

## ON IMPULSIVE REACTION-DIFFUSION MODELS IN HIGHER DIMENSIONS\*

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**Abstract.** We formulate a general impulsive reaction-diffusion equation model to describe the population dynamics of species with distinct reproductive and dispersal stages. The seasonal reproduction is modeled by a discrete-time map, while the dispersal is modeled by a reaction-diffusion partial differential equation. Study of this model requires a simultaneous analysis of the differential equation and the recurrence relation. When boundary conditions are hostile we provide critical domain results showing how extinction versus persistence of the species arises, depending on the size and geometry of the domain. We show that there exists an *extreme volume size* such that if  $|\Omega|$  falls below this size the species is driven extinct, regardless of the geometry of the domain. To construct such extreme volume sizes and critical domain sizes, we apply Schwarz symmetrization rearrangement arguments, the classical Rayleigh–Faber–Krahn inequality, and the spectrum of uniformly elliptic operators. The critical domain results provide qualitative insight regarding long-term dynamics for the model. Last, we provide applications of our main results to certain biological reaction-diffusion models regarding marine reserve, terrestrial reserve, insect pest outbreak, and population subject to climate change.

**Key words.** reaction-diffusion models, persistence versus extinction of species, eigenvalue problems for differential operators, rearrangement arguments, population dynamics

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

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**1. Introduction.** Impulsive reaction-diffusion equation models for species with distinct reproductive and dispersal stages were proposed by Lewis and Li in [24]. These models can be considered to be 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. The population of a species at the beginning of year  $m$  is denoted by  $N_m(x)$ . We assume that reproduction (or harvesting) occurs at the beginning of the year, via a discrete time map,  $g$ , after which there is birth, mortality, and dispersal via a reaction-diffusion for a population with density  $u^{(m)}(x, t)$ . At the end of this year the density  $u^{(m)}(x, 1)$  provides the population density for the start of year  $m + 1$ ,  $N_{m+1}(x)$ . We examine solutions of the following system for any  $m \in \mathbb{Z}^+$ :

$$(1.1) \quad \begin{cases} u_t^{(m)} = \operatorname{div}(A\nabla u^{(m)} - au^{(m)}) + f(u^{(m)}) & \text{for } (x, t) \in \Omega \times (0, 1], \\ u^{(m)}(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u^{(m)}(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u^{(m)}(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where  $\Omega$  is a set in  $\mathbb{R}^n$ ,  $A$  is a constant symmetric positive definite matrix, and  $a$  is a constant vector. We assume that the function  $g$  satisfies the following assumptions:

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- (G0)  $g$  is a continuous positive function in  $\mathbb{R}^+$  and  $g(0) = 0 < g'(0)$  and there exists a positive constant  $M \in (0, \infty]$  such that  $g(N)$  is nondecreasing for  $0 < N \leq M$ . In other words, monotonicity of  $g$  is required only on a subset of  $\mathbb{R}^+$ .
- (G1) There exists a positive constant  $\bar{M} \leq M$  such that  $g(N) \leq g'(0)N$  for  $0 < N < \bar{M}$ .
- (G2) There exists a differentiable function  $h$  for  $h(0) = h'(0) = 0$  and a constant  $\bar{M} \leq M$  so that  $g(N) \geq g'(0)N - h(N)$  for  $0 < N < \bar{M}$ .

Note that the linear function

$$(1.2) \quad g(N) = bN,$$

where  $b$  is a positive constant, satisfies all of the above assumptions. For the above  $g$  when  $b = 1$  and  $f(N) = N(1 - N)$ , model (1.1) recovers the classical Fisher's equation introduced by Fisher in [14] and Kolmogorov, Petrowsky, and Piscounoff (KPP) in [21] in 1937. One can consider nonlinear functions for  $g$  such as the Ricker function, that is

$$(1.3) \quad g(N) = Ne^{r(1-N)},$$

where  $r$  is a positive constant. For the optimal stocking rates for fisheries mathematical biologists often apply the Ricker model [37] introduced in 1954 to study salmon populations with scramble competition for spawning sites leading to overcompensatory dynamics. The Ricker function is nondecreasing for  $0 < N \leq M = \frac{1}{r}$  and satisfies all of the assumptions. Note also that the Beverton–Holt function

$$(1.4) \quad g(N) = \frac{(1 + \lambda)N}{1 + \lambda N}$$

for positive constant  $\lambda$  is an increasing function. The Beverton–Holt model was introduced to understand the dynamics of compensatory competition in fisheries by Beverton and Holt [4] in 1957. Another example is the Skellam function

$$(1.5) \quad g(N) = R(1 - e^{-bN}),$$

where  $R$  and  $b$  are positive constants. This function was introduced by Skellam in 1951 in [39] to study population density for animals, such as birds, which have contest competition for nesting sites that leads to compensatory competition dynamics. Note that the Skellam function behaves similarly to the Beverton–Holt function and it is nondecreasing for any  $N > 0$ . We shall use these functions in the application section (section 3). We refer interested readers to [41] for more functional forms with biological applications. We now provide some assumptions on the function  $f$ . We suppose the following:

- (F0)  $f(\cdot)$  is a continuous function and  $f(0) = 0$ . We also assume that  $f'(0) \neq 0$ .
- (F1) There exists a differentiable function  $h$  for  $h(0) = h'(0) = 0$  so that

$$f'(0)N - h(N) \leq f(N) \leq f'(0)N \quad \text{for } N \in \mathbb{R}^+.$$

Note that we do not have any assumption on the sign of  $f(\cdot)$  and  $f'(0)$ . Note that  $f(N) = N(1 - N)$ ,  $f(N) = bN$  for  $b \in \mathbb{R}$ , and  $f(N) = \alpha N - \beta N^2$  for  $\alpha \in \mathbb{R}$  and  $\beta \in \mathbb{R}^+$  satisfy the above assumptions (F0) and (F1).

Suppose that  $a = 0$  and  $A = 0$ ; then  $u(x, t)$  only depends on time and not space, meaning that individuals do not advect or diffuse. Assume that  $N_m$  represents the number of individuals at the beginning of the reproductive stage in the  $m$ th year. Then

$$(1.6) \quad \begin{cases} u_t(t) = f(u(t)) & \text{for } t \in (0, 1], \\ u(0) = g(N_m), \\ N_{m+1} := u(1). \end{cases}$$

Separation of variables shows that

$$(1.7) \quad \int_{g(N_m)}^{N_{m+1}} \frac{d\omega}{f(\omega)} = 1.$$

Note that a positive constant equilibrium of (1.6) satisfies

$$(1.8) \quad \int_{g(N)}^N \frac{d\omega}{f(\omega)} = 1.$$

Assume that  $f$  satisfies (F0)–(F1) and  $g$  satisfies (G0)–(G2); then

$$(1.9) \quad 1 = \int_{g(N)}^N \frac{d\omega}{f(\omega)} \geq \frac{1}{f'(0)} \int_{g(N)}^N \frac{d\omega}{\omega} = \frac{1}{f'(0)} \ln \left| \frac{N}{g(N)} \right| \geq \frac{1}{f'(0)} \ln \left| \frac{1}{g'(0)} \right|.$$

In light of the above computations, we assume that

$$(1.10) \quad e^{f'(0)} g'(0) > 1,$$

and an  $N^* > 0$  exists such that  $f \neq 0$  on the closed interval with endpoints  $N^*$  and  $g(N^*)$  and

$$(1.11) \quad \int_{g(N^*)}^{N^*} \frac{d\omega}{f(\omega)} = 1.$$

We also assume that  $g$  is nondecreasing on  $[0, N^*]$ ; that is equivalent to considering  $M := N^*$  in the assumption (G0). Note that for the case of equality in (1.9) there might only be the zero equilibrium; for examples, see (3.2) and (3.18) in the application section (section 3).

Equation (1.1) defines a recurrence relation for  $N_m(x)$  as

$$(1.12) \quad N_{m+1}(x) = Q[N_m(x)] \quad \text{for } x \in \Omega \subset \mathbb{R}^n,$$

where  $m \geq 0$  and  $Q$  is an operator that depends on  $A, a, f, g$ . While most of the results provided in this paper are valid in any dimensions, we shall focus on the case of  $n \leq 3$  for applications. For notational convenience we drop superscript ( $m$ ) for  $u^{(m)}(x, t)$ , rewriting it as  $u(x, t)$ . The remarkable point about the impulsive reaction-diffusion equation (1.1)–(1.12) is that it is a mixture of a differential equation and a recurrence relation. Therefore, one may expect that the analysis of this model requires a simultaneous analysis of the continuous and discrete type. If the yearlong activities are modeled by impulsive dynamical systems, models of the form (1.1) have a longer history and have been given various names: discrete time metered models [9], sequential-continuous models [6], and semidiscrete models [38]. We refer interested readers to [40] for more information.

In this paper, we provide critical domain size for extinction versus persistence of populations for impulsive reaction-diffusion models of the form (1.1) defined on domain  $\Omega \subset \mathbb{R}^n$ . It is known that the geometry of the domain has fundamental impacts on qualitative behavior of solutions of equations in higher dimensions. We consider domains with various geometric structures in dimensions  $n \geq 1$  including convex and concave domains and also domains with smooth and nonsmooth boundaries.

The discrete time models of the form (1.12) are studied extensively in the literature, in particular in the foundational work of Weinberger [45], where  $N_m(x)$  represents the gene fraction or population density at time  $n$  at the point  $x$  of the habitat and  $Q$  is an operator on a certain set of functions on the habitat. It is shown by Weinberger [45] that under a few biologically reasonable hypotheses on the operator  $Q$ , results similar to those for the Fisher and KPP types for models (1.12) hold. In other words, given a direction vector  $e$ , the recurrence relation (1.12) admits a non-increasing planar traveling wave solution for every  $c \geq c^*(e)$  and, more importantly, there will be a spreading speed  $c^*(e)$  in the sense that a new mutant or population which is initially confined to a bounded set spreads asymptotically at speed  $c^*(e)$  in direction  $e$ . This falls under the general Weinberger type given in (1.12).

Note that for the standard Fisher's equation with the drift in one dimension, that is,

$$(1.13) \quad u_t = du_{xx} - au_x + f(u) \quad \text{for } (x, t) \in \Omega \times \mathbb{R}^+,$$

the critical domain size for the persistence versus extinction is

$$(1.14) \quad L^* := \frac{2\pi d}{\sqrt{4df'(0) - a^2}}$$

when  $\Omega = (0, L)$  and the speeds of propagation to the right and left are

$$(1.15) \quad c_{\pm}^*(a) = 2\sqrt{df'(0)} \pm a$$

when  $\Omega = \mathbb{R}$ . For more information regarding the minimal domain size, we refer interested readers to Lewis, Hillen, and Lutscher [23], Murray and Sperb [33], Pachepsky et al. [34], Speirs and Gurney [42], and references therein. The remarkable point is that  $c_{\pm}^*(a)$  is a linear function of  $a$  and  $L^*$  as a function of  $a$  blows up to infinity exactly at roots of  $c_{\pm}^*(a)$ . For more information on analysis of reaction-diffusion models and on strong connections between persistence criteria and propagation speeds, we refer interested readers to [10, 23, 31, 32, 34] and references therein.

**NOTATION 1.1.** *Throughout this paper the matrix  $I = (\delta_{i,j})_{i,j=1}^n$  stands for the identity matrix, the matrix  $A$  is defined as  $A = (a_{i,j})_{i,j=1}^n$ , and the vector  $a$  is  $a = (a_i)_n$ . The matrix  $A$  and the vector  $a$  have constant components unless otherwise stated. We shall refer to vector fields  $a$  with  $\operatorname{div} a = 0$  as divergence free vector fields. The notation  $j_{m,1}$  stands for the first positive zero of the Bessel function  $J_m$  for any  $m \geq 0$  and  $\Gamma$  refers to the Gamma function.*

The organization of the paper is as follows. We investigate how the geometry and size of the domain  $\Omega$  affect persistence versus extinction of the species. We consider various types of domain, including an  $n$ -hyperrectangle, a ball of radius  $R$ , and a general domain with smooth boundary, to construct critical domain sizes and extreme volume size (section 2). We then provide applications of the main results to models for marine reserve, terrestrial reserve, insect pest outbreaks, and populations subject to climate change (section 3). At the end, we provide proofs for our main results and discussions.

**2. Geometry of the domain for persistence versus extinction.** A habitat boundary not only can be considered as a natural consequence of physical features such as rivers, roads, or (for aquatic systems) shorelines but also it can come from interfaces between different types of ecological habitats such as forests and grasslands. Boundaries can induce various effects in population dynamics. They can affect movement patterns, act as a source of mortality or resource subsidy, or function as a unique environment with its own set of rules for population interactions. See Fagan, Cantrell, and Cosner [11] for further discussion. Note that a boundary can have different effects on different species. For example, a road may act as a barrier for some species but as a source of mortality for others. Since a boundary can have different effects on different species, the presence of a boundary can influence community structure in ways that are not completely obvious from the ways in which they affect each species; see Cantrell and Cosner [7, 8] for more information.

In this section, we consider the following impulsive reaction-diffusion model on domains with hostile boundaries to explore persistence versus extinction

$$(2.1) \quad \begin{cases} u_t = \operatorname{div}(A\nabla u - au) + f(u) & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where  $\Omega$  is a bounded domain in  $\mathbb{R}^n$ ,  $a$  is a vector in  $\mathbb{R}^n$ , and  $A$  is a constant positive definite symmetric matrix.

In what follows we provide critical domain sizes for various domains depending on the geometry of the domain. We shall postpone the proofs of these theorems to the end of this section. We start with the critical domain size for a  $n$ -hyperrectangle ( $n$ -orthotope).

**THEOREM 2.1.** *Assume that  $\Omega = [0, L_1] \times \cdots \times [0, L_n]$ , where  $L_1, \dots, L_n$  are positive constants,  $A = d(\delta_{i,j})_{i,j=1}^n$ , and the advection  $a$  is a constant vector field in  $\mathbb{R}^n$ . Suppose also that  $f$  satisfies (F0)–(F1),  $g$  satisfies (G0)–(G2), and (1.10) holds. Then, critical domain dimensions  $L_1^*, \dots, L_n^*$  satisfy*

$$(2.2) \quad \sum_{i=1}^n \frac{1}{[L_i^*]^2} = \frac{1}{d\pi^2} \left[ \ln(e^{f'(0)}g'(0)) - \frac{|a|^2}{4d} \right],$$

where  $\ln(e^{f'(0)}g'(0)) > \frac{|a|^2}{4d}$ . More precisely, when

$$(2.3) \quad \sum_{i=1}^n \frac{1}{[L_i]^2} > \frac{1}{d\pi^2} \left[ \ln(e^{f'(0)}g'(0)) - \frac{|a|^2}{4d} \right],$$

and  $g$  satisfies (G0)–(G1), then  $N_m(x)$  decays to zero, that is,  $\lim_{m \rightarrow \infty} N_m(x) = 0$ , and when

$$(2.4) \quad \sum_{i=1}^n \frac{1}{[L_i]^2} < \frac{1}{d\pi^2} \left[ \ln(e^{f'(0)}g'(0)) - \frac{|a|^2}{4d} \right],$$

and  $g$  satisfies (G0)–(G2), then  $\liminf_{m \rightarrow \infty} N_m(x) \geq \bar{N}(x)$ , where  $\bar{N}(x)$  is a positive equilibrium. In addition, critical domain dimensions can be arbitrarily large when  $\ln(e^{f'(0)}g'(0)) < \frac{|a|^2}{4d}$ .

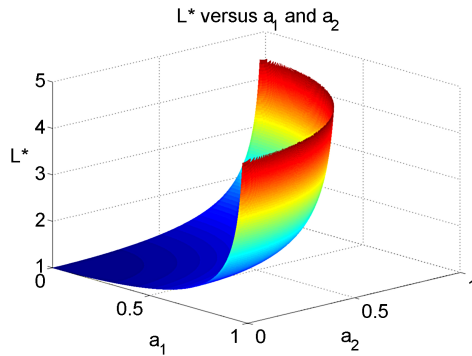


FIG. 1. Critical domain dimension  $L^*$  as a function of  $a = (a_1, a_2)$ .

Suppose that the domain  $\Omega$  is an  $n$ -hypercube. Then the critical domain size is explicitly given by the following corollary.

COROLLARY 2.1. *Suppose that assumptions of Theorem 2.1 hold. In addition, let  $L_1 = \dots = L_n = L > 0$ . Then the critical domain dimension is*

$$(2.5) \quad L^* := \begin{cases} 2\pi d \sqrt{\frac{n}{4d[f'(0) + \ln(g'(0))] - |a|^2}} & \text{if } 4d[f'(0) + \ln(g'(0))] - |a|^2 > 0, \\ \infty & \text{if } 4d[f'(0) + \ln(g'(0))] - |a|^2 < 0. \end{cases}$$

The above results are shown in Figure 1 to clarify the relationship between the critical domain dimension and the advection in two dimensions,  $n = 2$ .

Note that for the case  $n = 1$  and  $a = 0$ , the minimal domain size  $L^*$  was given by Lewis and Li in [24]. In addition, one can compare the critical domain dimension (2.5) for the impulsive reaction-diffusion model (1.1) in higher dimensions to the one given by (1.14) for the classical Fisher’s equation in one dimension. We now provide a similar result for a critical domain radius when the domain is a ball of radius  $R$ . In Theorems 2.2 and 2.3, we let the drift  $a$  be a divergence free vector field that is  $\text{div } a = 0$ .

THEOREM 2.2. *Suppose that  $\Omega = B_R$ , where  $B_R$  is the ball of radius  $R$  and centered at zero,  $A = d(\delta_{i,j})_{i,j=1}^m$ , and the drift  $a$  is a divergence free vector field that is not necessarily constant vector field. Suppose also that  $f$  satisfies (F0)–(F1),  $g$  satisfies (G0)–(G2), and (1.10) holds. Then the critical domain radius is*

$$(2.6) \quad R^* := j_{n/2-1,1} \sqrt{\frac{d}{\ln(g'(0)) + f'(0)}}$$

in the sense that if  $R < R^*$  and  $g$  satisfies (G0)–(G1), then  $\lim_{m \rightarrow \infty} N_m(x) = 0$ , and if  $R > R^*$  and if  $g$  satisfies (G0)–(G2), then  $\liminf_{m \rightarrow \infty} N_m(x) \geq \bar{N}(x)$ , where  $\bar{N}(x)$  is a positive equilibrium.

Theorem 2.2 is a generalized version of the standard island case (two-dimensional space) for discussing the persistence and extinction of a species.

From now on we consider a more general domain  $\Omega \subset \mathbb{R}^n$  with a smooth boundary. Our main goal is to provide sufficient conditions on the volume and on the geometry of the domain  $\Omega$  for the extinction of populations. To be able to work with general domains we borrow Schwarz symmetrization rearrangement arguments

from mathematical analysis. In what follows, we introduce this symmetrization argument and then we apply it to eigenvalue problems associated to (1.1). We refer interested readers to the lecture notes of Burchard [5] and references therein for more information.

Let  $\Omega$  be a measurable set of finite volume in  $\mathbb{R}^n$ . Its symmetric rearrangement  $\Omega^*$  is the following ball centered at zero whose volume agrees with  $\Omega$ :

$$(2.7) \quad \Omega^* := \{x \in \mathbb{R}^n; \alpha_n |x|^n < |\Omega|\}.$$

For any function  $\phi \in L^1(\Omega)$ , define the distribution function of  $\phi$  as

$$(2.8) \quad \mu_\phi(t) := |\{x \in \Omega; \phi(x) > t\}|$$

for all  $t \in \mathbb{R}$ . The function  $\mu_\phi$  is right-continuous and nonincreasing and as  $t \rightarrow \infty$  we have  $\mu_\phi \rightarrow 0$ . Similarly, as  $t \rightarrow -\infty$  we have  $\mu_\phi \rightarrow |\Omega|$ . Now for any  $x \in \Omega^* \setminus \{0\}$  define

$$(2.9) \quad \phi^*(x) := \sup\{t \in \mathbb{R}, \mu_\phi(t) \geq \alpha_n |x|^n\}.$$

The function  $\phi^*$  is clearly radially symmetric and nonincreasing in the variable  $|x|$ . By construction,  $\phi^*$  is equimeasurable with  $\phi$ . In other words, corresponding level sets of the two functions have the same volume,

$$(2.10) \quad \mu_\phi(t) = \mu_{\phi^*}(t),$$

for all  $t \in \mathbb{R}$ . An essential property of the Schwarz symmetrization is the following: if  $\phi \in H_0^1(\Omega)$ , then  $|\phi|^* \in H_0^1(\Omega^*)$  and

$$(2.11) \quad \|\phi^*\|_{L^2(\Omega^*)} = \|\phi\|_{L^2(\Omega)}$$

and

$$(2.12) \quad \|\nabla|\phi|^*\|_{L^2(\Omega^*)} = \|\nabla\phi\|_{L^2(\Omega)}.$$

One of the main applications of this rearrangement technique is the resolution of optimization problems for the eigenvalues of some second-order elliptic operators on  $\Omega$ . Let  $\lambda_1(\Omega)$  denote the first eigenvalue of the Laplace operator  $-\Delta$  with Dirichlet boundary conditions in an open bounded smooth set  $\Omega \subset \mathbb{R}^n$  that is given by the Rayleigh–Ritz formula

$$(2.13) \quad \lambda_1(\Omega) = \inf_{\|\phi\|_{L^2(\Omega)}=1} \|\nabla\phi\|_{L^2(\Omega)}^2.$$

It is well-known that  $\lambda_1(\Omega) \geq \lambda_1(\Omega^*)$  and that the inequality is strict unless  $\Omega$  is a ball. We refer interested readers to [13, 22] and references therein. Since  $\lambda_1(\Omega^*)$  can be explicitly computed, this result provides the classical Rayleigh–Faber–Krahn inequality, which states that

$$(2.14) \quad \lambda_1(\Omega) \geq \lambda_1(\Omega^*) = \left(\frac{|B_1|}{|\Omega|}\right)^{2/n} j_{n/2-1,1}^2,$$

where  $j_{m,1}$  is the first positive zero of the Bessel function  $J_m$ . More recently, Hamel, Nadirashvili, and Russ in [16] provided an extension of the above result to the operator

$$(2.15) \quad -\operatorname{div}(A\nabla) + a \cdot \nabla + V$$

with Dirichlet boundary conditions where the symmetric matrix field  $A$  is in  $W^{1,1}(\Omega)$ , the vector field (drift)  $a : L^1(\Omega) \rightarrow \mathbb{R}^n$  and potential  $V$  that is a continuous function in  $\bar{\Omega}$ . Throughout this paper, we call a matrix  $A$  *uniformly elliptic* on  $\bar{\Omega}$  whenever there exists a positive constant  $d$  such that for all  $x \in \bar{\Omega}$  and for all  $\zeta \in \mathbb{R}^n$ ,

$$(2.16) \quad A(x)\zeta \cdot \zeta \geq d|\zeta|^2.$$

Consider the following eigenvalue problem:

$$(2.17) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi = \lambda(A, a, \Omega)\phi & \text{in } \Omega, \\ u = 0 & \text{on } \partial\Omega; \end{cases}$$

when  $\Omega \in C^{2,\alpha}$  for some  $0 < \alpha < 1$ , the matrix  $A$  is uniformly elliptic and  $a : L^\infty(\Omega) \rightarrow \mathbb{R}^n$ , where  $\|a\|_\infty \leq \tau$  for  $\tau \geq 0$ . It is shown in [16] that the first eigenvalue of (2.17) admits the following lower bound:

$$(2.18) \quad \lambda_1(A, a, \Omega) \geq \lambda_1(d(\delta_{i,j}), \tau e_r, \Omega^*).$$

Here  $\Omega^* = B_R$  is the ball of radius

$$(2.19) \quad R = \left( \frac{|\Omega|}{\alpha_n} \right)^{1/n}$$

for  $\alpha_n := |B_1| = \frac{\pi^{n/2}}{\Gamma(1+\frac{n}{2})}$ . In addition, equality in (2.18) holds only when, up to translation,  $\Omega = \Omega^*$  and  $a = \tau e_r$  for  $e_r = \frac{x}{|x|}$ .

We are now ready to develop sufficient conditions for the extinction of population on various geometric domains. The remarkable point here is that the volume of the domain  $\Omega$  is the key point for the extinction rather than the other aspects of the domain. The following theorems imply that for some general domain  $\Omega$  there is an extreme volume size,  $V_{ex}$ , such that when  $|\Omega| < V_{ex}$  extinction must occur for the population living in the habitat. The following theorem provides an explicit formula for such an extreme volume size for any open bounded domain with a smooth boundary.

**THEOREM 2.3.** *Let  $A$  be uniformly elliptic,  $f$  satisfy (F0)–(F1),  $g$  satisfy (G0)–(G2), and (1.10) hold. Suppose that the vector field  $a$  is divergence free and  $\Omega \subset \mathbb{R}^n$  is an open bounded domain with smooth boundary. Then  $\lim_{m \rightarrow \infty} N_m(x) = 0$  for any  $x \in \Omega$  when  $|\Omega| < V_{ex}$  for*

$$(2.20) \quad V_{ex} := \frac{1}{\Gamma(1 + \frac{n}{2})} \left( \frac{d\pi j_{\frac{n}{2}-1,1}^2}{f'(0) + \ln(g'(0))} \right)^{\frac{n}{2}},$$

and  $j_{k,1}$  stands for the first positive root of the Bessel function  $J_k$ .

Theorem 2.3 states that the addition of incompressible flow to the impulse reaction-diffusion problem can only make the critical domain size larger but never smaller. Note that the above theorem, unlike Theorems 2.2 and 2.1, only deals with the extinction and not the persistence of species. This is due to the fact that, in our proofs, we apply the well-known Rayleigh–Faber–Krahn inequality (see (2.14)) and rearrangement arguments to estimate the first eigenvalue of elliptic operators. Unfortunately, these estimates are sharp only for the radial domains, that is, when  $\Omega = B_R$ . Note also that for the  $n$ -hyperrectangle, eigenvalues of elliptic operators are explicitly



known. In short, due to a lack of mathematical techniques, we provide criteria for the extinction of species and proving persistence under the assumption  $|\Omega| \geq V_{ex}$  seems to be more challenging and remains open.

**COROLLARY 2.2.** *In two dimensions, it is known that  $j_{\frac{n}{2}-1,1} = j_{0,1} \approx 2.408$ . Therefore the extreme volume size is*

$$(2.21) \quad V_{ex} = \frac{d\pi j_{0,1}^2}{f'(0) + \ln(g'(0))}.$$

**COROLLARY 2.3.** *In three dimensions,  $j_{\frac{n}{2}-1,1} = j_{1/2,1} = \pi$  and  $\Gamma(1+\frac{n}{2}) = \Gamma(\frac{5}{2}) = \frac{3\sqrt{\pi}}{4}$ . Therefore,*

$$(2.22) \quad V_{ex} = \frac{4\pi^4 d}{3} \sqrt{\frac{d}{[f'(0) + \ln(g'(0))]^3}}.$$

The fact that a hyperrectangle (or  $n$ -orthotope) does not have a smooth boundary implies that Theorem 2.3 is not applied to these types of geometric shapes. In what follows, we provide an extreme volume size result for a hyperrectangle in light of Theorem 2.1.

**THEOREM 2.4.** *Suppose that  $\Omega = [0, L_1] \times \cdots \times [0, L_n]$  and  $A = d(\delta_{i,j})_{i,j=1}^n$  where  $L_1, \dots, L_n$  and  $d$  are positive constants and  $a$  is a constant vector field. Assume that  $f$  satisfies (F0)–(F1) and  $g$  satisfies (G0)–(G2) and (1.10) holds. If  $|\Omega| \leq V_{ex}$  for*

$$(2.23) \quad V_{ex} := \begin{cases} \left( \frac{4d^2\pi^2 n}{4d[f'(0) + \ln(g'(0))] - |a|^2} \right)^{n/2} & \text{if } 4d[f'(0) + \ln(g'(0))] > |a|^2, \\ \infty, & \text{if } 4d[f'(0) + \ln(g'(0))] < |a|^2. \end{cases}$$

Then  $\lim_{m \rightarrow \infty} N_m(x) = 0$  for any  $x \in \Omega$ .

We shall end this section by briefly explaining the divergence free concept that appeared in Theorems 2.2 and 2.3. The assumption  $\operatorname{div} a = 0$  implies that the flow field is incompressible. This would be the case, for example, for water, but not for air. It also means that the integral

$$(2.24) \quad \int_{\partial\Gamma} a \cdot n \, dS = 0$$

vanishes by the divergence theorem. Here  $\Gamma$  is a smooth subset of the domain  $\Omega$  (possibly nonproper), and  $n$  is the outwardly oriented unit normal vector. The integral quantity is interpreted as the total flow out of  $\Gamma$ . This implies that the addition of incompressible flow to the problem cannot make the critical volume size any smaller, although it could make it larger. Indeed, even in the simple case of one dimension an incompressible flow term of the form  $a \equiv C$ , where  $C$  is a constant, can drive the critical domain size to infinity.

**3. Applications.** In this section, we provide applications of main theorems given in the past sections.

**3.1. Marine reserve.** A marine reserve is a marine area protected against fishing and harvesting. Marine reserves could increase species diversity, biomass, and fishery production, etc., within reserve areas (Lockwood, Hastings, and Botsford [28]).

We use our model here to show the dependence of the critical domain size on the advection flow speed and the mortality rate. Consider the model

$$(3.1) \quad \begin{cases} u_t = \operatorname{div}(d\nabla u - au) - \gamma u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where  $\gamma$  is the natural mortality rate, and  $g$  is either the Beverton–Holt function  $g(N_m) = \frac{(1+\lambda)N_m}{1+\lambda N_m}$  or the Ricker function  $g(N_m) = N_m e^{r(1-N_m)}$  for  $r, \lambda > 0$ . The assumption (1.10) is equivalent to  $\ln(1 + \lambda) > \gamma$  or  $r > \gamma$  for the Beverton–Holt or Ricker functions, respectively. Note that the positive equilibrium  $N^*$  exists for the Beverton–Holt and Ricker functions and they are of the form

$$(3.2) \quad N^* := \frac{1}{\lambda} [e^{-\gamma}(1 + \lambda) - 1] \quad \text{and} \quad N^* := \frac{r - \gamma}{r},$$

respectively. Note also that the Ricker function is nondecreasing in  $[0, N^*]$  when  $r \leq \gamma + 1$  and the Beverton–Holt function is increasing on the entire  $\mathbb{R}^+$ . We now provide the critical dimension size regarding extinction versus persistence for various geometric shapes.

*Case 1.* Consider the domain  $\Omega = [0, L] \times [0, L]$  in two dimensions. Then Theorem 2.1 implies that the critical dimension for the Beverton–Holt function is

$$(3.3) \quad L^*(a) = \frac{\pi\sqrt{2d}}{\sqrt{\ln(1 + \lambda) - \gamma - \frac{|a|^2}{4d}}}$$

when  $\ln(1 + \lambda) > \gamma + \frac{|a|^2}{4d}$  and  $L^*(a)$  can be arbitrarily large when  $\gamma < \ln(1 + \lambda) < \gamma + \frac{|a|^2}{4d}$ . Similarly, for the Ricker function the critical dimension is

$$(3.4) \quad L^*(a) = \frac{\pi\sqrt{2d}}{\sqrt{r - \gamma - \frac{|a|^2}{4d}}}$$

when  $\gamma + 1 \geq r > \gamma + \frac{|a|^2}{4d}$  and  $L^*(a)$  can be arbitrarily large when  $r - \gamma$  is close to  $\frac{|a|^2}{4d}$ . In other words, when  $L < L^*(a)$  the functional sequence  $N_m(x)$  satisfies  $\lim_{m \rightarrow \infty} N_m(x) = 0$  that refers to extinction and when  $L > L^*(a)$  we have the persistence that is  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for the positive equilibrium  $\bar{N}(x)$ .

*Case 2.* Consider the domain  $\Omega = B_R$ , where  $B_R$  is a disk in two dimensions with radius  $R$  and  $a$  is a divergence free vector field. Theorem 2.2 implies that the critical value dimension for the Beverton–Holt function is

$$(3.5) \quad R^*(\gamma) = j_{0,1} \sqrt{\frac{d}{\ln(1 + \lambda) - \gamma}},$$

and for the Ricker function the critical dimension is

$$(3.6) \quad R^*(\gamma) = j_{0,1} \sqrt{\frac{d}{r - \gamma}},$$

where  $j_{0,1} \approx 2.408$  is the first positive root of the Bessel function  $J_0$ . In other words, for subcritical radius, that is, when  $R < R^*(\gamma)$ , we have  $\lim_{m \rightarrow \infty} N_m(x) = 0$ , and for supercritical radius, that is, when  $R > R^*(\gamma)$ , we have  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for some positive equilibrium  $\bar{N}(x)$ .

*Case 3.* Consider a general domain  $\Omega$  in two dimensions with smooth boundary and area  $|\Omega|$ . In addition, let  $a$  be a divergence free vector field that is  $\operatorname{div} a = 0$ . We now apply Theorem 2.3 to find the extreme mortality parameter

$$(3.7) \quad \gamma_{ex} := \frac{dj_{0,1}^2}{|\Omega|} - \ln(1 + \lambda),$$

which implies that extinction occurs for  $\gamma < \gamma_{ex}$  and the Beverton–Holt function. Similarly for the Ricker function the extreme mortality parameter  $h$  is given by

$$(3.8) \quad \gamma_{ex} := \frac{dj_{0,1}^2}{|\Omega|} - r.$$

Note that our main results regarding the critical domain size and the extreme volume size (section 2) are valid in three dimensions as well.

*Case 4.* Consider the domain  $\Omega = [0, L] \times [0, L] \times [0, L]$  in three dimensions. The corresponding formulae to (3.3) and (3.4) are

$$(3.9) \quad L^*(a) = \frac{\pi\sqrt{3d}}{\sqrt{\ln(1 + \lambda) - \gamma - \frac{|a|^2}{4d}}} \quad \text{and} \quad L^*(a) = \frac{\pi\sqrt{3d}}{\sqrt{r - \gamma - \frac{|a|^2}{4d}}}$$

for the Beverton–Holt and Ricker functions, respectively, under the same assumptions on the parameters. We now suppose that  $\Omega = B_R$  when  $B_R$  is a disk in three dimensions with radius  $R$  and  $a$  is a divergence free vector field. The corresponding formulae to (3.5) and (3.6) are

$$(3.10) \quad R^*(\gamma) = \pi\sqrt{\frac{d}{\ln(1 + \lambda) - \gamma}} \quad \text{and} \quad R^*(\gamma) = \pi\sqrt{\frac{d}{r - \gamma}}$$

for the Beverton–Holt and Ricker functions, respectively. Last, we consider a general domain  $\Omega$  in three dimensions with smooth boundary and area  $|\Omega|$ . The corresponding extreme mortality parameters to (3.7) and (3.8) are

$$(3.11) \quad \gamma_{ex} := d \left( \frac{4\pi^4}{3|\Omega|} \right)^{\frac{2}{3}} - \ln(1 + \lambda) \quad \text{and} \quad \gamma_{ex} := d \left( \frac{4\pi^4}{3|\Omega|} \right)^{\frac{2}{3}} - r$$

for the Beverton–Holt and Ricker functions, respectively.

As an application of these results, one can consider the water volume of a marine reserve region for fish. Reserves are being applied commonly to conserve fish and other populations under threat; see [3, 30]. We know that because water is incompressible, the currents will give a divergence free vector field in three dimensions. Then Theorem 2.3 implies that ocean currents could not improve the persistence of the species, under the assumption of hostile boundary conditions at the exterior of the reserve.

**3.2. Terrestrial reserve.** A terrestrial reserve is a terrestrial protected area for conservation and economic purposes. Terrestrial reserves conserve biodiversity and protect threatened and endangered species from hunting [12]. We use our model here to show the dependence of terrestrial species persistence on the diffusion rate. Consider

$$(3.12) \quad \begin{cases} u_t = d\Delta u - \gamma u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where  $g$  is the Beverton–Holt function  $g(N_m) = \frac{(1+\lambda)N_m}{1+\lambda N_m}$ . Just like in section 3.1, the assumption (1.10) is equivalent to  $\ln(1 + \lambda) > \gamma$ .

*Case 1.* Consider the domain  $\Omega = [0, L_1] \times [0, L_2]$  in two dimensions, where  $L_1, L_2$  are positive. Then a direct consequence of Theorem 2.1 is that when the diffusion is greater than the critical diffusion

$$(3.13) \quad d^* := \frac{1}{\pi^2} [\ln(1 + \lambda) - \gamma] \frac{L_1^2 L_2^2}{L_1^2 + L_2^2},$$

that is, when  $d > d^*$ , we have  $\lim_{m \rightarrow \infty} N_m(x) = 0$  that refers to extinction. In addition, when  $d < d^*$  we have  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for some positive equilibrium  $\bar{N}(x)$ .

*Case 2.* We now consider a bounded domain  $\Omega$  in two dimensions with a smooth boundary and area  $|\Omega|$ . Theorem 2.3 implies that when the diffusion is greater than the extreme diffusion

$$(3.14) \quad d_{ex} := \frac{|\Omega|}{\pi j_{0,1}^2} [\ln(1 + \lambda) - \gamma],$$

that is, when  $d > d_{ex}$ , then the population must go extinct. Note that for the case of  $\Omega = B_R$ , Theorem 2.2 implies that the extreme diffusion given by (3.14) is the critical diffusion

$$(3.15) \quad d^* := \frac{R^2}{j_{0,1}^2} [\ln(1 + \lambda) - \gamma],$$

meaning that when  $d > d^*$  then  $\lim_{m \rightarrow \infty} N_m(x) = 0$  and for  $d < d^*$  we have  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for some positive equilibrium  $\bar{N}(x)$ . In Case 1, we considered a rectangular domain that does not have smooth boundaries, unlike the domain in Case 2. Comparing  $d^*$  and  $d_{ex}$  given by (3.13) and (3.14) one sees that  $d^* < d_{ex}$  when  $\Omega = [0, L_1] \times [0, L_2]$  and  $L_1 = L_2$ , since  $\pi j_{0,1}^2 \approx 18.21$  and  $2\pi^2 = 19.73$ .

**3.3. Insect pest outbreaks.** Insect pest outbreaks are a historic problem in agriculture and can have long-lasting effects. It may be necessary to control insect pests in order to maximize crop production [43]. We apply our model here to study the dependence of insect pest extirpation on the removal rate. Consider

$$(3.16) \quad \begin{cases} u_t = d\Delta u + r(1 - u)u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where  $g(N_m) = (1 - s)N_m$  and  $0 < s < 1$  is the surviving fraction of pests that contribute to the population a year later. The assumption (1.10) is equivalent to

$$(3.17) \quad e^r(1 - s) > 1.$$

Assuming that (3.17) holds, straightforward calculations show that the positive equilibrium  $N^*$  that solves (1.11) is of the form

$$(3.18) \quad N^* := \frac{(1 - s)e^r - 1}{(1 - s)(e^r - 1)},$$

and  $g$  is clearly increasing in  $[0, N^*]$ .

*Case 1.* Consider the rectangular domain  $\Omega = [0, L_1] \times [0, L_2]$  in two dimensions for positive  $L_1, L_2$ . We now apply Theorem 2.1 to conclude that the critical value for the parameter  $s$  regarding extinction versus persistence is

$$(3.19) \quad s^* := 1 - e^{-d\pi^2 \left[ \frac{L_1^2 + L_2^2}{L_1^2 L_2^2} \right] - r}.$$

More precisely, for  $s > s^*$  we have  $\lim_{m \rightarrow \infty} N_m(x) = 0$  and for  $s < s^*$  we have  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for the positive equilibrium  $\bar{N}(x)$ .

*Case 2.* Consider a slightly more general bounded domain  $\Omega$  in two dimensions with a smooth boundary and area  $|\Omega|$ . Here we introduce an extreme value for the parameter  $s$  as

$$(3.20) \quad s_{ex} := 1 - e^{-\frac{d\pi^2 j_{0,1}^2}{|\Omega|} - r},$$

meaning that when  $s$  is larger than  $s_{ex}$  the population must go extinct.

**3.4. Populations in moving habitats arising from climate change.** We end this part with mentioning that (3.1) can be applied to study a population subject to climate change. Climate change, especially global warming, has greatly changed the distribution and habitats of biological species. Uncovering the potential impact of climate change on biota is an important task for modelers [36]. We consider a rectangular domain, that is,  $\Omega = [0, L_1] \times [0, L_2]$ , moving in the positive  $x$ -axis direction at speed  $c$ . Outside this domain conditions are hostile to population growth, while inside the domain there is random media, mortality, and periodic reproduction. Using the approach of [36] this problem is transformed to a related problem on a stationary domain. Consider (3.16), where  $g$  is the Beverton–Holt function and the vector field  $a$  is nonzero in the  $x$ -axis direction that is  $a = (-c, 0)$ . Theorem 2.1 implies that for

$$(3.21) \quad \frac{1}{L_1^2} + \frac{1}{L_2^2} < \frac{1}{d\pi^2} \left[ \ln(1 + \lambda) - \gamma - \frac{c^2}{4d} \right],$$

when  $\ln(1 + \lambda) > \gamma + \frac{c^2}{4d}$  we have  $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$  for some positive equilibrium  $\bar{N}(x)$  which refers to persistence of population. In other words, (3.21) yields the parameter  $c$  must be bounded by

$$(3.22) \quad c^2 < 4d[\ln(1 + \lambda) - \gamma] - (2d\pi)^2 \left[ \frac{L_1^2 + L_2^2}{L_1^2 L_2^2} \right] < 4d[\ln(1 + \lambda) - \gamma].$$

This implies that persistence and ability to propagate should be closely connected. 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. We refer interested readers to Speirs and Gurney [42] and Pachepsky et al. [34] for similar arguments regarding Fisher's equation with advection.

**4. Discussion.** We examined impulsive reaction-diffusion equation models for species with distinct reproductive and dispersal stages on domains  $\Omega \subset \mathbb{R}^n$  when  $n \geq 1$  with diverse geometrical structures. Unlike standard partial differential equation models, study of impulsive reaction-diffusion models requires a simultaneous analysis of the differential equation and the recurrence relation. This fundamental fact rules out certain standard mathematical analysis theories for analyzing solutions of these types of models, but it opens up various ways to apply the model. These models can be considered as a description for a continuously growing and dispersing population with pulse harvesting and a population with individuals immobile during the winter. As a domain  $\Omega$  for the model, we considered bounded sets in  $\mathbb{R}^n$ , including convex and nonconvex domains with smooth or nonsmooth boundaries, and also the entire space  $\mathbb{R}^n$ . Since the geometry of the domain has tremendous impacts on the solutions of the model, we consider various types of domains to study the qualitative properties of the solutions. We refer interested readers to [7, 8, 11] and references therein regarding how habitat edges change species interactions.

On bounded rectangular and circular domains, we provided critical domain sizes regarding persistence versus extinction of populations in any space dimension  $n \geq 1$ . In order to find the critical domain sizes we used the fact that the first eigenpairs of the Laplacian operator for such domains can be computed explicitly. Note that for a general bounded domain in  $\mathbb{R}^n$ , with smooth boundaries, the spectrum of the Laplacian operator is not known explicitly. However, various estimates are known for the eigenpairs. As a matter of fact, study of the eigenpairs of differential operators is one of the oldest problems in the field of mathematical analysis and partial differential equations; see Faber [10], Krahn [22], Pólya [35], and references therein.

We applied several mathematical analysis methods such as Schwarz symmetrization rearrangement arguments, the classical Rayleigh–Faber–Krahn inequality, and lower bounds for the spectrum of uniformly elliptic operators with Dirichlet boundary conditions given by Li and Yau [27] to compute a novel quantity called extreme volume size. Whenever  $|\Omega|$  falls below the extreme volume size the species must be driven extinct, regardless of the geometry of the domain. In other words, the extreme volume size provides a lower bound (a necessary condition) for the persistence of population. In the context of biological sciences this can provide a partial answer to questions about how much habitat is enough (see also Fahrig [12] and references therein). We believe that this opens up new directions of research in both mathematics and sciences.

In this paper we presented applications of our main results in two and three space dimensions to certain biological reaction-diffusion models regarding marine reserve, terrestrial reserve, insect pest outbreaks, and population subject to climate change. Note that when  $n = 1$  our results recovers the results provided by Lewis and Li [24] and when  $g(N) = N$  and  $A = d(\delta_{i,j})_{i,j=1}^n$  our results on both bounded and unbounded domains coincide with the ones for the standard Fisher-KPP equation. Throughout this paper we assumed that the diffusion matrix and, for the most part, the advection vector field contain constant components. Study of the influence of nonconstant advection and nonconstant diffusion on persistence and extinction properties is considered in the work of Hamel and Nadirashvili [15], and Hamel, Nadirashvili, and Russ [16].

**5. Proofs.** In this section, we provide mathematical proofs for our main results.

**5.1. Proofs of Theorems 2.1 and 2.2.** We start with the proof of Theorem 2.1. The proof of Theorem 2.2 is very similar. For both of the proofs, the following

technical lemma plays a fundamental role. We shall omit the proof of the lemma since it is standard in this context.

LEMMA 5.1. *Suppose that  $\phi_1, \lambda_1$  are the first eigenvalue and the first eigenfunction of (2.17). Then*

$$(5.1) \quad \lambda_1(dI, a, [0, L_1] \times \cdots \times [0, L_n]) = \frac{|a|^2}{4d} + d\pi^2 \left( \frac{1}{L_1^2} + \cdots + \frac{1}{L_n^2} \right),$$

$$(5.2) \quad \lambda_1(dI, 0, B_R) = j_{n/2-1,1}^2 R^{-2}d,$$

where  $j_{m,1}$  is the first positive zero of the Bessel function  $J_m$ .

*Proof of Theorem 2.1.* Suppose that the recurrence relation  $\bar{N}_m(x)$  is a solution of the following linearized problem:

$$(5.3) \quad \begin{cases} u_t + a \cdot \nabla u = \operatorname{div}(A\nabla u) + f'(0)u & \text{for } (x, t) \in \Omega \times \mathbb{R}^+, \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times \mathbb{R}^+, \\ u(x, 0) = g'(0)\bar{N}_m(x) & \text{for } x \in \Omega, \\ \bar{N}_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega. \end{cases}$$

Let

$$(5.4) \quad u(x, t) = cg'(0)e^{\lambda t}\phi(x)$$

be a solution for the above linear problem (5.3) for some function  $\phi$  and constant  $c$ . It is straightforward to show that  $\phi$  satisfies

$$(5.5) \quad -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi = (f'(0) - \lambda)\phi \quad \text{in } \Omega.$$

Note that the initial condition is  $u(x, 0) = g'(0)\bar{N}_m(x) = cg'(0)\phi(x)$ . This implies that

$$(5.6) \quad \bar{N}_{m+1}(x) = u(x, 1) = cg'(0)e^{\lambda}\phi(x) = g'(0)e^{\lambda}\bar{N}_m(x).$$

In light of (5.5), we consider the Dirichlet eigenvalue problem

$$(5.7) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi = \lambda\phi & \text{in } \Omega, \\ \phi = 0 & \text{on } \partial\Omega, \\ \phi > 0 & \text{in } \Omega \end{cases}$$

and let the pair  $(\phi_1, \lambda_1(A, a, \Omega))$  be the first eigenpair of this problem. Setting  $\lambda := f'(0) - \lambda_1(A, a, \Omega)$  in (5.4) we get

$$(5.8) \quad u(x, t) = cg'(0)e^{(f'(0) - \lambda_1(A, a, \Omega))t}\phi_1(x).$$

This implies that

$$(5.9) \quad \bar{N}_{m+1}(x) = c \left( g'(0)e^{f'(0) - \lambda_1(A, a, \Omega)} \right)^m \phi_1(x).$$

Therefore, we get

$$(5.10) \quad \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0$$

when  $g'(0)e^{f'(0) - \lambda_1(A, a, \Omega)} < 1$ , that is, when

$$(5.11) \quad \lambda_1(A, a, \Omega) > \ln(e^{f'(0)}g'(0)).$$

Suppose that  $u(x, 0) = N_0(x)$  is an initial value for the original nonlinear problem (1.1). One can choose a sufficiently large  $c$  such that  $N_0(x) \leq \bar{N}_0(x)$ . Applying standard comparison theorems, together with the fact that  $g$  is linear, and induction arguments we obtain  $N_m(x) \leq \bar{N}_m(x)$  for all  $m \geq 0$ . This implies that

$$(5.12) \quad \lim_{m \rightarrow \infty} N_m(x) = 0$$

when (5.11) holds. We now analyze inequality (5.11) that involves the first eigenvalue of (5.7). Applying Lemma 5.1 to (5.7) when  $A = d(\delta_{i,j})_{i,j=1}^m$ ,  $\Omega = [0, L_1] \times \dots \times [0, L_n]$  we obtain

$$(5.13) \quad \lambda_1(dI, a, \Omega) = \frac{|a|^2}{4d} + d\pi^2 \left( \sum_{i=1}^n L_i^{-2} \right).$$

Equating this and (5.11) we end up with

$$(5.14) \quad \sum_{i=1}^n L_i^{-2} > \frac{1}{4d^2\pi^2} \left[ 4d[\ln(e^{f'(0)}g'(0))] - |a|^2 \right].$$

This proves the first part of the theorem. To show the second part we suppose that  $g$  satisfies (G0)–(G2) and we analyze the eigenvalue problem (5.7). Suppose that  $g'(0)e^{f'(0)-\lambda_1(A,a,\Omega)} > 1$ , that is, when the inequality (5.11) is reversed, namely,

$$(5.15) \quad \lambda_1(A, a, \Omega) < \ln(g'(0)) + f'(0).$$

Let  $\lambda > \lambda_1$  and  $\underline{g}$  such that  $\underline{g}e^{f'(0)-\lambda} > 1$ . Since  $g$  satisfies (G0)–(G2), there exists an  $\tilde{M}$  such that  $g(N) \geq g'(0)N - h(N)$  for  $0 < N < \tilde{M}$ . The fact that  $h$  is differentiable and  $h(0) = h'(0) = 0$  implies that there exists a positive constant  $\delta$  such that for  $N < \delta$  the fraction  $\frac{h(N)}{N}$  can be sufficiently small, let's say

$$(5.16) \quad \frac{h(N)}{N} < \min\{g'(0) - \underline{g}, \lambda - \lambda_1\}.$$

Now define

$$(5.17) \quad \underline{u}(x, t) = \epsilon \underline{g} e^{(f'(0)-\lambda)t} \phi_1(x).$$

Note that  $g(\underline{u}(x, t)) \geq g'(0)\underline{u}(x, t) - h(\underline{u}(x, t))$ . For sufficiently small  $\epsilon$  and  $t \in (0, 1]$ , we get

$$(5.18) \quad \frac{g(\underline{u}(x, t))}{\underline{u}(x, t)} \geq \underline{g} + (g'(0) - \underline{g}) - \frac{h(\underline{u}(x, t))}{\underline{u}(x, t)} \geq \underline{g},$$

where we have used the fact that  $\frac{h(\underline{u}(x, t))}{\underline{u}(x, t)} < g'(0) - \underline{g}$  when  $t \in (0, 1]$ . This implies that

$$(5.19) \quad g(\underline{u}(x, t)) \geq \underline{g} \underline{u}(x, t).$$

We now show that  $\underline{u}$  is a subsolution for the partial differential equation given in (1.1) when  $t \in (0, 1]$ , that is,

$$(5.20) \quad \begin{cases} u_t = \operatorname{div}(A\nabla u) + a \cdot \nabla u + f(u) & \text{for } (x, t) \in \Omega \times \mathbb{R}^+, \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times \mathbb{R}^+. \end{cases}$$



Since  $f$  satisfies (F0)–(F1), we get

$$(5.21) \quad f(\underline{u}) \geq f'(0)\underline{u} - h(\underline{u}) = \epsilon g e^{(f'(0)-\lambda)t} \phi_1 f'(0) - h(\underline{u}).$$

This implies that

$$(5.22) \quad \begin{aligned} & \underline{u}_t - \operatorname{div}(A\nabla\underline{u}) - a \cdot \nabla\underline{u} - f(\underline{u}) \\ & \leq \epsilon g e^{(f'(0)-\lambda)t} [(f'(0) - \lambda)\phi_1 - \operatorname{div}(A\nabla\phi_1) + a \cdot \nabla\phi_1 - f'(0)\phi_1] + h(\underline{u}) \\ & = \epsilon g e^{(f'(0)-\lambda)t} [-\operatorname{div}(A\nabla\phi_1) + a \cdot \nabla\phi_1 - \lambda_1\phi_1] \\ & \quad + \epsilon g e^{(f'(0)-\lambda)t} [\lambda_1 - \lambda] \phi_1 + h(\underline{u}). \end{aligned}$$

Note that  $\lambda_1$  is the first eigenvalue of (5.7) that yields

$$(5.23) \quad -\operatorname{div}(A\nabla\phi_1) + a \cdot \nabla\phi_1 - \lambda_1\phi_1 = 0.$$

Applying this in (5.22) we get

$$(5.24) \quad \begin{aligned} & \underline{u}_t - \operatorname{div}(A\nabla\underline{u}) - a \cdot \nabla\underline{u} - f(\underline{u}) \\ & \leq \epsilon g e^{(f'(0)-\lambda)t} [\lambda_1 - \lambda] \phi_1 + h(\underline{u}) \\ & = \underline{u} \left[ \lambda_1 - \lambda + \frac{h(\underline{u})}{\underline{u}} \right]. \end{aligned}$$

We now apply (5.16) to conclude that

$$(5.25) \quad \underline{u}_t - \operatorname{div}(A\nabla\underline{u}) - a \cdot \nabla\underline{u} - f(\underline{u}) \leq 0.$$

This proves our claim. Suppose that  $N_m(x)$  is a solution of (1.1); then

$$(5.26) \quad N_{m+1}(x) = Q[g(N_m)](x),$$

where the operator  $Q$  maps  $u(x, 0)$  to  $u(x, 1)$ . To be more precise, let  $u(x, t)$  solve

$$(5.27) \quad \begin{cases} u_t = \operatorname{div}(A\nabla u - au) + f(u) & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, 0) = u_0(x) & \text{for } x \in \Omega; \end{cases}$$

then  $u(x, 1) = Q[u_0](x)$ . It is straightforward to see that  $Q$  is a monotone operator due to comparison principles. Now, let  $M_0(x) = \epsilon\phi_1(x)$  and

$$(5.28) \quad M_{m+1}(x) = Q[g(M_m)](x).$$

We now apply the fact that  $\underline{u}$  is a subsolution of (5.27) together with (5.25) and (5.19) and the monotonicity of the operator  $Q$  to conclude

$$(5.29) \quad M_1(x) = Q[g(M_0)](x) \geq Q[\underline{g} \cdot M_0](x) \geq \underline{u}(x, 1) \geq M_0(x).$$

An induction argument implies that

$$(5.30) \quad M_{m+1}(x) \geq M_m(x) \quad \text{for } m \geq 0.$$

Note that  $g(0) = 0$  and  $Q$  is a continuous operator defined on the range of function  $g$ . This implies that for a sufficiently small  $\epsilon > 0$ , we have  $M_0(x) = \epsilon\phi_1(x) \leq M_1(x) = Q[g(\epsilon\phi_1(x))](x) \leq N^*$ , where  $N^*$  is a positive equilibrium for (1.8). Therefore,

$$(5.31) \quad M_m(x) \leq M_{m+1}(x) \leq N^*.$$

The sequence of function  $M_m(x)$  is bounded increasing that must be convergent to  $N(x)$ . Note also that for sufficiently small  $\epsilon$  one can show that  $M_0(x) = \epsilon\phi_1(x) \leq Q[g(u_0)](x) = Q[g(N_0)](x) = N_1(x)$ . We refer interested readers to [19] for a similar argument. Finally from comparison principles we have  $M_{m+1}(x) \leq N_m(x)$ . This and (5.31) imply that  $\liminf_{m \rightarrow \infty} N_m(x) \geq \liminf_{m \rightarrow \infty} M_m(x) = N(x)$ . This completes the proof.  $\square$

*Proof of Corollary 2.1.* Assuming that  $L_i = L > 0$  for any  $1 \leq i \leq n$ , from (5.14) we get the following:

$$(5.32) \quad nL^{-2} > \frac{1}{4d^2\pi^2} (4d[\ln(g'(0)) + f'(0)] - |a|^2).$$

This completes the proof.  $\square$

*Proof of Theorem 2.2.* Suppose that the recurrence relation  $\bar{N}_m(x)$  is a solution of the linearized problem (5.3) when  $\text{div } a = 0$  and  $A = d(a_{i,j})_{i,j=1}^m$ . Assume that the following function  $u(x, t)$  is a solution for the linear problem (5.3),

$$(5.33) \quad u(x, t) = cg'(0)e^{\lambda t}\phi(x),$$

for some constant  $c$  and where  $\phi$  satisfies

$$(5.34) \quad -d\Delta\phi + a \cdot \nabla\phi = (f'(0) - \lambda)\phi \text{ in } B_R.$$

Suppose that  $\lambda_1$  is the first eigenvalue of the following eigenvalue problem with Dirichlet boundary conditions:

$$(5.35) \quad \begin{cases} -d\Delta\phi + a \cdot \nabla\phi = \lambda(dI, a, B_R)\phi & \text{in } B_R, \\ \phi = 0 & \text{on } \partial B_R, \\ \phi > 0 & \text{in } B_R. \end{cases}$$

Under similar arguments as in the proof of Theorem 2.1, whenever

$$(5.36) \quad \lambda_1(dI, a, B_R) > \ln(e^{f'(0)}g'(0)),$$

we conclude the decay

$$(5.37) \quad \lim_{m \rightarrow \infty} N_m(x) = \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0 \text{ in } B_R,$$

and otherwise we get

$$(5.38) \quad \lim_{m \rightarrow \infty} N_m(x) \geq \lim_{m \rightarrow \infty} \bar{N}_m(x) \geq N(x) \text{ in } B_R.$$

Therefore, we only need to discuss the magnitude of  $\lambda_1$ . Lemma 5.1 implies that

$$(5.39) \quad \lambda_1(dI, 0, B_R) = d \left( \frac{|B_1|}{|B_R|} \right)^{2/n} j_{n/2-1,1}^2,$$

where  $j_{n/2-1,1}$  is the first positive zero of the Bessel function  $J_{n/2-1}$ . This and the fact that  $a$  is a divergence free vector field imply that

$$(5.40) \quad \lambda_1(dI, a, B_R) \geq dR^{-2}j_{n/2-1,1}^2.$$

Combining (5.40) and (5.36) provides proofs for (5.37) and (5.38) when  $R < R^*$  and  $R > R^*$ , respectively, where

$$(5.41) \quad R^* := \sqrt{\frac{d j_{n/2-1,1}^2}{\ln(g'(0)) + f'(0)}}.$$

This completes the proof.  $\square$

**5.2. Proofs of Theorems 2.3 and 2.4.** This part is dedicated to proofs of theorems regarding the extreme volume size for both a general domain  $\Omega \subset \mathbb{R}^n$  with a smooth boundary, Theorem 2.3, and also for a  $n$ -hyperrectangle domain  $\Omega = [0, L_1] \times \cdots \times [0, L_n]$  with nonsmooth boundaries, Theorem 2.4.

*Proof of Theorem 2.3.* With the same reasoning as in the proof of Theorem 2.1, the limit tends to zero, that is,

$$(5.42) \quad \lim_{m \rightarrow \infty} N_m(x) = \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0 \quad \text{in } \Omega,$$

when

$$(5.43) \quad \lambda_1(A, a, \Omega) > \ln(e^{f'(0)} g'(0)).$$

Here  $\lambda_1(A, a, \Omega)$  stands for the first eigenvalue of

$$(5.44) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi = \lambda_1(A, a, \Omega)\phi & \text{in } \Omega, \\ \phi = 0 & \text{on } \partial\Omega, \\ \phi > 0 & \text{in } \Omega. \end{cases}$$

From the fact that the vector field  $a$  is divergence free (in the sense of distributions), we have  $\lambda_1(A, a, \Omega) \geq \lambda_1(A, 0, \Omega)$ . This can be seen by multiplying (5.44) with  $\phi$  and integrating by parts over  $\Omega$  and using the fact that  $\operatorname{div} a = 0$ . We now apply the generalized Rayleigh–Faber–Krahn inequality (2.18), that is,

$$(5.45) \quad \lambda_1(A, a, \Omega) \geq \lambda_1(dI, 0, \Omega^*),$$

where  $\Omega^*$  is the ball  $B_R \subset \mathbb{R}^n$  for the radius  $R = (\frac{|\Omega|}{|B_1|})^{1/n}$  where  $|B_1|$  is the volume of the unit ball, that is,  $|B_1| = \frac{\pi^{\frac{n}{2}}}{\Gamma(1+\frac{n}{2})}$ . Note that Lemma 5.1 implies that

$$(5.46) \quad \lambda_1(dI, 0, \Omega^*) = j_{n/2-1,1}^2 R^{-2} d.$$

Combining (5.43), (5.45), and (5.46) shows that whenever

$$(5.47) \quad j_{n/2-1,1}^2 R^{-2} d > f'(0) + \ln(g'(0)),$$

the decay estimate (5.42) holds. Note that the radius  $R$  in (5.47) is  $(\frac{|\Omega|}{|B_1|})^{1/n}$ . This implies that for any domain with the volume  $|\Omega|$  that is less than

$$(5.48) \quad |\Omega| < |B_1| \left( \frac{d j_{n/2-1,1}^2}{f'(0) + \ln(g'(0))} \right)^{\frac{n}{2}},$$

the population must go extinct. This completes the proof.  $\square$

We now provide a proof for Theorem 2.4, that is, in regards to  $n$ -hyperrectangle domain

$$\Omega = [0, L_1] \times \cdots \times [0, L_n]$$

with nonsmooth boundaries.

*Proof of Theorem 2.4.* The idea of the proof is very similar to the ones provided in proofs of Theorems 2.3 and 2.1. The decay of the  $N_m(x)$  to zero as  $m$  goes to infinity refers to inequality (5.14), that is,

$$(5.49) \quad \frac{1}{L_1^2} + \cdots + \frac{1}{L_n^2} > \frac{1}{d\pi^2} \left[ f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d} \right].$$

Note that when the right-hand side of the above inequality is nonpositive then this is valid for any  $L_i$  for  $1 \leq i \leq n$ . So, we assume that  $f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d} > 0$ .

On the other hand, the following inequality of arithmetic and geometric means hold:

$$(5.50) \quad \frac{1}{L_1^2} + \dots + \frac{1}{L_n^2} \geq n \sqrt[n]{\frac{1}{L_1^2} \cdots \frac{1}{L_n^2}} = n \left( \frac{1}{L_1 \cdots L_n} \right)^{\frac{2}{n}} = n|\Omega|^{-\frac{2}{n}},$$

where the equality holds if and only if  $L_1 = \dots = L_n$ . Combining (5.49) and (5.50) yields that when

$$(5.51) \quad |\Omega| < \left( \frac{nd\pi^2}{f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d}} \right)^{n/2},$$

the population must go extinct. This completes the proof. □

**5.3. The spectrum of the Laplacian operator.** To find the the extreme volume size  $V_{ex}$  in Theorem 2.3 we applied the Schwarz symmetrization argument and the classical Rayleigh–Faber–Krahn inequality and its generalizations. In this part we discuss that one can avoid applying rearrangement-type arguments to obtain inequalities for eigenvalues of the Laplacian operator with Dirichlet boundary conditions for an arbitrary domain  $\Omega$ . However, the extreme volume size  $V_{ex}$  that we deduce with this argument is slightly smaller than the one given in (2.20). Suppose that

$$(5.52) \quad \begin{cases} -\Delta\phi = \lambda\phi & \text{in } \Omega, \\ \phi = 0 & \text{on } \partial\Omega, \\ \phi > 0 & \text{in } \Omega. \end{cases}$$

The discreteness of the spectrum of the Laplacian operator allows one to order the eigenvalues  $0 < \lambda_1 \leq \lambda_2 \leq \dots \leq \lambda_k \leq \dots$  monotonically. Proving lower bounds for  $\lambda_k$  has been a celebrated problem in the field of partial differential equations. We now mention key results in the field and then we apply the lower bounds to our models. In 1912, Weyl showed that the spectrum of (5.52) has the following asymptotic behavior as  $k \rightarrow \infty$ :

$$(5.53) \quad \lambda_k \sim (2\pi)^2 |B_1|^{-\frac{2}{n}} \left( \frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

In 1960, Pólya in [35] proved that for certain geometric shapes, that is, “plane-covering domain”  $\Omega \subset \mathbb{R}^n$ , the following holds for all  $k \geq 1$ :

$$(5.54) \quad \lambda_k \geq (2\pi)^2 |B_1|^{-\frac{2}{n}} \left( \frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

Then he conjectured that the above inequality should hold for general domains in  $\mathbb{R}^n$ . His original proof and his conjecture were provided for  $n = 2$ . Even though this conjecture is still an open problem there are many interesting results in this regard. The inequality

$$(5.55) \quad \lambda_k \geq C_n (2\pi)^2 |B_1|^{-\frac{2}{n}} \left( \frac{k}{|\Omega|} \right)^{\frac{2}{n}}$$

with a positive constant  $C_n < \frac{n}{n+2}$  was given for arbitrary domains by Lieb in [26] and references therein. Li and Yau [27] improved upon this result, proving that the following lower bound holds for all  $k \geq 1$ :

$$(5.56) \quad \lambda_k \geq \frac{n}{n+2} (2\pi)^2 |B_1|^{-\frac{2}{n}} \left( \frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

We now apply the lower bound (5.56) to get the following extreme volume size. Note that this  $V_{ex}$  is independent from Bessel functions.

**THEOREM 5.1.** *Let  $A = d(\delta_{i,j})_{i,j=1}^m$  for a positive constant  $d$  and the vector field  $a$  be divergence free. We assume that  $f$  satisfies (F0)–(F1),  $g$  satisfies (G0)–(G2), and (1.10) holds. Suppose that  $\Omega \subset \mathbb{R}^n$  is an open bounded domain with smooth boundary and  $|\Omega| < V_{ex}$ , where*

$$(5.57) \quad V_{ex} = \Gamma\left(1 + \frac{n}{2}\right) \left[ \frac{4dn\pi}{(n+2)[f'(0) + \ln(g'(0))]} \right]^{\frac{n}{2}}.$$

Then  $\lim_{m \rightarrow \infty} N_m(x) = 0$  for any  $x \in \Omega$ .

**COROLLARY 5.1.** *In two dimensions  $n = 2$ , the extreme volume size provided in (5.57) is*

$$(5.58) \quad V_{ex} = \frac{2d\pi}{f'(0) + \ln(g'(0))}.$$

Moreover, in three dimensions  $n = 3$ , the extreme volume size (5.57) simplifies to

$$(5.59) \quad V_{ex} = \frac{18\sqrt{3}\pi^2}{5\sqrt{5}} \left( \frac{d}{f'(0) + \ln(g'(0))} \right)^{\frac{3}{2}},$$

where we have used the fact that  $\Gamma(1 + \frac{n}{2}) = \Gamma(\frac{5}{2}) = \frac{3\sqrt{\pi}}{4}$ .

Note that  $V_{ex}$  given in (5.58) and (5.59) are slightly smaller than the ones given by (2.21) and (2.22) in Corollaries 2.2 and 2.3, respectively.

*Proof of Theorem 5.1.* Note that we have the following lower bound on the first eigenvalue as an immediate consequence of (5.56), that is,

$$(5.60) \quad \lambda_1(dI, 0, \Omega) \geq d \frac{n}{n+2} (2\pi)^2 (|B_1||\Omega|)^{-\frac{2}{n}}.$$

Following ideas provided in the proof of Theorem 2.3 one can complete the proof.  $\square$

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