

Climate Change and Integrodifference Equations in a Stochastic Environment

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Abstract Climate change impacts population distributions, forcing some species to migrate poleward if they are to survive and keep up with the suitable habitat that is shifting with the temperature isoclines. Previous studies have analysed whether populations have the capacity to keep up with shifting temperature isoclines, and have mathematically determined the combination of growth and dispersal that is needed to achieve this. However, the rate of isocline movement can be highly variable, with much uncertainty associated with yearly shifts. The same is true for population growth rates. Growth rates can be variable and uncertain, even within suitable habitats for growth. In this paper, we reanalyse the question of population persistence in the context of the uncertainty and variability in isocline shifts and rates of growth. Specifically, we employ a stochastic integrodifference equation model on a patch of suitable habitat that shifts poleward at a random rate. We derive a metric describing the asymptotic growth rate of the linearised operator of the stochastic model. This metric yields a threshold criterion for population persistence. We demonstrate that the variability in the yearly shift and in the growth rate has a significant negative effect on the persistence in the sense that it decreases the threshold criterion for population persistence. Mathematically, we show how the persistence metric can be connected to the principal eigenvalue problem for a related integral operator, at least for the case where isocline shifting speed is deterministic. Analysis of dynamics for the case where the dispersal kernel is Gaussian leads to the existence of a critical shifting speed, above which the population will go extinct, and below which the population will persist. This leads to

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clear bounds on rate of environmental change if the population is to persist. Finally, we illustrate our different results for butterfly population using numerical simulations and demonstrate how increased variances in isocline shifts and growth rates translate into decreased likelihoods of persistence.

Keywords Integrodifference equations · Climate change · Forced migration speed · Stochastic environment · Population persistence

Mathematics Subject Classification 45R05 · 45C05 · 92D25

1 Introduction

The consequences of climate change on population abundance and distribution have been widely investigated for the last two decades. One of these consequences is a modification of range distributions. Indeed, we know that, for a large variety of vertebrate and invertebrate species, climate change induces range shift towards the poles or higher altitudes, contraction or expansion of the habitat and habitat loss (Parmesan and Yohe 2003; Hickling et al. 2006; Menendez et al. 2014; Parmesan 2006; Lenoir et al. 2008, amongst other). Mathematical models and simulations that include climate change have predicted an effect of climate change on range distribution through habitat migration, habitat reduction and expansion and habitat loss (Parmesan and Yohe 2003; Ni 2000; Hu et al. 2015; Malcolm and Markham 2000; Polovina et al. 2011; Parr et al. 2012; Hazen et al. 2013). In this paper, we are interested in understanding, with the aid of a mechanistic model, the effect of shifting range on population persistence when the yearly range shifts and the population growth rates are stochastic.

Mechanistic models have been used to study the effect of shifting boundaries on population persistence, by considering a suitable habitat, which is a bounded domain where the population can grow, that is shifted towards the pole at a forced speed $c > 0$. Potapov and Lewis (2004) used a reaction–diffusion system with a moving suitable habitat to investigate the effect of climate change and shifting boundaries on population persistence when two populations compete with one another. Berestycki et al. (2009) used a similar equation, in a scalar framework, to study the persistence property of one population facing shifting range, and characterised persistence as it depends on the shifting speed. More recent papers also investigate the effect of shifting range on population persistence of single populations (Richter et al. 2012; Leroux et al. 2013; Li et al. 2014). In all these, reaction–diffusion equations are used to model the temporal evolution of the density u of a population in space and time. That is, individuals are assumed to disperse and grow simultaneously. In these models, dispersal is local in the sense that the population disperses to its closest neighbourhood, in a diffusive manner.

Another approach to modelling the temporal evolution of the density of a population is to consider populations that disperse and reproduce successively and to allow for nonlocal dispersal. In this case, integrodifference equations are the appropriate model for the dynamics of the density u . Integrodifference equations, introduced by Kot and Schaffer (1986) to model discrete-time growth-dispersal, assume time ($t = 0, 1, \dots$) to be discrete and space $\xi \in \Omega$ to be continuous. From one generation to the next, the

population grows, according to a nonlinear growth function $f(u)$ and then disperses according to a dispersal kernel K , so

$$u_{t+1}(\xi) = \int_{\Omega} K(\xi, \eta) f(u_t(\eta)) d\eta, \quad t \in \mathbb{N}. \tag{1}$$

Strictly, the dispersal kernel $K(\xi, \eta)$ is a probability density function describing the chance of dispersal from η to ξ .

We consider a self-regulating population, with negative density dependence so the slope of the growth is assumed to be monotonically decreasing with $f(u) > u$ for $0 < u < C$ and $f(u) < u$ for $u > C$, where $C > 0$ is the carrying capacity. As we consider a population that is not subject to an Allee effect, the standard assumption on the growth function is that the geometric growth rate is the largest at lowest density, that is, $f(u)/u$ achieves its supremum as u approaches 0. We denote $r = \lim_{u \rightarrow 0^+} f(u)/u = f'(0)$. When we wish to explicitly distinguish between populations with different geometric growth rates, we modify our notation, replacing $f(u)$ by $f_r(u)$. Within this framework, we consider two types of growth dynamics: compensatory and overcompensatory. The compensatory growth dynamics are monotonic with respect to density u , whereas the overcompensatory growth dynamics have a characteristic ‘‘hump’’ shape (Fig. 1).

The eigenvalue problem associated with the linearisation of (1) about $u \equiv 0$ is

$$\lambda \phi(\xi) = r \int_{\Omega} K(\xi, \eta) \phi(\eta) d\eta \tag{2}$$

and persistence of the population $u_t(\xi)$ depends upon whether λ falls above or below one (Kot and Schaffer 1986; VanKirk and Lewis 1997; Lutscher and Lewis 2004). An approximate method for calculating λ employs the so-called dispersal success approximation (VanKirk and Lewis 1997). Without loss of generality, one can assume that $\int_{\Omega} \phi(\eta) d\eta = 1$ and integrating the previous equation on Ω we get

$$\lambda = r \int_{\Omega} \int_{\Omega} K(\xi, \eta) \phi(\eta) d\eta = r \int_{\Omega} s(\eta) \phi(\eta) d\eta \tag{3}$$

where $s(\eta) = \int_{\Omega} K(\xi, \eta) d\xi$ is the dispersal success. This function represents the probability for an individual located at η to disperse to a point within the domain. The so-called dispersal success approximation $\phi(\eta) \approx \frac{1}{|\Omega|}$ therefore allows the principal eigenvalue λ to be estimated by (VanKirk and Lewis 1997).

$$\bar{\lambda} = \frac{r}{|\Omega|} \int_{\Omega} s(\eta) d\eta \tag{4}$$

This approximation gives $\bar{\lambda}$ as the growth rate times the estimated proportion of individuals that stay within the suitable habitat from one generation to the next. A modified dispersal success approximation recently introduced by Reimer et al. (2016) improves upon the dispersal success approximation assumption that the population is uniformly

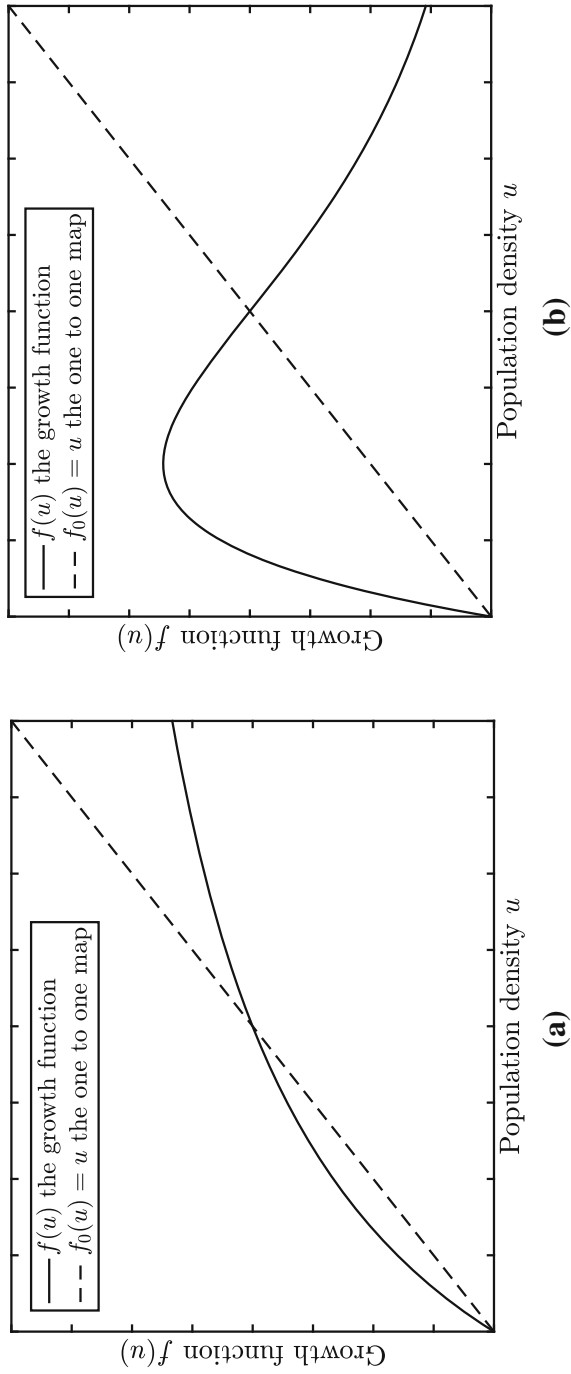


Fig. 1 Compensatory (a) and overcompensatory (b) growth with one positive fixed point

distributed within the favourable environment. [Reimer et al. \(2016\)](#) introduced a modified approximation that weights the dispersal success values by the proportion of the population at each point. They defined the modified dispersal success approximation by

$$\widehat{\lambda} = \frac{r}{|\Omega|} \int_{\Omega} \left(\frac{s(\eta)}{\bar{\lambda}} \right) s(\eta) d\eta \quad (5)$$

and showed that this gave a better approximation to the eigenvalue. We will employ both versions of the dispersal success approximation (4) and the modified dispersal success approximation (5) in our calculations later in this paper.

So far we have considered only the dependence of the growth on the density u . In the framework for climate change, the population can grow differently depending on where it is located with respect to space and time. To take this into account, we introduce a suitability function, $g_t(\eta)$ ($0 \leq g_t \leq 1$), which depends on space and time and multiplies the growth map f . As we consider populations whose suitable habitat shifts towards the pole, we choose a particular form for suitability function, $g_t(\eta) = g_0(\eta - s_t)$, where g_0 is the initial suitability function in the absence of climate change and s_t is a parameter standing for the centre of the suitable habitat. The simple case where the habitat shifts at a constant speed c is given by $s_t = ct$. However, as we describe below, it is also possible to allow s_t to vary randomly about ct .

Following the growth stage, the population disperses in space according to the dispersal kernel K . The kernel K is assumed to be positive everywhere, that is, the probability of dispersing to any point in space is always positive. Dispersal kernels are typically assumed to depend only on the signed distance between two points in space, i.e., only on the dispersal location relative to the source location. If the population has no preferred direction of dispersal, the kernel is symmetric, depending only upon the distance between source and dispersal locations. This is not the case, however, in rivers where the population is subjected to a stream flow, for example, or in environments with a prevailing wind direction that affects dispersal. In this paper, we consider the Gaussian and the Laplace kernel as examples of typical symmetric dispersal kernels (Fig. 2).

In this framework of discrete-time growth-dispersal models, [Zhou and Kot \(2011\)](#) investigated the effect of climate change and shifting range on the persistence of the population and highlighted the possible existence of a critical shifting speed for persistence. More recently, several works investigated the effect of shifting range in more general discrete-time growth-dispersal models ([Zhou and Kot 2013](#); [Harsch et al. 2014](#); [Phillips and Kot 2015](#)).

Recent research reports an increase in the environmental stochasticity in population dynamics, partly due to climate change and its effect on the frequency and the intensity of extreme climatic events covering large areas of the globe ([Saltz et al. 2006](#); [IPCC 2007](#); [Kreyling et al. 2011](#)). It is also known that the projected consequences for population ranges vary, depending on the different scenarios related to climate change (see, for example, [IPCC \(2014\)](#)).

In this paper, we focus on the effect of environmental stochasticity on population persistence in the presence of a shifting range, using a stochastic population model.

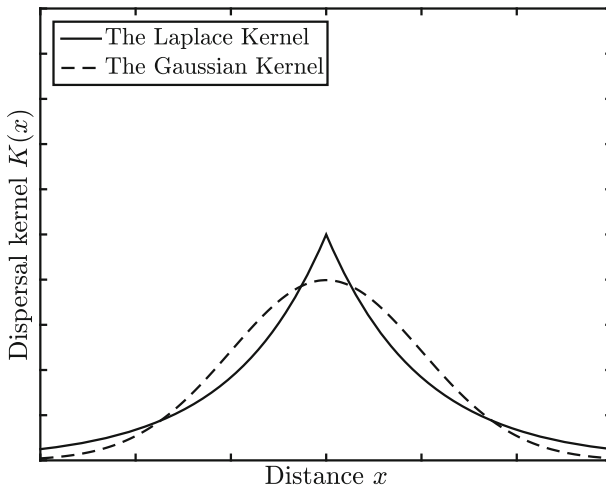


Fig. 2 Laplace and Gaussian dispersion kernel $x \mapsto K(x)$ centred at 0

The development of stochastic population models in population ecology was initially motivated by the study of the effect of environmental stochasticity on population dynamics and on the large time behaviour of the population (May 1973; Turelli 1977).

We incorporate stochasticity into our modelling framework in two ways: first with respect to the shifting speed for suitable habitat and second with respect to the growth rate within the suitable habitat. The model for the shifting speed gives the centre of the suitable habitat as $s_t = ct + \sigma_t$, where σ_t is a random variable. Here we assume that c is unknown but fixed, depending on the scenario considered for the severity of global warming ($c \in \{c_1, \dots, c_n\}$) (Fig. 3). Variability of the growth dynamics at each generation, for example, due to weather conditions or extreme climate events, is included through stochasticity in the growth function $f(u)$. Our approach is to incorporate the randomness into the geometric growth rate $r_t \in \{r_1, \dots, r_n\}$ (Fig. 4) and so in any given year the growth function is given by $f_{r_t}(u)$ where $r_t = f'_{r_t}(0)$.

Our goal is to mathematically analyse the effect of climate change and shifting range on population dynamics for a species that grows and then disperses at each generation, taking into account stochasticity induced by environmental variability and climate change. In Sect. 2, we derive the model and state model assumptions. In Sect. 3, we first define a persistence condition, derived from the papers of Hardin et al. (1988) and Jacobsen et al. (2015). We then detail computation of the persistence criterion and highlight the link between persistence of the population and principal eigenvalue of the operator linearised about 0 for the case where the shifting speed is not random ($\sigma_t \equiv 0$). We also prove that when the dispersal kernel is Gaussian and the speed is not random, there exists a critical shifting speed characterising persistence of the population. Speeds above this critical value will drive the population to extinction, while speeds below will allow the population to persist. In sect. 4, we apply the theory to an example in butterfly population subject to changing temperatures in Canada (Leroux et al. 2013) and use numerical simulations to investigate the dependence of the critical shifting speed on the variance of the dispersal Gaussian kernel. We

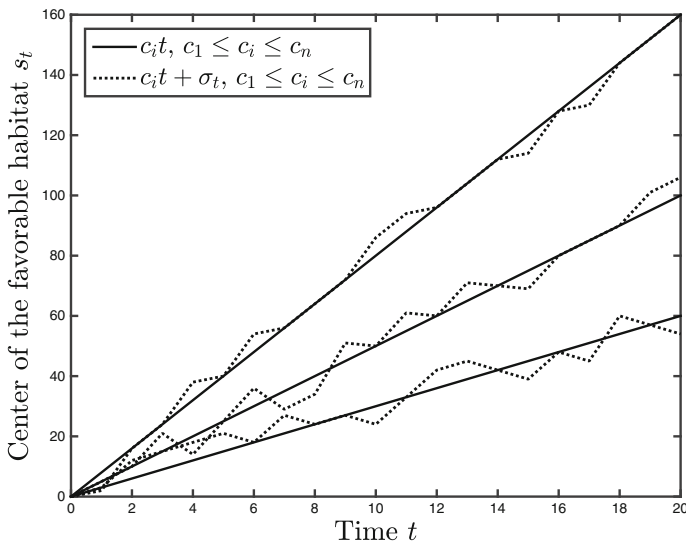


Fig. 3 Position of the centre of the suitable habitat depending of the generation t , the chosen shifting speed $c_i \in \{c_1, \dots, c_n\}$ and the random process σ_t . In this figure, there are three possible c and for each $c_i \in \{c_1, c_2, c_3\}$, the centre of the suitable habitat at generation t is located at $c_i t + \sigma_t$, $(\sigma_t)_t$ independently identically distributed

also compute the persistence criterion as a function of the variance of the dispersal kernel for Gaussian and Laplace kernel. Lastly we numerically investigate the effect of the variability in the yearly shift and in the growth rate on the persistence of the population. In Appendix, we draw on classical theory of invasion speeds for stochastic integrodifference equations to aid development of a heuristic link between the speed of the stochastic wave in the homogeneous framework and the critical domain size and persistence condition.

2 The Model

In this section, we derive the mechanistic model used to study population persistence facing global warming and habitat shifts. We explain the different assumptions made for each component throughout the derivation of the model and conclude by explaining how it results in the problem in a moving environment.

As already stated in the introduction, we use the theory of integrodifference equations to model the temporal dynamics of the density of the population u , as introduced by [Kot and Schaffer \(1986\)](#). In the classical homogeneous case, the model is as given in Eq. (1) with Ω given by \mathbb{R} and with u_0 given, nonnegative, compactly supported and bounded.

We make the following assumptions regarding the dispersal kernel K

- Hypothesis 1** (i) For all $\xi \in \mathbb{R}$, $\eta \in \mathbb{R}$, $K(\xi, \eta) = K(\xi - \eta)$.
(ii) $K(x)$ is well defined, continuous, uniformly bounded and positive in \mathbb{R} .

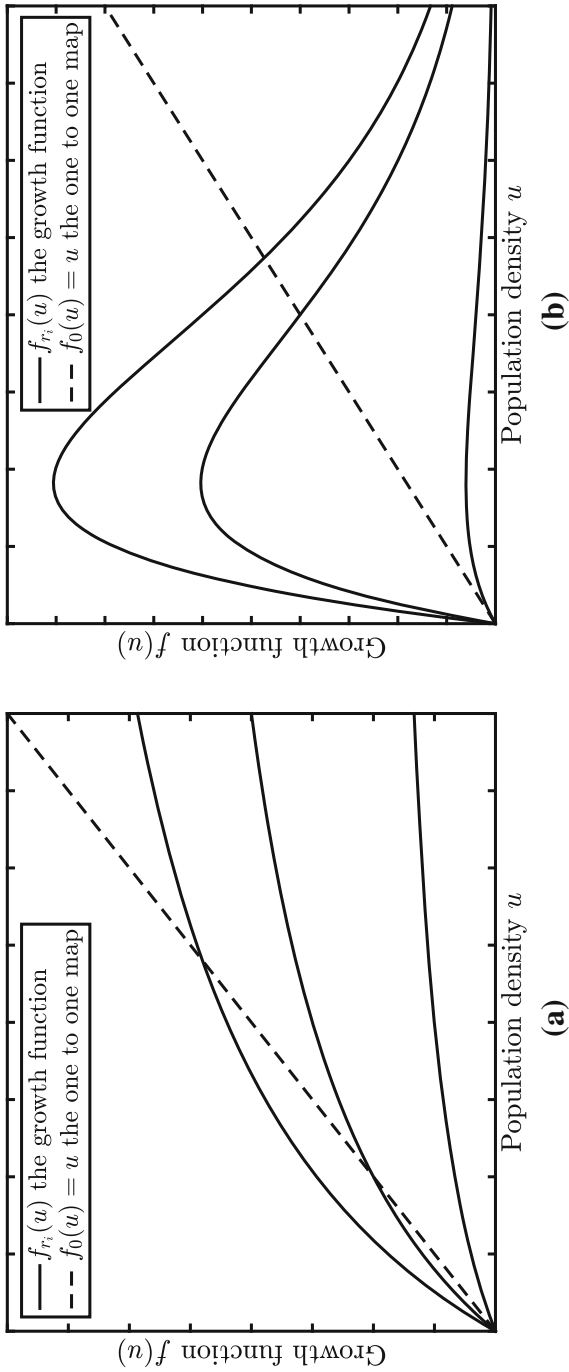


Fig. 4 Different realisations for the growth function f_r depending on the random process r for compensatory (a) and overcompensatory (b) growth. One notices that for some realisation $f_r'(0) < 1$ and there is no positive fixed point for this type of function f_r

The first hypothesis means that K takes the form of a difference kernel and depends only on the signed distance between ξ and η . The second holds for typical kernel, such as the Laplace and Gaussian (Fig. 2).

To include the effect of climate change on range distribution in this model, we assume that the suitability of the environment is heterogeneous in the sense that

$$u_{t+1}(\xi) = \int_{\mathbb{R}} K(\xi - \eta) g_t(\eta) f(u_t(\eta)) d\eta. \quad (6)$$

where the function $(t, \eta) \mapsto g_t(\eta)$ stands for the suitability of the environment at generation t and location η .

We make the following assumptions for the suitability function g_t :

- Hypothesis 2** (i) Denoting s_t as the reference point on a suitable habitat, we assume that $g_t(\eta) = g_0(\eta - s_t)$,
(ii) $g_0(x)$ is compactly supported, nonnegative, bounded by 1 and is nontrivial in \mathbb{R} .

Biologically these assumptions mean that the suitable environment has a constant profile g_0 that is shifted by s_t at generation t .

The model then becomes

$$u_{t+1}(\xi) = \int_{\mathbb{R}} K(\xi - \eta) g_0(\eta - s_t) f(u_t(\eta)) d\eta. \quad (7)$$

We denote Ω_0 as the support of g_0 , i.e., $\Omega_0 := \{x \in \mathbb{R}, g_0(x) > 0\}$. Notice that only the population located in $\Omega_0 + s_t := \{x \in \mathbb{R} \mid x = x' + s_t, x' \in \Omega_0\}$ contributes to the growth from generation t to generation $t + 1$. To introduce environmental stochasticity in our model, we assume that $(s_t)_{t \in \mathbb{N}}$ is a random process and $f(u) = f_{r_t}(u)$, with $(f_{r_t})_{t \in \mathbb{N}}$ a sequence of random functions. We interpret r_t as the geometric growth rate of the population at low density. These two forms of environmental stochasticity emphasise the dependence of the range shift and the growth rate on the strength of the climate change. Moreover, we can be more precise about the form of the shift variable s_t . Indeed, we assume that for all $t \in \mathbb{N}$, $s_t = ct + \sigma_t$, where $c > 0$ is a constant representing the asymptotic shifting speed and σ_t is a random variable representing the environmental stochasticity in the shift from one year to the next. In the introduction, we stated that the asymptotic shifting speed itself may be uncertain. However, from now on, we consider it to be a fixed constant c and study the problem of persistence of the population for different possible values of the asymptotic shifting speed c .

Denoting by $(\alpha_t)_t = (\sigma_t, r_t)_t$ and \mathcal{S} the set of possible outcomes for α at each generation, we assume that the elements $(\alpha_t)_t$ are independent, identically distributed and bounded by appropriate values, namely:

- Hypothesis 3** (i) $(\alpha_t)_t = (\sigma_t, r_t)_t$ is a sequence of independent, identically distributed random variables, with distribution \mathcal{P}_α
(ii) There exist $\underline{\sigma} < 0 < \bar{\sigma}$ such that for all $t \in \mathbb{N}$, $\underline{\sigma} \leq \sigma_t < \bar{\sigma}$ with probability 1
(iii) There exist $\bar{r} > \underline{r} > 0$ such that for all $t \in \mathbb{N}$, $\underline{r} \leq r_t < \bar{r}$ with probability 1

We consider a self-regulating population, with negative density dependence and make the following assumptions on the growth function f :

Hypothesis 4 For any r such that $\alpha \in \mathcal{S}$

- (i) $f_r: \mathbb{R} \rightarrow [0, +\infty)$ is continuous, with $f_r(u) = 0$ for all $u \leq 0$,
- (ii) There exists a constant $m > 0$ such that, for all r ,
 - a. $u \in \mathbb{R}^+ \mapsto f_r(u)$ is nondecreasing,
 - b. $0 < f_r(u) \leq m$ for all positive continuous function u ,
 - c. If u, v are constants such that $0 < v < u$ then $f_r(u)v < f_r(v)u$,
 - d. $u \in \mathbb{R} \mapsto f_r(u)$ is right differentiable at 0, uniformly with respect to $\alpha \in \mathcal{S}$.
- (iii) We denote $r = f'_r(0)$ as the right derivative of f_r at 0 and assume for now that
 - a. $\underline{r} \leq f'_r(0) \leq \bar{r}$, from Hypothesis 3(iii)
 - b. $\inf\{f_r(b), \alpha \in \mathcal{S}\} > 0$, with $b := m \sup_{x \in \mathbb{R}} K(x) \int_{\Omega_0} g_0(y) dy$.

Hypothesis 4(i) means that the population does not grow when no individuals are present in the environment. We also assume that the growth of the population is bounded (Hypothesis 4(ii)b) and consider a population not subject to an Allee effect, that is, the geometric growth rate is decreasing with the density of the population (Hypothesis 4(ii)c). Hypothesis 4(ii)d holds for typical growth functions as the ones illustrated by Fig. 1. Notice that because of Hypothesis 4(ii)a, we do not yet consider models with overcompensatory competition here. Indeed we will need this monotonicity assumption to prove large time convergence of the solution of our problem. Nevertheless, we can extend our result to the case with overcompensation where f is not assumed to be nondecreasing and so Hypothesis 4(ii)a no longer holds. More details are given in Corollary 1, stated in the next section. Hypothesis 4(iii)a assumes that the geometric growth rate at zero density is bounded from above and below by some positive constants, while Hypothesis 4(iii)b implies that the growth term at the maximal density is positive, for all the possible environments.

Finally, denoting by $F_{\alpha_t}(u) := \int_{\Omega} K(x - y + c)g_0(y - \sigma_t)f_r(u(y))dy$, we make a last assumption:

Hypothesis 5 There exists $\alpha^* \in \mathcal{S}$ such that

$$F_{\alpha}(u) \leq F_{\alpha^*}(u) \tag{8}$$

for all $\alpha \in \mathcal{S}$, u nonnegative continuous function.

This assumption means that there exists an environment α^* that has the better outcome than all other environments in terms of population growth.

The general problem becomes

$$u_{t+1}(\xi) = \int_{\mathbb{R}} K(\xi - \eta)g_0(\eta - s_t)f_r(u_t(\eta))d\eta. \tag{9}$$

We are interested in the large time behaviour of the density u . Using a similar approach to the one of Zhou and Kot (2011), we would like to study the problem in the shifted environment, so as to track the population. Considering the moving variables $\xi_{t+1} := \xi - s_{t+1}$, $\eta_t := \eta - s_t$ and letting $\bar{u}_t(\eta_t) := u_t(\eta + s_t)$ be the associated density in the moving frame (where the reference point is the centre of the suitable environment that is shifted by s_t at time t), we obtain a problem where the space

variables ξ_{t+1} and η_t are also random variables. To simplify the analysis, we consider the problem in the “asymptotic” moving frame. That is we consider $x = \xi - c(t + 1)$ and $y = \eta - ct$ and using Hypothesis 1(i), Eq. (9) can be written as

$$u_{t+1}(x + c(t + 1)) = \int_{\mathbb{R}} K(x - y + c)g_0(y - \sigma_t)f_{r_t}(u_t(y + ct))dy. \quad (10)$$

Letting $\bar{u}_t(y) := u_t(y + ct)$ be the associated density in the moving frame, we have

$$\bar{u}_{t+1}(x) = \int_{\mathbb{R}} K(x - y + c)g_0(y - \sigma_t)f_{r_t}(\bar{u}_t(y))dy. \quad (11)$$

Dropping the bar, we obtain the following problem, in the moving frame,

$$u_{t+1}(x) = \int_{\mathbb{R}} K(x - y + c)g_0(y - \sigma_t)f_{r_t}(u_t(y))dy, \quad (12)$$

where u_0 is given as a nonnegative, nontrivial and bounded function. Moreover, as stated in Hypothesis 3(ii), for all $t \in \mathbb{N}$, $\sigma_t \in (\underline{\sigma}, \bar{\sigma})$ and thus defining

$$\Omega := (\inf \Omega_0 + \underline{\sigma}, \sup \Omega_0 + \bar{\sigma}), \quad (13)$$

we only have to study Eq. (12) for all $x \in \Omega$, for all $t \in \mathbb{N}$. The problem in the moving frame becomes

$$u_{t+1}(x) = \int_{\Omega} K(x - y + c)g_0(y - \sigma_t)f_{r_t}(u_t(y))dy, \quad (14)$$

where u_0 is given as a nonnegative, nontrivial and bounded function. Notice that this problem is now defined on a compact set $\Omega \subset \mathbb{R}$.

Many results already exist for the deterministic version of (14). When $\sigma_t \equiv 0$ and f is deterministic, depending only on u , it has been shown that, if $g_0(y) = \mathbb{1}_{[-\frac{L}{2}, \frac{L}{2}]}$, the magnitude of the largest eigenvalue of the linearised operator around 0 determines the stability of the trivial solution and thus the persistence of the population (see Zhou and Kot (2011, 2013) for the one dimensional problem, Phillips and Kot (2015) for the two dimensional problem). Harsch et al. (2014) study a similar deterministic integrodifference equation modified to include age- and stage-structured population and show that if the magnitude of the principal eigenvalue of the linearised problem around 0 exceeds one, then 0 becomes stable and the population goes extinct. Zhou also studied the associated deterministic problem (12), for more general deterministic functions f and g_0 (Zhou 2013, chapter 4).

In this paper, we are interested in similar questions about persistence of the population, but now for a shifting environment that moves at a random speed and a population that reproduces at a growth rate, chosen randomly at each generation.

Mathematically the assumptions on K , f and F that we make are similar than those made by Jacobsen et al. (2015) in their study of the question of persistence of a population in temporally varying river environment. They assumed that the dispersal

kernel and growth terms are randomly distributed at each time step but also assumed asymmetric dispersal kernels to take the effects of water flow into account. They used the theory of [Hardin et al. \(1988\)](#) to develop a persistence criterion for the general model

$$u_{t+1}(x) = F_{\alpha_t}(u_t(x)), \quad (15)$$

where $t \in \mathbb{N}$, $x \in \Omega \subset \mathbb{R}^n$ and $(\alpha_t)_t$ are independently identically distributed random variables and related this persistence criterion to the long-term growth rate. In what follows, we use similar theory to study our integrodifference Eq. (14) where $\alpha_t = (\sigma_t, r_t)_t$.

3 Persistence Condition for Random Environments with Shifted Kernel

In this section, we derive a criterion that separates persistence from extinction for a population facing random environments and climate change. We highlight the dependence of this criterion on the asymptotic geometric growth rate at low density on the one hand and on the shifted dispersal success function on the other hand. We then develop a connection between persistence and the magnitude of the principal eigenvalue of a linearised operator for the case when only the growth rate is stochastic. This allows us to conclude on the existence of a critical shifting speed for the case of Gaussian dispersal kernel.

3.1 Conditions for Persistence

We first describe the derivation of the deterministic criterion characterising persistence from extinction of the population.

Define $(u_t)_t$ to be the solution of problem (14). Then, $(u_t)_t$, the sequence of population density at each generation $t \in \mathbb{N}$, is a random process and for each t positive, u_t takes values in $C_+(\Omega)$, the set of continuous, nonnegative function defined on Ω . Using the same notation as [Hardin et al. \(1988\)](#), we can rewrite Eq. (14) as follows

$$u_{t+1}(x) = F_{\alpha_t}[u_t](x), \quad (16)$$

for all $x \in \Omega$.

We have the following theorem about the large time behaviour of the solution

Theorem 1 *Assume that K , g_0 , f_r and $(\alpha_t)_t$ satisfy all the assumptions stated in Sect. 2 (Hypotheses 1–5), let $(u_t)_t$ be the solution of problem (14), with a bounded, nonnegative and nontrivial initial condition u_0 . Then u_t converges in distribution to a random variable u^* as time goes to infinity, independently of the initial condition u_0 , and u^* is a stationary solution of (14), in the sense that*

$$u^*(x) = \int_{\Omega} K(x - y + c)g_0(y - \sigma^*)f_{r^*}(u^*(y))dy, \quad (17)$$

with (σ^*, r^*) a random variable taking its values in \mathcal{S} with distribution \mathcal{P}_α (Hypothesis 3i). Denoting by μ^* the stationary distribution associated with u^* and $\mu^*(\{0\})$ the probability that $u^* \equiv 0$, we have that $\mu^*(\{0\}) = 0$ or $\mu^*(\{0\}) = 1$

The proof of this theorem follows from [Hardin et al. \(1988, Theorem 4.2\)](#) and is detailed in Appendix 1. One can then be more precise about the distribution μ^* . Define

$$\Lambda_t := \left(\int_{\Omega} \tilde{u}_t(x) dx \right)^{1/t}, \quad (18)$$

where $(\tilde{u}_t)_t$ is the solution of the linearised problem around 0, i.e., for all $x \in \Omega$

$$\tilde{u}_{t+1}(x) = \mathcal{L}_{\alpha_t} \tilde{u}_t(x) := \int_{\Omega} K(x - y + c) g_0(y - \sigma_t) r_t \tilde{u}_t(y) dy. \quad (19)$$

The metric Λ_t can be interpreted as the growth rate of the linearised operator up to time t and its limit, representing the asymptotic growth rate of the linearised operator. We have the following theorem

Theorem 2 *Let Λ_t be defined as in (18), then*

$$\lim_{t \rightarrow +\infty} \Lambda_t = \Lambda \in [0, +\infty), \text{ with probability } 1.$$

And,

- If $\Lambda < 1$, the population will go extinct, in the sense that $\mu^*(\{0\}) = 1$,
- If $\Lambda > 1$, the population will persist, in the sense that $\mu^*(\{0\}) = 0$.

The proof of this theorem follows from [Hardin et al. \(1988, Theorem 5.3\)](#) and [Jacobsen et al. \(2015, Theorem 2\)](#), and it is explained in Appendix 1. From these two theorems, one can then deduce a corollary, for the case where the growth function f is not assumed to be monotonic anymore.

Corollary 1 *Let K, f, g_0 and $(\alpha_t)_t$ satisfy the assumptions from Sect. 2 except assumption 4(ii)a, that is, f_r is not assumed to be nondecreasing. Let $(u_t)_t$ be the solution of (14), with a bounded initial condition u_0 . Let Λ_t be defined as in (18), then*

$$\lim_{t \rightarrow +\infty} \Lambda_t = \Lambda \in [0, +\infty), \text{ with probability } 1.$$

Also,

- If $\Lambda < 1$, the population will go extinct, in the sense that $\lim_{t \rightarrow +\infty} u_t(x) = 0$ for all $x \in \Omega$ with probability 1,
- If $\Lambda > 1$, the population will persist, in the sense that $\liminf_{t \rightarrow +\infty} \inf_{x \in \Omega} u_t(x) > 0$ with probability 1.

Proof First note that

$$\|F_\alpha(u)\|_\infty = \max_{x \in \Omega} \int_\Omega K(x - y + c)g_0(y - \sigma)f_r(u(y))dy \tag{20}$$

$$< m \cdot \sup_{x \in \mathbb{R}} K(x) \cdot \int_{\Omega_0} g_0(y)dy = b, \tag{21}$$

where m is defined in Hypothesis 4(ii)b. This implies that

$$u_t(x) \leq b, \tag{22}$$

for all $t \in \mathbb{N}^*$, for all $x \in \Omega$. Then define lower and upper nondecreasing functions that satisfy Hypothesis 4,

$$u \in C_+(\mathbb{R}) \mapsto \underline{f}_r(u), \quad u \in C_+(\mathbb{R}) \mapsto \overline{f}_r(u),$$

so their slopes match that of f_r at zero

$$\underline{f}'_r(0) = f'_r(0) = \overline{f}'_r(0) = r, \tag{23}$$

and they satisfy the inequalities

$$0 < \underline{f}_r(u) \leq f_r(u) \leq \overline{f}_r(u) < m \tag{24}$$

for all $u \in (0, b)$. For instance, we can choose the nondecreasing function

$$\underline{f}_r(u) = \min_{u \leq v \leq b} f_r(v) \text{ and } \overline{f}_r(u) = \max_{0 \leq v \leq u} f_r(v), \tag{25}$$

One can easily prove, using the definition of $\underline{f}_r, \overline{f}_r$ and the properties of f_r , that \underline{f}_r and \overline{f}_r as defined in (25) satisfy Hypothesis 4(i), (ii) and (iii) and are such that (23)–(24) are satisfied.

Then denoting $(v_t)_t$, respectively, $(w_t)_t$, as the solution of problem (14), with \underline{f}_r instead of f_r , respectively, \overline{f}_r instead of f_r , such that $v_0 \equiv u_0 \equiv w_0$, we have

$$v_t(x) \leq u_t(x) \leq w_t(x) \tag{26}$$

for all $t \in \mathbb{N}$, for all $x \in \Omega$. Applying the previous theorems (Theorems 1 and 2), we know that

- If $\Lambda > 1$ (where Λ is defined in Theorem 2), then the population associated with the process $(v_t)_t$ persists in the sense that $\mu_v^*(\{0\}) = P(\lim_{t \rightarrow +\infty} v_t \equiv 0) = 0$, which implies, using (26) that $\lim_{t \rightarrow +\infty} \inf_{x \in \Omega} u_t(x) > 0$ with probability 1,
- If $\Lambda < 1$, then the population associated with the process $(w_t)_t$ goes extinct in the sense that $\mu_w^*(\{0\}) = P(\lim_{t \rightarrow +\infty} w_t \equiv 0) = 1$, which implies, using again (26), that $\lim_{t \rightarrow +\infty} u_t(x) = 0$, for all $x \in \Omega$, with probability 1.

This completes the proof of Corollary 1. □

This means that the results about persistence and extinction extend to the case of overcompensatory growth as illustrated in Fig. 1, even though we cannot draw conclusions about the large time convergence of the solution.

Note that the persistence criterion as given by Theorem 2 or Corollary 1 is difficult to analyse further. It requires the calculation of the asymptotic growth rate of the linearised operator under random environmental conditions (Eq. (18)). However, we can proceed heuristically regarding a necessary condition for persistence of the population by comparing the asymptotic shifting speed c with the asymptotic invasion speed of the population in a homogeneous environment. Consider the population dynamics in a homogeneous environment ($g_0 \equiv 1$). Equation (19) becomes

$$\tilde{u}_{t+1}(x) = \int_{\mathbb{R}} K(x - y + c)r_t\tilde{u}_t(y)dy. \tag{27}$$

If we consider exponentially decaying solution of the form $\tilde{u}_t \propto h_t e^{-sx}$, $s > 0$, substitution into (27) yields

$$h_{t+1} = M(s)e^{-sc}h_t r_t \tag{28}$$

where M is the moment generating function of K

$$M(s) = \int_{\mathbb{R}} e^{sz} K(z)dz. \tag{29}$$

The pointwise growth rate of the solution is given asymptotically by

$$\lim_{t \rightarrow +\infty} \frac{1}{t} \ln \left(\frac{h_t}{h_0} \right) = \ln(M(s)) + \lim_{t \rightarrow +\infty} \frac{1}{t} \sum_{i=0}^{t-1} \ln(r_i) - cs \tag{30}$$

$$= E[\ln(r_0 M(s))] - cs \tag{31}$$

and is positive if $c < \bar{c}^*$ where

$$\bar{c}^* = \inf_{s>0} \frac{1}{s} E[\ln(r_0 M(s))]. \tag{32}$$

We interpret \bar{c}^* as the invasion speed of a population undergoing dispersal and stochastic growth in a spatially homogeneous environment. In the case where g_0 is diminished, so it is not equal to one at all point in space, $c < \bar{c}^*$ may no longer suffice to give a positive pointwise growth rate. On the other hand, if we consider a bounded, compactly supported initial condition, \tilde{u}_0 , and thus for all $s > 0$ there exists h_0 such that $\tilde{u}_0(x) \leq h_0 e^{-sx}$, then the population \tilde{u}_t , solution of (27) starting with the initial condition \tilde{u}_0 ,

$$\tilde{u}_{t+1}(x) \leq h_{t+1} e^{-sx}. \tag{33}$$

The pointwise growth rate of the solution \tilde{u}_t will thus be smaller than the pointwise growth rate of the solution $h_t e^{-sx}$, and $c < \bar{c}^*$ is necessary to give a positive pointwise growth rate of \tilde{u}_t .

3.2 Computation of the Persistence Criterion Λ

In this section, we detail possible computation of the persistence criterion Λ and highlight the link between Λ and the principal eigenvalue of the linearised operator around zero.

Using the analysis of the previous section, one can determine whether a population can track its favourable environment and thus persist ($\Lambda > 1$ in Theorem 2 and Corollary 1) or cannot keep pace with the shifting environment and goes extinct ($\Lambda < 1$ in Theorem 2 and Corollary 1). It would be interesting to understand the dynamics of $\Lambda := \lim_{t \rightarrow +\infty} \Lambda_t$ in terms of the different parameters of the problem. Using the definition of Λ_t (18), we have

$$\Lambda_1 = \int_{\Omega} \tilde{u}_1(x) dx \tag{34}$$

$$= \int_{\Omega} \int_{\Omega} K(x - y + c) g_0(y - \sigma_0) r_0 u_0(y) dy dx \tag{35}$$

where r_0, σ_0 are the realisations for the geometric growth rate and the yearly shift at generation 0. Continuing,

$$\Lambda_2 = \left(\int_{\Omega} \tilde{u}_2(x) dx \right)^{1/2} \tag{36}$$

$$= \left(\int_{\Omega} \int_{\Omega} K(x - y_1 + c) g_0(y_1 - \sigma_1) r_1 \tilde{u}_1(y_1) dy_1 dx \right)^{1/2} \tag{37}$$

$$= (r_1 r_0)^{1/2} \left(\int_{\Omega} \int_{\Omega} \int_{\Omega} K(x - y_1 + c) g_0(y_1 - \sigma_1) K(y_1 - y_2 + c) g_0(y_2 - \sigma_0) u_0(y_2) dy_2 dy_1 dx \right)^{1/2} \tag{38}$$

where r_1, σ_1 are the realisations for the geometric growth rate and the yearly shift at generation 1. In a similar manner, one can then derive the more general formula

$$\Lambda_t = R_t^{1/t} \cdot \kappa_t^{1/t} \tag{39}$$

where

$$R_t = \prod_{i=0}^{t-1} r_i \in \mathbb{R}^+, \tag{40}$$

the geometric mean of the geometric growth rate at zero and

$$\kappa_t = \underbrace{\int_{\Omega} \dots \int_{\Omega}}_{t+1 \text{ terms}} K(x - y_1 + c)g_0(y_1 - \sigma_{t-1}) \dots K(y_{t-1} - y_t + c) g_0(y_t - \sigma_0)u_0(y_t)dy_t \dots dy_1 dx \tag{41}$$

Considering

$$\ln(R_t^{1/t}) = \frac{1}{t} \sum_{i=0}^{t-1} \ln(r_i), \tag{42}$$

and using the strong law of large number we have

$$\ln(R_t^{1/t}) \rightarrow E[\ln(r_0)] \in \mathbb{R} \text{ as } t \rightarrow +\infty$$

with probability 1 and thus obtain

$$R_t^{1/t} \rightarrow e^{E[\ln(r_0)]} = \bar{R} \in (0, +\infty) \text{ as } t \rightarrow +\infty, \tag{43}$$

with probability 1. Combining Eqs. (39) and (43), the persistence criterion Λ becomes

$$\Lambda = e^{E[\ln(r_0)]} \cdot \lim_{t \rightarrow +\infty} \kappa_t^{1/t}. \tag{44}$$

This formula for Λ highlights the dependence of the persistence criterion on the different parameters of the problem. Notice that the distribution of the growth rate at zero affects the first part, whereas the distribution of the yearly shifts affects the second part of the formula. We further analyse the effect of the variation in r or the variation in σ using numerical simulation in Sect. 4.

Persistence Criterion Λ for Deterministic Shifting Speed

We turn our attention to further analysis of the persistence criterion Λ , as given in (44), when we assume that the shifting speed is not random. That is, we assume that $\sigma \equiv 0$ and thus randomness comes only from the growth term. We still consider a population that sees its favourable environment shifted at a speed c , but this speed is not assumed to have random variation from one generation to the next. In this case, $\Omega = \Omega_0$ and

$$\Lambda_t = R_t^{1/t} \cdot \left(\int_{\Omega_0} \dots \int_{\Omega_0} K(x - y_1 + c)g_0(y_1) \dots K(y_{t-1} - y_t + c) g_0(y_t)u_0(y_t)dy_t \dots dy_1 dx \right)^{1/t}. \tag{45}$$

Define \mathcal{K}_c the linear operator such that

$$\mathcal{K}_c[u](x) = \int_{\Omega_0} K(x - y + c)g_0(y)u(y)dy. \tag{46}$$

As K is positive and Ω_0 is compact, the operator \mathcal{K}_c is compact (Krasnosel'skii 1964) and strongly positive, that is, for any function $u \geq 0$, there exists $t \in \mathbb{N}$ such that $\mathcal{K}_c^t[u](x) := \mathcal{K}_c \left[\mathcal{K}_c \left[\dots [\mathcal{K}_c[u] \dots] \right] \right] (x) > 0$ for all $x \in \Omega_0$. Then, applying the Krein–Rutman theorem, it follows that this operator possesses a principal eigenvalue $\lambda_c > 0$ such that $|\lambda| < \lambda_c$ for all other eigenvalues λ and λ_c is the only eigenvalue associated with a positive principal eigenfunction ϕ_c . That is, $\lambda_c > 0$ and $\phi_c > 0$ satisfy

$$\lambda_c \phi_c(x) = \int_{\Omega_0} K(x - y + c) g_0(y) \phi_c(y) dy \tag{47}$$

for all $x \in \Omega_0$. One can always normalise ϕ_c such that $\int_{\Omega_0} \phi_c(y) dy = 1$. Now choosing the initial condition for Eq. (14) so that $u_0 \equiv \phi_c$, we have

$$\Lambda_t = R_t^{1/t} \cdot \lambda_c \tag{48}$$

so that

$$\Lambda = \bar{R} \cdot \lambda_c, \tag{49}$$

with $\bar{R} = e^{E[\ln(r_0)]}$ defined in (43).

One has to approximate the principal eigenvalue λ_c to be able to conclude about the persistence of the population. One can refer to the paper by Kot and Phillips (2015) for the description and implementation of different numerical or analytical methods to compute the principal eigenvalue of a linear operator.

In the specific case of Gaussian kernel with variance $(\sigma^K)^2$, that is,

$$K(x) = \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{x^2}{2(\sigma^K)^2}}, \tag{50}$$

the principal eigenvalue of the shifted linear operator \mathcal{K}_c can be expressed as a decreasing function of c . Indeed, we know that λ_c and ϕ_c satisfy for all $x \in \Omega_0$

$$\lambda_c \phi_c(x) = \int_{\Omega_0} \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{(x-y+c)^2}{2(\sigma^K)^2}} g_0(y) \phi_c(y) dy \tag{51}$$

$$= \int_{\Omega_0} \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{(x-y)^2}{2(\sigma^K)^2}} e^{-\frac{c^2}{2(\sigma^K)^2}} e^{-\frac{2c(x-y)}{2(\sigma^K)^2}} g_0(y) \phi_c(y) dy \tag{52}$$

The last equality is equivalent to

$$(e^{\frac{c^2}{2(\sigma^K)^2}} \lambda_c) \cdot (e^{\frac{cx}{(\sigma^K)^2}} \phi_c(x)) = \int_{\Omega_0} \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{(x-y)^2}{2(\sigma^K)^2}} g_0(y) (e^{\frac{cy}{(\sigma^K)^2}} \phi_c(y)) dy. \tag{53}$$

Letting $\phi_0 := e^{\frac{cx}{(\sigma^K)^2}} \phi_c$ and $\lambda_0 := e^{\frac{c^2}{2(\sigma^K)^2}} \lambda_c$, Eq. (53) becomes

$$\lambda_0 \phi_0 = \mathcal{K}_0[\phi_0] \tag{54}$$

and ϕ_0 is a positive function. Thus, one has that

$$\lambda_c = e^{-\frac{c^2}{2(\sigma^K)^2}} \lambda_0, \tag{55}$$

where λ_0 is the principal eigenvalue of the linear operator \mathcal{K}_0 (defined by (46) when $c = 0$) and

$$\Lambda = e^{-\frac{c^2}{2(\sigma^K)^2}} \lambda_0 \cdot \bar{R} \tag{56}$$

is decreasing with $c > 0$. Assuming that the parameters of the problem are chosen so that when $c = 0$ the population persists, that is

$$\bar{R} \cdot \lambda_0 > 1, \tag{57}$$

there exists a critical value $c^* > 0$ such that for all $c < c^*$ the population persists and when $c > c^*$ the population goes extinct (in the sense of Theorem 2 or Corollary 1). The critical value c^* is such that

$$e^{-\frac{(c^*)^2}{2(\sigma^K)^2}} \lambda_0 \cdot \bar{R} = 1 \tag{58}$$

that is,

$$c^* = \sqrt{2(\sigma^K)^2 (\ln(\lambda_0) + E[\ln(r_0)])}. \tag{59}$$

We can thus state the following proposition

Proposition 1 *Let K , f and F satisfy the assumption from Sect. 2. Assume also that $\sigma_t \equiv 0$ and K is a Gaussian kernel with variance $(\sigma^K)^2$, that is,*

$$K(x) = \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{x^2}{2(\sigma^K)^2}}. \tag{60}$$

There exists $c^ \geq 0$ such that*

- for all $c < c^*$, the population persists in the sense of Theorem 2 (or Corollary 1 when the growth map f is not necessarily monotonic),*
- for all $c > c^*$, the population goes extinct in the sense of Theorem 2 (or Corollary 1 when the growth map f is not necessarily monotonic).*

Moreover, if \bar{R} , defined in (43), and λ_0 the principal eigenvalue of \mathcal{K}_0 defined in (46) are such that $\bar{R} \cdot \lambda_0 > 1$, the critical shifting speed is given by

$$c^* = \sqrt{2(\sigma^K)^2 (\ln(\lambda_0) + E[\ln(r_0)])} > 0. \tag{61}$$

The critical shifting speed for persistence thus increases with the expected geometric growth rate. Heuristically one would imagine that when σ^K is small enough relative to Ω_0 then c^* should increase with the variance of the dispersal kernel, as the population becomes more mobile. On the other hand, when σ^K becomes too large relative to Ω_0 then the population would disperse outside its favourable environment and then c^* should decrease with the variance of the dispersal kernel.

Assuming that

$$g_0(y) = \mathbb{1}_{\Omega_0}(y) = \begin{cases} 1 & \text{if } y \in \Omega_0, \\ 0 & \text{otherwise.} \end{cases}$$

one can also approximate the principal eigenvalue λ_0 using the dispersal success approximation

$$\bar{\lambda}_0 = \frac{1}{|\Omega_0|} \int_{\Omega_0} s^0(y) dy \tag{62}$$

as defined in (4) or the modified dispersal success approximation

$$\hat{\lambda}_0 = \frac{1}{\Omega_0} \int_{\Omega_0} \left(\frac{s^0(y)}{\bar{\lambda}_0} \right) s^0(y) dy \tag{63}$$

as defined in (5), with $s^0(y) = \int_{\Omega_0} K(x - y) dx$ the dispersal success function when $c = 0$. We obtained similar conclusion than Reimer et al. (2016) when comparing the principal eigenvalue λ_0 , its dispersal success approximation $\bar{\lambda}_0$ and its modified dispersal success approximation $\hat{\lambda}_0$ (Fig. 5), observing that the modified dispersal success approximation gives a more accurate estimate of the principal eigenvalue λ_0 than the regular dispersal success approximation.

In this section, we derived a analytical tool to characterise the persistence of a population facing shifting range in a stochastic environment. We also analysed further the dependence of the criterion with respect to the parameters of the model and investigated the existence of a critical shifting speed c , separating persistence from extinction, in the particular case of Gaussian dispersal kernel.

4 Numerical Calculation of Persistence Conditions, with Application to Shifting Butterfly Populations

We now focus on applying the stochastic model and theory to butterfly populations responding to climatic change. Our goal is twofold, first to illustrate the calculation of Λ (44) and the critical shifting speed c^* (61) in a ecologically realistic problem and

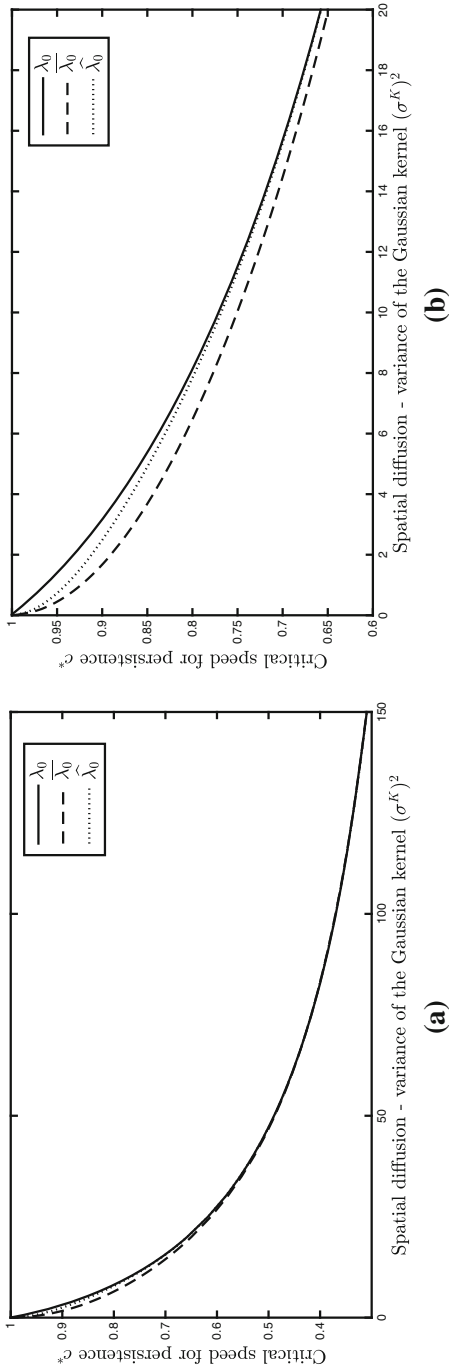


Fig. 5 Principal eigenvalue λ_0 , its dispersal success approximation $\hat{\lambda}_0$ and its modified dispersal success approximation $\tilde{\lambda}_0$ as a function of $(\sigma^K)^2$, the variance of the dispersal kernel, when K is a Gaussian kernel and $|\Omega_0| = 10$. On the *left panel* **a** $(\sigma^K)^2$ spans from 0:01 to 150. The *right panel* **b** shows a zoom of the *left panel* for small values of $(\sigma^K)^2$, where the error between the different approximations is the largest. The principal eigenvalue λ_0 was calculated using the power method

second to investigate the impact of variability in environmental shift (σ) and growth rate (r) on population persistence.

We assume that for each generation, there are only two possible environments, a good environment when $\alpha = \alpha_g$ and a bad environment when $\alpha = \alpha_b$, such that

$$P(\alpha = \alpha_b) = 0.5 \text{ and } P(\alpha = \alpha_g) = 0.5.$$

We consider $\sigma \in \{\underline{\sigma}, \bar{\sigma}\}$, and $r \in \{\underline{r}, \bar{r}\}$ with

$$\underline{\sigma} < 0 < \bar{\sigma} \text{ and } 0 < \underline{r} < \bar{r}. \tag{64}$$

To define good and bad environments, we assume that the larger the r , the better the environment and the smaller the σ , the better the environment and thus consider

$$\alpha_g = (\underline{\sigma}, \bar{r}) \text{ and } \alpha_b = (\bar{\sigma}, \underline{r}). \tag{65}$$

Leroux et al. (2013) study the effect of climate change and range migration for twelve species of butterflies in Canada. In their papers, the authors use a reaction–diffusion model to study the ecological dynamics of the population and its persistence properties. In their analyses, they estimate the shifting speed c and the growth rate r for each species to compute the critical diffusion coefficient that will determine the persistence of the population assuming no restriction on the length of the patch. Here we use their estimated means and standard deviation of c and r to fix the values of c , $\underline{\sigma}$, $\bar{\sigma}$, \underline{r} and \bar{r} defined above and

$$c = 3.25 \text{ km/year, } \underline{\sigma} = -1.36 \text{ km/year, } \bar{\sigma} = 1.36 \text{ km/year, } \underline{r} = 2.07, \bar{r} = 4.85$$

unless otherwise stated. We then study the persistence of the population in our stochastic framework for a fixed patch size $|\Omega_0| = 10 \text{ km}$.

4.1 Critical Shifting Speed for Gaussian Kernel

First, we assume that the shifting speed is fixed and deterministic, i.e., $\sigma \equiv 0$, and we investigate numerically the variation of the critical shifting speed c^* as a function of the variance of the dispersal kernel in the case of Gaussian dispersal kernel. Indeed, using the analysis of Sect. 3.2, we know that for Gaussian kernel, when $\sigma \equiv 0$, that is, the shifting speed is not stochastic anymore, then there exists a critical speed $c^* \geq 0$ such that for all $c < c^*$ the population persists in the moving frame whereas if $c > c^*$ the population goes extinct. Using Eq. (61), we know that $c^* = \sqrt{2(\sigma^K)^2 \ln(\lambda_0 \cdot \bar{R})}$, with λ_0 being the principal eigenvalue of the linear operation \mathcal{K}_0 defined in (46) when $c = 0$ and \bar{R} being the geometric average of the geometric growth rate, defined in (43). Notice from the derivation of c^* in the previous section that when $\lambda_0 \cdot \bar{R} < 1$, the critical speed is zero because for all $c \geq 0$, $\Lambda = e^{-\frac{c^2}{2(\sigma^K)^2}} \lambda_0 \cdot \bar{R}$ defined in (56), is always smaller than 1. As can be observed from Fig. 6, the critical shifting speed for persistence first increases with the variance of the dispersal kernel as the population

is more and more mobile and can track its favourable environment more easily. Then, the critical speed decreases for large values of $(\sigma^K)^2$ and converges to 0 as the patch size becomes too small for the population to persist even in a nonshifted environment. When the shifting speed $c = 3.25$ km/year, as it was suggested by Leroux et al. (2013), there exists three different regimes for the persistence of the population depending on the value of the variance $(\sigma^K)^2$ (Fig. 6b). When the variance of the dispersal kernel is small (point A), the critical speed for persistence c^* is smaller than the shifting speed $c = 3.25$ and thus population cannot keep pace with its environment. As the variance $(\sigma^K)^2$ increases (point B), the critical speed for persistence increases above 3.25 and thus the population persists. Nevertheless, when $(\sigma^K)^2$ becomes too large (compared to the patch size), the critical speed for persistence decreases below the shifting speed $c = 3.25$ to reach 0 (point C) and the population does not keep pace with its environment anymore. One can also note that in this framework the dispersal success approximation for the principal eigenvalue $\bar{\lambda}_0$, defined in (4), gives an accurate approximation of the critical speed for persistence (Fig. 6a).

4.2 Effect of the Dispersal on Persistence of Butterfly in Canada

In this section, we approximate the persistence criteria Λ , defined in (18), computing Λ_t for large t and study the change in the persistence criterion as a function of the variance of the dispersal kernel, when all the other parameters are fixed. We choose parameters based on the analysis by Leroux et al. (2013):

$$c = 3.25 \text{ km/year}, \underline{\sigma} = -1.36 \text{ km/year}, \bar{\sigma} = 1.36 \text{ km/year}, \underline{r} = 2.07, \bar{r} = 4.85.$$

We use two different kernels, the Laplace kernel

$$K(x) = \frac{\alpha}{2} e^{-\alpha|x|} \quad (66)$$

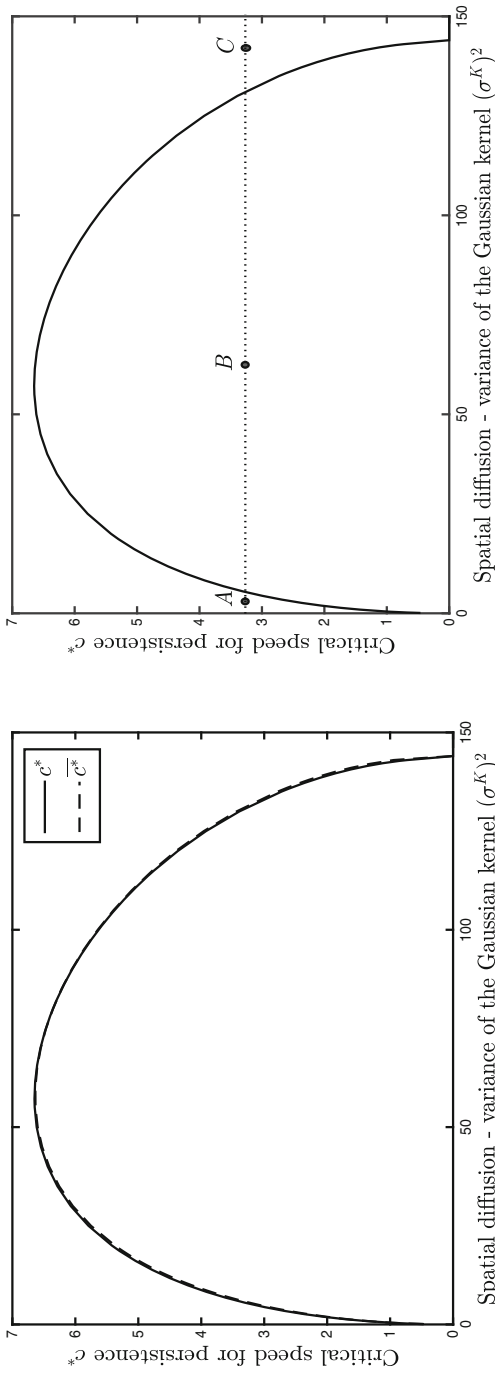
and the Gaussian kernel

$$K(x) = \frac{1}{\sqrt{2\pi(\sigma^K)^2}} e^{-\frac{x^2}{2(\sigma^K)^2}} \quad (67)$$

and consider for each kernel a variance $(\sigma^K)^2$, $((\sigma^K)^2 = (2/\alpha^2)$ for Laplace kernel) that spans from 0.1 to 150 km²/year. We approximate Λ , computing

$$\Lambda_t = \left(\int_{\Omega} \tilde{n}_t(x) dx \right)^{1/t} \quad (68)$$

for large t , as defined in (18) (Fig. 7). As can be expected from the computation of the critical speed in Fig. 6, the value of Λ increases with the variance of the dispersal kernel at first and then decreases when the variance becomes too large with respect to the patch size (Fig. 7). Whereas the persistence criteria Λ associated with the Laplace



(a)

(b)

Fig. 6 Critical speed for persistence c^* as defined in (61) and its approximation \bar{c}^* using the dispersal success approximation $\bar{\lambda}_0$ instead of the principal eigenvalue λ_0 , as a function of the dispersal Gaussian kernel variance (a). The principal eigenvalue λ_0 was calculated using the power method. On the right panel (b), the critical speed for persistence c^* is compared to a fixed shifting speed $c = 3.25$ km/year. Points A, B and C highlight the existence of three different persistence regime as the variance of the dispersal kernel increases. The parameter values are the following: $\sigma = \bar{\sigma} = 0$ km/year, $r = 2.07$, $\bar{r} = 4.85$ and $|\Omega_0| = 10$ km

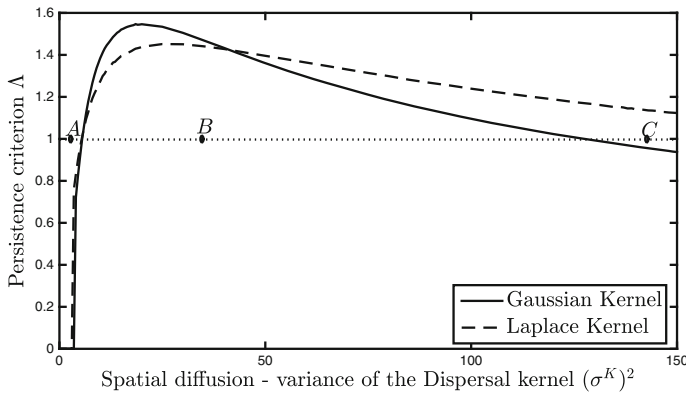


Fig. 7 Approximation of Λ as a function of the dispersal kernel variance, for Gaussian kernel (solid curve) and Laplace kernel (dashed curve). The value of Λ is compared to 1 (dotted curve). Points A, B and C highlight the existence of three different persistence regimes as the variance of the dispersal kernel increases. The parameter values are the following: $c = 3.25$ km/year, $\underline{\sigma} = -1.36$ km/year, $\bar{\sigma} = 1.36$ km/year, $\underline{r} = 2.07$, $\bar{r} = 4.85$ and $|\Omega_0| = 10$ km

kernel stay above 1 for large value of $(\sigma^K)^2$, the one associated with the Gaussian kernel decreases below 1 for large variance (Point C in Fig. 7).

4.3 Stochasticity of the Parameters and Persistence of the Population

We now turn our attention to investigating the effect of the stochasticity in the parameters on population persistence. We analyse the effects of increasing the variance of the yearly shift σ or increasing the variance of the growth rate r separately. In each case, we assume that the expectation of the random variable σ or r is fixed and the probability of a bad (respectively, good) environment is also fixed to 0.5. In this section, we used the values from Leroux et al. (2013) to fix the parameters values and assume that

$$c = 3.25 \text{ km/year, } |\Omega_0| = 10 \text{ km and } (\sigma^K)^2 = 25 \text{ km}^2/\text{year.}$$

We first analyse the variation of the persistence criterion Λ as a function of the variance of the yearly shift σ . To do so we fix \underline{r}, \bar{r} using again the values from Leroux et al. (2013) and assume that

$$\underline{r} = 2.07 \text{ and } \bar{r} = 4.85.$$

We approximate Λ , computing Λ_t for large t , as a function of the variance of σ , the yearly shift, assuming that $E[\sigma] = 0$ (Fig. 8a). For this analysis, we consider again two types of dispersal kernel: a Gaussian dispersal kernel and a Laplace dispersal kernel. As illustrated in Fig. 8a, the persistence criterion Λ decreases as the variance of σ increases, and thus persistence is harder to achieve in environment with high stochasticity. Moreover, when the variance of σ becomes too large, the population cannot persist anymore ($\Lambda < 1$ in Fig. 8a).

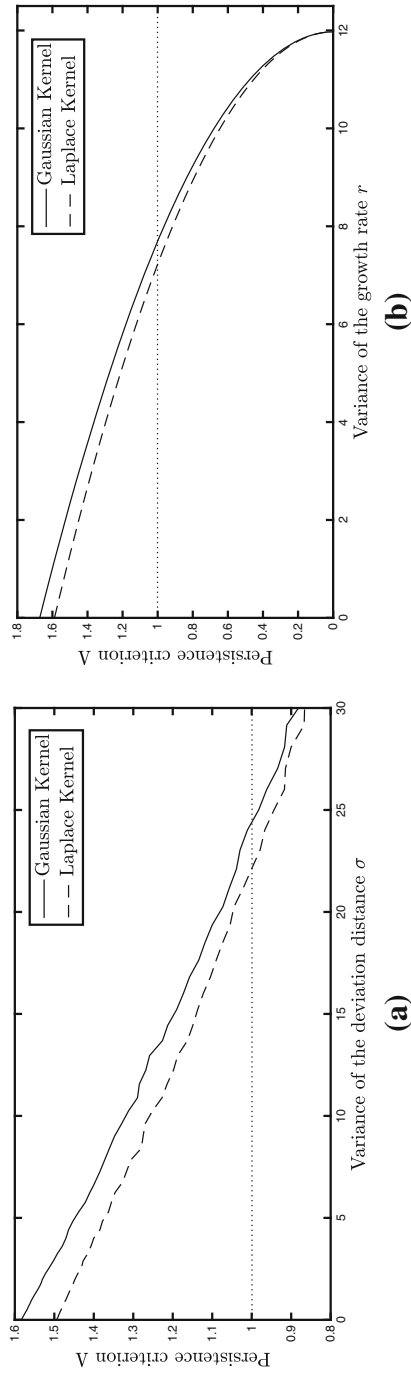


Fig. 8 Approximation of Δ as a function of the variance of the random shift σ (panel a) or as a function of the variance of the growth rate r (panel b) for Gaussian Kernel (solid line) and Laplace kernel (dashed line). The parameter value for these computations are $c = 3.25$ km/year, $|\Omega_0| = 10$ km and the variance of the dispersal kernel is $25 \text{ km}^2/\text{year}$. For the left panel, we fixed $\underline{r} = 2.07$, $\bar{r} = 4.85$, and for the right panel, we fixed $\underline{\sigma} = -1.36$, $\bar{\sigma} = 1.36$

Using a similar approach, we analyse the effect of increasing the variance of the growth rate r on the persistence criterion Λ . To do so we fix $\underline{\sigma}$ and $\bar{\sigma}$ using again the values from [Leroux et al. \(2013\)](#) and assume that

$$\underline{\sigma} = -1.36 \text{ and } \bar{\sigma} = 1.36.$$

As illustrated in [Fig. 8b](#), the persistence criterion is also decreasing as a function of the variance of the growth rate r . We thus conclude that adding variance to a model will impact negatively the persistence of the population.

In this section, we considered a simple example, applicable to butterfly populations, where there exists only two outcomes for the random variable: a bad or a good environment. We investigated the dependence of the persistence of the population on the variance of the dispersal kernel and concluded that at first the persistence criterion (and also the critical shifting speed in the particular case of Gaussian kernels) increases with the variance of the dispersal kernel as the population increases its mobility and thus its ability to follow its favourable habitat. On the other hand, the persistence criterion decreases as the variance of the dispersal kernel becomes too large, because the population flees its favourable habitat. We also investigated the dependence of the persistence of the population on the variability of the two stochastic variables in our model. We numerically analysed the persistence criterion as a function of the variance of the random variable σ , the yearly shift, or as a function of the variance of the random variable r , the growth rate. We observed that the persistence decreases with the variability of σ ([Fig. 8a](#)) and with the variability of r ([Fig. 8b](#)) and concluded that the variability of the asymptotic shifting speed or of the growth rate has a negative effect on population persistence.

5 Discussion

In this paper, we model and analyse persistence conditions for a population whose range distribution is shifted towards the pole at a stochastic speed. The problem arises from the effects of climate change on range distribution ([Parmesan 2006](#)). While previous mathematical analyses of this problem consider deterministic environment ([Zhou and Kot 2011, 2013](#); [Harsch et al. 2014](#); [Phillips and Kot 2015](#)), it has been highlighted that the presence of climate change increases the temporal variability of the environment, partly due to extreme climatic events ([IPCC 2007](#)). Therefore, understanding the effect of a random geometric growth rate and a random shifting speed of the favourable environment becomes necessary.

We first summarise the main results of our study.

- Convergence in distribution to an equilibrium (as time goes to infinity), when the population is assumed to have compensatory competition dynamics,
- Existence of a deterministic metric, having a biological interpretation in terms of a growth rate, which characterises persistence of the population in the case of compensatory and overcompensatory competition dynamics,
- Derivation of the persistence metric using the principal eigenvalue of a linear integral operator when the deviation of the shifting speed is fixed,

- Existence of a critical shifting speed separating persistence from extinction in the specific case of Gaussian dispersal kernel,
- Approximation of the critical shifting speed, using the dispersal success approximation (VanKirk and Lewis 1997) and the modified dispersal success approximation (Reimer et al. 2016),
- Analysis of the persistence of a population of butterfly facing climate change and range shift as a function of its dispersal capacity, through numerical simulation,
- Analysis of the qualitative effect of the variability in the yearly shift or in the growth rate on the persistence of a population in the particular case of butterfly.

More precisely, our model assumes that the geometric growth rate for low density in the favourable environment is random from one generation to the next and that the bounded favourable environment is shifted at some asymptotic speed c , with an additional random yearly shift σ_t . The centre of the favourable environment, s_t , is thus given by $s_t = ct + \sigma_t$. We use the theory of integrodifference equations to analyse the persistence of the population in this framework and employ a change of variables to study the problem in the shifted framework to track the favourable environment.

The theory of Hardin et al. (1988) and Jacobsen et al. (2015) applies to our shifted problem and provides a general measure for persistence in term of the linearised problem at zero. Indeed in these two papers, the authors prove that the persistence of the population depends on the magnitude of the metric Λ (Jacobsen et al. 2015) defined as the asymptotic growth rate of the linearised operator, or equivalently on the magnitude of the metric R (Hardin et al. 1988) defined as the asymptotic L^∞ norm of the linearised operator. The former metric defined by Jacobsen et al. (2015) has more biological meaning and is easier to compute numerically, which is why we chose to use it in this paper. Our paper thus provides a mathematical metric to measure persistence of the population facing climate change and shifted range distribution in a temporally variable environment. Note that we chose to study the problem in one dimension (i.e., $\Omega \subset \mathbb{R}$) but the theory can be extended to $\Omega \subset \mathbb{R}^n$, $n \geq 1$, and the results in Sect. 3 are straightforward to extend.

We use the analytical results of Sect. 3 to study the persistence of a butterfly population facing range shifts. We computed, for two different dispersal kernels (Laplace and Gaussian), the persistence metric as a function of the dispersal capacity (variance of the dispersal kernel). We find that for a fixed shifting speed (estimated from a paper by Leroux et al. (2013)), there exists three different regimes (Fig. 7). When the dispersal capacity of the population is small, the butterflies cannot keep track with their favourable environment and go extinct, when the dispersal capacity increases the persistence metric increases above one and the population persists. On the other hand, as the dispersal variance becomes too high, the population disperses outside its favourable habitat and goes extinct.

In the special case, where the shift is deterministic, that is the yearly variation is $\sigma_t = 0$ for all $t \in \mathbb{N}$, then the problem describes the dynamics of a population with variable growth, facing shifting ranges. In this case, we characterise the persistence of the population through the magnitude of the asymptotic growth rate

of a linear operator, similarly to the results by Zhou and Kot (2011) in the case of deterministic scalar integrodifference equations with shifting boundaries. We also show that in the case of Gaussian dispersal kernel, this asymptotic growth rate is decreasing with respect to c . This proves the existence of a critical speed c^* such that for all shifting speed c less than c^* , the asymptotic growth rate will be above one and the population will persist, whereas when the shifting speed is above c^* , the asymptotic growth rate is below one and the population converges to zero in its favourable environment. These results are also independent of the initial condition, as soon as it is nonnegative and nontrivial and in this sense is similar to the one proved by Berestycki et al. (2009) for deterministic scalar reaction–diffusion equations.

To analytically determine the critical speed for persistence, c^* , we need to compute the principal eigenvalue of the linearised operator around the trivial steady state. As the dispersal kernel is positive everywhere, this principal eigenvalue can be computed using the power method. Nevertheless in a biological framework, this principal eigenvalue can be approximated using the dispersal success function (VanKirk and Lewis 1997) or a modified dispersal success function (Reimer et al. 2016) (Fig. 5). In this case, the principal eigenfunction is either approximated by the probability to stay in the suitable habitat, after the dispersal stage, normalised by the size of the habitat (dispersal success approximation), or by the probability to stay within the favourable habitat, weighted by the proportion of individual at each point of the favourable domain, normalised again by the size of the habitat (Reimer et al. 2016). As illustrated in Fig. 6a, the dispersal success approximation gives accurate results for the computation of the critical speed for persistence. On the other hand, these approximations do not give accurate estimates of the principal eigenfunction when the dispersal kernel is shifted by c (if one wanted to estimate λ_c directly instead indirectly through λ_0). In these cases, one could use the methods described by Phillips and Kot (2015) to compute efficiently the principal eigenvalue of a given linear operator.

We also highlighted, using numerical simulation, the negative effect of the variability of the parameter on the persistence of the population. Indeed, as illustrated in Fig. 8, the persistence metric decreases with the variance of both parameters: σ the yearly shift and r the growth rate.

Finally, note that the asymptotic shifting speed c is actually uncertain in the sense that it depends on the severity of the climate change (IPCC 2014). In this paper, we assumed that c was known but if one would only know the distribution of the different outcomes for c , the asymptotic shifting speed, one can then compute the probability of persistence using our analysis. Indeed, in the specific case of Gaussian kernel and assuming that the yearly shift σ_t is zero for all t , then the probability of persistence would be given by the probability that c is less than c^* .

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Appendix 1: Proof of Theorem 1 and 2

The proof of Theorems 1 and 2 mostly follows from Hardin et al. (1988)[Theorem 4.2 and Theorem 5.3]. Indeed Hardin et al. (1988) study the general stochastic model

$$X_{t+1} = F_{\alpha_t}(X_t), \tag{69}$$

with $(X_t)_t$ a random process that takes values in the set on nonnegative continuous function in Ω , $(\alpha_t)_t$, independent identically distributed random variable taking values in the set \mathcal{S} . And they have the following assumption for F_α

- (H1) For each $\alpha \in \mathcal{S}$, F_α is a continuous map of $C_+(\Omega)$, into itself such that $F_\alpha(u) = 0 \in C_+(\Omega)$ if and only if $u = 0 \in C_+(\Omega)$.
- (H2) If $u, v \in C_+(\Omega)$ and $u \geq v$ then $F_\alpha(u) \geq F_\alpha(v)$.
- (H3) There exists some $b > 0$ such that for $u \in C_+(\Omega)$
 - (a) $\|F_\alpha(u)\|_\infty \leq b$ for all $\alpha \in \mathcal{S}$ and $\|u\|_\infty \leq b$,
 - (b) there exists some time t (depending on u_0) such that

$$\|F_{\alpha_t} \circ \dots \circ F_{\alpha_0} u_0\|_\infty < b, \tag{70}$$

for all $\alpha_0, \dots, \alpha_t \in \mathcal{S}$,

- (c) there exists some $d > 0$ such that

$$F_\alpha(b) \geq d \tag{71}$$

for all $\alpha \in \mathcal{S}$.

- (H4) Let $B_b := \{u \in C_+(\Omega) : \|u\|_\infty \leq b\}$, then there is some compact set $D \subset C_+(\Omega)$ such that $F_\alpha(B_b) \subset D$ for all $\alpha \in \mathcal{S}$.
- (H5) There exists some $h > 0$ such that

$$\|F_\alpha(u)\|_\infty \leq h\|u\|_\infty, \tag{72}$$

for all $\alpha \in \mathcal{S}$ and $u \in C_+(\Omega)$.

- (H6) There exists some $\xi > 0$ such that

$$F_\alpha(B_b) \subset K_\xi, \tag{73}$$

where $K_\xi := \{u \in C_+(\Omega) : u \geq \xi\|u\|_\infty\}$.

- (H7) For each $a > 0$, there exists a continuous function $\tau : (0, 1] \rightarrow (0, 1]$ such that $\tau(s) > s$ for all $s \in (0, 1)$ and such that

$$\tau(s)F_\alpha(u) \leq F_\alpha(su) \tag{74}$$

for all $\alpha \in \mathcal{S}$ and $u \in C_+(\Omega)$ such that $a \leq u \leq b$.

- (H8) F_α is Fréchet differentiable (with respect to $C_+(\Omega)$) at $0 \in C_+(\Omega)$. We denote by \mathcal{L}_α the operator $F'_\alpha(0)$

(H9) There exists a function $\mathcal{N} : \mathbb{R}_+ \rightarrow [0, 1]$ such that

$$\lim_{u \rightarrow 0, u > 0} \mathcal{N}(u) = 1 \text{ and } \mathcal{N}(\|u\|_\infty) \mathcal{L}_\alpha u \leq F_\alpha(u) \leq \mathcal{L}_\alpha u, \tag{75}$$

for all $u \in C_+(\Omega)$.

We want to prove that the previous hypotheses are satisfied in our framework and then apply Theorem 4.2, Theorem 5.3 by [Hardin et al. \(1988\)](#) and Theorem 2 by [Jacobsen et al. \(2015\)](#). One can check, as it is done by [Jacobsen et al. \(2015, Section 5.3\)](#), that under Hypotheses 1–5, the previous hypotheses (H1)–(H9) are satisfied and one can then apply Theorem 4.2, Theorem 5.3 from [Hardin et al. \(1988\)](#) and Theorem 2 from [Jacobsen et al. \(2015\)](#). For completeness, we will write the main steps referring most of the time to [Jacobsen et al. \(2015, Section 5.3\)](#). First, we denote by,

$$\overline{K} := \sup\{K(x), x \in \mathbb{R}\} < +\infty, \tag{76}$$

and

$$\underline{K} := \inf \{K(x), x \in (\inf \Omega - \sup \Omega + c, \sup \Omega - \inf \Omega + c)\} > 0. \tag{77}$$

These two constants will be used several times in the proof of (H1)–(H9) below.

- (H1) The continuity of F_α follows from the continuity of f_r , and the boundedness of K and $\int_\Omega g_0(y)dy$. K positive in \mathbb{R} , f_r and g_0 nonnegative yield the second statement.
- (H2) This follows from the monotonicity of f_r for all $\alpha \in \mathcal{S}$.
- (H3) The constant $b > 0$ will be defined later in the proof,
 - (a) for all $\alpha \in \mathcal{S}$, $u \in C_+(\Omega)$,

$$\|F_\alpha(u)\|_\infty = \max_{x \in \Omega} \int_\Omega K(x - y + c)g_0(y - \sigma)f_r(u(y))dy \tag{78}$$

$$< m \cdot \overline{K} \cdot \int_{\Omega_0} g_0(y)dy = b. \tag{79}$$

This proves the statement.

- (b) Using the same argument as before, for all $u_0 \in C_+(\Omega)$, $t \in \mathbb{N}^*$, $\alpha_t, \dots, \alpha_0 \in \mathcal{S}$,

$$\|F_{\alpha_t} \circ \dots \circ F_{\alpha_0}(u_0)\|_\infty = \|F_{\alpha_t}(u)\|_\infty < b, \tag{80}$$

where $u \in C_+(\Omega)$.

- (c) For all $x \in \Omega$,

$$F_\alpha(b)(x) \geq \inf_{\alpha \in \mathcal{S}} f_r(b) \int_\Omega K(x - y + c)g_0(y - \sigma)dy \geq \inf_{\alpha \in \mathcal{S}} f_r(b) \cdot d_1 \tag{81}$$

with

$$d_1 := \underline{K} \cdot \int_{\Omega_0} g_0(y)dy > 0 \tag{82}$$

One concludes using the positivity of K and Hypothesis 4(iii)b that there exists $d > 0$ such that for all $x \in \Omega$,

$$F_\alpha(b)(x) \geq d. \tag{83}$$

(H4) This statement follows from the continuity of K , uniform boundedness of F_α and f_r and Hypothesis 5, details can be found in [Jacobsen et al. \(2015\)](#)[Section 5.3].

(H5) From assumption 4(ii)c, we have that for all $u > 0$, $f'_r(0)u \geq f_r(u)$. Thus, using this inequality, with assumptions 1(ii), 2(ii) and 4 (iii)a, we get for all $u \in C_+(\Omega)$, for all $\alpha \in \mathcal{S}$,

$$\|F_\alpha(u)\|_\infty \leq h\|u\|_\infty, \tag{84}$$

with $h := \bar{r} \cdot \bar{K} \cdot \int_{\Omega} g_0(y)dy$.

(H6) First, notice that for all $\alpha \in \mathcal{S}$, $u \in B_b$

$$\begin{aligned} \|F_\alpha(u)\|_\infty &\leq \bar{r} \cdot \bar{K} \cdot \int_{\Omega} g_0(y - \sigma)u(y)dy \implies \int_{\Omega} g_0(y - \sigma)u(y) \\ &\geq \frac{\|F_\alpha(u)\|_\infty}{\bar{r} \cdot \bar{K}}, \end{aligned} \tag{85}$$

and using Hypothesis 4(ii)c,

$$f_\alpha(u) \geq \frac{f_\alpha(b)}{b}u. \tag{86}$$

Then for all $x \in \Omega$

$$F_\alpha(u)(x) \geq \underline{K} \cdot \frac{f_\alpha(b)}{b} \int_{\Omega} g_0(y - \sigma)u(y)dy \tag{87}$$

$$\geq \frac{\underline{K}}{\bar{K}} \cdot \frac{f_\alpha(b)}{b} \frac{\|F_\alpha(u)\|_\infty}{\bar{r}} \tag{88}$$

and the statement is proved.

(H7) This proof is also derived from [Jacobsen et al. \(2015\)](#). We want to find a continuous function $\tau : (0, 1] \rightarrow (0, 1]$ such that for all $s \in (0, 1)$,

$$\begin{aligned} \tau(s)F_\alpha(u) &\leq F_\alpha(su) \\ \Leftrightarrow \int_{\Omega} K(x - y + c)g_0(y - \sigma)\tau(s)f_r(u(y))dy &\leq \int_{\Omega} K(x - y + c) \\ g_0(y - \sigma)f_r(su(y))dy & \end{aligned}$$

Thus, it is sufficient to have $\tau(s) f_r(u(y)) \leq f_r(su(y))$ for all $y \in \Omega$. From Hypothesis 4(ii)c, as $s \in (0, 1)$, we have that for all $\alpha \in \mathcal{S}$

$$s < \frac{f_r(su)}{f_r(u)}, \tag{89}$$

and letting $\tau(s) = \min \left\{ \frac{f_r(su)}{f_r(u)}, \alpha \in \mathcal{S}, a \leq u \leq b \right\}$ we have, for all $s \in (0, 1)$, $\alpha \in \mathcal{S}$ and $u \in [a, b]$,

$$\tau(s) > s \text{ and } \frac{f_r(su)}{f_r(u)} \geq \tau(s) \tag{90}$$

and the statement is proved.

(H8) We want to prove that

$$\lim_{h \rightarrow 0} \frac{\|F_\alpha(0+h) - F_\alpha(0) - \mathcal{L}_\alpha h\|_\infty}{\|h\|_\infty} = 0, \tag{91}$$

where $\mathcal{L}_\alpha := F'_\alpha(0)$ is a linear operator. Using the differentiability of f_r at 0, one proves that the limit exists and $\mathcal{L}_\alpha h = r \int_\Omega K(x-y+c)g_0(y-\sigma)h(y)dy$.

(H9) The second part of the inequality follows from assumption 4(ii)c. For each $\alpha \in \mathcal{S}$ let $\mathcal{N}_\alpha : [0, +\infty) \rightarrow [0, 1]$ be such that

$$\mathcal{N}(u) = \begin{cases} \frac{f_\alpha(u)}{r \cdot u} & \text{if } u > 0, \\ 1 & \text{if } u = 0. \end{cases} \tag{92}$$

The function \mathcal{N}_α is continuous and defining $\mathcal{N}(u) = \min \{\mathcal{N}_\alpha(u), \alpha \in \mathcal{S}\}$, it gives the wanted statement (using the fact that $\mathcal{N}_\alpha(u(x)) \geq \mathcal{N}_\alpha(\|u\|_\infty)$).

We can thus apply Theorem 4.2 from Hardin et al. (1988) to prove Theorem 1 and use Theorem 5.3 by Hardin et al. (1988) and Theorem 2 by Jacobsen et al. (2015) to prove Theorem 2. For sake of completeness, we include the three Theorems from Hardin et al. (1988) and Jacobsen et al. (2015) below.

Theorem 3 [Hardin et al. (1988, Theorem 4.2)] *Suppose that Hypotheses (H1)–(H7) above and Hypothesis 3(i) in Sect. 2 are satisfied and that $u_0 \neq 0 \in C_+(\Omega)$ with probability one. Then u_t solution of (14) converges in distribution to a stationary distribution μ^* , independent of u_0 , such that either $\mu^*({0}) = 0$ or $\mu^*({0}) = 1$.*

The above Theorem from Hardin et al. (1988) states that the distribution μ^* is stationary in the sense that it satisfies

$$P\mu^* = \mu^* \tag{93}$$

where P is the Markov process given by

$$P\mu(B) = \int \mu(F_\alpha^{-1}(B))d\mathcal{P}_\alpha, \tag{94}$$

with $B \in \mathcal{B}(C_+(\Omega))$ the family of borel sets in $C_+(\Omega)$. This is equivalent to writing that the random variable u^* with distribution μ^* satisfies

$$u^* = F_\alpha^*[u^*] \quad (95)$$

for some α^* taking its values in \mathcal{S} with distribution \mathcal{P}_α .

Theorem 4 [Hardin et al. (1988, Theorem 5.3)] *Suppose that Hypotheses (H1)–(H9) above and Hypothesis 3(i) in Sect. 2 are satisfied and that $u_0 \neq 0 \in C_+(\Omega)$ with probability one. Let μ^* be as in Theorem 4.2 and define $R = \lim_{t \rightarrow +\infty} \|\mathcal{L}_{\alpha_t} \circ \cdots \circ \mathcal{L}_{\alpha_0}\|$, with \mathcal{L} the linearised operator around zero ((19))*

- (a) *If $R < 1$ then $\mu^*(\{0\}) = 1$ and $u_t \rightarrow 0$ with probability one.*
 (b) *If $R > 1$ then $\mu^*(\{0\}) = 0$.*

Theorem 5 [Jacobsen et al. (2015, Theorem 2)] *Let R be defined as in the previous theorem by $R = \lim_{t \rightarrow +\infty} \|\mathcal{L}_{\alpha_t} \circ \cdots \circ \mathcal{L}_{\alpha_0}\|$, then $\Lambda = R$ (Λ defined in (18)).*

Appendix 2: Persistence Condition and Invasion Speed

In this section, we derive an heuristic criteria for persistence inspired from Neubert et al. (2000) linking the critical patch size and the asymptotic invasion speed to get necessary conditions for persistence. We consider problem (9), where the suitability functions g_0 are indicator functions, that is

$$g_0(y) = \mathbb{1}_{\Omega_0} = \begin{cases} 1 & \text{if } y \in \Omega_0, \\ 0 & \text{otherwise.} \end{cases}$$

In addition to the assumptions made in Sect. 2, we will also assume that K is a thin tail dispersal kernel in the sense that it has exponentially bounded tails, i.e., there exists $s > 0$,

$$\int_{\mathbb{R}} e^{s|x|} K(x) dx < +\infty. \quad (96)$$

This last assumption guarantees that the moment generating function (29) exists on some open interval of the form $(0, s^+)$. This assumption was not necessary to derive the persistence condition in Sect. 3 but it will be used to study the speed of the stochastic wave.

Appendix 2.1: Critical Domain Size in the Constant Environment

Let us first consider the problem in the nonshifted frame and thus assume that $s_t \equiv 0$, where $(s_t)_t$, defined in Sect. 2, is the centre of the suitable habitat at generation t .

Thus, we consider the following integrodifference equation

$$u_{t+1}^0(x) = \int_{\Omega_0} K(\xi - \eta) f_{r_t}(u_t^0(\eta)) d\eta, \quad (97)$$

denoting by u^0 the solution in this nonshifted framework. Using the theorems in Sect. 3, we get that as time goes to infinity, u^0 persists if

$$E[\ln(r_0)] > -\ln(\lambda_0), \quad (98)$$

where $E[\cdot]$ is the expectation of a random variable and λ_0 is the principal eigenvalue of the linear operator \mathcal{K}_0 :

$$\mathcal{K}_0[u](x) = \int_{\Omega_0} K(x - y)u(y)dy. \quad (99)$$

Now assume that K , Ω_0 and $(r_t)_t$ are such that (98) is satisfied and study the problem in the nonmoving, homogeneous framework.

Appendix 2.2: Invasion Speed in a Stochastic Homogeneous Environment

Now we are interested in deriving the asymptotic invasion speed of the population in an homogeneous environment to compare it with the forced shifting speed c . We thus consider the homogeneous problem on \mathbb{R} in the nonmoving frame, i.e., let $(n_t)_t$ be the solution of the equation

$$n_{t+1}(\xi) = \int_{\mathbb{R}} K(\xi - \eta) f_{r_t}(n_t(\eta)) d\eta. \quad (100)$$

As we are considering the initial problem in the nonmoving frame, K does not depend on c and $g_0 \equiv 1$ in \mathbb{R} and thus the stochasticity comes only from the growth term. From the analysis of Neubert et al. (2000), there are two different approaches to estimate the invasion speed of the stochastic process $(n_t)_t$. One can either consider the invasion speed of the expected wave or the asymptotic speed of the stochastic wave. We will only consider the latter approach and assume that the speed is governed by the linearisation at 0. Denote by $(\tilde{n}_t)_t$, the solution of the linearised operator at 0, i.e., for all $t \in \mathbb{N}$,

$$\tilde{n}_{t+1}(\xi) = \int_{\mathbb{R}} K(\xi - \eta) r_t \tilde{n}_t(\eta) d\eta. \quad (101)$$

We define the random variable \mathcal{E}_t as the most rightward position such that \tilde{n}_t is greater than some threshold, i.e.,

$$\mathcal{E}_t = \sup \{ \xi \in \mathbb{R}, \tilde{n}_t > \bar{n} \}, \quad (102)$$

where $\bar{n} \in (0, 1)$ is a fixed critical threshold. Assume that $\forall \xi \in \mathbb{R}, n_0(\xi) = \alpha e^{-s\xi}$, for some $s > 0$, i.e., the initial condition has a wave shape, then for all $t \in \mathbb{N}, \xi \in \mathbb{R}$,

$$\tilde{n}_{t+1}(\xi) = \alpha \prod_{i=0}^t (r_i M(s)) e^{-s\xi}, \tag{103}$$

where M is the moment generating function of K ((29)). This function exists in some interval $(0, s^+)$ because of assumption (96). Moreover, $\bar{n} = n_0(\mathcal{E}_0) = \tilde{n}_{t+1}(\mathcal{E}_{t+1})$, thus denoting by $\bar{c}_t(s)$ the invasion speed of $(\mathcal{E}_t)_t$ starting with $n_0(\xi) = \alpha e^{-s\xi}$ for all $\xi \in \mathbb{R}^+$, we have

$$\begin{aligned} \bar{c}_{t+1}(s) &= \frac{\mathcal{E}_{t+1} - \mathcal{E}_0}{t + 1} \\ &= \frac{1}{t + 1} \sum_{i=0}^t \frac{1}{s} \ln(r_i M(s)) \\ &= \left(\frac{1}{s} \ln(M(s)) + \frac{1}{t + 1} \sum_{i=0}^t \frac{1}{s} \ln(r_i) \right). \end{aligned}$$

Thus, $(\bar{c}_t(s))$ is the sum of independent identically distributed variables and thus converges in distribution to a random variable that is normally distributed with mean $\mu(s)$ and variance $\sigma^2(s)$ such that

$$\mu(s) = E\left[\frac{1}{s} \ln(r_0 M(s))\right] \tag{104}$$

and

$$\sigma^2(s) = \lim_{t \rightarrow +\infty} \frac{1}{t} V \left[\frac{1}{s} \ln(r_0 M(s)) \right] = 0. \tag{105}$$

As $\sigma^2(s) \equiv 0$, this implies that $\bar{c}_t(s)$ converges in probability to the constant $\frac{1}{s} E[\ln(r_0 M(s))]$. This is true for all s such that $M(s)$ exists. Now if we want to consider the more general cases when n_0 is a compactly supported function, the minimal speed over all the s will be the relevant one and we have that the invasion speed of the stochastic wave at time t , \bar{c}_t , has mean $\mu = \inf_{s>0} \mu(s)$ and variance $(\sigma_t^*)^2 = \sigma_t^2(s^*)$, where s^* is such that $\mu(s^*) = \mu$, and thus converges in probability to

$$\bar{c}^* = \inf_{s>0} \frac{1}{s} E[\ln(r_0 M(s))]. \tag{106}$$

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