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Research article

Dynamics of a two-state reversible population model

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Abstract: The effect of the diffusion rate on the persistence of a nematode population with two reversible states in a spatially heterogeneous environment is investigated. In the absence of advection, it is shown that when the toxin distribution is not identically maximal, the system admits a unique positive equilibrium. As the diffusion rate tends to zero, this equilibrium converges to that of the corresponding non-spatial kinetic system, concentrating near locations where resources are abundant and toxin levels are low. As the diffusion rate tends to infinity, the equilibrium becomes spatially homogeneous and approaches a constant determined by the spatial averages of the resource, toxin, and competition coefficients. These results show that slow diffusion promotes exploitation of local favorable habitats, whereas fast diffusion smooths spatial heterogeneity, highlighting the joint influence of diffusion and environmental heterogeneity on persistence.

Keywords: evolution of dispersal; state transition; population dynamics; spatial heterogeneity
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1. Introduction

The interaction between diffusion and spatial heterogeneity has become a central topic in the study of population dynamics and species interactions, particularly within reaction-diffusion frameworks. Many existing studies assume spatial structure and homogeneous diffusion in populations. However, natural populations are often more complex, consisting of different life stages or other intrinsic traits. Recent studies suggest that such complexity may significantly influence the population growth and stability, especially in spatially heterogeneous environments [1, 3–5].

Free-living nematodes such as *Caenorhabditis elegans* exhibit remarkable behavioral plasticity in response to environmental changes. When food is abundant, individuals tend to remain in nutrient-rich patches with relatively low movement; when resources become scarce, they increase locomotion to seek more favorable conditions [1]. Moreover, the exposure to toxins induces stress responses that affect both movement and reproduction. Recent experiments by Baragary et al. [1] demonstrated that the spatial arrangement of nutrients and toxins-whether overlapping, separated, or including a refuge-has distinct effects on the population growth of nematode strains with different dispersal rates. In particular, faster diffusers may achieve higher final population sizes under certain configurations, contrary to the classical reduction principle [7]. These observations suggest that individuals may switch between physiological states, such as active feeding and quiescent reserve-accumulating states, in response to local environmental conditions. Such state transitions, together with the movement behavior, may play an important role in determining the population persistence.

Motivated by these biological findings, we propose the following reaction-diffusion-advection system to describe the dynamics:

$$\begin{cases} u_t = (\mu u_x + \alpha\sigma_x u)_x - r(x)u + k(1+b(1-\sigma(x)))v - \gamma_1(x)u^2 - \eta_1(x)uv, & 0<x<L,\ t>0,\\ v_t = (\mu v_x + \alpha\sigma_x v)_x - kv + r(x)u - \gamma_2(x)v^2 - \eta_2(x)uv, & 0<x<L,\ t>0,\\ \mu u_x(x,t) + \alpha\sigma_x u(x,t) = 0, \quad \mu v_x(x,t) + \alpha\sigma_x v(x,t) = 0, & x=0,\ L,\ t>0,\\ u(x,0) = u_0(x) \ge 0,\ u_0(x) \not\equiv 0, \quad v(x,0) = v_0(x) \ge 0,\ v_0(x) \not\equiv 0, & 0<x<L, \end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ denote the densities of nematodes with and without food reserve, respectively. The constants μ and α represent the diffusion and advection coefficients. The functions $r(x)$ and $\sigma(x)$ describe the resource and toxin, respectively, which satisfy $r(x) \ge 0, \not\equiv 0$ and $0 \le \sigma(x) \le 1$ on $[0,L]$. Nematodes exhibit directed movements away from toxins at a rate of α. Individuals in state $v(x,t)$ produce $b(1-\sigma(x))$ offspring at a rate of $k > 0$, independently of spatial location. The nonnegative functions $\gamma_i(x)$ and $\eta_i(x)$ represent the per-capita death rates and saturation effects, respectively, with $\gamma_i(x) > 0$ on $[0,L]$ for $i = 1,2$. To establish basic properties of system (1.1), we assume that $r(x)$, $\sigma(x)$, $\gamma_i(x)$, and $\eta_i(x) \in C^1([0,L])$. We note that when $\eta_1(x) \equiv \eta_2(x) \equiv 0$ on $[0,L]$, system (1.1) becomes cooperative, allowing the application of the monotone dynamical systems theory, which yields stronger conclusions such as uniqueness and global attractivity of positive steady states.

In our previous work [12], we investigated the asymptotic and monotonic properties of the principal eigenvalue of the associated linearized system, which characterizes the intrinsic growth rate of the population. That analysis showed that spatial heterogeneity alone may favor higher dispersal rates, extending results of Cantrell et al. [4] for two-stage models and challenging the classical reduction principle. However, the eigenvalue analysis in [12] is restricted to linear dynamics. The present study extends this framework to the full nonlinear steady-state problem. Focusing on the case without advection ($\alpha = 0$), we first establish the existence of a unique positive equilibrium under cooperative conditions ($\eta_i \equiv 0$) and prove its global attractivity (Theorem 2.4). Then, we analyze its asymptotic behavior in the regimes of small and large diffusion:

- As $\mu \to 0$, the positive equilibrium locally and uniformly converges to the equilibrium of the associated spatially heterogeneous kinetic system, concentrating near regions where local growth is favorable (Theorem 2.6).
- As $\mu \to \infty$, the equilibrium becomes spatially homogeneous and converges to a constant profile determined by spatial averages of the coefficients. Additionally, we provide conditions that ensure the existence and uniqueness of this limiting state (Theorem 2.7).

These results shed light on how diffusion and spatial heterogeneity jointly influence population persistence in stage-structured systems, thus complementing and extending existing results on two-stage reaction-diffusion models [3,4].

The rest of this paper is organized as follows: Section 2 presents the main results, including the existence and uniqueness of positive steady states (Theorem 2.4), and the asymptotic behavior for small and large diffusion (Theorems 2.6 and 2.7), together with the corresponding proofs; and Section 3 provides a discussion of biological implications and possible future directions.

2. Main results

This section is devoted to proving the existence of the positive steady state to system (1.1), and then analyzing its asymptotic behavior in the regimes of small and large diffusion.

By using the contraction rectangular method (see [5, 10]), we have the following result on the uniform boundedness of the solution for system (1.1).

Lemma 2.1. *There exist positive numbers $\hat{M}$ and $\hat{N}$ such that for $M \geq \hat{M}$ and $N \geq \hat{N}$, the rectangular region $[0, M] \times [0, N]$ is invariant and contracting from above. Then, any solution of system (1.1) with nonnegative bounded initial data exists for all $t \geq 0$, and eventually lies in the rectangular region $[0, \hat{M}] \times [0, \hat{N}]$.*

Proof. The local existence of classical solutions follows from standard results; see the discussions and references in [2, 11]. Let $\hat{u} = ue^{(\alpha/\mu)\sigma(x)}$ and $\hat{v} = ve^{(\alpha/\mu)\sigma(x)}$. Then, (1.1) becomes the following:

$$\begin{cases} \hat{u}_t = \mu\hat{u}_{xx} - \alpha\sigma_x\hat{u}_x - r(x)\hat{u} + k(1 + b(1 - \sigma(x)))\hat{v} - \gamma_1(x)\hat{u}^2e^{(-\alpha/\mu)\sigma(x)} - \eta_1(x)\hat{u}\hat{v}e^{-(\alpha/\mu)\sigma(x)}, \\ \hat{v}_t = \mu\hat{v}_{xx} - \alpha\sigma_x\hat{v}_x - k\hat{v} + r(x)\hat{u} - \gamma_2(x)\hat{v}^2e^{-(\alpha/\mu)\sigma(x)} - \eta_2(x)\hat{u}\hat{v}e^{-(\alpha/\mu)\sigma(x)}, \\ \hat{u}_x(x, t) = 0,\ \hat{v}_x(x, t) = 0,\ x = 0, L,\ t > 0, \\ \hat{u}(x, 0) = u_0(x)e^{(\alpha/\mu)\sigma(x)} \geq 0, \not\equiv 0, \hat{v}(x, 0) = v_0(x)e^{(\alpha/\mu)\sigma(x)} \geq 0, \not\equiv 0, \end{cases} \tag{2.1}$$

where $0 < x < L,\ \ t > 0$. Let

$$\begin{aligned} F_1(\hat{u}, \hat{v}) &= -(r(x) + \gamma_1(x)\hat{u}e^{-(\alpha/\mu)\sigma(x)})\hat{u} + (k + kb(1 - \sigma(x)) - \eta_1(x)\hat{u}e^{-(\alpha/\mu)\sigma(x)})\hat{v}, \\ F_2(\hat{u}, \hat{v}) &= -(k + \gamma_2(x)\hat{v}e^{-(\alpha/\mu)\sigma(x)})\hat{v} + (r(x) - \eta_2(x)\hat{v}e^{-(\alpha/\mu)\sigma(x)})\hat{u}. \end{aligned} \tag{2.2}$$

For system (2.1), it is easy to see that $F_1(0, \hat{v}) = k(1 + b(1 - \sigma(x)))\hat{v} > 0$, and $F_2(\hat{u}, 0) = r(x)\hat{u} > 0$ for any $\hat{u}, \hat{v} > 0$. Moreover, there exist $\hat{M}$ and $\hat{N}$ such that $k + kb(1 - \sigma(x)) - \eta_1(x)e^{-(\alpha/\mu)\sigma(x)}\hat{M} < 0$ and $r(x) - \eta_2(x)e^{-(\alpha/\mu)\sigma(x)}\hat{N} < 0$. Thus, there exists some small $\varepsilon > 0$ such that for $M \geq \hat{M} - \varepsilon$, $N \geq \hat{N} - \varepsilon$,

$$\begin{aligned} &F_1(M, \hat{v}) = -(r(x) + \gamma_1(x)Me^{-(\alpha/\mu)\sigma(x)})M + (k + kb(1 - \sigma(x)) - \eta_1(x)Me^{-(\alpha/\mu)\sigma(x)})\hat{v} < 0 \text{ for any } \hat{v} > 0, \\ &F_2(\hat{u}, N) = -(k + \gamma_2(x)Ne^{(\alpha/\mu)\sigma(x)})N + (r(x) - \eta_2(x)Ne^{-(\alpha/\mu)\sigma(x)})\hat{u} < 0 \ \text{ for any } \ \hat{u} > 0. \end{aligned}$$

Consequently, for any nonnegative bounded initial data $(\hat{u}_0, \hat{v}_0)$, the associated solution $(\hat{u}(x, t, \hat{u}_0), \hat{v}(x, t, \hat{v}_0))$ of system (2.1) is contained in $[0, M] \times [0, N]$ for all $t \geq 0$. Let

$$\begin{aligned} F_1^+(\hat{u}, \hat{v}) &= -(r(x) + \gamma_1(x)\hat{u}e^{-(\alpha/\mu)\sigma(x)})\hat{u} + [k + kb(1 - \sigma(x)) - \eta_1(x)\hat{u}e^{-(\alpha/\mu)\sigma(x)}]_+\hat{v}, \\ F_2^+(\hat{u}, \hat{v}) &= -(k + \gamma_2(x)\hat{v}e^{-(\alpha/\mu)\sigma(x)})\hat{v} + [r(x) - \eta_2(x)\hat{v}e^{-(\alpha/\mu)\sigma(x)}]_+\hat{u}, \end{aligned}$$

where $[x]_+ = \max\{x, 0\}$. Then, $F_1^+(\hat{u}, \hat{v})$ and $F_2^+(\hat{u}, \hat{v})$ are locally Lipschitz continuous in the rectangular region $[0, M] \times [0, N]$. Replacing $F_1(\hat{u}, \hat{v})$ and $F_2(\hat{u}, \hat{v})$ in system (2.1) by $F_1^+(\hat{u}, \hat{v})$ and $F_2^+(\hat{u}, \hat{v})$, respectively, then the solutions to the original system are sub-solutions to the modified system.

Let $(\hat{U}(t), \hat{V}(t))$ be the solution of the ordinary differential equation (ODE) system $\hat{U}_t = F_1^+(\hat{u}, \hat{v})$, $\hat{V}_t = F_2^+(\hat{u}, \hat{v})$ with $(\hat{U}_0, \hat{V}_0) = (M, N)$. This will be a solution for the system obtained by replacing $F_1(\hat{u}, \hat{v})$ and $F_1(\hat{u}, \hat{v})$ with $F_1^+(\hat{u}, \hat{v})$ and $F_2^+(\hat{u}, \hat{v})$, respectively, in system (2.1). Furthermore, based on the comparison theorem (see [9, Chapter 7]), we obtain $\hat{u}(x, t, \hat{u}_0) \leq \hat{U}(t)$ and $\hat{v}(x, t, \hat{v}_0) \leq \hat{V}(t)$ for any $t \geq 0$. Note that $\limsup_{t\to\infty} \hat{U}(t) \leq \hat{M} - \varepsilon$ and $\limsup_{t\to\infty} \hat{V}(t) \leq \hat{N} - \varepsilon$. Hence, $\hat{u}(x, t, \hat{u}_0)$ and $\hat{v}(x, t, \hat{v}_0)$ eventually lie in $[0, \hat{M}] \times [0, \hat{N}]$. Since $\hat{u} = ue^{(\alpha/\mu)\sigma(x)}$ and $\hat{v} = ve^{(\alpha/\mu)\sigma(x)}$, we can conclude that $u(x, t, u_0)$ and $v(x, t, v_0)$ eventually lie in $[0, \hat{M}] \times [0, \hat{N}]$. □

Corollary 2.2. *System* (1.1) *generates a semiflow* Φ_t *in*

$$\mathrm{Y} = \left\{(u_0, v_0) \in C([0, L]; \mathbb{R}_+^2) : u_0 \leq M, v_0 \leq N \text{ on } [0, L]\right\},$$

in the sense that for each initial data in Y, *the solution of system* (1.1) *satisfies* $(u(x,t), v(x,t)) \in \mathrm{Y}$ *for all* $t \geq 0$. *Furthermore,* Φ_t *is strictly subhomogeneous, in the case that* $\eta_i(x) = 0$, Φ_t *is strongly monotone.*

Proof. Since the first part of the corollary is derived from Lemma 2.1, we only need to show the second part.

For $0 < \chi < 1$, and $(u, v) \in \mathrm{Y}$, we obtain the following:

$$\begin{aligned} F_1(\chi u, \chi v) &= -r(x)\chi u + (k + kb(1 - \sigma(x)))\chi v - \gamma_1(x)(\chi u)^2 - \eta_1(x)\chi u \chi v, \\ &= \chi(-r(x)u + (k + kb(1 - \sigma(x)))v - \gamma_1(x)\chi u^2 - \eta_1(x)\chi uv), \\ &> \chi(-r(x)u + (k + kb(1 - \sigma(x)))v - \gamma_1(x)u^2 - \eta_1(x)uv), \\ &= \chi F_1(u, v). \end{aligned}$$

Similarly, we obtain $F_2(\chi u, \chi v) > \chi F_2(u, v)$. This implies that the reaction terms of (1.1) are strictly subhomogeneous. Then, by the similar arguments as in [6, Theorem 2.2], we get that for any $t > 0$, the semiflow $\Phi_t : \mathrm{Y} \to \mathrm{Y}$ is strictly subhomogeneous in the sense that for $0 < \chi < 1$, $(u_0, v_0) \in \mathrm{Y}$ with $(u_0, v_0) \gg 0$ such that $\Phi_t(\chi u_0, \chi v_0) \gg_{\mathbb{D}} \chi \Phi_t(u_0, v_0)$, where $\mathbb{D} := C^0([0, L], \mathbb{R}_+^2)$.

When $\eta_i(x) = 0$, the Jacobian matrix of the reaction terms in system (1.1) with respect to (u, v) takes the following form:

$$\mathcal{J} = \begin{pmatrix} -r(x) - 2\gamma_1(x)u & k + kb(1 - \sigma(x)) \\ r(x) & -k - 2\gamma_2(x)v \end{pmatrix}.$$

Note that the Jacobian matrix $\mathcal{J}$ has nonnegative off-diagonal entries; hence, the semiflow $\Phi_t : \mathrm{Y} \to \mathrm{Y}$ generated by system (1.1) is monotone under the partial order $\leq_{\mathbb{D}}$ generated by the cone $\mathbb{D}$. Moreover, since $r(x) \geq 0, \not\equiv 0$ on $x \in [0, L]$, we obtain that $\mathcal{J}$ is irreducible, which implies that Φ_t is strongly monotone in the interior of Y (see [9]). □

To determine the persistence of the nematodes, the principal eigenvalue, denoted as $\lambda_1(\mu, \alpha)$, of the following eigenvalue problem plays an important role in the analysis:

$$\begin{cases} (\mu\phi_x + \alpha\sigma_x\phi)_x - r(x)\phi + (k + kb(1 - \sigma(x)))\varphi + \lambda\phi = 0, & 0 < x < L, \\ (\mu\varphi_x + \alpha\sigma_x\varphi)_x - k\varphi + r(x)\phi + \lambda\varphi = 0, & 0 < x < L, \\ \mu\phi_x(x) + \alpha\sigma_x\phi(x) = \mu\varphi_x(x) + \alpha\sigma_x\varphi(x) = 0. & x = 0,\ L. \end{cases} \tag{2.3}$$

A classical result (see, e.g. [8, Chapter 4]) states that any positive solution (u, v) of system (1.1) satisfies the following:

$$\underline{c}e^{-\lambda_1(\mu,\alpha)t} \leq \min\{u, v\} \leq \max\{u, v\} \leq \overline{c}e^{-\lambda_1(\mu,\alpha)t} \qquad \text{for some constants } \overline{c} \geq \underline{c} > 0. \tag{2.4}$$

Lemma 2.3. *For each* $\mu > 0$*,* $\alpha \in \mathbb{R}$*, and* $0 \leq \sigma(x) \leq 1$*, the principal eigenvalue* $\lambda_1(\mu, \alpha)$ *of* (2.3) *satisfies* $\lambda_1(\mu, \alpha) \leq 0$*, and equality holds if and only if* $\sigma(x) \equiv 1$ *on* $[0, L]$.

Proof. The assertion is based on [12, Lemma 3.1] □

By applying Corollary 2.2, Lemma 2.3, and [13, Theorem 2.3.4], we are able to obtain the threshold dynamics of system (1.1).

Theorem 2.4. *For each* $\mu > 0$*,* $\alpha \in \mathbb{R}$ *and* $0 \leq \sigma(x) \leq 1$*, then the following statements are true.*

(i) *If* $\sigma(x) \equiv 1$ *on* $[0, L]$*, then the trivial solution* $(0, 0)$ *of system (1.1) is globally asymptotically stable.*

(ii) *If* $\sigma(x) \leq 1, \not\equiv 1$ *on* $[0, L]$*, then the system* (1.1) *is persistent and has at least one positive steady state solution. Furthermore, if* $\eta_i(x) = 0$*, then the system* (1.1) *admits a unique positive steady-state solution, denoted by* (u_e, v_e)*, which is the global attractor for all nonnegative, non-trivial solutions.*

Now, we proceed to study the asymptotic profiles of the positive steady state of system (1.1) as the diffusion rate becomes small or large.

Based on [12, Lemma 3.2], we have the following result.

Lemma 2.5. *Suppose that* $\alpha = 0$*. Then, the principal eigenvalue* $\lambda_1(\mu, 0)$ *of* (2.3) *satisfies*

$$\lim_{\mu\to 0} \lambda_1(\mu, 0) = \min_{x_0\in[0,L]} \frac{1}{2}[k + r(x_0) - \sqrt{(k + r(x_0))^2 + 4kbr(x_0)(1 - \sigma(x_0))}], \tag{2.5}$$

and

$$\lim_{\mu\to\infty} \lambda_1(\mu, 0) = \frac{1}{2}[k + \bar{r} - \sqrt{(k + \bar{r})^2 + 4kb\bar{r}(1 - \bar{\sigma})}], \tag{2.6}$$

where $\bar{r} = \frac{\int_0^L r(x)\,dx}{L}$, $\bar{\sigma} = \frac{\int_0^L \sigma(x)\,dx}{L}$.

Next, we will assume that $\eta_i(x) = 0$ on $[0, L]$, in which case, the system (1.1) is cooperative; by applying Theorem 2.4 and [3, Theorem 1], we obtain the asymptotic behavior of the positive equilibrium of system (1.1) when $\alpha = 0$ and μ is sufficiently small.

Theorem 2.6. *Assume that* $\alpha = 0$ *and* $\sigma(x_0) < 1$ *for some* $x_0 \in [0, L]$*. Then, there exists* $\mu_1 \ll 1$ *such that system* (1.1) *has a positive steady state for any* $\mu \in (0, \mu_1)$*, denoted as* (u_μ, v_μ)*. Moreover, if* $\eta_i(x) = 0$*, then* $(u_\mu, v_\mu) \to (U_e, V_e)$ *locally uniformly as* $\mu \to 0$*, where* (U_e, V_e) *is the unique positive equilibrium of the kinetic system of (1.1).*

Proof. By (2.5), there exists a $\mu_1 > 0$ such that if $\sigma(x_0) < 1$ for some x_0, the principal eigenvalue $\lambda_1(\mu, 0)$ of (2.3) is negative for all $0 < \mu < \mu_1$. Then, by Theorem 2.4, the system is persistent and has a positive equilibrium for a small μ. Moreover, if $\eta_i(x) = 0$, then the system has a unique globally attracting positive equilibrium.

Next, we prove the convergence $(u_\mu, v_\mu) \to (U_e, V_e)$ locally uniformly as $\mu \to 0$, under the additional assumption $\eta_i(x) \equiv 0$.

Step 1. The kinetic equilibrium. For each fixed $x \in [0, L]$, consider the following kinetic system obtained from (1.1) by setting $\mu = 0$:

$$\begin{cases} \dfrac{du}{dt} = -r(x)u + k(1 + b(1 - \sigma(x)))v - \gamma_1(x)u^2, \\ \dfrac{dv}{dt} = -kv + r(x)u - \gamma_2(x)v^2. \end{cases} \tag{2.7}$$

Since $\sigma(x_0) < 1$ for some $x_0 \in [0, L]$, the linearization of (2.7) at $(0, 0)$ has a positive principal eigenvalue at $x = x_0$. Consequently, for every x with $\sigma(x) < 1$, the kinetic system admits a unique positive equilibrium $(U_e(x), V_e(x))$, while for x with $\sigma(x) = 1$, the only nonnegative equilibrium is $(0, 0)$. Moreover, $(U_e(x), V_e(x))$ continuously depends on x and is globally asymptotically stable among nonnegative nontrivial solutions of (2.7) (see [4, Lemma 4]).

Step 2. Construction of a local subsolution. Fix any point x_0 with $\sigma(x_0) < 1$. Let $\Lambda(x_0) > 0$ be the principal eigenvalue of the matrix

$$A(x_0) = \begin{pmatrix} -r(x_0) & k(1 + b(1 - \sigma(x_0))) \\ r(x_0) & -k \end{pmatrix},$$

and let $p = (p_1, p_2)^T$ be a corresponding positive eigenvector. Choose a small interval $I_\rho = (x_0 - \rho, x_0 + \rho) \subset (0, L)$ such that $\sigma(x) < 1$ for all $x \in I_\rho$, and the coefficients $r(x), \sigma(x), \gamma_i(x)$ are close to their values at x_0. Let ψ be the positive principal eigenfunction of the Dirichlet problem

$$-\psi_{xx} = \lambda_1 \psi \quad \text{in } I_\rho, \qquad \psi(x_0 \pm \rho) = 0,$$

normalized by $\max_{I_\rho} \psi = 1$. Then, $\lambda_1 > 0$ and $\psi > 0$ in I_ρ. Extend ψ to $[0, L]$ by setting $\psi \equiv 0$ outside I_ρ. For a small constant $\delta > 0$, define the following:

$$\underline{w}_\mu(x) = \big(\underline{u}_\mu(x), \underline{v}_\mu(x)\big) = \delta\,\psi(x)\,p.$$

We claim that for sufficiently small μ, ρ, δ, the function $\underline{w}_\mu$ is a subsolution of the steady-state system for (1.1), i.e.,

$$\mu \underline{u}_\mu'' + F_1(x, \underline{u}_\mu, \underline{v}_\mu) \geq 0, \qquad \mu \underline{v}_\mu'' + F_2(x, \underline{u}_\mu, \underline{v}_\mu) \geq 0 \quad \text{in } [0, L],$$

where F_1, F_2 are the reaction terms in (1.1) with $\eta_i = 0$. Indeed, using $\underline{w}_\mu = \delta\psi p$ and $-\psi_{xx} = \lambda_1 \psi$, we have the following:

$$\mu \underline{u}_\mu'' = -\mu\lambda_1\delta\psi p_1, \qquad \mu \underline{v}_\mu'' = -\mu\lambda_1\delta\psi p_2.$$

Expanding F around $(0, 0)$ gives the following:

$$F(x, \delta\psi p) = \delta\psi\, A(x)p + O(\delta^2\psi^2).$$

Because $A(x)$ is close to $A(x_0)$ for $x \in I_\rho$ when ρ is small, and $A(x_0)p = \Lambda(x_0)p$, we can choose ρ so that

$$F(x, \delta\psi p) \geq \delta\psi\, \frac{\Lambda(x_0)}{2}\, p \quad \text{for all } x \in I_\rho.$$

Then, for $x \in I_\rho$,

$$\mu \underline{w}_\mu'' + F(x, \underline{w}_\mu) \geq \delta\psi\left(-\mu\lambda_1 p + \frac{\Lambda(x_0)}{2} p\right).$$

Taking μ sufficiently small such that $\mu\lambda_1 \leq \Lambda(x_0)/2$, the right-hand side is nonnegative. Outside I_ρ, $\underline{w}_\mu \equiv 0$, and $F(x, 0, 0) = 0$, so the inequality trivially holds. Hence, $\underline{w}_\mu$ is indeed a subsolution.

Step 3. A constant supersolution. Since the quadratic terms $-\gamma_1(x)u^2$ and $-\gamma_2(x)v^2$ dominate for large densities, there exists a constant $\bar{M} > 0$ (independent of μ) such that for all $x \in [0, L]$,

$$F_1(x, \bar{M}, \bar{M}) < 0, \qquad F_2(x, \bar{M}, \bar{M}) < 0.$$

Thus, $\overline{w} \equiv (\bar{M}, \bar{M})$ is an upper solution of the steady-state system for (1.1) .

Step 4. Monotone iteration and existence of the positive steady state. Because the system is cooperative ($\eta_i = 0$), the standard monotone iteration method applies: starting from $\underline{w}_\mu$ and $\overline{w}$, we construct increasing and decreasing sequences that converge to a solution of the steady-state system for (1.1). By the comparison principle, any solution lies between $\underline{w}_\mu$ and $\overline{w}$. The uniqueness of the positive steady state guarantees that the limit is precisely (u_μ, v_μ). Consequently,

$$\underline{w}_\mu(x) \leq (u_\mu(x), v_\mu(x)) \leq (\bar{M}, \bar{M}) \quad \text{for all } x \in [0, L].$$

Step 5. Convergence as $\mu \to 0$. Take any sequence $\mu_n \to 0$ and consider the corresponding positive steady states (u_{μ_n}, v_{μ_n}). By the uniform bound from Step 4 and standard elliptic estimates, a subsequence uniformly converges to some nonnegative limit $(\tilde{u}, \tilde{v})$. Passing to the limit in the weak formulation of the steady-state system for (1.1), shows that $(\tilde{u}, \tilde{v})$ satisfies the kinetic system pointwise:

$$F_1(x, \tilde{u}, \tilde{v}) = 0, \qquad F_2(x, \tilde{u}, \tilde{v}) = 0 \quad \text{for a.e. } x \in [0, L].$$

Hence, $(\tilde{u}(x), \tilde{v}(x))$ must equal either $(0, 0)$ or the positive kinetic equilibrium $(U_e(x), V_e(x))$ at each x. The subsolution constructed in Step 2 forces $\tilde{u}(x) \geq \underline{w}_\mu(x) > 0$ for x in a neighborhood of any x_0 with $\sigma(x_0) < 1$, provided μ is small enough. Therefore, $\tilde{u}(x) > 0$ and $\tilde{v}(x) > 0$ wherever $\sigma(x) < 1$, and $\tilde{u} = \tilde{v} = 0$ elsewhere. By uniqueness of the kinetic equilibrium, $(\tilde{u}, \tilde{v}) = (U_e, V_e)$. Since every convergent subsequence converges to the same limit, the whole family (u_μ, v_μ) locally and uniformly converges to (U_e, V_e) as $\mu \to 0$. This completes the proof. □

Next, we state our result on the asymptotic behavior of the positive equilibrium of system (1.1) when $\alpha = 0$ and μ is sufficiently large. We emphasize that Theorem 2.7 does not require the cooperative assumption; it holds for general nonnegative $\eta_i(x)$.

Theorem 2.7. *Assume that $\alpha = 0$, $\bar{\sigma} < 1$ and $\bar{\eta}_1\bar{\eta}_2 < \bar{\gamma}_1\bar{\gamma}_2$. Then, there exists $\mu_2 \gg 1$ such that system* (1.1) *has a positive steady state for any $\mu \in (\mu_2, \infty)$. Moreover, any positive solution (u_μ, v_μ) for $\mu \in (\mu_2, \infty)$ satisfies $(u_\mu, v_\mu) \to (u_\infty, v_\infty)$ uniformly as $\mu \to \infty$, where*

$$u_\infty = \frac{kv_\infty + \bar{\gamma}_2 v_\infty^2}{\bar{r} - \bar{\eta}_2 v_\infty}, \tag{2.8}$$

and v_∞ is a positive solution of the algebraic equation

$$\begin{aligned}(\bar{\gamma}_2\bar{\eta}_1\bar{\eta}_2 - \bar{\gamma}_1\bar{\gamma}_2^2)v_\infty^3 + (\bar{\eta}_1\bar{\eta}_2 + \bar{r}\bar{\gamma}_2\bar{\eta}_2 + k(1 + b(1 - \bar{\sigma}))\bar{\eta}_2 - 2\bar{\gamma}_1\bar{\gamma}_2 - \bar{r}\bar{\eta}_1\bar{\gamma}_2)v_\infty^2 \\ + (-\bar{r}^2\bar{\gamma}_2 - kb(1 - \bar{\sigma})\bar{r}\bar{\eta}_2 - \bar{\gamma}_1 - \bar{r}\bar{\eta}_1)v_\infty + kb(1 - \bar{\sigma})\bar{r}^2 = 0.\end{aligned} \tag{2.9}$$

In addition, if the discriminant of the derivative of the cubic polynomial in (2.9) *is negative, then the positive solution (u_∞, v_∞) is unique.*

Proof. Since $\bar{\sigma} < 1$, it is easy to obtain that $\lambda_1(\mu, 0) < 0$ for all $\mu > \mu_2$ via (2.6). Hence, there exists $\mu_2 > 0$ such that $\lambda_1(\mu, 0) < 0$ for all $\mu > \mu_2$. By Theorem 2.4, system (1.1) has a positive steady state (u_μ, v_μ) for every $\mu > \mu_2$. Now, we study its limit as $\mu \to \infty$.

Let $\mu_n \to \infty$ be an arbitrary sequence and denote $(u_n, v_n) = (u_{\mu_n}, v_{\mu_n})$. Then, (u_n, v_n) satisfies the following:

$$\begin{cases} \mu_n (u_n)_{xx} - r(x)u_n + k(1 + b(1 - \sigma(x)))v_n - \gamma_1(x)u_n^2 - \eta_1(x)u_n v_n = 0, \\ \mu_n (v_n)_{xx} - kv_n + r(x)u_n - \gamma_2(x)v_n^2 - \eta_2(x)u_n v_n = 0, \\ u_n'(0) = u_n'(L) = 0, \quad v_n'(0) = v_n'(L) = 0. \end{cases} \tag{2.10}$$

Step 1. Uniform bounds. Because $\eta_i \geq 0$, we have the following estimates:

$$\begin{aligned} &- r(x)u_n + k(1 + b(1 - \sigma(x)))v_n - \gamma_1(x)u_n^2 - \eta_1(x)u_n v_n \leq -r(x)u_n + k(1 + b(1 - \sigma(x)))v_n - \gamma_1(x)u_n^2, \\ &- kv_n + r(x)u_n - \gamma_2(x)v_n^2 - \eta_2(x)u_n v_n \leq -kv_n + r(x)u_n - \gamma_2(x)v_n^2. \end{aligned}$$

Since $\gamma_i(x) \geq \gamma_{i\min} > 0$, there exists a constant $K > 0$ (independent of μ_n) such that for all x,

$$-r(x)K + k(1 + b(1 - \sigma(x)))K - \gamma_1(x)K^2 \leq 0, \quad -kK + r(x)K - \gamma_2(x)K^2 \leq 0.$$

Thus, (K, K) is an upper solution of the steady-state system. A standard comparison argument yields $0 \leq u_n(x), v_n(x) \leq K$ for all x.

Step 2. Gradient estimates and compactness. Multiply the first equation in (2.10) by u_n and integrate over $[0, L]$. Using integration by parts and the Neumann boundary conditions, we obtain the following:

$$\mu_n \int_0^L (u_n')^2 dx = \int_0^L u_n(- ru_n + k(1 + b(1 - \sigma))v_n - \gamma_1 u_n^2 - \eta_1 u_n v_n)dx.$$

The right-hand side is bounded by a constant C_1 that only depends on K and the coefficients. Hence, $\int_0^L (u_n')^2 dx = O(1/\mu_n) \to 0$ as $n \to \infty$. Similarly, $\int_0^L (v_n')^2 dx \to 0$. Since (u_n) and (v_n) are uniformly bounded in $L^\infty(0, L)$, it follows from L^p estimates and the Sobolev embedding theorem that there exists a subsequence of $\{\mu_n\}$ (still denoted by $\{\mu_n\}$) such that the corresponding positive solutions (u_n, v_n) of (2.10) satisfies that $u_n \to u_\infty$, $v_n \to v_\infty$ in $C^1[0, L]$ as $n \to \infty$.

Step 3. Identification of the limit. Integrate the two equations in (2.10) over $[0, L]$ and use the boundary conditions:

$$\begin{aligned} 0 &= \int_0^L (- r(x)u_n + k(1 + b(1 - \sigma(x)))v_n - \gamma_1(x)u_n^2 - \eta_1(x)u_n v_n)dx, \\ 0 &= \int_0^L (- kv_n + r(x)u_n - \gamma_2(x)v_n^2 - \eta_2(x)u_n v_n)dx. \end{aligned}$$

Letting $n \to \infty$ and using uniform convergence, we obtain the following:

$$\begin{cases} -\bar{r}u_\infty + k(1 + b(1 - \bar{\sigma}))v_\infty - \bar{\gamma}_1 u_\infty^2 - \bar{\eta}_1 u_\infty v_\infty = 0, \\ -kv_\infty + \bar{r}u_\infty - \bar{\gamma}_2 v_\infty^2 - \bar{\eta}_2 u_\infty v_\infty = 0, \end{cases} \tag{2.11}$$

where $\bar{f} = \frac{1}{L}\int_0^L f(x)dx$ for any function f.

Step 4. Solving the algebraic system and uniqueness. From the second equation of (2.11), assuming $\bar{r} - \bar{\eta}_2 v_\infty > 0$, we solve for u_∞ as follows:

$$u_\infty = \frac{k v_\infty + \bar{\gamma}_2 v_\infty^2}{\bar{r} - \bar{\eta}_2 v_\infty}.$$

Substituting this into the first equation yields a cubic equation for v_∞. After simplification (using the expressions of the averages), we arrive at (2.9). Define the following:

$$P(v) = (\bar{\gamma}_2 \bar{\eta}_1 \bar{\eta}_2 - \bar{\gamma}_1 \bar{\gamma}_2^2) v^3 + (\cdots) v^2 + (\cdots) v + kb(1 - \bar{\sigma}) \bar{r}^2,$$

where the coefficients are as in (2.9). The condition $\bar{\eta}_1 \bar{\eta}_2 < \bar{\gamma}_1 \bar{\gamma}_2$ implies that the leading coefficient of P is negative, and $P(0) = kb(1 - \bar{\sigma})\bar{r}^2 > 0$ while $P(v) \to -\infty$ as $v \to \infty$. Hence $P(v) = 0$ has at least one positive root.

To ensure uniqueness, we consider the derivative $P'(v)$, which is a quadratic polynomial. If the discriminant of P' is negative, then $P'(v)$ does not change sign. Because the leading coefficient of P' is three times the leading coefficient of P, it is also negative. Consequently, $P'(v) < 0$ for all v, so P is strictly decreasing on $\mathbb{R}$. A strictly decreasing continuous function can cross zero at most once. Therefore, $P(v) = 0$ has exactly one positive root, which we denote by v_∞. Then, the corresponding u_∞ is uniquely determined by (2.8).

Since every convergent subsequence of (u_μ, v_μ) as $\mu \to \infty$ has a further subsequence that converges to the same limit (u_∞, v_∞), the whole family uniformly converges. This completes the proof. □

3. Conclusions and discussion

In this work, we investigate a reaction–diffusion model for a population with two reversible states (e.g., nematodes with and without food reserves) in a spatially heterogeneous environment. Our results show that the persistence and spatial distribution of the population are strongly influenced by the diffusion rate μ, even in the absence of directed movement ($\alpha = 0$).

When the diffusion rate is very small, the population tends to concentrate near locations where local conditions (resource $r(x)$ and toxin $\sigma(x)$) are most favorable, and the positive equilibrium approaches that of the corresponding non-spatial kinetic system (Theorem 2.6). In contrast, when the diffusion rate is large, the population becomes spatially homogenized, and its density converges to a constant determined by the spatial averages $\bar{r}$ and $\bar{\sigma}$ (Theorem 2.7). These two asymptotic regimes highlight a clear trade-off: slow diffusion allows the population to exploit favorable local conditions, whereas a fast diffusion averages out spatial heterogeneity and reduces the benefit of local adaptation.

From an ecological perspective, these results suggest a possible mechanism by which the movement rates affect the survival of stage-structured populations in heterogeneous and potentially toxic environments. For nematodes that switch between a low-energy state (u) and a high-energy state (v), the model indicates that an intermediate diffusion rate may be advantageous when resources and toxins are patchily distributed. This observation complements the recent work of Baragary et al. [1], where spatial heterogeneity alone was shown to select for increased movement rates in populations with state transitions. In addition, our eigenvalue analysis (Lemma 2.5) provides a concrete criterion for persistence: the principal eigenvalue $\lambda_1(\mu, 0)$ must be negative. In the limiting regimes, this condition reduces to quantities which are dependent on either local or spatially averaged values of $r(x)$ and $\sigma(x)$, linking spatially explicit models with their non-spatial counterparts.

Compared with related studies on two-stage reaction–diffusion systems [3, 4], the present model incorporates state-dependent birth rates $b(1 - \sigma(x))$ as well as toxin-dependent effects, which are relevant for organisms whose reproduction is sensitive to environmental quality. This leads to qualitatively different dynamics, since the reproduction of the v state is directly modulated by the environmental toxicity. While Cantrell et al. [3, 4] focused on the role of dispersal in systems without such dependence, our results highlight how the environmental toxicity can further shape the population persistence. The convergence to the kinetic system as $\mu \to 0$ (Theorem 2.6) is consistent with the general principle that very slow diffusion localizes the dynamics, whereas the homogenization as $\mu \to \infty$ (Theorem 2.7) is well known in single-species models and is extended here to a cooperative two-state system.

Finally, we note an important limitation of the present analysis: the asymptotic results in Theorems 2.6 and 2.7 are obtained under the assumption when $\alpha = 0$. The general case when $\alpha \neq 0$ is significantly more challenging, as the interplay between diffusion, advection, and spatial heterogeneity complicates even the analysis of the associated eigenvalue problem. For this reason, in this study, we focused on the case when $\alpha = 0$ to isolate the effect of random diffusion. Extending the asymptotic analysis to $\alpha \neq 0$ remains an open problem. Other possible directions include incorporating temporal environmental variation or more general nonlinear transition mechanisms between the two states.

Use of Generative-AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The author declares that she has no conflict of interest.

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