

Mathematical Models and Methods in Applied Sciences
© World Scientific Publishing Company

**STEADY STATE CONCENTRATION FOR A PHENOTYPIC
STRUCTURED PROBLEM MODELLING THE EVOLUTIONARY
EPIDEMIOLOGY OF SPORE PRODUCING PATHOGENS**

RAMSES DJIDJOU-DEMASSE

*Institut National de la Recherche Agronomique, UMR 1065,
F-33882 Villenave d'Ornon, France
ramses.djidjou-demasse@inra.fr **

ARNAUD DUCROT

*Université de Bordeaux, IMB, UMR CNRS 5251,
F-33076 Bordeaux, France
arnaud.ducrot@u-bordeaux.fr*

FRÉDÉRIC FABRE

*Institut National de la Recherche Agronomique, UMR 1065,
F-33882 Villenave d'Ornon, France
frederic.fabre@inra.fr*

Received (Day Month Year)
Revised (Day Month Year)
Communicated by (xxxxxxxxxx)

In this paper, we construct a model to describe the evolutionary epidemiology of spore producing asexual plant pathogens in a homogeneous host population. By considering the evolution in the space of the pathogen phenotypic values, we derive an integro-differential equation with nonlocal mutation terms. Our first main result is concerned with the existence and uniqueness of the endemic steady state of the model. Next assuming that the mutation kernel depends on a small parameter $\varepsilon > 0$ (the variance of the dispersion into the space of the pathogen phenotypic values), we investigate the concentration properties of the endemic steady state in the space of phenotypic values. In the context of this work, several Evolutionary Attractors (as defined in classical adaptive dynamics) may exist. However, in rather general situations, our results show that only one Evolutionary Attractor persists when the populations are at equilibrium and when ε is small enough. Our analysis strongly relies on a refined description of the spectral properties of some integral operator with a highly concentrated kernel. We conclude the paper by presenting some numerical simulations of the model to illustrate this concentration phenomenon.

Keywords: Evolutionary epidemiology; Spore producing pathogens; Population dynamics; Concentration phenomenon.

AMS Subject Classification: 92D15, 92D25

*ddramses@gmail.com

2 *R. Djidjou-Demasse et al.*

1. Introduction

The objective of this paper is to analyse the concentration property, in the space of phenotypic values, of the steady state solutions of an integro-differential model representing the evolutionary epidemiology of spore producing plant pathogens, typically fungal leaf pathogen. Fungi are the most frequent agents of plant disease in natural ecosystems and major causal agents of crop damage³⁷.

The inspiration of the current model was motivated by the emergence, during the last decade, of a trend in mathematical epidemiology aiming to integrate in the same modelling framework previously separate approaches dedicated, on one side, to model epidemic and, on the other side, to model evolution⁽³⁵⁾. This approach was first proposed by Day and Proulx in⁵ and re-explained in different contexts by Day and Gandon in⁴. Essentially, this analytical framework is inspired by quantitative genetics. It can be used to monitor the simultaneous dynamics of epidemics and dynamics of evolution of any pathogen life-history trait of interest. This is a major issue for public health policies but also for plant health management in agro-ecosystems. Indeed, similarly to Darwinian medicine⁽³⁵⁾, the sustainable management of plant disease has two distinct but interdependent goals : "an immediate epidemiological one of reducing the incidence, severity and frequency of disease epidemics and a longer-term evolutionary one of reducing the rate of evolution of new patho-types"⁽⁴³⁾. The longer-term evolutionary goal aims for example to preserve the efficiency of disease resistance genes used in cultivated plant varieties (cultivar).

In this work, we use a system of integro-differential equations to model both the epidemiological and the evolutionary dynamics of spore-producing pathogens in a homogeneous host population. The host population is subdivided into two compartments, Susceptible or healthy host tissue (S) and Infected tissue (i). Healthy tissue is transformed into infected tissue with the arrival and successful germination of a single fungal spore from the spore pool compartment (A). The host population does not represent individual plants, but rather leaf area densities (leaf surface area per m^2). The leaf surface is viewed as a set of individual patches corresponding to a restricted host surface area that can be colonized by a single pathogen individual¹⁸.

The model considers a continuum of different pathogen strains. It allows for example to tackle the issue of pathogen adaptation to quantitative resistance. This is important as up to now, most theoretical works deal with the adaptation of plant pathogen to qualitative resistance (see for example^{29,40,31,14,11,12,34}). On quantitatively resistant hosts, parasite exhibit a continuous distribution of their disease phenotype^(24,39): all the pathogen strains cause infection but each with its own level of quantitative pathogenicity^{23,43}. From the pathogen side, the adaptation to quantitative resistance is thus characterized by a gradual increase of the pathogenicity levels. From the host side, this process leads to a gradual erosion of the efficiency of quantitative resistance²⁴. More specifically, in the model, each pathogen strain

is characterized by its phenotypic value which affects the life-history traits of the pathogens expressed during the basic steps of the host-pathogen interaction: (i) infection efficiency (probability that a spore deposited on a receptive host surface produces a lesion), (ii) latent period (time interval between infection and the onset of sporulation), (iii) sporulation rate (amount of spore produced per lesion and per unit time) and (iv) infectious period (time from the beginning to the end of sporulation). We consider an asexually reproducing pathogen: the evolution in the space of phenotypic values is thus modeled with an integral operator with kernel m describing mutations from a pathogen strain with phenotypic value $y \in \mathbb{R}^N$ to another one with phenotypic value $x \in \mathbb{R}^N$.

The model we shall consider in this work reads as the following non-local age structured system of equations posed for $t > 0$, age since infection $a > 0$ and phenotypic value $x \in \mathbb{R}^N$, for some integer $N \geq 1$,

$$\begin{cases} \partial_t S(t) = \Lambda - \mu S(t) - S(t) \int_{\mathbb{R}^N} \beta(y) A(t, y) dy, \\ (\partial_t + \partial_a) i(t, a, x) = -\mu i(t, a, x), \\ i(t, 0, x) = \beta(x) S(t) A(t, x), \\ \partial_t A(t, x) = \int_{\mathbb{R}^N} \int_0^\infty m(x-y) r(a, y) i(t, a, y) da dy - \delta A(t, x). \end{cases} \quad (1.1)$$

Here $S(t)$, $i(t, a, x)$ and $A(t, x)$ respectively denote the density of healthy tissue, the density of infected tissue since the time $a > 0$ by the pathogen with phenotypic value $x \in \mathbb{R}^N$, and the density of airborne spores of pathogens with phenotypic value x . The parameters $\Lambda > 0$, $\mu > 0$ and $\delta > 0$ respectively represent the influx of new healthy host tissue, the death rate of the host tissue and the deposition rate of spores. The function m stands for the mutation kernel and describes the dispersion into the space of phenotypic values at each pathogen generation. The function $\beta = \beta(x)$ describes the infection efficiency of the pathogen while the age specific function $r = r(a, x)$ combines the life-history traits describing host-pathogen interaction: the sporulation rate, the latent period and the infectious period. The precise assumptions on these functions will be specified latter. Typically it takes the form

$$r(a, x) = p(x) \mathbf{1}_{[\tau(x), \tau(x)+l(x)]}(a),$$

where p , τ and l denote the strain specific sporulation rate, latent period and infectious period respectively. Here $\mathbf{1}_{[\tau(x), \tau(x)+l(x)]}$ is the indicator function such that $r(a, x) = p(x)$, if $a \in [\tau(x), \tau(x) + l(x)]$ and 0 elsewhere.

The formulation of Problem (1.1) assumed that there is no disease induced mortality of infected lesions. As it will be discussed further below, this model is particularly well adapted for the description of biotrophic host-pathogen interactions, for which the pathogens require a living host for their development. But, a more general model formulation including disease induced mortality will also be discussed in Section 3.

Model (1.1) appears, in a slightly different form, in ¹⁸ where the authors studied the evolutionary adaptation of a pathogen to quantitative resistance.

In this work we shall focus on the study of the stationary states of (1.1). We shall more specifically investigate the concentration properties in the space of phenotypic values of these stationary states when the mutation kernel m depends on a small parameter $\varepsilon > 0$ and is highly concentrated. We shall more specifically assume that it takes the form

$$m(x) = m_\varepsilon(x) := \varepsilon^{-N} m\left(\frac{x}{\varepsilon}\right), \quad \forall x \in \mathbb{R}^N. \quad (1.2)$$

Here the small parameter ε models the small variance of the dispersion into the space of phenotypic values. Note also that this does not imply that mutations are rare since they arise at each life cycle of the pathogen.

The formal limiting system with $\varepsilon = 0$ fully uncouples the different locations in the phenotypic trait space and it takes the form

$$\begin{cases} \partial_t S(t) = \Lambda - \mu S(t) - S(t) \int_{\mathbb{R}^N} \beta(y) A(t, y) dy, \\ (\partial_t + \partial_a) i(t, a, x) = -\mu i(t, a, x), \\ i(t, 0, x) = \beta(x) S(t) A(t, x), \\ \partial_t A(t, x) = \int_0^\infty r(a, x) i(t, a, x) da - \delta A(t, x). \end{cases}$$

Under specific assumptions on the model parameters, that will be provided in Assumptions 2.1 and 2.2 below, the above system of equations may admit an infinite number of endemic stationary states, in particular if the following threshold condition is satisfied

$$\mathcal{T}_0^0 := \frac{\Lambda}{\mu} \|\Psi\|_\infty > 1,$$

with

$$\Psi(x) = \frac{\beta(x)}{\delta} \int_0^\infty r(a, x) e^{-\mu a} da. \quad (1.3)$$

This function Ψ will be referred below as the fitness function. Here we will show that, under suitable conditions, when $\varepsilon > 0$, then the coupling in the phenotypic trait space is sufficiently strong to ensure the uniqueness of an endemic stationary state. Moreover, when ε is small enough, this endemic stationary state concentrates, in the trait space, on the points maximizing the fitness function Ψ . And, more deeply, we shall show that, under biologically reasonable assumptions, this concentration property selects a single trait (that will be characterized) even if the maximal fitness is achieved at several trait locations.

Let us mention that concentration properties for continuously structured models with small mutation in evolutionary dynamics have attracted a lot of interest in the last decade. Diekmann *et al.* in ⁸ introduced a Hamilton-Jacobi approach, roughly based on a suitable time rescaling argument and a change of unknown (usually called WKB ansatz), to study such concentration property in the phenotypic

values space for a resource-consumer problem. Such an approach has been fruitfully used to deeply understand the dynamical behaviour of concentration points for various problems, including non-local competition logistic equation and chemostat problem, involving small mutation parameter. We refer for instance to ^{6,27,28,32} and the references cited therein. We also refer to ² and the references therein for some results on the long time behaviour concentration for some non-local logistic like equation. Let us also mention the work of Calsina *et al.* in ³ where the authors formulate and study a selection mutation equation with a continuous phenotypic evolutionary trait and a non-local mutation operator. In this work, the authors prove a concentration property for the steady state solutions of their problem when the mutation rate is a small parameter, that is when the time scale for mutations is slower than the selection phenomena. They provide a refined description of the asymptotic profile for these steady states and show that their asymptotic profile is a Cauchy distribution. Note that the context of the aforementioned work is rather different from the one considered in this note. Indeed, as mentioned above, we do not assume a slow time scale for the mutation processes but a small variance of the dispersion into the phenotypic values space due to mutations at each life cycle of pathogens. In Gudelj *et al.* ¹⁵, the authors study the effect of small mutation on the phenotypic evolution of a pathogen population, modelled by a diffusion, coupled with the host heterogeneity. Depending on the trade-off relationship between the transmission rates on two host populations, using formal asymptotics expansions, the authors determine the maximum number of phenotypes a pathogen population can support in the long term.

In this work, our analysis of the steady states of Problem (1.1) relies on the spectral properties of the integral operator (involving the fitness function Ψ)

$$L\varphi(x) = \int_{\mathbb{R}^N} m(x-y)\Psi(y)\varphi(y)dy, \quad (1.4)$$

and a refined analysis of its counterpart with small parameter ε , that reads as the same operator with m replaced by m_ε . Such study follows some arguments proposed by Helffer and Sjöstrand in ¹⁷ (see also ^{21,36} and the references therein). Let us mention here that we will not assume that the mutation kernel has very fast decay at infinity. We allow fat tail's dispersion with fractional exponential decay rate restriction (see Assumption 2.4 (i) below). In that setting, one of the key point argument relies on the derivation of the fast decay estimates for the eigenvectors of some integral operator.

This manuscript is organized as follows. In Sections 2-3 we state and discuss the main results that will be obtained in this work. Section 4 is devoted to the derivation of simple conditions ensuring the existence of a principal eigenvalue for some non-local operator. Section 5 investigates preliminary spectral estimates. Section 6 is devoted to the derivation of eigenvector decay estimates. Finally Section 7 completes the proof of the main results of this work, that deal with the asymptotic expansion of some principal eigenvalue and the concentration property of the associated principal

6 *R. Djidjou-Demasse et al.*

eigenvector.

2. Main results

In this section we state the main results that will be proved in this work.

Our first main result is concerned with the existence and uniqueness of the endemic steady state of (1.1). Let us observe that $(S, i, A) \in (0, \infty) \times L^1_+((0, \infty) \times \mathbb{R}^N) \times L^1_+(\mathbb{R}^N)$ is a stationary state of (1.1) iff it satisfies

$$\begin{cases} \int_{\mathbb{R}^N} m(x-y)\Psi(y)A(y)dy = \frac{1}{S}A(x), \\ \Lambda - \mu S = S \int_{\mathbb{R}^N} \beta(y)A(y)dy \text{ and } i(a, x) = \beta(x)SA(x)e^{-\mu a}. \end{cases} \quad (2.1)$$

Hence, the term $\frac{1}{S}$ appears as an eigenvalue of the linear integral operator L given by the left hand side of the first equation of (2.1), namely defined as in (1.4) and where the fitness function Ψ is defined by (1.3).

Therefore the study of the stationary states of (1.1) strongly relies on the spectral properties of the operator L defined by (1.4).

Before stating our existence result, we shall first state the set of assumptions that will be needed to study the existence of stationary states for (1.1).

Assumption 2.1. (Fitness function) We assume that Λ , μ and δ are given positive parameters. The functions $\beta = \beta(x)$ and $r = r(a, x)$ respectively belong to $L^\infty_+(\mathbb{R}^N)$ and $L^\infty_+((0, \infty) \times \mathbb{R}^N)$. And, the function $\Psi : \mathbb{R}^N \rightarrow \mathbb{R}_+$, defined in (1.3), is assumed to be continuous on \mathbb{R}^N . It furthermore satisfies $\Psi \not\equiv 0$ and

$$\lim_{\|x\| \rightarrow \infty} \Psi(x) = 0.$$

Assumption 2.2. (Mutation kernel) The mutation kernel $m : \mathbb{R}^N \rightarrow \mathbb{R}$ satisfies

- (i) $m \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$ is non-negative, symmetric with respect to the origin, that is $m(-x) = m(x)$ a.e. in \mathbb{R}^N and it has a unit mass, that is $\int_{\mathbb{R}^N} m(x)dx = 1$.
- (ii) The function m is almost everywhere strictly positive.
- (iii) For each $R > 0$ the function $M_R : x \mapsto \sup_{\|y\| \leq R} m(x+y)$ belongs to $L^1(\mathbb{R}^N)$.

In order to state our existence result for an endemic stationary state, let us introduce further notation. We set

$$\Omega = \{x \in \mathbb{R}^N : \Psi(x) > 0\} \text{ and } \Theta(x) \equiv \Psi^{\frac{1}{2}}(x), \quad (2.2)$$

and we introduce the functional $\rho = \rho[m]$ defined by

$$\rho[m] = \sup_{\substack{\varphi \in L^2(\Omega) \\ \|\varphi\|_{L^2(\Omega)} = 1}} \iint_{\Omega \times \Omega} \Theta(x)\Theta(y)m(x-y)\varphi(x)\varphi(y)dx dy. \quad (2.3)$$

Together with this notation, the first main result reads as follows.

Theorem 2.1. *Let Assumptions 2.1 and 2.2 be satisfied. Define the number \mathcal{T}_0 by*

$$\mathcal{T}_0 = \frac{\Lambda}{\mu} \rho[m]. \quad (2.4)$$

When $\mathcal{T}_0 \leq 1$, then System (1.1) has a unique equilibrium point (S^0, i^0, A^0) defined by

$$(S^0, i^0, A^0) = \left(\frac{\Lambda}{\mu}, 0, 0 \right).$$

When $\mathcal{T}_0 > 1$, then System (1.1) has two different equilibrium points (S^0, i^0, A^0) defined as above and (S^, i^*, A^*) , where the components satisfy*

$$0 < S^* < S^0, \quad A^* \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N) \text{ with } A^* > 0 \text{ a.e.,}$$

$$\text{and } i^*(a, x) = \beta(x) S^* A^*(x) e^{-\mu a}.$$

As mentioned above, the proof of Theorem 2.1 is strongly relies on the spectral properties of the operator L . The set of assumptions stated above will, in particular, ensure the existence of a principal eigenpair for the operator L . In view of the definition of the threshold \mathcal{T}_0 and System (2.1), we shall also prove that the quantity $\rho[m]$ corresponds to the principal eigenvalue of the operator L .

We now assume that the mutation kernel m depends upon a small parameter $0 < \varepsilon \ll 1$. It is now denoted by m_ε and takes the form of (1.2).

We aim at describing the behaviour as $\varepsilon \rightarrow 0$ of the endemic equilibrium point $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$ of System (1.1) when m is replaced by m_ε . We shall more specifically be interested in describing the concentration properties of the function A_ε^* , that arises as the principal eigenvector of the linear operator L^ε defined by

$$L^\varepsilon \varphi(x) = \int_{\mathbb{R}^N} m_\varepsilon(x-y) \Psi(y) \varphi(y) dy. \quad (2.5)$$

The behaviour, as $\varepsilon \rightarrow 0$, of the endemic steady state of System 1.1 will follow from a detailed analysis of the principal eigenpair of the above linear integral operator, as $\varepsilon \rightarrow 0$. We will first collect some results related to the principal eigenpair of operator L^ε . Note that the existence and basic properties of the principal eigenpair will be ensured by Theorem 4.1 below. Then, as a corollary, we shall describe the behaviour of the endemic equilibrium of System (1.1) as $\varepsilon \rightarrow 0$.

To perform our analysis we shall need to impose more assumptions than the ones stated in Assumptions 2.1 and 2.2. In addition to these assumptions, we assume that

Assumption 2.3. In addition to Assumption 2.1, we assume that

- (i) The function $\Theta = \Psi^{\frac{1}{2}}$ is of the class C^∞ on \mathbb{R}^N .
- (ii) There exists a finite number of points $\{x_1^0, \dots, x_M^0\} \subset \mathbb{R}^N$ such that

$$\{x \in \mathbb{R}^N : \Psi(x) = \|\Psi\|_\infty\} = \{x_1^0, \dots, x_M^0\},$$

and for all $k = 1, \dots, M$, the Hessian matrix $-D^2\Theta(x_k^0)$ is positive definite.

8 *R. Djidjou-Demasse et al.*

Assumption 2.4. In addition to Assumption 2.2, the kernel function m arising in (1.2) satisfies the following properties:

(i) There exist some constants $M_0 > 0$, $\eta_0 > 0$ and $\gamma_0 \in (0, 1)$ such that

$$m(x) \leq M_0 \exp(-\eta_0 \|x\|^{\gamma_0}), \text{ a.e. } x \in \mathbb{R}^N.$$

(ii) The covariance matrix $\Sigma[m]$ of the probability measure $m(x)dx$ is positive definite. Here recall that $\Sigma[m] = (\Sigma_{i,j})_{i,j=1,\dots,N}$ is defined by

$$\Sigma_{i,j} = \int_{\mathbb{R}^N} y_i y_j m(y) dy, \quad i, j = 1, \dots, N.$$

Let us observe that Assumption 2.4 (i) implies in particular that Assumption 2.2 (iii) is satisfied. Moreover this assumption means that the dispersion decays rather fast at infinity but without being a thin tail kernel. This assumption allows a class of fat tail dispersal kernel. As a consequence, the Fourier transform of the kernel m cannot be analytically extended on a complex strip around the real axis, namely of the form $\{z \in \mathbb{C} : |\Im(z)| \leq \nu\}$ for some positive ν . This prevents us from using the methodology developed in ^{30,22,36} to derive Agmon type decay of the eigenvectors.

As discussed above we are concerned with properties of the principal eigenpair (see Theorem 4.1 below) of the operator L^ε for small $0 < \varepsilon \ll 1$, that is of the solution of the problem

$$L^\varepsilon \psi^\varepsilon(x) = \lambda^\varepsilon \psi^\varepsilon(x) \text{ with } \psi^\varepsilon \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N) \text{ and } \psi^\varepsilon > 0 \text{ a.e.} \quad (2.6)$$

Now we shall observe that, due to Assumption 2.4, one may reduce (and simplify) our next statements and computations to the case where the covariance matrix of the mutation kernel reads as $2I_N$, where I_N denotes the $N \times N$ -identity matrix. Indeed if $(\lambda^\varepsilon, \psi^\varepsilon)$ denotes a solution of (2.6), then the pair $(\rho^\varepsilon, \varphi^\varepsilon)$, with

$$\rho^\varepsilon = \frac{1}{\|\Psi\|_\infty} \lambda^\varepsilon \text{ and } \varphi^\varepsilon(x) = \psi^\varepsilon \left(\frac{\sqrt{2}}{2} \Sigma[m]^{\frac{1}{2}} x \right),$$

becomes a solution of the following linear problem

$$\begin{cases} \frac{1}{\varepsilon^N} \int_{\mathbb{R}^N} \widehat{m} \left(\frac{x-y}{\varepsilon} \right) \widehat{\Psi}(y) \varphi^\varepsilon(y) dy = \rho^\varepsilon \varphi^\varepsilon(x), \text{ a.e. } x \in \mathbb{R}^N, \\ \varphi^\varepsilon \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N) \text{ and } \varphi^\varepsilon > 0 \text{ a.e.} \end{cases}$$

Here, setting $\Sigma = \Sigma[m]$ for notational simplicity, we have set

$$\widehat{m}(x) = 2^{-\frac{N}{2}} \sqrt{\det(\Sigma)} m \left(\frac{\sqrt{2}}{2} \Sigma^{\frac{1}{2}} x \right) \text{ and } \widehat{\Psi}(x) = \frac{1}{\|\Psi\|_\infty} \Psi \left(\frac{\sqrt{2}}{2} \Sigma^{-\frac{1}{2}} x \right). \quad (2.7)$$

Therefore the pair $(\rho^\varepsilon, \varphi^\varepsilon)$ corresponds to a principal eigenpair of the operator L^ε with m and Ψ respectively replaced by \widehat{m} and $\widehat{\Psi}$.

Observe furthermore that \widehat{m} satisfies all the conditions stated in Assumptions 2.2 and 2.4 with $\Sigma[\widehat{m}] = 2I_N$ while the function $\widehat{\Psi}$ satisfies the conditions described

in Assumptions 2.1 and 2.3 together with $\|\widehat{\Psi}\|_\infty = 1$. In addition the set of points $\{x_j^0 : j = 1, \dots, M\}$ becomes

$$\{\widehat{x}_j^0 : j = 1, \dots, M\} = \{\widehat{\Psi} = 1\} \text{ with } \widehat{x}_j^0 = \sqrt{2\Sigma}^{\frac{1}{2}} x_j^0, j = 1, \dots, M. \quad (2.8)$$

Our first result is concerned with the asymptotic expansion, as an asymptotic series, of the principal eigenvalue λ^ε as $\varepsilon \rightarrow 0$. In order to state our result, we need to introduce further notation. Define for each $j = 1, \dots, M$ the (Hessian) matrix A_j by

$$A_j = -D^2\widehat{\Theta}(\widehat{x}_j^0) \text{ with } \widehat{\Theta}(x) = \widehat{\Psi}(x)^{\frac{1}{2}}. \quad (2.9)$$

Also denote by P_j , for $j = 1, \dots, M$, the elliptic operator defined by

$$P_j := -\Delta + \left\| A_j^{\frac{1}{2}} x \right\|^2, \quad (2.10)$$

and we define, for any $j = 1, \dots, M$, the function $\varphi_{0,j}$ by

$$\varphi_{0,j}(x) = (2\pi)^{-\frac{N}{2}} \sqrt{\det(A_j^{\frac{1}{2}})} \exp\left(-\frac{\|A_j^{\frac{1}{2}} x\|^2}{2}\right). \quad (2.11)$$

Observe that $\|\varphi_{0,j}\|_{L^2(\mathbb{R}^N)} = 1$ and $P_j \varphi_{0,j} = \text{tr}\left(A_j^{\frac{1}{2}}\right) \varphi_{0,j}$ for all $j = 1, \dots, M$.

In addition to these notation and definitions, one defines, for any $j = 1, \dots, M$, the sequences $\{\varphi_{k,j}\}_{k \geq 0} \subset L^2(\mathbb{R}^N)$ and $\{\lambda_{k,j}\}_{k \geq 0} \subset \mathbb{R}$ by the following recurrence relation:

$$\varphi_{0,j} \text{ is defined in (2.11) and } \lambda_{0,j} = -\text{tr}\left(A_j^{\frac{1}{2}}\right),$$

and for $k \geq 1$

$$\varphi_{k,j} \perp \varphi_{0,j} \text{ and } (P_j + \lambda_{0,j}) \varphi_{k,j} = -\sum_{p=0}^{k-1} \lambda_{k-p,j} \varphi_{p,j} + \sum_{p=0}^{k-1} \mathcal{D}_{j,k-p} \varphi_{p,j}. \quad (2.12)$$

Here the symbol \perp is used to refer to orthogonality with respect to the usual $L^2(\mathbb{R}^N)$ -inner product while the symbols $\mathcal{D}_{j,p} \in \mathbb{R}[x, \partial_x]$ denote, for any $j = 1, \dots, M$ and $p \geq 1$, a differential operator that will be specified in (5.9) below. However, at this stage, let us mention that these operators take the form

$$\mathcal{D}_{j,p} = \sum_{(\alpha,\beta,\gamma) \in \mathcal{I}_p} a_j^{(\alpha,\beta,\gamma)} x^\alpha \partial^\gamma + \sum_{(\alpha,\beta) \in \mathcal{J}_p} b_j^{(\alpha,\beta)} x^\alpha, \quad (2.13)$$

wherein the different coefficients can be expressed in terms of the derivatives of $\widehat{\Theta}$ at \widehat{x}_j^0 as well as different moments of the kernel \widehat{m} . The sets of summation index, \mathcal{I}_p and \mathcal{J}_p , depend on p but are independent of the point j . It is easy to see, using Fredholm solvability condition, that the above defined sequence is uniquely determined.

Using the sequences $\{\lambda_{k,j}\}_{k \geq 0}$ for $j = 1, \dots, M$, we shall define an order relation on the set $\{1, \dots, M\}$. For that purpose, let us recall that the set of real sequences

10 *R. Djidjou-Demasse et al.*

$\mathbb{R}^{\mathbb{N}}$ can be endowed by the usual (total) lexicographical order, denoted by \preceq , and defined as follows: for any pair of sequences $\{a_n\}_{n \geq 0}$ and $\{b_n\}_{n \geq 0}$ one has

$$\{a_n\}_{n \geq 0} \preceq \{b_n\}_{n \geq 0} \Leftrightarrow \begin{cases} \text{either } a_0 < b_0, \\ \text{either } \exists k \geq 0, a_p = b_p \forall p = 0, \dots, k \text{ and } a_{k+1} < b_{k+1}, \\ \text{or } a_p = b_p, \forall p \geq 0. \end{cases}$$

This total order for real sequences allows us to define the following total order \leq on the set $\{1, \dots, M\}$ as follows: for any $i, j \in \{1, \dots, M\}$ one has

$$i \leq j \Leftrightarrow \{\lambda_{k,i}\}_{k \geq 0} \preceq \{\lambda_{k,j}\}_{k \geq 0}. \quad (2.14)$$

Consider the set $\mathcal{M} \subset \{1, \dots, M\}$ defined by

$$\mathcal{M} = \max(\{1, \dots, M\}, \leq). \quad (2.15)$$

Observe that $\mathcal{M} \neq \emptyset$ since $\{1, \dots, M\}$ is finite and \mathcal{M} is not necessarily reduced to a single point. However, let us observe that if $i \neq j$ belongs to \mathcal{M} then $\lambda_{k,i} = \lambda_{k,j}$ for all $k \geq 0$.

We are now able to state our next main result that is concerned with the asymptotic expansion of the principal eigenvalue of the operator L^ε . Our precise result reads as follows.

Theorem 2.2. *Let Assumptions 2.1, 2.2, 2.3 and 2.4 be satisfied. Let λ^ε denote the principal eigenvalue of operator L^ε . Then λ^ε admits the following asymptotic series expansion as $\varepsilon \rightarrow 0$, for any $j \in \mathcal{M}$,*

$$\lambda^\varepsilon \sim \|\Psi\|_\infty \left(1 + \sum_{k=0}^{\infty} \varepsilon^{1+k} \lambda_{2k,j} \right), \quad (2.16)$$

in the sense that, for any $p \geq 0$ one has

$$\frac{1}{\|\Psi\|_\infty} \lambda^\varepsilon = 1 + \sum_{k=0}^p \varepsilon^{1+k} \lambda_{2k,j} + O(\varepsilon^{p+2}) \text{ as } \varepsilon \rightarrow 0.$$

Our next result is concerned with a concentration property of the principal eigenvector ψ^ε of L^ε as defined in (2.6). Our result reads as follows.

Theorem 2.3. *Let Assumptions 2.1, 2.2, 2.3 and 2.4 be satisfied. Let us assume that $\mathcal{M} = \{i\}$. Consider the principal eigenvector ψ^ε of L^ε normalized so that $\|\psi^\varepsilon\|_{L^1(\mathbb{R}^N)} = 1$. Then, for each $\nu \in (0, \gamma_0)$, there exists $\eta > 0$ such that the following concentration property holds true:*

$$\int_{\mathbb{R}^N \setminus B(x_i^0, \varepsilon^\nu)} \psi^\varepsilon(x) dx = O(\exp(-\eta \varepsilon^{\nu-\gamma_0})) \text{ as } \varepsilon \rightarrow 0.$$

In particular, one gets $\psi^\varepsilon \rightarrow \delta_{x_i^0}$ as $\varepsilon \rightarrow 0$ for the narrow topology. This means that for any continuous function $f \in C(\mathbb{R}^N)$ one has

$$\lim_{\varepsilon \rightarrow 0} \int_{\mathbb{R}^N} f(x) \psi^\varepsilon(x) dx = \int_{\mathbb{R}^N} f(x) \delta_{x_i^0}(dx) = f(x_i^0).$$

We are now able to come back to the study of the stationary states of System (1.1) with $m = m_\varepsilon$ given by (1.2). In that setting, the threshold quantity \mathcal{T}_0 depends upon the small parameter ε . In order to emphasize such a dependence, we shall denote it by $\mathcal{T}_0^\varepsilon$. Now recall that, according to Theorem 2.1, if $\mathcal{T}_0^\varepsilon > 1$ then System (1.1) has a unique endemic equilibrium point, denoted by $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$. Then the above theorems, namely Theorem 2.2 and Theorem 2.3, can be applied to obtain the following information on the asymptotic shape of the endemic stationary state of Problem (1.1) as $\varepsilon \rightarrow 0$.

Corollary 2.1. *Let Assumptions 2.1, 2.2, 2.3 and 2.4 be satisfied. Then the threshold $\mathcal{T}_0^\varepsilon$ satisfies*

$$\lim_{\varepsilon \rightarrow 0} \mathcal{T}_0^\varepsilon = \mathcal{T}_0^0 := \frac{\Lambda}{\mu} \|\Psi\|_\infty.$$

We furthermore assume that $\mathcal{T}_0^0 > 1$ and that the function β is continuous on \mathbb{R}^N . If $\mathcal{M} = \{i\}$ then the endemic steady state $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$, that is well defined for any $\varepsilon > 0$ small enough, satisfies the following asymptotic behaviour as $\varepsilon \rightarrow 0$:

$$\lim_{\varepsilon \rightarrow 0} S_\varepsilon^* = \frac{1}{\|\Psi\|_\infty},$$

and for any continuous function $f \in \mathcal{C}(\mathbb{R}^N)$, we also have

$$\lim_{\varepsilon \rightarrow 0} \int_{\mathbb{R}^N} f(x) A_\varepsilon^*(x) dx = \frac{\mathcal{T}_0^0 - 1}{\mu \beta(x_i^0)} f(x_i^0),$$

and

$$\lim_{\varepsilon \rightarrow 0} \int_{\mathbb{R}^N} f(x) i_\varepsilon^*(a, x) dx = \frac{\mathcal{T}_0^0 - 1}{\mu} f(x_i^0) e^{-\mu a} \text{ in } L^1(0, \infty) \cap L^\infty(0, \infty).$$

Remark 2.1. Assume that the trait is one-dimensional, namely $N = 1$ and that the fitness function Ψ is symmetric. If $\mathcal{M} = \{i, j\}$ with $i \neq j$ then, since the principal eigenvector is also symmetric, the endemic stationary state (equally) concentrates on these two points and this yields a dimorphic steady state.

In order to comment the above let us assume that $N = 1$. In that case it is easy to check that $i, j \in \mathcal{M}$ if and only if

$$\Theta^{(n)}(x_j^0) = \Theta^{(n)}(x_i^0), \quad \forall n \in \mathbb{N}.$$

From a biological point of view, if $\mathcal{M} = \{i\}$; then in that case, when the dispersal in the phenotypic trait space is small, namely $\varepsilon \ll 1$, the unique (endemic) steady state of (1.1) concentrates on a single trait, i.e. the equilibrium population is basically monomorphic.

3. Discussion

In this section, we first introduce the notion of singular strategies and discuss some numerical simulations of the model. These simulations illustrate how to use the model to monitor the evolutionary epidemiology of spore producing plant pathogens as introduced in ^{4,5}. We also discuss (i) the link between the pathogen fitness function Ψ and the well known basic reproduction number \mathcal{R}_0 in the context of epidemiology and (ii) how the model can encompassed the major trophic modes encountered in fungal parasitism. Throughout this discussion we consider the term strategy to be a synonym for phenotypic value.

Singular strategies. In order to introduce some vocabulary from the adaptive dynamics literature, we shall consider a slightly simplified version of System (1.1). Here we omit the age structure and we assume that the evolution of the density of airborne spores is a fast process. In that context we re-write (1.1) as follows

$$\begin{cases} \partial_t S_\varepsilon(t) = \Lambda - \mu S_\varepsilon(t) - S_\varepsilon(t) \int_{\mathbb{R}^N} \beta(y) A_\varepsilon(t, y) dy, \\ \partial_t I_\varepsilon(t, x) = \beta(x) S_\varepsilon(t) A_\varepsilon(t, x) - \left(\mu + \frac{1}{l(x)} \right) I_\varepsilon(t, x), \\ A_\varepsilon(t, x) = \frac{1}{\delta} \int_{\mathbb{R}^N} m_\varepsilon(x - y) p(y) I_\varepsilon(t, y) dy. \end{cases} \quad (3.1)$$

Here we take into account the (strain-specific) duration of the sporulation period, denoted by $l(x)$, while $p(x)$ denotes the (strain-specific) sporulation rate.

For the above model the fitness function Ψ takes the form

$$\Psi(x) = \frac{\beta(x)p(x)}{\delta(\mu + 1/l(x))},$$

and, the results presented in the previous section for (1.1) also hold true for the above slightly different system of equations.

Here we assume that $N = 1$ (i.e. $x \in \mathbb{R}$). Then it follows from classical adaptive dynamics ^{8,13,25} that the growth rate of a rare mutant strategy, y , in the resident x -population is given by the so-called *invasion exponent* defined by $f_x(y) := \left(\mu + \frac{1}{l(y)} \right) (S_x \Psi(y) - 1)$. Herein S_x denotes the stationary solution of (3.1) when $\varepsilon \rightarrow 0$ and the pathogen population is assumed to be monomorphic (see (3.2) below). To see this, note that formally taking the limit $\varepsilon \rightarrow 0$ into (3.1), this system becomes

$$\begin{cases} \partial_t S(t) = \Lambda - \mu S(t) - \frac{S(t)}{\delta} \int_{\mathbb{R}} \beta(y) p(y) I(t, y) dy, \\ \partial_t I(t, x) = \left(\mu + \frac{1}{l(x)} \right) [S(t) \Psi(x) - 1] I(t, x), \end{cases}$$

so that with a monomorphic pathogen population, $I(t, x) = I(t) \delta_x$, the previous

system further simplifies and yields

$$\begin{cases} \partial_t S(t) = \Lambda - \mu S(t) - \frac{\beta(x)p(x)}{\delta} S(t)I(t), \\ \partial_t I(t) = \left(\mu + \frac{1}{l(x)} \right) [S(t)\Psi(x) - 1] I(t). \end{cases} \quad (3.2)$$

Hence the invasion of mutant strategy y into a resident x -population is given by the following linearized equation with growth rate $f_x(y)$:

$$\partial_t I_y(t) = f_x(y)I_y(t).$$

Now the evolution of a trait x is then governed by the selection gradient defined by

$$D(x) := \left. \frac{\partial f_x}{\partial y} \right|_{y=x} = \left(\mu + \frac{1}{l(x)} \right) S_x \Psi'(x).$$

Equilibrium points of the adaptive dynamics (also called singular strategies) are solutions of $D(x^*) = 0$. The classification of singular points involves second order derivatives of the invasion exponent $f_x(y)$ by computing the following coefficients (see ^{8,10,13,25} and references therein):

$$c_{22} := \frac{\partial^2}{\partial y^2} f_{x^*}(x^*); \quad c_{12} = c_{21} := \frac{\partial^2}{\partial x \partial y} f_{x^*}(x^*) \text{ and } c_{11} := -(c_{22} + 2c_{12}).$$

According to ^{13,25}, a singular point x^* is called *Evolutionary Stable Strategy* (ESS) if $c_{22} < 0$ and *Convergent Stable Strategy* (CSS) if $c_{12} + c_{22} < 0$. *Evolutionary Attractor* (EA) is then a strategy that is both ESS and CSS.

Coming back to (3.1), singular points are the solutions of $D(x) = 0$, that is $S_x \Psi'(x) = 0$. Hence the singular points are critical points of the fitness function Ψ .

Now recalling the non-degeneracy hypothesis in Assumption 2.3, the points – globally – maximizing the fitness function Ψ are then EA, so that the set of global maximum points of the fitness function Ψ is contained in the EA-set. Indeed, note that we have $c_{22} = (\mu + l(x^*)^{-1}) S_{x^*} \Psi''(x^*) < 0$ and, since $S_x = \Psi(x)^{-1}$, $c_{12} = [l'(x^*)\Psi(x^*)l(x^*)^{-2} - (\mu + l(x^*)^{-1}) \Psi'(x^*)] \Psi(x^*)^{-2} \Psi'(x^*) = 0$, for any points x^* such that $\Psi(x^*) = \|\Psi\|_\infty$.

In the context of this work, several evolutionary attractors (as defined above) may exist. However, in rather general situations, our results show that only one EA persists (at least at equilibrium) when ε is small enough. This persistence property is described by using the set \mathcal{M} (see (2.15)). For this reason, the points in \mathcal{M} will be referred throughout this discussion as *Globally Stable Evolutionary Attractor* (GSEA for short).

Basic reproduction number. The basic reproduction number (usually denoted by \mathcal{R}_0) is one of the most important concepts in epidemiology, ^{9,42}. When there are no 'interactions' in the phenotypic space of pathogens (i.e. without mutations in Model (1.1): $\varepsilon = 0$) and using the next generation operator approach as in

^{7,19} we find the basic reproduction number. More specifically, the basic reproduction number $\mathcal{R}_0(x)$ of the pathogen strain with phenotypic value x is related to the fitness function $\Psi(x)$ given in (1.3) as follows

$$\mathcal{R}_0(x) := \frac{\Lambda}{\mu} \Psi(x) = \frac{\Lambda}{\mu} \times \frac{\beta(x)p(x)e^{-\mu\tau(x)}}{\delta\mu} \left[1 - e^{-\mu l(x)} \right].$$

The above expression of $\mathcal{R}_0(x)$ aggregates all the quantitative traits of pathogenicity of the disease cycle: infection efficiency ($\beta(x)$), latent period ($\tau(x)$), sporulation rate ($p(x)$) and infectious period ($l(x)$). It is a useful function combining these basic life-history traits into a single fitness metric ^{41,26}. In particular \mathcal{R}_0 can be used to measure and compare the fitness of pathogens with different quantitative traits, especially with different latent period. This is an important point in the context of agricultural system as pointed in ²³. Generally, by assuming that there is only one pathogen strain x^* which maximizes \mathcal{R}_0 , it's well known that x^* will be the strongest (or dominant) strain. We refer for example to ⁷ and references therein. However, the situation becomes more complicated to characterise the strongest strain when at least two pathogen strains maximize \mathcal{R}_0 . By taking into account the mutation in the space of the pathogen strains, the results obtained in this note allow us to do so. Roughly speaking, by introducing a mutation kernel describing the dispersion into the space of phenotypic values of pathogens, we provide a characterization of the dominant strain even in the case of multiple strains maximizing \mathcal{R}_0 . To end this paragraph, we emphasize that the decay of the mutation kernel considered here (namely Assumption 2.4 (i)) allows us to also consider some class of fat-tailed mutation kernel. This assumption is interesting in biological context where mutant offsprings can be significantly different from their progenitors at the first mutation generation. See for example ²⁰, where this point is also discussed.

Description of the model numerical simulation. Let us consider a field where a pathogen population has become monomorphic (concentrated around the phenotypic value x_0) because, for example, a single plant cultivar has been sown for a very long time. The simulations will describe the epidemiological and evolutionary dynamics following the deployment of a new plant cultivar in that field at time $t = 0$. Typically, this new cultivar is bearing a quantitative resistance. The function Ψ describes the fitness of the pathogen population on the cultivar considered. We set $\Psi := \pi G(x_1, \sigma_1) + (1 - \pi)G(x_2, \sigma_2)$ where $G(x_j, \sigma_j)$ states for the Gaussian function with expected value x_j , with variance σ_j^2 and $\pi \in (0, 1)$. This implies that the pathogen population is essentially constituted of two groups with dominant phenotypes x_1 and x_2 mixed in proportion π (see Figure 1). It defines an adaptive landscape with two local fitness peaks regrouping each individuals with close combinations of life-history traits.

From here, the simulations of the evolutionary epidemiology dynamics of the model are divided in two parts: the case of single maximum for Ψ and the case of at least two maximum points for Ψ . For all the simulations, the variance of the dispersion into the space of phenotypic values is fixed to $\varepsilon = 0.04$.

Dynamics with a single global maximum point for the fitness function Ψ . Here the fitness function Ψ is maximized by a single phenotypic value x_2 , but a local maximum fitness also exists around x_1 and is close to $\Psi(x_2)$ (Figure 2 (a)). In this case x_2 is the GSEA value (as defined in the Singular strategies section of the Discussion). Accordingly, the simulation shows that the pathogen population is concentrated around this phenotypic value x_2 as the time becomes large (see Figure 2 (b)). But, the transient dynamics before reaching the GSEA value is also interesting: the pathogen population lives during certain time around the initial dominant phenotypic value x_0 and then shifts by mutation and lives for a relatively long time around the local maximum fitness x_1 . In our applied case study, the duration of the transient dynamics is the time length needed for the complete erosion of the quantitative resistant cultivar. It measures the durability of the quantitative resistance gene considered. Said another way, this is the time length during which the quantitative resistant cultivar introduced at $t = 0$ still reduce epidemic relatively to epidemic intensity before its deployment.

Dynamics with at least two global maximum points for the fitness function Ψ . Here, the fitness function is maximized by two phenotypic values x_1 and x_2 (Figure 3 (a)). The natural question is: where will be the concentration in the space of phenotypic values of the pathogens with the long time dynamics? In other words, among these two EAs, which one will asymptotically persist? In the configuration described in Figure 3 (a), the phenotypic values x_1 and x_2 differ by their respective second derivative of the fitness function. Namely, we have $\Psi''(x_2) > \Psi''(x_1)$. According to the order defined in (2.14) on the set of maximum points of the fitness function, x_2 is the GSEA value. The simulation shows the concentration around x_2 in the large time behaviour (Figure 3 (b)). Before reaching the GSEA value, the pathogen population lives during certain time around the initial dominant phenotypic value x_0 and then shift by mutation and lives for a relatively long time around the EA value x_1 . Notice that the time needed to reach the GSEA value is longer than the previous case of a single maximum point for the fitness function (see Fig. 2 (c) compared to Fig. 3 (c)). Indeed, the phenotypic value x_1 is much more 'close' to the GSEA value x_2 than previously in the sense that here we have $\Psi(x_1) = \Psi(x_2)$, which was not the case before.

Another configuration is the case where we cannot 'classify' the two global maximum points x_1 and x_2 of the fitness function by using their second derivative, namely $\Psi''(x_1) = \Psi''(x_2)$. In this situation, we have to compute the higher order derivatives of the fitness function to determine the GSEA values using the total order provided by (2.14).

In the case of symmetric configuration of the fitness function with respect to the phenotypic values x_1 and x_2 , the system admits two GSEA values and, in that special case, the pathogen population equally concentrates on these two GSEA values and leading to a dimorphic pathogen population (see Figure 4 and also Remark 2.1). In the more general setting with non-symmetric configuration and two GSEAs, we are not able to describe the concentration property of the solutions. We suspect

that the pathogen population may be dimorphic with, possibly, different proportion for each GSEA.

Disease induced mortality of infected host tissue. Plant pathogens can be classified by their feeding relationships with their host: necrotrophs, biotrophs and hemibiotrophs¹⁶. The necrotrophs have to kill host tissues and then obtain food from the dead plant material. The biotrophs require a living host for nutrition and to successfully complete their life cycle. The hemibiotrophs combine both a biotrophic and a necrotrophic mode of nutrition. Typically there is a relatively short biotrophic phase followed by necrotrophy and the development of necrotic lesions.

Our model formulation in (1.1) assumed that there is not disease induced mortality of infected lesions, i.e. the pathogen considered is essentially biotrophs. But, notice that the model can encompass the other major trophic modes (necrotrophs and hemibiotrophs) encountered in fungal parasitism by taking into account the disease induced mortality. Actually, the i -equation of Model (1.1) can be written as

$$(\partial_t + \partial_a) i(t, a, x) = -(\mu + d(a, x))i(t, a, x);$$

wherein $d(a, x)$ is the disease induced mortality of the infected tissue by pathogen with phenotypic value x and which is infected since the time a . By taking into account the disease induced mortality of the infected tissue, the preceding results of this note remain true with the following fitness function

$$\Psi(x) = \frac{\beta(x)}{\delta} \int_0^\infty r(a, x) \exp\left(-\mu a - \int_0^a d(\sigma, x) d\sigma\right) da.$$

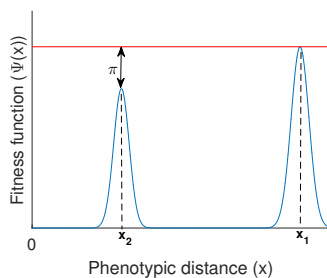


Fig. 1. An adaptive landscape with two local fitness peaks. The fitness function Ψ of the pathogen population is described by a Gaussian mixture model: $\Psi := \pi G(x_1, \sigma_1) + (1 - \pi)G(x_2, \sigma_2)$, wherein $G(x_j, \sigma_j)$ states for the Gaussian function with expected value x_j , with variance σ_j^2 and $\pi \in (0, 1)$. This implies that the pathogen population is essentially constituted of two groups with dominant phenotypes x_1 and x_2 mixed in proportion π .

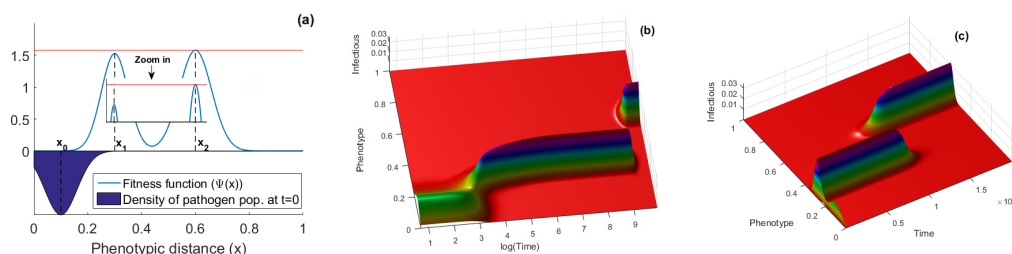


Fig. 2. Epidemiological and evolutionary dynamics of a spore producing pathogen with a single global maximum point for the fitness function. **(a)** The fitness function Ψ and the density of pathogen population at time $t = 0$ with respect to the phenotypic value space. The fitness function is maximized by a single phenotypic value x_2 and has a local maximum at x_1 . In this case, x_2 is the GSEA (Globally Stable Evolutionary Attractor) value. **(b)** Joint epidemiological and evolutionary dynamics of infectious tissues with respect to the phenotypic value space. Initially (at $t = 0$), the pathogen population is essentially concentrated around the phenotypic value x_0 . Then the graph displays how the density of infected tissue and the phenotypic composition of the pathogen population change jointly on the same time scale. The long time dynamics illustrates the concentration of the pathogen population around the GSEA value x_2 . Before reaching the phenotypic value x_2 , the pathogen population lives during certain time around the initial dominant phenotypic value x_0 and then shifts by mutation and lives for a relatively long time around the local maximum fitness x_1 . **(c)** Same as for (b) but without logarithmic time scale.

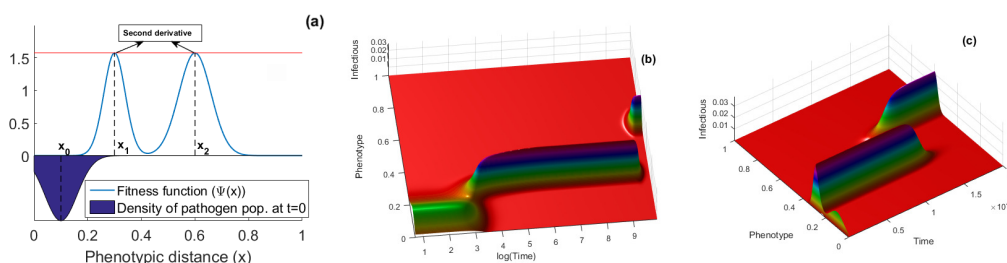


Fig. 3. Epidemiological and evolutionary dynamics of a spore producing pathogen with two global maximum points for the fitness function. **(a)** The fitness function Ψ and the density of pathogen population at time $t = 0$ with respect to the phenotypic value space. The fitness function is maximized by two EAs (Evolutionary Attractors) x_1 and x_2 . The phenotypic values x_1 and x_2 differ by their respective second derivative of the fitness: $\Psi''(x_2) > \Psi''(x_1)$. According to the order defined in (2.14) on the set of maximum points of the fitness function, x_2 is the GSEA (Globally Stable Evolutionary Attractor) value. **(b)** Joint epidemiological and evolutionary dynamics of infectious tissues with respect to the phenotypic value space. Evolutionary epidemiology dynamics of infectious tissues with respect to the phenotypic value space. Initially (at $t = 0$), the pathogen population is essentially concentrated around the phenotypic value x_0 . The long time dynamics illustrates the concentration of the pathogen population around the GSEA value x_2 . Before reaching the phenotypic value x_2 , the pathogen population lives during certain time around the initial dominant phenotypic value x_0 and then shifts by mutation and lives for a relatively long time around the phenotypic value x_1 . **(c)** Same as for (b) but without logarithmic time scale. Observed that, the time to reach the GSEA value is longer than the case of Figure 2 with a single maximum point for the fitness function.

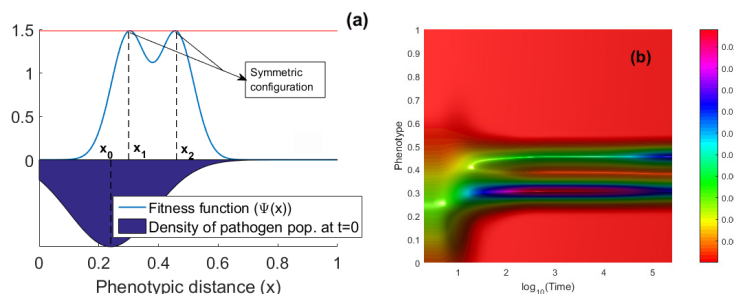


Fig. 4. Epidemiological and evolutionary dynamics of a spore producing pathogen in the case of symmetric configuration of the fitness function. **(a)** The fitness function Ψ and the density of pathogen population at time $t = 0$ with respect to the phenotypic value space. We have a symmetric configuration of the fitness function with respect to the phenotypic values x_1 and x_2 . Thus, according to the order defined in (2.14) on the set of maximum points of the fitness function, both phenotypic values x_1 and x_2 are GSEA (Globally Stable Evolutionary Attractor) values. **(b)** Joint epidemiological and evolutionary dynamics of infectious tissues with respect to the phenotypic value space. Evolutionary epidemiology dynamics of infectious tissues with respect to the phenotypic value space. Initially (at $t = 0$), the pathogen population is essentially concentrated around the phenotypic value x_0 . With the long-time dynamics, the pathogen population equally concentrates around the phenotypic values x_1 and x_2 leading to a dimorphic population.

4. Preliminaries and proof of Theorem 2.1

In this section we study some spectral properties of the linear operator L defined in (1.4), acting on Lebesgue spaces, and we prove Theorem 2.1.

To proceed, for each $p \in [1, \infty)$ we denote by L_p the linear operator L acting on the Lebesgue space $L^p(\mathbb{R}^N)$. Let us observe that since the kernel operator $m \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$, the operator L_p is a bounded linear operator. Using this notation, we shall split this section into two parts. We first study the existence of a principal eigenvalue of the operators L_p for any $1 \leq p < \infty$. And, using this property, we then turn to the proof of Theorem 2.1.

4.1. Principal eigenpair of operator L_p

As mentioned above, this section is devoted to the study of the principal eigenpair for the linear bounded operator L_p for $p \in [1, \infty)$. We refer to ¹ and the references therein for results about generalized principal eigenvalue for some non-local operators. In view of our applications, we prove in this section that Assumptions 2.1 and 2.2 are sufficient to ensure the existence of the principal eigenpair. The main result of this section reads as follows.

Theorem 4.1. *Let Assumptions 2.1 and 2.2 be satisfied. Then the following hold true:*

- (i) For each $p \in [1, \infty)$, the linear operator L_p is compact on $L^p(\mathbb{R}^N)$ and,

its spectral radius, denoted by $r(L_p)$, satisfies $r(L_p) > 0$. Moreover there exists a function $\phi_p \in L^p(\mathbb{R}^N)$ such that

$$\phi_p > 0 \text{ a.e. and } L_p \phi_p = r(L_p) \phi_p.$$

Furthermore, if $\phi \in L^p_+(\mathbb{R}^N) \setminus \{0\}$ satisfies for some $\alpha \in \mathbb{R}$ the equality $L_p \phi = \alpha \phi$, then $\phi > 0$ a.e., $\phi \in \text{span}(\phi_p)$ while $\alpha = r(L_p)$.

- (ii) One has $r(L_p) = r(L_q)$ and $\phi_q \in L^p(\mathbb{R}^N)$ for all $p, q \in [1, \infty)$.
- (iii) Recalling the definition of $\rho[m]$ in (2.3), the common value of these spectral radius is characterized as $r(L_p) = \rho[m]$ for any $p \in [1, \infty)$.

In order to prove this result we shall make use of the so-called Frobenius theorem, that generalizes the well known Krein-Rutmann theorem for positive, irreducible and compact linear operators in Banach lattices. Its precise statement can be found in Corollary 4.2.15 in ³³ (see also the references therein).

Recall that the open set Ω is defined in (2.2). Let us first observe that when $\Omega \neq \mathbb{R}^N$ then, for any $p \in [1, \infty)$, the operator L_p may not be irreducible on $L^p(\mathbb{R}^N)$. To be more precise, if $\mathbb{R}^N \setminus \Omega$ has a non empty interior, consider any function $\phi \in L^p_+(\mathbb{R}^N) \setminus \{0\}$ such that $\phi(x) = 0$ a.e. for $x \in \Omega$. Then $(L_p)^n \phi = 0$ for all $n \geq 1$ and the operator L_p is not irreducible.

Hence, despite the compactness of L_p we cannot directly apply the aforementioned result. To proceed, let us notice that by extending functions by zero outside Ω one may identify for each exponent $p \in [1, \infty)$ the space $L^p(\Omega)$ as a closed subspace of $L^p(\mathbb{R}^N)$. In addition, with such an identification, one may also consider, for each $p \in [1, \infty)$, the restriction operator $L_p|_{L^p(\Omega)}$ defined as a bounded linear operator from $L^p(\Omega)$ into $L^p(\mathbb{R}^N)$ but also the operator $M_p \in \mathcal{L}(L^p(\Omega))$ defined, for any $u \in L^p(\Omega)$, by

$$M_p[u](x) = \int_{\Omega} m(x-y)\Psi(y)u(y)dy = (L_p|_{L^p(\Omega)})[u](x), \text{ a.e. } x \in \Omega. \quad (4.1)$$

Despite the operator L_p is not irreducible in general, the operator M_p is irreducible. Hence our proof of Theorem 4.1 relies on the study on the spectral properties of the operator M_p .

Throughout this section, for any $p \in [1, \infty]$, we shall denote by p' the conjugated exponent of p , namely $\frac{1}{p} + \frac{1}{p'} = 1$.

Proof. [Proof of Theorem 4.1] The proof is split into several steps.

First step: In this first step we shall show that, for any $p \in [1, \infty)$, the operator L_p is compact in $L^p(\mathbb{R}^N)$.

To that aim let us denote, for each $h \in \mathbb{R}^N$ and each function $f : \mathbb{R}^N \rightarrow \mathbb{R}$, by $\tau_h f$ the translation of f by h , defined by $\tau_h f(x) = f(x+h)$ for all $x \in \mathbb{R}^N$.

Let $p \in [1, \infty)$ be given. Let $u \in L^p(\mathbb{R}^N)$ and $h \in \mathbb{R}^N$ be given. Then one has

$$\|\tau_h L_p[u] - L_p[u]\|_{L^p(\mathbb{R}^N)}^p = \int_{\mathbb{R}^N} \left| \int_{\mathbb{R}^N} [\tau_h m(x-y) - m(x-y)]\Psi(y)u(y)dy \right|^p dx.$$

20 *R. Djidjou-Demasse et al.*

Then Young inequality yields

$$\|\tau_h L_p[u] - L_p[u]\|_{L^p(\mathbb{R}^N)} \leq \|\tau_h m - m\|_{L^1(\mathbb{R}^N)} \|\Psi\|_\infty \|u\|_{L^p(\Omega)}.$$

Since $\|\tau_h m - m\|_{L^1(\mathbb{R}^N)} \rightarrow 0$ as $h \rightarrow 0$ one gets that

$$\lim_{h \rightarrow 0} \tau_h L_p[u] = L_p[u] \text{ in } L^p(\mathbb{R}^N),$$

wherein the above convergence holds uniformly on bounded sets on $L^p(\mathbb{R}^N)$.

On the other hand, let $u \in L^p(\mathbb{R}^N)$ and $s > 0$ be given. Then one has

$$\int_{\|x\|>s} |L_p[u](x)|^p dx \leq \int_{\|x\|>s} \left[\int_{\mathbb{R}^N} m(x-y) \Psi(y) |u(y)| dy \right]^p dx. \quad (4.2)$$

Let $R > 0$ be given. Consider a smooth and nonnegative function χ_R such that $0 \leq \chi_R \leq 1$, $\chi_R(y) = 1$ if $|y| \leq R$ and $\chi_R(y) = 0$ if $|y| \geq R+1$. Then, there exists some constant $C = C_p > 0$, such that Equation (4.2) becomes

$$\begin{aligned} \int_{\|x\|>s} |L_p[u](x)|^p dx &\leq C_p \int_{\|x\|>s} \left[\int_{\mathbb{R}^N} m(x-y) \Psi(y) |u(y)| \chi_R(y) dy \right]^p dx \\ &\quad + C_p \int_{\|x\|>s} \left[\int_{\mathbb{R}^N} m(x-y) \Psi(y) |u(y)| (1 - \chi_R(y)) dy \right]^p dx. \end{aligned}$$

Now observe that there exists some constant $C > 0$ independent of u (and R) such that one has

$$\begin{aligned} \int_{\|x\|>s} \left[\int_{\mathbb{R}^N} m(x-y) \Psi(y) |u(y)| \chi_R(y) dy \right]^p dx \\ \leq C \|m\|_\infty^{p-1} \|u\|_{L^p(\mathbb{R}^N)}^p \int_{\|x\|>s} \left[\sup_{\|x-y\| \leq R+1} m(y) \right] dx. \end{aligned}$$

Moreover, since $\|m\|_{L^1(\mathbb{R}^N)} = 1$, Young inequality ensures that

$$\int_{\|x\|>s} \left[\int_{\mathbb{R}^N} m(x-y) \Psi(y) |u(y)| (1 - \chi_R(y)) dy \right]^p dx \leq \sup_{\|y\| \geq R} |\Psi(y)|^p \|u\|_{L^p(\mathbb{R}^N)}^p.$$

Now, setting $B_p(1)$ the unit ball in $L^p(\mathbb{R}^N)$, one obtains from Assumption 2.2 (iii) that for all $R > 0$

$$\limsup_{s \rightarrow +\infty} \sup_{u \in B_p(1)} \int_{\|x\|>s} |L_p[u](x)|^p dx \leq C_p \sup_{\|y\| \geq R} |\Psi(y)|^p.$$

Finally recalling the last condition in Assumption 2.1, namely that $\Psi(x) \rightarrow 0$ as $\|x\| \rightarrow \infty$, one obtains

$$\lim_{s \rightarrow +\infty} \sup_{u \in B_p(1)} \|L_p[u]\|_{L^p(\{\|x\| \geq s\})} = 0.$$

Therefore the Fréchet-Kolmogorov theorem applies and ensures that L_p is a compact operator on $L^p(\mathbb{R}^N)$.

Second step: In this second step we shall prove that the spectral radius of the operator L_p is positive. As mentioned above, the operator L_p is not irreducible, in

general. This difficulty is overcome by using the operator $M_p \in \mathcal{L}(L^p(\Omega))$ defined in (4.1). Let us first observe that the operator M_p can be re-written as $M_p = r_p \circ L_p \circ j_p$, wherein the bounded linear operators $j_p : L^p(\Omega) \rightarrow L^p(\mathbb{R}^N)$ and $r_p : L^p(\mathbb{R}^N) \rightarrow L^p(\Omega)$ are defined by

$$j_p[u](x) = \begin{cases} u(x) & \text{a.e. } x \in \Omega \\ 0 & \text{else} \end{cases} \quad \text{and } r_p[u](x) = u|_{\Omega}(x) \text{ a.e. } x \in \Omega.$$

As a consequence of the first step M_p is a compact operator on $L^p(\Omega)$. Moreover, due to the definition of Ω in (2.2), and since $m > 0$ a.e., the operator M_p is irreducible on $L^p(\Omega)$. We deduce from this discussion that Frobenius theorem (see Theorem 4.2.13 and Corollary 4.2.15 in ³³) applies and ensures that its spectral radius $r(M_p)$ is positive and it is a simple eigenvalue of M_p associated to an eigenvector $\psi_p > 0$ a.e. in Ω . Moreover if $\alpha \in \mathbb{R}$ is an eigenvalue M_p associated to an eigenvector $\psi \in L^p_+(\Omega) \setminus \{0\}$ then $\alpha = r(M_p)$ and $\psi > 0$ a.e. in Ω .

As a consequence, if $\psi \in L^p(\Omega)$ is a principal eigenvector of M_p , then the function $\phi \in L^p(\mathbb{R}^N)$, defined by

$$\phi(x) = \begin{cases} \psi(x) & \text{if } x \in \Omega, \\ \frac{1}{r(M_p)} \int_{\Omega} m(x-y)\Psi(y)\psi(y)dy & \text{if } x \notin \Omega, \end{cases}$$

satisfies $L_p\phi = r(M_p)\phi$ so that $0 < r(M_p) \leq r(L_p)$.

As a consequence of the positivity of the spectral radius $r(L_p)$ (see Lemma 4.2.10 in ³³) there exists $\bar{\phi} \in L^p_+(\mathbb{R}^N) \setminus \{0\}$ such that $L_p\bar{\phi} = r(L_p)\bar{\phi}$. Hence the function $\psi := \bar{\phi}|_{\Omega} \in L^p_+(\Omega) \setminus \{0\}$ is such that $M_p\psi = r(L_p)\psi$. Therefore because of the properties of the spectral eigenpair stated above for the operator M_p , one concludes that

$$r(M_p) = r(L_p) \text{ and } \phi > 0 \text{ a.e. in } \mathbb{R}^N.$$

This argument coupled with the properties of the operator M_p completes the proof of Theorem 4.1 (i).

Third step: In this step we complete the proof of Theorem 4.1 (ii). By the first item (i) with $p = 1$, there exists a function $\phi_1 \in L^1(\mathbb{R}^N)$ with $\phi_1 > 0$ a.e. such that $r(L_1)\phi_1 = L_1\phi_1$. Now, let $q \geq 1$ be given. Because of (i), in order to show that $r(L_q) = r(L_1)$, it is sufficient to show that $\phi_1 \in L^q(\mathbb{R}^N)$. However note that this follows from Young inequality. Indeed since $\phi_1 \in L^1(\mathbb{R}^N)$ and $m \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$, then the convolution product $m * (\Psi\phi_1) \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$ and the result follows.

Fourth step: We now complete the proof of Theorem 4.1 by proving (iii).

To that aim, because of the result of (ii) and by the proof of the second step, it is sufficient to show that $\rho[m] = r(M_2)$, where the operator M_2 is defined in (4.1) with $p = 2$. Let $\psi \in L^2(\Omega)$ with $\psi > 0$ a.e. be a principal eigenvector of M_2 . Then, recalling the function Θ defined in (2.2) as $\Theta = \Psi^{\frac{1}{2}}$, it satisfies

$$\int_{\Omega} m(x-y)\Theta(y)\varphi(y)dy = r(M_2)\psi(x), \quad \forall x \in \Omega, \quad \text{with } \varphi(x) := \Theta(x)\psi(x).$$

22 *R. Djidjou-Demasse et al.*

Hence multiplying the above equation by $\Theta(x)$ yields

$$\Theta(x) \int_{\Omega} m(x-y)\Theta(y)\varphi(y)dy = r(M_2)\varphi(x), \forall x \in \Omega.$$

Next consider the linear bounded operator \widehat{M} on the Hilbert space $L^2(\Omega)$ defined by

$$\widehat{M}[\varphi](x) = \Theta(x) m * (\Theta\varphi)(x), \forall x \in \Omega, \forall \varphi \in L^2(\Omega).$$

Then observe that using similar arguments as the ones developed for the study of M_2 , the positive linear operator \widehat{M} is compact and irreducible. Since $\phi(\cdot) = \Theta(\cdot)\psi(\cdot) \in L^2(\Omega)$ with $\phi > 0$ a.e., one deduces that

$$r(M_2) = r(\widehat{M}).$$

Finally, due to the symmetry hypothesis on the mutation kernel m , the operator \widehat{M} is self-adjoint and then, the Rayleigh quotient formulation for the principal eigenvalue of \widehat{M} ensures that

$$r(M_2) = r(\widehat{M}) = \rho[m].$$

This completes the proof of (iii) and also completes the proof of Theorem 4.1. \square

Remark 4.1. From the above proof, we have obtained that if $(r, \phi) \in (0, \infty) \times L^1(\mathbb{R}^N)$ is a principal eigenpair of L_1 (and thus of L_p for any $p \geq 1$) then $(r, \phi|_{\Omega})$ (resp. $(r, \Theta\phi|_{\Omega})$) is a principal eigenpair of M_p (resp. \widehat{M}). One may also observe that if $(r, \varphi) \in (0, \infty) \times L^2(\Omega)$ is a principal eigenpair of \widehat{M} , then the function $\psi = \frac{\varphi}{\Theta} \in L^2(\Omega)$ and the pair (r, ψ) is a principal eigenpair of M_2 (and thus of M_p for any $p \geq 1$). From the construction of the second step of the proof above, the pair (r, ϕ) , where the function ϕ is defined by

$$\phi(x) = \frac{1}{r} \int_{\Omega} m(x-y)\Theta(y)\varphi(y)dy, \quad x \in \mathbb{R}^N,$$

is a principal eigenpair of L_2 , thus of L_p for any $p \geq 1$.

This remark provides a correspondence between the principal eigenpairs of the three types of operators L_p , M_p and \widehat{M} . This will be used in the sequel.

4.2. Proof of Theorem 2.1

This section is devoted to the proof of Theorem 2.1. For that purpose, let us observe that the trivial stationary state $(S^0, i^0, A^0) := \left(\frac{\Lambda}{\mu}, 0, 0\right)$ is an equilibrium of (1.1) whatever the value of the threshold \mathcal{T}_0 . In order to prove Theorem 2.1, it is sufficient to study System (2.1). Hence we look for non-trivial solution $(S, i, A) \in (0, \infty) \times L^1_+(\mathbb{R}^N) \times L^1_+(\mathbb{R}^N)$ satisfying (2.1). Here non-trivial means that $A \neq 0$.

Note that using the notation of the previous section, (2.1) re-writes as

$$\begin{cases} L_1[A](x) = \frac{1}{S}A(x), & x \in \mathbb{R}^N, \\ \Lambda - \mu S = S \int_{\mathbb{R}^N} \beta(y)A(y)dy & \text{and } i(a, x) = \beta(x)SA(x)e^{-\mu a}. \end{cases} \quad (4.3)$$

Because of Theorem 4.1 (i), one obtains that $r(L_1) = \frac{1}{S}$ and $A \in \text{span}(\phi_1)$, wherein $\phi_1 \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$ denotes the principal eigenfunction of L_1 normalized by $\|\phi_1\|_{L^1(\mathbb{R}^N)} = 1$ and such that $\phi_1 > 0$ a.e.. We write $A = \lambda\phi_1$ for some unknown constant $\lambda > 0$. Plugging this expression into the S -equation of Problem (4.3) one obtains that

$$\Lambda - \frac{\mu}{r(L_1)} = \frac{\lambda}{r(L_1)} \int_{\mathbb{R}^N} \beta(y)\phi_1(y)dy.$$

Hence, since the right hand side of the above equality is positive and recalling that due to Theorem 4.1 one has $r(L_1) = \rho[m]$, the condition $\mathcal{T}_0 > 1$ is a necessary condition for the existence of a non-trivial stationary state.

On the other hand, if $\mathcal{T}_0 > 1$, then System (4.3) admits a unique solution that is given by

$$S = \frac{1}{r(L_1)}, \quad A(x) = \frac{\Lambda r(L_1) - \mu}{\int_{\mathbb{R}^N} \beta(y)\phi_1(y)dy} \phi_1(x) \quad \text{and } i(a, x) = \beta(x)A(x)e^{-\mu a}.$$

(Here recall that since $\Psi \not\equiv 0$, then $\beta \not\equiv 0$ so that the integral arising in the expression of A is positive) This completes the proof of Theorem 2.1.

5. Preliminary spectral estimates and quasi-modes

This section is concerned with the derivation of preliminary asymptotic expansions of the eigenvalues of some linear operators.

For notational simplicity, throughout this section we write m, Ψ, Θ and x_i^0 , for $i = 1, \dots, M$, instead of $\hat{m}, \hat{\Psi}, \hat{\Theta}$ and \hat{x}_i^0 for $i = 1, \dots, M$ defined in (2.7) and (2.8).

5.1. Asymptotic spectral estimates

We shall analyse the limiting behaviour as $\varepsilon \rightarrow 0$ of the principal eigenvalue (or spectral radius) associated to the linear operator L^ε defined in (2.5). We denote the spectral radius of L^ε by λ^ε i.e. $\lambda^\varepsilon = r(L^\varepsilon)$. Because of Remark 4.1, it is also given as the principal eigenvalue of the symmetric linear operator M^ε acting on $L^2(\mathbb{R}^N)$ and defined by

$$M^\varepsilon[u](x) = \Theta(x) \int_{\Omega} m_\varepsilon(x-y)\Theta(y)u(y)dy, \quad x \in \mathbb{R}^N. \quad (5.1)$$

Thus we shall analyse the spectral properties as $\varepsilon \rightarrow 0$ of the linear operator M^ε on the Hilbert space $L^2(\mathbb{R}^N)$. Observe that, using the same arguments as in the proof of Theorem 4.1, for each $\varepsilon > 0$, the operator M^ε is self-adjoint, compact but may

24 *R. Djidjou-Demasse et al.*

not be irreducible if $\Omega \neq \mathbb{R}^N$. However its spectrum coincides with the one of its restriction to $L^2(\Omega)$, that is an irreducible operator.

Our analysis of the spectrum of M^ε relies on a suitable comparison between the linear operator M^ε and the so-called harmonic operators P_j^ε defined around each point of the set $\{x_j^0\}_{j=1,\dots,M}$ given in Assumption 2.3 (ii). Here to be more precise, the linear operators P_j^ε , for $j = 1, \dots, M$ and $\varepsilon > 0$, are defined on $L^2(\mathbb{R}^N)$ by

$$P_j^\varepsilon = -\varepsilon^2 \Delta + V_j(x) \text{ with } V_j(x) = \left\| A_j^{\frac{1}{2}} (x - x_j^0) \right\|. \quad (5.2)$$

Now for any $j = 1, \dots, M$, let us denote by $\omega_j = (\omega_{j,1}, \dots, \omega_{j,N})^T$ with $\omega_{j,l} > 0$ the vector of eigenvalues of the positive definite (see Assumption 2.3 (ii)) matrix $A_j^{\frac{1}{2}} = (-D^2 \Psi(x_j^0))^{\frac{1}{2}}$. Then the spectrum of P_j^ε is given by

$$\begin{cases} \sigma(P_j^\varepsilon) = \{\varepsilon e_{\alpha,j} : \alpha \in \mathbb{N}^N\}, \\ \text{with } e_{\alpha,j} = 2\alpha \cdot \omega_j + \text{tr}\left(A_j^{\frac{1}{2}}\right), \forall \alpha \in \mathbb{N}^N. \end{cases} \quad (5.3)$$

In the above formula, the symbol \cdot denotes the inner Euclidean product in \mathbb{R}^N .

In order to state our first result related to the spectrum of the operator M^ε , we reorder the set

$$\begin{aligned} \{e_{\alpha,j} : j = 1, \dots, M, \alpha \in \mathbb{N}^N\} &= \{e_1, e_2, \dots, e_n, \dots\}, \\ \text{with } e_1 &\leq e_2 \leq e_3 \leq \dots \leq e_n \leq \dots \end{aligned}$$

Here the elements appearing in the above sets are computed with multiplicity. Let us also note that, if we consider the linear operator $P^\varepsilon := \bigoplus_{j=1}^M P_j^\varepsilon$ acting on $\bigoplus_{j=1}^M L^2(\mathbb{R}^N)$, then its spectrum is given, for any $\varepsilon > 0$, by

$$\sigma(P^\varepsilon) = \{\varepsilon e_{\alpha,j} : j = 1, \dots, M, \alpha \in \mathbb{N}^N\}.$$

Also notice that the normalized eigenfunction of the operator P_j^ε associated to the eigenvalue $\varepsilon e_{\alpha,j}$ is given by

$$g_{\alpha,j}^\varepsilon(y) = \varepsilon^{-N/4} h_\alpha \left(\frac{y - x_j^0}{\sqrt{\varepsilon}} \right) \exp \left(-\frac{1}{2\varepsilon} \left\| A_j^{\frac{1}{2}} (y - x_j^0) \right\|^2 \right), \quad \alpha \in \mathbb{N}^N; \quad (5.4)$$

where $h_\alpha = h_{\alpha_1} \otimes \dots \otimes h_{\alpha_N}$ while h_l denotes the one-dimensional Hermite polynomial

$$h_l(y) = \frac{(-1)^l}{\sqrt{2^l l! \pi^{1/4}}} e^{y^2} \left(\frac{d}{dy} \right)^{(l)} e^{-y^2}.$$

With this notation, our first result reads as follows.

Proposition 5.1. *Let Assumptions 2.1, 2.2, 2.3 and 2.4 be satisfied. Let us denote by $E_1(\varepsilon) > E_2(\varepsilon) \geq \dots \geq E_n(\varepsilon) \geq \dots$, the eigenvalues of M^ε . Then for each $n \geq 1$, the following expansion holds true:*

$$E_n(\varepsilon) = 1 - \varepsilon e_n + O\left(\varepsilon^{6/5}\right) \text{ for } 0 < \varepsilon \ll 1.$$

The proof of this proposition is classical and based on the Rayleigh quotient formulation for the eigenvalues. The proof is omitted and we refer the reader to ³⁸ and ³⁶.

5.2. Construction of quasi-modes and properties of the sequences

$$\{\lambda_{k,j}\}_{k \geq 0}$$

In this section we shall construct suitable quasi-modes for the operator M^ε around x_j^0 for some fixed index $j \in \{1, \dots, M\}$ and we shall study properties of the sequences $\{\lambda_{k,j}\}_{k \geq 0}$ defined in (2.12).

To that aim we consider the unitary operators U_j^ε defined on $L^2(\mathbb{R}^N)$ by

$$U_j^\varepsilon[u](x) := \varepsilon^{-\frac{N}{4}} u \left(\varepsilon^{-\frac{1}{2}} (x - x_j^0) \right).$$

Here note that $(U_j^\varepsilon)^{-1}[u](x) = \varepsilon^{\frac{N}{4}} u \left(\varepsilon^{\frac{1}{2}} x + x_j^0 \right)$. Next observe that one has

$$(1 - M^\varepsilon)[u](x) = \int_{\mathbb{R}^N} (u(x) - u(x + \varepsilon y)) K_\varepsilon(x, y) dy + V_\varepsilon(x)u(x),$$

wherein we have set

$$\begin{cases} K_\varepsilon(x, y) = \Theta(x)\Theta(x + \varepsilon y)m(y), \\ V_\varepsilon(x) = 1 - \frac{\Theta(x)}{2} \int_{\mathbb{R}^N} [\Theta(x + \varepsilon y) + \Theta(x - \varepsilon y)] m(y) dy. \end{cases} \quad (5.5)$$

Note also that one has

$$\begin{aligned} M_j^\varepsilon[u](x) &:= \left((U_j^\varepsilon)^{-1} \circ (1 - M^\varepsilon) \circ U_j^\varepsilon \right) [u](x) \\ &= \int_{\mathbb{R}^N} \left(u(x) - u(x + \varepsilon^{\frac{1}{2}} y) \right) K_\varepsilon \left(\varepsilon^{\frac{1}{2}} x + x_j^0, y \right) dy + V_\varepsilon \left(\varepsilon^{\frac{1}{2}} x + x_j^0 \right) u(x). \end{aligned} \quad (5.6)$$

Recalling the definition of the sequence $\{(\lambda_{p,j}, \varphi_{p,j})\}_{p \geq 0}$ in (2.12), the following proposition holds true:

Proposition 5.2. *Let $n \geq 2$ be given. Let us define $u^{\varepsilon,n}$ by*

$$u^{\varepsilon,n} = \sum_{p=0}^n \varepsilon^{\frac{p}{2}} \varphi_{p,j}.$$

Then one has for $\varepsilon \ll 1$:

$$M_j^\varepsilon[u^{\varepsilon,n}] = - \left(\sum_{p=0}^n \varepsilon^{1+\frac{p}{2}} \lambda_{p,j} \right) u^{\varepsilon,n} + O \left(\varepsilon^{\frac{n+1}{2}} \right) \text{ in } L^2(\mathbb{R}^N).$$

Remark 5.1. Using the above proposition one may already prove Theorem 2.2 in the special case where

$$\text{card} \left\{ i = 1, \dots, M, \text{tr} \left(A_i^{\frac{1}{2}} \right) = \min_{j=1, \dots, M} \text{tr} \left(A_j^{\frac{1}{2}} \right) \right\} = 1. \quad (5.7)$$

26 *R. Djidjou-Demasse et al.*

Indeed in that case, because of Proposition 5.1, there exists a unique $i \in \{1, \dots, M\}$ such that

$$E_1(\varepsilon) = 1 - \varepsilon \operatorname{tr} \left(A_i^{\frac{1}{2}} \right) + O \left(\varepsilon^{\frac{6}{5}} \right),$$

while for any $j \geq 2$ one has

$$\lim_{\varepsilon \rightarrow 0} \frac{1}{\varepsilon} (1 - E_j(\varepsilon)) \neq \operatorname{tr} \left(A_i^{\frac{1}{2}} \right).$$

However, since M^ε is self-adjoint, note that for each $n \geq 2$, Proposition 5.2 ensures that

$$\operatorname{dist} \left(1 + \sum_{p=0}^n \varepsilon^{1+\frac{p}{2}} \lambda_{p,i}; \sigma(M^\varepsilon) \right) = O \left(\varepsilon^{\frac{n+1}{2}} \right).$$

Hence since $\lambda_{0,i} = -\operatorname{tr} \left(A_i^{\frac{1}{2}} \right)$, one obtains that

$$E_1(\varepsilon) = 1 + \sum_{p=0}^n \varepsilon^{1+\frac{p}{2}} \lambda_{p,i} + O \left(\varepsilon^{\frac{n+1}{2}} \right),$$

and Theorem 2.2 follows from Lemma 5.1 below in the particular case where (5.7) holds true.

Before going to the proof of Proposition 5.2, let us first observe that the functions $\varphi_{p,j}$ for $p \geq 0$ take the form of a polynomial multiplied by $\varphi_{0,j}$ (see (2.11)). Hence for each $p \geq 0$ and each multi-index $\alpha \in \mathbb{N}^N$, there exist some constant $C_{p,\alpha} > 0$ and some integer $N_{p,\alpha} \in \mathbb{N}$ such that

$$|\partial^\alpha \varphi_{p,j}(x)| \leq C_{p,\alpha} (1 + \|x\|^{N_{p,\alpha}}) \exp \left(-\frac{\|A_j^{\frac{1}{2}} x\|^2}{2} \right), \quad \forall x \in \mathbb{R}^N.$$

Next, the proof of the above proposition is based on the following estimate:

Claim 5.1. For each integer $m \geq 0$, $n \geq 0$ and $r \geq 0$, there exists some constant $C_{m,n,r} > 0$ such that for all $\varepsilon \in [0, 1]$ one has

$$\left\| \|\cdot\|^n \int_{\mathbb{R}^N} \|\cdot + \varepsilon^{\frac{1}{2}} y\|^r \exp \left(-\frac{\|A_j^{\frac{1}{2}} (\cdot + \varepsilon^{\frac{1}{2}} y)\|^2}{2} \right) \|y\|^m m(y) dy \right\|_{L^2(\mathbb{R}^N)} \leq C_{m,n,r}.$$

Proof. Let us observe that, for any $\varepsilon \in (0, 1]$, one has for all $x \in \mathbb{R}^N$:

$$\begin{aligned} & \|x\|^n \int_{\mathbb{R}^N} \|x + \varepsilon^{\frac{1}{2}}y\|^r \exp\left(-\frac{\|A_j^{\frac{1}{2}}(x + \varepsilon^{\frac{1}{2}}y)\|^2}{2}\right) \|y\|^m m(y) dy \\ & \leq \int_{\mathbb{R}^N} (\|x + \sqrt{\varepsilon}y\| + \sqrt{\varepsilon}\|y\|)^n \|x + \varepsilon^{\frac{1}{2}}y\|^r \exp\left(-\frac{\|A_j^{\frac{1}{2}}(x + \varepsilon^{\frac{1}{2}}y)\|^2}{2}\right) \|y\|^m m(y) dy \\ & \leq \sum_{k=0}^n \binom{n}{k} \varepsilon^{\frac{n-k}{2}} \int_{\mathbb{R}^N} \|x + \sqrt{\varepsilon}y\|^{r+k} \exp\left(-\frac{\|A_j^{\frac{1}{2}}(x + \varepsilon^{\frac{1}{2}}y)\|^2}{2}\right) \|y\|^{n-k+m} m(y) dy. \end{aligned}$$

By setting, for each integer $k \geq 0$, m_k the function defined by

$$m_k(y) = \|y\|^k m(y),$$

and recalling that $\varepsilon \in (0, 1]$, one gets for any $x \in \mathbb{R}^N$:

$$\begin{aligned} & \|x\|^n \int_{\mathbb{R}^N} \|x + \varepsilon^{\frac{1}{2}}y\|^r \exp\left(-\frac{\|A_j^{\frac{1}{2}}(x + \varepsilon^{\frac{1}{2}}y)\|^2}{2}\right) \|y\|^m m(y) dy \\ & \leq \sum_{k=0}^n \binom{n}{k} \left(\|\cdot\|^{k+r} \exp\left(-\frac{\|A_j^{\frac{1}{2}}\cdot\|^2}{2}\right) \right) * \left(\varepsilon^{-\frac{N}{2}} m_k\left(\frac{\cdot}{\varepsilon^{\frac{1}{2}}}\right) \right) (x). \end{aligned}$$

Finally, using Young convolution inequality, one obtains

$$\begin{aligned} & \left\| \|\cdot\|^n \int_{\mathbb{R}^N} \|\cdot + \varepsilon^{\frac{1}{2}}y\|^r \exp\left(-\frac{\|A_j^{\frac{1}{2}}(\cdot + \varepsilon^{\frac{1}{2}}y)\|^2}{2}\right) \|y\|^m m(y) dy \right\|_{L^2(\mathbb{R}^N)} \\ & \leq \sum_{k=0}^n \binom{n}{k} \left\| \|\cdot\|^{k+r} \exp\left(-\frac{\|A_j^{\frac{1}{2}}\cdot\|^2}{2}\right) \right\|_{L^2(\mathbb{R}^N)} \|m_k\|_{L^1(\mathbb{R}^N)}, \end{aligned}$$

and the claim follows for any $\varepsilon \in (0, 1]$ and also for $\varepsilon = 0$ because of Fatou lemma \square

Proof. [Proof of Proposition 5.2] Recalling that $\Psi = \Theta^2$ and setting $u = u^{\varepsilon, n}$, let us observe that one has

$$\begin{aligned} & \int_{\mathbb{R}^N} (u(x) - u(x + \varepsilon^{\frac{1}{2}}y)) K_\varepsilon\left(\varepsilon^{\frac{1}{2}}x + x_j^0, y\right) dy \\ & = \sum_{\substack{\beta \geq 0, \alpha \geq 0 \\ |\alpha| + 2|\beta| \leq n}} \varepsilon^{\frac{|\alpha|}{2} + |\beta|} a_j^{\alpha, \beta} x^\alpha \int_{\mathbb{R}^N} (u(x) - u(x + \varepsilon^{\frac{1}{2}}y)) y^\beta m(y) dy + \mathcal{R}^\varepsilon[u](x), \end{aligned}$$

wherein we have set

$$a_j^{\alpha, \beta} = \frac{\partial^\beta \Theta(x_j^0) \partial^\alpha \Psi(x_j^0)}{(\beta + \alpha)!}, \quad (5.8)$$

28 *R. Djidjou-Demasse et al.*

while the remainder satisfies that there exists some constant $C_n > 0$ such that for all $\varepsilon \in (0, 1]$:

$$|\mathcal{R}^\varepsilon[u](x)| \leq C_n \varepsilon^{\frac{n+1}{2}} (1 + \|x\|^{n+1}) \int_{\mathbb{R}^N} |u(x) - u(x + \varepsilon^{\frac{1}{2}}y)| (1 + \|y\|^{n+1}) m(y) dy.$$

Hence because of Claim 5.1 one obtains that

$$\mathcal{R}^\varepsilon[u] = O\left(\varepsilon^{\frac{n+1}{2}}\right) \text{ as } \varepsilon \rightarrow 0 \text{ in } L^2(\mathbb{R}^N).$$

Using once again Claim 5.1 we get

$$\begin{aligned} & - \int_{\mathbb{R}^N} \left(u(x) - u(x + \varepsilon^{\frac{1}{2}}y)\right) K_\varepsilon\left(\varepsilon^{\frac{1}{2}}x + x_j^0, y\right) dy \\ &= \sum_{\substack{\alpha, \beta \in \mathbb{N}^N, |\gamma| \geq 1, p \geq 0 \\ p + |\alpha| + |\gamma| + 2|\beta| \leq n}} \varepsilon^{p + \frac{|\alpha| + |\gamma|}{2} + |\beta|} a_j^{(\alpha, \beta, \gamma)} x^\alpha \partial^\gamma \varphi_{p,j}(x) + O\left(\varepsilon^{\frac{n+1}{2}}\right), \end{aligned}$$

wherein we have set

$$a_j^{(\alpha, \beta, \gamma)} = \frac{1}{\gamma!} a_j^{\alpha, \beta} \int_{\mathbb{R}^N} y^{\gamma + \beta} m(y) dy.$$

As a consequence we obtain

$$\begin{aligned} -M_j^\varepsilon[u^{\varepsilon, n}] &= \sum_{\substack{\alpha, \beta \in \mathbb{N}^N, |\gamma| \geq 1, p \geq 0 \\ p + |\alpha| + |\gamma| + 2|\beta| \leq n}} \varepsilon^{p + \frac{|\alpha| + |\gamma|}{2} + |\beta|} a_j^{(\alpha, \beta, \gamma)} x^\alpha \partial^\gamma \varphi_{p,j} \\ &+ \sum_{\substack{k \geq 0, |\alpha| + |\beta| \geq 1 \\ k + |\alpha| + 2|\beta| \leq n}} \varepsilon^{\frac{k + |\alpha|}{2} + |\beta|} b_j^{(\alpha, \beta)} x^\alpha \varphi_{k,j} + O\left(\varepsilon^{\frac{n+1}{2}}\right), \end{aligned}$$

with

$$b_j^{(\alpha, \beta)} = \frac{1 + (-1)^{|\beta|}}{2} \frac{\partial^\alpha \Psi(x_j^0) \partial^\beta \Theta(x_j^0)}{(\alpha + \beta)!} \int_{\mathbb{R}^N} y^\beta m(y) dy.$$

Now recalling that $\Psi(x_j^0) = \Theta(x_j^0) = 1$ and $\nabla \Psi(x_j^0) = \nabla \Theta(x_j^0) = 0$, straightforward computations yields

$$-M_j^\varepsilon[u^{\varepsilon, n}] = -\varepsilon (P_j + \lambda_{0,j}) \varphi_{0,j} + \varepsilon \sum_{p=1}^{n-2} \varepsilon^{\frac{p}{2}} \left(-(P_j + \lambda_{0,j}) \varphi_{p,j} + \sum_{k=0}^{p-1} \mathcal{D}_{j,pk} \varphi_{k,j} \right) + O\left(\varepsilon^{\frac{n+1}{2}}\right),$$

where P_j is the operator defined in (2.10) and the differential operators $\mathcal{D}_{j,p}$ are defined by

$$\mathcal{D}_{j,p} = \sum_{|\alpha| + 2|\beta| + |\gamma| = 2+p, |\gamma| \geq 1} a_j^{(\alpha, \beta, \gamma)} x^\alpha \partial^\gamma + \sum_{|\alpha| + 2|\beta| = 2+p} b_j^{(\alpha, \beta)} x^\alpha. \quad (5.9)$$

Finally recalling (2.12) completes the proof of Proposition 5.2. \square

We now give some further properties of the sequences $\{\lambda_{k,j}\}_{k \geq 0}$ for $j \in \{1, \dots, M\}$. To that aim recall that functions $\varphi_{k,j}$ are given by a polynomial multiplied by $\varphi_{0,j}$, defined in (2.11). We now write, for each $k \geq 0$ and $j \in \{1, \dots, M\}$:

$$\varphi_{k,j} = Q_{k,j} \varphi_{0,j} \text{ with } Q_{k,j} \in \mathbb{R}[X_1, \dots, X_N].$$

The next lemma ensures that the formal series $\sum_{k=0}^{\infty} \varepsilon^{\frac{k}{2}} \lambda_{k,j}$ does not contain any $\frac{1}{2}$ -degree terms.

Lemma 5.1. *Let $j \in \{1, \dots, M\}$ be given and fixed. Then the polynomials $Q_{k,j}$ satisfy*

$$Q_{k,j}(-X) = (-1)^k Q_{k,j}(X),$$

and the sequence $\{\lambda_{k,j}\}_{k \geq 0}$ satisfies

$$\lambda_{k,j} = 0 \text{ if } k \equiv 1 \pmod{2}.$$

Proof. During this proof, since the index j is fixed we write Q_k and λ_k respectively instead of $Q_{k,j}$ and $\lambda_{k,j}$. To prove this result, let us observe that the sequence $\{Q_k\}_{k \geq 0}$ satisfies the following equation for all $X = (X_1, \dots, X_N)^T$:

$$\begin{aligned} \varphi_{0,j}^{-1} (P_j + \lambda_{0,j}) [\varphi_{0,j} Q_k] &= \left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla \right) Q_k \\ &= - \sum_{p=0}^{k-1} \lambda_{k-p} Q_p + \sum_{p=0}^{k-1} \varphi_{0,j}^{-1} \mathcal{D}_{j,k-p} [\varphi_{0,j} Q_p]. \end{aligned}$$

Next let us write $\mathbb{R}[X_1, \dots, X_N] = E^+ \oplus E^-$ with

$$E^{\pm} = \{P \in \mathbb{R}[X_1, \dots, X_N] : P(-X) = \pm P(X)\}.$$

Next observe that $\left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla \right) E^{\pm} \subset E^{\pm}$ and that

$$\ker \left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla \right) = \{P \in \mathbb{R}[X_1, \dots, X_N] : P = P(0)\} = \mathbb{R} \subset E^+.$$

Next we shall prove, using an induction argument for $k \geq 0$, that

$$Q_{2p} \in E^+, Q_{2p+1} \in E^- \text{ and } \lambda_{2p+1} = 0, \forall p \in \{0, \dots, k\}. \quad (5.10)$$

Step $k = 0$: Let us first observe that $Q_0(X) = 1$ and that the function $\varphi_{1,j} = Q_1 \varphi_{0,j}$ satisfies the equation

$$(P_j + \lambda_{0,j}) \varphi_{1,j} = -\lambda_1 \varphi_{0,j} + \mathcal{D}_{j,1} [\varphi_{0,j}].$$

Recall that $\mathcal{D}_{j,1}$ is defined in (5.9), and reads as

$$\begin{aligned} \mathcal{D}_{j,1} &= \sum_{|\alpha|+2|\beta|+|\gamma|=3, |\gamma| \geq 1} a_j^{(\alpha, \beta, \gamma)} x^\alpha \partial^\gamma + \sum_{|\alpha|+2|\beta|=3} b_j^{(\alpha, \beta)} x^\alpha \\ &= \sum_{|\gamma|=3} a_j^{(0,0,\gamma)} \partial^\gamma + \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha + \sum_{|\alpha|=1, |\beta|=1} b_j^{(\alpha, \beta)} x^\alpha. \end{aligned}$$

30 *R. Djidjou-Demasse et al.*

Now looking at the definition of the coefficients $a_j^{(\alpha,\beta,\gamma)}$ and $b_j^{(\alpha,\beta)}$ above and recalling that m is symmetric, we get

$$\mathcal{D}_{j,1} = \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha.$$

Thus the equation for $\varphi_{1,j}$ reduces to

$$(P_j + \lambda_{0,j}) \varphi_{1,j} = -\lambda_1 \varphi_{0,j} + \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha \varphi_{0,j}.$$

Now Fredholm alternative ensures that

$$-\lambda_1 \varphi_{0,j} + \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha \varphi_{0,j} \perp \varphi_{0,j} \Rightarrow \lambda_1 = 0,$$

so that $\varphi_{1,j}$ and Q_1 respectively solve

$$(P_j + \lambda_{0,j}) \varphi_{1,j} = \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha \varphi_{0,j} \text{ and } \left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla\right) Q_1 = \sum_{|\alpha|=3} b_j^{(\alpha,0)} x^\alpha \in E^-.$$

This ensures that $Q_1 \in \mathbb{R} \oplus E^-$ while the condition $\varphi_{1,j} \perp \varphi_{0,j}$ ensures that $Q_1(0) = 0$. This re-writes as $Q_1 \in E^-$ and this completes the first step for $k = 0$.

Step from k to $k + 1$: Here we assume that (5.10) holds for some $k \geq 0$ and we shall prove that it also holds true for $k + 1$. To that aim let us first observe that

$$\sum_{p=0}^{2k+1} \lambda_{2k+2-p} Q_p = \sum_{p=0}^k \lambda_{2k+2-2p} Q_{2p} \in E^+.$$

On the other hand observe that

$$\begin{aligned} \sum_{p=0}^{2k+1} \varphi_{0,j}^{-1} \mathcal{D}_{j,2k+2-p} [\varphi_{0,j} Q_p] &= \sum_{|\alpha|+2|\beta|=4+2k-p} b_j^{(\alpha,\beta)} X^\alpha Q_p \\ &+ \sum_{p=0}^{2k+1} \sum_{\substack{|\alpha|+|\gamma|=2(2+k-|\beta|)-p \\ |\gamma| \geq 1}} a_j^{(\alpha,\beta,\gamma)} \varphi_{0,j}^{-1} X^\alpha \partial^\gamma (\varphi_{0,j} Q_p). \end{aligned}$$

However for each $|\alpha| = p \pmod 2$ one gets $X^\alpha Q_p \in E^+$ while, for each $|\alpha| + |\gamma| = p \pmod 2$ we have $\varphi_{0,j}^{-1} X^\alpha \partial^\gamma (\varphi_{0,j} Q_p) \in E^+$. Hence this yields

$$\left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla\right) Q_{2k+2} \in E^+ \text{ and } Q_{2k+2} \in E^+.$$

Now, using the same argument as above, let us show that $Q_{2k+3} \in E^-$. First note that

$$\sum_{p=1}^{2k+2} \lambda_{2k+3-p} Q_p = \sum_{p=0}^k \lambda_{2k+3-(2p+1)} Q_{2p+1} \in E^-.$$

Next note that

$$\begin{aligned} \sum_{p=0}^{2k+2} \varphi_{0,j}^{-1} \mathcal{D}_{j,2k+3-p} [\varphi_{0,j} Q_p] &= \sum_{|\alpha|+2|\beta|=5+2k-p} b_j^{(\alpha,\beta)} X^\alpha Q_p \\ &+ \sum_{p=0}^{2k+2} \sum_{\substack{|\alpha|+|\gamma|=1+2(2+k-|\beta|)-p \\ |\gamma|\geq 1}} a_j^{(\alpha,\beta,\gamma)} \varphi_{0,j}^{-1} X^\alpha \partial^\gamma (\varphi_{0,j} Q_p). \end{aligned}$$

Now note that for each $|\alpha| = 1 + p \pmod 2$ one gets $X^\alpha Q_p \in E^-$ while, for each $|\alpha| + |\gamma| = 1 + p \pmod 2$ we have $\varphi_{0,j}^{-1} X^\alpha \partial^\gamma (\varphi_{0,j} Q_p) \in E^-$. Thus we get

$$\left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla\right) Q_{2k+3} = -\lambda_{2k+3} + R \text{ with } R \in E^-.$$

Hence because of Fredholm solvability condition one gets

$$-\lambda_{2k+3} \int_{\mathbb{R}^N} \varphi_{0,j}^2(x) dx + \int_{\mathbb{R}^N} R(x) \varphi_{0,j}^2(x) dx = 0.$$

Next since $R \in E^-$ the second integral in the above solvability condition vanishes that ensures that $\lambda_{2k+3} = 0$. Moreover since $\left(-\Delta + 2A_j^{\frac{1}{2}} X \cdot \nabla\right) Q_{2k+3} \in E^-$ we obtain that $Q_{2k+3} \in \mathbb{R} \oplus E^-$. Finally since $\varphi_{0,j} \perp \varphi_{2k+3,j} = Q_{2k+3} \varphi_{0,j}$, this yields $Q_{2k+3} = 0$ and $Q_{2k+3} \in E^-$. This completes the proof of the induction step and thus the proof of the proposition. \square

6. Spectral properties with a single peak

As in the previous section, for notational simplicity, throughout this section we write m , Ψ , Θ and x_i^0 , for $i = 1, \dots, M$, instead of \widehat{m} , $\widehat{\Psi}$, $\widehat{\Theta}$ and \widehat{x}_i^0 for $i = 1, \dots, M$ defined by (2.7) and (2.8).

We shall work around a single peak of the fitness function Ψ . To proceed we fix $i \in \{1, \dots, M\}$ and a radius $r > 0$ such that

$$\Psi > 0 \text{ on } \overline{B}(x_i^0, r) \text{ and } \Psi(x) < \|\Psi\|_\infty \forall x \in \overline{B}(x_i^0, r) \setminus \{x_i^0\}.$$

Now we consider the linear operator $M_i^{\varepsilon,r}$ defined on $L^2(B(x_i^0, r))$ by

$$M_i^{\varepsilon,r}[u](x) = u(x) - \Theta(x) \int_{B(x_i^0, r)} m_\varepsilon(x-y) \Theta(y) u(y) dy, \quad x \in B(x_i^0, r). \quad (6.1)$$

The aim of this section is to study some spectral properties of this self-adjoint operator. Let us denote by $\{F_{i,k}(\varepsilon)\}_{k \geq 1}$ its sequence of eigenvalues ordered such that

$$F_{i,1}(\varepsilon) < F_{i,2}(\varepsilon) \leq \dots \leq F_{i,k}(\varepsilon) \leq \dots$$

Now let us mention that the asymptotic expansion derived in Proposition 5.1 also holds true for this operator. This means, in this context, that one has

$$F_{i,k}(\varepsilon) = \varepsilon e_k^i + O\left(\varepsilon^{\frac{6}{5}}\right),$$

32 *R. Djidjou-Demasse et al.*

wherein the sequence $\{e_k^i\}_{k \geq 1}$ denotes the increasing rearrangement of the set $\{e_{\alpha,i}, \alpha \in \mathbb{N}^N\}$ as defined in (5.3). We also would like to mention here that the construction of quasi-modes in the previous section for the operator M^ε is also valid for operator $M_i^{\varepsilon,r}$. Hence, since we work around as single peak x_i^0 , we deduce that the lowest eigenvalue $F_{i,1}(\varepsilon)$ of this operator has an asymptotic series. More precisely one has

$$F_{i,1}(\varepsilon) \sim \sum_{k=0}^{\infty} \varepsilon^{1+k} \lambda_{2k,i}. \quad (6.2)$$

In this section we establish Agmon like decay estimates for the eigenvectors of the operator $M_i^{\varepsilon,r}$ defined above in (6.1). The main result of this section reads as follows.

Theorem 6.1 (Decay estimates). *Let Assumptions 2.1, 2.2, 2.3 and 2.4 be satisfied. Fix $R_0 > 0$ large enough so that $[0, \varepsilon R_0] \cap \sigma(M_i^{\varepsilon,r}) \neq \emptyset$ for all $\varepsilon > 0$ small enough. Recalling the definition of γ_0 in Assumption 2.4 (i), then there exist $\eta_1 > 0$ small enough and some constant $C > 0$ such that for all $0 < \varepsilon \ll 1$ small enough and each $u^\varepsilon \in L^2(B(x_i^0, r))$, normalized (in L^2) eigenfunction of $M_i^{\varepsilon,r}$ associated to some eigenvalue $E \in [0, \varepsilon R_0]$, the following holds true:*

$$\left\| \exp\left(\eta_1 \frac{\|x_i^0 - \cdot\|}{\varepsilon^{\gamma_0}}\right) u^\varepsilon(\cdot) \right\|_{L^2(B(x_i^0, r))} \leq C \text{ for all } \varepsilon > 0 \text{ small enough.} \quad (6.3)$$

Proof. For notational simplicity, without loss of generality, we assume that $x_i^0 = 0$ and we write $M_i^{\varepsilon,r} \equiv M^{\varepsilon,r}$.

Recalling the definition of the function K_ε in (5.5), we define for $\eta > 0$ the non-negative function V_η^ε on $\overline{B}(0, r)$ by

$$V_\eta^\varepsilon(x) := \int_{B(-x, \frac{r}{\varepsilon})} \left[\cosh\left(\frac{\eta}{\varepsilon^{\gamma_0}} (\|x\| - \|x + \varepsilon y\|)\right) - 1 \right] K_\varepsilon(x, y) dy. \quad (6.4)$$

Next we claim that:

Claim 6.2. There exist $\eta_1 > 0$ and some constant $C > 0$ such that, for any $\varepsilon \in (0, 1)$, one has

$$0 \leq V_{\eta_1}^\varepsilon(x) \leq C \varepsilon^{1-\gamma_0}, \quad \forall x \in B(0, r).$$

Proof. [Proof of Claim 6.2] In order to prove this estimate, let us first observe that, for any $x \in B(0, r)$, any $y \in B(-x, \frac{r}{\varepsilon})$ and any $\varepsilon > 0$, one has, due to the triangular inequality,

$$\frac{\eta}{\varepsilon^{\gamma_0}} \|\|x\| - \|x + \varepsilon y\|\| \leq \eta \varepsilon^{1-\gamma_0} \|y\|.$$

Now note that, since $\cosh t - 1 \leq |t|e^{|t|}$, for all $t \in \mathbb{R}$, it comes, for any $x \in B(0, r)$ and $y \in B(-x, \frac{r}{\varepsilon})$, that

$$\cosh\left(\frac{\eta}{\varepsilon^{\gamma_0}} (\|x\| - \|x + \varepsilon y\|)\right) - 1 \leq \eta \varepsilon^{1-\gamma_0} \|y\| \exp(\eta \varepsilon^{1-\gamma_0} \|y\|).$$

Recalling that $K_\varepsilon(x, y) \leq \|\Theta\|_\infty^2 m(y)$, this yields, for any $x \in B(0, r)$,

$$V_\eta^\varepsilon(x) \leq L\varepsilon^{1-\gamma_0} \int_{B(0, \frac{r}{\varepsilon})} \|x - z\| \exp(\eta\varepsilon^{1-\gamma_0}\|x - z\|) m(x - z) dz,$$

wherein we have set $L = \|\Theta\|_\infty^2 \eta$. Now due to the decay estimate in Assumption 2.4 (i) it follows that, for any $x \in B(0, r)$, one has

$$V_\eta^\varepsilon(x) \leq M_0 L \varepsilon^{1-\gamma_0} \int_{B(0, \frac{r}{\varepsilon})} \|x - z\| \exp(\eta\varepsilon^{1-\gamma_0}\|x - z\| - \eta_0\|x - z\|^{\gamma_0}) dz. \quad (6.5)$$

On the other hand, for any $x \in B(0, r)$ and $z \in B(0, \frac{r}{\varepsilon})$, one has

$$\begin{aligned} \eta\varepsilon^{1-\gamma_0}\|x - z\| - \eta_0\|x - z\|^{\gamma_0} &\leq (\eta\varepsilon^{1-\gamma_0}\|x - z\|^{1-\gamma_0} - \eta_0) \|x - z\|^{\gamma_0} \\ &\leq \left(r^{1-\gamma_0}\eta(1 + \varepsilon)^{1-\gamma_0} - \eta_0\right) \|x - z\|^{\gamma_0}. \end{aligned} \quad (6.6)$$

Now let us fix $\eta_1 > 0$ such that for all $0 < \varepsilon < 1$

$$r^{1-\gamma_0}\eta_1(1 + \varepsilon)^{1-\gamma_0} \leq \frac{\eta_0}{2}.$$

So we infer from the above estimates, namely (6.5) and (6.6), that for all $\varepsilon \in (0, 1)$

$$V_\eta^\varepsilon(x) \leq M_0 \eta_1 \|\Theta\|_\infty^2 \varepsilon^{1-\gamma_0} \int_{B(0, \frac{r}{\varepsilon})} \|x - z\| \exp\left(-\frac{\eta_0}{2}\|x - z\|^{\gamma_0}\right) dz.$$

This completes the proof of Claim 6.2. \square

Equipped with Claim 6.2 we are able to deal with the last step of the proof of Theorem 6.1.

Recalling the definition of the function V_ε in (5.5) and since $B(0, r)$ is bounded, there exists some constant $C_1 > 0$ such that for all ε small enough one has

$$C_1\varepsilon^{1-\gamma_0} \geq C_1\varepsilon \geq V_\varepsilon(x) - V_0(x) \geq -C_1\varepsilon \geq -C_1\varepsilon^{1-\gamma_0}, \quad \forall x \in \overline{B}(0, r),$$

with $V_0(x) = 1 - \Psi(x)$. Now since $V_0(x) > 0$ for any $x \in \overline{B}(0, r) \setminus \{0\}$ and since $x_i^0 = 0$ is a non-degenerate minimum of V_0 , there exist some constants $C_2 > 0$ and $C_3 > 0$ such that $C_2\|x\|^2 \leq V_0(x) \leq C_3\|x\|^2$ for all $x \in \overline{B}(0, r)$. Hence we infer from Claim 6.2 that

$$C_3\|x\|^2 \geq V_0(x) - V_\eta^\varepsilon(x) \geq C_2\|x\|^2 - C\varepsilon^{1-\gamma_0}, \quad \forall x \in \overline{B}(0, r).$$

Thus, we deduce that for any $\varepsilon > 0$ small enough one has

$$\begin{aligned} V_\varepsilon(x) - V_\eta^\varepsilon(x) &\geq C_2\|x\|^2 - [C_1 + C]\varepsilon^{1-\gamma_0}, \\ V_\varepsilon(x) - V_\eta^\varepsilon(x) &\leq C_3\|x\|^2 + C_1\varepsilon^{1-\gamma_0}, \end{aligned} \quad \forall x \in \overline{B}(0, r).$$

Now, let $b \in [0, R_0]$ be given and define the sets

$$X_-^{\varepsilon, b} := \{x \in \overline{B}(0, r) : V_\varepsilon(x) - V_\eta^\varepsilon(x) - \varepsilon b < 0\} \quad \text{and} \quad X_+^{\varepsilon, b} = \overline{B}(0, r) \setminus X_-^{\varepsilon, b}.$$

Then, observe that

$$X_-^{\varepsilon, b} \subset \{x \in \overline{B}(0, r) : \|x\|^2 \leq \varepsilon^{1-\gamma_0} C_4\}, \quad \text{with} \quad C_4 = \frac{C + C_1}{C_2}.$$

34 *R. Djidjou-Demasse et al.*

Next define the functions $R_{\pm} : \overline{B}(0, r) \rightarrow [0, \infty)$ by

$$\begin{aligned} R_+(x) &:= \sqrt{\varepsilon^{1-\gamma_0} \mathbf{1}_{\{\|x\|^2 \leq \varepsilon^{1-\gamma_0} C_4\}}(x) + (V_\varepsilon(x) - V_{\eta_1}^\varepsilon(x) - \varepsilon b) \mathbf{1}_{X_+^{\varepsilon, b}}(x)}, \\ R_-(x) &:= \sqrt{\varepsilon^{1-\gamma_0} \mathbf{1}_{\{\|x\|^2 \leq \varepsilon^{1-\gamma_0} C_4\}}(x) - (V_\varepsilon(x) - V_{\eta_1}^\varepsilon(x) - \varepsilon b) \mathbf{1}_{X_-^{\varepsilon, b}}(x)}. \end{aligned}$$

With this notation, in order to complete the proof of Theorem 6.1, we claim that:

Claim 6.3. Consider the function Φ^ε defined by

$$\Phi^\varepsilon(x) = \exp\left(\frac{\eta_1 \|x\|}{\varepsilon^{\gamma_0}}\right). \quad (6.7)$$

By setting $R := R_+ + R_- > 0$, the following holds true for any $\varepsilon > 0$ small enough, any $b \in [0, R_0]$ and any $u \in L^2(B(0, r))$:

$$\|R\Phi^\varepsilon u\|_{L^2(B(0, r))}^2 \leq 4 \left\| \frac{1}{R} \Phi^\varepsilon (M^{\varepsilon, r} - \varepsilon b) u \right\|_{L^2(B(0, r))}^2 + 8 \|R_- \Phi^\varepsilon u\|_{L^2(B(0, r))}^2. \quad (6.8)$$

Before proving this claim, we first complete the proof of Theorem 6.1. To that aim observe that

$$R_+^2(x) - R_-^2(x) \equiv V_\varepsilon(x) - V_{\eta_1}^\varepsilon(x) - \varepsilon b.$$

Now note that there exists some constant $C_5 > 0$ (independent of $b \in [0, R_0]$ and ε) such that

$$R := R_+ + R_- \geq C_5 \varepsilon^{\frac{1-\gamma_0}{2}} \quad \text{and} \quad R_- \leq C_5 \varepsilon^{\frac{1-\gamma_0}{2}}. \quad (6.9)$$

As a consequence one gets for any $u \in L^2(B(0, r))$:

$$\begin{cases} \|R\Phi^\varepsilon u\|_{L^2(B(0, r))}^2 \geq C_5^2 \varepsilon^{1-\gamma_0} \|\Phi^\varepsilon u\|_{L^2(B(0, r))}^2, \\ \left\| \frac{1}{R} \Phi^\varepsilon (M^{\varepsilon, r} - \varepsilon b) u \right\|_{L^2(B(0, r))}^2 \leq C_5^{-2} \varepsilon^{-(1-\gamma_0)} \|\Phi^\varepsilon (M^{\varepsilon, r} - \varepsilon b) u\|_{L^2(B(0, r))}^2, \\ \|R_- \Phi^\varepsilon u\|_{L^2(B(0, r))}^2 \leq C_5^2 \varepsilon^{1-\gamma_0} \|u\|_{L^2(B(0, r))}^2. \end{cases}$$

Coupling the above estimates with the estimate provided by Claim 6.3 ensures that there exists some constant $C_6 > 0$ such that for all $u \in L^2(B(0, r))$, all $\varepsilon > 0$ small enough and $b \in [0, R_0]$:

$$\|\Phi^\varepsilon u\|_{L^2(B(0, r))}^2 \leq C_6 \left[\varepsilon^{-2(1-\gamma_0)} \|\Phi^\varepsilon (M^{\varepsilon, r} - \varepsilon b) u\|_{L^2(B(0, r))}^2 + \|u\|_{L^2(M_0)}^2 \right].$$

Choosing $u = u^\varepsilon \in L^2(B(0, r)) \setminus \{0\}$ and $b = b_\varepsilon$ such that $M^{\varepsilon, r} u^\varepsilon = \varepsilon b_\varepsilon u^\varepsilon$ and inserting into the above estimate completes the proof of Theorem 6.1.

Finally, it remains to prove Claim 6.3.

Proof. [Proof of Claim 6.3]. Notice that by the definition of K_ε in (5.5), we have for all nonnegative functions $\psi_1, \psi_2 \in L^2(\mathbb{R}^N)$,

$$\int_{\mathbb{R}^N \times \mathbb{R}^N} \psi_1(x + \varepsilon y) \psi_2(x) K_\varepsilon(x, y) dy dx = \int_{\mathbb{R}^N \times \mathbb{R}^N} \psi_1(x) \psi_2(x + \varepsilon y) K_\varepsilon(x, y) dy dx.$$

Then, by applying successively Lemmas 2.1 and 2.3 in ²², (6.8) follows and this ends the proof of Claim 6.3. \square

7. Proof of Theorem 2.2, Theorem 2.3

This section is devoted to the proof of the asymptotic expansion stated in Theorem 2.2 and of the concentration result stated in Theorem 2.3.

As in the previous sections, for notational simplicity, throughout this section we write m , Ψ , Θ and x_i^0 , for $i = 1, \dots, M$, instead of \widehat{m} , $\widehat{\Psi}$, $\widehat{\Theta}$ and \widehat{x}_i^0 for $i = 1, \dots, M$ defined by (2.7) and (2.8).

Let $s_0 := \min_{j \neq k} \|x_j^0 - x_k^0\|^2$ denote the minimum distance over all two different points x_l^0 , $l = 1, \dots, M$. Then for any $s \in (0, s_0)$ and $j = 1, \dots, M$, the ball of radius s centred at x_j^0 , denoted by $B(x_j^0, s)$, satisfies $x_k^0 \notin B(x_j^0, s)$ for $k \neq j$. Let us consider the set $\mathcal{N} \subset \{1, \dots, M\}$ defined by

$$\begin{aligned} \mathcal{N} &= \left\{ j \in \{1, \dots, M\} : \lambda_{0,j} = \max_{p=1, \dots, M} \lambda_{0,p} \right\} \\ &= \left\{ j \in \{1, \dots, M\}, \operatorname{tr} \left(A_j^{\frac{1}{2}} \right) = \min_{p=1, \dots, M} \operatorname{tr} \left(A_p^{\frac{1}{2}} \right) \right\}. \end{aligned}$$

Let us observe that if $\operatorname{card} \mathcal{N} = 1$, then Remark 5.1 already provides a proof of Theorem 2.2. Here we will prove Theorem 2.2 in the more general situation where \mathcal{N} is not reduced to a single peak and we also prove Theorem 2.3.

Recalling the definition of the set \mathcal{M} in (2.15), observe that $\mathcal{M} \subset \mathcal{N}$. In the sequel we set $K := \operatorname{card} \mathcal{N}$ and assume that $\mathcal{N} = \{1, \dots, K\}$.

Now recall that $E_1(\varepsilon) > E_2(\varepsilon) \geq \dots \geq E_K(\varepsilon) \geq \dots$ denotes the sequence of eigenvalues of the operator M^ε as defined in (5.1). Next, due to Proposition 5.1 there exists some constant $\kappa > 0$ such that for all $0 < \varepsilon \ll 1$ one has

$$\operatorname{dist}(\{E_1(\varepsilon), \dots, E_K(\varepsilon)\}; \sigma(M^\varepsilon) \setminus \{E_1(\varepsilon), \dots, E_K(\varepsilon)\}) \geq \kappa \varepsilon.$$

For $j = 1, \dots, K$, we also denote by $\psi_j^\varepsilon \in L^2(\mathbb{R}^N)$ the normalized eigenvector of the operator M^ε associated to the eigenvalue $E_j(\varepsilon)$.

Now fix $s \in (0, s_0)$ small enough such that

$$\overline{B}(x_j^0, s) \subset \Omega, \quad \forall j \in \mathcal{N}.$$

And, for each $j \in \mathcal{N}$ let us consider $F_{1,j}(\varepsilon) \in \mathbb{R}$ and $u_j^\varepsilon \in L^2(B(x_j^0, s))$ the principal eigenvalue and the normalized (in L^2) principal eigenvector of the operator $M_j^{\varepsilon,s}$ as defined in (6.1). For notational simplicity we write $F_j(\varepsilon)$ instead of $F_{1,j}(\varepsilon)$.

Then our next result reads as follows:

Theorem 7.1. *For each $\varepsilon > 0$ small enough, there exists a bijection b^ε from $\{E_1(\varepsilon), \dots, E_K(\varepsilon)\}$ into $\{F_1(\varepsilon), \dots, F_K(\varepsilon)\}$ such that we can find $\sigma > 0$ with*

$$b^\varepsilon(\lambda) = 1 - \lambda + O\left(e^{-\frac{\sigma}{\varepsilon^{7/6}}}\right).$$

36 *R. Djidjou-Demasse et al.*

Before proving Theorem 7.1, let us observe that as a consequence of this result,

$$E_1(\varepsilon) = 1 - \min_{j=1}^K F_j(\varepsilon) + O\left(e^{-\frac{\sigma}{\varepsilon^{\gamma_0}}}\right).$$

Recalling the asymptotic expansion of $F_j(\varepsilon)$ obtained in (6.2), this ensures that

$$F_j(\varepsilon) = F_k(\varepsilon) + O(\varepsilon^\infty), \quad \forall j, k \in \mathcal{M},$$

and

$$E_1(\varepsilon) \sim 1 + \sum_{k=0}^{\infty} \varepsilon^{1+k} \lambda_{2k,j}, \quad \forall j \in \mathcal{M}.$$

Finally recalling that λ^ε , the principal eigenvalue of L^ε , coincides with $E_1(\varepsilon)$ (see Section 4). This completes the proof of Theorem 2.2 by recalling that the above computations are performed with $\widehat{\Psi} = \Psi / \|\Psi\|_\infty$.

We shall now focus on proving Theorem 7.1. This proof will follow from several steps.

For each $j \in \mathcal{N}$, let us denote by χ_j^s the characteristic function of the ball $B(x_j^0, s)$. Next our first lemma reads as follows

Lemma 7.1. *There exists $\eta > 0$ such that, for all $j \in \mathcal{N}$ and $\varepsilon > 0$ small enough one has:*

$$(1 - M^\varepsilon)(\chi_j^s u_j^\varepsilon) = F_j(\varepsilon)(\chi_j^s u_j^\varepsilon) + r_j, \quad a.e. x \in \mathbb{R}^N,$$

where the remainder r_j satisfies

$$\|r_j\|_{L^2(\mathbb{R}^N)} = O\left(\exp\left(-\frac{\eta}{\varepsilon^{\gamma_0}}\right)\right). \quad (7.1)$$

Proof. Note first that one has

$$(1 - M^\varepsilon)(\chi_j^s u_j^\varepsilon)(x) = \chi_j^s(x) M_j^{\varepsilon,s}[u_j^\varepsilon](x) + r_j(x), \quad a.e. x \in \mathbb{R}^N,$$

wherein the remainder r_j takes the form

$$r_j(x) = -\chi_j^s(x) \Theta(x) \int_{B(x_j^0, s)} m_\varepsilon(x-y) \Theta(y) u_j^\varepsilon(y) dy, \quad \forall x \in \mathbb{R}^N.$$

Now recalling that

$$M_j^{\varepsilon,s}[u_j^\varepsilon] = F_j(\varepsilon) u_j^\varepsilon,$$

we get

$$(1 - M^\varepsilon)(\chi_j^s u_j^\varepsilon) = F_j(\varepsilon)(\chi_j^s u_j^\varepsilon) + r_j.$$

Now let us focus on proving (7.1). To that aim observe that one has, for all $x \in \mathbb{R}^N$:

$$|r_j(x)| \leq M_0 \|\Theta\|_\infty^2 \chi_j^s(x) \int_{B(x_j^0, s)} \varepsilon^{-N} e^{-\frac{\|x-y\|^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} \left(e^{\frac{\eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} u_j^\varepsilon(y) \right) dy.$$

Here η_1 is the constant provided by Theorem 6.1. Hence Hölder inequality yields, for all $x \in \mathbb{R}^N$:

$$|r_j(x)|^2 \leq M_0^2 \|\Theta\|_\infty^4 \chi_j^s(x) \int_{B(x_j^0, s)} \varepsilon^{-2N} e^{-2 \frac{\|x-y\|^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} dy \times \left\| e^{\frac{\eta_1 \|\cdot - x_j^0\|}{\varepsilon^{\gamma_0}}} u_j^\varepsilon \right\|_{L^2(B(x_j^0, s))}^2.$$

Due to Theorem 6.1, there exists some constant $C > 0$ such that for all $\varepsilon > 0$ small enough one has

$$|r_j(x)|^2 \leq C \chi_j^s(x) \int_{B(x_j^0, s)} \varepsilon^{-2N} e^{-2 \frac{\|x-y\|^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} dy, \quad \forall x \in \mathbb{R}^N.$$

In the sequel of this proof $C > 0$ denotes a constant, independent of ε , that may change from line to line. Now fix $\sigma > s$. Then one has for all $x \in \mathbb{R}^N$ such that $\|x - x_j^0\| \geq \sigma$:

$$\begin{aligned} |r_j(x)|^2 &\leq C \int_{\|y-x_j^0\| \leq s} \varepsilon^{-2N} e^{-2 \frac{\|x-x_j^0\|^{\gamma_0} (1 - \|x-x_j^0\|^{-1} \|y-x_j^0\|)^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} dy \\ &\leq C \int_{\|y-x_j^0\| \leq s} \varepsilon^{-2N} e^{-2 \frac{\|x-x_j^0\|^{\gamma_0} (1 - \frac{s}{\sigma})^{\gamma_0}}{\varepsilon^{\gamma_0}}} dy \\ &\leq C \varepsilon^{-2N} \exp\left(-2 \frac{\|x-x_j^0\|^{\gamma_0} (1 - \frac{s}{\sigma})^{\gamma_0}}{\varepsilon^{\gamma_0}}\right). \end{aligned}$$

Next, one gets for all $x \in \mathbb{R}^N$ such that $s \leq \|x - x_j^0\|$:

$$\begin{aligned} |r_j(x)|^2 &\leq C \int_{\|y-x_j^0\| \leq \frac{s}{2}} \varepsilon^{-2N} e^{-2 \frac{\|x-x_j^0\|^{\gamma_0} (1 - \|x-x_j^0\|^{-1} \|y-x_j^0\|)^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} dy \\ &\quad + C \int_{\frac{s}{2} \leq \|y-x_j^0\| \leq s} \varepsilon^{-2N} e^{-2 \frac{\|x-x_j^0\|^{\gamma_0} (1 - \|x-x_j^0\|^{-1} \|y-x_j^0\|)^{\gamma_0} + \eta_1 \|y-x_j^0\|}{\varepsilon^{\gamma_0}}} dy \\ &\leq C \int_{\|y-x_j^0\| \leq \frac{s}{2}} \varepsilon^{-2N} e^{-2 \frac{s^{\gamma_0}}{2^{\gamma_0} \varepsilon^{\gamma_0}}} dy + C \int_{\frac{s}{2} \leq \|y-x_j^0\| \leq s} \varepsilon^{-2N} e^{-\frac{\eta_1 s}{\varepsilon^{\gamma_0}}} dy \\ &\leq C \varepsilon^{-2N} \left[\exp\left(-\frac{2^{1-\gamma_0} s^{\gamma_0}}{\varepsilon^{\gamma_0}}\right) + \exp\left(-\frac{\eta_1 s}{\varepsilon^{\gamma_0}}\right) \right]. \end{aligned}$$

Coupling the above estimates completes the proof of (7.1) and thus the proof of Lemma 7.1. \square

Using the above lemma we are now in position to prove Theorem 7.1. For that purpose let us fix $0 < \sigma < \eta$. Here η is the constant provided by Lemma 7.1 above. Next applying Proposition 5.1 to the operators $M_j^{\varepsilon, s}$ with $j \in \mathcal{N}$ and M_ε , one obtains that there exist $\kappa > 0$ and $\kappa_1 > 0$ with $2\kappa_1 < \kappa$ such that, for all $\varepsilon \ll 1$ small enough, one has for all $\theta \in [0, \kappa_1]$:

$$\begin{aligned} \sigma(1 - M_\varepsilon) \cap [\theta\varepsilon, (\kappa - \theta)\varepsilon] &= \{1 - E_k(\varepsilon), k = 1, \dots, K\}, \\ \sigma(M_j^{\varepsilon, s}) \cap [\theta\varepsilon, (\kappa - \theta)\varepsilon] &= \{F_j(\varepsilon)\}, \quad \forall j \in \mathcal{N}. \end{aligned}$$

38 *R. Djidjou-Demasse et al.*

Now setting $I_\varepsilon = \left[\frac{\kappa_1}{2}\varepsilon, (\kappa - \frac{\kappa_1}{2})\varepsilon \right]$, the above statement re-writes as

$$\left[\sigma(1 - M_\varepsilon) \cup \bigcup_{j=1}^K \sigma(M_j^{\varepsilon,s}) \right] \cap \left[\left(I_\varepsilon + \left[-\frac{\kappa_1\varepsilon}{2}, \frac{\kappa_1\varepsilon}{2} \right] \right) \setminus I_\varepsilon \right] = \emptyset.$$

Next following Chapter 6 in ³⁶, we set $a_\varepsilon = e^{-\frac{\sigma}{\varepsilon\gamma_0}}$ and we consider, for any fixed $\varepsilon > 0$ small enough, disjoint intervals $I_1, \dots, I_{N_\varepsilon} \subset I_\varepsilon$ such that

$$\{1 - E_1(\varepsilon), \dots, 1 - E_K(\varepsilon), F_1(\varepsilon), \dots, F_K(\varepsilon)\} \subset \bigcup_{k=1}^{N_\varepsilon} I_k,$$

$$\text{dist}(I_k, I_{k'}) \geq 2a_\varepsilon, \forall k \neq k' \text{ and } \sup_{k=1}^{N_\varepsilon} |I_k| = O(a_\varepsilon).$$

Consider now for $k = 1, \dots, N_\varepsilon$ the sets of index

$$J_k = \{j \in \{1, \dots, K\} : F_j(\varepsilon) \in I_k\} \text{ and } L_k = \{j \in \{1, \dots, K\} : 1 - E_k(\varepsilon) \in I_k\},$$

as well as the vectors subspaces of $L^2(\mathbb{R}^N)$ defined by

$$\mathcal{E}_k = \bigoplus_{j \in J_k} \text{span}(\chi_j^s u_j^\varepsilon) \text{ and } \mathcal{F}_k = \text{span}\{\psi_j^\varepsilon, j \in L_k\}.$$

Together with the above notation, the proof of Theorem 7.1 directly follows from the following claim:

Claim 7.2. The following holds true:

$$\text{card } J_k = \text{card } L_k, \forall k = 1, \dots, N_\varepsilon.$$

Proof. [Proof of Claim 7.2] Let us observe that

$$\sum_{k=1}^{N_\varepsilon} \text{card } J_k = \sum_{k=1}^{N_\varepsilon} \text{card } L_k = K.$$

Hence in order to prove the above claim, it is sufficient to prove that

$$\text{card } J_k \leq \text{card } L_k, \forall k = 1, \dots, N_\varepsilon.$$

To that aim, consider $\Pi_{\mathcal{E}_k}$ and $\Pi_{\mathcal{F}_k}$ the spectral (orthogonal) projectors on \mathcal{E}_k and \mathcal{F}_k respectively. Next in order to prove the above collection of inequalities, it is sufficient to prove that there exists $\sigma' > 0$ such that, for all $k = 1, \dots, N_\varepsilon$ and all $\varepsilon > 0$ small enough, one has

$$\|\Pi_{\mathcal{E}_k} - \Pi_{\mathcal{F}_k} \Pi_{\mathcal{E}_k}\| = O\left(\exp\left(-\frac{\sigma'}{\varepsilon\gamma_0}\right)\right).$$

These estimates follow from the results derived in ¹⁷ (see Proposition 2.5 of this paper). Indeed, if $k \in \{1, \dots, N_\varepsilon\}$ is given such that $\text{card } J_j \geq 1$ then because of Lemma 7.1 one obtains

$$\|\Pi_{\mathcal{E}_k} - \Pi_{\mathcal{F}_k} \Pi_{\mathcal{E}_k}\| = O\left(\frac{1}{a_\varepsilon} \exp\left(-\frac{\eta}{\varepsilon\gamma_0}\right)\right) = O\left(\exp\left(-\frac{\eta - \sigma}{\varepsilon\gamma_0}\right)\right),$$

and the result follows since $\eta - \sigma > 0$. \square

We now turn to the proof of Theorem 2.3.

Proof. [Proof of Theorem 2.3] Here recall that we have assumed that $\mathcal{M} = \{i\} \subset \mathcal{N}$. Next observe that there exist some power $m_0 \geq 1$ and some constant $\kappa > 0$ such that for all $\varepsilon > 0$ small enough:

$$\text{dist}(1 - E_1(\varepsilon), \sigma(1 - M_\varepsilon) \setminus \{1 - E_1(\varepsilon)\}) \geq \kappa \varepsilon^{m_0}.$$

Using the notation introduced above, this implies that there exists $k_\varepsilon \in \{1, \dots, N_\varepsilon\}$ such that

$$1 - E_1(\varepsilon), F_i(\varepsilon) \in I_{k_\varepsilon} \text{ and } \text{card } J_{k_\varepsilon} = \text{card } L_{k_\varepsilon} = 1.$$

Due to the proof of Claim 7.2, one gets, for $k = k_\varepsilon$ and some $\sigma > 0$, that for ε small enough:

$$\|\Pi_{\mathcal{E}_k} - \Pi_{\mathcal{F}_k} \Pi_{\mathcal{E}_k}\| = O\left(\exp\left(-\frac{\sigma}{\varepsilon^{\gamma_0}}\right)\right).$$

This re-writes as follows:

$$\chi_i^s u_i^\varepsilon - \langle \chi_i^s u_i^\varepsilon, \psi_1^\varepsilon \rangle \psi_1^\varepsilon = O\left(\exp\left(-\frac{\sigma}{\varepsilon^{\gamma_0}}\right)\right) \text{ in } L^2(\mathbb{R}^N).$$

Here the symbol $\langle \cdot, \cdot \rangle$ is used to denote the usual inner product in $L^2(\mathbb{R}^N)$. Taking the L^2 -norm implies that

$$|\langle \chi_i^s u_i^\varepsilon, \psi_1^\varepsilon \rangle| = 1 + O\left(\exp\left(-\frac{\sigma}{\varepsilon^{\gamma_0}}\right)\right),$$

so that

$$\psi_1^\varepsilon = \chi_i^s u_i^\varepsilon + O\left(\exp\left(-\frac{\sigma}{\varepsilon^{\gamma_0}}\right)\right) \text{ in } L^2(\mathbb{R}^N).$$

Now recall that

$$E_1(\varepsilon)\psi_1^\varepsilon = M_\varepsilon[\psi_1^\varepsilon].$$

Hence it follows from Young inequality for the convolution product that for some constant $\kappa > 0$:

$$\|\psi_1^\varepsilon\|_{L^1(\mathbb{R}^N)} \geq \kappa \varepsilon^{-N/2}.$$

Thus, setting $\tilde{\psi}^\varepsilon = \|\psi_1^\varepsilon\|_{L^1(\mathbb{R}^N)}^{-1} \psi_1^\varepsilon$, one gets

$$E_1(\varepsilon)\tilde{\psi}^\varepsilon = M_\varepsilon[\tilde{\psi}^\varepsilon],$$

and

$$E_1(\varepsilon)\tilde{\psi}^\varepsilon = \|\psi_1^\varepsilon\|_{L^1(\mathbb{R}^N)}^{-1} M_\varepsilon[\chi_i^s u_i^\varepsilon] + O\left(\varepsilon^{-N} \exp\left(-\frac{\sigma}{\varepsilon^{\gamma_0}}\right)\right) \text{ in } L^1(\mathbb{R}^N).$$

However, using the same argument and computations as in the proof of Lemma 7.1, one obtains that there exists $\sigma' > 0$ such that

$$M_\varepsilon [\chi_i^s u_i^\varepsilon] = \chi_i^s u_i^\varepsilon + O\left(\exp\left(-\frac{\sigma'}{\varepsilon^{\gamma_0}}\right)\right) \text{ in } L^1(\mathbb{R}^N).$$

As a consequence, we get for some $\sigma'' > 0$ that

$$E_1(\varepsilon)\tilde{\psi}^\varepsilon = \|\psi_1^\varepsilon\|_{L^1(\mathbb{R}^N)}^{-1} \chi_i^s u_i^\varepsilon + O\left(\exp\left(-\frac{\sigma''}{\varepsilon^{\gamma_0}}\right)\right) \text{ in } L^1(\mathbb{R}^N).$$

Now let us fix $\eta \in (0, \gamma_0)$. Recalling Theorem 6.1 (for u_i^ε) one gets, using Hölder inequality, that there exists some constant $C > 0$ such that, for all $\varepsilon > 0$ small enough, it holds:

$$E_1(\varepsilon) \int_{\mathbb{R}^N \setminus B(x_i^0, \varepsilon^\nu)} \tilde{\psi}^\varepsilon dx \leq C \left[\int_{\varepsilon^\nu \leq y \leq s} \exp\left(-2\eta_1 \frac{\|y\|}{\varepsilon^{\gamma_0}}\right) dy \right]^{\frac{1}{2}} + O\left(\exp\left(-\frac{\sigma''}{\varepsilon^{\gamma_0}}\right)\right).$$

As a consequence, we get

$$E_1(\varepsilon) \int_{\mathbb{R}^N \setminus B(x_i^0, \varepsilon^\nu)} \tilde{\psi}^\varepsilon dx = O\left(\exp\left(-\eta_1 \varepsilon^{\nu-\gamma_0}\right)\right).$$

Since $E_1(\varepsilon) \rightarrow 1$ as $\varepsilon \rightarrow 0$, this proves the expected concentration property for the function $\tilde{\psi}^\varepsilon$. Finally, Theorem 2.3 follows from the link between the principal eigenvector of L^ε and M^ε discussed in Remark 4.1 together with the above concentration property. \square

Acknowledgment

R. Djidjou Demasse has received the support of the CIVB (Conseil Interprofessionnel du Vin de Bordeaux) under the CIVB project called "Recherche, expérimentation, études et outils", and also received the support of the EU in the framework of the Marie-Curie FP7 COFUND People Programme, through the award of an AgreeSkills/AgreeSkills+ fellowsh under grant agreement N° FP7-609398.

References

1. Berestycki, H., Coville, J. and Vo, H.H., 2016. On the definition and the properties of the principal eigenvalue of some nonlocal operators. *J. Funct. Anal.*, 271, pp. 2701-2751.
2. Bonnefon, O., Coville, J. and Legendre, G., 2015. Concentration Phenomenon in Some Non-Local Equation. Preprint.
3. Calsina, À., Cuadrado, S., Desvilletes, L. and Raoul, G., 2013. Asymptotics of steady states of a selection-mutation equation for small mutation rate. *Proc. Math. Roy. Soc. Edinb.*, 143, pp. 1123-1146.
4. Day, T. and Gandon, S., 2007. Applying population-genetic models in theoretical evolutionary epidemiology. *Ecol. Lett.*, 10, pp. 876-888.
5. Day, T. and Proulx, S.R., 2004. A general theory for the evolutionary dynamics of virulence. *Am. Nat.*, 163, pp. E40-E63.

6. Desvillettes, L., Jabin, P.E., Mischler, S. and Raoul, G., 2008. On selection dynamics for continuous structured populations. *Commun. Math. Sci.*, 6, pp. 729-747.
7. Djidjou Demasse R. and Ducrot A., 2013. An age-structured within-host model for multistrain malaria infections. *SIAM J. Appl. Math.*, 73, pp. 572-593.
8. Diekmann, O., Jabin, P.E., Mischler, S. and Perthame, B., 2005. The dynamics of adaptation: an illuminating example and a Hamilton-Jacobi approach. *Theor. Popul. Biol.*, 67, pp. 257-271.
9. Diekmann, O., Heesterbeek, J.A.P. and Metz, J.A., 1990. On the definition and the computation of the basic reproduction ratio R_0 in models for infectious diseases in heterogeneous populations. *J. Math. Biol.*, 28, pp. 365-382.
10. Doebeli, M., Hauert, C. and Killingback, T., 2004. The evolutionary origin of cooperators and defectors. *Science*, 306, pp. 859-862.
11. Fabre, F., Rousseau, E., Mailleret, L. and Moury, B., 2012. Durable strategies to deploy plant resistance in agricultural landscapes. *New Phytologist*, 193, pp. 1064-1075.
12. Fabre, F., Rousseau, E., Mailleret, L. and Moury, B., 2015. Epidemiological and evolutionary management of plant resistance: optimizing the deployment of cultivar mixtures in time and space in agricultural landscapes. *Evol. Appl.*, 8, pp. 919-932.
13. Geritz, S.A., Metz, J.A., Kisdi, É. and Meszéna, G., 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, 78(10), p.2024-2027.
14. Gilligan, C. A. and van den Bosch, F., 2008. Epidemiological models for invasion and persistence of pathogens. *Annu. Rev. Phytopathol.*, 46, pp. 385-418.
15. Gudelj, I., Coman, C.D. and Beardmore, R.E., 2006. Classifying the role of trade-offs in the evolutionary diversity of pathogens. *Proc. Math. Phys. Eng. Sci.*, 462, pp. 97-116.
16. Hammerschmidt, R., 2006. Hemibiotrophic growth: combining two forms of fungal parasitism. *Physiol. Mol. Plant P.*, 69, pp. 1-2.
17. Helffer, B. and Sjostrand, J., 1984. Multiple wells in the semi-classical limit I. *Comm. Part. Differ. Equat.*, 9, pp. 337-408.
18. Iacono, G.L., van den Bosch, F. and Paveley, N., 2012. The evolution of plant pathogens in response to host resistance: factors affecting the gain from deployment of qualitative and quantitative resistance. *J. Theo. Biol.*, 304, pp. 152-163.
19. Inaba, H., 2012. On a new perspective of the basic reproduction number in heterogeneous environments. *J. Math. Biol.*, 65, pp. 309-348.
20. Jourdain, B., Méléard, S. and Woyczynski, W.A., 2012. Lévy flights in evolutionary ecology. *J. Math. Biol.*, 65, pp. 677-707.
21. Klein, M. and Rosenberger, E., 2008. Agmon-type estimates for a class of difference operators. *Ann. Inst. H. Poincaré*, 9, pp. 1177-1215.
22. Klein, M., Léonard, C. and Rosenberger, E., 2014. Agmon-type estimates for a class of jump processes. *Math. Nachr.*, 287, pp. 2021-2039.
23. Lannou, C., 2012. Variation and selection of quantitative traits in plant pathogens. *Annu. Rev. Phytopathol.*, 50, pp. 319-338.
24. McDonald, B.A. and Linde, C., 2002. Pathogen population genetics, evolutionary potential, and durable resistance. *Annu. Rev. Phytopathol.*, 40, pp. 349-379.
25. Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., van Heerwaarden, J.S., 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M. (Eds.), *Stochastic and spatial Structures of Dynamical Systems*. North-Holland, Amsterdam, pp. 183-231.
26. Montarry, J., Hamelin, F.M., Glais, I., Corbière, R. and Andrivon, D., 2010. Fitness costs associated with unnecessary virulence factors and life history traits: evolutionary

42 *R. Djidjou-Demasse et al.*

- insights from the potato late blight pathogen *Phytophthora infestans*. *BMC Evol. Biol.*, 10, pp. 1-9.
27. Mirrahimi, S., Perthame, B., Bouin, E. and Millien, P., 2011. Population formulation of adaptative meso-evolution: theory and numerics. In *The mathematics of Darwin's legacy*, 159-174, *Math. Biosci. Interact.*, Birkhäuser/Springer Basel AG, Basel, 2011.
 28. Mirrahimi, S., Perthame, B. and Wakano, J.Y., 2012. Evolution of species trait through resource competition. *J. Math. Biol.*, 64, pp. 1189-1223.
 29. Mundt, C.C., 2014. Durable resistance: a key to sustainable management of pathogens and pests. *Infect. Genet. Evol.*, 27, pp. 446-455.
 30. Nakamura, S., 1998. Agmon-type exponential decay estimates for pseudodifferential operators, *J. Math. Sci. Univ. Tokyo*, 5, pp. 693-712.
 31. Ohtsuki, A. and Sasaki, A., 2006. Epidemiology and disease-control under gene-for-gene plantpathogen interaction. *J. Theor. Biol.*, 238, pp. 780-794.
 32. Perthame, B. and Barles, G., 2007. Dirac concentrations in lotka-volterra parabolic PDEs. *Indiana Univ. Math. J.*, 57, pp. 3275-3301.
 33. Meyer-Nieberg, P., 1991. *Banach Lattices*, Springer-Verlag Berlin Heidelberg.
 34. Poland, J.A., Balint-Kurti, P.J., Wisser, R.J., Pratt, R.C. and Nelson, R.J., 2009. Shades of gray: the world of quantitative disease resistance. *Trends Plant Sci.*, 14, pp. 21-29.
 35. Restif, O., 2009. Evolutionary epidemiology 20 years on: challenges and prospects. *Infect. Genet. Evol.*, 9, pp. 108-123.
 36. Rosenberger, E., 2006. *Asymptotic Spectral Analysis and Tunnelling for a class of Difference Operators*. Thesis, Universität Potsdam.
 37. Savary, S., Teng, P.S., Willocquet, L. and Nutter Jr, F.W., 2006. Quantification and modeling of crop losses: a review of purposes. *Annu. Rev. Phytopathol.*, 44, pp. 89-112.
 38. Simon, B., 1983. Semiclassical analysis of low lying eigenvalues. I. Non-degenerate minima: Asymptotic expansions. *Ann. Inst. H. Poincaré*, 38, pp. 295-308.
 39. St. Clair, D.A., 2010. Quantitative disease resistance and quantitative resistance loci in breeding. *Annu. Rev. Phytopathol.*, 48, pp. 247-268.
 40. Van den Bosch, F. and Gilligan, C.A., 2003. Measures of durability of resistance. *Phytopathology*, 93, pp. 616-625.
 41. Van den Bosch, F., McRoberts, N., Van den Berg, F. and Madden, L.V., 2008. The basic reproduction number of plant pathogens: matrix approaches to complex dynamics. *Phytopathology*, 98, pp. 239-249.
 42. Van den Driessche, P. and Watmough, J., 2008. Further notes on the basic reproduction number. *Mathematical epidemiology*, 159-178, *Lecture Notes in Math.*, 1945, Springer, Berlin.
 43. Zhan, J., Thrall, P.H., Papaïx, J., Xie, L. and Burdon, J.J., 2015. Playing on a pathogen's weakness: using evolution to guide sustainable plant disease control strategies. *Annu. Rev. Phytopathol.*, 53, pp. 19-43.