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Perturbations of Positive Semigroups and Applications to Population Genetics

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1. Introduction

The present article has its origin in a problem of population genetics, namely the investigation of a differential equation that describes the dynamical behavior of probability densities of certain types (e.g. genes) in a population, under the combined action of selection and mutation. A true understanding of such models is of some interest for evolutionary theory, as is indicated in Sect. 4 below. To cover a sufficiently wide range of applications, it turns out that an approach involving functional analysis and, in particular, the theory of strongly continuous semigroups of positive operators is useful.

The mathematical core of the present article is the investigation of the spectral properties of perturbations $A=T-U$ on a Banach lattice E, where $-T$ is the infinitesimal generator of a strongly continuous semigroup of contractions and U is a positive, bounded operator which satisfies a certain compactness condition. To treat this problem, the family of operators $K_\alpha=U(T+\alpha)^{-1}$, $\operatorname{Re}\alpha>0$, on E is investigated. The precise compactness condition that is required is power-compactness of all K_α with $\operatorname{Re}\alpha>0$. Based on results of Schaefer [19], which generalize the Perron-Frobenius Theorem for positive matrices and the Krein-Rutman Theorem, it is shown that the existence of some $\alpha>0$, such that the spectral radius of K_α satisfies $r(K_\alpha)>1$, implies the existence of a unique $\alpha_0>0$ such that $r(K_{\alpha_0})=1$, and, $-\alpha_0$ is the lowest eigenvalue of $\sigma(A)$. If U is irreducible $-\alpha_0$ has algebraic multiplicity one and its eigenspace is spanned by a quasi-interior point of $D(A)$. Furthermore, the existence of some α with $r(K_\alpha)>1$ is equivalent to the condition $s(-T+U)>s(-T)$. Here $s(-T+U)$ and $s(-T)$ denote the spectral bounds of $-T+U$ and $-T$, respectively. This generalizes similar results of Greiner (cf. [6] and [15]), because we require only power-compactness, which will be of importance, when U is a kernel operator on a L^1-space. In particular, the condition $s(-T+U)>s(-T)$ can be replaced by testing whether $r(K_\alpha)>1$, for some $\alpha>0$. The latter has the advantage of being much easier to check, since the K_α's are bounded operators. This is the contents of Sect. 2.

In Sect. 3 sufficient conditions for the existence and global stability of a unique equilibrium solution of the differential equation

$$\dot{p}(t)+A\,p(t)=p(t)\int(A\,p)(y,t)\,d\nu(y)$$

are derived. Here $p(t)$ denotes a probability density on a locally compact space M that carries a positive measure ν, and $A=T-U$, where T is a multiplication operator and U a kernel operator on $E=L^p(M,\nu)$. To study the spectral properties of the operator A the results of Sect. 1 are applied.

In Sect. 4, finally, some concrete applications to particular models from population genetics are treated.

2. Perturbations of Generators of Positive Semigroups

Throughout, let $(E,\|\ \|)$ denote a real or complex Banach lattice, for example $E=L^p(M,\nu)$, $1\leqq p<\infty$, ν a positive σ-finite measure on a locally compact space M. Let $E_+=\{f\in E: f\geqq 0\}$. A bounded linear operator $S\in L(E)$ is called *positive*, if $f\in E_+$ implies $Sf\in E_+$. In case, $E=L^p(M,\nu)$, $f\geqq 0$ means $f(x)\geqq 0$ ν-a.e. A one-parameter semigroup $(S(t))_{t\geqq 0}$ is called positive, if it is a C_0-semigroup, i.e., strongly continuous, and each operator $S(t)$ is positive. As general references for the theory of positive operators and semigroups of linear operators we mention Schaefer [19], Nagel [15] and Pazy [18], respectively.

In the sequel T and U denote linear operators $E\to E$ satisfying assumptions (A1), (A2) and (A3) which are stated below.

(A1) *T is closed with dense domain $D(T)$, such that $-T$ generates a positive semigroup $\{e^{-Tt}\}_{t\geqq 0}$ of contractions, that is $\|e^{-Tt}\|\leqq 1$, for $t\geqq 0$.*

(A2) *U is a positive, bounded operator on E.*

It is well known that a densely defined operator $-T$ is the infinitesimal generator of a semigroup of contractions, if and only if $-T$ is m-dissipative (or, equivalently, T is m-accretive). Hence $\operatorname{range}(T+\alpha)=E$ and

$$\|(T+\alpha)f\|\geqq\alpha\|f\| \tag{2.1}$$

for all $f\in D(T)$ and $\alpha>0$ (cf. Pazy [18], 1.4 and 3.3). Since $-T$ generates a positive semigroup, it follows from Nagel [15] that

$$|(T+\alpha)^{-1}f|\leqq(T+\operatorname{Re}\alpha)^{-1}|f| \tag{2.2}$$

for all $f\in E$ and $\operatorname{Re}\alpha>s(-T)$. Here $s(-T)=\sup\{\operatorname{Re}\alpha: -\alpha\in\sigma(T)\}$ denotes the spectral bound of $-T$ and $\sigma(T)$ the spectrum of T. In particular, $(T+\alpha)^{-1}$ is a positive operator whenever $\alpha>s(-T)$. Throughout, we assume that $s(-T)=0$.

Since T is a closed operator, $D(T)$ becomes a Banach space, denoted by F, under the graph norm $\|f\|_F=\|f\|+\|Tf\|$, $f\in D(T)$. The closed graph theorem together with the fact that $\operatorname{range}(T+\alpha)=E$, $\alpha>0$, implies that $(T+\alpha)^{-1}: E\to F$ is bounded. Inequality (2.2) shows that this is valid for arbitrary $\alpha\in\mathscr{D}$, where $\mathscr{D}$ denotes $\{z\in\mathbb{C}: \operatorname{Re}z>0\}$ throughout.

It is the purpose of this section to investigate the spectral properties of the operator

$$A: E \to E, \quad A := T - U, \quad D(A) = D(T). \tag{2.3}$$

Since T is closed and U is bounded, A is a closed operator with $D(A) = D(T)$ (Kato [9], III.2).

Now let us introduce the family of operators

$$K_\alpha: E \to E, \quad K_\alpha := U(T+\alpha)^{-1}, \quad \alpha \in \mathscr{D}. \tag{2.4}$$

These operators will play a central role in the investigation of the spectrum of A. Each K_α, $\alpha \in \mathscr{D}$, is a bounded operator on E, since U and $(T+\alpha)^{-1}$ are bounded. However, we will need more, namely we will require throughout that

(A 3) *K_α is power compact for all $\alpha \in \mathscr{D}$, that is, there is some fixed n such that $K_\alpha{}^n$ is compact for all $\alpha \in \mathscr{D}$.*

Remark 2.1. If U is T-compact, that is, if $U: F \to E$ is compact then K_α is compact, since $(T+\alpha)^{-1}: E \to F$ is bounded. If U is weakly T-compact, K_α is weakly compact and $K_\alpha{}^2$ is compact if E is an AL- or AM-space (cf. Schaefer [19], II.9). Power compactness of K_α is equivalent to T-power compactness of U as defined by Voigt [22].

Next we will collect some facts concerning the spectral properties of the operators K_α. Since K_α is power compact, the spectrum of K_α consists of eigenvalues with 0 as the only possible accumulation point and all eigenvalues $\neq 0$ have finite algebraic multiplicity. Let $r(\alpha) := r(K_\alpha)$ denote the spectral radius of K_α. If $\alpha > 0$, K_α is a positive operator and it follows from Schaefer ([19], V.4) that $r(\alpha)$ is an isolated eigenvalue of K_α with finite multiplicity (in fact a pole of the resolvent), provided that $r(\alpha) > 0$. If, additionally, K_α is irreducible (cf. [19], III.8), $r(\alpha)$ is an algebraically simple eigenvalue, whose eigenspace is spanned by a unique positive eigenvector f_α, which is a quasi-interior point of E_+ (in case $E = L^p$ this means that $f_\alpha > 0$ ν-a.e.). Furthermore, $r(\alpha)$ is the unique eigenvalue of K_α with a positive eigenvector (cf. [19], V.5).

Now we are able to state and prove the main results of this section. It is supposed that T and U satisfy the assumptions (A1), (A2) and (A3).

Proposition 2.1 (i) *If* $\operatorname{Re}\alpha > 0$, *$f_\alpha$ is an eigenfunction of A, corresponding to an eigenvalue $-\alpha$, i.e.,*

$$Af_\alpha = (T-U)f_\alpha = -\alpha f_\alpha, \quad f_\alpha \in D(A), \tag{2.5}$$

if and only if

$$K_\alpha g_\alpha = U(T+\alpha)^{-1} g_\alpha = g_\alpha, \quad g_\alpha \in E, \quad g_\alpha = (T+\alpha) f_\alpha \tag{2.6}$$

holds, that is, if 1 is an eigenvalue of K_α with eigenfunction g_α.

(ii) *Each $\lambda \in \sigma(A)$ with* $\operatorname{Re}\lambda < 0$ *is an isolated eigenvalue with finite algebraic multiplicity.*

Theorem 2.2. *The following assertions are equivalent:*

(i) *There exists $\alpha > 0$ with $r(\alpha) > 1$.*

(ii) *There exists a unique* $\alpha_0 > 0$ *with* $r(\alpha_0) = 1$. *In particular,*

$$\alpha_0 = s(-A) = \sup\{\operatorname{Re}\lambda:\ \lambda \in \sigma(-A)\}. \tag{2.7}$$

(iii) $s(-A) = s(-T+U) > s(-T)$.

This implies:

(a) $-\alpha_0$ *is an isolated eigenvalue of* A *of finite algebraic multiplicity with a positive eigenvector.*

(b) *If the semigroup generated by* $-T$ *is eventually norm continuous (e.g. analytic), then* $-\alpha_0 < \operatorname{Re}\lambda$ *for all* $\lambda \in \sigma(A)$, $\lambda \neq -\alpha_0$.

(c) *If* U *is irreducible,* $-\alpha_0$ *is a simple eigenvalue, whose eigenspace is spanned by a quasi-interior point of* $E_+ \cap D(A)$.

To prove these results we need some lemmas.

Lemma 1. $\operatorname{Re}\alpha_1 \geqq \alpha_2 > 0$ *implies* $r(\alpha_1) \leqq r(\alpha_2)$ *and* $\lim_{\alpha\to\infty} r(\alpha) = 0$.

The *proof* of the first assertion follows easily from relation (2.2) together with the positivity of U and $(T+\alpha_2)^{-1}$ and the fact that $(T+\alpha)^{-1}$ is monotone decreasing. The second assertion holds, since $r(\alpha) \leqq \|K_\alpha\| \leqq \alpha^{-1}\|U\|$.

Lemma 2. $\alpha \mapsto r(\alpha)$ *is continuous for* $\operatorname{Re}\alpha > 0$.

Proof. Let $\alpha, \alpha_1 \in \mathscr{D}$. A simple computation shows that

$$K_\alpha = K_{\alpha_1}(T+\alpha_1)(T+\alpha)^{-1} = K_{\alpha_1} + (\alpha_1 - \alpha) K_{\alpha_1}(T+\alpha)^{-1}.$$

This implies

$$\|K_\alpha - K_{\alpha_1}\| \leqq \|K_{\alpha_1}\| \frac{|\alpha_1 - \alpha|}{\operatorname{Re}\alpha}.$$

It follows that K_α converges to K_{α_1}, if α converges to α_1. Denote by $\mathscr{S}$ the set of all compact subsets of $\mathbb{C}$, endowed with the Hausdorff distance. Then, by a result of Newburgh [17], the mapping s: $L(E) \to \mathscr{S}$, given by $s(B) = \sigma(B)$ is continuous at B, if $\sigma(B)$ is totally disconnected. The assertion of the lemma follows easily.

Proof of Proposition 2.1. (i) An easy calculation shows that (2.5) and (2.6) are formally equivalent. Since $(T+\alpha)^{-1}$: $R \to F$ is bounded, $f_\alpha \in D(T)$ if and only if $g_\alpha = (T+\alpha) f_\alpha \in E$.

(ii) $\alpha \mapsto K_\alpha$ is an analytic function on $\mathscr{D}$ and K_α^n is compact for some $n \geqq 1$. Now, Corollary 1 of [20] implies one of the following alternatives: (a) If $1 - K_\alpha^n$ is somewhere invertible on $\mathscr{D}$, then $(1-K_\alpha)^{-1}$ is a meromorphic function on $\mathscr{D}$, or (b) $1 - K_\alpha^n$ is invertible for no $\alpha \in \mathscr{D}$. In case (a) this proves assertion (ii), since

$$(A+\alpha)^{-1} = (T+\alpha)^{-1}(1-K_\alpha)^{-1} \tag{2.8}$$

holds and $\alpha \mapsto (T+\alpha)^{-1}$ is analytic on $\mathscr{D}$. Case (b), however, cannot occur due to Lemma 1.

Remark 2.2. Part (ii) of Proposition 2.1 is also a consequence of Theorem 1.1 of Voigt [22] (together with Lemma 1). However, elements of the above proof will be needed below.

Lemma 3. *$\alpha \mapsto r(\alpha)$ is strictly monotone decreasing for $\alpha \in (0, \infty)$.*

Proof. Assume the contrary, i.e., the existence of $0<\alpha_1<\alpha_2$ such that $r(\alpha_1) = r(\alpha_2) = c > 0$. Lemmas 1 and 2 imply that $r(\alpha) = c$ for all $\alpha \in [\alpha_1, \alpha_2]$. Since K_α is positive, 1 is an eigenvalue of $c^{-1} K_\alpha$ for each $\alpha \in [\alpha_1, \alpha_2]$, in contradiction to the meromorphic nature of $(1-c^{-1}K_\alpha)^{-1}$ (see the proof of Proposition 2.1).

Proof of Theorem 2.2. (i)$\Rightarrow$(ii) The existence of a unique α_0 is the consequence of Lemmas 1, 2, and 3. The validity of (2.7) is a consequence of Lemmas 1 and 3, since $\lambda \in \sigma(-A)$ with $\operatorname{Re}\lambda > \alpha_0$ would imply $r(\lambda) \leqq r(\operatorname{Re}\lambda) < r(\alpha_0) = 1$, which, together with Proposition 2.1 (i), leads to a contradiction.

(ii)$\Rightarrow$(iii) This is obvious, since $s(-A) = \alpha_0 > 0 = s(-T)$.

(iii)$\Rightarrow$(i) Suppose that $r(\alpha) \leqq 1$ for all positive α. Then, in fact, $r(\alpha) < 1$ holds for all positive α, because of Lemma 3. This implies, by Lemma 1, that $r(\alpha) < 1$ for all $\alpha \in \mathscr{D}$. Hence $(1-K_\alpha)^{-1}$ exists for all $\alpha \in \mathscr{D}$. Since $s(-T) = 0$, also $(T+\alpha)^{-1}$ exists for all $\alpha \in \mathscr{D}$. Using (2.8), it follows that $(A+\alpha)^{-1}$ exists for all $\alpha \in \mathscr{D}$. This yields $s(-A) \leqq 0 = s(-T)$, the desired contradiction.

(a) That $-\alpha_0$ is an isolated eigenvalue of A of finite algebraic multiplicity follows from Proposition 2.1 (ii). The existence of a positive eigenvector of A, corresponding to $-\alpha_0$, follows from the fact that $r(\alpha_0) = 1$ is a simple pole of the resolvent of K_{α_0} ([19], V.Ex.7) together with Proposition 2.1 (i). In case U, and hence K_α, is compact, this is just part of the Krein-Rutman theorem.

(b) This assertion follows from (2.7) and (a) together with C.III Corollary 2.13 of Nagel [15].

(c) In view of what has already been shown, it is sufficient to prove irreducibility of K_α, $\alpha > 0$, and to apply Theorem 5.2 of Schaefer [19] to K_α. Recall that an operator S is irreducible if and only if for each $0 < f \in E$ and each $0 < \phi \in E'$ some $n \in \mathbb{N}$ exists such that $\langle S^n f, \phi \rangle > 0$ ([19], III.8). Since $-T$ generates a positive C_0-semigroup, $\langle g, \psi \rangle > 0$ for $0 < g \in E$ and $0 < \psi \in E'$ implies

$$\langle (T+\alpha)^{-1} g, \psi \rangle = \int_0^\infty e^{-\alpha t} \langle e^{-Tt} g, \psi \rangle \, dt > 0$$

for all $\alpha > 0$. In particular, $\langle Uf, \psi \rangle = \langle f, U'\psi \rangle > 0$ entails $\langle (T+\alpha)^{-1} f, U'\psi \rangle = \langle K_\alpha f, \psi \rangle > 0$, $\alpha > 0$. Now we proceed by induction and assume that $\langle U^{n-1} f, \phi \rangle > 0$ implies $\langle K_\alpha{}^{n-1} f, \phi \rangle > 0$. Since $\langle U^n f, \phi \rangle > 0$ is equivalent to $\langle U^{n-1} f, U'\phi \rangle > 0$, $\langle K_\alpha{}^{n-1} f, U'\phi \rangle > 0$ follows by assumption. As we have seen above this implies $\langle (T+\alpha)^{-1} K_\alpha{}^{n-1} f, U'\phi \rangle > 0$, which in turn is equivalent to $\langle K_\alpha{}^n f, \phi \rangle > 0$. This proves that irreducibility of U implies irreducibility of K_α, $\alpha > 0$. This finishes the prove Theorem 2.2.

Remark 2.3. Greiner ([6]; see also [15], C-III, Prop. 3.18) has proved that, condition (iii) of Theorem 2.2 implies (a), if U is T-compact. In Theorem 2.2 we have replaced T-compactness of U by power compactness of K_α, which is useful, when the Banach lattice E is an L^1-space, for example. In particular, the theorem stated above seems to be more useful for concrete applications, since the validity of the condition $r(K_\alpha) > 1$ for some $\alpha > 0$ is more easily to check then the condition $s(-T+U) > s(-T)$, that has been used by Greiner.

Remark 2.4. It is possible, to generalize the above results, to T-bounded perturbations U. In that case one needs an additional condition, namely the existence of some $\alpha>0$, such that $r(\alpha)<1$. This is automatically satisfied, if U is bounded, but can be shown to be valid also for certain unbounded operators (see Remark 3.1). In particular, it can be shown that this condition implies closedness of the operator A (which is not the case for general T-bounded perturbations). For, consider the right hand side of Eq. (2.8). This is a bounded operator for sufficiently large α, i.e. if $r(\alpha)<1$, and it can be shown as in Pazy ([18], 3.1) that it is just the resolvent of A. Hence, $A+\alpha$ is closed for large $\alpha>0$, which implies closedness for every α, in particular for $\alpha=0$.

3. Asymptotic Behavior of the Solutions of an Initial Value Problem

It is the purpose of this section to investigate the asymptotic behavior of the solutions of the initial value problem

$$\dot{p}(t)+A\,p(t)=p(t)\cdot\int (A\,p)(y,t)\,d\nu(y), \qquad p(0)=p_0\in L^q. \tag{3.1}$$

Here the operator $A\colon L^q\to L^q$ is the sum of a multiplication and a kernel operator, as defined below. Throughout, let $E=L^q(M,\nu)$, where M is locally compact, ν is a positive σ-finite measure on M and $1\leqq q<\infty$. To define the operator A we introduce functions w and u satisfying the following assumptions.

(T 1) $w\colon M\to\mathbb{R}_+$ is measurable and $\operatorname{ess\,inf} w=0$.
(T 2) $(w+1)^{-1}\in L^{q'}$, $1/q+1/q'=1$.
(U 1) $u\colon M\times M\to\mathbb{R}_+$ is measurable.
(U 2) $u_1(x)=\int u(y,x)\,d\nu(y)\in L^\infty$.
(U 3) If $q>1$ then $u_2(x)=\int u(x,y)\,d\nu(y)\in L^\infty$.
(U 4) If $q=1$ then $\int \operatorname*{ess\,sup}_{y\in M}\dfrac{u(x,y)}{w(y)+1}\,dx<\infty$.

$$\text{If } q>1 \text{ then } \left\{\int\left[\int\left(\frac{u(x,y)}{w(y)+1}\right)^{q'}d\nu(y)\right]^{q/q'}d\nu(x)\right\}^{1/q}<\infty.$$

Now define

$$T\colon E\to E, \qquad Tf(x)=w(x)\,f(x), \qquad D(T)=\{f\in E\colon wf\in E\}, \tag{3.2}$$
$$U\colon E\to E, \qquad Uf(x)=\int u(x,y)\,f(y)\,d\nu(y), \qquad D(U)=E, \tag{3.3}$$
$$A\colon E\to E, \qquad A=T-U, \qquad D(A)=D(T). \tag{3.4}$$

F is just the Banach space $L^q(M,\nu_q)$ with $\nu_q=(w+1)^q\,\nu$. An equivalent norm is given by $\|f\|+\|Tf\|$. According to (2.4) we have

$$K_\alpha\colon E\to E, \qquad K_\alpha f(x)=\int\frac{u(x,y)}{w(y)+\alpha}f(y)\,d\nu(y), \qquad \alpha\in\mathscr{D}. \tag{3.5}$$

Let us collect some properties of T, U and K_α.

Proposition 3.1. *Let T, U and K_α be defined as in* (3.2), (3.3) *and* (3.5), *respectively. Then*

(i) $\sigma(T) = \operatorname{ess\,range}(w) \subseteq [0, \infty)$ *and* $s(-T) = 0$. *In particular,* $-T$ *generates a positive analytic semigroup. If* $q = 2$, T *is selfadjoint.*

(ii) U *is a positive, bounded operator on* E *and* U *is irreducible if and only if*

$$\int_{M \setminus S} \int_S u(x, y)\, d\nu(x)\, d\nu(y) > 0 \tag{3.6}$$

for each measurable set $S \subseteq M$ *such that* $\nu(S) > 0$ *and* $\nu(M \setminus S) > 0$.

(iii) K_α *is a bounded positive operator for every* $\alpha > 0$ *which is irreducible if* U *is irreducible.*

(iv) *If* $q > 1$ *then* K_α *is compact for every* $\alpha \in \mathscr{D}$.
If $q = 1$ *then* K_α^2 *is compact for every* $\alpha \in \mathscr{D}$.

Proof. (i) Recall that $\lambda \notin \operatorname{ess\,range}(w)$ if and only if an ε_0 exists such that for $I_{\lambda, \varepsilon_0} := \{x : |w(x) - \lambda| < \varepsilon_0\}$, $\nu(I_{\lambda, \varepsilon_0}) = 0$. This implies that $|\lambda - w(x)|^{-1}$ is essentially bounded by ε_0^{-1}. For arbitrary $g \in L^q$ define

$$f(x) = \begin{cases} g(x)/(\lambda - w(x)), & x \notin I_{\lambda, \varepsilon_0} \\ 0, & x \in I_{\lambda, \varepsilon_0}. \end{cases}$$

It follows that $(\lambda - T) f = g$ and

$$\|f\|_q = \left\| g \frac{1}{\lambda - w} \right\|_q = \Big\{ \int_{M \setminus I_{\lambda, \varepsilon_0}} |g(x)|^q |(\lambda - w(x))^{-1}|^q \, d\nu(x) \Big\}^{1/q} \leqq \|g\|_q \varepsilon_0^{-1}.$$

This proves that $\sigma(T) = \operatorname{ess\,range}(w)$. Since $\operatorname{ess\,inf} w = 0$, we have $s(-T) = 0$. It follows that T is m-accretive, sectorial, positive and selfadjoint if $q = 2$, which implies the other assertions of (i).

(ii) Positivity of U follows from (U 1). The statement concerning irreducibility may be found in Schaefer ([19], V.6). Next we show boundedness of U, if $q > 1$. Applying Hölder's inequality we obtain

$$\begin{aligned} \|Uf\|_q^q &= \int \Big(\int u(x, y) f(y)\, d\nu(y)\Big)^q d\nu(x) \\ &\leqq \int \Big(\int u(x, y)\, d\nu(y)\Big)^{q/q'} \cdot \Big(\int u(x, y) f(y)^q\, d\nu(y)\Big)\, d\nu(x) \\ &\leqq \|u_2\|_\infty^{q/q'} \iint u(x, y) f(y)^q\, d\nu(y)\, d\nu(x) \leqq \|u_2\|_\infty^{q/q'} \|u_1\|_\infty \|f\|_q^q. \end{aligned}$$

If $q = 1$, one obtains similarly $\|Uf\|_1 \leqq \|u_1\|_\infty \|f\|_1$.

(iii) is obvious.

(iv) K_α is given by the kernel $\dfrac{u(x, y)}{w(y) + \alpha}$ which satisfies the condition stated under (U 4), since $\left\| \dfrac{w+1}{w+\alpha} \right\|_\infty$ is finite, if $\alpha \in \mathscr{D}$. Hence, each K_α is a so-called Hille-Tamarkin operator on L^q and therefore compact, if $q > 1$. If $q = 1$ then K_α^2 is compact (cf. Jörgens [8]).

Although no simple general conditions ensuring compactness of kernel operators between L^1-spaces are valid, in special cases stronger results can be derived. For convolution operators the following proposition, which is a special case of Corollary 3.6 of Feichtinger [4], can be derived.

Proposition 3.2. *Let M be a locally compact abelian group, e.g., $M=\mathbb{R}^k$ or $M=\mathbb{Z}^k$, and let $u(x,y)=u(x-y)$ and $(w+1)^{-1}\in C_0(M)$. Then U: $L^1(M,v_1)\to L^1(M,v)$ is compact if and only if $u\in L^1(M,v)$.*

It should also be noticed that if $(w+1)^{-1}$ does not vanish at infinity, no compact convolution operator exists.

Corollary 3.3. *The statements of Proposition 2.1 and Theorem 2.2 are valid for the operator A (3.4). In particular, A generates a positive analytic semigroup on E which satisfies $s(-A)=\alpha_0>0$, if an $\alpha>0$ exists, such that $r(\alpha)>1$ holds.*

The first assertion is obvious, since Proposition 3.1 implies that (A1), (A2) and (A3) are fulfilled. The second is a consequence of the positivity and boundedness of U.

Remark 3.1. If conditions (U2) and (U3) are omitted U is in general not bounded. However, it is not difficult to show that $\|K_\alpha\|$ and, therefore, also $r(\alpha)$ tends to zero as $\alpha\to\infty$, if for every compact subset $K\subseteq M$ the integral $\int_K (\int_K u(x,y)^{q'}\,dv(y))^{q/q'}\,dv(x)$ is finite. This is obviously the case, if u is bounded on $M\times M$. This shows that generalizations along the lines of Remark 2.4 may be useful, sometimes.

Next let us derive a simple condition that ensures the existence of an $\alpha>0$ with $r(\alpha)>1$.

Proposition 3.4. *Let $x_0\in M$ be such that $w(x_0)=0$. Define $I_\alpha:=\{x\in M\colon w(x)\leqq\alpha\}\cap U(x_0)$, where $U(x_0)$ is a small neighborhood of x_0. If there exists $u_0>0$ such that*

$$\frac{1}{v(I_\alpha)}\inf_{x\in I_\alpha}\int_{I_\alpha} u(x,y)\,dv(y)\geqq u_0 \tag{3.7}$$

holds for all small $\alpha>0$, and if

$$\frac{u_0}{2}\lim_{\alpha\to 0}\frac{v(I_\alpha)}{\alpha}>1 \tag{3.8}$$

then there exists $\alpha>0$ such that $r(\alpha)>1$.

Proof. First note that there exist x_0 and $U(x_0)$ such that $v(I_\alpha)>0$, $\alpha>0$, since $0\in\text{ess range}(w)$. Let φ_α denote the characteristic function of I_α. Then we have

$$K_\alpha\varphi_\alpha(x)=\int_{I_\alpha}\frac{u(x,y)}{w(y)+\alpha}\,dv(y)\geqq\frac{1}{2\alpha}\int_{I_\alpha} u(x,y)\,dv(y)\geqq\frac{u_0\,v(I_\alpha)}{2\alpha}\,\varphi_\alpha(x).$$

This implies that $\|K_\alpha{}^n\|^{1/n}\geqq\dfrac{u_0\,v(I_\alpha)}{2\alpha}$ and, therefore, the assertion follows from (3.8).

Condition (3.7) is satisfied, for example, if $u(x,y)\geqq u_0$ in a neighborhood of (x_0, x_0). (3.8) is a cusp condition on w, that is, at a minimum $w(x_0)=0$ there must not be a cusp. Conditions like (3.7) and (3.8) are in fact necessary to ensure that $r(\alpha)>1$ for small α, as the subsequent example shows.

Example. Choose $M=[0,1]$ and $E=L^1(M,\nu)$, ν the Lebesgue measure. Suppose that $u(x,y)=u(x)$. Then

$$K_\alpha u(x)=\int_M \frac{u(y)}{w(y)+\alpha}\,d\nu(y)\cdot u(x).$$

Since K_α is positive, compact (which is obvious) and u is strictly positive (as a consequence of (3.6)) it follows that

$$r(\alpha)=\int_M \frac{u(y)}{w(y)+\alpha}\,d\nu(y).$$

Hence, there exists an equilibrium density in L^1 if and only of this expression is greater than 1 for some $\alpha>0$. Suppose that $\|u\|_\infty<1/2$ and $w(x)=\sqrt{x}$. Then

$$r(\alpha)=\int_0^1 \frac{u(y)}{w(y)+\alpha}\,d\nu(y)\leqq \tfrac{1}{2}\int_0^1 (\sqrt{y}+\alpha)^{-1}\,d\nu(y)=1-\alpha\ln\frac{1+\alpha}{\alpha}<1$$

for all positive α.

Throughout the sequel, we assume that an α with $r(\alpha)>1$ exists and that, besides of (T1), (T2) and (U1)–(U4), (3.6) holds. This implies the existence of a unique, nondegenerate "ground state" of A with a strictly positive eigenvector. The rest of this section is devoted to the proof of the following theorem.

Theorem 3.5. *There exists a unique, strictly positive probability distribution $\bar{p}\in D(T)$ which is an equilibrium of* (3.1). *Moreover, $\bar{p}$ is globally, asymptotically stable (in a sense specified below).*

Proof. First we will investigate the asymptotic behavior of the solutions of

$$\dot{n}(t)+(A+\alpha_0)\,n(t)=0. \tag{3.9}$$

Since $-A$ is the generator of a positive, analytic semigroup, the same is true for $-(A+\alpha_0)$. Therefore, (3.9) has a unique solution in $D(A)=D(T)$, existing for all $t>0$ and for any $n_0\in E$ (cf. Pazy [18], 4.2). If n_0 is positive, so is $n(t)$, for every $t>0$. Moreover, by Hölder's inequality we have $\|f\|_1\leqq \|(w+1)f\|_q\,\|(w+1)^{-1}\|_{q'}<\infty$, due to (T2). This implies that $D(T)\subseteq L^1$. Hence, every solution of (3.9) is in L^1 for $t>1$.

Set $A_0=A+\alpha_0$. Then the eigenvalue $\lambda_0=0$ of A_0 has algebraic multiplicity 1. Let P denote the corresponding spectral projection and let $E_1=PE$ and $E_2=(I-P)E$. In the present case we have $E_1=\ker A_0=\{r\bar{p}\colon r\in\mathbb{C}\}$, where $\bar{p}$ is the uniquely determined, strictly positive eigenvector of A_0 corresponding to $\lambda_0=0$ such that $\int\bar{p}(x)\,d\nu(x)=1$. This normalization is possible, since $\bar{p}\in D(T)\subseteq L^1$. Then $E=E_1\oplus E_2$ and the E_i are invariant under A_0, and if A_i denotes the restriction of A_0 to E_i then A_1 is the 0-operator on E_1 and $D(A_2)=D(A_0)\cap E_2$ and $\sigma(A_2)=\sigma(A_0)\setminus\{0\}$ (see Henry [7], Th. 1.5.2 or Kato [9], III.6.4). Moreover, $-A_2$ generates an analytic semigroup $\{e^{-A_2t}\}_{t\geqq 0}$ which is just the restriction of $\{e^{-A_0t}\}_{t\geqq 0}$. (The latter leaves each E_i invariant.) Since, due to Theorem 2.2(b), the spectral bound $s(-A_2)<0$, and because e^{-A_2t} is analytic (and therefore growth and spectral bound coincide) there exists $\beta>0$ such that

$$\|e^{-A_2t}\|\leqq Ce^{-\beta t} \quad \text{and} \quad \|A_2e^{-A_2t}\|\leqq Ce^{-\beta t}/t \tag{3.10}$$

for all $t>0$ (see Henry [7], Th. 1.5.3).

According to the above decomposition, for every $n_0\in E$ unique elements $r\in\mathbb{C}$ and $v_0\in E_2$ exist, such that $n_0=r\bar{p}+v_0$. It follows that $e^{-A_0t}n_0=r\bar{p}+e^{-A_2t}v_0$ and (3.10) yields

$$\|e^{-A_0t}n_0-r\bar{p}\|=\|e^{-A_2t}v_0\|\leqq Ce^{-\beta t}\|v_0\|$$

and

$$\|A_0e^{-A_0t}n_0-r\bar{p}\|=\|A_2e^{-A_2t}v_0\|\leqq Ce^{-\beta t}\|v_0\|/t.$$

Since $A_0=T+(\alpha_0-U)$ and since U is bounded, an easy estimate shows that

$$\lim_{t\to\infty}\|e^{-A_0t}n_0-r\bar{p}\|_F=0. \tag{3.11}$$

If $n_0\geqq 0$ and n_0 is not identical zero, then $r>0$. For, assume $r=0$ ($r<0$ cannot happen, since the semigroup is positive). Then we have $n_0=v_0\geqq 0$. 0 is also a simple eigenvalue of the adjoint A_0' with strictly positive eigenvector $\bar{p}'$, since K_α' is power compact and positive on E' and our results hold therefore also for A_0'. It follows that $v_0\perp\ker A_0'=\{z\bar{p}' \colon z\in\mathbb{C}\}$, which is a contradiction. Thus we have shown that for $n_0\in E$ there is a unique $r\in\mathbb{C}$ such that $\lim_{t\to\infty}n(t)=r\bar{p}$ (in F!). If $n_0\geqq 0$ and not identical zero then $r>0$. In particular, it follows that $\int n(x,t)\,dv(x)\geqq\varepsilon(r)>0$ for all $t>0$.

Now we turn to (3.1). (3.1) is obtained from (3.9) through the transformation $p(t)=n(t)/\int n(x,t)\,dv(x)$. This is a well defined positive element in $D(T)$ with $\int p(x,t)\,dv(x)=1$, whenever $n(0)=n_0\in E$, $n_0>0$. If $E=L^1$ it is obvious that $Ap(t)\in L^1$ for all t and, therefore, the integral on the right hand side of (3.1) is finite. If $E=L^q$ this needs not to be the case. However, if $n_0\in L^q_{q'}=\{f\in L^q\colon (1+x^2)^{1/q'}f\in L^q\}$ then $n(t)\in\{f\in L^q\colon (1+x^2)^{1/q'}wf\in L^q\}$ and it follows that $An(t)$ and, hence, $Ap(t)$ are in $L^q_{q'}\subseteq L^1$ for every $t>0$. Together with (3.11) and $\int n(x,t)\,dv(x)\geqq\varepsilon(r)>0$, which has been shown above, this implies that for any positive $p_0\in L^1(M)$, resp. $p_0\in L^q_{q'}(M)$, a unique positive solution $p(t)$ of (3.1) exists for all $t>0$ and converges to $\bar{p}$ in F and hence in L^1, as $t\to\infty$. This proves Theorem 3.5.

4. Applications to Some Problems of Population Genetics

In this section a general population biological model is presented and analyzed that describes the dynamics of a haploid population under the influence of selection and mutation. The model covers numerous special cases that have been investigated earlier (cf. [1, 5, 10–14, 16, 21]).

We consider a population that is infinitely large and has overlapping generations. Individuals are characterized by their type x, where x is a vector in a (locally compact) subset $M \subseteq \mathbb{R}^k$, $k \geqq 1$. M is the state space and is endowed with a positive measure. The components of x may be, for example, numerical values of quantitative characters or alleles at a certain gene locus. $p(x, t)$ denotes the normalized density of type x in the population at time t. $p(t)$ denotes the corresponding element in $L^1(M, \nu)$. It is positive and has norm 1. Throughout, let $E = L^1(M, \nu)$.

The mutation term will be denoted by $u(x, y) \geqq 0$, i.e., $u(x, y)\,dt$ is the fraction of individuals of type x originating through mutation from individuals of type y in the time interval dt. Let us assume that u satisfies assumptions (U1), (U2) and (U4) (or the assumption of Proposition 3.2). $m(x)$ denotes Malthusian fitness, that is, the intrinsic growth rate of type x. We assume that $m(x) \leqq$ const. (ν-a.e.) and that $m: M \to \mathbb{R}$ is measurable. Set $d = \operatorname{ess\,inf}(-m + u_1)$ and $w = -m + u_1 - d$, then w fulfills (T1) and (T2). (Note that $q = 1$, now.)

Employing standard modelling techniques from population genetics (cf. Kimura, [10]) the differential equation describing the dynamical behavior of type densities $p(x, t)$ is derived to

$$\frac{\partial p(x,t)}{\partial t} = [m(x) - \bar{m}(t)]\, p(x,t) + \int_M u(x,y)\, p(y,t)\, d\nu(y) - u_1(x)\, p(x,t) \qquad (4.1)$$

where $\bar{m}(t) = \int_M m(x)\, p(x,t)\, d\nu(x)$ denotes the mean fitness of the population. Defining the operators T, U, and A as in Sect. 3, it is easily seen that Eq. (4.1) yields just Eq. (3.1) and Theorem 3.5 applies, if (3.6) holds and if $r(\alpha) > 1$ for sufficiently small $\alpha > 0$. Subsequently, we will treat several special cases.

A. One Locus with a Finite Number of Alleles

If M is a finite set (with measure ν normalized such that $\nu(x) = 1$, $x \in M$), each x may be considered as an allele at some gene locus. Mutation from y to x occurs with probability $u(x, y) \geqq 0$, such that $\sum_{x \in M} u(x, y) = 1$. Moreover, to each allele x a finite fitness value $m(x)$ is assigned. Hence (T1), (T2), (U1), (U2) and (U4) are satisfied. To apply Theorem 3.5, we have to require additionally that the operator U, or in the present case, the matrix with entries $u(x, y)$, is irreducible. And, we have to show that there exists an $\alpha > 0$ with $r(\alpha) > 1$. Let $x_0 \in M$ be such that $w(x_0) = 0$. Since U is irreducible there is a sequence $x_1, \ldots, x_{s-1}$ such that $u(x_0, x_1) > 0, \ldots, u(x_{s-1}, x_0) > 0$. (Usually one has $u(x_0, x_0) > 0$, since $u(x_0, x_0) = 0$ is biologically not very sensible.) It follows that $K_\alpha \varphi_{x_i} \geqq c_i \varphi_{x_{i-1}}$, for $i = 1, \ldots, s-1$ and $c_i > 0$, and that $K_\alpha \varphi_{x_0} \geqq \frac{c_0}{\alpha} \varphi_{x_{s-1}}$, where φ_{x_i} denotes the characteristic function of $\{x_i\}$. Hence

$$K_\alpha^{sn} \varphi_{x_0} \geqq (c/\alpha)^n \varphi_{x_0}, \qquad c = \prod c_i > 0$$

for all $n \in \mathbb{N}$. This implies

$$\|K_\alpha^{sn}\|^{1/sn} \geqq (c/\alpha)^{1/s}$$

for all $n \in \mathbb{N}$, which proves that $\lim_{\alpha \to 0} r(\alpha) = \infty$. Therefore, Theorem 3.5 is applicable.

It follows that in the classical selection-mutation model for a haploid population a unique, globally stable equilibrium exists, for arbitrary fitness functions (unimodal or not) and arbitrary irreducible mutation operators. For finite M equation (4.1) is just a system of ordinary differential equations. Although they are well known in population genetics (cf. Crow and Kimura [3], 6.4), it seems that no complete analysis has been published, so far. However, for a closely related discrete time model, i.e. for a difference equation, an analogous result was first proved in full generality by Moran [13], using the Perron-Frobenius theory of positive matrices.

B. One Locus with an Infinite Number of Alleles

If M is an infinite, countable discrete set (with measure v normalized such that $v(x) = 1$, $x \in M$) and each $x \in M$ is considered as an allele at some gene locus, one arrives at models like those investigated by Moran ([13, 14]) and Kingman [11]. They, however, used discrete time models with a slightly different modelling. Theorem 3.5 can be applied, if (U2), (U4) and (3.6) are fulfilled (the other conditions hold automatically) and if some $\alpha > 0$ exists with $r(\alpha) > 1$. Due to Proposition 3.4 this is the case, for example, if $u(x_0, x_0) > 0$, whenever $w(x_0) = 0$. This condition is satisfied in most biological applications and may also be found in Kingman [11]. Moran and Kingman (loc. cit.) presented also some other assumptions that lead to a unique and stable equilibrium.

C. Models with Continuous Allelic Effects

It was Kimura [10], who analyzed in an influential paper a model with a continuum of allelic effects. Such models may be of considerable importance, because most metric characters (like brain weight, body size, etc.) vary continuously. In the present terminology he chose $M = \mathbb{R}$ with Lebesgue measure v and interpreted $x \in M$ as an average allelic effect on the quantitative character under consideration. He assumed $m(x) = -sx^2$, s the selection coefficient, and $u(x, y) = \mu(2\pi\gamma^2)^{-1/2} e^{-(x-y)^2/2\gamma^2}$, μ the mutation rate. He derived Eq. (4.1), approximated it by a diffusion equation and calculated mean and variance of the equilibrium distribution – which is Gaussian – of this diffusion equation. Kimura's model has been further analyzed by Fleming [5] and Nagylaki [16], still using approximation techniques. These authors conjectured the existence of a unique, stable equilibrium distribution. Only recently, it was proved in [1], using spectral theory of selfadjoint operators, that a unique equilibrium distribution exists and that every solution $p(t)$ with $(1 + x^2)^{1/2} p(0) \in L^2(\mathbb{R})$ converges to this unique equilibrium. An exact analysis of models of this kind is of importance for one of the basic problems of evolutionary theory, namely the maintenance of genetic variability (cf. Turelli [21], and Bürger [1, 2]).

The present analysis allows to generalize Kimura's model in various directions. Instead of the special mutation and fitness terms he used, one can take all functions u and m (or w) such that the hypothesis of Theorem 3.5 is fulfilled. For example, one can put $u(x, y)=u(x-y)$ with $u \in L^1(M)$ (e.g. compactly supported) and $\operatorname{ess\,inf} u>0$ in a neighborhood of 0. If, moreover, m has no cusp at its optimum and satisfies $\lim_{|x|\to\infty} m(x)=-\infty$ then Proposition 3.2 together with Theorem 3.5 prove the existence of a unique globally stable equilibrium. If u and m are chosen as in Kimura [10] or in [1] (see above) and if $E=L^2(\mathbb{R})$ one arrives just at the main result of [1]. The choice $E=L^1(\mathbb{R})$ improves that result, because it follows that every solution $p(t)$ such that $p(0) \in L^1(\mathbb{R})$ converges to the unique equilibrium.

If, however, m has a cusp at its optimum, an equilibrium density in L^1 does not necessarily exist, as the example before Theorem 3.5 shows. It appears that at equilibrium an atom of probability occurs at the optimal fitness value and thus it may be conjectured that an equilibrium exists in the space of probability measures $C_0(M)'$. This observation may be of practical importance, since there is some empirical evidence that fitness landscapes may be rather jagged. Also Kingman's [12] house-of-cards model, i.e. the choice $u(x, y)=u(x)$, u strictly positive and in L^1, fits well into our context. Then U is compact and irreducible, independent of the choice of m and therefore, Theorem 3.5 applies. Kingman discovered a condition for the existence of a unique equilibrium in his model, that corresponds precisely to our condition in the example before Theorem 3.5 (which is of the house-of-cards type).

Instead of $M=\mathbb{R}$ one can also take $M=\mathbb{R}^k$ or $M=I^k$, I some interval. This means that many characters can be considered and the scale of measurement can be chosen arbitrarily. The latter is of importance, if each $x \in M$ is considered as a vector of measurements of quantitative characters. Typical choices of m and u in case $M=\mathbb{R}^k$, that satisfy all our assumptions, are $m=-x^t A x$, A a positive definit $k \times k$ matrix, $u(x, y)=u(x-y)$ with $u \in L^1$ and positive and strictly positive near 0. If M is compact, then for bounded u (U4) is a consequence of (T2). Hence, the only additional assumptions one has to impose are irreducibility of U and a condition like that in Proposition 3.4. Applications of the present results to the problem of the maintenance of genetic variability are given in [2].

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