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Lionel Roques, Mickaël D. Chekroun

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BY

LIONEL ROQUES
MICKAËL D. CHEKROUN

Unité Biostatistique et Processus Spatiaux
Institut National de la Recherche Agronomique
Avignon, France
http://www.biosp.org

On population resilience to external perturbations

Lionel Roques[*]   Mickaël D. Chekroun[†]

Abstract

We study a spatially-explicit harvesting model in periodic or bounded environments. The model is governed by a parabolic equation with a space-dependent nonlinearity of KPP type, and a negative external forcing term. The domain is either the whole space $\mathbb{R}^N$, with periodic coefficients, or a bounded domain. Analyzing the stationary states, we define two main types of solutions: the "significant" solutions, which always stay above a certain small threshold value, and the "remnant" solutions, which are always below this value. Using sub- and supersolution methods, the characterization of the first eigenvalue and first eigenfunction of some linear elliptic operators, we obtain existence and nonexistence results, as well as results on the number of stationary solutions. We also characterize the asymptotic behavior of the evolution equation as a function of the forcing term amplitude. In particular, we define critical thresholds on the forcing term below which the population density converges to a significant state, while it converges to a remnant state whenever the forcing term lies above the highest threshold. These bounds were shown to be useful in studying the influence of environmental fragmentation on the long-time behavior of the population density, in terms of the forcing term amplitude. We also present numerical results in the case of stochastic environments.

Keywords: reaction-diffusion, heterogeneous media, harvesting models, stochastic environments, periodic environments.

1   Introduction

Overexploitation has led to the extinction of many species [4]. Traditionally, models of ordinary differential equations (ODEs) or difference equations

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[*]Unité Biostatistique et Processus Spatiaux (BioSP), INRA, Domaine St Paul - Site Agroparc, 84914 Avignon Cedex 9, France

[†]Environmental Research and Teaching Institute, École Normale Supérieure, 24 rue Lhomond, 75231 Paris Cedex 05, France

have been used to estimate the maximum sustainable yields from populations and perform quantitative analysis of harvesting policies and management strategies [17]. Occulting age or stage structures as well as delay mechanisms, which will not be treated by the present paper, the ODEs models are generally of the type:

$$\frac{dU}{dt} = F(U) - Y(U), \qquad (1.1)$$

where U is the population biomass at time t, $F(U)$ is the growth function and $Y(U)$ corresponds to the harvest function. In these models, the most commonly used growth function is logistic, with $F(U) = U(\mu - \nu U)$ ([5], [25], [35]), where $\mu > 0$ is the intrinsic growth rate of the population and $\nu > 0$ models its susceptibility to crowding effects.

Different harvesting strategies $Y(U)$ have been considered in the literature, and are used in practical resource management. A very common one is the *constant-yield harvesting* strategy, where a constant number of individuals are removed per unit of time: $Y(U) = \delta$, with δ a positive constant. This harvesting function naturally appears when a quota is set on the harvesters ([31], [32], [38]). Another frequently used harvesting strategy is the *proportional harvesting* strategy (also called *constant-effort harvesting*), where a constant proportion of the population is removed. It leads to a harvesting function of the type $Y(U) = \delta U$.

Much less has been done in this field using reaction-diffusion models (but see [23], [26], [29]). The aim of this paper is to perform an analysis of some harvesting models, within the framework of reaction-diffusion equations.

One of the most celebrated reaction-diffusion model has been introduced by Fisher [15] and Kolmogorov, Petrovsky and Piskunov [22] in 1937. Since then, it has been widely used to model spatial propagation or spreading of biological species into homogeneous environments (see books [25], [28] and [40] for review). The corresponding equation is

$$u_t = D\nabla^2 u + u(\mu - \nu u), \qquad (1.2)$$

where $u = u(t, x)$ is the population density at time t and space position x, D is the diffusion coefficient, and μ and ν still correspond to the *constant* intrinsic growth rate and susceptibility to crowding effects. In the 80's, this model has been extended to heterogeneous environments by Shigesada et al. [37]. The corresponding model (which we denote by *SKT-model* in this paper) is of the type:

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u). \qquad (1.3)$$

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The coefficients $\mu(x)$ and $\nu(x)$ now depend on the space variable x, and can therefore include some effects of environmental heterogeneity. More recently, this model revealed that the heterogeneous character of the environment played an essential role on species persistence, in the sense that for different spatial configurations of the environment, a population can survive or become extinct, depending on the habitat spatial structure ([8], [12], [34], [36]).

As mentioned above, the combination of a harvesting model with a Fisher-KPP population dynamics model, leading to an equation of the form $u_t = D\nabla^2 u + u(\mu - \nu u) - Y(x, u)$ has been considered in recent papers, either using a spatially dependent proportional harvesting term $Y(x, u) = q(x)u$ in [26] [29], or a spatially dependent and time-constant harvesting term $Y(x) = h(x)$ in [23]. In these papers, the models were considered in bounded domains with Dirichlet (lethal) boundary conditions.

Here we study a population dynamics model of the SKT-type, with a spatially dependent harvesting term $Y(x, u)$:

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - Y(x, u). \qquad (1.4)$$

We mainly focus on a "quasi-constant-yield" case, where the harvesting term only depends on u for very low population densities (ensuring the nonnegativity of u). We consider two types of domains and boundary conditions. In the first case, the domain is bounded with Neumann (reflective) boundary conditions; this framework is often more realistic for modelling species which cannot cross the domain boundary. In the second case, we consider the model (1.4) in the whole space $\mathbb{R}^N$ with periodic coefficients. This last situation, though technically more complex, is useful, for instance, for studying spreading phenomena ([7], [9]), and for studying the effects of environmental fragmentation, independently of the boundary effects. Lastly, note that the effects of variability in time of the harvesting function will be investigated in a forthcoming publication [13].

In § 2, we define a quasi-constant-yield harvesting reaction-diffusion model. We prove, on a firm mathematical basis, existence and nonexistence results for the equilibrium equations, as well as results on the number of possible stationary states. We also characterize the asymptotic behavior of the solutions of (1.4). In § 3, we illustrate the practical usefulness of the results of § 2, by studying the effects of the amplitude of the harvesting term on the population density in terms of environmental fragmentation. Lastly, in § 4, we give new results for the proportional harvesting case $Y(x, u) = q(x)u$.

2 Mathematical analysis of a quasi-constant-yield harvesting reaction-diffusion model

For the sake of readability, the proofs of the results of § 2 are postponed to § 2.5.

2.1 Formulation of the model

In this paper, we consider the model:

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - \delta h(x)\rho_\varepsilon(u), \ (t,x) \ \in \ \mathbb{R}_+ \times \Omega. \qquad (2.5)$$

The function $u = u(t,x)$ denotes the population density at time t and space position x. The coefficient D, assumed to be positive, denotes the diffusion coefficient. The functions $\mu(x)$ and $\nu(x)$ respectively stand for the spatially dependent intrinsic growth rate of the population, and for its susceptibility to crowding effects. Two different types of domains Ω are considered: either $\Omega = \mathbb{R}^N$ or Ω is a smooth bounded and connected domain of $\mathbb{R}^N$ ($N \geq 1$). We qualify the first case as the *periodic case*, and the second one as the *bounded case*. In the periodic case, we assume that the functions $\mu(x)$, $\nu(x)$ and $h(x)$ depend on the space variables in a periodic fashion. For that, let $L = (L_1, \ldots, L_N) \in (0, +\infty)^N$. We recall the definition:

Definition 2.1 A function g is said to be *L-periodic* if $g(x + k) = g(x)$ for all $x = (x_1, \cdots, x_N) \in \mathbb{R}^N$ and $k \in L_1\mathbb{Z} \times \cdots \times L_N\mathbb{Z}$.

Thus, in the periodic case, we assume that μ, ν and h are L-periodic. In the bounded case we assume that Neumann boundary conditions hold: $\dfrac{\partial u}{\partial n} = 0$ on $\partial\Omega$, where n is the outward unit normal to $\partial\Omega$. The period cell C is defined by

$$C := (0, L_1) \times \cdots \times (0, L_N),$$

in the periodic case, and in the bounded case, we set

$$C := \Omega,$$

for the sake of simplicity of some forthcoming statements.

We furthermore assume that the functions μ and ν satisfy

$$\mu, \ \nu \ \in \ L^\infty(\Omega) \text{ and } \exists \ \underline{\nu}, \overline{\nu} \ \in \ \mathbb{R} \text{ s.t. } 0 < \underline{\nu} < \nu(x) < \overline{\nu}, \ \forall \ x \ \in \ \Omega. \qquad (2.6)$$

Regions with higher values of $\mu(x)$ and lower values of $\nu(x)$ will be qualified as being *more favorable*, while, on the other hand, regions with lower $\mu(x)$ and higher $\nu(x)$ values will be considered as being *less favorable* or equivalently, *more hostile*.

The last term in (2.5), $\delta h(x)\rho_\varepsilon(u)$, corresponds to a *quasi-constant-yield* harvesting term. Indeed, the function ρ_ε satisfies:

$$\rho_\varepsilon \in C^1(\mathbb{R}), \rho_\varepsilon' \geq 0, \; \rho_\varepsilon(s) = 0 \text{ for all } s \leq 0, \text{ and } \rho_\varepsilon(s) = 1 \text{ for all } s \geq \varepsilon, \tag{2.7}$$

where ε is a non-negative parameter. With such a harvesting function, the yield is constant in time whenever $u \geq \varepsilon$, while it depends on the population density when $u < \varepsilon$. In the sequel, the parameter ε is taken to be very small. As we prove in the next sections, there are many situations where the solutions of the model always remain larger than ε. For these reasons, we qualify our model as *quasi-constant-yield harvesting SKT-model*, the "dominant" regime being the constant-yield one. Note that the function ρ_ε ensures the non-negativity of the solutions of (2.5). From a biological point of view, ε can correspond to a threshold below which harvesting is progressively abandoned. Considering constant-yield harvesting functions without this threshold value would be unrealistic since it would lead to harvest on zero-populations.

Finally, we specify that $\delta \geq 0$ and that h is a function in $L^\infty(\Omega)$ such that

$$\text{there exists } \alpha > 0 \text{ with } \alpha \leq h(x) \leq 1 \text{ for all } x \in \Omega. \tag{2.8}$$

We call h the *harvesting scalar field*, and δ designates by this way the amplitude of this field.

Before starting our analysis of this model, we consider the no-harvesting case, i.e. when $\delta = 0$. We recall the main known results in this case. These results will indeed be necessary for the analysis of the quasi-constant-yield harvesting SKT-model.

2.2 The no-harvesting case

When $\delta = 0$ in equation (2.5), our model reduces to the SKT-model described by equation (1.3). The behavior of the solutions of this model has been extensively studied in [8] and [9].

Results are formulated in terms of first (smallest) eigenvalue λ_1 of the Schrödinger operator $\mathcal{L}_\mu$ defined by

$$\mathcal{L}_\mu \phi := -D\nabla^2 - \mu(x)I,$$

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with either periodic boundary conditions (on the period cell C) in the periodic case or Neumann boundary conditions in the bounded case. This operator is the linearized one of the full model around the trivial solution. Recall that λ_1 is defined as the unique real number such that there exists a function $\phi > 0$, the first eigenfunction, which satisfies

$$\begin{cases} -D\nabla^2\phi - \mu(x)\phi = \lambda_1\phi \text{ in } C, \\ \phi > 0 \text{ in } C, \ \|\phi\|_\infty = 1, \end{cases} \tag{2.9}$$

with either periodic or Neumann boundary conditions, depending on Ω. The function ϕ is uniquely defined by (2.9) ([7]), and belongs to $W^{2,\tau}(C)$ for all $1 \leq \tau < \infty$ (see [1] and [2] for further details). We set

$$\underline{\phi} := \min_{x \in C} \phi(x).$$

We recall that a stationary state p of equation (1.3) satisfies the equation,

$$-D\nabla^2 p = p(\mu(x) - \nu(x)p). \tag{2.10}$$

The following result on the stationary states of (2.10) is proved in [8].

Theorem 2.2 *(i) If $\lambda_1 < 0$, the equation* (2.10) *admits a unique nonnegative, nontrivial and bounded solution, p_0.*
(ii) If $\lambda_1 \geq 0$, the only nonnegative and bounded solution of (2.10) *is 0.*

Moreover, in the periodic case, the solution p_0 is L-periodic. Throughout this paper, p_0 always denotes the stationary solution given by Theorem 2.2, Part (i).

In order to emphasize that this solution can be "far" from 0 (see Definition 2.5, and the commentary following (2.14)), we give a lower bound for p_0.

Proposition 2.3 *Assume that $\lambda_1 < 0$, then $p_0 \geq \dfrac{-\lambda_1\underline{\phi}}{\overline{\nu}}$ in Ω.*

The asymptotic behavior of the solutions of (1.3) is also detailed in [8]. It is proved that $\lambda_1 < 0$ is a necessary and sufficient condition for species persistence, whatever the initial population u^0 is:

Theorem 2.4 *Let u^0 be an arbitrary bounded and continuous function in Ω such that $u^0 \geq 0$, $u^0 \not\equiv 0$. Let $u(t, x)$ be the solution of (1.3), with initial datum $u(0, x) = u^0(x)$.*
(i) If $\lambda_1 < 0$, then $u(t, x) \to p_0(x)$ in $W^{2,\tau}_{loc}(\Omega)$, for all $1 \leq \tau < \infty$, as $t \to +\infty$ (uniformly in the bounded case).
(ii) If $\lambda_1 \geq 0$, then $u(t, x) \to 0$ uniformly in Ω as $t \to +\infty$.

The situation (i) corresponds to persistence, while in the case (ii) the population tends to extinction. In the sequel, unless otherwise specified, we therefore always assume that $\lambda_1 < 0$, so that the population survives, at least when there is no harvesting. We are now in position to start our main analysis of steady states and related asymptotic behavior of the solutions of (2.5).

2.3 Stationary states analysis

As it is classically demonstrated in finite dimensional dynamical system theory and many problems in the infinite dimensional setting (see e.g. [39]), the asymptotic behavior of the solutions of (2.5) is governed in part by the steady states and their relative stability properties. In that respect, we study in this section the positive stationary solutions of (2.5), namely the solutions of

$$-D\nabla^2 p_\delta = p_\delta(\mu(x) - \nu(x)p_\delta) - \delta h(x)\rho_\varepsilon(p_\delta), \ x \ \in \ \Omega, \qquad (2.11)$$

in the periodic and bounded cases. When needed, we may note (2.11,δ) instead of (2.11).

Note that, provided $p_\delta \geq \varepsilon$ in Ω, p_δ is equivalently a solution of the simpler equation

$$-D\nabla^2 p_\delta = p_\delta(\mu(x) - \nu(x)p_\delta) - \delta h(x), \ x \ \in \ \Omega. \qquad (2.12)$$

This last equation has been analyzed in the case of Dirichlet boundary conditions in [29], in the particular case of constant coefficients μ and ν.

Because of the type of harvesting function considered here, we are lead to introduce the definition:

Definition 2.5 Set $\varepsilon_0 := \dfrac{\varepsilon}{\underline{\phi}} \geq \varepsilon$. We say that a nonnegative function σ is *remnant* whenever $\max\limits_C \sigma < \varepsilon_0$, whereas it is *significant* if it is a bounded function satisfying $\min\limits_C \sigma \geq \varepsilon_0$.

Remark 1: The concepts of remnant and significant solutions, as well as the harvesting term $\delta h(x)\rho_\varepsilon(u)$, are not classical. In order to clarify these notions, we present in Fig. 1 a short graphical study of the non-spatial model:

$$\frac{dU}{dt} = U(\mu - \nu U) - \delta\rho_\varepsilon(U) =: k(U), \ t \in \mathbb{R}_+, \qquad (2.13)$$
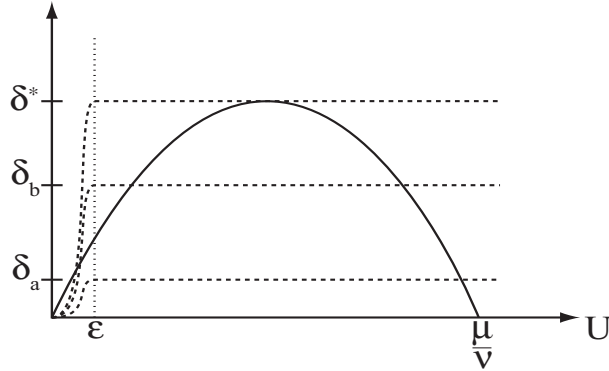
Figure 1: The logistic growth function $U \mapsto U(\mu - \nu U)$ (solid line), and the harvesting function $U \mapsto \delta \rho_\varepsilon(U)$ for three values of δ (dashed lines). The abscissae of the points of intersection of the solid and dashed lines correspond, respectively, to remnant (if smaller than ε) and significant (if strictly larger than ε) stationary solutions of (2.13). We observe that the number of significant solutions is: one, if $\delta < k(\varepsilon)$ (case $\delta = \delta_a$); two, if $k(\varepsilon) \leq \delta < \mu^2/(4\nu)$ (case $\delta = \delta_b$); one, if $\delta = \mu^2/(4\nu)$ (case $\delta = \delta^*$); zero, if $\delta > \mu^2/(4\nu)$. The number of nonzero remnant solutions is zero or more, if $\delta \leq k(\varepsilon)$ (depending on the shape of ρ_ε); one or more, if $\delta > k(\varepsilon)$, since, from (2.7), $\rho'_\varepsilon(0) = 0$. We assumed here that $\varepsilon_0 = \varepsilon$.

with constant coefficients $\mu, \nu > 0$.

Since ε_0 is assumed to be small in our model, the remnant solutions of (2.11) correspond to very low population densities. On the other hand, significant solutions are everywhere above ε_0. In particular, a constant-yield is ensured in that case. Contrarily to the ODE case, stationary solutions which are neither remnant nor significant may exist, as outlined in the next theorems. However, as we will see while studying the long-time behavior of the solutions of the model (2.5), they are of less importance (see Theorem 2.11 and § 3). The threshold ε_0 is different from ε in general. We had to define remnant and significant functions using ε_0 for technical reasons (see the proof of Theorem 2.10, part (ii), equation (2.31)). Since ε is assumed to be very small, it has no implication on the biological interpretation of our results. Moreover, most of our results still work when ε_0 is replaced by ε.

Let us now start our analysis of equation (2.11). In the sequel, we always

assume that

$$\varepsilon_0 < \frac{-\lambda_1 \underline{\phi}}{4\overline{\nu}}, \tag{2.14}$$

so that, in particular, from Proposition 2.3, the solution p_0 of (2.10) is significant.

We begin by proving that there exists a threshold δ^* such that, if the amplitude δ is below δ^*, the equation (2.11) admits significant solutions, while it does not in the other case.

Theorem 2.6 *Assume that $\lambda_1 < 0$, then there exists $\delta^* \geq 0$ such that*

(i) if $\delta \leq \delta^*$ there exists at least a positive significant solution $p_\delta \leq p_0$ of (2.11).

(ii) if $\delta > \delta^*$, there is no positive significant solution of (2.11).

Remark 2: There is no positive bounded solution of (2.11) whenever $\lambda_1 \geq 0$.

Under stronger hypotheses, we are able to prove that (2.11) admits *at most* two significant solutions. In order to state this result, we need some definitions. Let G be the space defined by

$$G := H^1(C), \tag{2.15}$$

in the bounded case, and by

$$G := H^1_{per} = \left\{ \psi \in H^1_{loc}(\mathbb{R}^N) \text{ such that } \psi \text{ is L-periodic} \right\}, \tag{2.16}$$

in the periodic case. Let us define the standard Rayleigh quotient, for all $\psi \in G$, $\psi \not\equiv 0$, and for all $\sigma \in L^\infty(C)$,

$$\mathcal{R}_\sigma(\psi) := \frac{\displaystyle\int_C D|\nabla\psi|^2 - \sigma(x)\psi^2}{\displaystyle\int_C \psi^2}. \tag{2.17}$$

According to the Courant-Fischer Theorem (see e.g. [6]), the second smallest eigenvalue λ_2 of the operator $\mathcal{L}_\mu$ can be characterized by:

$$\lambda_2 = \min_{E_k \subset G, \dim(E_k)=2} \max_{\psi \in E_k, \ \psi \not\equiv 0} \mathcal{R}_\mu(\psi). \tag{2.18}$$

This characterization is equivalent to the classical one given in [18].

We are now in position to state the theorem:

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Theorem 2.7 *Assume that $\lambda_1 < 0 \leq \lambda_2$, then, in the bounded case, the equation (2.11) admits at most two significant solutions. In the periodic case, (2.11) admits at most two L'-periodic significant solutions for all $L' \in (0, +\infty)^N$. Moreover, under these hypotheses, if two solutions $p_{1,\delta}$ and $p_{2,\delta}$ exist, they are ordered in the sense that, for instance, $p_{1,\delta} < p_{2,\delta}$ in Ω.*

Remark 3: Similar methods also allow us to assess a result on the number of solutions of equation (2.12). Indeed, if $\lambda_1 < 0 \leq \lambda_2$, then we obtain that (2.12) admits at most two non-negative bounded (and periodic in the periodic case) solutions. If these solutions exist, they are ordered.

In the periodic case, Theorem 2.7 also gives some information on the periodicity of the significant solutions of (2.11), which are actually found to have the same periodicity as the coefficients of the equation (2.11):

Corollary 2.8 *Assume that $\lambda_1 < 0 \leq \lambda_2$. Then, in the periodic case, the significant periodic solutions of (2.11) are L-periodic.*

The fact that $\lambda_1 < 0$ is directly related to the instability of the trivial solution in the SKT-model. The additional condition $\lambda_2 \geq 0$ in this theorem is linked to the existence of a stable manifold or center manifold of the steady state 0 of the SKT-model, in some appropriate functional spaces (see [39]). Therefore, the assumptions of Theorem 2.7, and the Krein Rutmann theory, allow us to conclude that under these assumptions, the unstable manifold of 0 is of dimension equal to *one* or equivalently the stable manifold is of codimension one. Such results on multiplicity of solutions of elliptic nonlinear equations with a source or sink term have been investigated in the past, and are known nowadays as being of Ambrosetti-problem type. These results also involve manifolds of codimension 1 (in the functional space of forcing), and first and second eigenvalues (for the Laplace operator only) (see [27] for a survey of these results).

In any event, Theorem 2.7 relies on the assumption that $\lambda_2 \geq 0$. In the next proposition, we give conditions under which λ_2 may become positive.

Proposition 2.9 *(i) In the bounded case, if C is a (smooth) domain with diameter $d := \max\limits_{x,y \in C} \|x - y\|_{\mathbb{R}^N}$, $\lambda_2(C) \geq D \left(\dfrac{\pi}{d}\right)^2 - \max\limits_C \mu$.*

(ii) In the periodic case, $\lambda_2(C) \geq D \left(\dfrac{\pi}{L_d}\right)^2 - \max\limits_C \mu$, where L_d denotes the length of the longest diagonal of the period cell C.

For instance, when $C = [0, 1] \times [0, 1]$, we have $d = L_d = \sqrt{2}$; thus, for $D = 1$ and $\max_C \mu = 4$, we get $\lambda_2 > 0.9$. However, this lower bound is far from being optimal. Indeed, in all our computations of § 3, and under the same hypothesis on C and D, we always had $\lambda_2 > 0$, while $\max_C \mu = 10$. Sharper lower bounds for λ_2 can be found in [11]; however, these bounds are also more sensitive to the geometry of the domain, and thus less general. They are therefore not detailed here.

We now introduce a result which is important for more applied ecological questions. Indeed, one of the main drawbacks of Theorem 2.6 is that it gives no computable bound for δ^*. Obtaining information on the value of δ^* is precious for more inclined ecological questions such as the study of the relationships between δ^* and the environmental heterogeneities. The next theorem states some computable estimates of δ^*.

Let us define

$$\delta_1 := \frac{\lambda_1^2 \underline{\phi}}{\overline{\nu}(1 + \underline{\phi})^2} \text{ and } \delta_2 := \frac{\lambda_1^2}{4\alpha\underline{\nu}}. \tag{2.19}$$

Note that neither δ_1 nor δ_2 depend on δ and ε.

Theorem 2.10 *(i) If $\lambda_1 < 0$ and $\delta \leq \delta_1$, then there exists a positive significant (and $L-$periodic in the periodic case) solution p_δ of (2.11) such that*
$p_\delta \geq -\dfrac{\lambda_1 \phi}{\overline{\nu}(1 + \underline{\phi})}.$

(ii) If $\lambda_1 < 0$ and $\delta > \delta_2$, the only possible positive bounded solutions of (2.11) are remnant.

The lower bound of Part (i), for p_δ, does not depend on ε. Thus, there is a clear distinction between the remnant and significant solutions. Note that, of course, $\delta_1 \leq \delta_2$.

The formulae (2.19) allow numerical evaluations. An important quantity to compute is the size of the gap $\delta_2 - \delta_1$, and its fluctuations in terms of environmental configurations. This question is addressed in § 3 through a numerical study.

2.4   Asymptotic behavior

In this section, we prove that the quantity δ^* in fact corresponds to a maximum sustainable yield, in the sense that when δ is smaller than δ^*, the population density $u(t, x)$ converges to a significant stationary state of (2.5) as $t \to \infty$, whereas when δ is larger than δ^*, the population density converges to a stationary state which is not significant. In fact, when δ is larger

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than the quantity δ_2 defined by (2.19) we even prove that the population converges to a remnant stationary state of (2.5).

We assume here that the harvesting starts on a stabilized population governed by the standard SKT-model with $\delta = 0$. From Theorem 2.4, this means that we study the behavior of the solutions $u(t, x)$ of our model (2.5), starting with the initial datum $u(0, x) = p_0(x)$. Since we have assumed that $\lambda_1 < 0$, it follows from Theorem 2.2, Proposition 2.3 and (2.14) that p_0 is well defined and significant.

Let us describe, with the next theorem, the long-time behavior of the population density.

Theorem 2.11 *Let $u(t, x)$ be the solution of (2.5) with initial datum $u(0, x) = p_0(x)$. Then u is non-increasing in t and,*

(i) if $\delta \leq \delta^*$, $u(t, x) \to p_\delta(x)$ uniformly in Ω as $t \to +\infty$, where p_δ is the maximal significant solution of (2.11). Moreover p_δ is L-periodic in the periodic case;

(ii) if $\delta > \delta^*$, then the function $u(t, \cdot)$ converges uniformly in Ω to a solution of (2.11) which is not significant;

(iii) if $\delta > \delta_2$, the function $u(t, \cdot)$ converges uniformly in Ω to a remnant solution of (2.11).

Remark 4: If, in addition, we assume that $\lambda_2 \geq 0$, then Theorem 2.7 says that, whenever $\delta \leq \delta^*$, the equation (2.5) admits at most two significant stationary states (which are periodic stationary states in the periodic case). In that case, the stationary state p_δ selected at large times is the higher one. If we do not assume that $\lambda_2 \geq 0$, this stationary state can still be defined as "the maximal one" that can be constructed by a sub- and super- solution method (see [3]).

From the above theorem, we observe that, whenever $\delta \leq \delta^*$, the solution $u(t, x)$ of (2.5), with initial datum p_0, remains significant for all times $t \geq 0$. This ensures a constant yield in time, and justifies the name of the model.

Similar results could be obtained for a wider class of initial data. Indeed, with similar methods, the convergence of $u(t, x)$ to a significant solution of (2.11) can be obtained whenever $\delta \leq \delta^*$ for all bounded and continuous initial data $u(0, x)$ which are larger than the smallest significant solution of (2.11). In particular, when $u(0, x)$ is larger than the maximal significant solution of (2.11), $u(t, x)$ converges to this maximal significant solution as $t \to +\infty$. A more detailed analysis of the basin of attraction related to the maximal significant solution will be further investigated in the forthcoming paper [13].

Theorem 2.11 shows that the practical determination of δ^* is directly linked to the size of the gap $\delta_2 - \delta_1$. As we will see in § 3, this gap (δ_1, δ_2) can be very narrow in certain situations. In those cases, the numerical computation of δ_1 and δ_2 therefore gives a sharp localization of the maximum sustainable quota $\delta^* \in [\delta_1, \delta_2]$, that can be of non-negligible ecological interest.

2.5 Proofs of the results of § 2

Proof of Proposition 2.3: Let ϕ be defined by (2.9), with the appropriate boundary conditions. Set $\kappa_0 := \dfrac{-\lambda_1}{\overline{\nu}}$. Then the function $\kappa_0 \phi$ satisfies

$$
\begin{aligned}
-D\nabla^2(\kappa_0\phi) - \mu(x)\kappa_0\phi + \nu(x)(\kappa_0\phi)^2 &= \lambda_1\kappa_0\phi + \nu(x)(\kappa_0\phi)^2, \\
&= \kappa_0\phi(\lambda_1 + \nu(x)\kappa_0\phi) \leq 0.
\end{aligned}
$$

Thus $\kappa_0\phi$ is a subsolution of the equation (2.10) satisfied by p_0. Since for $M \in \mathbb{R}$ large enough, M is a supersolution of (2.10), it follows from the uniqueness of the positive bounded solution p_0 of (2.10) that $p_0 \geq \kappa_0\phi \geq \dfrac{-\lambda_1\phi}{\overline{\nu}}$.
□

Before proving Theorem 2.6, we begin with the following lemma.

Lemma 2.12 *For all $\delta > 0$, if p_δ is a nonnegative bounded solution of (2.11), then $p_\delta \leq p_0$.*

Proof of Lemma 2.12: Assume that there exists $x_0 \in \Omega$ such that $p_\delta(x_0) > p_0(x_0)$. The function p_δ satisfies

$$
-D\nabla^2 p_\delta - p_\delta(\mu(x) - \nu(x)p_\delta) = -\delta h(x)\rho_\varepsilon(p_\delta) \leq 0,
$$

thus p_δ is a subsolution of the equation (2.10) satisfied by p_0. Since for $M \in \mathbb{R}$ large enough, M is a supersolution of (2.10) we can apply a classic iterative method to infer the existence of a solution p_0' of (2.10) (with Neumann boundary conditions in the bounded case since both p_δ and M satisfy Neumann boundary conditions) such that $p_\delta \leq p_0' \leq M$. In particular $p_0'(x_0) > p_0(x_0)$, which is in contradiction with the uniqueness of the positive bounded solution of (2.10). □

Proof of Theorem 2.6: Let us define

$$\delta^* := \sup\{\delta \geq 0, (2.11) \text{ admits a significant solution}\}.$$

For $\delta = 0$, we know from Proposition 2.3 that p_0 is a significant solution of (2.11). Moreover, for δ large enough, the nonexistence of significant solutions of (2.11) is a direct consequence of the maximum principle (it is also a consequence of the proof of Theorem 2.10, Part (ii)). Thus δ^* is well defined and bounded.

Assume that $\delta^* > 0$, and let us prove that equation (2.11,δ^*) admits a significant solution. By definition of δ^*, there exists a sequence $(p_{\delta_k})_{k \in \mathbb{N}}$ of solutions of (2.11,δ_k) with $0 < \delta_k \leq \delta^*$ and $\delta_k \to \delta^*$ as $k \to +\infty$. Moreover, from Lemma 2.12, $\varepsilon_0 \leq p_{\delta_k} \leq p_0$ for all $k \geq 0$. Thus, from standard elliptic estimates and Sobolev injections, the sequence $(p_{\delta_k})_{k \in \mathbb{N}}$ converges (up to the extraction of some subsequence) in $W_{loc}^{2,\tau}$, for all $1 \leq \tau < \infty$, to a significant solution p_{δ^*} of (2.11,δ^*).

Now, let $0 \leq \delta < \delta^*$. Then

$$-D\nabla^2 p_{\delta^*} - p_{\delta^*}(\mu(x) - \nu(x)p_{\delta^*}) + \delta h(x) = (\delta - \delta^*)h(x) < 0,$$

thus p_{δ^*} is a subsolution of (2.11,δ). Since p_0 is a supersolution of (2.11,δ), and $p_{\delta^*} \leq p_0$, a classical iterative method gives the existence of a significant solution p_δ of (2.11,δ) (with Neumann boundary conditions in the bounded case since both p_0 and p_δ satisfy Neumann boundary conditions). This concludes the proof of Theorem 2.6. $\square$

Proof of Theorem 2.7: As a preliminary, we prove that if two solution exist, then they cannot intersect. Let $p_{1,\delta}$ and $p_{2,\delta}$ be two significant solutions of (2.11). In the bounded case, we assume that $p_{1,\delta}$ and $p_{2,\delta}$ satisfy Neumann boundary conditions. In the periodic case, we assume that there exists $L' \in (0, +\infty)^N$ such that $p_{1,\delta}$ and $p_{2,\delta}$ are L'-periodic, we then denote the period cell by C'. Let us set $q_\delta := p_{2,\delta} - p_{1,\delta}$. Then q_δ verifies

$$-D\nabla^2 q_\delta - [\mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})]q_\delta = 0, \qquad (2.20)$$

thus, setting $\rho(x) := \mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})$, we obtain

$$-D\nabla^2 q_\delta - \rho(x)q_\delta = 0, \qquad (2.21)$$

with the same boundary conditions that were satisfied by $p_{1,\delta}$ and $p_{2,\delta}$.

Let $\widehat{\lambda_1}$ and $\widehat{\lambda_2}$ be respectively the first and second eigenvalues of the operator $\mathcal{L}_\rho := -D\nabla^2 - \rho I$. Let $\mathcal{R}_\sigma(\phi)$, be defined by equation (2.17). Since $\rho(x) < \mu(x) - 2\underline{\nu}\varepsilon_0$ for all $x \in \Omega$, we get

$$\mathcal{R}_\rho(\varphi) \geq \mathcal{R}_\mu(\varphi) + 2\underline{\nu}\varepsilon_0,$$

for all $\varphi \in G'$, where $G' := H^1(C)$ in the bounded case and

$$G' := H^1_{per} = \left\{ \varphi \in H^1_{loc}(\mathbb{R}^N) \text{ such that } \varphi \text{ is L'-periodic} \right\},$$

in the periodic case. Thus, by the classical min-max formula (2.18), it follows that

$$\widehat{\lambda_2} \geq \lambda_2 + 2\underline{\nu}\varepsilon_0 > 0. \tag{2.22}$$

Furthermore, from (2.21), 0 is an eigenvalue of the operator $\mathcal{L}_\rho$. Thus, (2.22) implies that $\widehat{\lambda_1} = 0$. As a consequence, q_δ is a principal eigenfunction of the operator $\mathcal{L}_\rho$. The principal eigenfunction characterization thus implies that q_δ has a constant sign. Finally, we get that $p_{1,\delta}$ and $p_{2,\delta}$ do not intersect each other.

Let us now prove that equation (2.11) admits at most two significant solutions. Arguing by contradiction, we assume that there exist three significant (L'-periodic in the periodic case, for some $L' \in (0, +\infty)^N$) solutions $p_{1,\delta}$, $p_{2,\delta}$, and $p_{3,\delta}$ of (2.11). From the above result, we may assume, without loss of generality, that $p_{3,\delta} > p_{2,\delta} > p_{1,\delta} > \varepsilon_0$. Set $q_{2,1} := p_{2,\delta} - p_{1,\delta}$ and $q_{3,2} := p_{3,\delta} - p_{2,\delta}$, then these functions satisfy the equations

$$-D\nabla^2 q_{2,1} - \rho_{2,1}(x)q_{2,1} = 0, \tag{2.23}$$

and

$$-D\nabla^2 q_{3,2} - \rho_{3,2}(x)q_{3,2} = 0, \tag{2.24}$$

with $\rho_{2,1} := \mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})$ and $\rho_{3,2} := \mu(x) - \nu(x)(p_{2,\delta} + p_{3,\delta})$. Moreover, $q_{2,1} > 0$ and $q_{3,2} > 0$. Thus 0 is the first eigenvalue of the operators $\mathcal{L}_{\rho_{2,1}} := -D\nabla^2 - \rho_{2,1}I$ and $\mathcal{L}_{\rho_{3,2}} := -D\nabla^2 - \rho_{3,2}I$ with either Neumann or L'-periodic boundary conditions.

From the strong maximum principle (see e.g. [18]) (together with Hopf's Lemma in the bounded case, and using the L'-periodicity of $q_{3,2}$ in the periodic case), we obtain the existence of $\theta > 0$ such that $q_{3,2} > \theta$. Since the operator $\mathcal{L}_{\rho_{3,2}}$ is self-adjoint, we have the following formula for its first eigenvalue $\widehat{\lambda_1}^{3,2}$,

$$\widehat{\lambda_1}^{3,2} = \min_{\varphi \in G'} \mathcal{R}_{\rho_{3,2}}(\varphi),$$

thus

$$\widehat{\lambda_1}^{3,2} = \min_{\varphi \in G'} \left\{ \mathcal{R}_{\rho_{2,1}}(\varphi) + \frac{\int_C \nu(p_{3,\delta} - p_{1,\delta})\varphi^2}{\int_C \varphi^2} \right\} \geq \min_{\varphi \in G'} \left\{ \mathcal{R}_{\rho_{2,1}}(\varphi) \right\} + \underline{\nu}\theta,$$

$$\geq \widehat{\lambda_1}^{2,1} + \underline{\nu}\theta,$$

where $\widehat{\lambda_1}^{2,1}$ is the first eigenvalue of the operator $\mathcal{L}_{\rho_{2,1}}$. Since the first eigenvalues of the operators $\mathcal{L}_{\rho_{2,1}}$ and $\mathcal{L}_{\rho_{3,2}}$ are both 0, we deduce that $0 \geq 0 + \underline{\nu}\theta > 0$, hence a contradiction. $\square$

Proof of Corollary 2.8: Let p_δ be a significant L'-periodic solution of (2.11), and let $k \in \prod_{i=1}^N L_i \mathbb{Z}$. From the L-periodicity of the equation (2.11), $p_\delta(\cdot + k)$ is also a solution of (2.11). By periodicity of p_δ, the functions p_δ and $p_\delta(\cdot + k)$ intersect each other. Thus, from Theorem 2.7, since p_δ and $p_\delta(\cdot + k)$ are both L'-periodic, $p_\delta \equiv p_\delta(\cdot + k)$. Therefore, p_δ is a L-periodic function. $\square$

Proof of Proposition 2.9: In the bounded case, let $\tilde{C}$ be the convex hull of the set C. It was proved in [30] that the second Neumann eigenvalue of the Laplace operator $-D\nabla^2$ on $\tilde{C}$ was larger than $D\left(\frac{\pi}{d}\right)^2$. Since $C \subset \tilde{C}$, we have $H^1(C) \subset H^1(\tilde{C})$. Using formula (2.18), we thus obtain that the second eigenvalue of $\mathcal{L}_\mu$ in the bounded case satisfies $\lambda_2 \geq D\left(\frac{\pi}{d}\right)^2 - \max_C \mu$. This proves part (i) of Proposition 2.9.

In the periodic case, since H^1_{per} can be seen as a subset of $H^1(C)$, it follows from (2.18) that,

$$\lambda_2 \geq \min_{E_k \subset H^1(C), \dim(E_k)=2} \max_{\psi \in E_k, \ \psi \not\equiv 0} \mathcal{R}_\mu(\psi). \tag{2.25}$$

The period cell C is convex but not smooth enough to assert that the right-hand side of (2.25) is equal to the second eigenvalue in the bounded case. Let L_d be the longest diagonal of C. Then C is included in a ball B_{L_d} of diameter L_d. Thus, from formula (2.18), the right-hand side of (2.25) is larger than the second eigenvalue of $\mathcal{L}_\mu$ on B_{L_d}. From (i), the conclusion of (ii) follows. $\square$

Proof of Theorem 2.10, Part (i): Let λ_1 and ϕ be defined by (2.9), and let

κ be a nonnegative real number such that $\kappa > \varepsilon_0$. Then we have

$$
\begin{aligned}
-D\nabla^2(\kappa\phi) - \kappa\phi(\mu(x) - \kappa\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\kappa\phi) &\leq \lambda_1\kappa\phi + \kappa^2\phi^2\nu(x) + \delta \\
&\leq \kappa\phi(\lambda_1 + \kappa\phi\nu(x)) + \delta \\
&\leq \max_{\tau\in I}\{\tau(\lambda_1 + \tau\overline{\nu})\} + \delta,
\end{aligned}
\tag{2.26}
$$

where $I = \{\kappa\phi(x),\ x \in C\}$. Setting $g(\tau) := \tau(\lambda_1 + \tau\overline{\nu})$, since $\|\phi\|_\infty = 1$, and since g is a convex function, it follows from (2.26) that

$$
-D\nabla^2(\kappa\phi) - \kappa\phi(\mu(x) - \kappa\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\kappa\phi) \leq \max\{g(\kappa), g(\kappa\underline{\phi})\} + \delta.
\tag{2.27}
$$

Let us take κ_0 be such that $g(\kappa_0) = g(\kappa_0\underline{\phi})$, namely $\kappa_0 = -\dfrac{\lambda_1}{\overline{\nu}(1 + \underline{\phi})}$ (note that $\kappa_0\phi > \varepsilon$). We get

$$
-D\nabla^2(\kappa_0\phi) - \kappa_0\phi(\mu(x) - \kappa_0\phi\nu(x)) + \delta h(x) \leq -\frac{\lambda_1^2\underline{\phi}}{\underline{\nu}(1 + \underline{\phi})^2} + \delta \leq 0, \quad (2.28)
$$

from the hypothesis on δ of Theorem 2.10, Part (i). Therefore, $\kappa_0\phi$ is a subsolution of (2.11) with either L-periodic or Neumann boundary conditions. Moreover, if M is a large enough constant, M is a supersolution of (2.11) with L-periodic or Neumann boundary conditions. Thus, it follows from a classical iterative method that there exists a solution $\underline{p_\delta}$ of (2.11), with the required boundary conditions, and which satisfies $\kappa_0\phi \leq \underline{p_\delta} \leq M$ in Ω. Moreover, in the periodic case, since $\kappa_0\phi$ and M are L-periodic and since the equation (2.11) is also L-periodic, it follows that p_δ is L-periodic. Theorem 2.10, Part (i) is proved. $\square$

Proof of Theorem 2.10, Part (ii): Assume that $\lambda_1 < 0$, $\delta > \delta_2$ and that there exists a positive bounded solution p_δ of (2.11) which is not remnant, i.e.

$$
\text{there exists } x_0 \text{ with } p_\delta(x_0) \geq \varepsilon_0. \tag{2.29}
$$

Since ϕ is bounded from below away from 0 and p_δ is bounded, we can define

$$
\gamma^* = \inf\{\gamma > 0,\ \gamma\phi > p_\delta \text{ in } \Omega\} > 0. \tag{2.30}
$$

It follows from the definition of γ^* that $\gamma^*\phi \geq p_\delta$ in Ω, and in particular, $\gamma^*\phi(x_0) \geq p_\delta(x_0) \geq \varepsilon_0$. Since $\|\phi\|_\infty = 1$, we get $\gamma^* \geq \varepsilon_0$. Thus,

$$
\gamma^*\phi \geq \varepsilon_0\underline{\phi} = \varepsilon, \tag{2.31}
$$

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which implies $\rho_\varepsilon(\gamma^*\phi) = 1$. Thus, $h(x)\rho_\varepsilon(\gamma^*\phi) \geq \alpha$, and we get,

$$-D\nabla^2(\gamma^*\phi)-\gamma^*\phi(\mu(x)-\gamma^*\phi\nu(x))+\delta h(x)\rho_\varepsilon(\gamma^*\phi) \geq \gamma^*\phi(\lambda_1+\gamma^*\phi\nu(x))+\delta\alpha,$$

on Ω. Moreover, since $\gamma^*\phi > 0$ and $\nu \geq \underline{\nu}$, we have $\gamma^*\phi(\lambda_1 + \gamma^*\phi\nu(x)) \geq -\dfrac{\lambda_1^2}{4\underline{\nu}}$. Using the fact that $\delta > \delta_2 = \dfrac{\lambda_1^2}{4\alpha\underline{\nu}}$, we thus get:

$$-D\nabla^2(\gamma^*\phi)-\gamma^*\phi(\mu(x)-\gamma^*\phi\nu(x))+\delta h(x)\rho_\varepsilon(\gamma^*\phi) \geq -\frac{\lambda_1^2}{4\underline{\nu}} + \delta\alpha > 0, \quad (2.32)$$

on Ω. Therefore, $\gamma^*\phi$ is a supersolution of (2.11). Set $z := \gamma^*\phi - p_\delta$. From the definition of γ^*, we know that $z \geq 0$, and that there exists a sequence $(x_n)_{n\in\mathbb{N}}$ in Ω such that $z(x_n) \to 0$ as $n \to +\infty$.

In the bounded case, up to the extraction of some subsequence, $x_n \to \overline{x} \in \Omega$ as $n \to +\infty$. By continuity, $z(\overline{x}) = 0$. Moreover, subtracting (2.11) to (2.32), we get

$$-D\nabla^2 z + [\nu(x)(\gamma^*\phi + p_\delta) + \chi(x) - \mu(x)]z > 0 \text{ in } \Omega, \quad (2.33)$$

where the function χ is defined by $\chi(x) = \delta h(x)\frac{\rho_\varepsilon(\gamma^*\phi(x))-\rho_\varepsilon(p_\delta(x))}{\gamma^*\phi(x)-p_\delta(x)}$ whenever $\gamma^*\phi(x) - p_\delta(x) \neq 0$, and $\chi(x) = \rho'_\varepsilon(p_\delta(x))$ otherwise. Since ρ_ε is C^1, χ is bounded. Thus $b(x) := \nu(x)(\gamma^*\phi + p_\delta) + \chi(x) - \mu(x)$ is a bounded function. Using the strong elliptic maximum principle, we deduce from (2.33) that $z \equiv 0$. Thus $\gamma^*\phi \equiv p_\delta$ is a positive solution of (2.11). It is in contradiction with (2.32).

In the periodic case, we must also consider the situation where the sequence $(x_n)_{n\in\mathbb{N}}$ is not bounded. Let $(\overline{x}_n) \in \overline{C}$ be such that $x_n - \overline{x}_n \in \prod_{i=1}^N L_i\mathbb{Z}$. Up to the extraction of some subsequence, we can assume that there exists $\overline{x}_\infty \in \overline{C}$ such that $\overline{x}_n \to \overline{x}_\infty$ as $n \to +\infty$. Set $\phi_n(x) = \phi(x+x_n)$ and $p_{\delta,n}(x) = p_\delta(x + x_n)$. From standard elliptic estimates and Sobolev injections, it follows that (up to the extraction of some subsequence) $p_{\delta,n}$ converge in $W_{loc}^{2,\tau}$, for all $1 \leq \tau < \infty$, to a function $p_{\delta,\infty}$ satisfying

$$-\nabla^2(Dp_{\delta,\infty})-p_{\delta,\infty}(\mu(x+\overline{x}_\infty)-p_{\delta,\infty}\nu(x+\overline{x}_\infty))+\delta h(x+\overline{x}_\infty)\rho_\varepsilon(p_{\delta,\infty}) = 0,$$

in $\mathbb{R}^N$, while $\gamma^*\phi_n$ converges to $\gamma^*\phi_\infty := \gamma^*\phi(\cdot + \overline{x}_\infty)$, and

$$-\nabla^2(D\gamma^*\phi_\infty)-\gamma^*\phi_\infty(\mu(x+\overline{x}_\infty)-\gamma^*\phi_\infty\nu(x+\overline{x}_\infty))+\delta h(x+\overline{x}_\infty)\rho_\varepsilon(\gamma^*\phi_\infty) > 0,$$

in $\mathbb{R}^N$. Let us set $z_\infty(x) := \gamma^*\phi_\infty(x)-p_{\delta,\infty}(x)$. Then $z_\infty(x) = \lim_{n\to+\infty} z(x+x_n)$, therefore $z_\infty \geq 0$ and $z_\infty(0) = 0$. Moreover, there exists a bounded function b_∞ such that

$$-D\nabla^2 z_\infty + b_\infty z_\infty > 0 \text{ in } \mathbb{R}^N. \quad (2.34)$$

It then follows from the strong maximum principle that $z_\infty \equiv 0$ and we again obtain a contradiction. Finally, we necessarily have $p_\delta \leq \varepsilon_0$, and the proof of Theorem 2.10, Part (ii) is complete. $\square$

Proof of Theorem 2.11, Part (i): Assume that $\delta \leq \delta^*$. Let p_δ be the unique maximal significant solution defined in the proof of Theorem 2.10, Part (i). Then, from Lemma 2.12,

$$p_\delta(x) \leq p_0(x) = u(0, x), \ \forall \ x \ \in \ \Omega, \tag{2.35}$$

which implies

$$p_\delta(x) \leq u(t, x) \text{ in } \mathbb{R}_+ \times \Omega, \tag{2.36}$$

since p_δ is a stationary solution of (2.5). Moreover, since p_0 is a supersolution of (2.11), u is nonincreasing in time t, and standard parabolic estimates imply that u converges in $W_{loc}^{2,\tau}(\Omega)$, for all $1 \leq \tau < \infty$, to a bounded stationary solution u_∞ of (2.5). Furthermore, from (2.36) we deduce that $p_\delta \leq u_\infty \leq p_0$. Since p_δ is the maximal positive solution of (2.11), it follows that $u_\infty \equiv p_\delta$. Moreover, in the periodic case, since p_0 and the equation (2.5) are L-periodic, $u(t, x)$ is also L-periodic in x. Therefore the convergence is uniform in Ω. Part (i) of Theorem 2.11 is proved. $\square$

Proof of Theorem 2.11, Parts (ii) and (iii): Assume that $\delta > \delta^*$. Since 0 is a stationary solution of (2.5) and $u(0, x) = p_0 > 0$, we obtain that $u(t, x) > 0$ in $\mathbb{R}^+ \times \Omega$, and again, from standard parabolic estimates, we know that u converges in $W_{loc}^{2,\tau}(\Omega)$ (for all $1 \leq \tau < \infty$) to a bounded stationary solution $\underline{u_\infty} \geq 0$ of (2.5) as $t \to +\infty$. Moreover, in the periodic case, from the L-periodicity of the initial data and of the equation (2.5), we know that $u(t, \cdot)$ and $\underline{u_\infty}$ are L-periodic. Therefore the convergence is uniform in Ω. It follows from Theorem 2.6, Part (ii) that $\underline{u_\infty}$ cannot be a significant solution of (2.11). Moreover, if $\delta > \delta_2$, Theorem 2.10, Part (ii) ensures that $\underline{u_\infty}$ is a remnant solution of (2.11). $\square$

3 Numerical investigation of the effects of environmental fragmentation

We propose here to apply the results of §2, on the estimation of the maximum sustainable yield, to the study of the effects of environmental fragmentation. A theoretical investigation of the relationships between maximum sustainable yield and fragmentation is difficult to achieve (see Remark 5).

To overcome this difficulty, we propose a numerical study in the case of stochastic environments. Firstly, we show that the gap $\delta_2 - \delta_1$, obtained from (2.19) and Theorem 2.10, remains small whatever the degree of fragmentation is. This gap corresponds to the numerical values of the harvesting quota δ for which we do not know whether the population density will converge to a significant or a remnant solution of the stationary equation (2.11). Secondly, we show that there is a monotone increasing relationship between the maximal sustainable yield δ^* and the habitat aggregation.

Remark 5: In a periodic environment, a simple way of changing the degree of fragmentation without changing the relative spatial pattern (favorable area/unfavourable area ratio), is to modify the size of the period cell C. Assume that $\mu(x) = \eta\left(\frac{x}{L}\right)$, for some $1-$periodic function η with positive integral, and for some $L > 0$. This means that the environment consists in square cells of side L. Setting $\lambda_{1,L} := \lambda_1$, and $\phi_L := \phi$, we then have $-D\Delta\phi_L - \eta\left(\frac{x}{L}\right)\phi_L = \lambda_{1,L}\phi_L$ on $[0, L]^N$. The function $\psi_L(x) := \phi_L(Lx)$ thus satisfies $-D\Delta\psi_L - L^2\eta(x)\psi_L = L^2\lambda_{1,L}\psi_L$ in $[0,1]^N$, with 1-periodicity. From the Rayleigh formula we thus obtain:

$$\lambda_{1,L} = \min_{\psi \in H^1_{per}} \frac{D}{L^2} \frac{\int_{[0,1]^N} |\nabla\psi|^2}{\int_{[0,1]^N} \psi^2} - \frac{\int_{[0,1]^N} \eta\psi^2}{\int_{[0,1]^N} \psi^2},$$

therefore $\lambda_{1,L} < 0$ (since $\psi \equiv 1 \in H^1_{per}$), and $\lambda_{1,L}$ decreases with L. It implies that δ_2 increases with L. The relationship between δ_1 and L is less clear since, $\underline{\phi_L} = \min_C \phi_L$ may not always be an increasing function of L.

In order to lessen the boundary effects, and to focus on fragmentation, we place ourselves in the periodic case. For our numerical computations, we assume that the environment is made of two components, favorable and unfavorable regions. It is expressed in the model (2.5) through the coefficient $\mu(x)$, which takes two values μ^+ or μ^-, depending on the space variable x. We also assume that

$$\mu^+ > \mu^-, \ \nu(x) \equiv 1, \ h(x) \equiv 1 \text{ and } D = 1.$$

Using a stochastic model for landscape generation [34], we built 2000 samples of binary environments, on the 2-dimensional period cell $C = [0, 1]^2$, with different degrees of fragmentation. In all these environments, the favorable region, where $\mu(x) = \mu^+$, occupies 20% of the period cell. The environmental fragmentation is defined as follows. We discretize the cell C into $n_C = 50 \times 50$ equal squares C_i. The lattice made of the cells C_i is equipped with a 4-neighborhood system $V(C_i)$ (see Fig. 2), with toric
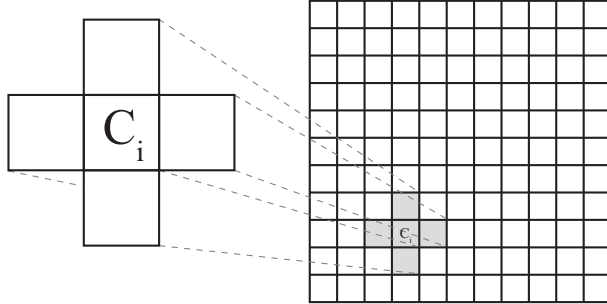
20

Figure 2: The 4-neighborhood system: an element C_i of C and its four neighbors.

conditions. On each cell C_i, we assume that the function μ either takes the value μ^+ or μ^-, while the number $n_+ = \text{card}\{i, \mu \equiv \mu^+ \text{ on } C_i\}$ is fixed to $n_C \times \frac{20}{100} = 500$. For each landscape sample $\omega = (\mu(C_i))_{i=1...n_C}$, we set

$$s(\omega) = \frac{1}{2} \sum_{C_i \subset C} \sum_{C_j \in V(C_i)} \mathbb{1}\{\mu(C_j) = \mu(C_i)\},$$ the number of pairs of neighbors

(C_i, C_j) such that μ takes the same value on C_i and C_j ($\mathbb{1}\{\cdot\}$ is the indicator function). The number $s(\omega)$ is directly linked to the environmental fragmentation: a landscape pattern is all the more aggregated as $s(\omega)$ is high, and all the more fragmented as $s(\omega)$ is small (Fig. 3). Thus, we shall refer to s as the "habitat aggregation index".

Remark 6: There exist several ways of obtaining hypothetical landscape distributions. The commonest are neutral landscape models, originally introduced by Gardner et al. [16]. They can include parameters which regulate the fragmentation [20]. We preferred to use a stochastic landscape model presented in [34], since it allows an exact control of the favorable and unfavorable surfaces, and is therefore well adapted for analyzing the effects of fragmentation *per se.* This model is inspired from statistical physics. The number of pairs of similar neighbors s is controlled during the process of landscape generation. This quantity can be measured *a posteriori* on the landscape samples. Other measures of fragmentation could have been used, such as fractal dimension (see [24]). For a discussion on the different ways of measuring habitat fragmentation in real-world situations the interested reader can refer to [14].

For our computations, we took $\mu^+ = 10$ and $\mu^- = 0$, and we computed the corresponding values of λ_1^i, δ_1^i and δ_2^i on each landscape sample ω^i of aggregation index s^i, for $i = 1 \ldots 2000$. The eigenvalues λ_1^i were computed

(a) $s = 3400$ (b) $s = 3800$ (c) $s = 4200$
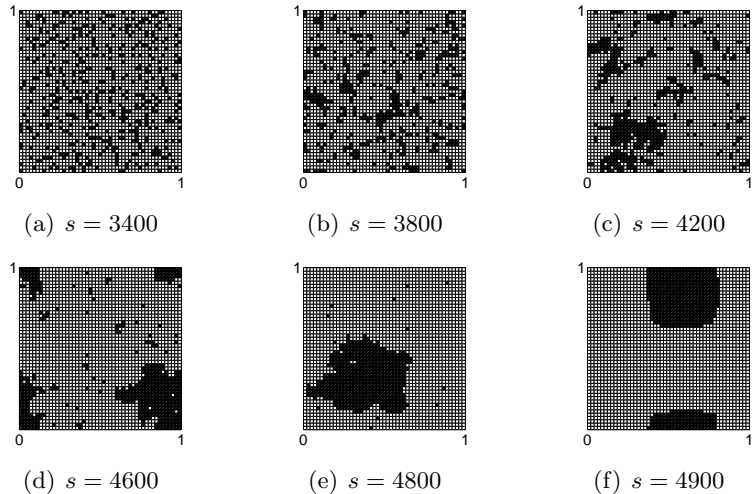
(d) $s = 4600$ (e) $s = 4800$ (f) $s = 4900$

Figure 3: Some samples of the landscapes used for the computations of δ_1 and δ_2, with different values of the habitat aggregation index s. The black areas correspond to more favorable environment, where $\mu(x) = \mu^+$.

with a finite elements method. We fitted the data sets $\{(s^i, \delta_1^i)\}_{i=1...2000}$ and $\{(s^i, \delta_2^i)\}_{i=1...2000}$ using ninth degree polynomials (it is enough to assess if the relations between s and δ_1, δ_2 tend to be monotonic or not). The resulting fitted curves $\delta_{1,f}$ and $\delta_{2,f}$ are presented in Fig. 4. Under the assumption of normally distributed values of δ_1 and δ_2 for fixed s values, we computed a lower prediction bound ($\delta_{1,lo}$) for new observation of δ_1 and an upper prediction bound for δ_2 ($\delta_{2,up}$), with a level of certainty of 99%. Thus, given a configuration ω, with a fixed value of s, when δ is smaller than $\delta_{1,lo}$, we take a 0.5% chance of being above δ_1, while when δ is larger than $\delta_{2,up}$, we take a 0.5% chance of being below δ_2. The small thickness of the intervals $(\delta_{1,lo}, \delta_{2,up})$ emphasizes the quality of the relationship between the habitat aggregation index s and the maximum sustainable yield $\delta^* \in [\delta_1, \delta_2]$. This also indicates that the criteria of Theorems 2.10 and 2.11 are close to be optimal, at least in some situations.

Furthermore, as we can observe, the values of δ_1 and δ_2 tend to increase as s increases, and thus as the environment aggregates. Since $\delta^* \in [\delta_1, \delta_2]$, we deduce from the computations presented in Fig. 4 that δ^* tends to increase with environmental aggregation.

These tests were performed for particular values of μ^+ and μ^-. However, the thickness of the interval (δ_1, δ_2) can be determined for all values of μ^+,
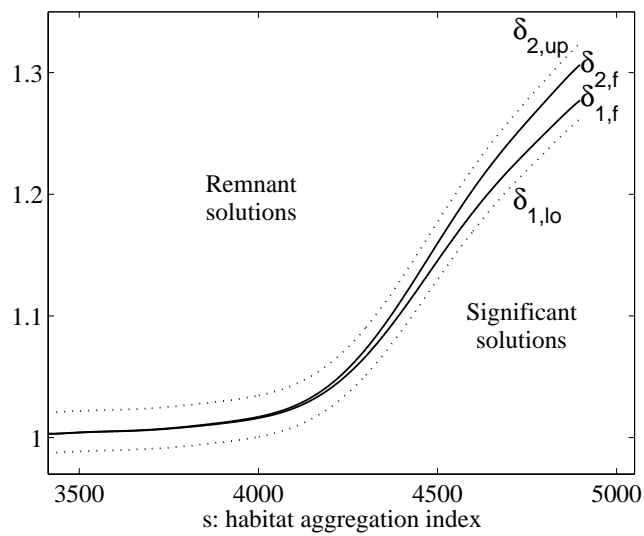
Figure 4: Solid lines: $\delta_{1,f}$ and $\delta_{2,f}$ correspond respectively to the data sets $\{(s^i, \delta_1^i)\}_{i=1\ldots2000}$ and $\{(s^i, \delta_2^i)\}_{i=1\ldots2000}$, fitted with ninth degree polynomials. Dashed lines: $\delta_{1,lo}$ is a lower prediction bound for new observations of δ_1 and $\delta_{2,up}$ an upper prediction bound for new observations of δ_2, with in both cases a level a certainty of 99%.

μ^- without further numerical computations, provided that $\mu^+ - \mu^- = 10$. Indeed, let us set $B := \mu^+ - \mu^-$. For a fixed value of B, let $\mu_0(x)$ be a given L-periodic function in $L^\infty(\mathbb{R}^N)$ taking only the two values $\mu_0^+ = B$ and $\mu_0^- = 0$. Let $\lambda_{1,0}$ be the first eigenvalue of the operator $-\nabla^2 - \mu_0 I$ on C, with L-periodicity conditions, ϕ_0 the associated eigenfunction with minimal value $\underline{\phi_0}$ and

$$\delta_{1,0} := \frac{\lambda_{1,0}^2 \underline{\phi_0}}{(1 + \underline{\phi_0})^2} \text{ and } \delta_{2,0} := \frac{\lambda_{1,0}^2}{4}.$$

We have the following proposition:

Proposition 3.1 *Assume that $\mu(x) = \mu_0(x) + \mu^-$, with $\mu^- > \lambda_{1,0}$. Let δ_1 and δ_2 be defined by (2.19). Then we have $\delta_2 - \delta_1 = \left(1 - \dfrac{\mu^-}{\lambda_{1,0}}\right)^2 (\delta_{2,0} - \delta_{1,0})$.*

This result also indicates that the information on δ^* is all the more precise as the growth rate function takes low values. However, the "relative thickness" of the interval (δ_1, δ_2), compared to δ_1, $\dfrac{\delta_2 - \delta_1}{\delta_1}$, does not depend on μ^-, as it can be easily noticed.

Proof of Proposition 3.1: The relation $\lambda_1[\mu(x)] = \lambda_{1,0} - \mu^-$ is a direct consequence of the uniqueness of the first eigenvalue λ_1. We assume that $\mu^- > \lambda_{1,0}$, so that $\lambda_1[\mu(x)] < 0$. From the uniqueness of the eigenfunction ϕ associated to λ_1, ϕ does not depend on μ^-. Therefore, δ_1 and δ_2 satisfy $\delta_1 = \dfrac{(\lambda_{1,0} - \mu^-)^2 \underline{\phi_0}}{(1 + \underline{\phi_0})^2}$ and $\delta_2 = \dfrac{(\lambda_{1,0} - \mu^-)^2}{4}$. The result immediately follows. $\square$

4 A few comments on the proportional harvesting model

In this model, the population density u is governed by the equation

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - q(x)u, \ x \in \Omega, \qquad (4.37)$$

with L-periodicity of the functions $\mu(x)$, $\nu(x)$ and $q(x)$ in the periodic case, and with Neumann or Dirichlet boundary conditions in the bounded case. Setting

$$\tau(x) := \mu(x) - q(x),$$

this model becomes equivalent to the SKT-model (1.3). Hence, many properties of the solutions of this model are described in the existing literature.

In particular the existence, nonexistence and uniqueness results of Theorems 2.2 and 2.4 apply. The condition $\lambda_1[\mu(x) - q(x)] < 0$ is therefore necessary and sufficient for species persistence. Furthermore, the theoretical results of [8], [12], [33], [34] on the effects of habitat arrangement on species persistence are also true for this model.

For instance, when the function $\mu(x)$ is constant, with $\mu(x) \equiv \mu_1 > 0$, and if the domain Ω is convex and symmetric with respect to each axis $\{x_1 = 0\}, ..., \{x_N = 0\}$, the next result is a straightforward consequence of the paper [8],

Theorem 4.1 *(i) In the periodic case, $\lambda_1[\mu_1 - q_k^*(x)] \leq \lambda_1[\mu_1 - q(x)]$.*

(ii) In the bounded Dirichlet case, $\lambda_1[\mu_1 - q_k^*(x)] \leq \lambda_1[\mu_1 - q(x)]$,

(iii) In the bounded Neumann case, if Ω is a rectangle, $\lambda_1[\mu_1 - q_k^\sharp(x)] \leq \lambda_1[\mu_1 - q(x)]$.

Here q_k^* denotes the symmetric decreasing Steiner rearrangement of the function q with respect to the variable x_k, and $q_k^\sharp$ denotes the monotone rearrangement of q with respect to x_k (see [8] and [10] for the definition of these rearrangements). These rearrangements of a function q not only preserve its mean value, but also its distribution function. This means that if, for instance, q corresponds to a "patch" function taking the values q_1, q_2 and q_3 in some regions A_1, A_2 and A_3 respectively, with $A_1 + A_2 + A_3 = |C|$, then the areas of the regions where the rearranged functions q^* and $q^\sharp$ take the values q_1, q_2 and q_3 remain equal to A_1, A_2 and A_3 respectively.

Theorem 4.1, combined with Theorem 2.4 say that the spatially rearranged harvesting strategies are better for species survival. This result can be helpful from a resource management point of view. Indeed, the authorities can rearrange the position of the harvested areas in order to improve the chances of population persistence. The result of Theorem 4.1 shows that, in the framework of these models, the creation of a large reserve gives persistence more chances than the creation of several small reserves, and is in accordance with the former results of [23] and [26] in the Dirichlet case. See Fig. 5 for some illustrations in the bounded case with Dirichlet and Neumann boundary conditions.

5   Discussion

We have proposed a model for the study of populations in heterogeneous environments, for populations submitted to an external negative forcing term.
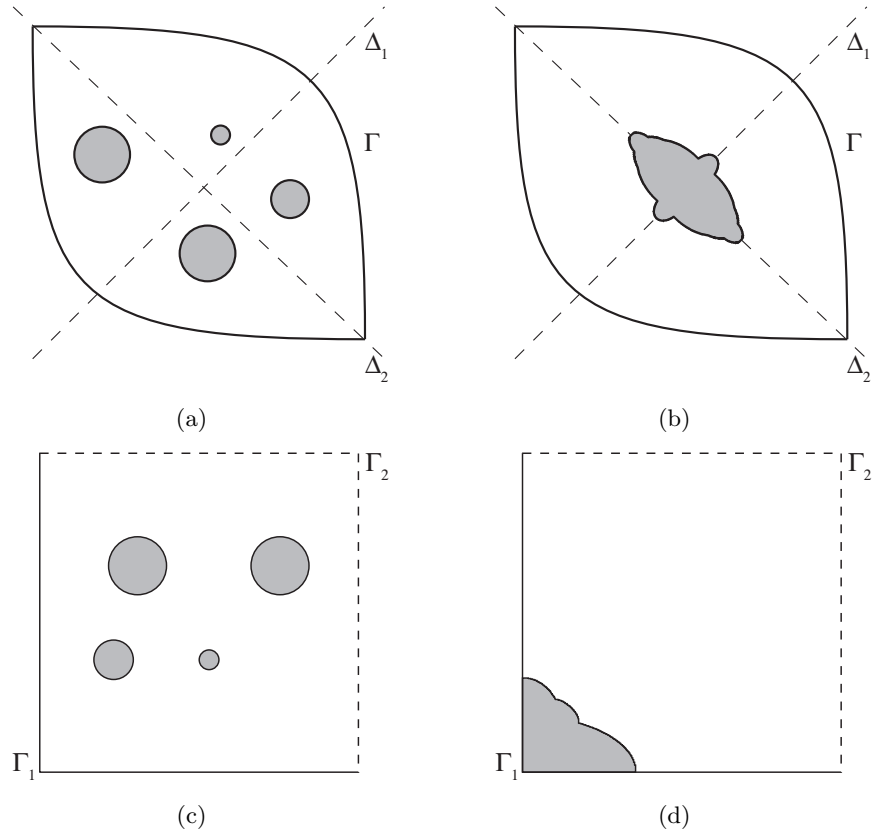
Figure 5: Examples of applications of Theorem 4.1, Parts (ii) and (iii) to reserves management. In the figures (a) and (b), the boundary Γ of Ω is lethal (Dirichlet boundary conditions). (a): The initial effort function $q(x)$ takes two values, $q^+ > 0$ in the white area and $q^- = 0$ in the shadowed regions, which correspond to reserves. (b): Position of the reserves after a symmetric decreasing Steiner rearrangement along the Δ_1 and Δ_2 axes, successively. The rearranged configuration (b) always give more chances of species persistence. In the figures (c) and (d), the boundary Γ is divided into two parts: $\Gamma = \Gamma_1 \cup \Gamma_2$. Γ_1 is represented with a solid line and can correspond to a coast, while Γ_2 is represented with a dashed line, and can correspond to a non-physical limit that the species cannot cross (Neumann boundary conditions). (c): The effort function $q(x)$ again takes two values, $q^+ > 0$ in the white area and $q^- = 0$ in the reserves. (d): Position of the reserves after monotone rearrangement along the horizontal and vertical axes, successively. The chances of persistence are better in the rearranged configuration (d).

This forcing term could be regarded as a "quasi-constant-yield" harvesting, depending only on the population density u when u is below a certain small threshold ε. The introduction of such a threshold ε was necessary for ensuring the nonnegativity of the solutions of our model, and therefore its actuality.

We carried out new mathematical results on the elliptic equation satisfied by the stationary states of the model, and on the associated parabolic equation. Both qualitative and quantitative results were obtained.

From the qualitative point of view, we described the behavior of the model solutions in terms of the harvesting amplitude δ. Two main types of stationary solutions were found: the remnant solutions, always below a small threshold ε_0 and therefore close to 0, and the significant solutions, always above this threshold, thus ensuring a time-constant yield. We discussed the maximum number of significant stationary solutions, which we found equal to 2, under an hypothesis of positivity of the second eigenvalue λ_2 of a linear operator. We further investigated the long-time behavior of the solution of our model, starting from a non-harvested population at equilibrium. We found a critical value δ^* of the harvesting term amplitude, below which the population density tends over time to a significant stationary solution, and above which it converges to a stationary solution which is not significant. We also established quantitative formulae for some lower and upper bounds for δ^*: δ_1 and δ_2 respectively. The threshold δ_2 has the additional property that, whenever the amplitude δ is above δ_2, the population density decreases to a remnant stationary solution.

The quantitative aspects of our study mainly consisted in discussing the effect of environmental fragmentation on these thresholds δ_1 and δ_2, and therefore on the interactions between environmental fragmentation and maximum sustainable yield. Namely, when computing the values of δ_1 and δ_2 on 2000 samples of stochastically obtained patchy environments, with different levels of fragmentation, we found an increasing relationship between these two coefficients and an environmental aggregation index s. This indicates that, for given areas of favorable and unfavorable regions, the harvesting quota that a species can sustain, while ensuring and time-constant yield, is higher when the favorable regions are aggregated.

The reader may note that, in our model, the species mobility was not affected by the environmental heterogeneity. Such a dependence could be modelled by using a more general dispersion term, of the form $\nabla \cdot (A(x)\nabla u)$, instead of $D\nabla^2 u$, where $A(x)$ stands for the diffusion matrix (see [8], [36]). In fact, most of our results still work when the matrix A is of class $C^{1,\alpha}$ (with $\alpha > 0$) and uniformly elliptic; i.e. when it exists $\tau > 0$ such that

$A(x) \geq \tau I_N$ for all $x \in \Omega$. Indeed, Theorems 2.2, 2.4, 2.7, 2.10, 2.11 remain true under this more general assumption. However, the effects of environmental heterogeneity may differ, depending on the way $A(x)$ and $\mu(x)$ are correlated (see [21]). In the proportional harvesting case, the results of § 4 on the effects of the arrangements of the harvested regions may also not be valid with this dispersion term. However, in situations where $A(x)$ takes low values (slow motion) when $q(x)$ is low ("reserves", see § 4), as underlined in [33], a simultaneous rearrangement of the functions $A(x)$ and $q(x)$ would lead to lower λ_1 values and therefore to higher chances of species survival.

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