PERSISTENCE AND PROPAGATION OF A PDE AND DISCRETE-TIME MAP HYBRID ANIMAL MOVEMENT MODEL WITH HABITAT SHIFT DRIVEN BY CLIMATE CHANGE*

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Abstract. Persistence or extinction of moving animal species is a fundamental question in spatial ecology. This paper focuses on the impact of habitat shift driven by climate change on the persistence and propagation of a population with birth pulse. We first present a class of impulsive reaction-diffusion models with heterogeneous nonlinear reaction in high-dimensional space and study their threshold dynamics. We provide the persistence criterion of the system in bounded domains, and prove the existence, uniqueness, and global attraction of a positive steady state. Then we extend the results from bounded domains to the whole space. Our results indicate how the speed of the shifting habitat edge and impulsive reproduction (or harvesting) rate determine the persistence and extinction of the population. Numerical simulations are presented to illustrate the theoretical results.

Key words. PDE and discrete-time map hybrid model, impulsive reaction-diffusion equation, shifting habitat, persistence, propagation

AMS subject classifications. 92B05, 35K57, 92D40, 92D50, 92D25

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1. Introduction. Climate change caused by the greenhouse effect and environmental pollution has become a global crisis, which poses a major threat to many living organisms and ecosystems. Evidence has been accumulated to illustrate species extinctions driven by global climate change [1, 2, 3]. Spatial distributions of persistent species at the continental scale are partly driven by climate change [4]. Adapting to the environmental change, many species have shifted from low latitudes to high latitudes, or from low elevations to high elevations [5, 6].

The pioneering work to address climate-driven habitat shift in spatial ecological models was proposed by Potapov and Lewis in [7]. The reaction-diffusion equation is described by

(1.1)
$$u_t = u_{xx} + f(x - ct, u), \quad x \in \mathbb{R},$$

where c > 0 is the shifting speed of the environment due to global climate change. It has been used to study the effect of climate change on the dispersal and evolution of species. Recently, the effect of climate change on the survival of ecological species has attracted a great deal of attention (e.g., [8, 9, 10, 11] and the references therein). In [8, 9, 10, 11], the authors discussed the persistence and propagation of a species under shifting habitat for a scalar reaction-diffusion equation. They presented a critical threshold for the shifting speed, namely, below this threshold the species survives and

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above it the species goes extinct. The same problem was studied in the framework of integrodifference equations, in which time is assumed to be discrete and dispersion is nonlocal [12, 13, 14, 40]. Berestycki and Rossi [9] extended the results of [8] to high dimension n and to a greater generality in the assumptions on f. They studied the following higher-dimensional models of (1.1):

(1.2)
$$\partial_t u = \Delta u + f(x - cte, u), \quad t > 0, \quad x \in \mathbb{R}^n,$$

where $f : \mathbb{R}^n \times [0, +\infty) \to \mathbb{R}, c > 0$, and $e \in \mathbb{R}^n$. They established a necessary and sufficient condition for the existence of traveling wave solutions, that is, solutions of the type u(x,t) = U(x - cte). The sign of the generalized principal eigenvalue λ_1 of an associated linear elliptic operator in \mathbb{R}^n has become the criterion to judging the existence of traveling wave solutions. With this criterion, they completely described the large time dynamics for this equation.

Remarkably, many species (e.g., fishes, birds, or large mammals) give birth only at a particular time of each year. Such species have a birth pulse, that is, reproduction takes place in a fixed short time period each year. Between birth pulses, mortality takes place and the population decreases. The population dynamics are generated by a composition of a discrete-time map and a PDE operator. PDE and discrete-time map hybrid models can be considered as a description for a seasonal birth pulse plus nonlinear mortality and dispersal throughout the year. Alternatively, they can describe seasonal harvesting plus nonlinear birth and mortality as well as dispersal throughout the year. In recent years such impulsive reaction-diffusion models without habitat shift have been studied in [15, 16, 17, 18, 19]. Considering the high-dimensional space, Fazly, Lewis, and Wang [18, 19] developed a general impulsive reaction-diffusion-advection equation model to describe the population dynamics of species with different reproductive and diffusion stages. When boundary conditions are hostile, they provided critical domain size results for the extinction or persistence of a species depending on the size and geometry of the domain. In the entire space \mathbb{R}^n , they provided an explicit formula for the spreading speed of propagation in any direction $e \in \mathbb{R}^n$ in terms of the same set of model parameters used for computing critical domain sizes and extreme volume sizes, and proved the existence of monostable traveling wave solutions. Recently, Wu and Zhao [20] extended the relevant conclusions to an impulsive integrodifferential equation model.

This paper focuses on the effects of habitat shift driven by climate change on propagation and persistence of a population with birth pulse. We first present the PDE and discrete-map hybrid model with habitat shift:

(1.3)
$$\begin{cases} \partial_t \tilde{u}^{(m)} = \Delta \tilde{u}^{(m)} + f(\tilde{x} - cte, \tilde{u}^{(m)}), & (\tilde{x}, t) \in \mathbb{R}^n \times (0, 1], \\ \tilde{u}^{(m)}(\tilde{x}, 0) = g(N_m(\tilde{x})), & \tilde{x} \in \mathbb{R}^n, \\ N_{m+1}(\tilde{x}) = \tilde{u}^{(m)}(\tilde{x}, 1), & \tilde{x} \in \mathbb{R}^n. \end{cases}$$

The dynamics in the dispersal stage is described by a nonlinear reaction-diffusion equation in an unbounded domain. By the change of variable $u(t, x) = \tilde{u}(t, \tilde{x} + cte)$, the system

(1.4)
$$u_t = \Delta u + ce \cdot \nabla u + f(x, u), \quad t > 0, \quad x \in \mathbb{R}^n, \quad n \ge 1, \quad c \ge 0,$$

is equivalent to the system

$$\partial_t \tilde{u} = \Delta \tilde{u} + f(\tilde{x} - cte, \tilde{u}), \quad t > 0, \quad \tilde{x} \in \mathbb{R}^n.$$

Therefore, if we study the dynamic behaviors of the system (1.3), we only need to investigate the following system:

(1.5)
$$\begin{cases} u_t^{(m)} = \Delta u^{(m)} + ce \cdot \nabla u^{(m)} + f(x, u^{(m)}), & (x, t) \in \mathbb{R}^n \times (0, 1], \\ u^{(m)}(x, 0) = g(N_m(x)), & x \in \mathbb{R}^n, \\ N_{m+1}(x) = u^{(m)}(x, 1), & x \in \mathbb{R}^n. \end{cases}$$

In this paper, all notations are the same as in [18]. The population of a species at the beginning of year m is denoted by $N_m(x)$. We study the dynamics of a population at the beginning of a reproductive (or harvesting) stage within a year. We use g to describe the population density at the end of a reproductive (or harvesting) stage as a function of the population density at the beginning of the stage. At the end of this year the density $u^{(m)}(x, 1)$ provides the population density for the start of year m+1, denoted by $N_{m+1}(x)$. For convenience, we rewrite the above mathematical model as

(1.6)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f(x, u), & (x, t) \in \mathbb{R}^n \times (0, 1], \\ u(x, 0) = g(N_m(x)), & x \in \mathbb{R}^n, \\ N_{m+1}(x) = u(x, 1), & x \in \mathbb{R}^n. \end{cases}$$

The system (1.6) defines a recurrence relation for $N_m(x)$ as

(1.7)
$$N_{m+1}(x) = \hat{Q}[N_m(x)] = Q_1 \circ g[N_m(x)] \text{ for } x \in \mathbb{R}^n,$$

where Q_1 is the time-one solution map of the evolution system $u_t = \Delta u + ce \cdot \nabla u + f(x, u)$ and an operator \hat{Q} depends on e, f, g. Note $N_{m+1} = \hat{Q}[N_m(x)] = \hat{Q}^{m+1}[N_0]$, where \hat{Q}^{m+1} is the (m+1)th iteration of \hat{Q} .

To analyze the dynamic behaviors of (1.6), we make the following assumptions throughout the paper.

- (H1) The nonlinearity $f(x, u) \in C^{1+\gamma}(\mathbb{R}^n \times \mathbb{R}^+, \mathbb{R})$ satisfies the following assumptions:
 - **H1.1** $f(x,0) = 0, f_u(x,0) \neq 0$ for $x \in \mathbb{R}^n$; $\exists M > 0$ such that $f(x,u) \leq 0$ for $u \geq M$ and for $x \in \mathbb{R}^n$;
 - **H1.2** $u \mapsto f(x, u)/u$ is strictly decreasing for $x \in \mathbb{R}^n$;
 - **H1.3** $\exists \delta > 0$ such that $u \mapsto f(x, u) \in C^1([0, \delta])$, uniformly for $x \in \mathbb{R}^n$, $u \mapsto f(x, u)$ is locally Lipschitz continuous, uniformly for $x \in \mathbb{R}^n$.
- (H2) The function g satisfies the following assumptions:
 - **H2.1** g(N) is continuous for $N \ge 0$, g(0) = 0, g'(0) > 0, g(N) > 0 for N > 0, and g(N) is nondecreasing for N > 0;
 - **H2.2** g(N)/N is nonincreasing for N, and there exists $\overline{N} > 0$ such that $g(\overline{N}) \leq \overline{N}$;
 - **H2.3** $N \mapsto g(N)$ is locally Lipschitz continuous, uniformly for $N \in \mathbb{R}^+$.
- (H3) There exist real numbers $G > 0, F > 0, \sigma_g > 0, \sigma_f > 0, \nu_g > 1$, and $\nu_f > 1$ such that $g(N) \ge g'(0)N GN^{\nu_g}$ for $0 \le N \le \sigma_g$, and $f(x, u) \ge f_u(x, 0)u Fu^{\nu_f}$ for $0 \le u < \sigma_f$.

Unlike [18, 19], we choose f(x, u) as a heterogeneous type of nonlinearity. In this paper, we assume that $r(x) := f_u(x, 0)$ is a bounded function and monotonically increasing in some direction, and the value of r(x) reflects the amount of available resources at x. The assumptions (H1)–(H3) essentially limit consideration to nonlinearity of the form uf(x, u). A typical example of f satisfying (H1)–(H3) is f(x, u) = u(r(x) - u). In addition, the monotonicity of the function $r(x) \in C^{\gamma}(\mathbb{R}^n, \mathbb{R})$ usually expresses monotonicity in the direction e. For example, for any $x, y \in \mathbb{R}^n$, $e \cdot (y - x)(r(y) - r(x)) > 0$ is established, and we call the function r(x) a monotone increasing function (in the direction e).

The rest of this paper is organized as follows. In section 2, we present some preliminary lemmas. In section 3, we use the method of upper and lower solutions to discuss the threshold dynamics for system (1.6) in a bounded or unbounded domain. In section 4, we give some numerical simulations to illustrate our analytic results. In section 5, we summarize the main findings and propose some future research directions.

2. Preliminaries. In order to derive the main results, we enumerate some classical properties of a class of semilinear elliptic problems. Here, we consider the form of a general linear elliptic operator,

$$Lu = a_{ij}(x)\partial_{ij}u + b_i(x)\partial_i u + c(x)u$$

in general domains $\Omega \subset \mathbb{R}^n$. We assume that $a_{ij}, b_i, c : \Omega \to \mathbb{R}$ are bounded and the matrix field (a_{ij}) is continuous, symmetric, and uniformly elliptic, that is

$$\underline{a}|\xi|^2 \le a_{ij}(x)\xi_i\xi_j \le \overline{a}|\xi|^2 \ \forall x \in \Omega, \xi \in \mathbb{R}^r$$

for some constants $0 < \underline{a} \leq \overline{a}$. An operator L is a self-adjoint operator, which means that it has the form

$$Lu = \partial_i \left(a_{ij}(x)\partial_j u \right) + c(x)u$$

with a_{ij} uniformly Lipschitz continuous.

In this paper, we will use some results on two generalized principal eigenvalues of a linear elliptic operator -L in a domain $\Omega \subset \mathbb{R}^n$ (Ω may be \mathbb{R}^n); see [23] and [24]. These two definitions are as follows:

$$\begin{split} \lambda_1(-L,\Omega) &:= \sup \left\{ \lambda \in \mathbb{R} | \exists \phi \in C^2(\Omega) \cap C^1_{loc}(\Omega), \phi > 0 \text{ and } (L+\lambda)\phi \leq 0 \text{ in } \Omega \right\}, \\ \lambda_1'(-L,\Omega) &:= \inf \left\{ \lambda | \exists \phi \in C^2(\Omega) \cap C^1_{loc}(\bar{\Omega}) \cap W^{2,\infty}(\Omega), \phi > 0 \text{ and } - (L+\lambda)\phi \leq 0 \\ & \text{ in } \Omega, \phi = 0 \text{ on } \partial\Omega \text{ if } \partial\Omega \neq \emptyset \right\}. \end{split}$$

In the absence of confusion, we may abbreviate the above eigenvalues as λ_1 and λ'_1 , respectively. We recall that the Dirichlet principal eigenvalue of -L in Ω is the unique real number λ_{Ω} such that the problem

$$\begin{cases} -L\varphi_{\Omega} = \lambda_{\Omega}\varphi_{\Omega} & \text{ in } \Omega, \\ \varphi_{\Omega} = 0 & \text{ on } \partial\Omega, \end{cases}$$

admits a positive solution φ_{Ω} (called the Dirichlet principal eigenfunction, which is unique up to scalar multiplication).

The following technical lemmas play a fundamental role.

LEMMA 2.1 (see [29, Theorem 1.7, Propositions 2.3 and 2.5]).

- 1. If Ω is smooth, then $\lambda'_1(-L,\Omega) \leq \lambda_1(-L,\Omega)$.
- 2. If Ω is bounded and smooth, then $\lambda_{\Omega} = \lambda_1(-L, \Omega) = \lambda'_1(-L, \Omega)$.
- 3. For a fixed $\Omega \subset \mathbb{R}^n$ and assuming that $a_1(x) \ge a_2(x)$ for all $x \in \Omega$. Then $\lambda_1(-L+a_1,\Omega) \ge \lambda_1(-L+a_2,\Omega)$.

4. Let Ω be a general domain in \mathbb{R}^n and $(\Omega_n)_{n\in\mathbb{N}}$ be a sequence of nonempty open sets such that $\Omega_n \subset \Omega_{n+1}$, $\bigcup_{n\in\mathbb{N}} \Omega_n = \Omega$. Then $\lambda_1(-L,\Omega_n) \searrow \lambda_1(-L,\Omega)$ as $n \to +\infty$. Furthermore, there exists a function $\varphi > 0$ such that

$$-L\varphi = \lambda_1(-L,\Omega)\varphi \quad in \ \Omega.$$

5. Let L be self-adjoint and Ω be a general domain in \mathbb{R}^n . Then we have

$$\lambda_1(-L,\Omega) = \inf_{\phi \in H_0^1(\Omega)} \frac{\int_\Omega \left(a_{ij}(x)\partial_i \phi \partial_j \phi - c(x)\phi^2\right)}{\int_\Omega \phi^2}$$

Back to the system (1.6), we set

$$\mathcal{L}w = \Delta w + ce \cdot \nabla w + f_u(x,0)w$$

and

$$\tilde{\mathcal{L}}w := \Delta w + \left(f_u(x,0) - c^2/4\right)w.$$

From the definition of the generalized principal eigenvalue and the Liouville transformation, we obtain the following lemma.

LEMMA 2.2 (see [9, Proposition 2]). For any domain Ω in \mathbb{R}^n the following identity holds:

$$\lambda_1(-\mathcal{L},\Omega) = \lambda_1(-\mathcal{L},\Omega).$$

Note the operator $\mathcal{L}_0 w := \Delta w + f_u(x, 0)w$ and set $\lambda_0 := \lambda_1(-\mathcal{L}_0, \mathbb{R}^n)$. Then we define critical speed c_0 as

(2.1)
$$c_0 := \begin{cases} 2\sqrt{-\lambda_0}, & \lambda_0 < 0, \\ 0, & \lambda_0 \ge 0 \end{cases}$$

By Lemma 2.2, we have

$$\lambda_1(-\mathcal{L},\mathbb{R}^n) = \lambda_1\left(-\mathcal{L}_0 + \frac{c^2}{4},\mathbb{R}^n\right) = \lambda_0 + \frac{c^2}{4}.$$

3. Threshold dynamics. Inspired by [7], using the moving coordinate transformation, $x \mapsto x - cte$, we can transform the study of the dynamic behavior of system (1.3) in an evolution (unbounded) domain $\Omega(t)$ into system (1.6) with advection in the fixed (bounded) space domain Ω . So this section will start with the study of persistence criteria in a bounded domain. It should be noted that the solutions of (1.6) are not equivalent to those of the original system (1.3) in an unbounded domain. However, the associated system has the same persistence conditions and the same well-posedness of solutions as the original system.

The purpose of this section is to study the persistence criterion for (1.6), namely, the criterion classifying the global dynamics of (1.6). We first treat successively the existence of a positive steady state of (1.6), its uniqueness, and global attractivity. Then we generalize the conclusions from bounded domains to whole space. Last, we discuss the impact of the shifting speed c on the propagation and persistence of species. **3.1.** Persistence criterion in a bounded domain Ω . In this subsection, we consider the following impulsive reaction-diffusion model on a bounded domain with Dirichlet boundary condition to explore persistence versus extinction:

(3.1)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f(x, u), & (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0, & (x, t) \in \partial \Omega \times (0, 1], \\ u(x, 0) = g \left(N_m(x) \right), & x \in \Omega, \\ N_{m+1}(x) := u(x, 1), & x \in \Omega, \end{cases}$$

where Ω is a bounded smooth domain in \mathbb{R}^n , and $\partial \Omega \in C^{2+\gamma}$.

The system (3.1) defines a recurrence relation for $N_m(x)$ as

(3.2)
$$N_{m+1}(x) = \hat{Q}[N_m(x)] = Q_1 \circ g[N_m(x)] \text{ for } x \in \Omega,$$

where Q_1 is the time-one solution map of the evolution system $u_t = \Delta u + ce \cdot \nabla u + f(x, u)$ for $x \in \Omega$. We proceed by linearizing model (3.1) at zero in the bounded domain:

(3.3)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f_u(x, 0)u, \quad (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0, \quad (x, t) \in \partial \Omega \times (0, 1], \\ u(x, 0) = g'(0)N_m(x), \quad x \in \Omega, \\ N_{m+1}(x) = u(x, 1), \quad x \in \Omega. \end{cases}$$

Let S_1 be the time-one solution map of the linear evolution system

$$u_t = \Delta u + ce \cdot \nabla u + f_u(x,0)u, \ x \in \Omega$$

Then $N_m(x)$ of model (3.3) satisfies the recursion system

(3.4)
$$N_{m+1}(x) = S_1[g'(0)N_m(x)] = \hat{S}[N_m(x)], x \in \Omega, \forall m \ge 0$$

where $\hat{S} = S_1 \circ g'(0)$.

It is assumed that u_0, v_0 are nonnegative continuous functions and $u_0(x) \geq v_0(x)$ for all $x \in \Omega$. We use $Q_t[u_0]$ and $Q_t[v_0]$ to represent the solutions of $u_t = \Delta u + ce \cdot \nabla u + f(x, u)$ with initial conditions u_0 and v_0 . By the monotonicity assumption on g and the comparison principle for reaction-diffusion equations, one can get $g(u_0(x)) \geq g(v_0(x))$ for all $x \in \Omega$, and $Q_t[u_0] \geq Q_t[v_0]$ for all $x \in \Omega, 0 < t \leq 1$. This result implies that the operator $\hat{Q} = Q_1[g(\cdot)]$ has the same monotonicity property. In conclusion, if nonnegative continuous initial value $N_{10}(x) \geq N_{20}(x)$ for all $x \in \Omega$, then $\hat{Q}[N_{10}(x)] \geq \hat{Q}[N_{20}(x)]$. If we further assume that $N_{10}(x) \neq N_{20}(x)$, then $\hat{Q}[N_{10}(x)] > \hat{Q}[N_{20}(x)]$, that is, \hat{Q} is order preserving. Obviously, the same statement is valid for the linearized operator \hat{S} . It is easy to verify that if (H1) and (H2) hold, \hat{Q} is linearly bounded, that is, $\hat{Q}[N(x)] \leq \hat{S}[N(x)]$. It should be pointed out that these statements are also valid when x belongs to the whole space \mathbb{R}^n .

Then we consider the Dirichlet eigenvalue problem

$$\begin{cases} -\mathcal{L}\phi = \lambda\phi & \text{in }\Omega, \\ \phi = 0 & \text{on }\partial\Omega, \\ \phi > 0 & \text{in }\Omega, \end{cases}$$

and let the pair $(\phi^*; \lambda_1(f_u(x, 0); \Omega))$ be the first eigenpair of this problem. Setting $\lambda_\Omega = \lambda_1(f_u(x, 0); \Omega)$, that is, λ_Ω is the principal eigenvalue of the following problem:

$$-\lambda\phi(x) = \triangle\phi(x) + ce \cdot \nabla\phi(x) + f_u(x,0)\phi(x), x \in \Omega$$

and associates with a positive eigenfunction ϕ^* . It follows that

$$N_m(x) = \left(g'(0)e^{-\lambda_\Omega}\right)^m \phi^*(x), x \in \Omega, \forall m \ge 0$$

is a solution of system (3.4). Below we will show that $g'(0)e^{-\lambda_{\Omega}}$ serves as a threshold value which determines whether the species can persist.

Let $\tilde{X} = \{\psi : \Omega \to \mathbb{R} \mid \psi \text{ is bounded in } \overline{\Omega}, \psi \in W_p^2(\Omega), \psi = 0 \text{ on } \partial\Omega\}$ with norm $\|\cdot\|_{\tilde{X}} = \|\cdot\|_{W_p^2(\Omega)}$ and p > 1 + n/2. It then follows that $(\tilde{X}, \|\cdot\|_{\tilde{X}})$ is a Banach space. For $\phi, \psi \in \tilde{X}$, we write $\phi \ge (\gg)\psi$ if $\phi(x) \ge (>)\psi(x)$ for all $x \in \overline{\Omega}$, and $\phi > \psi$ if $\phi \ge \psi$ but $\phi \ne \psi$. Define $\tilde{X}_+ = \{\psi \in \tilde{X} : \psi(x) \ge 0, \forall x \in \overline{\Omega}\}$. Then \tilde{X}_+ is a positive cone of \tilde{X} and induces a partial ordering on \tilde{X} .

For simplicity, we write the following theorem under more strict assumptions and prove it by three lemmas.

THEOREM 3.1. Assume that (H1), (H2), and (H3) hold. The following statements are valid:

- 1. If $g'(0)e^{-\lambda_{\Omega}} < 1$, then $\lim_{m \to +\infty} N_m(x) = 0$ uniformly for $x \in \overline{\Omega}$.
- 2. If $g'(0)e^{-\lambda_{\Omega}} > 1$, then system (3.2) has a unique positive steady state $N^* \in C^2(\bar{\Omega})$ with $N^* \gg 0$, which is globally attractive in the sense that for any $N_0 \in \tilde{X}_+$ with $N_0 > 0$, there holds $\lim_{m \to +\infty} N_m(x) = N^*(x)$ uniformly for $x \in \Omega$.

LEMMA 3.2 (extinction). Assume that f(x, u), g(u) satisfy properties (H1), (H2), and $g'(0)e^{-\lambda_{\Omega}} < 1$. Then all nonnegative solutions of (3.2) converge to zero.

Proof. Let $\overline{N}_m(x) = \delta(g'(0)e^{-\lambda_\Omega})^m \phi^*(x)$ for all $m \ge 0$, where δ is a positive constant. We claim that $\overline{N}_m(x)$ satisfies the following linear problem:

$$\begin{split} u_t &= \Delta u + ce \cdot \nabla u + f_u(x,0)u, \quad (x,t) \in \Omega \times (0,1], \\ u(x,t) &= 0, \quad (x,t) \in \partial \Omega \times (0,1], \\ u(x,0) &= g'(0)\overline{N}_m(x), \quad x \in \Omega, \\ \overline{N}_{m+1}(x) &:= u(x,1), \quad x \in \Omega. \end{split}$$

Clearly, $u(x,t) = g'(0)e^{-\lambda_{\Omega}t}[\delta\phi^*(x)]$ is a solution of the linear equation

$$u_t = \Delta u + ce \cdot \nabla u + f_u(x, 0)u$$
 for $(x, t) \in \Omega \times \mathbb{R}^+$

satisfying $u(x,0) = g'(0)[\delta\phi^*(x)] := g'(0)[\overline{N}_0(x)]$. This implies that

$$\overline{N}_1(x) = u(x,1) = \hat{S}[\overline{N}_0(x)] = g'(0)e^{-\lambda_\Omega}[\overline{N}_0(x)].$$

Thus, we have $\hat{Q}[\overline{N}_0(x)] \leq \hat{S}[\overline{N}_0(x)] = g'(0)e^{-\lambda_\Omega}[\overline{N}_0(x)]$. It is easy to see that the function $\overline{N}_0(x)$ is the eigenfunction of the operator \hat{S} corresponding to the eigenvalue $g'(0)e^{-\lambda_\Omega}$. By iteration, we find $\hat{Q}^m[\overline{N}_0(x)] \leq (g'(0)e^{-\lambda_\Omega})^m\overline{N}_0(x)$. By assumption, we have $0 < g'(0)e^{-\lambda_\Omega} < 1$, hence, it obtains $\hat{Q}^m[\overline{N}_0(x)] \to 0$ as $m \to \infty$. For any given initial value $N_0(x)$ in the original nonlinear system (1.6), we choose δ sufficiently large such that $N_0(x) \leq \overline{N}_0(x)$. By monotonicity and iteration, we have $\hat{Q}^m[\overline{N}_0(x)] \leq \hat{Q}^m[\overline{N}_0(x)]$ and, hence, $\lim_{m \to +\infty} N_m(x) = 0$ uniformly for $x \in \overline{\Omega}$.

LEMMA 3.3 (existence). Assume that f and g satisfy properties (H1)–(H3) above and assume that $g'(0)e^{-\lambda_{\Omega}} > 1$. Then there exists at least one positive steady state solution of (3.2). *Proof.* Let $Q_1[g(N_m(x))]$ be u(1,x) with u(x,t) the solution of the initial value problem

$$u_t = \Delta u + ce \cdot \nabla u + f(x, u), \quad u(x, 0) = g(N_m(x)).$$

Let a function $N(x) \in C^2(\overline{\Omega})$ be an upper (lower) solution of (3.2) if $N(x) \geq (\leq)\hat{Q}[N(x)]$.

If $e^{-\lambda_{\Omega}}g'(0) > 1$, then we can choose $\tilde{\lambda} < -\lambda_{\Omega}$ and $\underline{g} < g'(0)$ such that $e^{\bar{\lambda}}\underline{g} > 1$. Let $v(x,t) = \varepsilon \underline{g} e^{\tilde{\lambda} t} \phi^*(x)$. It follows from (H3) that for sufficiently small $\varepsilon > 0$ and $0 < t \leq 1$, we have $g(v(x,t)) \geq \underline{g}v(x,t) + v(x,t)([g'(0)-\underline{g}] - G\varepsilon^{\nu_g-1}[\underline{g}e^{\tilde{\lambda} t}\phi^*(x)]^{\nu_g-1}) \geq \underline{g}v(x,t)$. From (H3), we have $f(x,v) \geq f_u(x,0)v - Fv^{\nu_f}$ and, hence,

$$(3.5) \qquad \frac{\partial v}{\partial t} - \left[\Delta v + ce\nabla v - f(x,v)\right]$$
$$\leq \varepsilon \underline{g} \tilde{\lambda} e^{\tilde{\lambda} t} \phi^* - \varepsilon \underline{g} e^{\tilde{\lambda} t} \left[\Delta \phi^* + ce \cdot \nabla \phi^* - f_u(x,0)\phi^*\right] + F\left[\varepsilon \underline{g} e^{\tilde{\lambda} t} \phi^*\right]^{\nu_f}$$
$$= v\left(\left(\tilde{\lambda} + \lambda_\Omega\right) + F\varepsilon^{\nu_f - 1} \left[\underline{g} e^{\tilde{\lambda} t} \phi^*\right]^{\nu_f - 1} \right) \leq 0,$$

which shows that v(x, t) is a lower solution of system (1.4) with Dirichlet boundary conditions, where $x \in \Omega$. Thus, there exists a sufficiently small ε_0 such that for any given $\varepsilon \in (0, \varepsilon_0]$, $M_0 > \varepsilon \phi^*(x)$, and

$$\hat{Q}\left[\varepsilon\phi^*(x)\right] = Q_1\left[g\left(\varepsilon\phi^*(x)\right)\right] \ge Q_1\left[\underline{g}\varepsilon\phi^*(x)\right] \ge v(x,1) \ge \varepsilon\phi^*(x).$$

It implies that

$$M_0 \ge \hat{Q}^{m+1}\left[\varepsilon\phi^*(x)\right] \ge \hat{Q}^m\left[\varepsilon\phi^*(x)\right], x \in \Omega, \ \forall m \ge 0.$$

Since M_0 is an upper solution of system (3.2), we have $\hat{Q}[\rho M_0] \leq \rho \hat{Q}[M_0] \leq \rho M_0$ for any given $\rho > 1$ and, hence, $\hat{Q}^{m+1}[\rho M_0] \leq \hat{Q}^m[\rho M_0] \leq \rho M_0$.

Note $\underline{N}_0 = \varepsilon \phi^*$ and $\overline{N}_0 = M_0$, we have $\underline{N}_1 = \hat{Q} [\underline{N}_0] \geq \underline{N}_0$ and $\overline{N}_1 = \hat{Q} [\overline{N}_0] \leq \overline{N}_0$. By induction, we see that $\underline{N}_{m+1} \geq \underline{N}_m$ for all $m \in \mathbb{N}$, i.e., the sequence is monotone increasing. Since $\hat{Q}(N) \leq \rho M_0$, the sequence is also bounded. Hence, the pointwise limit $N_*(x) = \lim_{m \to \infty} \underline{N}_m(x)$ exists. In the same way, the pointwise limit $N^*(x) = \lim_{m \to \infty} \overline{N}_m(x)$ exists.

Define a set

$$\Gamma = \left\{ N_0 \in \tilde{X}_+ : \underline{N}_0(x) \le g(N_0(x)) \le \overline{N}_0(x) \text{ in } \overline{\Omega} \right\}.$$

Then Γ is a closed convex subset of \tilde{X}_+ . For any given $N_0 \in \Gamma$, let us investigate the parabolic equation

(3.6)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f(x, u), & (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0, & (x, t) \in \partial \Omega \times (0, 1], \\ u(x, 0) = g(N_0(x)), & x \in \Omega. \end{cases}$$

Obviously, $\bar{u} = u(x,t;g(\overline{N}_0(x)))$ and $\underline{u} = u(x,t;g(\underline{N}_0(x)))$ are the upper and lower solutions of (3.6), respectively. Thus (3.6) admits a unique solution $u(x,t) \in W_p^{2,1}(\Omega \times (0,1])$ and satisfies

$$\underline{N}_0(x) \le u(x,1) \le \overline{N}_0(x).$$

Set F = f(x, u(x, t)). We get $F \in C^{\alpha, \alpha/2}(\bar{Q}_T)$ by $u \in W_p^{2,1}(\Omega \times (0, 1]) \hookrightarrow C^{\alpha, \alpha/2}(\bar{Q}_T)$. Based on the embedding theorem and the regularity theory, we have

$$u \in W_n^{2,1}(\Omega \times (0,1]) \cap C^{2+\alpha,1+\alpha/2}(\bar{\Omega} \times (0,1]).$$

Hence $u(x, 1) = N_1(x) \in \Gamma \cap C^{2+\alpha}$. Applying the classical theory of PDEs, we obtain that Q_1 is continuous and compact in the topology of uniform convergence on every bounded interval. Since g is continuous, we have that \hat{Q} is continuous and compact in the topology of uniform convergence on every bounded interval. Compactness together with monotonicity implies that $\{\hat{Q}[\underline{N}_m]\}_m$ and, hence, $\{\underline{N}_m\}_m$, converges in the space of continuous functions. By continuity of \hat{Q} , we have

$$\hat{Q}[N_*] = \hat{Q}\left[\lim_{m \to \infty} \underline{N}_m\right] = \lim_{m \to \infty} \hat{Q}[\underline{N}_m] = \lim_{m \to \infty} \underline{N}_{m+1} = N_*.$$

Hence, N_* is a fixed point of \hat{Q} . In a similar way, N^* is also a fixed point of \hat{Q} .

LEMMA 3.4 (uniqueness and attractivity). Assume that f and g satisfy properties (H1)–(H3) above and assume that $g'(0)e^{-\lambda_{\Omega}} > 1$. Then system (3.2) has a unique positive steady state N^* , which is globally attractive.

Proof. Observe that for any $N_0(x) \in \Gamma$, system (3.1) has a unique nonnegative solution $u(x, t, g(N_0(x)))$ with initial condition $u(x, 0) = g(N_0(x))$. Since $\frac{g(N)}{N}$ is nonincreasing, $\frac{g(M)}{M} \geq \frac{g(N)}{N}$ for $N \geq M$. Set $M = \eta N \leq N$ for $0 \leq \eta \leq 1$ and apply the above inequality to get $g(\eta N) \geq \eta g(N)$, so we can see that g(N) is subhomogeneous. We can verify that Q_1 is strongly subhomogeneous in the sense that $Q_1(\eta\varphi) \gg \eta Q_1(\varphi)$ for all $\varphi \in \Gamma, \eta \in (0, 1)$. Thus, $\hat{Q} = Q_1 \circ g$ is strongly subhomogeneous (also see [19]). Moreover, \hat{Q} admits at most one strongly positive fixed point in Γ . Indeed, let ψ_1 and ψ_2 be in Γ such that $\hat{Q}(\psi_i) = \psi_i(i = 1, 2)$. By [41, Lemma 2.3.1], it follows that $\psi_1 = \tau \psi_2$ for some $\tau \in (0, 1]$. We further claim $\tau = 1$, that is, $\psi_1 = \psi_2$. Otherwise, we have $0 < \tau < 1$ and, hence, $\psi_1 = \hat{Q}(\psi_1) = \hat{Q}(\tau\psi_2) \gg \tau \hat{Q}(\psi_2) = \tau \psi_2 = \psi_1$. This is a contradiction. Consequently, N_* and N^* in Lemma 3.3 are equal.

For any given $N_0 = \varphi \in \tilde{X}_+$ with $\varphi > 0$, we have $g(\varphi) \in \tilde{X}_+$ with $g(\varphi) > 0$. It follows that $u(x, 1; g(\varphi)) \gg 0$ and, hence, $N_1 = u(x, 1; g(\varphi)) \gg 0$ and $N_1 \in W_p^2(\Omega) \cap C^{2+\alpha}(\bar{\Omega})$. We set N_1 as an initial datum and further choose a sufficiently small $\varepsilon \in (0, \varepsilon_0]$ and a sufficiently large $\rho > 1$ such that $\varepsilon \phi^* \leq N_1 \leq \rho M_0$. Thus, $\hat{Q}^m(\varepsilon \phi^*) \leq \hat{Q}^m(N_1) \leq \hat{Q}^m(\rho M_0)$. It follows that $\lim_{m \to +\infty} \hat{Q}^m(\varphi)(x) = N^*(x)$ uniformly for $x \in \Omega$.

Remark 3.5. The uniqueness proof of Theorem 3.1 is not superfluous. This is a significant difference between our hybrid model and the classical parabolic equations. In other words, for parabolic equations, the uniqueness of the solution obtained by the upper and lower solution method is almost self-evident, but for our hybrid system, this good property is not inherited. Conditions (H1.2) and (H2.2) make f and g satisfy concave conditions, respectively, so that the strongly subhomogeneous condition is satisfied for operator \hat{Q} , thus the uniqueness of the positive steady state is obtained.

3.2. Persistence criterion in the whole space \mathbb{R}^n . Let $X = BC(\mathbb{R}^n, \mathbb{R})$ be the set of all bounded and continuous functions from \mathbb{R}^n to \mathbb{R} with the usual supreme norm. For $\phi, \psi \in X$, we write $\phi \ge (\gg)\psi$ if $\phi(x) \ge (>)\psi(x)$ for all $x \in \mathbb{R}^n$, and $\phi > \psi$ if $\phi \ge \psi$ but $\phi \ne \psi$. Let $X_+ = \{\psi \in X : \psi(x) \ge 0 \ \forall x \in \mathbb{R}^n\}$. Then X_+ is a closed cone of X and its induced partial ordering makes X into an ordered Banach space. In this subsection we extend the conclusion of Theorem 3.1 to an unbounded domain. Here, two generalized principal eigenvalues λ_1 and λ'_1 represent $\lambda_1(-\mathcal{L}, \mathbb{R}^n)$ and $\lambda'_1(-\mathcal{L}, \mathbb{R}^n)$, respectively. We introduce different definitions of persistence. The population is weakly uniformly persistent if

$$\limsup_{m \to \infty} \sup_{x \in \mathbb{R}^n} N_m(x) > \varepsilon.$$

In other words, there exists some $\varepsilon > 0$ such that for all $m > m^*$, there exists $x_m \in \mathbb{R}^n$ such that $N_m(x_m) > \varepsilon$. And the population is locally persistent if

$$\sup_{x \in \mathbb{R}^n} \liminf_{m \to \infty} N_m(x) > \varepsilon.$$

In other words, there exist $\varepsilon > 0$ and $x_0 \in \mathbb{R}^n$, such that for all $m > m^*$, there exists $N_m(x_0) > \varepsilon$ (see [17, 21, 30]).

LEMMA 3.6 (weakly uniform persistence). Assume that f(x, u), g(u) satisfy properties (H1)–(H3), then $g'(0)e^{-\lambda'_1} > 1$ is a sufficient condition for weakly uniform persistence for system (1.7).

Proof. We only need to prove that the semiflow induced by \hat{Q} is weakly uniformly persistent. We adopt the method of contradiction. Suppose that the semiflow is not weakly uniformly persistent. Then for any $\varepsilon_0 > 0$, there exists some $N_0(x) \in X_+ \setminus \{0\}$ and $m^* \in \mathbb{N}$ such that $N_m(x) = \hat{Q}_{-}^m[N_0(x)] < \varepsilon_0$ for all $m \ge m^*$.

According to the definition of λ'_1 and $g'(0)e^{-\lambda'_1} > 1$, we can find $\mu > 1$ and $\phi \in X_+ \setminus \{0\}$ such that $\hat{S}\phi \ge \mu\phi > \phi$. Set $\epsilon \in (0,1)$ such that $\mu(1-\epsilon) > 1$.

Combined with assumptions (H1.1)–(H1.2), (H2.1)–(H2.2), and H_3 , it is easy to verify $\hat{S}[N(x)] \geq \hat{Q}[N(x)] \geq (1-\epsilon)\hat{S}[N(x)]$ for any $N(x) \in X_+$ with $0 \leq N(x) \leq \varepsilon_0$. Since the semiflow is not weakly uniformly persistent, after a forward shift in time, we can assume that $N_0(x) := N_{m^*}(x) \in X_+ \setminus \{0\}$ and $\hat{Q}^m[N_0(x)] < \varepsilon_0$ for $m \geq 0$. Since $N_{m+1}(x) = \hat{Q}[N(x)]$, we have $N_m(x) \leq \varepsilon_0$ for all $m \in \mathbb{Z}_+$. Using mathematical induction, we can get

(3.7)
$$N_m(x) \ge (1-\epsilon)^m \hat{S}^m[N_0(x)].$$

We can find a $p^* \in \mathbb{N}$ such that $N_{p^*}(x) \geq \theta \phi$ for some $\theta > 0$. For $\phi \in X_+$, we set the functional $[N(x)]_{\phi} := \sup\{\alpha \geq 0, N(x) \geq \alpha \phi(x)\}, N(x) \in X_+$. Since X_+ is closed, $N(x) \geq [N(x)]_{\phi} \phi, N(x) \in X_+$. Then $[\cdot]_{\phi}$ is order preserving, bounded, and homogeneous (i.e., [30, Lemma 4.3]).

After another forward shift in time, we assume that $[N_0]_{\phi} > 0$ and (3.7). Thus

$$[N_m]_{\phi} \ge (1-\epsilon)^m \left[\hat{S}^m \left(N_0 \right) \right]_{\phi}.$$

For any $N_0(x) \in X_+$,

$$\hat{S}(N(x)) \ge \hat{S}\left([N(x)]_{\phi}\phi\right) \ge [N(x)]_{\phi}\hat{S}(\phi) \ge [N(x)]_{\phi}\mu\phi$$

By using induction again, $[\hat{S}^m(N_0(x))]_{\phi} \ge \mu^m [N_0(x)]_{\phi}$. We combine the inequalities, if $m \to \infty$, then

$$[N_m(x)]_{\phi} \ge [\mu(1-\epsilon)]^m [N_0(x)]_{\phi} \to \infty.$$

Since the functional $[\cdot]_{\phi}$ is bounded, this contradicts the boundedness of $N_m(x)$. \Box

Furthermore, a nontrivial solution exists. In fact, according to the definition of the generalized eigenvalue λ'_1 , there is a bounded positive function ϕ^* , which makes inequality (3.5) true, that is, a lower solution of system (1.7) can be determined. Similarly to the proof of Lemma 3.3, there is at least one positive solution for system (1.7).

Then we will discuss the uniqueness of the solution. Our uniqueness result only applies to the solution satisfying $\inf_{x \in \mathbb{R}^n} N_0(x) > 0$ is unique.

LEMMA 3.7 (uniqueness). If $N^*(x)$ and $N_*(x)$ are two bounded positive solutions of system (1.7) such that $\inf_{x \in \mathbb{R}^n} N^*(x) > 0$ and $\inf_{x \in \mathbb{R}^n} N_*(x) > 0$, then $N^*(x) = N_*(x)$.

Proof. According to the boundedness of the positive solutions, we can find a constant ε so that $0 < \varepsilon \phi^*(x) = N_0(x) \le N_*(x)$. Let u(x,t) be the unique solution of the initial value problem

$$u_t = \Delta u + ce \cdot \nabla u + f(x, u), \quad u(x, 0) = g(\varepsilon \phi^*(x)).$$

Since $N_1(x) = u(x, 1)$, we have $N_0(x) \leq N_1(x) \leq N_*(x)$ by the comparison principle. Application of induction we can prove that $N_m(x)$ is increasing in m and $\varepsilon \phi^*(x) \leq N_m(x) \leq N_*(x)$ in $x \in \mathbb{R}^n$. So, there exists a positive function $\underline{N}(x)$ such that $N_m(x) \to \underline{N}(x)$ pointwise in \mathbb{R}^n as $m \to \infty$.

Based on the argument in the proof of [26, Lemma 3.2], it can be shown that $N_m(x) \to \underline{N}(x)$ in $C^2_{loc}(\mathbb{R}^n)$ as $m \to \infty$. Thus $\underline{N}(x)$ is a positive solution of (1.7).

According to the boundedness of the positive solutions, we can find a constant $\sigma > 0$ so that $\sigma = \inf_{x \in \mathbb{R}^n} \frac{\underline{N}(x)}{N_*(x)}$. Clearly, $\sigma \leq 1$ and $\underline{N}(x) \geq \sigma N_*(x)$ in \mathbb{R}^n . Assume that $\sigma < 1$, then $\underline{N}(x) \not\equiv \sigma N_*(x)$. Since $\hat{Q} = Q_1 \circ g$ is strongly subhomogeneous, we have

$$\underline{N}(x) = \hat{Q}[\underline{N}(x)] \ge \hat{Q}[\sigma N_*(x)] > \sigma \hat{Q}[N_*(x)] = \sigma N_*(x).$$

The same as above, there exists $\varepsilon > 0$ such that $\underline{N}(x) \ge (\sigma + \varepsilon)N_*(x)$ in \mathbb{R}^n . This is a contradiction with the definition of σ , and so $\underline{N}(x) = N_*(x)$.

In the same way, we can get
$$\underline{N}(x) = N^*(x)$$
, so $N_*(x) = N^*(x)$.

LEMMA 3.8 (attractivity). If $N_*(x)$ is a unique positive solution of system (1.7) satisfying $\inf_{x \in \mathbb{R}^n} N_0(x) > 0$, then $N_m(x) \to N_*(x)$ as $m \to \infty$ in $C^2_{loc}(\mathbb{R}^n)$.

Proof. Assume that $\inf_{x\in\mathbb{R}^n} N_0(x) > 0$, we can find $0 < \varepsilon \ll 1$ and $\rho \gg 1$ such that

$$\varepsilon \phi^*(x) \le g(N_0) \le \rho N_*(x).$$

It's obvious that $\rho N_*(x)$ is an upper solution of (1.7). Let w_m and W_m be solutions of (1.7) with initial value functions $\varepsilon \phi^*(x)$ and $\rho N_*(x)$, respectively. Then $w_1(x) \leq$ $N_1(x) \leq W_1(x)$ by the comparison principle. Using induction, we can get $w_m(x) \leq$ $N_m(x) \leq W_m(x)$ for $m \in \mathbb{N}$.

From the discussions of Lemma 3.7, we see that

$$\lim_{m \to +\infty} w_m(x) = N_*(x)$$

Similarly,

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$$\lim_{m \to +\infty} W_m(x) = N_*(x)$$

To sum up, we can see that $\lim_{m \to +\infty} N_m(x) = N_*(x)$ in $C^2_{loc}(\mathbb{R}^n)$.

As a summary, we obtain the following theorem.

THEOREM 3.9. Assume that (H1), (H2), and (H3) hold. If $g'(0)e^{-\lambda_1} > 1$, then system (1.7) has a unique positive steady state $N_*(x) \in C^2_{loc}(\mathbb{R}^n)$ with $N_*(x) > 0$, which is globally attractive in the sense that for any $N_0(x)$ with $\inf_{x \in \mathbb{R}^n} N_0(x) > 0$, there holds $\lim_{m \to +\infty} N_m(x) = N_*(x)$ uniformly for $x \in \mathbb{R}^n$.

According to Lemma 2.1 (see also [29, Theorem 1.7]), we obtain that $\lambda'_1(-\mathcal{L}, \Omega) \leq \lambda_1(-\mathcal{L}, \Omega)$ holds for Ω , where Ω is a smooth (possibly unbounded) domain. By slightly modifying the proof process in [29], one can show that, for any $\lambda > \lambda_1(-\mathcal{L}, \mathbb{R}^n)$, $\lambda'_1(-\mathcal{L}, \mathbb{R}^n) \leq \lambda$, that is, $\lambda'_1 \leq \lambda_1$ for \mathbb{R}^n . We will show that if we strengthen the condition $g'(0) > e^{\lambda'_1}$ to $g'(0) > e^{\lambda_1}$, then the long-term viability of species can be enhanced. This has some implications for the assisted reproductive strategy for endangered species.

Let B_R be the open ball of \mathbb{R}^N , with center 0 and radius R. Let y be an arbitrary point in \mathbb{R}^n and $\mathcal{L}^y w = \triangle w + ce \cdot \nabla w + f_u(x+y,0)w$. It is well known that there exists a principal eigenvalue λ_R^y and a principal eigenfunction φ_R^y in $C^2(\overline{B_R})$ satisfying

$$\begin{cases} -\mathcal{L}^{y}\varphi_{R}^{y} = \lambda_{R}^{y}\varphi_{R}^{y} & \text{ in } B_{R}, \\ \varphi_{R}^{y} = 0 & \text{ on } \partial B_{R}, \\ \varphi_{R}^{y} > 0 & \text{ in } B_{R}, \\ \|\phi^{y}\|_{\infty} = 1. \end{cases}$$

Since both λ_R^y and φ_R^y are unique, standard elliptic estimates and compactness arguments imply that the maps $y \mapsto \varphi_R^y$ and $y \mapsto \lambda_R^y$ are continuous with respect to y.

Let $\tilde{\lambda}_1^y$ be the principal eigenvalue and ϕ_{∞}^y be the principal eigenfunction of

$$\begin{cases} -\mathcal{L}^{y}\phi_{\infty}^{y} = \lambda_{1}^{y}\phi_{\infty}^{y} & \text{ in } \mathbb{R}^{n}, \\ \phi_{\infty}^{y} > 0 & \text{ in } \mathbb{R}^{n}, \\ \|\phi^{y}\|_{\infty} = 1. \end{cases}$$

We can verify that the first eigenvalue $\tilde{\lambda}_1^y$ does not depend on y. In other words, $\tilde{\lambda}_1^y = \lambda_1$ for all $y \in \mathbb{R}^n$. By Lemma 2.1, it can directly reach the following lemma.

LEMMA 3.10. For all $y \in \mathbb{R}^n$, the function $R \mapsto \lambda_R^y$ is decreasing in R > 0, and $\lim_{R \to +\infty} \lambda_R^y = \lambda_1$ uniformly in $y \in \mathbb{R}^n$.

THEOREM 3.11. Assume that $g'(0)e^{-\lambda_1} > 1$ and f(x, u), g(u) satisfy properties (H1), (H2), and (H3). Then $N_*(x)$ is a positive bounded solution of (1.7) that satisfies $\inf_{x \in \mathbb{R}^n} N_*(x) > 0$. Moreover, N_* is a unique positive steady state and globally attractive.

Proof. From Lemma 3.10, there exists $R_0 = \inf\{R|g'(0)e^{-\lambda_R} = 1\} > 0$ such that

$$\forall R \ge R_0 \; \forall y \in \mathbb{R}^n, g'(0)e^{-\lambda_R^y} > 1.$$

Note $u^y(x) := u(x+y)$. The function $N^y_*(x)$ satisfies

(3.8)
$$\begin{cases} u_t^y = \Delta u^y + ce \cdot \nabla u^y + f(x+y, u^y), & (x,t) \in \mathbb{R}^n \times (0,1], \\ u^y(x,0) = g(N_m^y(x)), & x \in \mathbb{R}^n, \\ N_{m+1}^y(x) = u^y(x,1), & x \in \mathbb{R}^n, \end{cases}$$

that is, $N_*^y(x) = \hat{Q}[N_*^y(x)] = \hat{Q}[N_*(x+y)]$ in \mathbb{R}^n .

Choosing $R \geq R_0$ and positive $\kappa < \kappa_0$, from the proof of Lemma 3.3, we can see that $\kappa \varphi_R^y$ is a lower solution of system (3.8) in $\Omega = B_R$. We want to prove that $N_*^y \geq \kappa_0 \varphi_R^y$ in $\overline{B_R}$. If it's not true, there exist $0 < \kappa^* \leq \kappa_0$ and $x_0 \in \overline{B_R}$ such that $\kappa^* \varphi_R^y(x_0) = N_*^y(x_0)$ and $N_*^y \geq \kappa^* \varphi_R^y$ in $\overline{B_R}$. Next, since $\varphi_R^y \equiv 0$ on ∂B_R , it follows that $x_0 \in B_R$. On the other hand, the above computations show that the function $\kappa^* \varphi_R^y$ is still a lower solution of (3.8). The strong maximum principle gives that $\kappa^* \varphi_R^y \equiv N_*^y$ in $\overline{B_R}$, which is in contradiction with the conditions on ∂B_R .

Thus, we have $N_*^y > \kappa_0 \varphi_R^y$ in $\overline{B_R}$, and $N_*^y(0) = N_*(y) > \kappa_0 \varphi_R^y(0)$. In other words, $N_*^y > \kappa_0 \varphi_R^y(0)$ for all $y \in \mathbb{R}^n$. Since the function $y \mapsto \kappa_0 \varphi_R^y(0)$ is continuous and positive over \mathbb{R}^n , there exists $\epsilon > 0$ such that $N_*^y > \kappa_0 \varphi_R^y(0) > \epsilon$ for all $y \in \mathbb{R}^n$.

Then, we prove the boundedness of the positive solution. We study the following impulsive reaction-diffusion model for any $m \in \mathbb{Z}^+$:

$$u_t^{(m)} = \Delta u^{(m)} + ce\nabla u^{(m)} + f(x, u^{(m)}) \text{ for } (x, t) \in K \times (0, 1],$$

$$u^{(m)}(x, t) = 0 \text{ for } (x, t) \in \partial K \times (0, 1],$$

$$u^{(m)}(x, 0) = g(N_m(x)) \text{ for } x \in K,$$

$$N_{m+1}(x) = u^{(m)}(x, 1) \text{ for } x \in K,$$

where K is a compact subset of \mathbb{R}^n . By the classical parabolic estimates, we get that there exists M > 0 such that $\|u^{(m)}(x,t)\|_{C^{1+\gamma/2,2+\gamma}([0,1]\times K)} < M$ for all $m > m^*$. Thus, one can extract a subsequence (that we still call $\{u^{(m)}\}_m$ that converges in $C^{1,2}_{loc}([0,1]\times K)$. Using a diagonal method, one can extract a subsequence such that $u^{(m)} \to u^{(\infty)}$ in $C^{1,2}_{loc}([0,1]\times \mathbb{R}^n)$. Thus, $N_*(x) = u^{(\infty)}(x,1) \in C^2_{loc}(\mathbb{R}^n)$.

Let $N_0 \in C^0(\mathbb{R}^n)$ be a nonnegative, bounded, and nonnull initial datum. Thus, $\rho > 1$ can be large enough to make $||g(N_0)|| \le \rho M$. We already know that ρM is the super solution of system (1.7). Therefore, using the same method as before, we can prove that $N_*(x) \le \rho M$ for all $x \in \mathbb{R}^n$. Therefore, $N_*(x)$ is bounded. Similarly to the proof of Lemmas 3.7 and 3.8, the uniqueness and attractiveness of the solution $N_*(x)$ can be obtained.

Theorem 3.11 implies that $g'(0)e^{-\lambda_1} > 1$ is a sufficient condition for locally persistence for system (1.7), that is, there exist $\varepsilon > 0$ and $x_0 \in \mathbb{R}^n$, such that for all $m > m^*$ there exists $N_m(x_0) > \varepsilon$. In addition, combining the proofs of Theorem 3.11 and Lemma 3.2, we can directly get the following conclusions.

PROPOSITION 3.12. Assume that (H1), (H2), and (H3) are satisfied and $g'(0)e^{-\lambda_1} < 1$. If $N_0(x) \neq 0$ is a continuous nonnegative function and compactly supported, then $N_m(x) \to 0$ as $m \to \infty$ uniformly on the compact subsets of \mathbb{R}^n .

We end this subsection by studying the situation $e^{\lambda'_1} < g'(0) < e^{\lambda_1}$. This inequality may be valid when considering an unbounded domain. More detailed information about the relationship between generalized eigenvalues λ_1 and λ'_1 can be found in [25, 27, 28, 29, 36]. In this case, the so-called grounding phenomenon will occur. The following corollary can be obtained directly from Proposition 3.12 and Theorem 3.9. This corollary shows that under $e^{\lambda'_1} < g'(0) < e^{\lambda_1}$, the asymptotic behavior of the solutions of system (1.7) depends on the properties of the initial datum.

COROLLARY 3.13. Assume that $e^{\lambda'_1} < g'(0) < e^{\lambda_1}$ and that hypotheses (H1), (H2), and (H3) are satisfied. Let $N_0 \in C^0(\mathbb{R}^n)$ be a nonnegative, bounded, and nonnull initial datum.

1. If N_0 is compactly supported, then $N_m(x) \to 0$ as $m \to +\infty$ locally uniformly with respect to $x \in \mathbb{R}^n$.

2. If $\inf_{\mathbb{R}^n} N_0 > 0$, then $N_m(x) \to N_*(x)$ as $m \to +\infty$ in $\mathcal{C}^2_{loc}(\mathbb{R}^n)$, where $N_*(x)$ is the unique positive solution of (1.7).

3.3. Effects of the habitat shifting speed. In this subsection, we investigate the influence of the habitat shifting speed driven by climate change on the persistence criterion. Set

$$R_0 := g'(0)e^{-\lambda_1(-\mathcal{L}_0,\mathbb{R}^n)},$$

where $\lambda_1(-\mathcal{L}_0, \mathbb{R}^n)$ depend on r(x). Similarly to the definition (2.1), we redefine critical speed

$$C_0^* := \begin{cases} 2\sqrt{\ln g'(0) - \lambda_1(-\mathcal{L}_0, \mathbb{R}^n)}, & R_0 > 1, \\ 0, & R_0 \le 1. \end{cases}$$

Combining Lemma 2.1 with the above definition, we can directly obtain the following conclusion.

LEMMA 3.14. The following statements about C_0^* hold:

- 1. C_0^* is a strictly monotone increasing function of g'(0).
- 2. C_0^* is a monotone increasing function of r(x).

Since $\lambda_1(-\Delta - r(\infty)) < \lambda_1(-\mathcal{L}_0, \mathbb{R}^n) = \lambda_1(-\Delta - r(x)) < \lambda_1(-\Delta - r(-\infty))$, we can denote $R_0(\pm \infty) := g'(0)e^{r(\pm \infty)}, C_0^*(\infty) := 2\sqrt{\ln g'(0) + r(\infty)}$.

THEOREM 3.15. The following statements hold:

- 1. If $R_0(\infty) < 1$, then $g'(0)e^{-\lambda_1} < 1$ for all c.
- 2. If $R_0(-\infty) < 1$ and $R_0(\infty) > 1$, then $g'(0)e^{-\lambda_1} > 1$ for $c \in (0, C_0^*(\infty))$, and $g'(0)e^{-\lambda_1} < 1$ for $c > C_0^*(\infty)$.
- 3. If $R_0(-\infty) > 1$, then $g'(0)e^{-\lambda_1} > 1$ for $c \in (0, C_0^*(\infty))$, and $g'(0)e^{-\lambda_1} < 1$ for $c > C_0^*(\infty)$.

We omit the proof of Theorem 3.15. Theorem 3.15 shows that the persistence and propagation depend on the speed of the shifting habitat edge c and a number $C_0^*(\infty)$.

Combining the continuous dependence of the solution on the parameters, the uniqueness, and attractiveness of the nontrivial solution, we consider two auxiliary systems

(3.9)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f(\infty, u), & (x, t) \in \Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)), & x \in \Omega, \\ N_{m+1}(x) = u(x, 1), & x \in \Omega, \end{cases}$$

and

(3.10)
$$\begin{cases} u_t = \Delta u + ce \cdot \nabla u + f(-\infty, u), & (x, t) \in \Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)), & x \in \Omega, \\ N_{m+1}(x) = u(x, 1), & x \in \Omega, \end{cases}$$

where $r(x) = f_u(x, u)$ and $r(\pm \infty) = f_u(\pm \infty, u)$, and the so-called x tends to $\pm \infty$, actually referring to $x \cdot e \to \pm \infty$. Similarly to [19], we can define two discrete semiflows $\{Q_{\pm}^m\}_{m\geq 0}$, then the maps $Q_{\pm}: X_+ \to X_+$ admit the following properties:

- 1. $T_y[Q_{\pm}[\phi]] = Q_{\pm}[T_y[\phi]]$ for all $(y, \phi) \in \mathbb{R}^n \times X_+$.
- 2. Q_{\pm} is monotone in the sense that $Q_{\pm}[\phi] \leq Q_{\pm}[\psi]$ for all $\phi, \psi \in X_{+}$ with $\phi \leq \psi$.
- 3. $T_{-y} \circ \hat{Q}^m \circ T_y[\varphi] \to Q^m_-[\varphi] \text{ in } X_+ \text{ as } y \cdot e \to -\infty \text{ and } T_{-y} \circ \hat{Q}^m \circ T_y[\varphi] \to Q^m_+[\varphi]$ in X_+ as $y \cdot e \to \infty$ for all $\varphi \in X_+$ and $m \in \mathbb{N}$.

- 4. $Q_{-}[\phi] \leq \hat{Q}[\phi] \leq Q_{+}[\phi]$ for all $\phi \in X_{+}$. 5. If $g'(0)e^{r(+\infty)} > 1$, $Q_{+} : \mathbb{R}_{+} \to \mathbb{R}_{+}$ has the unique positive fixed point $\beta(\infty)$ in \mathbb{R}_+ , and it is globally attractive. If $q'(0)e^{r(-\infty)} > 1$, $Q_-: \mathbb{R}_+ \to \mathbb{R}_+$ has the unique fixed point $\beta(-\infty)$, and it is globally attractive.

According to conclusions in [17, 19], for each unit direction vector ξ in the habitat, system (3.9) has downstream spreading speed $c^*(\xi; \infty)$ and upstream spreading speed $c^*(-\xi;\infty)$, where

$$c^*(\pm\xi;\infty) = 2\sqrt{r(\infty) + \ln(g'(0))} \mp ce \cdot \xi.$$

If the continuous initial function $u_0(x) = 0$ when $|x \cdot \xi|$ is large enough, and there is some real number L > 0 such that for any constant σ with $0 < \sigma < \beta(\infty), u_0(x) > \sigma$ for all $x \in \mathbb{R}^n$ with $|x \cdot \xi| \leq L$, then the solution u_m of the integral recursion has the following properties:

$$\lim_{m \to \infty} \sup_{x \cdot \xi \in (-\infty, -c_2m] \cup [c_1m, +\infty)} u_m(x) = 0,$$

where $c_1 > c^*(\xi)$ and $c_2 > c^*(-\xi)$, and

$$\lim_{m \to \infty} \sup_{x \cdot \xi \in [-c_2 m, c_1 m]} (\beta(\infty) - u_m(x)) = 0,$$

where $-c^*(-\xi) < -c_2 < c_1 < c^*(\xi)$. In addition, for any $c \ge c^*(\xi)$ there exists a continuous nonincreasing traveling wave solution $W(x \cdot \xi - cm)$ with $W(-\infty) = \beta(\infty)$ and $W(+\infty) = 0$.

In this paper we only consider forced traveling waves, that is, we take $\xi = e$. Thus, $c^*(e) = 2\sqrt{r(\infty)} + \ln(g'(0)) - c = C_0^*(\infty) - c, c^*(e) > 0$, if and only if $c < C_0^*(\infty)$. This is the case from a biological perspective as well. For example, if a population cannot propagate upstream but is washed downstream, it will not persist. By the definition of upstream (e-direction) spreading speed, if an observer moves upstream faster than the upstream spreading speed, the observer sees the uninvaded steady state. On the other hand, if the observer moves upstream slower than the upstream spreading speed, the observer sees the carrying capacity steady state $\beta(\infty)$. We have

$$\lim_{m \to \infty} \sup_{x \cdot e > (c^*(e) + \epsilon)t} u_m(x, 0) = 0$$

and

$$\lim_{m \to \infty} \sup_{0 < x \cdot e < (c^*(e) - \epsilon)t} |u_m(x, 0) - \beta(\infty)| = 0$$

for small enough ϵ , that is $0 < \epsilon < c^*(e)$. Let $x = \tilde{x} - cte$. It is easy to verify that the results in [10] are equivalent to the case when n = 1, e = 1, g(N) = N, c > 0 in our model (1.6), specifically, it means that if $c > C_0^*(\infty)$, then the species will go extinct in the habitat, and that if $c < C_0^*(\infty)$, then the species will persist and spread along the shifting habitat gradient at an asymptotic spreading speed $C_0^*(\infty)$.

4. Numerical simulations. In this section, we present some simulations to support our results and illustrate persistence and extinction of the population. We consider the model (1.6) with n = 1, e = 1, and we take the simplest case f(x, u) =u(r(x) - u), where $r(x) = \frac{2e^x - e^{-x}}{e^x + e^{-x}}$ is monotonically increasing and bounded with respect to x. We truncate the infinite domain \mathbb{R} to finite domain [-l, l], where l = 100

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FIG. 1. A numerical approximation to the graph of $N_m(x)$ for (1.7) with c = 2. Figures (a) and (b) represent the extinction of the population, (c) and (d) represent the persistence of the population, respectively. (a) $g'(0)e^{r(-\infty)} < g'(0)e^{r(+\infty)} < 1$ and $g'(0)e^{-\lambda_1} < 1$, (b) $g'(0)e^{r(-\infty)} < 1$, $g'(0)e^{r(+\infty)} > 1$ and $g'(0)e^{-\lambda_1} < 1$, (c) $g'(0)e^{r(-\infty)} < 1$, $g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} > 1$, (d) $g'(0)e^{r(-\infty)} > 1$, $g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} > 1$.

is sufficiently large, and the initial function

$$f_0(x) = \begin{cases} 0, & -100 \le x \le -5, \\ 0.4 \cos(\frac{\pi x}{10}), & -5 < x < 5, \\ 0, & 5 \le x \le 100. \end{cases}$$

To describe the effect of g'(0) on population persistence, we choose $c = 2, g(N) = kN, N_0(x) = f_0(x)$, and four different values for the parameter k as follows: $k_1 = 0.12, k_2 = 0.36, k_3 = 2$, and $k_4 = 4$. Note that when k < 1, the discrete map g means harvesting with the harvesting percentage 1 - k; when k > 1, the discrete map g means reproduction. From Figure 1, we can see that pulse reproduction (or harvesting) plays an important role in the persistence and extinction of the population. As g'(0) becomes larger, it promotes the survival of the population. In particular, we have that excessive compensation can even keep a certain amount of population in a harsh environment without extinction when the speed of the shifting habitat edge $c < C_0^*(\infty)$. These results provide important insights on the persistence and extinction of animal species.

We want to explore the impact of the shifting speed c on the persistence of the population. We first select g(N) = 2N; except for c we keep the same values of the parameters as in the numerical simulation above. Figures 2(a) and 1(c) have the same



FIG. 2. A numerical approximation to the graph of $N_m(x)$ for (1.7) with g'(0) = 2. Figure (a) represents the persistence of the population and (b) represents the extinction of the population, respectively. (a) $g'(0)e^{r(-\infty)} < 1, g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} > 1$, (b) $g'(0)e^{r(-\infty)} < 1, g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} < 1$.

parameter values, and $C_0^*(\infty) = 3.282$ can be obtained directly by simple calculation. We can observe the impact of shifting speed c on population persistence through Figure 2. Figure 2(a) describes the persistence of species and Figure 2(b) indicates the extinction of species in habitat.

Figures 2(a) and 1(c) have the same parameter values, and $C_0^*(\infty) = 3.282$ can be obtained directly by simple calculation. We can observe the impact of shifting speed c on population persistence through Figure 2. Figure 2(a) describes the persistence of species and Figure 2(b) indicates the extinction of species in habitat.

To verify our conclusion, we take the function g(N) = 4N and keep the other parameters fixed. We can obtain $C_0^*(\infty) = 3.680$. Figure 3(a) describes the persis-

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FIG. 3. A numerical approximation to the graph of $N_m(x)$ for (1.7) with g'(0) = 4. Figure (a) represents the persistence of the population and (b) represents the extinction of the population at any given location. (a) $g'(0)e^{r(-\infty)} > 1$, $g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} > 1$, (b) $g'(0)e^{r(-\infty)} > 1$, $g'(0)e^{r(+\infty)} > 1$, and $g'(0)e^{-\lambda_1} < 1$.

tence of species and Figure 3(b) indicates the extinction of species in habitat. Our results suggest that if climate change is slow, the species survives in the sense that the population persists at some locations, while if climate change is fast, the species goes extinct in the sense that the population cannot persist at any given location.

In order to verify the properties of the positive solution, we use the function g(N) = 4N, c = 2, and keep the other parameters unchanged. Obviously, we have $g'(0)e^{-\lambda_1} = g'(0)e^{-\lambda'_1} > 1$. We have chosen different initial functions $f_1(x) = 0.1$ and $f_2(x) = 1$. Figure 4 describe the persistence of the species. More importantly, our numerical results show that there is only one positive periodic solution for system (1.6) and it is globally attractive for different initial functions.



FIG. 4. A numerical approximation to the graph of $N_m(x)$ for (1.7) with c = 2, g'(0) = 4. Figures (a) and (b) both represent the persistence of species. In addition, Figures (a) and (b) show that although the system begins to evolve from different initial value functions, eventually the same positive periodic solution can be obtained.

In order to verify Corollary 3.13, we use the function g(N) = 4N, c = 9 and keep other parameters unchanged. By explicit formulas for λ_1 and λ'_1 in [36], one can get $e^{\lambda'_1} < g'(0) < e^{\lambda_1}$. We have chosen different initial functions $f_3(x) = 0.5$ and

$$f_4(x) = \begin{cases} 0, & -100 \le x \le -10, \\ 0.4 \cos(\frac{\pi x}{20}), & -10 < x < 10, \\ 0, & 10 \le x \le 100. \end{cases}$$

Figure 5(a) describes the local persistence of the species, and Figure 5(b) shows the weak persistence of the species in the habitat rather than the local persistence, that is, the species is extinct in the sense that it cannot survive for a long time in any given location.

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FIG. 5. A numerical approximation to the graph of $N_m(x)$ for (1.7) with c = 9, g'(0) = 4. Figure (a) represents the persistence of the population and (b) represents the extinction of the population at any given location.

5. Discussion. The climate-driven habitat shifts in spatial ecological models are getting more and more attention; see [7, 8, 9, 10, 11, 12, 13, 14, 31, 32, 33, 34, 35, 37, 39]. It should be mentioned that many species (e.g., fishes or large mammals) give birth only at a particular time of each year, and the reproduction of these species takes place in a very short period of time every year. This paper focuses on the impact of habitat shift driven by climate change on the propagation and persistence of a population with birth pulse. We have presented a class of impulsive reaction-advection-diffusion models, in which the advection term is driven by climate change. Unlike [15, 16, 17, 18, 19], we have used f(x, u) as a heterogeneous type of nonlinearity instead of a homogeneous type. As far as we know, there exist no papers dealing with impulsive PDEs in heterogeneous landscapes. In a bounded domain $\Omega \subset \mathbb{R}^n$, we

have obtained the persistence criterion of the system, which controls the persistence and extinction of the population, and proved the existence, uniqueness, and global attraction of a nontrivial steady state using eigenvalue theory, upper and lower solution methods, and other techniques. Then the persistence criterion has been extended from bounded domains Ω to the whole space \mathbb{R}^n . In addition, we also have indicated that the speed of the shifting habitat edge and impulsive reproduction (or harvesting) rate have important effects on persistence or extinction. The work in this article provides a new framework for the propagation and persistence of animal species under climate change.

Recently, Fang, Lou, and Wu [36] derived explicit formulas for λ_1 and λ'_1 in a one-dimensional environment, for the special case where r'(x) > 0. These formulas are

$$\lambda_1 = -r(\infty) + \frac{c^2}{4}, \quad \lambda_1' = \begin{cases} -r(\infty), & c \le 0, \\ \lambda_1, & c \in \left(0, 2\sqrt{r(\infty) - r(-\infty)}\right), \\ -r(-\infty), & c \ge 2\sqrt{r(\infty) - r(-\infty)}. \end{cases}$$

Moreover, when $r(\infty) > 0 > r(-\infty)$ and $c = 2\sqrt{r(\infty)}$, we have $\lambda'_1 = \lambda_1 = 0$. If c is large enough, we obtain a set of seemingly contradictory results, that is, $g'(0)e^{-\lambda_1} < 1$ but $g'(0)e^{-\lambda'_1} > 1$. To explain this phenomenon, we introduce different definitions of persistence. On an unbounded domain, it is much more practical to formulate this persistence condition in terms of upstream and downstream spreading speeds. Namely, a population persists if its spreading speeds in both directions are positive (also see [22]). Distinguishing weak persistence from local persistence can help understand the biological interpretations represented by persistence thresholds under different eigenvalue definitions, more specifically, the formula $q'(0)e^{-\lambda'_1} > 1$ describes that the population satisfies weak persistence, while the formula $q'(0)e^{-\lambda_1} < 1$ describes that the population does not satisfy local persistence, that is, the grounding phenomenon occurs (see [38]). In [37], the authors proved that there are minimum and maximum forcing waves within the appropriate parameter range, denoted by u_{\min} and $u_{\rm max}$, respectively. Considering the heteroclinic solution in the motion frame, they constructed two heteroclinic orbits connecting zero to these two special forcing waves. However, our result implies that there is a unique heteroclinic orbit Γ in system (1.4), where $\Gamma(-\infty) = \beta(-\infty)$ and $\Gamma(+\infty) = \beta(\infty)$. In addition, our numerical simulations illustrate that weak persistence can give rise to a population whose density is increasing but is being washed out because it cannot stay at any given location. It is reasonable to believe that a species that persists only weakly is at risk of being washed out of the system when the habitat fragmentation occurs.

Most studies on impulsive reaction-diffusion models focus on single species. It would be intriguing and challenging to derive and analyze multispecies models in this direction. For successful mating, the population density needs to be greater than some threshold value, which is called the Allee effect. It is increasingly recognized that considering the Allee effect has theoretical and practical significance in the study of population dynamics. Considering an impulsive reproduction function with a bistable structure (Allee effect) will lead to complex dynamics. Another interesting question is whether there is an equivalent result of the ideal free distribution for impulsive PDEs in heterogeneous habitats. We leave these questions for future investigation.

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