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Population dynamics under climate change: persistence criterion and effects of fluctuations

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Abstract

The present paper is devoted to the investigation of population dynamics under climate change. The evolution of species is modelled by a reaction-diffusion equation in a spatio-temporally heterogeneous environment described by a climate envelope that shifts with a time-dependent speed function. For a general almost-periodic speed function, we establish the persistence criterion in terms of the sign of the approximate top Lyapunov exponent and, in the case of persistence, prove the existence of a unique forced wave solution that dominates the population profile of species in the long run. In the setting for studying the effects of fluctuations in the shifting speed or location of the climate envelope, we show by means of matched asymptotic expansions and numerical simulations that the approximate top Lyapunov exponent is a decreasing function with respect to the amplitude of fluctuations, yielding that fluctuations in the shifting speed or location have negative impacts on the persistence of species, and moreover, the larger the fluctuation is, the more adverse the effect is on the species.

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In addition, we assert that large fluctuations can always drive a species to extinction. Our numerical results also show that a persistent species under climate change is invulnerable to mild fluctuations, and becomes vulnerable when fluctuations are so large that the species is endangered. Finally, we show that fluctuations of amplitude less than or equal to the speed difference between the shifting speed and the critical speed are too weak to endanger a persistent species.

Keywords Population dynamics · Climate change · Reaction-diffusion equation · Persistence criterion · Approximate top Lyapunov exponent · Forced wave solution · Fluctuations

Mathematics Subject Classification 92D25 · 92D40 · 35K57 · 35C07

Contents

1 Introduction

Climate change is known to have a great impact on the evolution of species. It alters and shifts the habitat that species reside in, and thus, forces species to shift/expand their range accordingly in order to remain persistent. Understanding whether a species can keep up with the shifting habitat and how the answer to this question depends on the species and shifting habitat are fundamental questions, which have been attracting a lot of attention in biological and ecological literature [see Walther et al. (2002), Parmesan (2006), Lenoir et al. (2008), Menendez et al. (2014) and references therein]. Mathematically, reaction–diffusion equations of the form

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

have been proposed to study the effects of climate change on evolving species, where $c \geq 0$ is the shifting speed of the habitat, and f is the growth rate function taking for example the form

$$f(x,u) = \begin{cases} Ru\left(1-\frac{u}{K}\right), & x \in \left(-\frac{L}{2}, \frac{L}{2}\right), \\ -Du, & x \in \mathbb{R}\backslash\left(-\frac{L}{2}, \frac{L}{2}\right) \end{cases} \tag{1.2}$$

for some $L > 0$ standing for the size of the climate envelope (Potapov and Lewis 2004; Berestycki et al. 2009) within which species can grow. In terms of (1.1), studying aforementioned fundamental questions is more or less equivalent to ask about the long term dynamics of non-negative solutions, representing the evolution of the spatial distribution of the species, as well as their dependence on c, L and the shape of f. In the paper by Berestycki et al. (2009), the authors established the persistence criterion for (1.1) with a more general growth rate function of logistic type. More precisely, they proved that solutions vanish as time elapses when the net reproduction number, defined to be the generalized principal eigenvalue of the operator $u \mapsto du_{xx}+cu_x+f_u(x,0)u$, is non-positive. When the net reproduction number crosses zero, a unique travelling wave with speed c exists and attracts solutions. They also studied the dependence of the net reproduction number on the shifting speed c and the size of the climate envelope L. The genetic consequences of climate change have been studied in Garnier and Lewis (2016), where the authors separate the population profile into neutral fractions and study the dynamics of each fraction to show that range shifts under slow climate change preserve genetic diversity.

The work (Berestycki et al. (2009)) has been extended in many aspects [see Berestycki and Rossi (2008), Berestycki and Rossi (2009), Bouhours and Nadin (2015), Vo (2015) and references therein] to

$$u_t = d\Delta u + f(t, x-ct, y, u), \quad (x,y) \in \mathbb{R}\times\Omega \subset \mathbb{R}\times\mathbb{R}^{N-1}, \tag{1.3}$$

where f is periodic in t, and for fixed t and y, the function $(x,u) \mapsto f(t,x,y,u)$ maintains key features of (1.2). When Ω is a bounded domain in $\mathbb{R}^{N-1}$ with smooth boundary, the equation (1.3) is equipped with homogeneous Neumann boundary condition on $\mathbb{R}\times\partial\Omega$. When $\Omega = \mathbb{R}^{N-1}$, the periodicity of f in y is assumed. Comparable results have been established for integrodifference equations (Zhou and Kot 2011, 2013; Phillips and Kot 2015; Bouhours and Lewis 2016; Lewis et al. 2018), and nonlocal dispersal equations (De Leenheer et al. 2020). Also, there exist relevant works when the habitat is growing or receding due to climate change [see Li et al. (2014), Hu and Li (2015), Fang et al. (2016), Hu and Zou (2017), Berestycki and Fang (2018), Li et al. (2018), Bouhours and Giletti (2019), Fang et al. (2021) and references therein].

In all aforementioned works, the climate envelope is assumed to have fixed size and shifts with a constant speed, and therefore, its location is predetermined. However, changes in environments driven by climate change are rather fluctuating and unpredictable [see e.g. Saltz et al. (2006); Kreyling et al. (2011)], resulting in fluctuations in the size, shifting speed and location of the climate envelope, which are respectively characterized by L, c and ct in the model (1.1) and (1.2). The purpose of the present paper is to study the effects of almost-periodic fluctuations in the shifting speed and location, two closely related components of the climate envelope, by considering the following model:

$$u_t = du_{xx} + f\left(x - \int_0^t c(s)ds, u\right), \quad x \in \mathbb{R}, \tag{1.4}$$

where $c : \mathbb{R} \to \mathbb{R}$ is an almost-periodic function. In the model (1.4), $c(t)$ and $\int_0^t c(s)ds$ are respectively the shifting speed and location of the climate envelope. Choosing special $c(t)$ allows us to discuss about the effects of fluctuations in the shifting speed and location. Indeed, setting $c(t) = c + \sigma(t)$ for some constant $c \neq 0$ and almost-periodic function $\sigma(t)$ in (1.1) results in

$$u_t = du_{xx} + f\left(x - ct - \int_0^t \sigma(s)ds, u\right), \quad x \in \mathbb{R}.$$

Assuming $\sigma(t)$ has zero average in the sense that $\lim_{t\to\infty} \frac{1}{t}\int_0^t \sigma(s)ds = 0$ so that $\sigma(t)$ has lower order than that of c, we can consider $\sigma(t)$ as fluctuations around the shifting speed c. If, in addition, the function $t \mapsto \int_0^t \sigma(s)ds$ is an almost-periodic function [if and only if it is bounded; see e.g. Fink (1974)] and has zero average, then we can regard $\int_0^t \sigma(s)ds$ as fluctuations around the location ct. Note that any continuously differentiable almost-periodic fluctuation $\Sigma(t)$ with $\Sigma(0) = 0$ (which is not a restriction) around the location ct can be written in this form, that is, $\Sigma(t) = \int_0^t \sigma(s)ds$, where $\sigma = \Sigma'$.

Our analysis and results are divided into two parts. In the first part, we conduct mathematical analysis of (1.4) in order to establish the criterion for extinction and persistence and study the global dynamics to capture the asymptotic population profile of the species when persistence happens. In the second part, we study the effects of fluctuations in the shifting speed and location of the climate envelope on this criterion to understand population extinction or persistence as the outcome of such fluctuations.

Persistence criterion To establish the persistence criterion and study the global dynamics, we consider the model (1.4) and make the following assumptions. Denote $\mathbb{R}_+ = [0, \infty)$.

(H) The diffusion coefficient $d > 0$ is fixed. The function $c : \mathbb{R} \to \mathbb{R}$ is Hölder continuous and almost-periodic. The growth rate function $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$ is given by $f(x, u) = ug(x, u)$, where $g : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$ is continuously differentiable, and is uniformly continuous and bounded on $\mathbb{R} \times [0, \delta]$ for any $\delta > 0$, and satisfies the following conditions:

- (i) $g_u(x, u) \leq 0$ for all $(x, u) \in \mathbb{R} \times \mathbb{R}_+$, and there is an open interval $I_0 \subset \mathbb{R}$ such that $u \mapsto g(x, u)$ is decreasing on $\mathbb{R}_+$ for each $x \in I_0$,
- (ii) $\limsup_{|x|\to\infty} g(x, 0) < 0$,
- (iii) there is $M_0 > 0$ such that $\sup_{x\in\mathbb{R}} g(x, u) < 0$ for all $u \geq M_0$.

The assumptions on f in (H) are standard. The condition in (i) says that the local growth rate decreases as the population size increases, and hence, f is of generalized logistic type. By (ii), the favorable habitat where species can grow is contained in a bounded region. The number M_0 in (iii) gives an upper bound for the carrying capacity.

It is convenient to consider (1.4) in the moving frame by introducing the change of variable $v(t,x) = u(t, x + \int_0^t c(s)ds)$. Then, $v(t,x)$ satisfies

$$v_t = dv_{xx} + c(t)v_x + f(x,v), \quad x \in \mathbb{R}. \tag{1.5}$$

Obviously, $v \equiv 0$ is a solution of (1.5), and its stability is expected to determine the extinction or persistence dynamics of (1.5). To study the stability of $v \equiv 0$, we examine the linearization of (1.5) at $v \equiv 0$, namely,

$$w_t = dw_{xx} + c(t)w_x + g(x,0)w, \quad x \in \mathbb{R}. \tag{1.6}$$

Denote by λ_L the *top Lyapunov exponent* of (1.6) restricted on $(-L, L)$ and equipped with zero Dirichlet boundary condition on $\pm L$. We refer the reader to Sect. 2 for more details. In the case that $c(t)$ is a periodic function, λ_L is nothing but the principal eigenvalue of the periodic parabolic operator $-\partial_t + d\partial_{xx}^2 + c(t)\partial_x + g(x,0)$ restricted on $(-L, L)$ and equipped with zero Dirichlet boundary condition at $x = \pm L$. It is shown in Lemma 2.2 that λ_L is non-decreasing in L and bounded above by $\sup_{x\in\mathbb{R}} g(x,0) < \infty$, and hence, $\lambda_\infty := \lim_{L\to\infty} \lambda_L$ is well-defined and called the *approximate top Lyapunov exponent* of (1.6) as suggested by its definition. We refer the reader to Sects. 3.3 and 4.4 for some characterizations of λ_∞. In particular, we show in Proposition 3.1 (2) that λ_∞ always has the same sign as that of the top Lyapunov exponent λ of (1.6) (see Definition 3.2 for the definition of λ).

The approximate top Lyapunov exponent λ_∞ is essentially a non-autonomous version of the generalized principal eigenvalue for (1.6) with a constant shifting speed $c(t) \equiv c$. Because of the success in using the generalized principal eigenvalue in Berestycki et al. (2009) to establish the persistence criterion, the approximate top Lyapunov exponent λ_∞ is expected to do a similar job in the current situation. To state the results, we let

$$X = \{u \in C(\mathbb{R}) : u \text{ is bounded and uniformly continuous}\}$$

be equipped with the supremum norm $\|u\|_\infty = \sup_{x\in\mathbb{R}} |u(x)|$. Set

$$X^+ = \{u \in X : u \geq 0\}.$$

For each initial data $u_0 \in X^+$, (1.4) admits a unique solution, denoted by $u(t, x; u_0)$, satisfying $u(t, \cdot; u_0) \in X^+$ for all $t \geq 0$. Our persistence criterion reads as follows.

Theorem A (Persistence criterion) *Assume (H).*

(1) *If $\lambda_\infty < 0$, then for any $u_0 \in X^+$, there holds $\|u(t, \cdot; u_0)\|_\infty \to 0$ as $t \to \infty$.*
(2) *If $\lambda_\infty > 0$, then for any $u_0 \in X^+ \setminus \{0\}$, there holds*

$$\liminf_{t\to\infty} \inf_{x\in[-L,L]} u\left(t, x + \int_0^t c(s)ds; u_0\right) > 0, \quad \forall L > 0.$$

Theorem A establishes the sharp threshold for extinction and persistence of (1.4) in terms of the sign of the approximate top Lyapunov exponent λ_∞. When $\lambda_\infty > 0$, the result clearly says that the species is well-adapted to the climate change by keeping pace with the shifting habitat, and therefore, persists in the long run. However, when $\lambda_\infty < 0$, the species is unable to keep pace with the shifting habitat, leading to the eventual extinction. Therefore, λ_∞ can be seen as the "integrated" per capita growth rate when the population density is very low. In literature, the persistence criterion for a species whose evolution is modelled by an evolutionary equation is often stated by means of the *basic reproduction number* R_0, which can be defined as $R_0 = e^{\lambda_\infty}$ here. In terms of the basic reproduction number, the persistence criterion becomes $R_0 < 1$ and $R_0 > 1$ implying extinction and persistence, respectively.

We point out that the infimum over an arbitrary $[-L, L]$ can not be replaced by that over $\mathbb{R}$ as $u(t, x; u_0) \to 0$ as $|x| \to \infty$ due to the adverse environment away from the climate envelope.

To better characterize the persistence dynamics of (1.4) that sheds light on the asymptotic population profile of species, we study the existence, uniqueness and stability of *forced wave solutions* when $\lambda_\infty > 0$. A forced wave solution of (1.4) is defined as follows.

Definition 1.1 (*Forced wave solution*) An entire solution u of (1.4) is called a *forced wave solution* if there is a bounded, positive and almost-periodic entire solution v of (1.5) such that

$$u(t, x) = v\left(t, x - \int_0^t c(s)ds\right), \quad (t, x) \in \mathbb{R} \times \mathbb{R}.$$

In the next result, we show that in the case of persistence, a unique forced wave solution is found to govern the asymptotic population profile.

Theorem B (Forced wave solution) *Assume (H). If $\lambda_\infty > 0$, then (1.4) has a unique forced wave solution u^*. Moreover, for any $u_0 \in X^+ \backslash \{0\}$, there holds $\|u(t, \cdot; u_0) - u^*(t, \cdot)\|_\infty \to 0$ as $t \to \infty$.*

When $c(t)$ is a periodic function, we obtain the following result.

Theorem C *Assume (H) and that $c(t)$ is periodic.*

(1) *If $\lambda_\infty \leq 0$, then for any $u_0 \in X^+$, there holds $\|u(t, \cdot; u_0)\|_\infty \to 0$ as $t \to \infty$.*
(2) *If $\lambda_\infty > 0$, then (1.4) has a unique forced wave solution u^*. Moreover, for any $u_0 \in X^+ \backslash \{0\}$, there holds $\|u(t, \cdot; u_0) - u^*(t, \cdot)\|_\infty \to 0$ as $t \to \infty$.*

Remark 1.1 We make some comments on Theorem C. Suppose $c(t)$ is T-periodic.

- It is shown in Proposition 4.1 that if the approximate top Lyapunov exponent λ_∞ satisfies the condition $\lambda_\infty > \limsup_{|x| \to \infty} g(x, 0)$, then it is the principal eigenvalue of the T-periodic parabolic operator $-\partial_t + d\partial_{xx}^2 + c(t)\partial_x + g(x, 0)$ considered in the space of T-periodic functions in X. Moreover, this condition can not be removed in general as pointed out in Remark 4.1.

- The extinction dynamics in the critical case $\lambda_\infty = 0$ is established.
- When $\lambda_\infty > 0$, the unique forced wave solution u^* has a T-periodic profile function, that is, $u^*\left(t, x + \int_0^t c(s)ds\right)$ is the unique bounded, positive and T-periodic solution of (1.5).

In Theorems A–C, we have established the persistence criterion and asymptotic population profile, in terms of the approximate top Lyapunov exponent λ_∞, for a species whose evolution is modelled by (1.4). To have a better understanding of the effects that the climate change has on the evolution of the species, it is natural to ask about the dependence of λ_∞ on the climate envelope. This is well studied in Berestycki et al. (2009) when the climate envelope is assumed to shift with a constant speed $c(t) \equiv c$. In particular, provided the species persists in the absence of climate change, there exists a critical shifting speed $c^* > 0$ such that the species persists if and only if the climate envelope shifts with a slower speed. Moreover, a semi-explicit formula for λ_∞ as a function of c is found by the Liouville transform.

Assuming that the climate envelope shifts with a constant speed $c \in [0, c^*)$ so that the species persists, we are interested in the effects that fluctuations on the shifting speed c have on the evolution of the species. More precisely, if the shifting speed function $c(t) = c + \sigma(t)$ for some fluctuation $\sigma(t)$, we would like to examine the dependence of λ_∞ on $\sigma(t)$. In particular, we would like to see if the fluctuation $\sigma(t)$ can drive the species to extinction and how large it needs to be in order to make this happen. Theorems A–C lay the solid foundation for investigating these issues. Now, we state the questions in details and present our findings.

Effects of fluctuations We investigate effects of fluctuations on the shifting speed and location of the climate envelope. To do so, we consider the following specified model:

$$u_t = du_{xx} + f\left(x - ct - A\int_0^t \sigma(s)ds, u\right), \quad x \in \mathbb{R}, \tag{1.7}$$

where d and f are as in (*H*), $c \geq 0$, $A \geq 0$ and $\sigma : \mathbb{R} \to \mathbb{R}$ is Hölder continuous. The linearization of (1.7) in the moving frame around the extinction state 0 reads

$$w_t = dw_{xx} + [c + A\sigma(t)]w_x + g(x, 0)w, \quad x \in \mathbb{R}. \tag{1.8}$$

Here, we focus on periodic fluctuations, that is, $\sigma(t)$ is a periodic function and has zero average. Hence, $A\sigma(t)$ is the fluctuation on the shifting speed c. Since $\sigma(t)$ is periodic and has zero average, $A\int_0^t \sigma(s)ds$ is the periodic fluctuation on the location ct. The parameter A therefore characterizes the amplitude of fluctuations. We study the influence of A on the approximate top Lyapunov exponent λ_∞^A of (1.8) in three aspects:

- effects of large fluctuations, namely, properties of λ_∞^A for large A;
- the monotonicity of λ_∞^A with respect to A;
- the (unique) solution of $\lambda_\infty^A = 0$ (as an equation of A) and its relation to the speed difference $c^* - c$, where $c^* > 0$ is the critical shifting speed in the absence of fluctuations and $c \in [0, c^*)$.

Denote by λ^A the top Lyapunov exponent of (1.8) and by λ_L^A restricted on $(-L, L)$ and equipped with zero Dirichlet boundary condition on $\pm L$. Then, $\lambda_\infty^A = \lim_{L\to\infty} \lambda_L^A$ for any $A \geq 0$. Trivially, $\lambda_\infty^A \leq \lambda^A$.

We first give some characterizations of the effects of large fluctuations.

Theorem D (Effects of large fluctuations) *Suppose (H) and σ is periodic and has zero average. The following hold.*

(1) $\lambda_\infty^A \geq -\frac{c^2}{4d} + \inf_{x\in\mathbb{R}} g(x, 0)$ *for all* $A > 0$.
(2) *If σ has only isolated zeros, then*

$$\limsup_{A\to\infty} \lambda^A \leq \limsup_{|x|\to\infty} g(x, 0).$$

Moreover, if the limits $g(\pm\infty, 0) := \lim_{x\to\pm\infty} g(x, 0)$ *exist and coincide, then*

$$\lim_{A\to\infty} \lambda^A = g(\pm\infty, 0).$$

(3) *If σ is continuously differentiable and has only isolated and non-degenerate zeros, then for each $L > 0$ there exist $C_1 = C_1(L) > 0$ and $C_2 = C_2(L) > 0$ such that*

$$\lambda_L^A \leq -C_1 A + C_2, \quad \forall A > 0.$$

Since $\limsup_{|x|\to\infty} g(x, 0) < 0$ by (H)(ii), Theorem D (2) implies that $\lambda_\infty^A < 0$ for all $A \gg 1$, saying that large fluctuations can always drive a species to extinction. The biological mechanism behind this can be made clear. When there are periodic large fluctuations, the climate envelope shifts regularly between the regions $\{x \in \mathbb{R} : x \ll -1\}$ and $\{x \in \mathbb{R} : x \gg 1\}$, resulting in the regular exposure of species to detrimental environments, where the drop of the number of species happens quickly and is eventually dominated by the per capita growth rate $g(x, 0)$ in $\{x \in \mathbb{R} : |x| \gg 1\}$. As λ_∞^A can be seen as the "integrated" per capita growth rate when the number of species is very low as mentioned earlier, it must be connected with $g(\pm\infty, 0)$ in the large fluctuation limit $A \to \infty$. Theorem D(1) says that the adverse effects of large fluctuations are limited, that is, large fluctuations can not make λ_∞^A arbitrarily negative. This seemingly counterintuitive result is a consequence of the facts that, in the model, the whole environment is unbounded, allowing species to migrate to anywhere, and its unfavorableness is uniformly limited with respect to spatial locations. For a species living in a finite whole environment, large fluctuations are likely to have great negative impacts. This is more or less reflected in the result of Theorem D(3), yielding in particular $\lim_{A\to\infty} \lambda_L^A = -\infty$. Such a result is expected as species can hardly keep pace with the shifting climate envelope and die immediately when arriving at the boundary of the habitat. Note that Theorem D(1) and (3) imply that the limit $\lambda_\infty^A = \lim_{L\to\infty} \lambda_L^A$ is NOT uniform in $A \gg 1$.

Next, we study the monotonicity of λ_∞^A with respect to A. We focus on the case that the species persists when there is no fluctuation, namely, $\lambda_\infty^0 > 0$. Using matched asymptotic expansion and numerical simulations, we find the following properties of λ_∞^A in terms of A:

(*P1*) there is $C_0 > 0$ such that

$$\lambda_\infty^A = \lambda_\infty^0 - C_0 A^2 + o(A^2) \quad \text{as} \quad A \to 0^+;$$

(*P2*) for each $A_0 \in (0, \infty)$ such that $\lambda_\infty^{A_0} > \limsup_{|x|\to\infty} g(x, 0)$, there is $C_{A_0} > 0$ such that

$$\lambda_\infty^A = \lambda_\infty^{A_0} - C_{A_0}(A - A_0) + o(|A - A_0|) \quad \text{as} \quad |A - A_0| \to 0;$$

(*P3*) the function $A \mapsto \lambda_\infty^A$ is non-increasing on $(0, \infty)$. Hence, there is $A_* \in (0, \infty]$ such that $\lambda_\infty^A > \limsup_{|x|\to\infty} g(x, 0)$ if and only if $A \in [0, A_*)$.

Formulas for C_0 and C_{A_0} are derived to numerically determine their signs. (*P1*) yields a quadratic dependence of λ_∞^A on A for small A. (*P1*)–(*P3*) together imply in particular that the function $A \mapsto \lambda_\infty^A$ is decreasing on $[0, A_*)$ and non-increasing on $[A_*, \infty)$, saying that the larger the fluctuation in the shifting speed or location is, the harder the species can keep up with the shifting habitat, and therefore, the harder the species can survive or persist. Besides, our numerical simulations show the existence of two windows $[0, A_1]$ and $[A_1, A_2]$ (where λ_∞^A crosses 0) such that λ_∞^A decreases slowly for $A \in [0, A_1]$ and much faster for $A \in [A_1, A_2]$ (see Figs. 3, 4), saying that a persistent species under climate change is adapted to mild fluctuations in the shifting speed or location of the climate envelope, while the dependence becomes somewhat sensitive once the species is endangered by fluctuations.

Finally, we examine the solution of $\lambda_\infty^A = 0$ and its relation to the speed difference $c^* - c$ under the assumption that the critical shifting speed $c^* > 0$ and $c \in [0, c^*)$ so that the species persists in the absence of fluctuations. To fix the idea, we assume $\min_{t\in\mathbb{R}} \sigma(t) = -1$ and $\max_{t\in\mathbb{R}} \sigma(t) = 1$ such that A is indeed the amplitude of fluctuations. For each $c \in [0, c^*)$, properties (*P1*)–(*P3*) ensure that the equation $\lambda_\infty^A = 0$ admits a unique solution A_c. We show

(*P4*) $A_c > c^* - c$ for all $c \in [0, c^*)$, or equivalently, $\lambda_\infty^{c^*-c} > 0$ for all $c \in [0, c^*)$.

The property (*P4*) says that fluctuations of amplitude less than or equal to the speed difference $c^* - c$ can not drive a species to extinction. Our numerical results (see Fig. 5) actually show that much larger fluctuations are required. To understand this, we first note that with $A = c^* - c$, the speed function $c + A\sigma(t)$ oscillates periodically between $2c - c^*$ and c^*. In consideration of the facts that $\sigma(t)$ has zero average, and at least in the absence of fluctuations, the faster the climate envelope shifts the smaller λ_∞^A is, fluctuations of amplitude $A = c^* - c$ are too weak to endanger a persistent species.

The rest of the paper is organized as follows. In Sect. 2, we study the Eqs. (1.5) and (1.6) truncated on bounded domains with zero Dirichlet boundary in preparation for the investigation of (1.5) or equivalently (1.4). In particular, we define the top Lyapunov exponent and study its monotonicity with respect to the domain size. Section 3 is devoted to the establishment of the persistence criterion and global dynamics for (1.5). Theorems A and B are proven in this section. Besides, we establish the connection between the approximate top Lyapunov exponent and the top Lyapunov exponent of

(1.6). In Sect. 4, we first prove Theorem C, then perform numerical simulations to support our theoretical study, and finally, give a characterization of the approximate top Lyapunov exponent. In Sect. 5, we study the effects of fluctuations in the shifting speed and location of the climate envelope. In particular, we prove Theorem D and justify (*P1*)–(*P4*).

2 Truncated equations

In this section, we study top Lyapunov exponents of (1.6) truncated on bounded domains with zero Dirichlet boundary condition. For each $L > 0$, we consider the following linear problem:

$$\begin{cases} w_t = dw_{xx} + c(t)w_x + g(x,0)w, & x \in (-L, L), \\ w(t,-L) = 0 = w(t,L). \end{cases} \tag{2.1}$$

As $c(t)$ is almost-periodic, it is more convenient to consider the following family:

$$\begin{cases} w_t = dw_{xx} + \tilde{c}(t)w_x + g(x,0)w, & x \in (-L, L), \\ w(t,-L) = 0 = w(t,L), \end{cases} \tag{2.2}$$

where $\tilde{c} \in \mathcal{H} := \overline{\{c(\cdot + t) : t \in \mathbb{R}\}}$. The closure is taken under the topology of local uniform convergence. For $\tilde{c} \in \mathcal{H}$, we write $\tilde{c} \cdot t$ for $\tilde{c}(\cdot + t)$.

Let

$$X_L = \{v \in C([-L, L]) : v(-L) = v(L) = 0\}$$

be equipped with the maximum norm, namely, $\|v\|_\infty = \max_{[-L,L]} |v|$. Denote by $\Phi_L(t, \tilde{c})w_0$ the unique classical solution of (2.2) with initial condition $\Phi_L(0, \tilde{c})w_0 = w_0 \in X_L$. The operator norm of $\Phi_L(t, \tilde{c})$ is denoted by $\|\Phi_L(t, \tilde{c})\| := \sup_{w \in X_L, \|w\|_\infty = 1} \|\Phi_L(t, \tilde{c})w\|_\infty$.

Definition 2.1 (*Top Lyapunov exponent*) The number

$$\lambda_L := \sup_{\tilde{c} \in \mathcal{H}} \limsup_{t \to \infty} \frac{\ln \|\Phi_L(t, \tilde{c})\|}{t}$$

is called the top Lyapunov exponent of (2.1).

Note that

$$\ln \|\Phi_L(t+s, \tilde{c})\| = \ln \|\Phi_L(t, \tilde{c} \cdot s) \circ \Phi_L(s, \tilde{c})\| \le \ln \|\Phi_L(t, \tilde{c} \cdot s)\| + \ln \|\Phi_L(s, \tilde{c})\|$$

for any $\tilde{c} \in \mathcal{H}$ and $t, s \geq 0$. It then follows from the almost-periodicity of $c(t)$ and the subadditive ergodic theorem [see e.g. Kingman (1973)] that

$$\lim_{t\to\infty} \frac{\ln \|\Phi_L(t, \tilde{c})\|}{t} = \lambda_L, \quad \forall \tilde{c} \in \mathcal{H} \tag{2.3}$$

See also Mierczyński and Shen (2008, Corollary 3.2.2) or Shen and Yi (1998, Remark 4.3) for the limit (2.3). In the next lemma, we collect some well-known results related to the top Lyapunov exponent λ_L. Set $X_L^+ = \{w \in X_L : w \geq 0\}$.

Lemma 2.1 *There is a continuous function $w_L : \mathcal{H} \to X_L^+ \setminus \{0\}$ such that the following hold for any $\tilde{c} \in \mathcal{H}$:*

(1) $\|w_L(\tilde{c})\|_\infty = 1$,
(2) $\Phi_L(t, \tilde{c})w_L(\tilde{c}) = \|\Phi_L(t, \tilde{c})w_L(\tilde{c})\|_\infty w_L(\tilde{c} \cdot t)$,
(3) $\lim_{t\to\infty} \dfrac{\ln \|\Phi_L(t, \tilde{c})w_L(\tilde{c})\|_\infty}{t} = \lambda_L$,
(4) *For any $w_0 \in X_L^+ \setminus \{0\}$, $\lim_{t\to\infty} \dfrac{\ln \|\Phi_L(t, \tilde{c})w_0\|_\infty}{t} = \lambda_L$.*

Proof (1)–(3) can be found in Shen and Yi (1998, Theorem II.4.4 and Proposition II.4.10) [see also the arguments in Hutson et al. (2001, Theorem 3.14)]. (4) follows from (3), the comparison principle and Hopf's lemma. □

Remark 2.1 Lemma 2.1 was originally established for $\Phi_L(t, \tilde{c})$ acting on a fractional power space $\tilde{X}_L$ related to $-\partial_{xx}^2$ that is compactly embedded into $C^1([-L, L])$. We refer the reader to Henry (1981) and Pazy (1983) for more details about the fractional power space. Lemma 2.1 then follows because of the fact that the top Lyapunov exponents of $\Phi_L(t, \tilde{c})$ acting on $\tilde{X}_L$ and X_L coincide.

Lemma 2.2 *λ_L is non-decreasing in L. Moreover, $\lambda_L \leq \max_{[-L,L]} g(\cdot, 0)$.*

Proof For $L > 0$, let w_L be as in Lemma 2.1. Fix $0 < L_1 < L_2$ and $\tilde{c} \in \mathcal{H}$. Then, there exists $\epsilon_0 \in (0, 1)$ such that $\epsilon_0 w_{L_1}(\tilde{c}) < w_{L_2}(\tilde{c})$ on $[-L_1, L_1]$. It follows from the comparison principle that

$$\epsilon_0 \Phi_{L_1}(t, \tilde{c})w_{L_1}(\tilde{c}) \leq \Phi_{L_2}(t, \tilde{c})w_{L_2}(\tilde{c}) \quad \text{in} \quad [-L_1, L_1].$$

Hence,

$$\begin{aligned}
\lambda_{L_2} &= \lim_{t\to\infty} \frac{\ln \|\Phi_{L_2}(t, \tilde{c})w_{L_2}(\tilde{c})\|_\infty}{t} \\
&\geq \lim_{t\to\infty} \frac{\ln \|\epsilon_0 \Phi_{L_1}(t, \tilde{c})w_{L_1}(\tilde{c})\|_\infty}{t} = \lim_{t\to\infty} \frac{\ln \epsilon_0 + \ln \|\Phi_{L_1}(t, \tilde{c})w_{L_1}(\tilde{c})\|_\infty}{t} \\
&= \lambda_{L_1}.
\end{aligned}$$

Let $g_L = \max_{[-L,L]} g(\cdot, 0)$. Then, $e^{g_L t}$ is a supersolution of (2.2), and thus, $\Phi_L(t, \tilde{c})w_L(\tilde{c}) \leq e^{g_L t}$ in $[-L, L]$ for all $t \geq 0$. It follows that $\lambda_L \leq \lim_{t\to\infty} \frac{\ln e^{g_L t}}{t} = g_L$. This completes the proof. □

Observe that the top Lyapunov exponent of (2.1) plays an important role in the study of the dynamics of the following Dirichlet boundary value problem

$$\begin{cases} v_t = dv_{xx} + \tilde{c}(t)v_x + f(x, v), & x \in (-L, L), \\ v(t, -L) = 0 = v(t, L). \end{cases} \tag{2.4}$$

In fact, assumptions on f and a priori estimates for parabolic equations [see e.g. Henry (1981), Hess (1991)] ensure the local well-posedness of (2.4) in X_L. This together with the comparison principle yields the globally well-posedness of (2.4) in X_L^+. For each $v_0 \in X_L^+$, we denote by $v(t, \cdot; v_0, \tilde{c})$ the unique global solution of (2.4) with $v(0, \cdot; v_0, \tilde{c}) = v_0$. The following result can be found in Zhao (2003, Theorem 3.1) and the claims in its proof.

Proposition 2.1 *Assume (H). Let λ_L be the top Lyapunov exponent of* (2.1)*. Then, the following hold.*

(1) *If $\lambda_L < 0$, then $\lim_{t\to\infty} \|v(t, \cdot; v_0, \tilde{c})\|_\infty = 0$ for all $v_0 \in X_L^+$ and $\tilde{c} \in \mathcal{H}$.*
(2) *If $\lambda_L > 0$, then* (2.4) *admits a unique positive almost-periodic solution $v^*(t, \tilde{c})$. Moreover, for any $v_0 \in X_L^+ \backslash \{0\}$ and $\tilde{c} \in \mathcal{H}$, there holds $\lim_{t\to\infty} \|v(t, \cdot; v_0, \tilde{c}) - v^*(t, \tilde{c})\|_\infty = 0$.*

3 Persistence criterion and forced waves

In this section, we study the global dynamics of (1.4) and prove Theorems A and B . We assume (*H*) throughout this section. Recall that λ_L is the top Lyapunov exponent of (2.1). Since $\sup_{\mathbb{R}} g(\cdot, 0) < \infty$, Lemma 2.2 ensures that

$$\lambda_\infty := \lim_{L\to\infty} \lambda_L$$

is well-defined and finite, and is called the *approximate top Lyapunov exponent* of (1.6).

3.1 Spectral criterion for persistence

Recall from Sect. 1 that X^+ is the set of non-negative, bounded and uniformly continuous functions on $\mathbb{R}$. The theory of semigroups and comparison principles ensure that for any initial data $v_0 \in X^+$, (1.5) admits a unique global solution, denoted by $v(t, x; v_0)$, satisfying $v(t, \cdot; v_0) \in X^+$ for all $t \geq 0$.

Theorem 3.1 *The following statements hold.*

(1) *If $\lambda_\infty < 0$, then $\lim_{t\to\infty} \|v(t, \cdot; v_0)\|_\infty = 0$ for all $v_0 \in X^+$.*
(2) *If $\lambda_\infty > 0$, then*

$$\liminf_{t\to\infty} \inf_{x\in[-L,L]} v(t, x; v_0) > 0, \quad \forall L > 0 \quad \text{and} \quad v_0 \in X^+\backslash\{0\}.$$

Theorem A follows directly from Theorem 3.1, whose proof needs the following lemma.

Lemma 3.1 *Let $v_0 \in X^+$. For any $\epsilon > 0$, there exist $T(\epsilon), L(\epsilon) > 0$ such that*

$$v(t, x; v_0) < \epsilon, \quad \forall t > T(\epsilon), \ |x| > L(\epsilon).$$

In particular, $\lim_{\substack{t\to\infty \\ |x|\to\infty}} v(t, x; v_0) = 0$.

Proof Fix $v_0 \in X^+$, and write $v(t, x)$ for $v(t, x; v_0)$. Suppose on the contrary that the conclusion fails. Then there are $\epsilon_0 > 0$, $\{t_n\} \subset [0, \infty)$ satisfying $t_n \to \infty$ as $n \to \infty$, and $\{x_n\} \subset \mathbb{R}$ satisfying $|x_n| \to \infty$ such that $v(t_n, x_n) \geq \epsilon_0$ for all n. We may assume without loss of generality that $x_n \to \infty$ as $n \to \infty$.

For each n, let $v^n(t, x) = v(t + t_n, x + x_n)$. Obviously, v^n satisfies

$$v_t^n = dv_{xx}^n + c(t + t_n)v_x^n + f(x_n + x, v^n).$$

Due to a priori estimates for parabolic equations and the almost-periodicity of $c(t)$, we may assume without loss of generality that there are v^* and c^* such that

$$\lim_{n\to\infty} v^n(t, x) = v^*(t, x) \quad \text{locally uniformly in } (t, x) \in \mathbb{R} \times \mathbb{R},$$
$$\lim_{n\to\infty} c(t + t_n) = c^*(t) \quad \text{uniformly in } t \in \mathbb{R}.$$

Then, v^* satisfies $v^*(0, 0) \geq \epsilon_0$ and is a sub-solution of the following linear equation

$$w_t = dw_{xx} + c^*(t)w_x - \alpha w, \quad \forall (t, x) \in \mathbb{R} \times \mathbb{R}, \tag{3.1}$$

where $\alpha > 0$ is such that $\limsup_{x\to\infty} g(x, 0) \leq -\alpha$.

Note that $M := \sup_{\mathbb{R}\times\mathbb{R}} v^* < \infty$. Clearly, for any fixed $t_0 \in \mathbb{R}$, $w(t, x) = e^{-\alpha(t-t_0)}M$ is a solution of (3.1). The comparison principle then yields $v^*(t, x) \leq e^{-\alpha(t-t_0)}M$ for all $(t, x) \in [t_0, \infty) \times \mathbb{R}$, which implies $v^*(0, x) \leq e^{\alpha t_0}M$ for any $x \in \mathbb{R}$ and $t_0 < 0$. If we choose $t_0 \ll -1$ such that $e^{\alpha t_0}M < \epsilon_0$, then $v^*(0, x) < \epsilon_0$ for all $x \in \mathbb{R}$, which contradicts the fact $v^*(0, 0) \geq \epsilon_0$. This completes the proof. □

We now prove Theorem 3.1.

Proof of Theorem 3.1 (1) Fix $v_0 \in X^+$, and write $v(t, x)$ for $v(t, x; v_0)$. Clearly,

$$v_t = dv_{xx} + c(t)v_x + f(x, v) \leq dv_{xx} + c(t)v_x + g(x, 0)v.$$

By Lemma 3.1, for any $\delta > 0$, there are $T \geq 0$ and $\tilde{L} > 0$ such that

$$v(t, x) < \delta, \quad \forall t \geq T, \ |x| \geq \frac{\tilde{L}}{2}. \tag{3.2}$$

Replacing v_0 by $v(T, \cdot)$, we may assume without loss of generality that $T = 0$.

Obviously, $v^\delta := v - \delta$ satisfies

$$v_t^\delta \le d v_{xx}^\delta + c(t) v_x^\delta + g(x,0) v^\delta + \delta g(x,0), \quad \forall t \ge 0,\ x \in \mathbb{R}. \tag{3.3}$$

Since $\lambda_\infty < 0$, there exists $L > \tilde{L}$ such that $\lambda_L < 0$. Let $\eta : \mathbb{R} \to [0,1]$ be a smooth function satisfying $\eta(x) = 1$ for $|x| \le \frac{L}{2}$ and $\eta(x) = 0$ for $|x| \ge \frac{3L}{4}$. Set $m_0 := \min_{[-L,L]} v_0$ and $v_0^\delta := \eta(v_0 - m_0)$. Clearly, $v_0^\delta \in X^+$. Let $v(t,x;v_0^\delta)$ be the unique solution of the following problem:

$$\begin{cases} v_t = d v_{xx} + c(t) v_x + g(x,0) v + \delta g(x,0), & t > 0,\ -L < x < L, \\ v(t,-L) = v(t,L) = 0, & t > 0, \\ v(0,x) = v_0^\delta(x), & x \in [-L,L]. \end{cases}$$

Then, the variation of constants formula yields

$$v(t,\cdot;v_0^\delta) = \Phi_L(t,c) v_0^\delta + \delta \int_0^t \Phi_L(t-s, c\cdot s) g(\cdot,0) ds,$$

where we recall that $\Phi_L(t,c)$ is the solution operator of (2.2) with $\tilde{c}(t) = c(t)$. It follows from the fact $\lambda_L \le \lambda_\infty < 0$ and (2.3) that there is $M > 0$ (independent of L) such that

$$v(t,\cdot;v_0^\delta) \le \Phi_L(t,c) v_0^\delta + \delta M \quad \text{in} \quad (-L,L), \quad \forall t \ge 0. \tag{3.4}$$

Observe that $v^\delta(t,\pm L) < 0$ for all $t \ge 0$ and $v^\delta(0,x) = v_0(x) - \delta \le v_0^\delta(x)$ for all $x \in [-L,L]$. It follows from (3.3) and the comparison principle that $v^\delta(t,x) \le v(t,x;v_0^\delta)$ for all $t \ge 0$ and $-L < x < L$, which together with (3.4) yields

$$v^\delta(t,\cdot) \le \Phi_L(t,c) v_0^\delta + \delta M \quad \text{in} \quad (-L,L), \quad \forall t \ge 0.$$

Since $\lambda_L < 0$ and (2.3) ensure the existence of $T_\delta > 0$ such that $\Phi_L(t,c) v_0^\delta \le \delta$ in $(-L,L)$ for all $t \ge T_\delta$, we find $v^\delta(t,x) \le (1+M)\delta$ for all $t \ge T_\delta$ and $-L < x < L$. This together with (3.2) and $v = v^\delta + \delta$ implies that $v(t,x) \le (2+M)\delta$ for all $t \ge T_\delta$ and $x \in \mathbb{R}$. Since $\delta > 0$ is arbitrary, we conclude $\lim_{t\to\infty} \sup_{x\in\mathbb{R}} v(t,x) = 0$. This proves (1).

(2) Since $\lambda_\infty > 0$, there holds $\lambda_L > 0$ for all $L \gg 1$. Since non-negative solutions of (1.5) give rise to super-solution of (2.4) with $\tilde{c}(t) = c(t)$, the result follows directly from Proposition 2.1 (2). □

3.2 Forced wave solutions

In this subsection, we study the existence and uniqueness of forced wave solutions of (1.4). Again, we focus on the Eq. (1.5).

Definition 3.1 An entire solution $v(t,x)$ of (1.5) is called a *profile function* if it is bounded, positive and almost-periodic in t for any fixed x.

Theorem 3.2 *Assume* $\lambda_\infty > 0$.

(1) *The Eq.* (1.5) *admits a unique profile function* v^**. It is also unique in the class of bounded positive entire solutions* v *of* (1.5) *satisfying* $\inf_{\mathbb{R}\times[-L,L]} v > 0$ *for all* $L > 0$.
(2) *For any* $v_0 \in X^+\backslash\{0\}$*, there holds* $\lim_{t\to\infty} \|v(t,\cdot;v_0) - v^*(t,\cdot)\|_\infty = 0$.

Theorem B follows directly from Theorem 3.2. We prove several lemmas before proving Theorem 3.2. The next result follows from arguments as in the proof of Lemma 3.1.

Lemma 3.2 *Let* v *be a bounded positive entire solution of* (1.5)*. Then,* $\lim_{|x|\to\infty} \sup_{t\in\mathbb{R}} v(t,x) = 0$.

We need the following uniqueness result.

Lemma 3.3 *For each* $i = 1, 2$*, let* v_i *be a bounded positive entire solution of* (1.5) *and satisfy* $\inf_{\mathbb{R}\times[-L,L]} v_i > 0$ *for all* $L > 0$*. Then,* $v_1 = v_2$.

Proof Switching the role of v_1 and v_2, we only need to show $v_1 \leq v_2$. For any $\epsilon > 0$, let $K_\epsilon = \{\kappa \geq 1 : v_1 - \epsilon \leq \kappa v_2\}$. By Lemma 3.2,

$$\lim_{|x|\to\infty} \sup_{t\in\mathbb{R}} v_i(t,x) = 0, \quad i = 1, 2. \tag{3.5}$$

This together with the uniform positivity of v_2 on $\mathbb{R}\times[-L,L]$ for all $L > 0$ implies that $K_\epsilon \neq \emptyset$. Set $\kappa_\epsilon := \inf\{\kappa : \kappa \in K_\epsilon\}$. It is clear that κ_ϵ is non-increasing in $\epsilon > 0$, and thus, $\kappa_0 := \lim_{\epsilon\to 0} \kappa_\epsilon$ exists and belongs to $[1,\infty]$. We show

$$\kappa_0 = 1, \tag{3.6}$$

which clearly yields $v_1 \leq v_2$.

For each $\epsilon > 0$, the definition of κ_ϵ ensures $\inf_{\mathbb{R}\times\mathbb{R}} (\kappa_\epsilon v_2 - v_1 + \epsilon) = 0$. Thus, there is a sequence $\{t_n^\epsilon\} \subset \mathbb{R}$ such that $\lim_{n\to\infty} \inf_{x\in\mathbb{R}} \left[\kappa_\epsilon v_2(t_n^\epsilon, x) - v_1(t_n^\epsilon, x) + \epsilon\right] = 0$. We may assume without loss of generality that there are $v_i^\epsilon(t,x), i = 1, 2$ and $c^\epsilon \in \mathcal{H}$ such that

$$\begin{aligned} v_i^\epsilon(t,x) &= \lim_{n\to\infty} v_i(t + t_n^\epsilon, x) \quad \text{locally uniform in } (t,x) \in \mathbb{R}\times\mathbb{R}, \quad i = 1, 2, \\ c^\epsilon(t) &= \lim_{n\to\infty} c(t + t_n^\epsilon) \quad \text{uniformly in } t \in \mathbb{R}. \end{aligned}$$

Then, $v_i^\epsilon, i = 1, 2$ are bounded positive entire solutions of (1.5) with c replaced by c^ϵ. Moreover, there hold $\kappa_\epsilon v_2^\epsilon \geq v_1^\epsilon - \epsilon$ and $\inf_{x\in\mathbb{R}} \left[\kappa_\epsilon v_2^\epsilon(0,x) - v_1^\epsilon(0,x) + \epsilon\right] = 0$. It follows from (3.5) that there is $x_\epsilon \in \mathbb{R}$ such that $\kappa_\epsilon v_2^\epsilon(0, x_\epsilon) = v_1^\epsilon(0, x_\epsilon) - \epsilon$. In particular, the function $t \mapsto \kappa_\epsilon v_2^\epsilon(t, x_\epsilon) - v_1^\epsilon(t, x_\epsilon) + \epsilon$ attains its minimum value at

0, and the function $x \mapsto \kappa_\epsilon v_2^\epsilon(0,x) - v_1^\epsilon(0,x) + \epsilon$ attains its minimum value at x_ϵ. Hence,

$$\begin{aligned}
0 &= \kappa_\epsilon v_{2,t}^\epsilon(0,x_\epsilon) - v_{1,t}^\epsilon(0,x_\epsilon)\\
&= d\left[\kappa_\epsilon v_{2,xx}^\epsilon(0,x_\epsilon) - v_{1,xx}^\epsilon(0,x_\epsilon)\right] + \tilde{c}^\epsilon(0)\left[\kappa_\epsilon v_{2,x}^\epsilon(0,x_\epsilon) - v_{1,x}^\epsilon(0,x_\epsilon)\right]\\
&\quad + \kappa_\epsilon v_2^\epsilon(0,x_\epsilon) g(x_\epsilon, v_2^\epsilon(0,x_\epsilon)) - v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, v_1^\epsilon(0,x_\epsilon)\\
&\geq \kappa_\epsilon v_2^\epsilon(0,x_\epsilon) g(x_\epsilon, v_2^\epsilon(0,x_\epsilon)) - v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, v_1^\epsilon(0,x_\epsilon))\\
&\geq \kappa_\epsilon v_2^\epsilon(0,x_\epsilon) g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon)) - v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, v_1^\epsilon(0,x_\epsilon))\\
&= \kappa_\epsilon v_2^\epsilon(0,x_\epsilon) g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon)) - v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon))\\
&\quad + v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon)) - v_1^\epsilon(0,x_\epsilon) g(x_\epsilon, v_1^\epsilon(0,x_\epsilon))\\
&= \left[\kappa_\epsilon v_2^\epsilon(0,x_\epsilon) - v_1^\epsilon(0,x_\epsilon)\right]\left[g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon)) + v_1^\epsilon(0,x_\epsilon) g_u(x_\epsilon,\eta_\epsilon)\right],
\end{aligned}$$

where we used the monotonicity of $v \mapsto g(x_\epsilon, v)$ in the second inequality, and the first order Taylor's expansion of the function $v \mapsto g(x_\epsilon, v)$ in the last equality. Hence, η_ϵ is between $\kappa_\epsilon v_2^\epsilon(0,x_\epsilon)$ and $v_1^\epsilon(0,x_\epsilon)$. Since $\kappa_\epsilon v_2^\epsilon(0,x_\epsilon) - v_1(0,x_\epsilon) < 0$, we deduce from $g_u \leq 0$ that

$$g(x_\epsilon, 0) \geq g(x_\epsilon, \kappa_\epsilon v_2^\epsilon(0,x_\epsilon)) + v_1^\epsilon(0,x_\epsilon) g_u(x_\epsilon,\eta_\epsilon) \geq 0.$$

As $\limsup_{|x|\to\infty} g(x,0) < 0$, there must hold the boundedness of $\{x_\epsilon\}_\epsilon$. Since $\kappa_\epsilon = \frac{v_1^\epsilon(0,x_\epsilon)-\epsilon}{v_2^\epsilon(0,x_\epsilon)}$, we conclude the boundedness of $\{\kappa_\epsilon\}$, and thus, $\kappa_0 \in [1,\infty)$.

Then, there is a sequence $\{\epsilon_n\}$ satisfying $\epsilon_n \to 0$ as $n \to \infty$, a point $x_* \in \mathbb{R}$ and functions v_i^*, $i = 1, 2$ and c^* such that

$$\begin{aligned}
x^* &= \lim_{n\to\infty} x_{\epsilon_n},\\
v_i^*(t,x) &= \lim_{n\to\infty} v_i^{\epsilon_n}(t,x) \quad \text{locally uniformly in } (t,x) \in \mathbb{R}\times\mathbb{R},\\
c^*(t) &= \lim_{n\to\infty} c^{\epsilon_n}(t) \quad \text{uniformly in } t \in \mathbb{R}.
\end{aligned}$$

Clearly, v_i^*, $i = 1, 2$ are bounded positive entire solutions of (1.5) with c replaced by c^*. Moreover, $\kappa_0 v_2^* \geq v_1^*$ and $\kappa_0 v_2^*(0,x^*) - v_1^*(0,x^*) = 0$.

Note that $w := \kappa_0 v_2^* - v_1^*$ satisfies $w(0,x^*) = 0$ and

$$\begin{aligned}
w_t &= dw_{xx} + c^*(t)w_x + \kappa_0 v_2^* g(x, v_2^*) - v_1^* g(x, v_1^*)\\
&\geq dw_{xx} + c^*(t)w_x + \kappa_0 v_2^* g(x, \kappa_0 v_2^*) - v_1^* g(x, v_1^*)\\
&= dw_{xx} + c^*(t)w_x + \kappa_0 v_2^* g(x, \kappa_0 v_2^*) - v_1^* g(x, \kappa_0 v_2^*)\\
&\quad + v_1^* g(x, \kappa_0 v_2^*) - v_1^* g(x, v_1^*)\\
&= dw_{xx} + c^*(t)w_x + [g(x, \kappa_0 v_2^*) + v_1^* g_u(x,\eta)]w, \quad \forall t \in \mathbb{R},
\end{aligned}$$

where $\eta = \eta(t,x)$ is a function between $\kappa_0 v_2^*(t,x)$ and $v_1^*(t,x)$. The strong maximum principle then implies $w \equiv 0$. This together with the fact that both v_1^* and v_2^* satisfy

(1.5) with c replaced by c^* yields $g(x, v_1^*(t,x)) = g(x, v_2^*(t,x))$ for all $(t,x) \in \mathbb{R}\times\mathbb{R}$, and hence,

$$g(x, v_2^*(t,x)) = g(x, v_1^*(t,x)) = g(x, \kappa_0 v_2^*(t,x)), \quad \forall (t,x) \in \mathbb{R}\times\mathbb{R},$$

leading to (3.6). This completes the proof. $\square$

To indicate the dependence of $v(t,x;v_0)$ on the almost-periodic function c, we write $v(t,x;v_0,c)$ for $v(t,x;v_0)$. We use both notations interchangeably whenever needed. For each $t_0 \in \mathbb{R}$, we write $c\cdot t_0 = c(\cdot + t_0)$. It follows from the uniqueness of solutions that

$$v(t+s,\cdot;v_0,c\cdot\tau) = v(t,\cdot;v(s,\cdot;v_0,c\cdot\tau),c\cdot(s+\tau)), \quad \forall t,s \geq 0,\ \tau \in \mathbb{R}, \tag{3.7}$$

where $v(\cdot,\cdot;v_0,c\cdot t_0)$ denotes the unique solution of (1.5) with c replaced by $c\cdot t_0$ and initial condition $v(0,\cdot;v_0,c\cdot t_0) = v_0$.

Proof of Theorem 3.2 (1) The proof is broken into two steps.

Step 1 We show the existence of a unique bounded positive entire solution v^* of (1.5) satisfying $\inf_{\mathbb{R}\times[-L,L]} v^* > 0$ for all $L > 0$.

Let $v(t,x;v_0,c)$ be a solution of (1.5) with initial condition $v(0,\cdot;v_0,c) = v_0 \in X^+\backslash\{0\}$. Since c is an almost-periodic function, there exists $t_n \to \infty$ such that $c\cdot t_n \to c$ uniformly as $n\to\infty$. By a priori estimates for parabolic equations, we may assume without loss of generality the existence of v^* such that $v(t+t_n,x;v_0,c)$ converges to $v^*(t,x)$ locally uniformly in $(t,x)\in\mathbb{R}\times\mathbb{R}$ as $n\to\infty$. It follows from Theorem 3.1(2) and Lemma 3.3 that v^* is the unique bounded positive entire solution of (1.5) satisfying $\inf_{\mathbb{R}\times[-L,L]} v^* > 0$ for all $L > 0$.

Step 2 We show that v^* is almost-periodic in t uniformly for x in bounded sets. Hence, it is a profile function.

Since c is an almost-periodic function, for any given sequences $\{\alpha_n'\}, \{\beta_n'\} \subset \mathbb{R}$, there are subsequences $\{\alpha_n\} \subset \{\alpha_n'\}$ and $\{\beta_n\} \subset \{\beta_n'\}$ such that

$$\lim_{n\to\infty}\lim_{m\to\infty} c(t+\alpha_n+\beta_m) = \lim_{n\to\infty} c(t+\alpha_n+\beta_n), \quad \forall t \in \mathbb{R}.$$

See Fink (1974, Theorem 1.17).

We write $v^*(t,x;c)$ for $v^*(t,x)$ to indicate the dependence on c. Schauder estimates ensure that $v^*(t,x;c)$ is uniformly continuous in $(t,x)\in\mathbb{R}\times\mathbb{R}$. To show that $v^*(t,x;c)$ is almost-periodic in t uniformly for x in bounded sets, we only need to prove that the limit

$$\lim_{n\to\infty}\lim_{m\to\infty} v^*(t+\alpha_n+\beta_m,x;c) = \lim_{n\to\infty} v^*(t+\alpha_n+\beta_n,x;c) \tag{3.8}$$

holds for all $t\in\mathbb{R}$ and uniformly for x in bounded subsets of $\mathbb{R}$.

We may assume without without loss of generality

$$
\begin{aligned}
&c' = \lim_{m\to\infty} c\cdot\beta_m, \quad c'' = \lim_{n\to\infty} c\cdot(\alpha_n+\beta_n),\\
&v'(x) = \lim_{m\to\infty} v^*(\beta_m, x; c) \text{ locally uniformly in } x\in\mathbb{R},\\
&v''(x) = \lim_{n\to\infty} v^*(\alpha_n+\beta_n, x; c) \text{ locally uniformly in } x\in\mathbb{R}.
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
v(t,x;v',c') &= \lim_{m\to\infty} v^*(t+\beta_m, x; c) \text{ locally uniformly in } (t,x)\in\mathbb{R}\times\mathbb{R},\\
v(t,x;v'',c'') &= \lim_{n\to\infty} v^*(t+\alpha_n+\beta_n, x; c) \text{ locally uniformly in } (t,x)\in\mathbb{R}\times\mathbb{R}.
\end{aligned}
\tag{3.9}
$$

where $v(t,x;v',c')$ and $v(t,x;v'',c'')$ are bounded positive entire solutions of (1.5) with c replaced by c' and c'', respectively. Moreover, arguments as in **Step 1** ensure that $\inf_{\mathbb{R}\times[-L,L]} v(\cdot,\cdot;v',c')>0$ and $\inf_{\mathbb{R}\times[-L,L]} v(\cdot,\cdot;v'',c'')>0$ for all $L>0$.

Let

$$
v'(t,x) := \lim_{n\to\infty} v(t+\alpha_n, x; v', c') \text{ locally uniformly in } (t,x)\in\mathbb{R}\times\mathbb{R}.
$$

Since $\lim_{n\to\infty} c'\cdot\alpha_n = c''$, we conclude that $v'(t,x)$ is a bounded positive entire solutions of (1.5) with c replaced by c'' and satisfies $\inf_{\mathbb{R}\times[-L,L]} v'(t,x)>0$ for all $L>0$. Hence, Lemma 3.3 guarantees that

$$
v'(t,x) = v(t,x;v'',c''), \quad \forall (t,x)\in\mathbb{R}\times\mathbb{R}.
$$

It follows from (3.9) that

$$
\begin{aligned}
&\lim_{n\to\infty}\lim_{m\to\infty} v^*(t+\alpha_n+\beta_m, x; c)\\
&\quad = \lim_{n\to\infty} v(t+\alpha_n, x; v', c') = v(t,x;v'',c'') = \lim_{n\to\infty} v^*(t+\alpha_n+\beta_n, x; c)
\end{aligned}
$$

holds for all $t\in\mathbb{R}$ and uniformly for x in bounded subsets. This proves (3.8), and hence, $v^*(t,x;c)$ is almost-periodic in t uniformly for x in bounded sets. This proves (1)

(2) Let $v_0\in X^+\setminus\{0\}$ and suppose on the contrary that the conclusion fails. Then, there exist $\epsilon_0>0$, and sequences $\{x_n\}\subset\mathbb{R}$ and $\{t_n\}\subset(0,\infty)$ satisfying $t_n\to\infty$ as $n\to\infty$ such that

$$
|v(t_n,x_n;v_0,c) - v^*(t_n,x_n;c)| \ge \epsilon_0, \quad \forall n. \tag{3.10}
$$

We may assume without loss of generality that $c\cdot t_n\to c'$ as $n\to\infty$. We consider two cases.

Case (i) $\{x_n\}$ is bounded. We may assume that $x_n \to x'$ as $n \to \infty$. By a prior estimates, we may assume that

$$v(t+t_n, x; v_0, c) \to v_1(t, x; c') \text{ locally uniformly in } (t, x) \in \mathbb{R} \times \mathbb{R},$$
$$v^*(t+t_n, x; c) \to v_2(t, x; c') \text{ locally uniformly in } (t, x) \in \mathbb{R} \times \mathbb{R},$$

where for each $i = 1, 2$, $v_i(t, x; c')$ is a bounded positive entire solution of (1.5) with c replaced by c' and satisfies $\inf_{\mathbb{R}\times[-L,L]} v_i(\cdot, \cdot; c') > 0$ for all $L > 0$. Note that the positivity of $v_1(t, x; c')$ follows from Theorem 3.1 (2). Hence, by Lemma 3.3, $v_1(t, x; , c') = v_2(t, x; c')$ for all $(t, x) \in \mathbb{R} \times \mathbb{R}$, which contradicts the fact that $|v_1(0, x'; c') - v_2(0, x'; c')| \geq \epsilon_0$.
Case (ii) $\{x_n\}$ is unbounded. By Lemma 3.1, $\lim_{n\to\infty} v^*(t_n, x_n; c) = 0$ and $\lim_{n\to\infty} v(t_n, x_n; v_0, c) = 0$. This is in contradictory to (3.10).

This proves (2), and hence, completes the proof of the theorem. □

3.3 Characterization of the approximate top Lyapunov exponent: I

In this subsection, we study the connections between λ_∞ and the *top Lyapunov exponent* of (1.6).

Consider the following family of equations:

$$w_t = dw_{xx} + \tilde{c}(t)w_x + g(x, 0)w, \quad x \in \mathbb{R}, \tag{3.11}$$

where $\tilde{c} \in \mathcal{H}$. Let X and X^+ be as in Sect. 1, that is, X is the space of bounded and uniformly continuous functions on $\mathbb{R}$ and is equipped with the supremum norm $\|u\|_\infty = \sup_{x\in\mathbb{R}} |u(x)|$, and $X^+ = \{u \in X : u \geq 0\}$. Denote by $\Phi(t, \tilde{c})w_0$ the unique classical solution of (3.11) with initial condition $\Phi(0, \tilde{c})w_0 = w_0 \in X$. The operator norm of $\Phi(t, \tilde{c})$ is denoted by $\|\Phi(t, \tilde{c})\| := \sup_{w\in X, \|w\|_\infty=1} \|\Phi(t, \tilde{c})w\|_\infty$.

Definition 3.2 (*Top Lyapunov exponent*) The number

$$\lambda := \sup_{\tilde{c}\in\mathcal{H}} \limsup_{t\to\infty} \frac{\ln \|\Phi(t, \tilde{c})\|}{t}$$

is called the top Lyapunov exponent of (1.6).

Note that

$$\ln \|\Phi(t+s, \tilde{c})\| = \ln \|\Phi(t, \tilde{c}\cdot s) \circ \Phi(s, \tilde{c})\| \leq \ln \|\Phi(t, \tilde{c}\cdot s)\| + \ln \|\Phi(s, \tilde{c})\|$$

for any $\tilde{c} \in \mathcal{H}$ and $t, s \geq 0$. It follows from the almost-periodicity of $c(t)$ and the subadditive ergodic theorem [see e.g. Kingman (1973)] that $\lim_{t\to\infty} \frac{\ln \|\Phi(t,\tilde{c})\|}{t} = \lambda$ for all $\tilde{c} \in \mathcal{H}$.

It is clear that $\lambda_\infty \leq \lambda$. Thanks to Theorem 3.1 (1), we are able to prove the following connections between λ_∞ and λ.

Proposition 3.1 *The following hold.*

(1) *If* $\lambda_\infty \geq \limsup_{|x|\to\infty} g(x,0)$*, then* $\lambda_\infty = \lambda$.
(2) λ_∞ *and* λ *have the same sign, that is,* $\lambda_\infty > 0$, $\lambda_\infty = 0$ *and* $\lambda_\infty < 0$ *if and only if* $\lambda > 0$, $\lambda = 0$ *and* $\lambda < 0$*, respectively.*

Proof We write $\lambda_\infty(a)$ and $\lambda(a)$ for λ_∞ and λ, respectively to indicate the dependence on $a = g(\cdot, 0)$.

(1) Assume that $\lambda_\infty(a) < \lambda(a)$. Without loss of generality, we may assume that

$$\lambda_\infty(a) < 0 < \lambda(a).$$

For otherwise, we can take $\lambda_0 \in (\lambda_\infty, \lambda)$ and replace $a(x)$ by $a_0(x) = a(x) - \lambda_0$. Then $\lambda_\infty(a_0) = \lambda_\infty(a) - \lambda_0 < 0 < \lambda - \lambda_0 = \lambda(a_0)$, and $\limsup_{|x|\to\infty} a_0(x) < 0$. Let $v_0^* \equiv 1$ and $\tilde{a}(t,x) = g(x, v(t,\cdot; v_0^*))$, where $v(t,x;v_0^*)$ denotes the solution of (1.5) with $v(0,\cdot;v_0^*) = v_0^* \in X^+$. Theorem A (1) ensures that $\lim_{t\to\infty} \|v(t,\cdot;v_0^*)\|_\infty = 0$. This together with the uniform continuity of g on $\mathbb{R} \times [0,\delta]$ for any $\delta > 0$ implies the existence of some $T > 0$ such that

$$a(x) \leq \tilde{a}(t,x) + \frac{\lambda(a)}{2}, \quad \forall t \geq T,\ x \in \mathbb{R}.$$

It follows from the comparison principle for parabolic equations that

$$\Phi(t, c\cdot T) v(T,\cdot;v_0^*) \leq e^{\frac{\lambda(a)}{2}t} v(t+T,\cdot;v_0^*), \quad \forall t \geq 0.$$

Note that $\inf_{x\in\mathbb{R}} v(T,x;v_0^*) > 0$, which is guaranteed by the uniform positivity of v_0^* and the lower boundedness of $g : \mathbb{R} \times [0,\delta) \to \mathbb{R}$ for any $\delta > 0$. Hence, there is $M > 0$ such that for any $v_0 \in X$ with $\|v_0\|_\infty = 1$,

$$-Mv(T,\cdot;v_0^*) \leq v_0 \leq Mv(T,\cdot;v_0^*).$$

Then by the comparison principle for parabolic equations again,

$$-M\Phi(t,c\cdot T)v(T,\cdot;v_0^*) \leq \Phi(t,c\cdot T)v_0 \leq M\Phi(t,c\cdot T)v(T,\cdot;v_0^*), \quad \forall t \geq 0.$$

This implies that $\|\Phi(t,c\cdot T)\| \leq M\|\Phi(t,c\cdot T)v(T,\cdot;v_0^*)\|$. It then follows that $0 < \lambda(a) \leq \frac{\lambda(a)}{2}$, which is a contradiction. Therefore, $\lambda_\infty(a) = \lambda(a)$.

(2) Given (1), it suffices to show $\lambda < 0$ when $\lambda_\infty < \limsup_{|x|\to\infty} g(x,0)$. Suppose on the contrary that $\lambda \geq 0$. Then, there is $\lambda_0 > 0$ such that

$$\lambda_\infty(a) + \lambda_0 < \limsup_{|x|\to\infty} g(x,0) + \lambda_0 < 0 < \lambda(a) + \lambda_0.$$

Let $a_0(x) = g(x,0) + \lambda_0$. Then, $\lambda_\infty(a_0) < \limsup_{|x|\to\infty} a_0(x) < 0 < \lambda(a_0)$. Arguments as in the proof of (1) gives $\lambda(a_0) < \frac{\lambda(a_0)}{2}$, which is a contradiction. Hence $\lambda < 0$. □

We end this section with the following remark.

Remark 3.1 The analysis conducted for the model (1.4) can be adapted to treat the following more general one:

$$u_t = du_{xx} + f(t, x - \int_0^t c(s)ds, u), \quad x \in \mathbb{R}, \tag{3.12}$$

where $(x, u) \mapsto f(t, x, u)$ satisfies (H) uniformly in $t \in \mathbb{R}$, and $t \mapsto f(t, x, u)$ is almost periodic (or even uniquely ergodic) locally uniformly in $(x, u) \in \mathbb{R} \times [0, \infty)$.

Indeed, in the moving frame, (3.12) becomes

$$v_t = dv_{xx} + c(t)v_x + f(t, x, v), \quad x \in \mathbb{R}. \tag{3.13}$$

Its linearization at $v \equiv 0$ reads

$$w_t = dw_{xx} + c(t)w_x + f_u(t, x, 0)w, \quad x \in \mathbb{R}. \tag{3.14}$$

Then, the approximate top Lyapunov exponent can be defined by considering (3.14) and its truncated equations.

Note that for (3.13), the almost-periodicity also appears in the nonlinear term and this is basically the only point where (3.13) differs from (1.5). But, the mathematical analysis reacts insensitively to this difference. Therefore, modifying the arguments in a straightforward way, we can prove the persistence criterion and global dynamics for (3.13) as well as the characterization of the approximate top Lyapunov exponent. These information then carries over to (3.12).

4 Persistence criterion and forced waves: the periodic case

In this section, we study the global dynamics of (1.4) in the periodic case, and prove Theorem C. We also perform numerical simulations to support our theoretical study.

4.1 Persistence and forced waves

Recall that $v(t, x; v_0)$ denotes the solution of (1.5) with $v(0, \cdot; v_0) = v_0 \in X^+$. Theorem C follows from the following result.

Theorem 4.1 *Suppose that $c(t)$ is T-periodic for some $T > 0$. The following statements hold.*

(1) *If $\lambda_\infty \le 0$, then $\lim_{t\to\infty} \|v(t, \cdot; v_0)\|_\infty = 0$ for all $v_0 \in X^+$.*
(2) *If $\lambda_\infty > 0$, then (1.5) admits a unique bounded positive T-periodic solution v^*. Moreover, there holds*

$$\lim_{t\to\infty} \|v(t, \cdot; u_0) - v^*(t, \cdot)\|_\infty = 0, \quad \forall u_0 \in X^+ \setminus \{0\}.$$

We present the following result on exponential separations before proving Theorem 4.1. Let

$$\Psi(t,s)w_0 = w(t,\cdot;s,w_0),$$

where $w(t,\cdot;s,w_0)$ is the solution of (1.6) with $w(s,\cdot;s,w_0) = w_0 \in X$. We write $w(t,\cdot;0,w_0)$ as $w(t,\cdot;w_0)$.

Lemma 4.1 *If $\lambda_\infty > \limsup_{|x|\to\infty} g(x,0)$, then there exist complementary closed subspaces $X_1(t)$ and $X_2(t)$ of X such that*

(1) *$X = X_1(t) \oplus X_2(t)$, where $X_1(t) = \operatorname{span}\{w_1(t,\cdot)\}$ for some positive entire solution w_1 of (1.6) and any $w_2 \in X_2(t)\backslash\{0\}$ changes sign on $\mathbb{R}$, and X_2 is invariant in the sense:*

$$\Psi(t,s)X_1(s) = X_1(t), \quad t \ge s,$$
$$\Psi(t,s)X_2(s) \subset X_2(t), \quad t \ge s;$$

(2) *there are $C, \gamma > 0$ such that for any $w_2 \in X_2(s)$, there holds*

$$\frac{\|\Psi(t,s)w_2\|_\infty}{\|w_1(t-s,\cdot)\|_\infty} \le Ce^{-\gamma(t-s)}\frac{\|w_2\|_\infty}{\|w_1(s,\cdot)\|_\infty}, \quad t \ge s.$$

Proof We write $\lambda_\infty(a)$ for λ_∞ to indicate the dependence on $a := g(\cdot,0)$. Note that for any $\lambda_0 \in \mathbb{R}$, $\lambda_\infty(a+\lambda_0) = \lambda_\infty(a)+\lambda_0$. Without loss of generality, we may assume that $\lambda_\infty(a) > 0$. For otherwise, we may choose $\lambda_0 \in (-\lambda_\infty(a), -\limsup_{|x|\to\infty} a(x))$ and replace $a(x)$ by $a_0(x) = a(x) + \lambda_0$. It is clear that $\lambda_\infty(a_0) > 0$ and $\limsup_{|x|\to\infty} a_0(x) < 0$. Then by Lemma 2.1, the conditions in Húska and Poláčik (2008, Theorem 9.2) are satisfied and the lemma then follows from Húska and Poláčik (2008, Theorem 9.2). □

Proof of Theorem 4.1 By Theorems 3.1 and 3.2 , we only need to prove the theorem when $\lambda_\infty = 0$.

Suppose on the contrary that the conclusion fails. Then, we can follow the proof of Theorem B to find a maximal bounded positive T-periodic solution v^* of (1.5). Write $v^*(t)$ for $v^*(t,x)$. By the variation of constants formula,

$$\begin{aligned} v^*(0) = v^*(nT) &= \Psi(nT,0)v^*(0) \\ &\quad + \int_0^{nT} \Psi(nT,s)\left[g(\cdot,v^*(s)) - g(\cdot,0)\right] v^*(s)ds. \end{aligned} \tag{4.1}$$

Let $w_1 \in X_1(0)$ and $w_2 \in X_2(0)$ be such that $v^*(0) = w_1 + w_2$. It follows from (4.1), $g(x,v) \le g(x,0)$ for all $x \in \mathbb{R}$ and $v \ge 0$, and Lemma 4.1 (2) that

$$\begin{aligned} v^*(0) &\le \Psi(nT,0)v^*(0) = \Psi(nT,0)w_1 + \Psi(nT,0)w_2 \\ &= w_1 + \Psi(nT,0)w_2 \to w_1 \quad \text{as} \quad n \to \infty, \end{aligned}$$

leading to $v^*(0) \leq w_1$, and hence, $w_2 \leq 0$. This implies that $w_2 = 0$ for otherwise w_2 must change its sign due to Lemma 4.1(1). Hence, $v^*(0) = w_1 \in X_1(0)$, which together with (4.1) implies that $g(\cdot, v^*(s)) = g(\cdot, 0)$, leading to a contradiction. $\square$

4.2 Numerical simulations for extinction and persistence

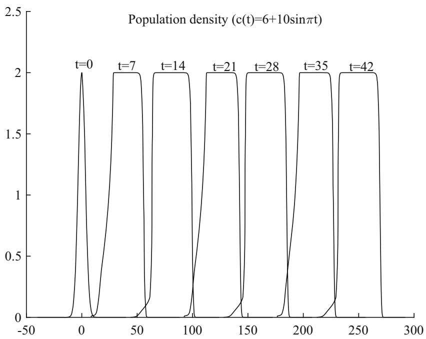
In this subsection, we perform numerical simulations to complement theoretical results for extinction and persistence proven in earlier subsections. To do so, we first fix d, f and $c(t)$ appearing in the model (1.4). We set $d = 1$, let f be given in (1.2) with parameters $K = 2$, $D = 2$ and $R = 10$, and choose $c(t) = c + A \sin \pi t$ with period 2, where $c \in \mathbb{R}$ and $A \geq 0$ are control parameters. We also fix the initial data $u_0(x) = 2e^{-\frac{x^2}{20}}$.

We actually simulate the solution $v(t, x)$ of (1.5) with initial data $v_0 = u_0$. Then,

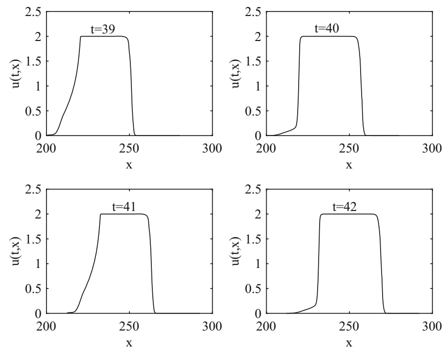
$$u(t, x) = v\left(t, x - \int_0^t c(s)ds\right), \quad (t, x) \in [0, \infty) \times \mathbb{R}.$$

To simulate $v(t, x)$, we truncate (1.5) and consider it on $(-L, L) = (-40, 40)$ with zero Dirichlet boundary condition on $\pm L$. We compute the solution of this initial-boundary value problem by the finite difference method in space and Runge–Kutta method in time. In all numerical simulations, the space step size and time step size are respectively taken as 0.05 and 0.001.

Figures 1 and 2 provide two typical behaviors of $u(t, x)$ in the case $c = 6$. Figure 1 shows when $A = 10$, the species persists and approaches a forced wave solution exhibiting the 2-periodicity in the moving frame. In Fig. 1a, shapes of $u(t, x)$ at odd time points $t = 7, 21, 35$ are similar; so are the shapes at even time points $t = 14, 28, 42$. The 2-periodicity in the moving frame is clearly reflected in Fig. 1b, where shapes of $u(t, x)$ at $t = 41$ and $t = 42$ look exactly the same as that at $t = 39$ and $t = 40$, respectively. Figure 2 shows when $A = 70$, the species is not able to keep pace with the shifting climate envelope and eventually becomes extinct.



(a)



(b)

Fig. 1 Numerical simulation of $u(t, x)$ with $c = 6$ and $A = 10$

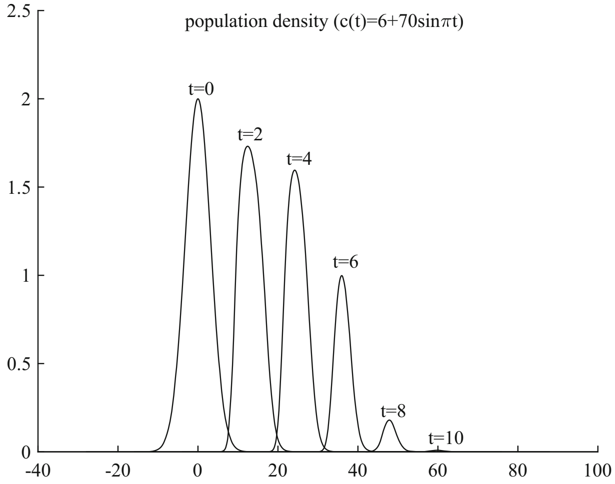


Fig. 2 Numerical simulation of $u(t,x)$ with $c=6$ and $A=70$

4.3 Numerical simulations for the approximate top Lyapunov exponent

In this subsection, we calculate the approximate top Lyapunov exponent λ_∞. Consider the following problem:

$$\begin{cases} w_t = w_{xx} + c(t)w_x + a(x)w, & x \in (-L, L), \\ w(t,-L) = 0 = w(t,L), \end{cases} \tag{4.2}$$

where $c(t) = c + A\sin\pi t$, $L = 40$, $a(x) = f_u(x,0)$ (with the same f as used in Sect. 4.2) is given by

$$a(x) = \begin{cases} 10, & |x| \le 20, \\ -2, & |x| > 20. \end{cases} \tag{4.3}$$

Denote by $w(t,x)$ the solution of (4.2) with initial condition $w(0,\cdot)$ given by

$$w(0,\cdot) = w_0 = \begin{cases} 1, & |x| \le 10, \\ 0, & |x| > 10. \end{cases}$$

We write λ_∞^A in place of λ_∞ to indicate the dependence on A. Because of Lemma 2.1(4), we can use $w(t,x)$ to calculate the approximate top Lyapunov exponent λ_∞^A (approximated by the top Lyapunov exponent λ_{40}^A), that is, we calculate $\frac{\ln\|w(t,\cdot)\|_\infty}{t}$ for sufficiently large t.

Due to possible exponential growth of the solution, Matlab would process $w(t,x)$ as infinity or negative infinity if we compute it for a large t. To overcome this overflow issue, we compute $w(t,x)$ by a piece-by-piece approach following Benettin et al.

(1980a, b). The theoretical foundation is as follows. Denote by $\Psi(t,s)$ the evolution family generated by (4.2). Fix some $T_*>0$, the period multiplied by a positive integer. Then, $\Psi(t+T_*, s+T_*)=\Psi(t,s)$. Writing $w_{nT_*}=w(nT_*,\cdot)$ for each $n\in\mathbb{N}$, we find

$$w_{nT_*}=\Psi(T_*,0)w_{(n-1)T_*}=\left[\Psi(T_*,0)\frac{w_{(n-1)T_*}}{\|w_{(n-1)T_*}\|_\infty}\right]\|w_{(n-1)T_*}\|_\infty.$$

Taking the norm $\|\cdot\|_\infty$ and then ln on both sides leads to

$$\ln\|w_{nT_*}\|_\infty=\ln\left\|\Psi(T_*,0)\frac{w_{(n-1)T_*}}{\|w_{(n-1)T_*}\|_\infty}\right\|_\infty+\ln\|w_{(n-1)T_*}\|_\infty.$$

Iterating the above identity gives

$$\ln\|w_{nT_*}\|_\infty=\sum_{i=1}^{n-1}\ln\left\|\Psi(T_*,0)\frac{w_{iT_*}}{\|w_{iT_*}\|_\infty}\right\|_\infty+\ln\|w_{T_*}\|_\infty,\quad n\in\mathbb{N}.$$

The approximate top Lyapunov exponent is approximated by $\frac{\ln\|w_{nT_*}\|_\infty}{nT_*}$ for a sufficiently large n. Note that in each step, we only need to solve (4.2) on $[0,T_*]$ with the normalized initial data.

We calculate the approximate top Lyapunov exponent λ_∞^A by fixing $c=6$ and varying A from 0 to 80. Figure 3a plots the curve of λ_{40}^A in terms of A, showing that the approximate top Lyapunov exponent decreases with respect to $A\geq 0$. We study this in details in Section 5. Moreover, Figure 3a shows the existence of two windows $[0,A_1]$ and $[A_1,A_2]$ (where the approximate top Lyapunov exponent crosses 0) such that λ_{40}^A decreases slowly for $A\in[0,A_1]$ and much faster for $A\in[A_1,A_2]$. Similar patterns are found for different choices of $c(t)$ (see Figs. 3b and 4). These patterns imply that (i) mild fluctuations have almost no effect on a persistent species under climate change, showing the adaptability of the species; (ii) the species becomes sensitive to fluctuations that are large enough to drive it to extinction.

We point out that when A is very large, the approximate of λ_∞^A by λ_{40}^A is invalid according to Theorem D(1) and (3), and there are substantial errors in numerical simulations.

4.4 Characterization of the approximate top Lyapunov exponent: II

Consider

$$\mathcal{L}:=-\partial_t+d\partial_{xx}^2+c(t)\partial_x+g(x,0) \tag{4.4}$$

as an unbounded operator in the space of T-periodic functions in X. Denote by $\mathcal{L}_L$ the operator $\mathcal{L}$ restricted on $(-L,L)$ and equipped with zero Dirichlet boundary condition on $\pm L$. It is considered as an unbounded operator in the space of T-periodic functions in X_L.

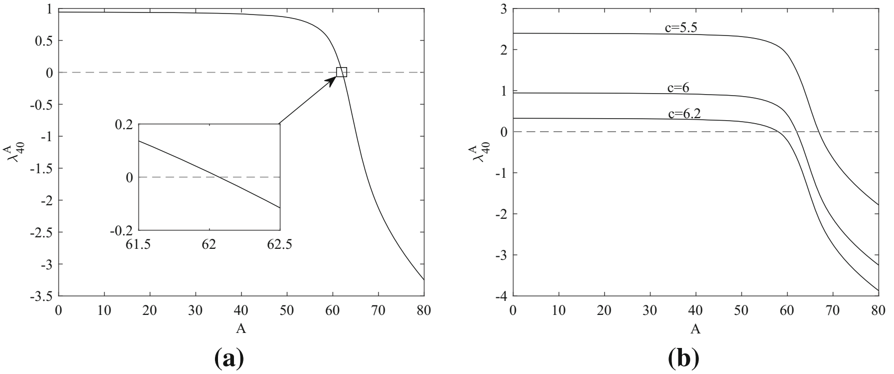


Fig. 3 **a** Numerical calculation of the approximate top Lyapunov exponent with $c = 6$ and A varying from 0 to 80. **b** Numerical calculation of the approximate top Lyapunov exponent with $c = 5.5, 6, 6.2$ and A varying from 0 to 80

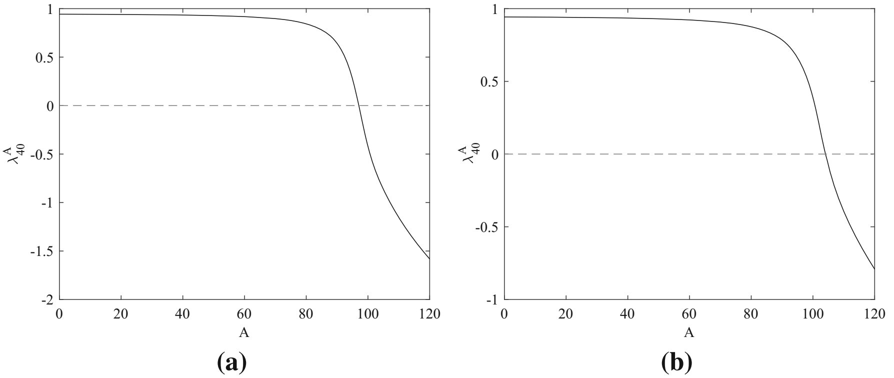


Fig. 4 **a** Numerical calculation of the approximate top Lyapunov exponent with $c(t) = 6 + A\frac{\sin(\pi t)+\sin(2\pi t)}{\max_t[\sin(\pi t)+\sin(2\pi t)]}$ and A varying from 0 to 120. **b** Numerical calculation of the approximate top Lyapunov exponent with $c(t) = 6 + A\frac{\sin(\pi t)+\sin(2\pi t)+\sin(4\pi t)}{\max_t[\sin(\pi t)+\sin(2\pi t)+\sin(4\pi t)]}$ and A varying from 0 to 120

Proposition 4.1 *Suppose that $c(t)$ is T-periodic. If $\lambda_\infty > \limsup_{|x|\to\infty} g(x, 0)$, then λ_∞ is the principal eigenvalue of $\mathcal{L}$.*

Proof Note that for $L > 0$, λ_L is the principal eigenvalue of $\mathcal{L}_L$. Thus, there exists a bounded positive T-periodic function w^L solving

$$\begin{cases} w^L_t = dw^L_{xx} + c(t)w^L_x + (g(x,0) - \lambda_L)w^L, & x \in (-L, L), \\ w^L(t, -L) = 0 = w^L(t, L). \end{cases} \tag{4.5}$$

We normalize w^L so that $\max_{\mathbb{R}\times(-L,L)} w^L = 1$. By the parabolic regularity, we may assume the existence of w^∞ such that $w^L(t, x) \to w^\infty(t, x)$ locally uniformly in $(t, x) \in \mathbb{R} \times \mathbb{R}$ as $L \to \infty$. Therefore, w^∞ is bounded, non-negative and T-periodic, and satisfies $\mathcal{L}w^\infty = \lambda_\infty w^\infty$.

To see $w^{\infty} > 0$, let $(t_L, x_L) \in [0, T] \times (-L, L)$ be such that $w^L(t_L, x_L) = 1$. Examining (4.5) at the point (t_L, x_L) yields $0 = dw^L_{xx}(t_L, x_L) + (g(x_L, 0) - \lambda_L) \leq g(x_L, 0) - \lambda_L$. Since $\limsup_{|x|\to\infty} g(x, 0) < \lambda_\infty$, we deduce the boundedness of $\{x_L\}_{L\gg 1}$. Thus, we may assume without loss of generality that $(t_L, x_L) \to (t_*, x_*)$ as $L \to \infty$, leading to $w^{\infty}(t_*, x_*) = 1$. Harnack's inequality then yields $w^{\infty} > 0$.

By Lemma 4.1, λ_∞ is simple and isolated, and hence, is the principal eigenvalue. □

Remark 4.1 We point out that the condition $\lambda_\infty > \limsup_{|x|\to\infty} g(x, 0)$ is sharp in the following sense: if $c(t) \equiv c \neq 0$ and the limits $\lim_{x\to\pm\infty} g(x, 0) = g_\pm$ are exponential, then

$$\max\{g_+, g_-\} = \sup \sigma_{ess}(d\partial^2_{xx} + c\partial_x + g(x, 0)).$$

In fact, it is easy to see from the arguments in Kapitula and Promislow (2013, Section 3.1.1.4) that $\sigma_{ess}(d\partial^2_{xx} + c\partial_x + g(x, 0))$ is the closure of the region in $\mathbb{C}$ bounded by the curves $\{-dk^2 + ick + g_- : k \in \mathbb{R}\}$ and $\{-dk^2 + ick + g_+ : k \in \mathbb{R}\}$. From which, the conclusion follows.

5 Effects of fluctuations

In this section, we study the effects of fluctuations on the shifting speed or location of the climate envelope. In particular, we prove Theorem D and use analytic methods (mainly, matched asymptotic expansions) and perform numerical simulations to justify (*P1*)–(*P3*) described in Sect. 1.

Consider (1.7) and assume that σ is non-zero and T-periodic for some $T > 0$, and has zero average, namely, $\int_0^T \sigma(s)ds = 0$. Thus, $A\sigma$ and $A\int_0^t \sigma(s)ds$ are respectively fluctuations on the shifting speed c and the location ct of the climate envelope. The parameter A is the amplitude of fluctuations.

In preparation for the analysis, we consider the following T-periodic parabolic operator

$$\mathcal{L}_A = -\partial_t + d\partial^2_{xx} + [c + A\sigma(t)]\,\partial_x + g(x, 0).$$

Denote by λ^A_L the principal eigenvalue of $\mathcal{L}_{A,L}$, which is $\mathcal{L}_A$ restricted on $(-L, L)$ and equipped with the zero Dirichlet boundary condition on $\pm L$. By Lemma 2.2, the approximate top Lyapunov exponent $\lambda^A_\infty := \lim_{L\to\infty} \lambda^A_L$ is well-defined and finite. By Theorem C, λ^A_∞ is a criterion for extinction and persistence of (1.7).

If A_0 is such that $\lambda^{A_0}_\infty > \limsup_{|x|\to\infty} g(x, 0)$, Proposition 4.1 ensures that $\lambda^{A_0}_\infty$ is the principal eigenvalue of $\mathcal{L}_{A_0}$ with the principal eigenfunction ψ_{A_0}, namely, a unique (up to multiplication by constants) positive, bounded and T-periodic eigenfunction. Classical analytic perturbation theory (see e.g. Kato (1995, Chapter 7, Section 2) or Reed and Simon (1978, Theorem XII.9)) ensures that for all A in a small neighborhood of A_0, λ^A_∞ is the principal eigenvalue of $\mathcal{L}_A$ with the principal eigenfunction ψ_A. Moreover, λ^A_∞ and ψ_A have asymptotic expansions in A near A_0.

5.1 Proof of Theorem D

(1) Fix $A > 0$. Obviously, $\lambda_L^A \geq \Lambda_L + \inf_{x\in\mathbb{R}} g(x,0)$, where Λ_L is the principal eigenvalue of the T-periodic operator $-\partial_t + d\partial_{xx}^2 + [c + A\sigma(t)]\,\partial_x$ restricted on $(-L, L)$ and equipped with zero Dirichlet boundary condition on $\pm L$. Denote by ϕ_L the positive eigenfunction associated to Λ_L.
Set $\Phi_L(t,y) = \phi_L(t,x)$, where $y = x + A\int_0^t \sigma(s)ds$. Obviously, Φ_L is a T-periodic function on the T-periodic domain $D_T := \bigcup_{t\in\mathbb{R}} \Big(\{t\} \times \Big[-L + A\int_0^t \sigma(s)ds, L + A\int_0^t \sigma(s)ds\Big]\Big)$ and satisfies

$$\begin{cases} -\partial_t \Phi_L + d\partial_{yy}^2 \Phi_L + c\partial_y \Phi_L = \Lambda_L \Phi_L & \text{in} \quad \mathrm{int}(D_T), \\ \Phi_L = 0 & \text{on} \quad \partial D_T, \\ \Phi_L > 0 & \text{in} \quad \mathrm{int}(D_T). \end{cases}$$

Let $\tilde{L} > 0$ be the largest number such that $\mathbb{R} \times [-\tilde{L} - 1, \tilde{L} + 1] \subset D_T$. Such a $\tilde{L}$ always exists as long as L is sufficiently large. Moreover, $\tilde{L} \to \infty$ as $L \to \infty$. Clearly, restricted on $\mathbb{R} \times [-\tilde{L}, \tilde{L}]$, Φ_L is T-periodic and satisfies $\inf \Phi_L > 0$ and

$$-\partial_t \Phi_L + d\partial_{yy}^2 \Phi_L + c\partial_y \Phi_L = \Lambda_L \Phi_L \quad \text{in} \quad \mathbb{R} \times (-\tilde{L}, \tilde{L}).$$

It follows from the comparison principle for parabolic equations that $\Lambda_L \geq \tilde{\Lambda}$, where $\tilde{\Lambda}$ is the principal eigenvalue of the operator $d\frac{d^2}{dy^2} + c\frac{d}{dy}$ restricted on $(-\tilde{L}, \tilde{L})$ and equipped with zero Dirichlet boundary condition on $\pm\tilde{L}$. Elementary calculations yield $\tilde{\Lambda} = -\frac{1}{4d}(c^2 + \frac{\pi^2 d^2}{\tilde{L}^2})$, and hence, $\lambda_L^A \geq -\frac{1}{4d}(c^2 + \frac{\pi^2 d^2}{\tilde{L}^2}) + \inf_{x\in\mathbb{R}} g(x,0)$. Letting $L \to \infty$, we conclude that $\lambda_\infty^A \geq -\frac{c^2}{4d} + \inf_{x\in\mathbb{R}} g(x,0)$.

(2) For clarity, we provide a proof for the case that $d = 1$, $c = 0$, and $\sigma(t)$ has only one zero in $(0, T)$. The general case can be proven in the same manner.
Let $t^* \in (0, T)$ be the zero of $\sigma(t)$ in $(0, T)$. We may assume without loss of generality that $\sigma > 0$ on $(0, t^*)$. So, $\sigma < 0$ on (t^*, T).
Set $a = g(\cdot, 0)$. For any given $0 < \epsilon \lll 1$, let $a^\infty < 0$ be such that $\limsup_{|x|\to\infty} a(x) < a^\infty < \limsup_{|x|\to\infty} a(x) + \epsilon$. Clearly, there is $L^* \gg 1$ such that $a(x) \leq a^\infty$ for all $|x| \geq L^*$. Then, there exists a smooth function $a^* : \mathbb{R} \to \mathbb{R}$ satisfying $a^* \geq a$ and $a^*(x) = a^\infty$ for all $|x| \geq L^*$. We claim that

Claim 1 There are $\delta > 0$ and a continuous T-periodic function $\phi : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ such that

$$0 < \inf \phi \leq \sup \phi < \infty \tag{5.1}$$

and, for all $A \gg 1$,

$$\begin{aligned} -\phi_t + \phi_{xx} + A\sigma(t)\phi_x + a^*(x)\phi \le (a^\infty + 4\epsilon)\phi \quad \text{in} \\ ((0,T)\backslash\{\delta, t^*-\delta, t^*+\delta, T-\delta\}) \times \mathbb{R}. \end{aligned} \tag{5.2}$$

In the case that the limits $a(\pm\infty) := \lim_{x\to\pm\infty} a(x)$ exist and coincide, for given $0 < \epsilon \ll 1$, there are $L_* > 0$ and a smooth function $a_*(x)$ such that $a_*(x) = a_\infty := a(\pm\infty) - \epsilon$ for $|x| \ge L_*$ and $a_*(x) \le a(x)$ for $x \in \mathbb{R}$. We claim that

Claim 2 There are $\delta > 0$ and a continuous T-periodic function $\tilde{\phi} : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ such that

$$0 < \inf \tilde{\phi} \le \sup \tilde{\phi} < \infty \tag{5.3}$$

and, for all $A \gg 1$,

$$\begin{aligned} -\tilde{\phi}_t + \tilde{\phi}_{xx} + A\sigma(t)\tilde{\phi}_x + a_*(x)\tilde{\phi} \ge (a_\infty - 4\epsilon)\tilde{\phi} \quad \text{in} \\ ((0,T)\backslash\{\delta, t^*-\delta, t^*+\delta, T-\delta\}) \times \mathbb{R}. \end{aligned} \tag{5.4}$$

Claim 1 together with the comparison principle for parabolic equations implies that $\lambda^A_\infty \le a^\infty + 4\epsilon$ for all $A \gg 1$. Hence, $\limsup_{A\to\infty} \lambda^A \le \limsup_{|x|\to\infty} a(x)$.

Claim 2 together with the comparison principle for parabolic equations implies that, if the limits $a(\pm\infty) := \lim_{x\to\pm\infty} a(x)$ exist and coincide, then $\lambda^A \ge a_\infty - 4\epsilon$ for all $A \gg 1$. Hence, $\liminf_{A\to\infty} \lambda^A \ge a(\pm\infty)$. It then follows that $\lim_{A\to\infty} \lambda^A$ exists and $\lim_{A\to\infty} \lambda^A = a(\pm\infty)$.

It remains to prove Claims 1 and 2. We first prove Claim 1, that is, we construct a continuous T-periodic function ϕ satisfying (5.1) and (5.2). Such a function ϕ is constructed to be of the form $\gamma(t)\beta(t,x)$ such that (5.2) holds for t near 0, t^*, and T due to $\gamma(t)$ and for other t's due to $\beta(t,x)$.

We first construct the function β, which is a T-periodic extension of $\beta : [0,T) \times \mathbb{R} \to \mathbb{R}$ defined as follows:

- for $t \in \{0, t^*\}$, $\beta(t,x) = 1$ for all $x \in \mathbb{R}$,
- for $t \in (0, t^*)$,

$$\beta(t,x) = \begin{cases} 1 + e^{-\frac{1}{\frac{(t^*)^2}{4} - (t-\frac{t^*}{2})^2}} \cdot e^{-\frac{1}{16(L^*)^4}}, & x \le -L^*, \\ 1 + e^{-\frac{1}{\frac{(t^*)^2}{4} - (t-\frac{t^*}{2})^2}} \cdot e^{-\frac{1}{16(L^*)^4 - (x+L^*)^4}}, & x \in (-L^*, L^*), \\ 1, & x \ge L^*, \end{cases}$$

- for $t \in (t^*, T)$,

$$\beta(t,x) = \begin{cases} 1, & x \le -L^*, \\ 1 + e^{-\frac{1}{\frac{(T-t^*)^2}{4} - (t-\frac{T+t^*}{2})^2}} \cdot e^{-\frac{1}{16(L^*)^4 - (x-L^*)^4}}, & x \in (-L^*, L^*), \\ 1 + e^{-\frac{1}{\frac{(T-t^*)^2}{4} - (t-\frac{T+t^*}{2})^2}} \cdot e^{-\frac{1}{16(L^*)^4}}, & x \ge L^*. \end{cases}$$

By the properties of the standard smooth mollifer, it is easy to see that $\beta \in C^{1,2}(\mathbb{R}\times\mathbb{R})$ satisfies $0 < \inf \beta \le \sup \beta < \infty$ and $\sup(|\beta_t| + |\beta_x| + |\beta_{xx}|) < \infty$. Note that

$$\sigma(t)\beta_x(t,x) < 0, \quad \forall\, t \in (0,t^*) \cup (t^*,T),\ \ x \in (-L^*, L^*) \tag{5.5}$$

and for any $\delta_1, \delta_2 > 0$,

$$\sup_{\substack{t\in[\delta_1,t^*-\delta_1]\cup[t^*+\delta_1,T-\delta_1]\\ x\in(-L^*+\delta_2,L^*-\delta_2)}} \sigma(t)\beta_x(t,x) < 0. \tag{5.6}$$

Note also that, for any $0 < \epsilon \ll 1$, there is a $\delta_2 > 0$ such that

$$\begin{cases} a^\infty - a^*(x) \ge -\epsilon, & x \in [-L^*, -L^*+\delta_2] \cup [L^*-\delta_2, L^*] \\ \beta_t(t,x) \ge -\epsilon\beta(t,x), & t \in (0,t^*) \cup (t^*,T),\ \ x \in [-L^*, -L^*+\delta_2] \cup [L^*-\delta_2, L^*] \\ \beta_{xx}(t,x) \le \epsilon\beta(t,x), & t \in (0,t^*) \cup (t^*,T),\ \ x \in [-L^*, -L^*+\delta_2] \cup [L^*-\delta_2, L^*]. \end{cases} \tag{5.7}$$

Next, for any $0 < \epsilon \ll 1$, let $\delta_1 > 0$ and $\gamma : \mathbb{R} \to \mathbb{R}$ be a T-periodic function such that

$$\gamma(t) = \begin{cases} e^{kt}, & t \in [0,\delta_1), \\ e^{-\epsilon(t-\delta_1)}e^{k\delta_1}, & t \in [\delta_1, t^*-\delta_1), \\ e^{k(t-t^*+\delta_1)}e^{k\delta_1}e^{-\epsilon(t^*-2\delta_1)}, & t \in [t^*-\delta_1, t^*+\delta_1), \\ e^{-\epsilon(t-t^*-\delta_1)}e^{3k\delta_1}e^{-\epsilon(t^*-2\delta_1)}, & t \in [t^*+\delta_1, T-\delta_1), \\ e^{k(t-T+\delta)}e^{3k\delta_1}e^{-\epsilon(T-4\delta_1)}, & t \in [T-\delta_1, T), \end{cases}$$

where k is a positive constant satisfying $\delta_1 = \frac{\epsilon T}{4k+4\epsilon}$ and

$$k > \sup_{t\in[0,T],x\in\mathbb{R}} \Big(a^\infty - a^*(x) + \beta_t(t,x) - \beta_{xx}(t,x)\Big).$$

It is easy to see that γ satisfies

$$\begin{cases} \inf_{t\in[0,T]} \gamma(t) > 0, \\ \gamma_t(t) \ge -\epsilon\gamma(t) \quad \text{for} \ \ t \in (0,T)\backslash\{\delta_1, t^*-\delta_1, t^*+\delta_1, T-\delta_1\}, \\ \gamma_t(t) \ge \sup_{t\in[0,T],x\in\mathbb{R}} \Big(a^\infty - a^*(x) + \beta_t(t,x) - \beta_{xx}(t,x)\Big)\gamma(t) \\ \qquad\qquad \text{for}\ t \in (0,\delta_1) \cup (t^*-\delta_1, t^*+\delta_1) \cup (T-\delta_1, T). \end{cases} \tag{5.8}$$

Now, for any $0 < \epsilon \ll 1$, let $\phi(t,x) = \gamma(t)\beta(t,x)$. It follows from (5.5) to (5.8) that there is $A^* > 0$ such that for any $A \ge A^*$, there holds

$$
\begin{aligned}
&\phi_t - \phi_{xx} - A\sigma(t)\phi_x - a^*(x)\phi(t,x)\\
&\quad = -a^\infty\phi(t,x) + (a^\infty - a^*(x))\phi(t,x) + \gamma_t(t)\beta(t,x) + \gamma(t)\beta_t(t,x)\\
&\qquad - \gamma(t)\beta_{xx}(t,x) - A\sigma(t)\beta_x(t,x)\\
&\quad \geq -(a^\infty + 4\epsilon)\phi(t,x), \quad \forall\, t\in(0,T)\backslash\{\delta_1, t^*-\delta_1, t^*+\delta_1, T-\delta_1\},\ x\in\mathbb{R}.
\end{aligned}
$$

Claim 1 is thus proven.

Next, we prove Claim 2. We construct a continuous T-periodic function $\tilde{\phi}$, which satisfies (5.3) and (5.4) and is of the form $\tilde{\gamma}(t)\tilde{\beta}(t,x)$ such that (5.4) holds for t near 0, t^*, and T due to $\tilde{\gamma}(t)$ and for other t's due to $\tilde{\beta}(t,x)$. The idea to construct $\tilde{\beta}(t,x)$ and $\tilde{\gamma}(t)$ is similar to the idea to construct $\beta(t,x)$ and $\gamma(t)$, but changing the monotonicity. To be more precise, we define $\tilde{\beta}(t,x)$ to be $\beta(t,-x)$, that is, $\tilde{\beta}$ restricted on $[0,T)\times\mathbb{R}$ reads as follows:

- for $t\in\{0,t^*\}$, $\tilde{\beta}(t,x)=1$ for all $x\in\mathbb{R}$,
- for $t\in(0,t^*)$,

$$
\tilde{\beta}(t,x) = \begin{cases}
1, & x\leq -L_*,\\
1 + e^{-\frac{1}{\frac{(t^*)^2}{4}-(t-\frac{t^*}{2})^2}}\cdot e^{-\frac{1}{16(L^*)^4-(x-L_*)^4}}, & x\in(-L_*,L_*),\\
1 + e^{-\frac{1}{\frac{(t^*)^2}{4}-(t-\frac{t^*}{2})^2}}\cdot e^{-\frac{1}{16(L_*)^4}}, & x\geq L_*,
\end{cases}
$$

- for $t\in(t^*,T)$,

$$
\tilde{\beta}(t,x) = \begin{cases}
1 + e^{-\frac{1}{\frac{(T-t^*)^2}{4}-(t-\frac{T+t^*}{2})^2}}\cdot e^{-\frac{1}{16(L_*)^4}}, & x\leq -L_*,\\
1 + e^{-\frac{1}{\frac{(T-t^*)^2}{4}-(t-\frac{T+t^*}{2})^2}}\cdot e^{-\frac{1}{16(L_*)^4-(x+L_*)^4}}, & x\in(-L_*,L_*),\\
1, & x\geq L_*.
\end{cases}
$$

For any $0<\epsilon\ll 1$ and $\tilde{k}\gg 1$, let $\tilde{\gamma}:\mathbb{R}\to\mathbb{R}$ be a T-periodic function such that

$$
\tilde{\gamma}(t) = \begin{cases}
e^{-\tilde{k}t}, & t\in[0,\tilde{\delta}_1),\\
e^{\epsilon(t-\tilde{\delta}_1)}e^{-\tilde{k}\tilde{\delta}_1}, & t\in[\tilde{\delta}_1, t^*-\tilde{\delta}_1),\\
e^{-\tilde{k}(t-t^*+\tilde{\delta}_1)}e^{-\tilde{k}\tilde{\delta}_1}e^{\epsilon(t^*-2\tilde{\delta}_1)}, & t\in[t^*-\tilde{\delta}_1, t^*+\tilde{\delta}_1),\\
e^{\epsilon(t-t^*-\tilde{\delta}_1)}e^{-3\tilde{k}\tilde{\delta}_1}e^{\epsilon(t^*-2\tilde{\delta}_1)}, & t\in[t^*+\tilde{\delta}_1, T-\tilde{\delta}_1),\\
e^{-\tilde{k}(t-T+\tilde{\delta}_1)}e^{-3\tilde{k}\tilde{\delta}_1}e^{\epsilon(T-4\tilde{\delta}_1)}, & t\in[T-\tilde{\delta}_1, T),
\end{cases}
$$

where $\tilde{\delta}_1 = \frac{\epsilon T}{4\tilde{k}+4\epsilon}$. Then, by arguments as in Claim 1, both (5.3) and (5.4) hold with $\tilde{\phi}(t,x) = \tilde{\beta}(t,x)\tilde{\gamma}(t)$ when $A\gg 1$. Claim 2 is thus proven.

(3) Fix $L>0$. Shifting σ slightly if necessary, we may assume without loss of generality that $\sigma(0)\neq 0$ so that $\sigma(nT)\neq 0$ for all $n\in\mathbb{Z}$. Let $N\in\mathbb{N}$ be the number of zeros of σ in $(0,T)$, which are labeled as $0<t_1<t_2<\cdots<t_N<T$. Note that N is at least 2. Set $t_0 = t_N - T$ and $t_{N+1} = t_1 + T$.

Fix $\delta > 0$ so small that the intervals $[t_i - \delta, t_i + \delta]$, $i \in \{1, \dots, N\}$ are disjoint and all contained in $(0, T)$, and σ' admits no zero in the union of these intervals.

For $i \in \{0, 1, \dots, N+1\}$, we set

$$L_i = \begin{cases} L+1 & \text{if } \ \sigma'(t_i) > 0, \\ -L-1 & \text{if } \ \sigma'(t_i) < 0, \end{cases}$$

and define

$$\Phi(t,x) = e^{-\frac{c+A\sigma(t)}{2d}(x-L_i)}, \quad (t,x) \in [t_i - \delta, t_i + \delta] \times (-L, L).$$

This in particular defines Φ on $\cup_{i=1}^N [t_i - \delta, t_i + \delta] \times (-L, L)$. We extend Φ to $[0, T] \times (-L, L)$ by linear interpolation in the spatial variable as the time variable changes. More precisely, for $i \in \{0, 1, \dots, N\}$, we define

$$\Phi(t,x) = e^{-\frac{c+A\sigma(t)}{2d}\left[\frac{t-(t_i+\delta)}{t_{i+1}-\delta-(t_i+\delta)}(x-L_{i+1}) + \frac{t_{i+1}-\delta-t}{t_{i+1}-\delta-(t_i+\delta)}(x-L_i)\right]},$$
$$(t,x) \in (t_i + \delta, t_{i+1} - \delta) \times (-L, L).$$

Thus, we have defined Φ on $[0, T] \times (-L, L)$. Clearly, $\inf \Phi > 0$ and $\Phi(0, \cdot) = \Phi(T, \cdot)$.

It is straightforward to check that for $i \in \{1, \dots, N\}$,

$$\begin{aligned} \mathcal{L}_{A,L}\Phi(t,x) &= \left\{ \frac{A\sigma'(t)}{2d}(x - L_i) - \frac{[c + A\sigma(t)]^2}{4d} + g(x, 0) \right\} \Phi(t,x) \\ &\le [-\alpha_i A + g(x,0)]\, \Phi(t,x), \quad \forall (t,x) \in (t_i - \delta, t_i + \delta) \times (-L, L), \end{aligned}$$

where $\alpha_i = \frac{1}{2d} \inf_{(t,x)\in(t_i-\delta,t_i+\delta)\times(-L,L)} \sigma'(t)(L_i - x) > 0$. For $i \in \{0, 1, \dots, N\}$,

$$\begin{aligned} &\mathcal{L}_{A,L}\Phi(t,x) \\ &= \left\{ \frac{A\sigma'(t)}{2d} \left[\frac{t-(t_i+\delta)}{t_{i+1}-\delta-(t_i+\delta)}(x - L_{i+1}) + \frac{t_{i+1}-\delta-t}{t_{i+1}-\delta-(t_i+\delta)}(x - L_i) \right] \right. \\ &\quad \left. + \frac{c + A\sigma(t)}{2d} \frac{L_i - L_{i+1}}{t_{i+1}-\delta-(t_i+\delta)} - \frac{[c + A\sigma(t)]^2}{4d} + g(x,0) \right\} \Phi(t,x) \\ &\le \left\{ \beta_i A - \gamma_i A^2 + \kappa_i \right\} \Phi(t,x), \quad \forall (t,x) \in (t_i + \delta, t_{i+1} - \delta) \times (-L, L), \end{aligned}$$

where $\beta_i = \beta_i(L) > 0$, $\gamma_i = \frac{1}{4d} \inf_{t\in(t_i+\delta,t_{i+1}-\delta)} \sigma(t)^2 > 0$ and $\kappa_i = \kappa_i(L) > 0$. Hence, there are $C_1 = C_1(L) > 0$ and $C_2 = C_2(L) > 0$ such that $\mathcal{L}_{A,L}\Phi \le (-C_1 A + C_2)\Phi$ a.e. in $(0, T) \times (-L, L)$. It follows from the comparison principle for parabolic equations that $\lambda_L^A \le -C_1 A + C_2$.

5.2 Justification of (*P1*)

Recall that we focus on the case that the species persists in the absence of fluctuations, namely, $\lambda_\infty^0 > 0$. Since $\limsup_{|x|\to\infty} g(x,0) < 0$, λ_∞^A is the principal eigenvalue of $\mathcal{L}_A$ with the principal eigenfunction ψ_A for all small A. Moreover, λ_∞^A and ψ_A have asymptotic expansions in A near 0.

For $0 < A \ll 1$, we set $\epsilon = A$. Then,

$$-\partial_t\psi_\epsilon + d\partial_{xx}\psi_\epsilon + [c + \epsilon\sigma(t)]\,\partial_x\psi_\epsilon + g(x,0)\psi_\epsilon = \lambda_\infty^\epsilon\psi_\epsilon. \tag{5.9}$$

Consider asymptotic expansions of λ_∞^ϵ and ψ_ϵ at $\epsilon = 0$:

$$\begin{aligned}\lambda_\infty^\epsilon &= \lambda_0 + \epsilon\lambda_1 + \epsilon^2\lambda_2 + \cdots,\\ \psi_\epsilon &= \phi_0 + \epsilon\phi_1 + \epsilon^2\phi_2 + \cdots,\end{aligned}$$

where $\lambda_0, \lambda_1, \lambda_2, \ldots$ are real numbers and $\phi_0, \phi_1, \phi_2, \ldots$ are T-periodic in t. Inserting these expansions into (5.9) and collecting terms of orders ϵ^0, ϵ^1 and ϵ^2, we find

$$\begin{aligned}&\text{order } \epsilon^0: \quad \mathcal{L}_0\phi_0 - \lambda_0\phi_0 = 0,\\ &\text{order } \epsilon^1: \quad \mathcal{L}_0\phi_1 - \lambda_0\phi_1 = \lambda_1\phi_0 - \sigma(t)\partial_x\phi_0,\\ &\text{order } \epsilon^2: \quad \mathcal{L}_0\phi_2 - \lambda_0\phi_2 = \lambda_1\phi_1 + \lambda_2\phi_0 - \sigma(t)\partial_x\phi_1.\end{aligned}$$

From the equation of order ϵ^0, we see that (λ_0, ϕ_0) is the principal eigenpair of $\mathcal{L}_0$, and of the elliptic operator $d\partial_{xx}^2 + c\partial_x + g(x,0)$. Hence, $(\lambda_0, \phi_0) = (\lambda_\infty^0, \psi_0)$ and $\psi_0(t,x) = \psi_0(x)$ is independent of t. Denote by $\mathcal{L}_0^*$ the adjoint operator of $\mathcal{L}_0$, namely, $\mathcal{L}_0^* = -\partial_t + d\partial_{xx}^2 - c\partial_x + g(x,0)$. Then, λ_∞^0 is also the principal eigenvalue of $\mathcal{L}_0^*$ as well as the elliptic operator $d\partial_{xx}^2 - c\partial_x + g(x,0)$. Denote by $\psi_0^*(t,x) = \psi_0^*(x)$ the associated positive eigenfunction.

Since ϕ_1 solves the equation of order ϵ^1, there must hold due to the Fredholm alternative that

$$\int_0^T \int_{\mathbb{R}} \psi_0^*(x)\,[\lambda_1\psi_0(x) - \sigma(t)\partial_x\psi_0(x)]\,dxdt = 0,$$

which together with $\int_0^T \sigma(t)dt = 0$ and the positivity of ψ_0 and ψ_0^* yields $\lambda_1 = 0$. Similarly, since ϕ_2 solves the equation of order ϵ^2, there must be true that $\int_0^T \int_{\mathbb{R}} \psi_0^*(x)\,[\lambda_2\psi_0(x) - \sigma(t)\partial_x\phi_1(t,x)]\,dxdt = 0$, where we used $\lambda_1 = 0$. It follows that

$$\lambda_2 = \frac{\displaystyle\int_0^T \int_{\mathbb{R}} \sigma(t)\psi_0^*(x)\partial_x\phi_1(t,x)dxdt}{\displaystyle T\int_{\mathbb{R}} \psi_0^*(x)\psi_0(x)dx} = \frac{\displaystyle-\int_0^T \int_{\mathbb{R}} \sigma(t)\partial_x\psi_0^*(x)\phi_1(t,x)dxdt}{\displaystyle T\int_{\mathbb{R}} \psi_0^*(x)\psi_0(x)dx}. \tag{5.10}$$

Table 1 Numerical calculation of λ_2

c	2	3	4	5	6	7	8
λ_2	−0.9080	−0.8971	−1.5982	−1.9851	−2.2876	−0.0549	−12.3161

Note that $\int_{\mathbb{R}} \psi_0^*(x)\psi_0(x)dx > 0$. Due to the cancellation in the integral $\int_0^T \int_{\mathbb{R}} \sigma(t) \psi_0^*(x)\partial_x\phi_1(t,x)dxdt$ or $\int_0^T \int_{\mathbb{R}} \sigma(t)\partial_x\psi_0^*(x)\phi_1(t,x)dxdt$, it is in general hard to determine the sign of λ_2 analytically. We show numerically that $\lambda_2 < 0$, and hence,

$$\lambda_\infty^\epsilon = \lambda_\infty^0 + \epsilon^2\lambda_2 + \cdots \quad \text{for} \quad 0 < \epsilon \ll 1.$$

This justifies *(P1)*.

For numerical simulations, we use the same parameters as in the previous cases, that is, $\sigma(t) = \sin \pi t$, $g(x, 0) = a(x)$ is given in (4.3) and $L = 40$, and treat c as the control parameter. We numerically calculate λ_2 by choosing several c. Results are listed in Table 1.

Below, we mention some considerations for the numerical calculations of λ_2.

(i) While ψ_0, ψ_0^* and ϕ_1 are not uniquely determined, λ_2 is independent of particular choices of them. Indeed, ψ_0 and ψ_0^* are unique up to multiplication by constants. Denote by Φ a particular T-periodic solution of the equation of order ϵ^1 with $\phi_0 = \psi_0$. Then, all possible ϕ_1 are given by $\{c_1\psi_0 + \Phi : c_1 \in \mathbb{R}\}$. If we solve the same equation with $\phi_0 = c\psi_0$ for some arbitrarily fixed $c \in \mathbb{R}$, all possible ϕ_1 are given by $\{c_1\psi_0 + c\Phi : c_1 \in \mathbb{R}\}$. It follows from $\int_0^T \sigma(s)ds = 0$ that

$$\frac{\displaystyle\int_0^T \int_{\mathbb{R}} \sigma(t)[c^*\psi_0^*(x)]\partial_x[c_1\psi_0(x) + c\Phi(t,x)]dxdt}{\displaystyle T\int_{\mathbb{R}} [c^*\psi_0^*(x)][c\psi_0(x)]dx} = \frac{\displaystyle\int_0^T \int_{\mathbb{R}} \sigma(t)\psi_0^*(x)\partial_x\Phi(t,x)dxdt}{\displaystyle T\int_{\mathbb{R}} \psi_0^*(x)\psi_0(x)dx}$$

is independent of c, c^* and c_1.

(ii) The computation of ψ_0 and ψ_0^* are conducted by the Matlab eigenfunction command.

(iii) The computation of ϕ_1 needs extra attention, as the homogeneous equation associated to the equation for ϕ_1 is at a critical state. More precisely, since 0 is the largest eigenvalue of the operator $\mathcal{L}_0 - \lambda_\infty^0$, direct computation could cause exponentially large errors as time elapses. We proceed by approximation. Let $0 < \delta \ll 1$ and consider the following inhomogeneous linear equation:

$$\mathcal{L}_0\phi_1 - (\lambda_\infty^0 + \delta)\phi_1 = -\sigma(t)\partial_x\psi_0.$$

It admits a unique T-periodic solution given by

$$\phi_1^\delta(t,\cdot)=\int_{-\infty}^t \sigma(s)e^{\mathcal{L}_e^\delta(t-s)}\partial_x\psi_0 ds,\quad t\in\mathbb{R}, \tag{5.11}$$

where $\{e^{\mathcal{L}_e^\delta t}\}_{t\geq 0}$ is the semigroup on X generated by $\mathcal{L}_e^\delta := d\partial_{xx}^2+c\partial_x+g(x,0)-(\lambda_\infty^0+\delta)$, where we recall from Section 1 that X is the space of bounded and uniformly continuous functions on $\mathbb{R}$ equipped with the supremum norm $\|\cdot\|_\infty$. The subscript “e” stands for “elliptic”. Then,

$$\{\phi_1^\delta\}_{0<\delta\ll 1} \text{ is uniformly bounded,} \tag{5.12}$$

which we justify immediately. Applying the regularity theory for parabolic equations, ϕ_1^δ converges to some ϕ_1 as $\delta\to 0$ along subsequences. Based on this, we calculate ϕ_1^δ for a small δ that gives an approximation of ϕ_1. The calculation of ϕ_1^δ is much more stable as the semigroup $\{e^{\mathcal{L}_e^\delta t}\}_{t\geq 0}$ is exponentially stable.

It remains to verify (5.12). Note that there is $C_1>0$ such that

$$\|e^{\mathcal{L}_e^\delta t}\|\leq C_1 e^{-\delta t},\quad \forall t\geq 0 \tag{5.13}$$

for all $0<\delta\ll 1$, where $\|e^{\mathcal{L}_e^\delta t}\| := \sup_{\phi\in X,\|\phi\|_\infty=1}\|e^{\mathcal{L}_e^\delta t}\phi\|_\infty$. Set $\mathcal{L}_e := d\partial_{xx}^2 + c\partial_x + g(x,0)-\lambda_\infty^0$ and denote by $\{e^{\mathcal{L}_e t}\}_{t\geq 0}$ the semigroup on X generated by $\mathcal{L}_e$. Clearly, $e^{\mathcal{L}_e^\delta t}=e^{-\delta t}e^{\mathcal{L}_e t}$ for all $t\geq 0$. Let $\mathcal{P}$ be the projection onto span$\{\psi_0\}$ (the eigenspace corresponding to the principal eigenvalue 0 of $\mathcal{L}_e$) and $\mathcal{Q}$ be its complement. Then, there are $C_2>0$ and $\gamma>0$ such that

$$\|e^{\mathcal{L}_e t}|_{\mathrm{ran}\mathcal{Q}}\|\leq C_2 e^{-\gamma t},\quad \forall t\geq 0. \tag{5.14}$$

For $t\in\mathbb{R}$, let N_t be the largest integer such that $N_tT\leq t$. Then, we can rewrite (5.11) as

$$\begin{aligned}\phi_1^\delta(t,\cdot) &= \sum_{n=-\infty}^{N_t}\int_{(n-1)T}^{nT}\sigma(s)e^{\mathcal{L}_e^\delta(t-s)}\mathcal{P}\partial_x\psi_0 ds\\ &\quad+\int_{N_tT}^t \sigma(s)e^{\mathcal{L}_e^\delta(t-s)}\mathcal{P}\partial_x\psi_0 ds+\int_{-\infty}^t\sigma(s)e^{\mathcal{L}_e^\delta(t-s)}\mathcal{Q}\partial_x\psi_0 ds\\ &=: \sum_{n=-\infty}^{N_t} I_n(t,\delta)+I(t,\delta)+II(t,\delta).\end{aligned}$$

Since $0 \le t - N_t T \le T$, it is easy to see from (5.13) that $\sup_{0<\delta\ll 1}\sup_{t\in\mathbb{R}} \|I(t,\delta)\|_\infty < \infty$. Set $\sigma_* = \max_{\mathbb{R}} |\sigma|$. By (5.14), we deduce

$$\|II(t,\delta)\|_\infty \le C_2\sigma_*\|\partial_x\psi_0\|_\infty \int_{-\infty}^t e^{-\gamma(t-s)}ds = \frac{C_2\sigma_*}{\gamma}\|\partial_x\psi_0\|_\infty,$$
$$\forall t \in \mathbb{R},\ 0 < \delta \ll 1.$$

Note that $e^{\mathcal{L}_e^\delta t}\mathcal{P} = e^{-\delta t}e^{\mathcal{L}_e t}\mathcal{P} = e^{-\delta t}\mathcal{P}$. For each $n \le N_t$,

$$\begin{aligned}
\|I_n(t,\delta)\|_\infty &= \left|\int_{(n-1)T}^{nT} \sigma(s)e^{-\delta(t-s)}ds\right| \|\mathcal{P}\partial_x\psi_0\|_\infty \\
&\le \left|\int_{(n-1)T}^{nT} \sigma(s)\left[e^{-\delta(t-s)} - e^{-\delta(t-(n-1)T)}\right]ds\right| \|\partial_x\psi_0\|_\infty \\
&\le \sigma_*\|\partial_x\psi_0\|_\infty \int_{(n-1)T}^{nT}\left(\int_{t-s}^{t-(n-1)T} \delta e^{-\delta\tau}d\tau\right)ds \\
&\le \sigma_*\|\partial_x\psi_0\|_\infty \delta T\int_{(n-1)T}^{nT} e^{-\delta(t-s)}ds,
\end{aligned}$$

where we used the fact that σ has zero average in the first inequality. It follows that

$$\left\|\sum_{n=-\infty}^{N_t} I_n(t,\delta)\right\|_\infty \le \sigma_*\|\partial_x\psi_0\|_\infty\delta T\int_{-\infty}^{N_tT} e^{-\delta(t-s)}ds$$
$$\le \sigma_*\|\partial_x\psi_0\|_\infty\delta T\int_{-\infty}^{t} e^{-\delta(t-s)}ds = \sigma_*T\|\partial_x\psi_0\|_\infty, \quad \forall t\in\mathbb{R},\ 0<\delta\ll 1.$$

Hence, (5.12) follows.

Analytical justification in a special case In the case that $c = 0$ and $g(x,0)$ is symmetric with respect to $x = 0$ (or $x = x_0$ by spatial translation), we are able to justify $\lambda_2 < 0$ analytically. In this case, ψ_0^* can be chosen to be ψ_0, and thus, (5.10) gives

$$\lambda_2 = -\frac{1}{T}\int_0^T\int_{\mathbb{R}} \sigma(t)\partial_x\psi_0(x)\phi_1(t,x)dxdt,$$

where we normalized ψ_0 so that $\int_{\mathbb{R}} |\psi_0(x)|^2dx = 1$. Multiplying the equation of order ϵ^1 by ϕ_1 and integrating the resulting equation over $[0,T]\times\mathbb{R}$, we find from $\lambda_1 = 0$ that

$$\lambda_2 T = \int_0^T\left[-d\int_{\mathbb{R}} |\partial_x\phi_1(t,x)|^2dx + \int_{\mathbb{R}} g(x,0)|\phi_1(t,x)|^2dx - \lambda_\infty^0\int_{\mathbb{R}}|\phi_1(t,x)|^2dx\right]dt.$$

We then conclude $\lambda_2 < 0$ from the following facts:

(1) Note that the functional

$$\phi \mapsto -d\int_{\mathbb{R}} |\partial_x \phi(x)|^2 dx + \int_{\mathbb{R}} g(x,0)|\phi(x)|^2 dx - \lambda_\infty^0 \int_{\mathbb{R}} |\phi(x)|^2 dx$$

has maximal value 0, which is attained only on span$\{\psi_0\}$.

(2) $\hat{\phi}_1 := \frac{1}{T}\int_0^T \phi_1(t,\cdot)dt \in$ span$\{\psi_0\}$. Indeed, taking the time average of the equation of order ϵ^1 leads to $d\partial_{xx}^2\hat{\phi}_1 + a(x)\hat{\phi}_1 - \lambda_0\hat{\phi}_1 = 0$.

(3) It follows from (1), (2) and $\phi_1 \not\equiv \hat{\phi}_1$ that there is $I \subset [0,T]$ with $|I| > 0$ such that

$$\begin{aligned}
&-d\int_{\mathbb{R}} |\partial_x \phi_1(t,x)|^2 dx + \int_{\mathbb{R}} g(x,0)|\phi_1(t,x)|^2 dx \\
&\quad -\lambda_\infty^0 \int_{\mathbb{R}} |\phi_1(t,x)|^2 dx \le 0, \qquad t \in [0,T]\backslash I, \\
&-d\int_{\mathbb{R}} |\partial_x \phi_1(t,x)|^2 dx + \int_{\mathbb{R}} g(x,0)|\phi_1(t,x)|^2 dx \\
&\quad -\lambda_\infty^0 \int_{\mathbb{R}} |\phi_1(t,x)|^2 dx < 0, \quad t \in I.
\end{aligned}$$

Hence, $\lambda_2 < 0$.

5.3 Justification of (*P2*)

Fix $A_0 \in (0,\infty)$ such that $\lambda_\infty^{A_0} > \limsup_{|x|\to\infty} g(x,0)$. For $A \approx A_0$, we set $\epsilon = A - A_0$. Then, $\mathcal{L}_A\psi_A = \lambda_\infty^A\psi_A$ can be written as

$$-\partial_t\psi_A + d\partial_{xx}^2\psi_A + [c + A_0\sigma(t) + \epsilon\sigma(t)]\,\partial_x\psi_A + g(x,0)\psi_A = \lambda_\infty^A\psi_A. \quad (5.15)$$

Consider asymptotic expansions of λ_∞^A and ψ_A at $A = A_0$:

$$\begin{aligned}
\lambda_\infty^A &= \lambda_0 + \epsilon\lambda_1 + \cdots, \\
\psi_A &= \phi_0 + \epsilon\phi_1 + \cdots,
\end{aligned}$$

where $\lambda_0, \lambda_1, \ldots$ are real numbers and $\phi_0, \phi_1, \ldots$ are T-periodic functions. Inserting these expansions into (5.15) and collecting terms of orders ϵ^0 and ϵ^1, we find

$$\begin{aligned}
\text{order } \epsilon^0 &: \ \mathcal{L}_{A_0}\phi_0 - \lambda_0\phi_0 = 0, \\
\text{order } \epsilon^1 &: \ \mathcal{L}_{A_0}\phi_1 - \lambda_0\phi_1 = \lambda_1\phi_0 - \sigma(t)\partial_x\phi_0,
\end{aligned}$$

It follows from the equation of order ϵ^0 that (λ_0, ϕ_0) is the principal eigenpair of $\mathcal{L}_{A_0}$, namely, $(\lambda_0, \phi_0) = (\lambda_\infty^{A_0}, \psi_{A_0})$.

Denote by $\mathcal{L}_{A_0}^*$ the adjoint operator of $\mathcal{L}_{A_0}$. Then, $\lambda_\infty^{A_0}$ is also the principal eigenvalue of $\mathcal{L}_{A_0}^*$. Denote by $\psi_{A_0}^*$ the positive eigenfunction of $\mathcal{L}_{A_0}^*$ associated

Table 2 Numerical calculation of λ_1

A	10	20	30	40	50	60	70
λ_1	$-2.7343(10)^{-4}$	$-7.3638(10)^{-4}$	-0.0077	-0.0885	-0.0955	-0.0948	-0.1331

to $\lambda_\infty^{A_0}$. Since ϕ_1 solves the equation of order ϵ^1, the Fredholm alternative gives $\int_0^T \int_{\mathbb{R}} \psi_{A_0}^*(t,x)\left[\lambda_1 \psi_{A_0}(t,x) - \sigma(t)\partial_x \psi_{A_0}(t,x)\right] dxdt = 0$, leading to

$$\lambda_1 = \frac{\displaystyle\int_0^T \int_{\mathbb{R}} \sigma(t)\psi_{A_0}^*(t,x)\partial_x \psi_{A_0}(t,x)dxdt}{\displaystyle\int_0^T \int_{\mathbb{R}} \psi_{A_0}^*(t,x)\psi_{A_0}(t,x)dxdt}.$$

Note that $\int_0^T \int_{\mathbb{R}} \psi_{A_0}^*(t,x)\psi_{A_0}(t,x)dxdt > 0$. However, it is in general hard to determine the sign of λ_1 analytically thanks to the cancellation in the integral $\int_0^T \int_{\mathbb{R}} \sigma(t)\psi_{A_0}^*(t,x)\partial_x \psi_{A_0}(t,x)dxdt$. We show numerically that $\lambda_1 < 0$, and hence,

$$\lambda_\infty^A = \lambda_\infty^{A_0} + \epsilon\lambda_1 + \cdots \quad \text{for} \quad |\epsilon| \ll 1.$$

This justifies (*P2*).

For numerical simulations, we use the same parameters as in the previous cases, that is, $\sigma(t) = \sin \pi t$, $g(x,0) = a(x)$ is given in (4.3) and $L = 40$, fix $c = 6$ and treat A as the control parameter. We numerically calculate λ_1 by choosing several A. Results are listed in Table 2.

We make some comments on the numerical calculations of λ_1. Since ψ_{A_0} and $\psi_{A_0}^*$ are unique up to multiplication by constants, λ_1 is independent of particular choices of ψ_{A_0} and $\psi_{A_0}^*$. Our calculation of ψ_{A_0} is guided by the following well-known fact [see e.g. Poláčik and Tereščák (1993)]: if $w(t,x)$ solves $w_t = dw_{xx} + [c + A_0\sigma(t)]w_x + g(x,0)w$ with initial condition $w_0 \gneqq 0$, then for any $t \in [0,T]$,

$$\frac{w(t+nT,\cdot)}{\|w(nT,\cdot)\|_\infty} \to \frac{\psi_{A_0}(t,\cdot)}{\|\psi_{A_0}(0,\cdot)\|_\infty} \quad \text{as} \quad n \to \infty. \tag{5.16}$$

We then compute $w(t+nT,x)$ for $t \in [0,T]$ and a sufficiently large n to obtain an approximation of ψ_{A_0} as well as its spatial partial derivative on $[0,T]$. The computation of $\psi_{A_0}^*$ is done in the same way.

A formal justification of (5.16) is straightforward. In fact, considering the time-T map and using the projection onto $\mathrm{span}\{\psi_{A_0}(0,\cdot)\}$ and its complement, it is not hard to see that $w(nT,\cdot) = Ce^{\lambda_\infty^{A_0} nT}\psi_{A_0}(0,\cdot) + R_n$ for all $n \geq 0$, where $C > 0$ (due to the non-negativity of w_0) and R_n satisfies $e^{-\lambda_\infty^0 nT}\|R_n\|_\infty \to 0$ exponentially fast as

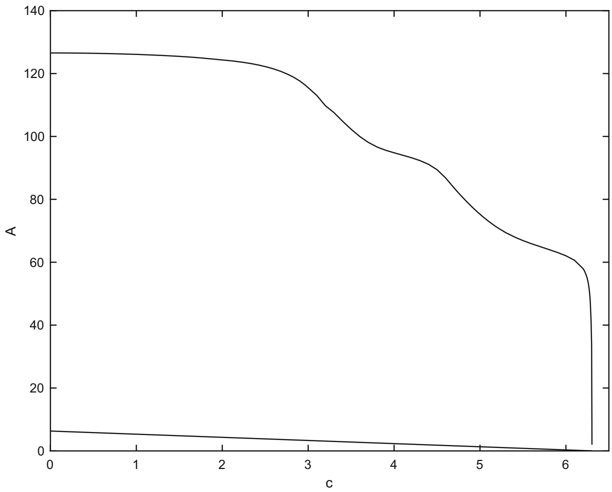


Fig. 5 Plot of $c \mapsto A_c$ (the curve) and $c \mapsto c^* - c$ (the straight line)

$n \to \infty$ (due to the spectral gap). Then,

$$\frac{w(nT,\cdot)}{\|w(nT,\cdot)\|_\infty} = \frac{C\psi_{A_0}(0,\cdot) + e^{-\lambda_\infty^{A_0} nT} R_n}{\|C\psi_{A_0}(0,\cdot) + e^{-\lambda_\infty^{A_0} nT} R_n\|_\infty} \to \frac{\psi_{A_0}(0,\cdot)}{\|\psi_{A_0}(0,\cdot)\|_\infty} \quad \text{as} \quad n \to \infty.$$

This leads to (5.16).

5.4 Justification of (*P3*)

The justification done in Sect. 5.3 for λ_∞^A carries over to λ_L^A. Hence, $\frac{d\lambda_L^A}{dA} < 0$ on $(0,\infty)$. It follows that for any $0 < A_1 < A_2 < \infty$,

$$\lambda_L^{A_2} - \lambda_L^{A_1} = \int_{A_1}^{A_2} \frac{d\lambda_L^A}{dA} dA < 0,$$

implying that $A \mapsto \lambda_L^A$ is decreasing on $(0,\infty)$. Since the function $A \mapsto \lambda_\infty^A$ is the pointwise limit of decreasing functions $\{A \mapsto \lambda_L^A\}_{L \gg 1}$, it is non-increasing.

5.5 Justification of (*P4*)

Recall that we assume that $\min_{t\in\mathbb{R}} \sigma(t) = -1$ and $\max_{t\in\mathbb{R}} \sigma(t) = 1$ such that A is indeed the amplitude of fluctuations. To highlight the dependence of λ_∞^A on c, we write $\lambda_\infty^A(c)$. We further assume that $\lambda_\infty^0(0) > 0$ so that the species persists in the absence of climate change and fluctuations. It is shown in Berestycki et al. (2009, Eq. (46)) by means of the Liouville transform that

$$\lambda_{\infty}^{0}(c) = \lambda_{\infty}^{0}(0) - \frac{c^2}{4d}, \tag{5.17}$$

which implies the existence of a unique $c^* > 0$ such that $\lambda_{\infty}^{0}(c) > 0$ for $c \in [0, c^*)$ and $\lambda_{\infty}^{0}(c) < 0$ for $c > c^*$. If we allow c to take negative values, then $\lambda_{\infty}^{0}(c) > 0$ for $|c| < c^*$ and $\lambda_{\infty}^{0}(c) < 0$ for $|c| > c^*$.

For each $c \in [0, c^*)$, properties $(P1)$–$(P3)$ ensure that the equation $\lambda_{\infty}^{A}(c) = 0$ admits a unique solution A_c such that $\lambda_{\infty}^{A}(c) > 0$ for $A \in [0, A_c)$ and $\lambda_{\infty}^{A}(c) < 0$ for $A > A_c$. We show numerically that $A_c > c^* - c$ for all $c \in [0, c^*)$, justifying $(P4)$.

To perform numerical simulations, we consider (4.2) and choose $c(t)$, L, $a(x)$ and $w(0, \cdot)$ to be the same as those used in Sect. 4.3. We calculate $\lambda_{\infty}^{0}(0) \approx 9.9940$, which together with the formula (5.17) with $d = 1$ gives the critical speed $c^* \approx 6.3227$. In Fig. 5, we plot the curve $c \mapsto A_c$ and the straight line $c \mapsto c^* - c$ for $c \in [0, c^*)$, showing $A_c > c^* - c$ for all $c \in [0, c^*)$, or equivalently $\lambda_{\infty}^{c^*-c} > 0$ for all $c \in [0, c^*)$.

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