2(\mu,\xi).\end{aligned}$$

Therefore,

$$\begin{aligned}\lambda_2(\mu,\xi) &= \frac{1}{\#(D_2)}\sum_{j\in D_2}\left(\nu_2\sum_{k\in K}(e^{-\mu k\cdot\xi}\frac{\phi_{j+k}}{\phi_j}-1)+a_2(j)\right)\\ &= \nu_2\sum_{k\in K}\left(e^{-\mu k\cdot\xi}\left[\frac{1}{\#(D_2)}\sum_{j\in D_2}\frac{\phi_{j+k}}{\phi_j}\right]-1\right)\\ &\quad+\frac{1}{\#(D_2)}\sum_{j\in D_2}a_2(j).\end{aligned}$$

Note that $\overline{a}_2 = 1/\#(D_2)\sum_{j\in D_2} a_2(j)$. Then

$$\lambda_2(\mu,\xi) = \nu_2\sum_{k\in K}\left(e^{-\mu k\cdot\xi}\left[\frac{1}{\#(D_2)}\sum_{j\in D_2}\frac{\phi_{j+k}}{\phi_j}\right]-1\right)+\overline{a}_2. \tag{3.4}$$

Since $\phi_{j+\mathbf{p}_2}=\phi_j$, $\prod_{j\in D_2}(\phi_{j+k})/\phi_j = 1$ for fixed $k\in K$. By (3.1), we have for any fixed $k\in K$ that

$$\frac{1}{\#(D_2)}\sum_{j\in D_2}\frac{\phi_{j+k}}{\phi_j}\geq\left(\prod_{j\in D_2}\frac{\phi_{j+k}}{\phi_j}\right)^{1/\#(D_2)} = 1. \tag{3.5}$$

Furthermore, we get equality if and only if all ϕ_{j+k}/ϕ_j are equal for $j\in D_2$. Thus, (2.2), (3.4) and (3.5) yield $\lambda_2(\mu,\xi)\geq\overline{\lambda}_2(\mu,\xi)$ and $\lambda_2(\mu,\xi)=\overline{\lambda}_2(\mu,\xi)$ if and only if all ϕ_{j+k}/ϕ_j are equal for $j\in D_2$. We claim that all ϕ_{j+k}/ϕ_j are equal for $j\in D_2$ if and only if $a_2(j)\equiv\overline{a}_2$. Suppose that $a_2(j)\equiv\overline{a}_2$. Then all ϕ_j are equal for $j\in D_2$, and so all ϕ_{j+k}/ϕ_j are equal for $j\in D_2$. On the other hand, suppose that all ϕ_{j+k}/ϕ_j are equal for $j\in D_2$. Then $1=\prod_{l\in D_2}\phi_{l+k}/\phi_l = (\phi_{j+k}/\phi_j)^{\#(D_2)}$ for any $j\in D_2$ and fixed $k\in K$, and therefore $\phi_{j+k}=\phi_j$ for any $j\in D_2$ and fixed $k\in K$. Since $\phi_{j+\mathbf{p}_2}=\phi_j$, we have that all ϕ_j are equal for $j\in D_2$. By (3.3) and (3.4), $a_2(j)\equiv\overline{a}_2$. This completes the proof. □

Proof of Theorem 2.1 (2). Suppose that $\phi(x)$ is a strictly positive principal eigenvector (1.7). First we divide both sides of (1.7) by $\phi(x)$ and obtain

$$\frac{\nu_3[\int_{\mathbf{R}^N}e^{-\mu(y-x)\cdot\xi}k_\delta(y-x)\phi(y)\,dy-\phi(x)]+a_3(x)\phi(x)}{\phi(x)} = \lambda_3(\delta,\mu,\xi),$$
$$x\in\mathbf{R}^N.$$

Integrating with respect to x over D_3 yields

$$\int_{D_3}\left[\frac{\nu_3[\int_{\mathbf{R}^N} e^{-\mu(y-x)\cdot\xi}k_\delta(y-x)\phi(y)\,dy-\phi(x)]+a_3(x)\phi(x)}{\phi(x)}\right]dx = \int_{D_3}\lambda_3(\delta,\mu,\xi)\,dx$$

or

$$\lambda_3(\delta,\mu,\xi)=\nu_3\left[\frac{1}{|D_3|}\int_{D_3}\int_{\mathbf{R}^N}\frac{e^{-\mu(y-x)\cdot\xi}k_\delta(y-x)\phi(y)}{\phi(x)}\,dy\,dx-1\right] + \frac{1}{|D_3|}\int_{D_3}a_3(x)\,dx.$$

Since $\overline{\lambda}_3(\delta,\mu,\xi) = \nu_3[\int_{\mathbf{R}^N} e^{-\mu y\cdot\xi}k_\delta(y)\,dy - 1] + \overline{a}_3$, $\lambda_3(\delta,\mu,\xi) \geq \overline{\lambda}_3(\delta,\mu,\xi)$ follows from

$$\frac{1}{|D_3|}\int_{D_3}\int_{\mathbf{R}^N}\frac{e^{-\mu(y-x)\cdot\xi}k_\delta(y-x)\phi(y)}{\phi(x)}\,dy\,dx \geq \int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\,dz$$

or

$$\frac{1}{|D_3|}\int_{D_3}\int_{\mathbf{R}^N}\frac{e^{-\mu z\cdot\xi}k_\delta(z)\phi(x+z)}{\phi(x)}\,dz\,dx \geq \int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\,dz$$

or

$$\frac{1}{|D_3|}\int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\int_{D_3}\frac{\phi(x+z)}{\phi(x)}\,dx\,dz \geq \int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\,dz. \tag{3.6}$$

Moreover, $\lambda_3(\delta,\mu,\xi)=\overline{\lambda}_3(\delta,\mu,\xi)$ if and only if

$$\frac{1}{|D_3|}\int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\int_{D_3}\frac{\phi(x+z)}{\phi(x)}\,dx\,dz = \int_{\mathbf{R}^N} e^{-\mu z\cdot\xi}k_\delta(z)\,dz. \tag{3.7}$$

To prove (3.6), it suffices to prove that

$$\frac{1}{|D_3|}\int_{D_3}\frac{\phi(x+z)}{\phi(x)}\,dx \geq 1 \quad \text{for all } z\in\mathbf{R}^N. \tag{3.8}$$

Note that $F(x) = -\ln x$ is a strictly convex function on $(0, \infty)$. By (3.2),

$$-\frac{1}{|D_3|}\int_{D_3} \ln\left[\frac{\phi(x+z)}{\phi(x)}\right] dx \geq -\ln\left[\frac{1}{|D_3|}\int_{D_3} \frac{\phi(x+z)}{\phi(x)} dx\right]. \tag{3.9}$$

By the periodicity of $\phi(x)$, we have $\int_{D_3} \ln\phi(x+z)\, dx = \int_{D_3} \ln\phi(x)\, dx$ for any $z \in \mathbf{R}^N$. Hence, (3.9) implies that

$$\begin{aligned}\ln\left[\frac{1}{|D_3|}\int_{D_3} \frac{\phi(x+z)}{\phi(x)}\, dx\right] &\geq \frac{1}{|D_3|}\int_{D_3} \ln\left[\frac{\phi(x+z)}{\phi(x)}\right] dx \\ &= \frac{1}{|D_3|}\int_{D_3} \ln[\phi(x+z)]\, dx \\ &\quad - \frac{1}{|D_3|}\int_{D_3} \ln[\phi(x)]\, dx \\ &= 0.\end{aligned}$$

Therefore, $1/|D_3| \int_{D_3} (\phi(x+z))/\phi(x)\, dx \geq 1$, and thus $\lambda_3(\delta, \mu, \xi) \geq \overline{\lambda}_3(\delta, \mu, \xi)$. Moreover, by (3.7), $\lambda_3(\delta, \mu, \xi) = \overline{\lambda}_3(\delta, \mu, \xi)$ if and only if

$$\frac{1}{|D_3|}\int_{D_3} \frac{\phi(x+z)}{\phi(x)}\, dx = 1 \quad \text{for all } z \in \mathbf{R}^N. \tag{3.10}$$

By (3.2) again, the equality occurs in (3.9) if and only if $\phi(x+z)/\phi(x) \equiv 1$ for any $z \in \mathbf{R}^N$, which is equivalent to $\phi(x) \equiv$ constant since z is arbitrary. This implies that $\lambda_3(\delta, \mu, \xi) = \overline{\lambda}_3(\delta, \mu, \xi)$ if and only if $a_3(x) \equiv \overline{a}_3$. The proof is thus completed. □

We end this section with two propositions which will be used in the next section. To indicate the dependence of $\lambda_3(\delta, \mu, \xi)$ on $a_3(\cdot)$, we may write $\lambda_3(\delta, \mu, \xi, a_3)$.

Proposition 3.1. *Assume that $a_3(x) \leq \widetilde{a}_3(x)$. If, for given $\delta > 0$, $\mu \in \mathbf{R}$ and $\xi \in S^{N-1}$, both $\lambda_3(\delta, \mu, \xi, a_3)$ and $\lambda_3(\delta, \mu, \xi, \widetilde{a}_3)$, exist, then*

$$\lambda_3(\delta, \mu, \xi, a_3) \leq \lambda(\delta, \mu, \xi, \widetilde{a}_3).$$

Proof. Consider the following two evolution equations,

(3.11)
$$\frac{\partial u}{\partial t} = \nu_3\bigg[\int_{\mathbf{R}^N} e^{-\mu(y-x)\cdot\xi} k_\delta(y-x)u(t,y)dy - u(t,x)\bigg] + a_3(x)u(t,x)$$

and

(3.12)
$$\frac{\partial u}{\partial t} = \nu_3\bigg[\int_{\mathbf{R}^N} e^{-\mu(y-x)\cdot\xi} k_\delta(y-x)u(t,y)dy - u(t,x)\bigg] + \widetilde{a}_3(x)u(t,x).$$

For a given $u^0 \in X_3$, let $u(t,\cdot;u^0)$ and $\widetilde{u}(t,\cdot;u^0)$ be the solutions of (3.11) and (3.12) with $u(0,\cdot;u^0) = u^0$ and $\widetilde{u}(0,\cdot;u^0) = u^0$, respectively. Put

$$\Phi(t)u^0 = u(t,\cdot;u^0), \qquad \widetilde{\Phi}(t)u^0 = \widetilde{u}(t,\cdot;u^0).$$

Let $r(\Phi(1))$ and $r(\widetilde{\Phi}(1))$ be the spectral radius of $\Phi(1)$ and $\widetilde{\Phi}(1)$, respectively. By [**45**, Lemma 3.1],

$$\lambda_3(\delta,\mu,\xi,a_3) = \ln r(\Phi(1))$$

and

$$\lambda_3(\delta,\mu,\xi,\widetilde{a}_3) = \ln r(\widetilde{\Phi}(1)).$$

By $a_3 \le \widetilde{a}_3$ and [**45**, Proposition 2.1], we have that, for any $u^0 \ge 0$, $\Phi(t,\cdot;u^0) \le \widetilde{\Phi}(t,\cdot;u^0)$ for any $t \ge 0$. It then follows that $r(\Phi(1)) \le r(\widetilde{\Phi}(1))$ and then $\lambda_3(\delta,\mu,\xi,a_3) \le \lambda_3(\delta,\mu,\xi,\widetilde{a}_3)$. □

Proposition 3.2. (1) *If $a_1(x) \equiv a_1$ is independent of x, then*

$$\lambda_1(\mu,\xi) = \nu_1\mu^2 + a_1.$$

(2) *If $a_2(j) \equiv a_2$ is independent of j, then*

$$\lambda_2(\mu,\xi) = \nu_2\bigg[\sum_{k\in K}(e^{-\mu k\cdot\xi} - 1)\bigg] + a_2.$$

(3) *If $a_3(x) \equiv a_3$ is independent of x, then $\lambda_3(\delta,\mu,\xi)$ exists for any $\delta > 0$, $\mu \in \mathbf{R}$, and $\xi \in S^{N-1}$, and*

$$\lambda_3(\delta,\mu,\xi) = \nu_3\left[\int_{\mathbf{R}^N} e^{-\mu y\cdot\xi} k_\delta(y)\,dy - 1\right] + a_3.$$

Moreover, $\lambda_3(\delta,\mu,\xi)$ is strictly increasing in $\delta > 0$, and $\lambda_3(\delta,\mu,\xi) \to a_3$ as $\delta \to 0$ and $\lambda_3(\delta,\mu,\xi) \to \infty$ as $\delta \to \infty$ uniformly in $\xi \in S^{N-1}$.

Proof. (1) It follows trivially.

(2) It also follows trivially.

(3) Observe that $\lambda = \nu_3[\int_{\mathbf{R}^N} e^{-\mu y\cdot\xi} k_\delta(y)\,dy - 1] + a_3 (> -\nu_3 + a_3)$ is an eigenvalue of (1.7) with an eigenfunction $\phi(x) \equiv 1$. By [**45**, Proposition 3.1], $\lambda_3(\delta,\mu,\xi)$ exists and $\lambda_3(\delta,\mu,\xi) = \nu_3[\int_{\mathbf{R}^N} e^{-\mu y\cdot\xi} k_\delta(y)\,dy - 1] + a_3$.

Let

$$g(\delta,\mu,\xi) = \int_{\mathbf{R}^N} e^{-\mu y\cdot\xi} k_\delta(y)\,dy - 1 = \int_{\mathbf{R}^N} e^{-\mu\delta z\cdot\xi} k(z)\,dz - 1.$$

Let $m_k(\xi) = 1/k! \int_{\mathbf{R}^n} (-z\cdot\xi)^k k(z)\,dz$ with $k \in \mathbf{N}$. Note that $m_k(\xi) > 0$ if k is even, and 0 if k is odd. Then

$$\begin{aligned} g(\delta,\mu,\xi) &= \int_{\mathbf{R}^N} e^{-\mu\delta z\cdot\xi} k(z)\,dz - 1 \\ &= \sum_{k=0}^{\infty} \int_{\mathbf{R}^n} \frac{1}{k!}(-\mu\delta z\cdot\xi)^k k(z)\,dz - 1 \\ &= \sum_{k=1}^{\infty} \frac{1}{2k!} m_{2k}(\xi)\delta^{2k}\mu^{2k}. \end{aligned}$$

Since each $m_{2k}(\xi)\delta^{2k} (k \in \mathbf{N})$ is a strictly increasing continuous function with respect to δ over $(0,\infty)$, the same holds for $g(\delta,\mu,\xi)$ and therefore for $\lambda_3(\delta,\mu,\xi)$, that is, $\lambda_3(\delta_1,\mu,\xi) > \lambda_3(\delta_2,\mu,\xi)$ for every $\delta_1 > \delta_2 > 0$.

Clearly, $\lambda_3(\delta,\mu,\xi) = \nu_3 \sum_{k=1}^{\infty} 1/2k! m_{2k}(\xi)\delta^{2k}\mu^{2k} + a_3 \to a_3$ as $\delta \to 0$ and $\lambda_3(\delta,\mu,\xi) \to \infty$ as $\delta \to \infty$ uniformly in $\xi \in S^{N-1}$. □

4. Spreading speeds. In this section, we study the effects of spatial variations and dispersal strategies on the spreading speeds of (1.1)–(1.3) and prove Theorems 2.2 and 2.3.

First of all, we have the following variational principle for the spreading speeds of (1.1)–(1.3) (if it exists).

Proposition 4.1. (1) *For any* $\xi \in S^{N-1}$, *there is a* $\mu^*(\xi) > 0$ *such that*

$$c_1^*(\xi) = \inf_{\mu>0} \frac{\lambda_1(\mu,\xi)}{\mu} = \frac{\lambda_1(\mu^*(\xi),\xi)}{\mu^*(\xi)}.$$

(2) *For any* $\xi \in S^{N-1}$, *there is a* $\mu^*(\xi) > 0$ *such that*

$$c_2^*(\xi) = \inf_{\mu>0} \frac{\lambda_2(\mu,\xi)}{\mu} = \frac{\lambda_2(\mu^*(\xi),\xi)}{\mu^*(\xi)}.$$

(3) *Given* $\delta > 0$, *assume that* $\lambda_3(\delta,\mu,\xi)$ *exists for any* $\mu \in \mathbf{R}$ *and* $\xi \in S^{N-1}$. *Then, for any* $\xi \in S^{N-1}$, $c_3^*(\delta,\xi)$ *exists and there is a* $\mu^*(\delta,\xi) > 0$ *such that*

$$c_3^*(\delta,\xi) = \inf_{\mu>0} \frac{\lambda_3(\delta,\mu,\xi)}{\mu} = \frac{\lambda_3(\delta,\mu^*(\delta,\xi),\xi)}{\mu^*(\delta,\xi)}.$$

Proof. (1) It follows from [**6**] (see also [**51**]).

(2) It follows from [**18**] (also see [**51**]).

(3) It follows from [**45**]. □

Proof of Theorem 2.2. (1) First, by Proposition 4.1, for any $\xi \in S^{N-1}$, there is a $\mu^*(\xi) > 0$ such that

$$c_2^*(\xi) = \frac{\lambda_2(\mu^*(\xi),\xi)}{\mu^*(\xi)}.$$

Then, by Theorem 2.1 and Proposition 4.1,

$$c_2^*(\xi) = \frac{\lambda_2(\mu^*(\xi),\xi)}{\mu^*(\xi)} \geq \frac{\overline{\lambda}_2(\mu^*(\xi),\xi)}{\mu^*(\xi)} \geq \overline{c}_2^*(\xi).$$

Now if, for some $\xi \in S^{N-1}$, $c_2^*(\xi) = \overline{c}_2^*(\xi)$, then we must have

$$\frac{\lambda_2(\mu^*(\xi), \xi)}{\mu^*(\xi)} = \frac{\overline{\lambda}_2(\mu^*(\xi), \xi)}{\mu^*(\xi)}.$$

By Theorem 2.1 again, we must have $a_2(j) \equiv \overline{a}_2$.

(2) It can be proved by similar arguments as in (1). □

Proof of Theorem 2.3. To indicate the dependence of $\lambda_3(\delta, \mu, \xi)$ and $c_3^*(\delta, \xi)$ on a_3, we may write $\lambda_3(\delta, \mu, \xi, a_3)$ and $c_3^*(\delta, \xi, a_3)$, respectively.

(1) Assume that $\nu_1 = \nu_3$ and $a_1(x) \equiv a_3(x) \equiv a_3$ is independent of x. By (H1), we must have $a_3 > 0$.

Observe that $\lambda_1(\mu, \xi) = a_3 + \nu_1 \mu^2$ for any $\xi \in S^{N-1}$ and $\mu \in \mathbf{R}$ and so $c_1^*(\xi) = \inf_{\mu > 0}\{\lambda_1(\mu, \xi)/\mu\} = 2\sqrt{a_3 \nu_1}$ is a constant.

By Proposition 3.2, $\lambda_3(\delta, \mu, \xi)$ is strictly increasing in $\delta > 0$. Then, by Proposition 4.1, $c_3^*(\delta, \xi)$ is strictly increasing in $\delta > 0$.

By Proposition 3.2 again, we have

$$\lambda_3(\delta, \xi, \mu, a) = \nu_3 \left[\int_{\mathbf{R}^N} e^{-\mu y \cdot \xi} k_\delta(y) dy - 1 \right] + a_3, \tag{4.1}$$

or

$$\frac{\lambda_3(\delta, \xi, \mu, a_3)}{\mu} = \frac{\nu_3 [\int_{\mathbf{R}^N} e^{-\mu y \cdot \xi} k_\delta(y)\, dy - 1] + a_3}{\mu}.$$

Given $\varepsilon > 0$, there exists an $M > 0$ such that

$$\frac{a_3}{M} < \frac{\varepsilon}{2}.$$

Note that

$$\lim_{\delta \to 0} \frac{\nu_3 [\int_{\mathbf{R}^N} e^{-M y \cdot \xi} k_\delta(y)\, dy - 1]}{M} = 0$$

uniformly in $\xi \in S^{N-1}$; hence, there is a $\delta_0 > 0$ such that

$$\frac{\nu_3 [\int_{\mathbf{R}^N} e^{-M y \cdot \xi} k_\delta(y) dy - 1]}{M} < \frac{\varepsilon}{2}$$

for all $0 < \delta < \delta_0$ and $\xi \in S^{N-1}$. Therefore,

$$\frac{\lambda_3(\delta,\xi,M,a_3)}{M} = \frac{\nu_3[\int_{\mathbf{R}^N} e^{-My\cdot\xi}k_\delta(y)dy - 1] + a_3}{M} < \frac{\varepsilon}{2} + \frac{\varepsilon}{2} = \varepsilon$$

for all $0 < \delta < \delta_0$. Thus, $c_3^*(\delta,\xi,a) = \inf_{\mu>0}\lambda_3(\delta,\xi,\mu,a_3)/\mu \leq \lambda_3(\delta,\xi,M,a)/M \to 0$ as $\delta \to 0$ uniformly in $\xi \in S^{N-1}$.

By the same arguments as in Proposition 3.2, one obtains

$$\begin{aligned}\lambda_3(\delta,\xi,\mu,a_3) &= \nu_3\left[\int_{\mathbf{R}^N} e^{-\mu\delta z\cdot\xi}k(z)\,dz - 1\right] + a_3\\ &= \nu_3\sum_{k=1}^{\infty}\frac{1}{2k!}m_{2k}(\xi)(\mu\delta)^{2k} + a_3\\ &\geq \frac{\nu_3 m_2(\xi)(\mu\delta)^2}{2} + a_3.\end{aligned}$$

Therefore,

$$\frac{\lambda_3(\delta,\xi,\mu,a_3)}{\mu} \geq \frac{1}{2}\frac{\nu_3 m_2(\xi)(\mu\delta)^2 + 2a_3}{\mu} \geq \sqrt{\nu_3 m_2 a_3}\,\delta,$$

for $\xi \in S^{N-1}$. Thus, $c_3^*(\delta,\xi,a_3) = \inf_{\mu>0}\lambda_3(\delta,\mu,\xi,a_3)/\mu \geq \sqrt{\nu_3 m_2(\xi) a_3}\,\delta \to \infty$ as $\delta \to \infty$ uniformly in $\xi \in S^{N-1}$.

Therefore, for any $\xi \in S^{N-1}$, there is a $\delta_0^*(\xi) > 0$ such that

$$c_1^*(\xi)\begin{cases} > c_3^*(\delta,\xi) & \text{for } 0 < \delta < \delta_0^*(\xi)\\ < c_3^*(\delta,\xi) & \text{for } \delta > \delta_0^*(\xi).\end{cases}$$

(2) By Propositions 3.1 and 4.1, $c_3^*(\delta,\xi,a_3) \leq c_3^*(\delta,\xi,\max_{x\in\mathbf{R}^N}|a_3(x)|)$. By Theorem 2.2, $c_3^*(\delta,\xi,\overline{a}_3) \leq c_3^*(\delta,\xi,a_3)$. We then have $c_3^*(\delta,\xi,a_3) \to 0$ as $\delta \to 0$ and $c_3^*(\delta,\xi,a_3) \to \infty$ as $\delta \to \infty$. Hence, for any $\xi \in S^{N-1}$, there are $0 < \delta_1^*(\xi) \leq \delta_2^*(\xi) < \infty$ such that

$$c_1^*(\xi)\begin{cases} > c_3^*(\delta,\xi) & \text{for } 0 < \delta < \delta_1^*(\xi)\\ < c_3^*(\delta,\xi) & \text{for } \delta > \delta_2^*(\xi).\end{cases} \qquad \square$$

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