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Maximization of the total population in reaction-diffusion models with logistic growth

Summary



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Abstract

This thesis is concerned with a nonlinear optimization problem that naturally arises in population biology. We consider the effect of spacial heterogeneity on the total population of a biological species at a steady state, using a reaction-diffusion model, or multi-patch model with logistic growth. Our objective is to maximize the total population when resources are distributed in some patches to control the intrinsic growth rate, but the total amount of resources is limited. It is shown that global maximizer is of “bang-bang” type under some constraint. Further, global maximizer can be expressed in a patchy environment for any number of patches with sufficiently small and large diffusion constant. To this purpose, we compute asymptotic expansion of the total population by using perturbation theory in a reaction diffusion model. In the case patchy environment, we use Taylor expansion and recurrence relation.

Summary

This is a summary of the author's Ph.D thesis [19] at Tokyo Institute of Technology.

Reaction-diffusion model with logistic growth

In this thesis, we first consider the boundary value problem for a semilinear elliptic equation

$$\begin{cases} \Delta u + u(m(x) - u) = 0 & \text{in } \Omega, \\ \frac{\partial u}{\partial \nu} = 0 & \text{on } \partial\Omega. \end{cases} \quad (1)$$

Here, Ω is a bounded domain in \mathbb{R}^d with a smooth boundary $\partial\Omega$, ν is an outward unit normal vector on $\partial\Omega$, and m is a bounded Lebesgue measurable function. Our interest is in the dependency of $\int_{\Omega} u dx$ on the weight m , specifically with relation to the reaction-diffusion logistic equation.

The problem (1) appears as a stationary problem for the following model of biological population growth introduced by Skellam [23], which plays an important role in studying the effects of dispersal and spatial heterogeneity in population dynamics:

$$\begin{cases} v_t = \Delta v + v(m(x) - v) & \text{in } \Omega \times \mathbb{R}_+, \\ \frac{\partial v}{\partial \nu} = 0 & \text{on } \partial\Omega \times \mathbb{R}_+, \\ v(x, 0) \geq 0, v(x, 0) \not\equiv 0 & \text{in } \overline{\Omega}, \end{cases} \quad (2)$$

where $v(x, t)$ represents the density of a species at location x and time t , and $v(x, 0) \in C(\overline{\Omega})$ is the initial data. In regards to biology, Ω is the habitat of a species and the function $m(x)$ represents the intrinsic growth rate of a species at location x . If $m(x) > 0$, then it is favorable to the species, whereas if $m(x) < 0$, then it is unfavorable. The zero-flux boundary condition in (1) means that no individuals cross the boundary of the habitat.

The trivial steady state $u \equiv 0$ corresponds to the extinction of the species. If the trivial solution is unstable, then the species can survive, that is, there is a unique positive steady state. Conversely, if $u \equiv 0$ is stable, then the species has

no chance to survive, that is, the solution tends to 0 as $t \rightarrow \infty$ uniformly on Ω . Therefore, the stability of the trivial steady state is crucial for the survival of the species. We refer to [2, 4, 5, 14, 15] and reference therein for previous works on (2).

Thus, if $v \equiv 0$ is unstable, the total population satisfies

$$\int_{\Omega} v(x, t) dx \rightarrow \int_{\Omega} u(x) dx \quad \text{as } t \rightarrow \infty,$$

where u is the positive solution of (1). Note that the solution u of (1) depends only on the function m . Hence we may denote the total population at steady state as

$$J(m) := \int_{\Omega} u dx.$$

Our objective is to maximize the total population $J(m)$ under the following constraints on m :

$$\text{(M1)} \quad \underline{m}(x) \leq m(x) \leq \overline{m}(x) \quad \text{a.e. in } \Omega,$$

$$\text{(M2)} \quad \int_{\Omega} m(x) dx \leq M,$$

$$\text{(M3)} \quad v \equiv 0 \text{ is unstable,}$$

where \underline{m} , \overline{m} are given bounded and continuous functions in Ω , and M is a given constant satisfying

$$\int_{\Omega} \underline{m}(x) dx < M < \int_{\Omega} \overline{m}(x) dx.$$

We define the feasible set of m by

$$\mathcal{M} := \{m \in L^{\infty}(\Omega) : m(x) \text{ satisfies (M1), (M2), and (M3)}\}, \quad (3)$$

and assume that \mathcal{M} is not empty.

These constraints (M1), (M2), and (M3) are derived from preservation of an endangered species which may not be able to survive without protection. The constraint (M1) implies that the intrinsic growth rate at location x is given by $\underline{m}(x)$ if there is no protection, and that the growth rate becomes at most $\overline{m}(x)$ if some protection is provided. The integral $\int_{\Omega} m dx$ represents the total amount of resources for protection, and (M2) implies that the resource is not enough. Though (M3) does not impose constraint on the function m explicitly, it is a necessary and sufficient condition for the existence of a positive solution of (1) [4, 5, 10, 15]. We also refer to [3, 11, 22] for related work on the existence and stability conditions for the population.

If a function $m^* \in \mathcal{M}$ satisfies

$$J(m^*) = \max_{m \in \mathcal{M}} J(m),$$

we call m^* a maximizer (or an optimal control) of J . Ding et al. [6] carried out numerical simulation in the case where $\underline{m} \equiv 0$ and $\overline{m} \equiv 1$, and addressed the following conjecture:

Conjecture A. *Assume that weight $m \in L^\infty(\Omega)$ satisfies $0 \leq m(x) \leq 1$ and $\int_\Omega m dx = M$, where $0 < M < |\Omega|$. Then there exists a measurable set E such that the optimal control of $J(m)$ satisfies $m(x) = 0$ on E and $m(x) = 1$ on $\Omega \setminus E$.*

Here $m \in \mathcal{M}$ is said to have a “bang-bang” property if m is expressed as $m(x) = \overline{m}(x)\chi_E + \underline{m}(x)\chi_{\Omega \setminus E}$ a.e. for some measurable set $E \subset \Omega$, where χ_A denotes the characteristic function. In this paper, we show that a similar situation of this conjecture holds true in a more general situation where the upper bound \overline{m} and lower bound \underline{m} of (M2) are not constant.

Our main result can be stated as follows:

Theorem 1. *$m \in \mathcal{M}$ is not a local maximizer of $J(m)$ if there exists $\delta > 0$ and a nonempty open set Ω_δ such that $\underline{m}(x) + \delta < m(x) < \overline{m}(x) - \delta$ almost everywhere in Ω_δ .*

As is well known, if m is Riemann integrable, then m is continuous almost everywhere. Hence the following corollary follows immediately.

Corollary 2. *Suppose that $m \in \mathcal{M}$ is Riemann integrable. If m is a local maximizer of $J(m)$, then m is of bang-bang type.*

When m is not of bang-bang type, the set

$$\{x \in \Omega : \underline{m}(x) < m(x) < \overline{m}(x)\}$$

has a positive measure, but may not have an interior point. In this case, it is very difficult to show the bang-bang property of local maximizers.

To show the bang-bang property, it might be useful to consider rearrangement argument when upper and lower bound of m are constant (see, e.g., [17, 18]). However, this method is not effective in our case. In this paper, we adopt a different approach, namely, we apply the perturbation method, and carry out careful analysis on the first and second variations of J when $m \in \mathcal{M}$ varies.

Multi-patch model

Understanding the effect of dispersal in heterogeneous environment on population dynamics is an important issue in spatial ecology [5]. Generally large diffusion tends to reduce the spatial variations in population distributions, while small diffusion might help organisms adapt to the local environment. In this paper we are interested in the impact of dispersal upon the total population of a single species residing in a spatially heterogeneous patchy environment. More specifically, we ask the following question: Given the total amount of resources, how should we distribute the resources across the habitat in order to maximize the total population of a species?

To address this question, we consider the following system of ordinary differential equations for a single species with logistic growth in a patchy environment:

$$\begin{cases} \frac{d}{dt}v_i(t) = v_i(m_i - v_i) + \delta(v_{i-1} + v_{i+1} - 2v_i), & i \in \Omega^*, t \in \mathbb{R}_+, \\ v_0(t) = v_1(t), v_{N+1}(t) = v_N(t), & t \in \mathbb{R}_+, \\ v_i(0) \geq 0, \sum_{i=1}^N v_i(0) > 0, & i \in \Omega^*, \end{cases} \quad (4)$$

where $N \geq 2$, $\Omega^* := \{1, 2, \dots, N\}$, and $\{m_i\}_{i \in \Omega^*} \subset \mathbb{R}$ is a sequence which satisfies

$$m_i \geq 0, \quad \sum_{i=1}^N m_i = m > 0. \quad (5)$$

The problem (4) was first studied by Levins [13], as a multi-patch model for a single species, where N is the total number of patches and $\delta > 0$ is the diffusion rate. The unknown function $v_i(t)$, $i \in \Omega^*$, $t \in \mathbb{R}_{\geq 0} := [0, \infty)$, denotes the number of individuals in i -th patch at time t . The constant m_i , $i \in \Omega^*$, represents the intrinsic growth rate of the species in i -th patch. If $m_i > 0$, then i -th patch is favorable to the species. The second equation in (4) means that no individuals cross the boundary of the habitat, so system (4) is closed. The constraint (5) means that the total amount of resources is limited.

Under assumption (5) it is well known that (4) has a unique positive steady state $\{u_i\}_{i \in \Omega^*}$, which satisfies

$$\begin{cases} u_i(m_i - u_i) + \delta(u_{i-1} + u_{i+1} - 2u_i) = 0, & i \in \Omega^*, \\ u_0 = u_1, u_{N+1} = u_N. \end{cases} \quad (6)$$

Furthermore, the unique positive steady state is globally stable and the total population of (4) satisfies

$$\sum_{i=1}^N v_i(t) \rightarrow \sum_{i=1}^N u_i \quad \text{as } t \rightarrow \infty.$$

Our purpose is to maximize the total population $U := \sum_{i=1}^N u_i$ at equilibrium under the constraint (5). See [7, 9, 12, 24] for related works.

This sort of multi-patch model is called “island chain” model or “stepping stone” model. Such model views the space as a collection of discrete patches. We treat each patch as a point, and view the overall population of a single species as a vector, with each component corresponding to the number of individuals in each patch. Furthermore, we can treat the dispersal in this model as a discrete analogue of the continuous diffusion. For more details see [1, 5, 8] and references therein. For this reason, this work is closely relevant to the investigation of the reaction-diffusion equation (2) in one-dimensional case. We also refer to [5, 15] and references therein for previous works of (2).

The maximization of the total population for the steady state of (2) has recently been studied by [16, 21] in $\Omega \subset \mathbb{R}^d$. They showed under some conditions that any global maximizer of the total population for the steady state must be of “bang-bang” type, which gives a partial answer to the conjecture raised by Ding et al. [6]. More recently, Mazari et al. [16] proved that if $\delta > 0$ is sufficiently large, then the global maximizer is given by $m(x) := \chi_E$, where either $E = (0, m)$ or $(1 - m, 1)$. Their numerical simulation results indicated that if the diffusion constant is sufficiently small, then fragmentation may occur in the one-dimensional case. However, it is extremely difficult to explicitly determine the maximizer for the steady state of (2) in general.

This motivates us to study the maximization problem for the difference equation (6), for which the computations of the total population can be done (but still fairly non-trivial) for small and large diffusion rates. Our results show that the global maximizer depends crucially on the diffusion rate δ , and the answers are completely different for small δ and large δ . In several cases we are able to show that the global maximizer is of the “bang-bang” type and to determine the maximizers explicitly by finding the specific guiding rules of fragmentation in the multi-patch model (6). In particular, fragmentation occurs when the diffusion rate is sufficiently small, which echoes the numerical findings in [16]. In this paper, we do not assume the upper bound for the resource distribution in each patch.

We define the set

$$\mathfrak{M} := \{\{m_i\}_{i \in \Omega^*} \mid \{m_i\}_{i \in \Omega^*} \text{ satisfies (5)}\} \subset \mathbb{R}^N.$$

For convenience, we express $\{m_i\}_{i \in \Omega^*}$ by \mathbf{m} or (m_1, m_2, \dots, m_N) . Note that the solution of (6) depends on the diffusion constant $\delta > 0$ and resources $\mathbf{m} \in \mathfrak{M}$. We denote the total population at stable equilibrium as $U = U(\mathbf{m}, \delta)$.

Our first main result is stated as follows:

Theorem 3 (Global maximizer for large δ). *Suppose that $\mathbf{m} \in \mathfrak{M}$ is given by*

$$\mathbf{m} = (0, 0, 0, \dots, m) \text{ or } \mathbf{m} = (m, 0, 0, \dots, 0).$$

Then there exists a positive constant $\Delta_{N,m} > 0$ such that for any $\delta > \Delta_{N,m}$ and for any $\tilde{\mathbf{m}} \in \mathfrak{M} \setminus \{\mathbf{m}\}$, the total population satisfies $U(\mathbf{m}, \delta) > U(\tilde{\mathbf{m}}, \delta)$.

Note that this theorem is consistent with the result of [16] for (2).

The next theorem shows that the global maximizer for sufficiently small δ is fragmented, and there are some rules of fragmentation in the multi-patch model (6).

Theorem 4 (Global maximizer for small δ). *Let $p > 0$ and $r > 0$ be any two positive integers. Define $\mathbf{P}_m = (0, m/p, 0)$, $\mathbf{P}_{m_*} = (0, m_*, 0)$, $\mathbf{m}^* = (0, m^*, 0, m^*, 0)$, where*

$$m^* = \frac{(1 + \sqrt{2})^2 m}{2\{4(p-1) + (1 + \sqrt{2})^2\}}, \quad m_* = \frac{4m}{4(p-1) + (1 + \sqrt{2})^2}.$$

Choose $\eta \in (0, p^*]$ arbitrarily, where

$$p^* := \begin{cases} m/p & \text{if } N = 3p, 3p+1, \\ m^* & \text{if } N = 3p+2. \end{cases}$$

Define a set

$$\mathfrak{M}_\eta := \{\mathbf{m} \in \mathfrak{M} \mid m_i \geq \eta \text{ or } m_i = 0 \text{ for all } i \in \Omega^*\}.$$

Suppose that $\mathbf{m} \in \mathfrak{M}_\eta$ is given as follows:

(i) If $N = 3p$, then

$$\mathbf{m} = (\underbrace{\mathbf{P}_m, \mathbf{P}_m, \dots, \mathbf{P}_m}_p).$$

(ii) If $N = 3p+1$, there are 3 cases:

(a) For $p = 1$, then

$$\mathbf{m} = (0, \mathbf{P}_m), \text{ or } \mathbf{m} = (\mathbf{P}_m, 0).$$

(b) For $p = 2r$, then

$$\mathbf{m} = (\underbrace{\mathbf{P}_m, \dots, \mathbf{P}_m}_r, \overset{3r+1}{\underset{\sim}{0}}, \underbrace{\mathbf{P}_m, \dots, \mathbf{P}_m}_r).$$

(c) For $p = 2r+1$, then

$$\mathbf{m} = (\underbrace{\mathbf{P}_m, \dots, \mathbf{P}_m}_r, \overset{3r+1}{\underset{\sim}{0}}, \underbrace{\mathbf{P}_m, \dots, \mathbf{P}_m}_{r+1}),$$

or

$$\mathbf{m} = (\underbrace{P_m, \dots, P_m}_{r+1}, \overset{3(r+1)+1}{\underset{0}{\check{0}}}, \underbrace{P_m, \dots, P_m}_r).$$

(iii) If $N = 3p + 2$, there are 3 cases:

(a) For $p = 1$, then

$$\mathbf{m} = \left(0, \frac{m}{2}, 0, \frac{m}{2}, 0\right).$$

(b) For $p = 2r$, then

$$\mathbf{m} = (\underbrace{P_{m_*}, \dots, P_{m_*}}_{r-1}, \mathbf{m}^*, \underbrace{P_{m_*}, \dots, P_{m_*}}_r),$$

or

$$\mathbf{m} = (\underbrace{P_{m_*}, \dots, P_{m_*}}_r, \mathbf{m}^*, \underbrace{P_{m_*}, \dots, P_{m_*}}_{r-1}).$$

(c) For $p = 2r + 1$, then

$$\mathbf{m} = (\underbrace{P_{m_*}, \dots, P_{m_*}}_r, \mathbf{m}^*, \underbrace{P_{m_*}, \dots, P_{m_*}}_r).$$

Then there exists positive constant $\delta_{N,m,\eta} > 0$ such that for any $\delta \in (0, \delta_{N,m,\eta})$ and any $\tilde{\mathbf{m}} \in \mathfrak{M}_\eta \setminus \{\mathbf{m}\}$, it follows that $U(\mathbf{m}, \delta) > U(\tilde{\mathbf{m}}, \delta)$.

Remark 5. Let $\mathbf{m} \in \mathfrak{M}$ be given as in Theorem 4. Choose $\tilde{\mathbf{m}} \in \mathfrak{M} \setminus \{\mathbf{m}\}$ arbitrarily. The proof of theorem 4 implies that there exists positive number $\delta_{\tilde{\mathbf{m}}}$ such that for any $\delta \in (0, \delta_{\tilde{\mathbf{m}}})$, it follows that $U(\mathbf{m}, \delta) > U(\tilde{\mathbf{m}}, \delta)$. Hence $\tilde{\mathbf{m}} \in \mathfrak{M} \setminus \{\mathbf{m}\}$ is not global maximizer for sufficiently small δ .

This theorem refers to a global-maximizer when there is minimum amount of resources $\eta > 0$ for each patches. When $\eta = 0$, it is very difficult to determine a global maximizer. However, in the two patches case, we obtain global maximizers for all $\delta > 0$.

Theorem 6 (Global maximizer for two patches). *In the case $N = 2$, Suppose that $\mathbf{m} \in \mathfrak{M}$ is given as*

$$\mathbf{m} = (0, m), \text{ or } \mathbf{m} = (m, 0).$$

Then for any $\tilde{\mathbf{m}} \in \mathfrak{M} \setminus \{\mathbf{m}\}$, it follows that $U(\mathbf{m}, \delta) > U(\tilde{\mathbf{m}}, \delta)$ for all $\delta > 0$.

Remark 7 (Global minimizer). *It is known that a global minimizer of the total population of (2) is constant. It still holds when we use the multi-patch model, that is, $m_i \equiv m/N$ for all $i \in \Omega^*$ is the global minimizer for all $\delta > 0$.*

We conclude this summary by noting that the author's Ph.D thesis [19] is based on [20, 21].

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