

# Evolution Operators and Algebras of Sex Linked Inheritance

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*Abstract.* In this short Letter we review recently obtained results for discrete-time dynamical systems and evolution algebras of sex linked inheritance. Moreover, we discuss several open problems related to such inheritance.

## 1. Introduction

Evolutionary theory is important to a proper understanding of living populations at all levels. Thus the analysis of gene frequency arrays assuredly has a part to play in anthropological comparisons and observations of animal behaviour patterns that may lead to a better quantification of the genetics and environmental components of behavioural traits. Mathematics, as the language of quantitative measurement, is clearly central to these pursuits. The relevant mathematics undoubtedly requires hybridisation of nonlinear analyses, compounded stochastic processes modelling, innovative statistical analysis of complex data, and the creative implementation of the gigantic computer methodology and all its ramifications [9].

Some mathematical methods have been applied successfully to population genetics for a long time. Even the quite elementary ideas used initially proved amazingly effective. For example, the famous Hardy–Weinberg law (1908) is basic to many calculations in population genetics. The mathematics in the classical works of Fisher, Haldane and Wright was also not very complicated but was of great help for the theoretical understanding of evolutionary processes. More recently, the methods of mathematical genetics have become more sophisticated. In use are probability theory, stochastic processes, nonlinear differential and difference equations and non-associative algebras. First contacts with topology have been established. Now in addition to the traditional movement of mathematics for genetics, inspiration is flowing in the opposite direction, yielding mathematics from genetics. The book [12] reflects to some degree both patterns but especially the latter one. A pioneer of this synthesis was S N Bernstein. He raised and partially solved the problem of characterising all stationary evolutionary operators, and this work was continued by Yu I Lyubich [12]. This problem has not been completely solved, but it appears that only certain

operators devoid of any biological significance remain to be addressed.

In [12], the dynamics of populations and their formal analogue are also studied. When selection is absent a very effective algebraic approach was introduced by Reiersöl (1961). This approach was extended by Lyubich (1971) to describe explicit solutions of the general evolution equation. Some more abstract algebraic-dynamical theory, were discovered by Etherington (1939).

The dynamics of selection require different methods. Here the leading role goes to Fisher's "fundamental theorem" concerning the increase of mean fitness of a population due to natural selection. An approach based on this theory uses a relatively complicated "relaxation" technique to establish the global convergence to equilibrium under conditions more general than have been previously achieved. Several topics which could be studied using these methods: polyploidy, overlapping generations, migration, etc.

Recently in [18], a new type of evolution algebra is introduced. This algebra also describes some evolution laws of genetics and it is an algebra  $E$  over a field  $K$  with a countable natural basis  $e_1, e_2, \dots$  and multiplication given by  $e_i e_i = \sum_j a_{ij} e_j$ ,  $e_i e_j = 0$  if  $i \neq j$ . Therefore,  $e_i e_i$  is viewed as "self-reproduction".

There exist several classes of non-associative algebras (baric, evolution, Bernstein, train, stochastic, etc.), whose investigation has provided a number of significant contributions to theoretical population genetics. Such classes have been defined different times by several authors, and all algebras belonging to these classes are generally called "genetic". Etherington introduced the formal language of abstract algebra to the study of the genetics (see for example, [2]). In recent years many authors have tried to investigate the difficult problem of classification of these algebras. The most comprehensive references for the mathematical research done in this area are [12, 13, 18, 20].

The paper [9] gives a comprehensive survey of problems in evolutionary theory studied by mathematical methods, both with regard to past developments, the present state of the subject and probable future trends. Many of the models considered are actually within the scope of mathematical population genetics, although the general ideas

discussed have implications for a much wider area. Anyone currently engaged in this field will find the viewpoints expressed interesting, placing the problems which are being studied extensively today into a wider perspective. At the same time this paper may stimulate further interest among mathematicians in biological applications.

In very recent paper [7] several mathematical problems are formulated which suggested by structural patterns present in biomolecular assemblies.

In this short Letter we review recently obtained results for discrete-time dynamical systems and evolution algebras of sex linked inheritance. Moreover, we discuss several open problems related to such inheritance. The next section contains very interesting preliminaries from biology. Section 3 is devoted to the results on free population. In Sec. 4 we discuss sex linked populations.

## 2. Preliminaries from Biology

The action of genes is manifested statistically in sufficiently large communities of matching individuals (belonging to the same species). These communities are called *populations* [12]. The population exists not only in space but also in time, i.e. it has its own life cycle. The basis for this phenomenon is reproduction by mating. Mating in a population can be free or subject to certain restrictions.

A *free population* (or *panmixia*) means random mating in the population. A *panmictic population* is one where all individuals are potential partners. This assumes that there are no mating restrictions, neither genetic or behavioural, upon the population, and that therefore all recombination is possible. The Wahlund effect assumes that the overall population is panmictic [6].

In genetics, *random mating* involves the mating of individuals regardless of any physical, genetic, or social preference. In other words, the mating between two organisms is not influenced by any environmental, hereditary, or social interaction. Hence, potential mates have an equal chance of being selected. Random mating is a factor assumed in the Hardy–Weinberg principle and is distinct from lack of natural selection: in viability selection for instance, selection occurs before mating.

The whole population in space and time comprises discrete generations  $F_0, F_1, \dots$ . The generation  $F_{n+1}$  is the set of individuals whose parents belong to the  $F_n$  generation. A *state* of a population is a distribution of probabilities of the different types of organisms in every generation.

A *sex-determination system* is a biological system that determines the development of sexual characteristics in an organism. Most sexual organisms have two sexes. Occasionally there are

hermaphrodites in place of one or both sexes. There are also some species that are only one sex due to parthenogenesis, the act of a female reproducing without fertilisation.

In many cases, sex determination is *genetic*: males and females have different alleles or even different genes that specify their sexual morphology. In animals, this is often accompanied by *chromosomal* differences. Genetic determination is generally through chromosome combinations of XY (for example: humans, mammals), ZW (birds), X0 (in this variant of the XY system, females have two copies of the sex chromosome (XX) but males have only one (X0). The 0 denotes the absence of a second sex chromosome. Generally in this method, the sex is determined by amount of genes expressed across the two chromosomes. This system is observed in a number of insects, including the grasshoppers and crickets of order Orthoptera and in cockroaches. A small number of mammals also lack a Y chromosome, Z0 (lepidoptera), WXY (platyfishes). Moreover, some organisms have multiple sex chromosomes: X1X2Y (for example, *Hoplias malabaricus*), X1X2X3X4X5Y (for example, *Tegegnaria ferruginea*), X1X2X3X4X5Y1Y2Y3Y4Y5 (*Ornithorhynchus anatinus*), etc. Sexual differentiation is generally started by a main gene, a sex locus, then a multitude of other genes follow in a domino effect.

In other cases, sex is determined by *environmental* variables such as *temperature*. For example, in some species of reptiles, including alligators, some turtles, the tuatara, and a few birds, sex is determined by the temperature at which the egg is incubated during a temperature sensitive period. For some, this is achieved by hotter temperatures being one sex and cooler temperatures being the other. For others, the extreme temperatures are one sex and the middle temperature is the other. Sex also can be determined by social variables (the *size of an organism* relative to other members of its population).

Environmental sex determination occurred before genetic; it is thought that a temperature-dependent reptile was the common ancestor to sex chromosomes. Some species, such as some snails, practice *sex change*: adults start out male, then become female. In tropical clown fish, the dominant individual in a group becomes female while the other ones are male, and blue head wrasses are the reverse. In the marine worm *Bonellia viridis*, larvae become males if they make physical contact with a female, and females if they end up on the bare sea floor. This is triggered by the presence of a chemical produced by the females, bonellin. Some species, however, have no sex-determination system. Hermaphrodites include the common earthworm and certain species

of snails. A few species of fish, reptiles, and insects reproduce by parthenogenesis and are female altogether. There are some reptiles, such as the boa constrictor and komodo dragon that can reproduce sexually and asexually, depending if a mate is available.

In some arthropods, sex is determined by *infection*, as when bacteria of the genus *Wolbachia* alter their sexuality; some species consist entirely of ZZ individuals, with sex determined by the presence of *Wolbachia*. If a male ZZ is infected by the bacteria *Wolbachia*, ZZ + w, then it becomes female. In this case there are three female genotypes: WZ, WZ + w and ZZ + w.

*Haemophilia* is a group of hereditary genetic disorders that impair the body's ability to control blood clotting or coagulation, which is used to stop bleeding when a blood vessel is broken.

Other unusual systems: swordtail fish, the *Chironomus* midge species, the Platypus has 10 sex chromosomes but lacks the mammalian sex-determining gene SRY, meaning that the process of sex determination in the Platypus remains unknown. Zebrafish go through juvenile hermaphroditism, but what triggers this is unknown. The Platypus has W, X, and Y chromosomes. This allows WY, WX, or XX females or YY and XY males [17].

**Remark 2.1.** The details of some sex-determination systems are not yet fully understood. A search in MathSciNet gives about 15 mathematical papers which are related to sex determination models (see for example, [3], [9], [10]). In papers [5], [15] we attempted to introduce thermodynamic methods in biology. In [19] an algebra associated to a sex change is constructed.

### 3. Free Population (Panmixia)

In this section we shall give evolution operators and algebras of a free population.

Consider a population consisting of  $m$  species. Let  $x^0 = (x_1^0, \dots, x_m^0)$  be the probability distribution (where  $x_i^0 = P(i)$  is the probability of  $i$ ,  $i = 1, 2, \dots, m$ ) of species in the initial generation, and  $P_{ij,k}$  the probability that individuals in the  $i$ th and  $j$ th species interbreed to produce an individual  $k$ , more precisely  $P_{ij,k}$  is the conditional probability  $P(k|i, j)$  that  $i$ th and  $j$ th species interbreed successfully, then they produce an individual  $k$ .

In this section we consider models of free population, i.e. there is no difference of sex and in any generation the "parents"  $ij$  are independent, i.e.  $P(i, j) = P(i)P(j) = x_i^0 x_j^0$ . Then the probability distribution  $x' = (x'_1, \dots, x'_m)$  (the state) of the species in the first generation can be found by

the total probability

$$x'_k = \sum_{i,j=1}^m P(k|i, j)P(i, j) = \sum_{i,j=1}^m P_{ij,k}x_i^0 x_j^0, \quad k = 1, \dots, m. \tag{3.1}$$

This means that the association  $x^0 \rightarrow x'$  defines a map  $V$  called the *evolution operator*. The population evolves by starting from an arbitrary state  $x^0$ , then passing to the state  $x' = V(x^0)$  (in the next "generation"), then to the state  $x'' = V(V(x^0))$ , and so on. Thus, states of the population described by the following discrete-time dynamical system

$$x^0, \quad x' = V(x^0), \quad x'' = V^2(x^0), \quad x''' = V^3(x^0), \dots \tag{3.2}$$

where  $V^n(x) = \underbrace{V(V(\dots V(x)))}_n$  denotes the  $n$  times iteration of  $V$  to  $x$ .

Note that  $V$  (defined by (3.1)) is a *quadratic stochastic operator* (QSO), and it is higher dimensional if  $m \geq 3$ . Higher dimensional dynamical systems are important, but there are relatively few dynamical phenomena that are currently understood [1].

The main problem for a given dynamical system is to describe the limit points of  $\{x^{(n)}\}_{n=0}^\infty$  for arbitrary given  $x^{(0)}$ .

In [4], we have discussed the recently obtained results on the problem, and also gave several open problems related to the theory of QSOs. See also [12] for more detailed theory of QSOs. Moreover, in [12] an evolution algebra  $\mathcal{A}$  associated to the free population is introduced and using this non-associative algebra, many results are obtained in explicit form, e.g. the explicit description of stationary quadratic operators, and the explicit solutions of a nonlinear evolutionary equation in the absence of selection, as well as general theorems on convergence to equilibrium in the presence of selection.

The algebra  $\mathcal{A}$  is defined as follows. Recall that any vector  $x \in \mathbb{R}^m$  can be written as  $x = \sum_{i=1}^m x_i e_i$  with  $\{e_1, \dots, e_m\}$  the canonical basis on  $\mathbb{R}^m$  with

$$e_1 = (1, 0, \dots, 0), \quad e_2 = (0, 1, 0, \dots, 0), \quad \dots, \\ e_m = (0, 0, \dots, 0, 1) \in \mathbb{R}^m.$$

Now introduce on  $\mathbb{R}^m$  a multiplication defined by

$$e_i e_k = \sum_{j=1}^m P_{ik,j} e_j. \tag{3.3}$$

Thus we identify the coefficients of inheritance as the structure constants of an algebra  $\mathcal{A}$ , i.e. a bilinear mapping  $\mathbb{R}^m \times \mathbb{R}^m$  to  $\mathbb{R}^m$ ,  $x \times y \rightarrow xy$ . The general formula for multiplication is the extension of (3.3) by bilinearity for multiplication:

$$xy = \sum_{i,k,j=1}^m (P_{ik,j} x_i y_k) e_j. \tag{3.4}$$

In particular, the evolution operator defined in coordinate form by (3.1) can be written as  $x' = V(x) = x^2$ . See [12] for properties of the algebra  $\mathcal{A}$ .

#### 4. Bisexual Population

Type partition is called differentiation. The simplest example is sex differentiation. In bisexual population (BP) any kind of differentiation must agree with the sex differentiation, i.e. all the organisms of one type must belong to the same sex. Thus, it is possible to speak of male and female types.

*Evolution operator.* In this subsection, following [12], we describe the evolution operator of a BP.

Assuming that the population is bisexual, we suppose that the set of females can be partitioned into finitely many different types indexed by  $\{1, 2, \dots, n\}$  and, similarly, that the male types are indexed by  $\{1, 2, \dots, \nu\}$ . The number  $n + \nu$  is called the dimension of the population. The population is described by its state vector  $(x, y)$  in  $S^{n-1} \times S^{\nu-1}$ , the product of two unit simplexes in  $\mathbb{R}^n$  and  $\mathbb{R}^\nu$  respectively. Vectors  $x$  and  $y$  are the probability distributions of the females and males over the possible types:

$$x \in S^{n-1} = \left\{ x \in \mathbb{R}^n : x_i \geq 0, \sum_{i=1}^n x_i = 1 \right\};$$

$$y \in S^{\nu-1} = \left\{ y \in \mathbb{R}^\nu : y_i \geq 0, \sum_{i=1}^\nu y_i = 1 \right\}.$$

Denote  $S = S^{n-1} \times S^{\nu-1}$ . We call the partition into types hereditary if for each possible state  $z = (x, y) \in S$  describing the current generation, the state  $z' = (x', y') \in S$  is uniquely defined describing the next generation. This means that the association  $z \mapsto z'$  defines a map  $V: S \rightarrow S$  called the evolution operator.

For any point  $z^{(0)} \in S$  the sequence  $z^{(t)} = V(z^{(t-1)})$ ,  $t = 1, 2, \dots$  is called the trajectory of  $z^{(0)}$ .

Let  $P_{ik,j}^{(f)}$  and  $P_{ik,l}^{(m)}$  be inheritance coefficients defined as the probability that a female offspring is type  $j$  and, respectively, that a male offspring is of type  $l$ , when the parental pair is  $ik$  ( $i, j = 1, \dots, n$ ; and  $k, l = 1, \dots, \nu$ ). We have

$$P_{ik,j}^{(f)} \geq 0, \sum_{j=1}^n P_{ik,j}^{(f)} = 1; \quad P_{ik,l}^{(m)} \geq 0, \sum_{l=1}^\nu P_{ik,l}^{(m)} = 1. \quad (4.1)$$

Let  $z' = (x', y')$  be the state of the offspring population at the birth stage. This is obtained from inheritance coefficients as

$$x'_j = \sum_{i,k=1}^{n,\nu} P_{ik,j}^{(f)} x_i y_k; \quad y'_l = \sum_{i,k=1}^{n,\nu} P_{ik,l}^{(m)} x_i y_k. \quad (4.2)$$

We see from (4.2) that for a BP the evolution operator is a quadratic mapping of  $S$  into itself.

The dynamics of this operator has not been completely studied yet.

See [14] for some results about the dynamical system generated by the operator (4.2).

*Evolution algebra of BP.* Now following [11], we give an algebra structure on the vector space  $\mathbb{R}^{n+\nu}$  which is closely related to the map (4.2).

Consider  $\{e_1, \dots, e_{n+\nu}\}$  the canonical basis on  $\mathbb{R}^{n+\nu}$  and divide the basis as  $e_i^{(f)} = e_i$ ,  $i = 1, \dots, n$  and  $e_i^{(m)} = e_{n+i}$ ,  $i = 1, \dots, \nu$ .

Now introduce on  $\mathbb{R}^{n+\nu}$  a multiplication defined by

$$e_i^{(f)} e_k^{(m)} = e_k^{(m)} e_i^{(f)} = \frac{1}{2} \left( \sum_{j=1}^n P_{ik,j}^{(f)} e_j^{(f)} + \sum_{l=1}^\nu P_{ik,l}^{(m)} e_l^{(m)} \right),$$

$$e_i^{(f)} e_j^{(f)} = 0, \quad i, j = 1, \dots, n; \quad e_k^{(m)} e_l^{(m)} = 0, \quad k, l = 1, \dots, \nu. \quad (4.3)$$

The general formula for the multiplication is the extension of (4.3) by bilinearity, i.e. for  $z, t \in \mathbb{R}^{n+\nu}$ ,

$$z = (x, y) = \sum_{i=1}^n x_i e_i^{(f)} + \sum_{j=1}^\nu y_j e_j^{(m)},$$

$$t = (u, v) = \sum_{i=1}^n u_i e_i^{(f)} + \sum_{j=1}^\nu v_j e_j^{(m)}$$

using (4.3), we obtain

$$zt = \frac{1}{2} \sum_{k=1}^n \left( \sum_{i=1}^n \sum_{j=1}^\nu P_{ij,k}^{(f)} (x_i v_j + u_i y_j) \right) e_k^{(f)} + \frac{1}{2} \sum_{l=1}^\nu \left( \sum_{i=1}^n \sum_{j=1}^\nu P_{ij,l}^{(m)} (x_i v_j + u_i y_j) \right) e_l^{(m)}. \quad (4.4)$$

From (4.4) and using (4.2), in the particular case that  $z = t$ , i.e.  $x = u$  and  $y = v$ , we obtain

$$zz = z^2 = \sum_{k=1}^n \left( \sum_{i=1}^n \sum_{j=1}^\nu P_{ij,k}^{(f)} x_i y_j \right) e_k^{(f)} + \sum_{l=1}^\nu \left( \sum_{i=1}^n \sum_{j=1}^\nu P_{ij,l}^{(m)} x_i y_j \right) e_l^{(m)} = V(z) \quad (4.5)$$

for any  $z \in S$ .

This algebraic interpretation is very useful. For example, a BP state  $z = (x, y)$  is an equilibrium (fixed point,  $V(z) = z$ ) precisely when  $z$  is an idempotent element of the set  $S$ .

If we write  $z^{[t]}$  for the power  $(\dots(z^2)\dots)$  ( $t$  times) with  $z^{[0]} \equiv z$  then the trajectory with initial state  $z$  is  $V^t(z) = z^{[t]}$ .

The algebra  $\mathcal{B} = \mathcal{B}_V$  generated by the evolution operator  $V$  (see (4.2)) is called the *evolution algebra of the bisexual population* (EABP).

**Remark 4.1.** 1. If a population is free then the male and female types are identical and, in particular

$n = \nu$ , the inheritance coefficients are the same for male and female offsprings, i.e.

$$P_{ik,j} = P_{ik,j}^{(f)} = P_{ik,j}^{(m)}.$$

The evolution algebra  $\mathcal{A}$  associated with the free population is commutative when the condition of symmetry  $P_{ik,j} = P_{ki,j}$  is satisfied, but it is not in general associative. In [11] we showed that algebra  $\mathcal{B}$  of bisexual population is commutative without any symmetry condition. Hence the algebra  $\mathcal{A}$  is a particular case of the algebra  $\mathcal{B}$ .

2. It is easy to see that the EA introduced in [18] is different from EABP,  $\mathcal{B}$ .

3. The algebra  $\mathcal{B}$  is a natural generalisation of a *zygotic algebra* for sex linked inheritance (see [2, 8, 13, 20]).

In [11], the basic properties of the algebra  $\mathcal{B}$  are studied. We proved that this algebra is commutative (and hence flexible), not associative and not necessarily power associative. We showed that  $\mathcal{B}$  is not a baric algebra, but a dibaric algebra and hence its square is baric. Moreover, the algebra is a Banach algebra. The set of all derivations of the algebra is described. We found necessary conditions for a state of the population to be a fixed point or a zero point of the evolution operator (4.2) which corresponds to the algebra  $\mathcal{B}$ . We also established upper estimate of the limit points set for trajectories of the evolution operator (4.2). Using the necessary conditions a detailed analysis of a special case of the evolution algebra (bisexual population of which has a preference on type "1" of females and males) is given. For such a special case the full set of idempotent elements and the full set of absolute nilpotent elements are obtained. These investigations are only at starting point, the algebra  $\mathcal{B}$  has not been completely studied yet.

*Gonosomal evolution operator.* As it was mentioned above in many cases, the sex determination is genetic, in particular, it is controlled by two chromosomes called gonosomes.

Suppose that the set of female types is  $\{1, 2, \dots, n\}$  and the set of male types is  $\{1, 2, \dots, \nu\}$ .

Let  $\gamma_{ik,j}^{(f)}$  and  $\gamma_{ik,l}^{(m)}$  be some inheritance coefficients (not necessary probabilities) with

$$\sum_{j=1}^n \gamma_{ik,j}^{(f)} + \sum_{l=1}^{\nu} \gamma_{ik,l}^{(m)} = 1. \tag{4.6}$$

Note that the condition (4.1) is a particular case of the condition (4.6) which is obtained when  $\gamma_{ik,j}^{(f)} = \frac{1}{2}P_{ik,j}^{(f)} \geq 0$ .

Consider an evolution operator  $W : \mathbb{R}^{n+\nu} \rightarrow \mathbb{R}^{n+\nu}$  defined as

$$x'_j = 2 \sum_{i,k=1}^{n,\nu} \gamma_{ik,j}^{(f)} x_i y_k; \quad y'_l = 2 \sum_{i,k=1}^{n,\nu} \gamma_{ik,l}^{(m)} x_i y_k. \tag{4.7}$$

This operator is called gonosomal evolution operator.

*Gonosomal algebra.* An algebra  $\mathcal{G}$  is gonosomal (see [19]) if there is a basis  $B = \{e_i^{(f)}\}_{i=1}^n \cup \{e_i^{(m)}\}_{i=1}^{\nu}$  on  $\mathcal{G}$  such that for every  $1 \leq i, j \leq n$  and  $1 \leq p, q \leq \nu$ , we have

$$e_i^{(f)} e_p^{(m)} = e_p^{(m)} e_i^{(f)} = \sum_{j=1}^n \gamma_{ip,j}^{(f)} e_j^{(f)} + \sum_{l=1}^{\nu} \gamma_{ip,l}^{(m)} e_l^{(m)},$$

$$e_i^{(f)} e_j^{(f)} = 0, \quad i, j = 1, \dots, n; \quad e_k^{(m)} e_l^{(m)} = 0, \quad k, l = 1, \dots, \nu, \tag{4.8}$$

where  $\gamma_{ij,k}^{(\cdot)}$  satisfies (4.6).

**Remark 4.2.** Note that operator (4.7) describes evolution of a haemophilia (a lethal recessive X-linked disorder: a female carrying two alleles for haemophilia dies). The dynamical systems generated by gonosomal operator (4.7) have not been studied yet. In [16] a similar operator is considered. Some constructions of the gonosomal algebra  $\mathcal{G}$  are given in [19].

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