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Model of phenotypic evolution in hermaphroditic populations

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Abstract We consider an individual based model of phenotypic evolution in hermaphroditic populations which includes random and assortative mating of individuals. By increasing the number of individuals to infinity we obtain a nonlinear transport equation, which describes the evolution of phenotypic distribution. The main result of the paper is a theorem on asymptotic stability of trait distribution. This theorem is applied to models with the offspring trait distribution given by additive and multiplicative random perturbations of the parental mean trait.

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1 Introduction

This paper studies the evolution of phenotypic traits in hermaphroditic populations, i.e. populations where every individual has both male and female reproductive system. A great part of these populations has formed various defense mechanisms against self-fertilization (*autogamy*) to guarantee genetic diversification (e.g. a proper shape of a flower can inhibit self-pollination in some species of plants). In that case, individuals can only mate with others to copulate and cross-fertilize. Nonetheless, cross-fertilisation occurs in some hermaphroditic species. Hermaphroditic populations are plentiful among both water and terrestrial animals as well as plants. Some of examples include Sponge (*Porifera*), *Turbelleria*, Cestoda (*Cestoidea*), *Lumbricidae*, some of mollusks such as sea slug Blue Dragon (*Glaucus atlanticus*) and various kinds of land snails or majority of flowering plants (angiosperms).

A considerable amount of literature has been published on modelling asexual populations by means of microscopic description of trait evolution. Macroscopic approximations of that models were derived in the forms of deterministic processes or superprocesses (see Champagnat 2006; Champagnat et al. 2008; Fournier and Méléard 2004; Ferrière and Tran 2009; Méléard and Tran 2009). In this paper we formulate an individual based model to describe the phenotypic evolution in hermaphroditic populations. We consider a large population of small individuals characterized by their traits. The traits are assumed to be unchanged during lifetime, and their examples include skin colour, the shape of a leaf and shell pattern. All the individuals are capable of mating or self-fertilizing to give birth to an offspring.

We consider a general model of mating, which includes both random and assortative mating. The first particular case is a semi-random mating model. This model is based on the assumption that each individual has an initial capability of mating depending on its trait. This mating model is similar to models describing aggregation processes in phytoplankton dynamics (see Arino and Rudnicki 2004; Rudnicki and Wieczorek 2006a, b). The second particular case is an assortative mating model. In this model, the individuals with similar traits mate more often than they would choose a partner randomly. We adapt a model based on a preference function Doebeli et al. (2007), Gavrilets and Boake (1998), Matessi et al. (2001), Polechová and Barton (2005), Schneider and Bürger (2006), Schneider and Peischl (2011), usually used in two-sex populations, to the hermaphrodites. The consequence of mating or self-fertilization is a birth of a new individual. The trait of this individual is given by a random variable that depends only on traits of the parents. Each individual can die naturally or when competing with others. We consider a continuous time model, and we assume that all above-mentioned events happen randomly.

The model presented in this paper is a hermaphroditic analogue of the asexual model introduced by Bolker and Pacala (1997), Law and Dieckmann (2002) and studied by Fournier and Méléard (2004). Despite the vast literature concerning individual based models and their macroscopic approximations, only a few models involving mating processes have appeared so far (Collet et al. 2013; Remenik 2009).

One of our aims is to study a macroscopic deterministic approximation of the model. We obtain it by increasing the number of individuals in the population to infinity, with simultaneous decrease in the mass of each individual. After suitable scaling of

parameters, the limit passage leads to an integro-differential equation. Solutions of the equation describe the evolution of trait distribution. We also study the existence and uniqueness of the solutions. We investigate extinction and persistence of the population and convergence of its size to some stable level.

The main aim of our paper is to prove asymptotic stability of trait distribution. Asymptotic behavior of the solutions is characterized by conservation of mean phenotypic trait. We apply our main theorem to two specific models. In these models the offspring trait is the parental mean trait randomly perturbed by some external environmental effects or genetic mutations. In the first model, the noise is additive. The property of additivity allows us to derive a formula for the stationary phenotypic distribution. The second model contains multiplicative noise, and it includes, as a special case, the Tjon–Wu version of the classic Boltzmann equation (see Bobylev 1976; Krook and Wu 1977; Tjon and Wu 1979). The Tjon–Wu equation describes the distribution of energy of particles. As a by-product of our investigation we give a simple proof of the theorem of Lasota and Traple (see Lasota 2002; Lasota and Traple 1999) concerning asymptotic stability of this equation. Addtionally, an example of the trait reduction is given. In this case, in a long period of time, all traits reduce to a particular one, which is the mean trait of the initial population.

The scheme of the paper is following. In Sect. 2 we collect all assumptions on the dynamics of the population. In Sect. 3 we introduce a stochastic process corresponding to our individual based model. Section 4 is devoted to the macroscopic approximation, the limiting equation and its solutions. In particular, we give results about extinction and persistence of the population and stabilization of its size. In Sect. 5 we formulate the results concerning the asymptotic stability, and we give examples of their applications. Finally, in the last section we discuss problems for future investigation concerning assortative mating models.

2 Individual-based model

Let us fix a positive integer d. We assume that every individual is described by a phenotypic trait x, which belongs to some closed and convex subset F of $\mathbb{R}^d$, whose interior is nonempty. The trait of an individual does not change during its lifetime.

2.1 Random mating

In sexually reproducing populations a mating process highly depends on a given species. We will consider both random and assortative mating. In classical genetics individuals mate randomly—the choice of partner is not influenced by the traits (*panmixia*). Random mating occurs often in plants, but it is also observed in some hermaphroditic animals (Baur 1992). We study a semi-random mating model in which the mating rate depends on the trait. An individual described by the trait x is capable of mating/self-fertilizing with rate $p(x)$, where p is a positive function of the trait.

Consider a population which consists of n individuals with traits $x_1, \ldots, x_n$. Since two different individuals may have the same trait, it is useful to describe the state of the population as the multiset

$$\mathbf{x} = \{x_1, \ldots, x_n\}.$$

We recall that a *multiset* (or *bag*) is a generalization of the notion of a set in which the members are allowed to appear more than once. We suppose that any individual can mate with an individual of trait x_j with the following probability

$$\frac{p(x_j)}{\sum_{l=1}^{n} p(x_l)}.$$

Thus the mating rate of individuals with traits x_i and x_j is given by

$$m(x_i, x_j; \mathbf{x}) = \frac{p(x_i)p(x_j)}{\sum_{l=1}^{n} p(x_l)}. \tag{1}$$

The figure $m(x_i, x_i; \mathbf{x})$ is a self-fertilization rate. In the case of populations without self-fertilization we assume that

$$m(x_i, x_j; \mathbf{x}) = \frac{p(x_i)p(x_j)}{2} \left(\frac{1}{\sum_{l \neq i} p(x_l)} + \frac{1}{\sum_{l \neq j} p(x_l)} \right) \tag{2}$$

if $i \neq j$ and $m(x_i, x_i; \mathbf{x}) = 0$. Let us observe that in both cases the mating rate is a symmetric function of x_i and x_j but only in the first case we have $\sum_{j=1}^{n} m(x_i, x_j; \mathbf{x}) = p(x_i)$. If we pass with the number of individuals to infinity, and replace the discrete model by the infinitesimal model with trait distribution described by a continuous measure μ, then the mating rate in both cases is given by

$$m(x, y; \mu) = \frac{p(x)p(y)}{\int_F p(z)\mu(dz)}. \tag{3}$$

2.2 Assortative mating

Now we consider models with assortative mating, i.e. when individuals of the similar traits mate more often than they choose a partner randomly. Assortative mating can be modelled in different ways. For example one can use matching theory, according to that, each participant ranks all the potential partners according to its preferences, and attempts to pair with the highest-ranking one (Almeida and de Abreu 2003; Puebla et al. 2012). Such models are very interesting but difficult to analyze. The most popular models of assortative mating are based on the assumption that a random encounter between two individuals with traits x and y depends on a preference function $a(x, y)$ (Doebeli et al. 2007; Gavrilets and Boake 1998; Matessi et al. 2001; Polechová and Barton 2005; Schneider and Bürger 2006; Schneider and Peischl 2011). We consider only the case when all the individuals have the same initial capability of mating $p(x) = 1$.

Usually, it is assumed that $a(x, y) = \varphi(\|x - y\|)$, where $\varphi : [0, \infty) \to [0, \infty)$ is a continuous and decreasing function. It means that if the population consists of n members with traits $x_1, \ldots, x_n$, then individuals of traits x_i, x_j mate with rate

$$m(x_i, x_j; \mathbf{x}) = \frac{a(x_i, x_j)}{\sum_{l=1}^{n} a(x_i, x_l)} = \frac{\varphi(\|x_i - x_j\|)}{\sum_{l=1}^{n} \varphi(\|x_i - x_l\|)}. \tag{4}$$

Note that in general, the function m is not symmetric in x_i and x_j, and usually it describes mating in two-sex populations. Then the first argument in m refers to a female. Females are assumed to mate only once, whereas males may participate in multiple matings. We have $\sum_{j=1}^{n} m(x_i, x_j; \mathbf{x}) = 1$ for each i, which means that all females mate with the same rate. The mating rate in the infinitesimal model is of the form

$$m(x, y; \mu) = \frac{a(x, y)}{\int_F a(x, z)\mu(dz)}. \tag{5}$$

While considering hermaphroditic populations, one can expect a model with a symmetric mating rate. We obtain such a model assuming that the mating rate is of the form

$$m(x_i, x_j; \mathbf{x}) = \frac{a(x_i, x_j)}{2 \sum_{l=1}^{n} a(x_i, x_l)} + \frac{a(x_i, x_j)}{2 \sum_{l=1}^{n} a(x_j, x_l)}, \tag{6}$$

where $a(x, y)$ is a symmetric nonnegative preference function, e.g. $a(x, y) = \varphi(\|x - y\|)$ (in the case of populations without self-fertilization we eliminate the terms with $i = l$ and $j = l$ from the denominators). The mating rate in the infinitesimal model is now of the form

$$m(x, y; \mu) = \frac{a(x, y)}{2 \int_F a(x, z)\mu(dz)} + \frac{a(x, y)}{2 \int_F a(y, z)\mu(dz)}. \tag{7}$$

In the rest of the paper we will assume that the mating rate $m(x_i, x_j; \mathbf{x})$ is of the form (1) or (6).

2.3 Birth of a new individual

After mating/self-fertilization an offspring is born with probability 1. The trait of the offspring is drawn from a distribution $K(x_i, x_j, dz)$, where x_i and x_j are parental traits. We suppose that for every $x, y \in F$ the measure $K(x, y, \cdot)$ is a Borel probability measure with support contained in the set F, and assume that there exist positive constants c_1, c_2, c_3 such that

$$\int_F |z| K(x, y, dz) \leq c_1 + c_2|x| + c_3|y|, \tag{8}$$

and

$$\int_F z K(x, y, dz) = \frac{x + y}{2}. \tag{9}$$

The above condition has a simple biological interpretation, namely, the expected offspring's trait is the parental mean trait. Moreover, we suppose that for every $x, y \in F$ and for every Borel set $A \subset F$

$$K(x, y, A) = K(y, x, A), \tag{10}$$

and the function

$$(x, y) \mapsto K(x, y, A) \tag{11}$$

is measurable.

2.4 Competition and death rates

An individual from the population can die naturally or when competing with others. Let us denote by $I(x_i)$ the rate of interaction of the individual with trait x_i. We assume that I is a nonnegative function. For individuals with traits x_i and x_j we define a competition kernel $U(x_i, x_j)$, which is assumed to be a nonnegative and symmetric function. Competition always leads to death of one of the competitors. We assume that the natural death rate of the individual with trait x_i is expressed by a number $D(x_i)$, and suppose that D is a nonnegative function.

3 Stochastic process corresponding to the model

3.1 The dynamics of the population

We present the dynamics of the ecological system that we are interested in. The process starts at time $t = 0$ from an initial distribution. Individuals with traits x_i and x_j can mate at rate $m(x_i, x_j; \mathbf{x})$ of the form (1) or (6). After mating an offspring is born with probability one. An individual with trait x_i dies naturally at rate $D(x_i)$ or by competition at rate $I(x_i) \sum_j U(x_i, X_j(t))$, where the sum extends over all living individuals at time t, and $X_j(t)$ are their traits. We assume that all the events (mating, natural death, competition) are independent.

3.2 The phase space

We denote by $\mathbb{N}$ the set of all positive integers, δ_x stands for the Dirac measure concentrated at a point x, and $\mathbb{1}_A$ denotes the indicator function of a set A. We consider the space $M(F)$ of all finite positive Borel measures on F equipped with the topology of weak convergence of measures. We introduce the set $\mathcal{M} \subset M(F)$ of the form

$$\mathcal{M} = \left\{ \sum_{i=1}^{n} \delta_{x_i} : \ n \in \mathbb{N}, \ x_i \in F \right\}. \tag{12}$$

For any measure $\mu \in M(F)$ and any measurable function f we define $\langle \mu, f \rangle = \int_F f \, d\mu$. In particular, $\langle \mu, f \rangle = \sum_{i=1}^{n} f(x_i)$ if $\mu = \sum_{i=1}^{n} \delta_{x_i}$. We write $\mathcal{D}([0, \infty), \mathcal{M})$ for the Skorokhod space of all cad-lag functions from the interval $[0, \infty)$ to the set $\mathcal{M}$ (see for details, e.g., Ethier and Kurtz 1986, Skorokhod 1956).

3.3 Generator of the process

We consider a continuous time $\mathcal{M}$-valued stochastic process $(\nu_t)_{t \geq 0}$ with the infinitesimal generator L given for all bounded and measurable functions $\phi : \mathcal{M} \to \mathbb{R}$ by the formula

$$L\phi(\nu) = \int_F \int_F \int_F [\phi(\nu + \delta_z) - \phi(\nu)] m(x, y; \nu) K(x, y, dz) \nu(dx) \nu(dy)$$

$$+ \int_F [\phi(\nu - \delta_x) - \phi(\nu)] \left(D(x) + I(x) \int_F U(x, y) \nu(dy) \right) \nu(dx). \tag{13}$$

The first term in the right-hand side describes the mating and birth processes with the dispersal of traits. The second term stands for two kinds of death. The death part of the generator was previously studied in Fournier and Méléard (2004). Notice that, on the contrary to Fournier and Méléard (2004), the operator L has the first term nonlinear with respect to ν.

We assume that there are positive constants $\underline{a}, \overline{a}, \overline{D}, \overline{I}, \overline{U}$ such that for every $x, y \in F$

$$\underline{a} \leq a(x, y) \leq \overline{a}, \quad p(x) \leq \overline{p}, \quad D(x) \leq \overline{D}, \quad I(x) \leq \overline{I}, \quad U(x, y) \leq \overline{U}. \tag{14}$$

Under the above assumptions, if the initial measure $\nu_0 \in \mathcal{M}$ satisfies $\mathbb{E}\big(\langle \nu_0, 1 \rangle^q \big) < \infty$ for some number $q \geq 1$, then

$$\mathbb{E}\left(\sup_{0 \leq t \leq T} \langle \nu_t, 1 \rangle^q \right) < \infty$$

for any $T < \infty$. Consequently, the standard approach of Fournier and Méléard can be easily applied to prove the existence of the Markov process $(\nu_t)_{t \geq 0}$ with the infinitesimal generator given by formula (13) (see Fournier and Méléard 2004, Remenik (2009) for detailed proofs).

4 Macroscopic model

4.1 Macroscopic approximation

This section contains an approximation of the process which was introduced and studied in the previous sections. The idea is to normalize the initial model and pass with the number of individuals to infinity, assuming that the "mass" of each individual becomes negligible. In this approximation mating and death rates remain unchanged. Only the intensity of interaction is rescaled, and tends to 0 with an unbounded growth of the population. This approach leads to a deterministic nonlinear integro-differential equation whose solutions describe an evolution of trait distribution.

We consider a sequence of populations indexed by numbers $N \in \mathbb{N}$. If the Nth population consists of individuals $\mathbf{x}^N = \{x_1^N, \ldots, x_{n(N)}^N\}$, then

(a) individuals with traits x_i^N and x_j^N can mate with rate $m(x_i^N, x_j^N; \mathbf{x}^N)$ of the form (1) or (6),
(b) a new offspring's trait is drawn from a distribution $K(x_i^N, x_j^N, dz)$, where x_i^N, x_j^N are the traits of parents,
(c) an individual with trait x_i^N can die with rate $D(x_i^N)$,
(d) an individual with trait x_i^N interacts with other individuals with intensity $I(x_i^N)/N$,
(e) a competition kernel of individuals with traits x_i^N, x_j^N is a symmetric, nonnegative function $U(x_i^N, x_j^N)$.

The Nth population is described by a process $(v_t^N)_{t\geq 0}$ which is defined in the same way as the process $(v_t)_{t\geq 0}$ but with the corresponding coefficients. We define the $\mathcal{M}^N$-valued Markov process $(\mu_t^N)_{t\geq 0}$ by the formula $\mu_t^N = v_t^N/N$. The value space for the process $(\mu_t^N)_{t\geq 0}$ is thus

$$\mathcal{M}^N = \left\{ \frac{1}{N} v : v \in \mathcal{M} \right\}.$$

The generator L^N of the process $(\mu_t^N)_{t\geq 0}$ is given by

$$L^N \phi(v) = N \int_F \int_F \int_F \left(\phi\left(v + \frac{1}{N}\delta_z\right) - \phi(v) \right) m(x, y; v) K(x, y, dz)\, v(dx)\, v(dy)$$

$$+ N \int_F \left(\phi\left(v - \frac{1}{N}\delta_x\right) - \phi(v) \right) \left(D(x) + I(x) \int_F U(x, y)\, v(dy) \right) v(dx).$$

for any measurable and bounded map $\phi \colon \mathcal{M}^N \to \mathbb{R}$.

Theorem 1 *We assume that condition (14) holds, and the functions a, p, k, D, I, U are continuous. We suppose that $\mathbb{E}\big(\langle \mu_0^N, 1 \rangle^q \big) < \infty$ for some $q \geq 2$ and all $N \in \mathbb{N}$, and almost each sequence $(\mu_0^N)_{N\in\mathbb{N}}$ converges weakly to a deterministic finite measure*

μ_0, as $N \to \infty$. Then for all $T > 0$ the sequence of processes $(\mu_t^N)_{N \in \mathbb{N}}$ converges in distribution in $\mathcal{D}([0, T], M(F))$ to a deterministic and continuous measure-valued function $[0, T] \ni t \mapsto \mu_t \in M(F)$, satisfying the following equation

$$
\langle \mu_t, f \rangle = \langle \mu_0, f \rangle + \int_0^t \int_F \int_F \int_F f(z) m(x, y; \mu_s) K(x, y, dz) \, \mu_s(dx) \, \mu_s(dy) \, ds
$$

$$
- \int_0^t \int_F f(x) \Big(D(x) + I(x) \int_F U(x, y) \, \mu_s(dy) \Big) \mu_s(dx) \, ds \qquad (15)
$$

for every bounded and measurable function $f : F \to \mathbb{R}$.

The standard proof of the above theorem is based on Ethier and Kurtz (1986) Corollary 8.16, Chapter 4, and since mating is described by the Lipschitz continuous operator on the space of positive and finite Borel measures with total variation norm, it can be directly adapted for example, from Rudnicki and Wieczorek (2006a).

4.2 Strong solutions in the space of measures

According to Theorem 1 the solutions of (15) are continuous in the topology of weak convergence of measures. In this part we show a stronger result that they are also continuous in the total variation norm $\|\nu\|_{TV} = \sup\{|\langle \nu, f \rangle| : \ f - \text{measurable}, \sup_{x \in F} |f(x)| \leq 1\}$. We use the following formal notation

$$
\frac{d}{dt} \mu_t(dz) = \int_F \int_F m(x, y; \mu_t) \, K(x, y, dz) \mu_t(dx) \mu_t(dy)
$$

$$
- \Big(D(z) + I(z) \int_F U(z, y) \mu_t(dy) \Big) \mu_t(dz), \qquad (16)
$$

of equation (15) in the space of positive, finite Borel measures $M(F)$ on the set F with the total variation norm.

Theorem 2 *Assume that the functions a, p, D, I, U and (11) are measurable, and condition (14) holds. Moreover, suppose that there exist positive constants $\underline{p}, \underline{I}, \underline{U}$ such that*

$$
p(x) \geq \underline{p}, \quad I(x) \geq \underline{I}, \quad U(x, y) \geq \underline{U}, \qquad (17)
$$

for all $x, y \in F$. If $\mu_0 \in M(F)$, then there exists a unique solution μ_t, $t \geq 0$, of Eq. (16) with the initial condition μ_0. The function $t \mapsto \mu_t$ is bounded and continuous in the norm $\| \cdot \|_{TV}$.

Proof Let us fix $T \geq 0$, $\delta > 0$ and consider the space $C_T = C([T, T + \delta], M(F))$ with the norm $\|\mu.\|_T = \sup_{t \in [T, T+\delta]} \|\mu_t\|_{TV}$. Define the operator $\Lambda : C_T \to C_T$ by the formula

$$(\Lambda\mu.)(t)(dz) = \mu_T(dz) + \int\limits_T \int\limits_F \int\limits_F m(x, y; \mu_s) K(x, y, dz)\, \mu_s(dx)\, \mu_s(dy)\, ds$$

$$- \int\limits_T \left(D(z) + I(z) \int\limits_F U(z, y)\mu_s(dy) \right) \mu_s(dz)\, ds,$$

where $\mu_T \in M(F)$ is some measure. Notice that from assumption (14) there are constants $\overline{m}, \hat{m}$ depending on $\overline{p}$ in the case of semi-random mating, and on $\underline{a}, \overline{a}$ in the case of assortative mating, such that for any $y \in F$ and measures $\mu, \nu \in M(F)$

$$\int\limits_F m(x, y; \nu)\, \nu(dx) \le \overline{m}, \tag{18}$$

and

$$\int\limits_F \int\limits_F |m(x, y; \mu) - m(x, y; \nu)|\, \mu(dx)\, \nu(dy) \le \hat{m}\|\mu - \nu\|_{TV}. \tag{19}$$

Take functions $\mu., \nu. \in C_T$ from the ball $B(0, 2\|\mu_T\|_{TV})$. Then

$$\|\Lambda\mu.\|_T \le \|\mu_T\|_{TV} + 2\delta(\overline{m} + \overline{D})\|\mu_T\|_{TV} + 4\delta\overline{IU}\|\mu_T\|_{TV}^2, \tag{20}$$

and

$$\|\Lambda\mu. - \Lambda\nu.\|_T \le \delta\left(\overline{D} + 2\overline{m} + 4\hat{m}\|\mu_T\|_{TV}^2\right)\|\mu. - \nu.\|_T + 4\delta\overline{IU}\|\mu_T\|_{TV}\|\mu. - \nu.\|_T. \tag{21}$$

Taking $\delta > 0$ sufficiently small, from (20) and (21) it follows that Λ transforms the ball $B(0, 2\|\mu_T\|_{TV})$ into itself, and is Lipschitz continuous with some constant $L < 1$. By the Banach fixed point theorem the operator Λ has a unique fixed point and, consequently, (16) has a unique local solution.

In order to extend a local solution to the whole interval $[0, \infty)$ it is sufficient to show that the solution is bounded. Notice that

$$\frac{d}{dt}\|\mu_t\|_{TV} \le \|\mu_t\|_{TV}\left(\overline{m} - \underline{I}\,\underline{U}\|\mu_t\|_{TV}\right), \tag{22}$$

and consequently

$$\|\mu_t\|_{TV} \le \max\left\{\|\mu_0\|_{TV}, \frac{\overline{m}}{\underline{I}\,\underline{U}}\right\},$$

which completes the proof of the global existence and uniqueness.

Eventually, we show that the measure μ_t is positive for $t > 0$. Indeed, for any Borel set A we can write $\frac{d}{dt}\mu_t(A) \geq -\phi(t)\mu_t(A)$, where $\phi(t) = \left(\overline{D} + \overline{IU}\mu_t(F)\right)$. Hence

$$\mu_t(A) \geq \mu_0(A)\exp\left\{-\int_0^t \phi(s)\,ds\right\} \geq 0.$$

$\square$

A straight-forward conclusion is the following statement about solutions in L^1 space.

Corollary 1 *Suppose that for each $x, y \in F$ the measure $K(x, y, dz)$ is absolutely continuous with respect to the Lebesgue measure and*

$$K(x, y, dz) = k(x, y, z)\,dz. \tag{23}$$

Under the assumptions of Theorem 2, if μ_0 has a density $u_0 \in L^1$ with respect to the Lebesgue measure, then μ_t also has a density $u(t, \cdot) \in L^1$ and $u(t, z)$ is the unique solution of the following equation

$$\frac{\partial}{\partial t}u(t, z) = \int_F \int_F m(x, y; u(t, \xi)d\xi)\,k(x, y, z)u(t, x)u(t, y)\,dx\,dy$$

$$- \left(D(z) + I(z)\int_F U(z, y)u(t, y)\,dy\right)u(t, z), \tag{24}$$

with the initial condition $u(0, \cdot) = u_0(\cdot)$.

Proof Take a Borel set A with zero Lebesgue measure. Since the measure $K(x, y, dz)$ is absolute continuous with respect to the Lebesgue measure, $K(x, y, A) = 0$ for every $x, y \in F$, and consequently $\frac{d}{dt}\mu_t(A) \leq -\underline{D}\,\mu_t(A)$, and $\mu_0(A) = 0$. Therefore $\mu_t(A) = 0$ for all $t > 0$, and the statement comes from the Radon-Nikodym theorem. $\square$

4.3 Boundedness, extinction and persistence

From the proof of Theorem 2 it follows that the function $M(t) = \mu_t(F)$ is upper-bounded. Now we analyze further properties of $M(t)$. Let us recall that a population *becomes extinct* if $\lim_{t\to\infty} M(t) = 0$, and *is persistent* provided $\lim\inf_{t\to\infty} M(t) > 0$.

Proposition 1 *If $\inf_z D(z) \geq \sup_z p(z)$ in the case of random mating and $\inf_z D(z) \geq 1$ in the case of assortative mating, then the population becomes extinct. If $\sup_z D(z) < \inf_z p(z)$ in the case of random mating and $\sup_z D(z) < 1$ in the case of assortative mating, then the population is persistent.*

Proof In the case of random mating these properties follow simply from the inequalities

$$M'(t) \leq M(t) \left(\bar{p} - \underline{D} - \underline{I}\,\underline{U}M(t) \right)$$

and

$$M'(t) \geq M(t) \left(\underline{p} - \overline{D} - \overline{I}\,\overline{U}M(t) \right).$$

In the case of assortative mating we use similar inequalities with $\bar{p}$ and $\underline{p}$ replaced by 1. □

4.4 Equation on a global attractor

In order to describe more precisely asymptotic behavior of $M(t)$, we need to assume that the functions p, D, I, U do not depend on x, and are positive. To avoid extinction of the population, we additionally assume that $D < p$ in the case of random mating and $D < 1 =: p$ in the case of assortative mating (see Proposition 1). Then $M(t)$ satisfies the following equation

$$M'(t) = pM(t) - (D + IUM(t))M(t),$$

and $\bar{M} = (p - D)/(IU)$ is a stationary solution of this equation. Using basic facts from the theory of differential equations, it is easy to see that

$$\lim_{t \to \infty} M(t) = \bar{M}. \tag{25}$$

The number $\bar{M}$ is an analogue of *carrying capacity* studied in Bolker and Pacala (1997) and Fournier and Méléard (2004). In our case $\bar{M}$ is a number of individuals per unit of volume after long time.

From (25) it follows that all positive solutions converge to the set

$$\mathcal{A} = \left\{ \mu \in M(F) \colon \ \mu(F) = \bar{M} \right\},$$

which is invariant with respect to Eq. (16), i.e., if an initial condition μ_0 belongs to $\mathcal{A}$, then $\mu_t \in \mathcal{A}$ for $t > 0$. It means that $\mathcal{A}$ is a *global attractor* for Eq. (16). If $\mu_0 \in \mathcal{A}$ then the function $t \mapsto \mu_t$ satisfies the following equation

$$\frac{d}{dt}\mu_t(dz) = \int_F \int_F m(x, y; \mu_t)\, K(x, y, dz)\, \mu_t(dx)\, \mu_t(dy) - p\mu_t(dz). \tag{26}$$

Let μ_t be a positive solution of (16). If we substitute $\bar{\mu}_t = \frac{\bar{M}}{M(t)}\mu_t$, then the function $t \mapsto \bar{\mu}_t$ also satisfies (26). Therefore, the long-time behaviour of solutions of (26) is completely characterized by the dynamics on the attractor $\mathcal{A}$.

Now we consider only solutions on the set $\mathcal{A}$. If we replace $\mu_t(dx)$ by $\bar{M}\mu_t(dx)$ and t by pt in (26), then $\mu_t(dz)$ becomes a probability measure for all $t \geq 0$. The function $t \mapsto \mu_t$ satisfies

$$\frac{d}{dt}\mu_t(dz) + \mu_t(dz) = \int_F \int_F K(x, y, dz)\mu_t(dx)\mu_t(dy), \qquad (27)$$

in the case of random mating, and

$$\frac{d}{dt}\mu_t(dz) + \mu_t(dz) = \int_F \int_F \psi(x, y; \mu_t)K(x, y, dz)\mu_t(dx)\mu_t(dy), \qquad (28)$$

in the case of assortative mating, where

$$\psi(x, y; \mu) = \frac{a(x, y)}{2 \int_F a(x, r)\mu(dr)} + \frac{a(x, y)}{2 \int_F a(y, r)\mu(dr)}.$$

5 Asymptotic stability in the case of random mating

5.1 General remarks

In this section we study the convergence of solutions of Eq. (27) to some stationary solutions. Equation (27) can be treated as an evolution equation

$$\mu_t' = \mathcal{P}\mu_t - \mu_t, \qquad (29)$$

where the operator $\mathcal{P}$ acting on the space of all probability Borel measures on F is given by the formula

$$(\mathcal{P}\mu)(A) = \int_F \int_F K(x, y, A)\,\mu(dx)\,\mu(dy). \qquad (30)$$

The solution of (29) with an initial measure μ_0 is the deterministic process μ_t given by Theorem 2. The set $\mathcal{O}(\mu_0) := \{\mu_t : t \geq 0\}$ is called the *orbit* of μ_0.

Since the problem of the asymptotic stability of the solutions of Eq. (29) in an arbitrary d-dimensional space seems to be quite difficult, we consider only the case when $d = 1$ and F is a closed interval with nonempty interior. Generally, Eq. (29) has a lot of different stationary measures and it is rather difficult to predict a limit of a given solution. Assumption (9) allows us to omit this difficulty. Indeed, if a measure μ has a finite first moment q, then according to (8) and (9) we have

$$\int\limits_F |z| \, (\mathcal{P}\mu)(dz) = \int\limits_F \int\limits_F \int\limits_F |z| K(x, y, dz) \, \mu(dx) \, \mu(dy)$$

$$\leq \int\limits_F \int\limits_F (c_1 + c_2|x| + c_3|y|) \, \mu(dx) \, \mu(dy)$$

$$\leq c_1 + (c_2 + c_3) \int\limits_F |x| \, \mu(dx) < \infty$$

and

$$\int\limits_F z \, (\mathcal{P}\mu)(dz) = \int\limits_F \int\limits_F \int\limits_F z K(x, y, dz) \, \mu(dx) \, \mu(dy) = \int\limits_F \int\limits_F \frac{x + y}{2} \, \mu(dx) \, \mu(dy) = q.$$

Therefore, any solution μ_t of Eq. (29) has the same first moment for all $t \geq 0$. It means that we can restrict our consideration only to probability Borel measures with the same first moment.

The following example shows why we consider solutions of Eq. (29) with values in the space of probability Borel measures instead of the space of probability densities. In this example all the stationary solutions are the Dirac measures, and any solution converges in the weak sense to some stationary measure.

Example 1 Let Z be a random variable with values in the interval $[-1, 1]$ such that $\mathbb{E}Z = 0$ and $|Z| \not\equiv 1$. Assume that if x and y are parental traits, then the trait of an offspring is given by

$$\frac{x + y}{2} + Z \frac{|x - y|}{2},$$

i.e., the trait of an offspring is distributed between the traits of parents according to the law of Z. For a random variable X we denote by $m_1(X)$ and $m_2(X)$ its first and second moments and by $D(X)$ its variance, i.e., $D(X) = m_2(X) - (m_1(X))^2$. Let μ_t, $t \geq 0$, be a solution of (29) with a finite second moment, and let X_t, $t \geq 0$, be random variables with distribution measures μ_t. Then $\bar{x} := m_1(X_t)$ is a constant, and

$$\frac{d}{dt} D(X_t) = -\frac{1}{2}(1 - D(Z))D(X_t). \tag{31}$$

Since $D(Z) < 1$, we have $\lim_{t \to \infty} D(X_t) = 0$. Consequently, μ_t converges weakly to $\delta_{\bar{x}}$.

5.2 The Wasserstein distance

In order to investigate asymptotic properties of the solutions, we recall some basic facts concerning the Wasserstein distance between measures. For $\alpha \geq 1$ we denote by $\mathcal{M}_\alpha$ the set of all probability Borel measures μ on F such that $\int_F |z|^\alpha \, \mu(dz) < \infty$ and

by $\mathcal{M}_{\alpha,q}$ the subset of $\mathcal{M}_\alpha$ which contains all the measures such that $\int_F z\,\mu(dz) = q$. For any two measures μ, $\nu \in \mathcal{M}_1$, we define the *Wasserstein distance* by the formula

$$d(\mu, \nu) = \sup_{f \in \mathrm{Lip}_1} \int_F f(z)(\mu - \nu)(dz), \tag{32}$$

where Lip_1 is the set of all continuous functions $f : F \to \mathbb{R}$ such that for any x, $y \in F$

$$|f(x) - f(y)| \leq |x - y|.$$

The following lemma is of a great importance in the subsequent part of the paper.

Lemma 1 *The Wasserstein distance between measures μ, $\nu \in \mathcal{M}_1$ can be computed by the formula*

$$d(\mu, \nu) = \int_F |\Phi(x)|\,dx, \tag{33}$$

where $\Phi(z) = (\mu - \nu)(F \cap (-\infty, z])$ is the cumulative distribution function of the signed measure $\mu - \nu$.

Proof Let Φ_μ and Φ_ν be the cumulative distribution functions of the measures μ and ν. Since these measures have finite first absolute moments we have

$$\lim_{x \to -\infty} |x|\Phi_\mu(x) = \lim_{x \to -\infty} |x|\Phi_\nu(x) = 0$$

and

$$\lim_{x \to \infty} x(1 - \Phi_\mu(x)) = \lim_{x \to \infty} x(1 - \Phi_\nu(x)) = 0.$$

This gives

$$\limsup_{x \to \pm\infty} |f(x)|\Phi(x) \leq \lim_{x \to \pm\infty} |x|\Phi(x) = 0 \quad \text{for } f \in \mathrm{Lip}_1$$

and if F is bounded from below or from above, then we have $\Phi(x) = 0$ for $x \notin F$. Since f is a locally absolutely continuous function, integrating by parts leads to the formula

$$d(\mu, \nu) = \sup_{f \in \mathrm{Lip}_1} \int_F f(z)\,d\Phi(z) = \sup_{f \in \mathrm{Lip}_1} - \int_F f'(z)\Phi(z)\,dz.$$

Clearly the supremum is taken when $f'(z) = -\operatorname{sgn}\Phi(z)$. $\square$

Consider probability measures μ and μ_n, $n \in \mathbb{N}$, on the set F. We recall that the sequence (μ_n) converges *weakly* (or *in a weak sens*) to μ, if for any continuous and bounded function $f : F \to \mathbb{R}$

$$\int_F f(x)\,\mu_n(dx) \to \int_F f(x)\,\mu(dx),$$

as $n \to \infty$. It is well-known that the convergence in the Wasserstein distance implies the weak convergence of measures. Moreover, the space of probability Borel measures on any complete metric space is also a complete metric space with the Wasserstein distance (see e.g. Bolley 1934; Rachev 1991). The convergence of the sequence μ_n to μ in the space $\mathcal{M}_{1,q}$ is equivalent to the following condition (see Villani (2008), Definition 6.7 and Theorem 6.8)

$$\mu_n \to \mu \text{ weakly, as } n \to \infty \quad \text{and} \quad \lim_{R\to\infty} \limsup_{n\to\infty} \int_{F_R} |x|\mu_n(dx) = 0, \quad \text{(C)}$$

where $F_R := \{x \in F : |x| \geq R\}$. Fix $q \in F$, $\alpha > 1$, and $m > 0$. Consider a set $\widetilde{\mathcal{M}} \subset \mathcal{M}_{1,q}$ such that

$$\int_F |x|^\alpha \mu(dx) \leq m \tag{34}$$

for all $\mu \in \widetilde{\mathcal{M}}$. Then the set $\widetilde{\mathcal{M}}$ is relatively compact in $\mathcal{M}_{1,q}$. Indeed, by Markov inequality, $\mu(\{x : |x| \leq R\}) \geq 1 - m/R^\alpha$ for all $\mu \in \widetilde{\mathcal{M}}$, what means that the set $\widetilde{\mathcal{M}}$ is tight, and thus $\widetilde{\mathcal{M}}$ is relatively compact in the topology of weak convergence (see e.g. Billingsley (1995)). Moreover, for $\mu \in \widetilde{\mathcal{M}}$ we have

$$\int_{F_R} |x|\mu_k(dx) \leq \frac{1}{R^{\alpha-1}} \int_{F_R} |x|^\alpha \mu_k(dx) \leq \frac{m}{R^{\alpha-1}},$$

which implies the second condition in (C). Consequently, the set $\widetilde{\mathcal{M}}$ is relatively compact in $\mathcal{M}_{1,q}$.

5.3 Theorems on asymptotic stability

We use the script letter $\mathcal{K}$ for the cumulative distribution function of the measure K, i.e.,

$$\mathcal{K}(x, y, z) = K(x, y, F \cap (-\infty, z]).$$

The main result of this section is the following.

Theorem 3 *Fix $q \in F$. Suppose that*

(i) for all $y, z \in F$ the function $\mathcal{K}(x, y, z)$ is absolutely continuous with respect to x and for each $a, b, y \in F$ we have

$$\int_F \left| \frac{\partial}{\partial x} \mathcal{K}(a, y, z) - \frac{\partial}{\partial x} \mathcal{K}(b, y, z) \right| dz < 1, \tag{35}$$

(ii) there are constants $\alpha > 1$, $L < 1$, and $C \geq 0$ such that for every $\mu \in \mathcal{M}_{\alpha,q}$ we have

$$\int\limits_{F} |x|^{\alpha} \mathcal{P}\mu(dx) \leq C + L \int\limits_{F} |x|^{\alpha}\mu(dx). \tag{36}$$

Then for every initial measure $\mu_0 \in \mathcal{M}_{1,q}$ there exists a unique solution μ_t, $t \geq 0$, of Eq. (27) with values in $\mathcal{M}_{1,q}$. Moreover, there exists a unique measure $\mu^* \in \mathcal{M}_{1,q}$ such that $\mathcal{P}\mu^* = \mu^*$ and for every initial measure $\mu_0 \in \mathcal{M}_{1,q}$ the solution μ_t, $t \geq 0$, of Eq. (27) converges to μ^* in the space $\mathcal{M}_{1,q}$.

We split the proof of Theorem 3 into a sequence of lemmas. Denote by $\mathcal{F}_q$ the set of all cumulative distribution functions of the signed measures of the form $\mu - \nu$, where $\mu, \nu \in \mathcal{M}_{1,q}$.

Lemma 2 *Suppose that for all $y \in F$ and $\Phi \in \mathcal{F}_q$, $\Phi \not\equiv 0$, we have*

$$2 \int\limits_{F} \left| \int\limits_{F} \mathcal{K}(x, y, z)\Phi(dx) \right| dz < \int\limits_{F} |\Phi(x)| \, dx. \tag{37}$$

Then

$$d(\mathcal{P}\mu, \mathcal{P}\nu) < d(\mu, \nu) \tag{38}$$

for $\mu, \nu \in \mathcal{M}_{1,q}$, $\mu \neq \nu$. In particular, for every initial measure $\mu_0 \in \mathcal{M}_{1,q}$ there exists a unique solution μ_t, $t \geq 0$, of Eq. (27) with values in $\mathcal{M}_{1,q}$. ☐

Proof Since $K(x, y, \cdot) = K(y, x, \cdot)$, we can write

$$\mathcal{P}\mu - \mathcal{P}\nu = 2 \int\limits_{F} \int\limits_{F} K(x, y, \cdot)(\mu - \nu)(dx)\,\bar{\mu}(dy),$$

where $\bar{\mu} = (\mu + \nu)/2$. If $\Phi(x)$ is the cumulative distribution function of $\mu - \nu$, then the signed measure $\mathcal{P}\mu - \mathcal{P}\nu$ has the cumulative distribution function of the form

$$2 \int\limits_{F} \int\limits_{F} \mathcal{K}(x, y, z)\,\Phi(dx)\,\bar{\mu}(dy).$$

Hence

$$d(\mathcal{P}\mu, \mathcal{P}\nu) = 2 \int\limits_{F} \left| \int\limits_{F} \int\limits_{F} \mathcal{K}(x, y, z)\,\Phi(dx)\,\bar{\mu}(dy) \right| dz$$

$$\leq 2 \int\limits_{F} \int\limits_{F} \left| \int\limits_{F} \mathcal{K}(x, y, z)\,\Phi(dx) \right| dz\,\bar{\mu}(dy)$$

$$< \int\limits_{F} \int\limits_{F} |\Phi(x)| \, dx\,\bar{\mu}(dy) = \int\limits_{F} |\Phi(x)| \, dx = d(\mu, \nu).$$

☐

Lemma 3 *Suppose that condition (i) of Theorem 3 is fulfilled. Then condition (37) holds.*

Proof Take a $\Phi \in \mathcal{F}_q$ and denote $\Phi^+(x) = \max\{0, \Phi(x)\}$ and $\Phi^-(x) = \max\{0, -\Phi(x)\}$. Since Φ is the cumulative distribution function of $\mu - \nu$, where $\mu, \nu \in \mathcal{M}_{1,q}$, we have

$$\int\limits_F \Phi(x)\, dx = -\int\limits_F x\, \Phi(dx) = \int\limits_F x\, \Phi_\nu(dx) - \int\limits_F x\, \Phi_\mu(dx) = 0,$$

and, consequently,

$$\int\limits_F \Phi^+(x)\, dx = \int_F \Phi^-(x)\, dx = \frac{1}{2}\int\limits_F |\Phi(x)|\, dx. \tag{39}$$

Since Φ^+ and Φ^- are nonnegative functions and have the same integral, condition (35) implies

$$\int\limits_F \left| \int\limits_F \frac{\partial}{\partial x}\mathcal{K}(x, y, z)\Phi^+(x)\, dx - \int\limits_F \frac{\partial}{\partial x}\mathcal{K}(x, y, z)\Phi^-(x)\, dx \right| dz < \int\limits_F \Phi^+(x)\, dx. \tag{40}$$

Integrating $\int_F \mathcal{K}(x, y, z)\Phi(dx)$ by parts we obtain

$$\int\limits_F \mathcal{K}(x, y, z)\Phi(dx) = -\int\limits_F \frac{\partial}{\partial x}\mathcal{K}(x, y, z)\Phi(x)\, dx. \tag{41}$$

From (40) and (41) it follows

$$2\int\limits_F \left| \int\limits_F \mathcal{K}(x, y, z)\Phi(dx) \right| dz < 2\int\limits_F \Phi^+(x)\, dx = \int\limits_F |\Phi(x)|\, dx.$$

$\square$

Lemma 4 *Assume that $d(\mathcal{P}\mu, \mathcal{P}\nu) < d(\mu, \nu)$ for all $\mu, \nu \in \mathcal{M}_{1,q}$, $\mu \neq \nu$. Let $\mu_0, \nu_0 \in \mathcal{M}_{1,q}$ and denote by μ_t and ν_t, respectively, the solutions of Eq. (29) in the space of probability Borel measures on F. Then $\mu_t, \nu_t \in \mathcal{M}_{1,q}$ for $t \geq 0$ and $d(\mu_t, \nu_t) < d(\mu_r, \nu_r)$ for $0 \leq r < t \leq T$ provided that $\mu_T \neq \nu_T$.*

Proof Since $\mathcal{P}(\mathcal{M}_{1,q}) \subset \mathcal{M}_{1,q}$ every solution of (29) with an initial value from the set $\mathcal{M}_{1,q}$ remains in this set for all $t \geq 0$. Any solution μ_t of (29) satisfies the following integral equation

$$\mu_t = e^{r-t}\mu_r + \int\limits_r^t e^{s-t}\mathcal{P}\mu_s\, ds. \tag{42}$$

Let μ_t and ν_t be solutions of (29) with values in $\mathcal{M}_{1,q}$ and such that $\mu_T \neq \nu_T$. Then $\mu_t \neq \nu_t$ for $t \leq T$ and from (42) it follows that

$$
d(\mu_t, \nu_t) \leq e^{r-t} d(\mu_r, \nu_r) + \int_r^t e^{s-t} d(\mathcal{P}\mu_s, \mathcal{P}\nu_s)\, ds
$$

$$
< e^{r-t} d(\mu_r, \nu_r) + \int_r^t e^{s-t} d(\mu_s, \nu_s)\, ds
$$

for $0 \leq r < t \leq T$. Let $\alpha(s) = e^s d(\mu_s, \nu_s)$. Then

$$
\alpha(t) < \alpha(r) + \int_r^t \alpha(s)\, ds
$$

and from Gronwall's lemma it follows that $\alpha(t) < \alpha(r)e^{t-r}$, which gives $d(\mu_t, \nu_t) < d(\mu_r, \nu_r)$. $\qquad\square$

Lemma 5 *Assume that condition (ii) of Theorem 3 is fulfilled. Then for every initial measure $\mu_0 \in \mathcal{M}_{\alpha,q}$ its orbit $\mathcal{O}(\mu_0)$ is a relatively compact subset of $\mathcal{M}_{1,q}$. Moreover, $\mathrm{cl}\,\mathcal{O}(\mu_0) \subset \mathcal{M}_{\alpha,q}$, where $\mathrm{cl}\,\mathcal{O}(\mu_0)$ denotes the closure of $\mathcal{O}(\mu_0)$ in $(\mathcal{M}_{1,q}, d)$.*

Proof Take a $\mu_0 \in \mathcal{M}_{\alpha,q}$ and let μ_t be a solution of (29) with the initial condition μ_0. Let $m_0 = C/(1 - L)$, $m_\alpha = \int_F |x|^\alpha \mu_0(dx)$, and $m = \max\{m_0, m_\alpha\}$. We check that $\mu_t \in \mathcal{M}_{\alpha,q}$ for $t \geq 0$ and

$$
\int_F |x|^\alpha \mu_t(dx) \leq m \text{ for } t \geq 0. \tag{43}
$$

To see this, we define the set

$$
\mathcal{M}_{\alpha,q,m} = \left\{ \mu \in \mathcal{M}_{1,q} : \int_F |x|^\alpha \mu(dx) \leq m \right\}.
$$

Then $\mathcal{M}_{\alpha,q,m}$ is a closed and convex subset of $\mathcal{M}_{1,q}$. Hence $C([0, T], \mathcal{M}_{\alpha,q,m})$ is a closed subset of $C([0, T], \mathcal{M}_{1,q})$. For a sufficiently small $T > 0$, the map

$$
(\Lambda\mu)_t = e^{-t}\mu_0 + \int_0^t e^{s-t}\mathcal{P}\mu_s\, ds
$$

is a contraction on the space $C([0, T], \mathcal{M}_{1,q})$ and the function $t \mapsto \mu_t$, $0 \leq t \leq T$, is its fixed point. In order to prove that $\mu_t \in \mathcal{M}_{\alpha,q}$ for $t \geq 0$ and that (43) holds,

it is sufficient to check that the set $C([0, T], \mathcal{M}_{\alpha,q,m})$ is invariant with respect to Λ. Indeed, since $C + Lm \leq m$ we have

$$
\begin{aligned}
\int_F |x|^\alpha \, (\Lambda\mu)_t(dx) &= e^{-t} \int_F |x|^\alpha \, \mu_0(dx) + \int_0^t e^{s-t} \int_F |x|^\alpha \, \mathcal{P}\mu_s(dx) \, ds \\
&\leq e^{-t} \int_F |x|^\alpha \, \mu_0(dx) + \int_0^t e^{s-t} \left(C + L \int_F |x|^\alpha \, \mu_s(dx) \right) ds \\
&\leq e^{-t} m + \int_0^t e^{s-t} (C + Lm) \, ds \leq m.
\end{aligned}
$$

Thus, there exists $m > 0$ depending on μ_0 and $\alpha > 1$ such that (43) holds. Consequently, the orbit is a relatively compact subset of $\mathcal{M}_{1,q}$ and $\mathrm{cl}\,\mathcal{O}(\mu_0) \subset \mathcal{M}_{\alpha,q}$. $\qquad\square$

Let $\{S(t)\}_{t \geq 0}$ be a family of transformations of $\mathcal{M}_{1,q}$ defined by $S(t)\mu_0 = \mu_t$, where μ_t is the solution of (29) with the initial condition μ_0. For $\mu \in \mathcal{M}_{1,q}$ we define the ω-*limit set* by

$$
\omega(\mu) = \left\{ \nu \colon \nu = \lim_{n \to \infty} \mu_{t_n} \text{ for a sequence } (t_n)_{n \in \mathbb{N}} \text{ with } \lim_{n \to \infty} t_n = \infty \right\}.
$$

Proof of Theorem 3 Take a measure $\mu \in \mathcal{M}_{\alpha,q}$. According to Lemma 5 the orbit of μ is a relatively compact subset of $\mathcal{M}_{1,q}$. From this it follows that $\omega(\mu)$ is a nonempty compact set and for $t > 0$ we have $S(t)(\omega(\mu)) = \omega(\mu)$. First we check that $\omega(\mu)$ is a singleton. Indeed, if $\omega(\mu)$ has more than one element, then since $\omega(\mu)$ is a compact set, we can find two elements ν_1 and ν_2 in $\omega(\mu)$ with maximum distance $d(\nu_1, \nu_2)$. But since $S(t)(\omega(\mu)) = \omega(\mu)$, then for given $t > 0$ there exist $\bar\nu_1$ and $\bar\nu_2$ in $\omega(\mu)$ such that $S(t)\bar\nu_1 = \nu_1$ and $S(t)\bar\nu_2 = \nu_2$. Now from condition (i) and Lemmas 2, 3, and 4 it follows that

$$
d(\nu_1, \nu_2) = d(S(t)\bar\nu_1, S(t)\bar\nu_2) < d(\bar\nu_1, \bar\nu_2),
$$

which contradicts the definition of ν_1 and ν_2. Let $\omega(\mu) = \{\mu^*\}$. Then $S(t)\mu^* = \mu^*$ for $t \geq 0$ and, consequently, $\mathcal{P}\mu^* = \mu^*$. Since the orbit $\mathcal{O}(\mu)$ is relatively compact, we have $\lim_{t \to \infty} S(t)\mu = \mu^*$. According to Lemmas 2 and 3 the operator $\mathcal{P}$ has only one fixed point what means that the limit $\lim_{t \to \infty} S(t)\mu$ does not depend on $\mu \in \mathcal{M}_{\alpha,q}$. Now, we consider a measure $\mu \in \mathcal{M}_{1,q}$. The set $\mathcal{M}_{\alpha,q}$ is dense in the space $\mathcal{M}_{1,q}$. Thus, for every $\varepsilon > 0$ we can find $\bar\mu \in \mathcal{M}_{\alpha,q}$ such that $d(\mu, \bar\mu) < \varepsilon$. Moreover, since $\lim_{t \to \infty} S(t)\bar\mu = \mu^*$ we find t_ε such that $d(S(t)\bar\mu, \mu^*) < \varepsilon$ for $t \geq t_\varepsilon$. As the operators $S(t)$ are contractions we have

$$
d(S(t)\mu, \mu^*) \leq d(S(t)\mu, S(t)\bar\mu) + d(S(t)\bar\mu, \mu^*) < 2\varepsilon
$$

for $t \geq t_\varepsilon$, which completes the proof. $\qquad\square$

We can strengthen the thesis of Theorem 3, if we additionally assume that for all $x, y \in F$ the measure $K(x, y, dz)$ has a density $k(x, y, z)$ and k is a bounded and continuous function.

Theorem 4 *Assume that k is a bounded and continuous function, and k satisfies assumptions of Theorem 3. Then the stationary measure μ^* is absolutely continuous with respect to the Lebesgue measure and has a continuous and bounded density $u_*(x)$. Moreover, for every $\mu_0 \in \mathcal{M}_{1,q}$ the solution μ_t of Eq. (27) can be written in the form $\mu_t = e^{-t}\mu_0 + \nu_t$, where ν_t are absolutely continuous measures, have continuous and bounded densities $\nu_t(x)$, which converge uniformly to $u_*(x)$.*

Proof Since k is a continuous and bounded function and μ^* is a probability measure,

$$u_*(z) := \int\limits_F \int\limits_F k(x, y, z)\, \mu^*(dx)\, \mu^*(dy)$$

is a continuous bounded function and u_* is a density of μ^* because μ^* is a fixed point of the operator $\mathcal{P}$. For any initial measure $\mu_0 \in \mathcal{M}_{1,q}$ the solution μ_t of (27) satisfies the equation

$$\mu_t = e^{-t}\mu_0 + \int\limits_0^t e^{s-t}\mathcal{P}\mu_s \, ds.$$

For each $s \geq 0$ the measure $\mathcal{P}\mu_s$ has a continuous and bounded density $\bar{u}_s(x)$. Since the function $\varphi \colon [0, \infty) \to \mathcal{M}_{1,q}$ given by $\varphi(s) = \mu_s$ is continuous and $\lim_{s\to\infty} \mu_s = \mu^*$, the function $\psi \colon [0, \infty) \to C_b(F)$ given by $\psi(s) = \bar{u}_s$ is continuous and $\lim_{s\to\infty} \bar{u}_s = u_*$. Thus the measures $\nu_t = \int_0^t e^{s-t}\mathcal{P}\mu_s \, ds$ have continuous and bounded densities $\nu_t(x)$ and ν_t converges uniformly to u_* as $t \to \infty$. $\qquad\square$

5.4 Examples

Now, we study two biologically reasonable forms of K, which satisfy conditions (i) and (ii) of Theorem 3.

Example 2 We suppose that if x and y are parental traits, then the trait of the offspring is of the form

$$\frac{x + y}{2} + Z,$$

where Z is a 0-mean random variable, $\mathbb{E}Z^2 < \infty$ and Z has a positive density h. Then

$$k(x, y, z) = h\left(z - \tfrac{x+y}{2}\right) \tag{44}$$

and

$$\frac{\partial}{\partial x}\mathcal{K}(x, y, z) = -\frac{1}{2}h\left(z - \tfrac{x+y}{2}\right).$$

The condition (i) is equivalent to the inequality

$$\int_{-\infty}^{\infty} |h(z - \alpha) - h(z - \beta)| \, dz < 2$$

for all $\alpha, \beta \in \mathbb{R}$, which is a simple consequence of the assumption that h is a positive density. Now we check that condition (ii) holds with $\alpha = 2$. We have

$$
\begin{aligned}
\int_{-\infty}^{\infty} z^2 (\mathcal{P}\mu)(dz) &\leq \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \left((z - \tfrac{x+y}{2})^2 + (z - \tfrac{x+y}{2})(x + y) + \tfrac{(x+y)^2}{4} \right) \\
&\quad \times h\left(z - \tfrac{x+y}{2}\right) dz \, \mu(dx)\mu(dy) \\
&\leq \mathbb{E}Z^2 + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \tfrac{(x+y)^2}{4} \mu(dx)\mu(dy) \\
&\leq \mathbb{E}Z^2 + \frac{1}{2}q^2 + \frac{1}{2} \int_{-\infty}^{\infty} x^2 \mu(dx).
\end{aligned}
$$

If we additionally assume that the density h is a continuous function, then according to Theorem 4 the limit measure μ^* has a continuous and bounded density u_*, $\mu_t = e^{-t}\mu_0 + v_t(x) \, dx$, and v_t converges uniformly to u_*.

Now we determine the limiting distribution μ^*. Densities of the measures μ^* and μ_0 have the same first moment q and u_* satisfies the equation

$$u_*(z) = \int_{\mathbb{R}} \int_{\mathbb{R}} h\left(z - \frac{x+y}{2}\right) u_*(x) \, u_*(y) \, dx \, dy. \tag{45}$$

Observe that if a probability density f satisfies (45) and $\int_{\mathbb{R}} x f(x) \, dx = 0$, then $f(x - q)$ also satisfies (45) and has the first moment q. Since u_* is a unique solution of (45) with the first moment q we have $u_*(x) = f(x - q)$ for $x \in \mathbb{R}$. Now we construct the density f. Consider an infinite sequence of i.i.d. random variables

$$Z_{01}, Z_{11}, Z_{12}, Z_{21}, \ldots, Z_{24}, Z_{31}, \ldots, Z_{38}, \ldots$$

with density h and define the random variable

$$Y = Z_{01} + \frac{Z_{11} + Z_{12}}{2} + \frac{Z_{21} + \cdots + Z_{24}}{4} + \frac{Z_{31} + \cdots + Z_{38}}{8} + \cdots .$$

Then $\mathbb{E}Y = 0$. If Y_1 and Y_2 are two independent copies of Y and Z is a random variable with density h independent of Y_1 and Y_2, then

$$Y \stackrel{d}{=} Z + \frac{Y_1 + Y_2}{2}. \tag{46}$$

It means that the density f of Y satisfies (45). Let $h_n(x) = 2^n h(2^n x)$ for $n \geq 0$ and $x \in \mathbb{R}$. From the definition of the random variable Y it follows that

$$f = h_0 * h_1^{*2} * h_2^{*4} * h_3^{*8} * \ldots,$$

where $f * g$ denotes the convolution of f and g.

From (46) it follows immediately that $\mathbb{E}Y^2 = 2\mathbb{E}Z^2$. For instance, if Z has a normal distribution with zero mean and standard deviation σ, then Y has also a normal distribution with zero mean and standard deviation $\sqrt{2}\sigma$.

Example 3 As in Example 2 we suppose that if x and y are parental traits, then the trait of the offspring is of the form

$$(x + y)Z,$$

where Z is a random variable with values in the interval $[0, 1]$, and has a density h such that

$$\int_0^\infty x h(x)\, dx = \frac{1}{2}. \tag{47}$$

Then $F = [0, \infty)$ and the function k is of the form

$$k(x, y, z) = \frac{1}{x + y} h\left(\frac{z}{x + y}\right) \tag{48}$$

for $z \in [0, x + y]$ and $k(x, y, z) = 0$ otherwise. Equation (29) with kernel k given by (48) is known as the *general version of Tjon–Wu equation*. If $h = \mathbb{1}_{[0,1]}$, then this equation is the Tjon–Wu version of the Boltzmann equation (see Bobylev 1976; Krook and Wu 1977; Tjon and Wu 1979). The asymptotic stability of the classical Tjon–Wu equation in L^1 space was proven by Kiełek (see Kiełek 1990). Lasota and Traple (see Lasota 2002; Lasota and Traple 1999) proved stability in the general case but in the sense of the weak convergence of measures. If we assume additionally that the support of h contains an interval $(0, \varepsilon)$, $\varepsilon > 0$, then this result follows immediately from Theorem 3. Indeed, in that case one can easily compute

$$\frac{\partial}{\partial x}\mathcal{K}(x, y, z) = -h\left(\frac{z}{x + y}\right)\frac{z}{(x + y)^2}.$$

Now, condition (35) is equivalent to the inequality

$$\int_0^\infty \left| h(\tfrac{z}{\alpha})\tfrac{z}{\alpha^2} - h(\tfrac{z}{\beta})\tfrac{z}{\beta^2} \right| dz < 1 \tag{49}$$

for all $\alpha, \beta > 0$. This inequality is a simple consequence of positivity of h on the interval $(0, \varepsilon)$ and of the following condition

$$\int\limits_0^\infty h(\tfrac{z}{\alpha})\tfrac{z}{\alpha^2}\, dz = \int\limits_0^\infty h(x)x\, dx = \tfrac{1}{2}.$$

Now we check that the condition (ii) holds with $\alpha = 2$. We have

$$\int\limits_0^\infty z^2 (\mathcal{P}\mu)(dz) \leq \int\limits_0^\infty \int\limits_0^\infty \int\limits_0^\infty \frac{z^2}{x+y} h\left(\frac{z}{x+y}\right) dz\, \mu(dx)\mu(dy)$$

$$\leq \mathbb{E}Z^2 \int\limits_0^\infty \int\limits_0^\infty (x+y)^2\, \mu(dx)\mu(dy)$$

$$\leq \mathbb{E}Z^2 \left(2q^2 + 2\int\limits_0^\infty y^2\, \mu(dy)\right) \leq 2q^2 \mathbb{E}Z^2 + L \int\limits_0^\infty y^2\, \mu(dy),$$

where $L = 2\mathbb{E}Z^2$. Since $0 \leq Z \leq 1$, we have $L = 2\mathbb{E}Z^2 < 2\mathbb{E}Z = 1$.

Remark 1 The kernel k in Example 3 is not a continuous function even if the density h is a continuous and we cannot apply directly Theorem 4 in this case. But it not difficult to check that if $q > 0$ then $\mu^*(\{0\}) = 0$ and to prove that the invariant measure μ^* has a density u_*, and u_* is a continuous function on the interval $(0, \infty)$. Moreover, repeating the proof of Theorem 4 one can check that $\mu_t = e^{-t}\mu_0 + v_t(x)\, dx$, and v_t converges uniformly to u_* on the sets $[\varepsilon, \infty)$, $\varepsilon > 0$. In particular, if we consider Eq. (29) on the space of probability densities, then every solution converges to u_* in $L^1[0, \infty)$.

6 Conclusion

In the paper we presented some phenotype structured population models with a sexual reproduction. We consider both random and assortative mating. Our starting point is the individual-based model which clearly explains all interactions between individuals. The limit passage with the number of individuals to infinity leads to the macroscopic model which is a nonlinear evolution equation. We give some conditions which guarantee the global existence of solutions, persistence of the population and convergence of its size to some stable level. Next, we consider only a population with random mating and under suitable assumptions we prove that a phenotypic profile of the population converges to a stationary profile.

It would be interesting to study analytically long-time behavior of a phenotypic profile of population with assortative mating. Some numerical results presented in the paper Doebeli et al. (2007) suggest that also in this case one can expect convergence of a phenotypic profile to multimodal limit distributions. This result suggests that

assortative mating can lead to a polymorphic population and adaptive speciation. We hope that our methods invented to asymptotic analysis of populations with random mating will be also useful in the case of assortative mating. In order to do it, we probably need to modify the model of assortative mating (7) presented in Sect. 2, because it has a disadvantage that the mating rate does not satisfy the condition $\sum_{j=1}^{n} m(x_i, x_j) = 1$ for all i. We can construct a new model which corresponds to the same preference function $a(x, y)$ with a symmetric mating rate m which has the above property. In order to do this we look for constants $c_1, \ldots, c_n$ depending on the state of population such that

$$m(x_i, x_j; \mathbf{x}) = (c_i + c_j)a(x_i, x_j) \tag{50}$$

and $\sum_{j=1}^{n} m(x_i, x_j; \mathbf{x}) = 1$ for all i. In this way we obtain a system of linear equations for $c_1, \ldots, c_n$:

$$\sum_{j=1}^{n} b_{ij}c_j = 1, \quad \text{for } i = 1, \ldots, n, \tag{51}$$

where $b_{ij} = a(x_i, x_j)$ for $i \neq j$ and $b_{ii} = a(x_i, x_i) + \sum_{l=1}^{n} a(x_i, x_l)$. Since the matrix $[b_{ij}]$ has positive entries and the dominated main diagonal, system (51) has a unique and positive solution. The passage with the number of individuals to infinity leads to the following mating rate

$$m(x, y; \mu) = (c(x; \mu) + c(y; \mu))a(x, y), \tag{52}$$

where the function $c(x; \mu)$ depends on a phenotypic distribution μ, and satisfies the following Fredholm equation of the second kind

$$c(x; \mu) \int_F a(x, y)\, \mu(dy) + \int_F c(y; \mu)a(x, y)\, \mu(dy) = 1. \tag{53}$$

One can introduce a general model which covers both semi-random and assortative mating. Let $p(x)$ be the initial capability of mating of an individual with trait x and $a(x, y)$ be a symmetric nonnegative preference function. Now we can define a *cumulative preference function* by $\bar{a}(x, y) = a(x, y)p(x)p(y)$. The mating rate m is a symmetric function given by (50) with a replaced by $\bar{a}$ and we assume that $\sum_{j=1}^{n} m(x_i, x_j; \mathbf{x}) = p(x_i)$ for each i, j. The mating rate in an infinitesimal model is of the form

$$m(x, y; \mu) = (c(x; \mu) + c(y; \mu))a(x, y)p(x)p(y), \tag{54}$$

where the function $c(x; \mu)$ satisfies the following equation

$$c(x; \mu) \int_F a(x, y)p(y)\, \mu(dy) + \int_F c(y; \mu)a(x, y)p(y)\, \mu(dy) = 1. \tag{55}$$

In particular, in the semi-random case we have $a \equiv 1$ and $c \equiv 1/\int_F 2p(y)u(y)\, \mu(dy)$ and the mating rate is given by (3). Let us recall that in the general case c is not only

a function of x but it is also depends on μ and therefore, the proofs of results from Sects. 3 and 4 cannot be automatically adopted to these models.

References

Almeida CR, de Abreu FV (2003) Dynamical instabilities lead to sympatric speciation. Evol Ecol Res 5:739–757

Arino O, Rudnicki R (2004) Phytoplankton dynamics. C R Biol 327:961–969

Baur B (1992) Random mating by size in the simultaneously hermaphroditic land snail Arianta arbustorum: experiments and an explanation. Anim Behav 43:511–518

Billingsley P (1995) Probability and measure, 3rd edn. John Wiley and Sons, New York

Bobylev AV (1976) Exact solutions of the Boltzmann equation. Soviet Phys Dokl 20:822–824

Bolker B, Pacala S (1997) Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theor Popul Biol 52:179–197

Bolley F (1934) Separability and completeness for the Wasserstein distance. Sémin Probabl XLI Lect Notes Math 2008:371–377

Champagnat N (2006) A microscopic interpretation for adaptive dynamics trait substitution sequence models. Stoch Process Appl 116:1127–1160

Champagnat N, Ferrière R, Méléard S (2008) From individual stochastic processes to macroscopic models in adaptive evolution. Stoch Models 24:2–44

Collet P, Meleard S, Metz JAJ (2013) A rigorous model study of the adaptive dynamics of Mendelian diploids. J Math Biol 67:569–607

Doebeli M, Blok HJ, Leimar O, Dieckmann U (2007) Multimodal pattern formation in phenotype distributions of sexual populations. Proc R Soc B 274:347–357

Ethier SN, Kurtz TG (1986) Markov processes: characterization and convergence. John Wiley and Sons, New York

Ferrière R, Tran VC (2009) Stochastic and deterministic models for age-structured populations with genetically variable traits. ESAIM Proc 27:289–310

Fournier N, Méléard S (2004) A microscopic probabilistic description of locally regulated population and macroscopic approximations. Ann Appl Probab 14:1880–1919

Gavrilets S, Boake CRB (1998) On the evolution of premating isolation after a founder event. Am Nat 152:706–716 S

Kiełek Z (1990) Asymptotic behaviour of solutions of the Tjon–Wu equation. Ann Polon Math 52:109–118

Krook M, Wu TT (1977) Exact solutions of the Boltzmann equation. Phys Fluids 20:1589–1595

Law R, Dieckmann U (2002) Moment approximations of individual-based models. In: Dieckmann U, Law R, Metz JAJ (eds.) The Geometry of Ecological Interactions. Cambridge Univ. Press, Cambridge, pp 252–270

Lasota A (2002) Asymptotic stability of some nonlinear Boltzmann-type equations. J Math Anal Appl 268:291–309

Lasota A, Traple J (1999) An application of the Kantorovich-Rubinstein maximum principle in the theory of the Tjon–Wu equation. J Differ Equ 159:578–596

Matessi C, Gimelfarb A, Gavrilets S (2001) Long-term buildup of reproductive isolation promoted by disruptive selection: How far does it go? Selection 2:41–64

Méléard S, Tran VC (2009) Trait substitution sequence process and canonical equation for age-structured populations. J Math Biol 58:881–921

Polechová J, Barton NH (2005) Speciation through competition: a critical review. Evolution 59(2005):1194–1210

Puebla O, Bermingham E, Guichard F (2012) Pairing dynamics and the origin of species. Proc Biol Sci 279:1085–1092

Rachev ST (1991) Probability metrics and the stability of stochastic models. John Willey and Sons, Chich-
    ester
Remenik D (2009) Limit theorems for individual-based models in economics and finance. Stoch Process
    Appl 119:2401–2435
Rudnicki R, Wieczorek R (2006a) Fragmentation–coagulation models of phytoplankton. Bull Polish Acad
    Sci 54:175–191
Rudnicki R, Wieczorek R (2006b) Phytoplankton dynamics: from the behaviour of cells to a transport
    equation. Math Mod Nat Phenomena 1:83–100
Schneider KA, Bürger R (2006) Does competitive divergence occur if assortative mating is costly? J Evol
    Biol 19:570–588
Schneider KA, Peischl S (2011) Evolution of assortative mating in a population expressing dominance.
    PLoS ONE 6(4):e16821
Skorokhod SV (1956) Limit theorems for stochastic processes. Theory Prob Appl 1:261–290
Tjon JA, Wu TT (1979) Numerical aspects of the approach to a Maxwellian distribution. Phys Rev A
    19:883–888
Villani C (2008) Optimal transport, old and new, Grundlehren der Mathematischen Wissenschaften, 338.
    Springer, Berlin