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Algebraic Isotopy in Genetics

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It is shown that many of the algebras arising in nonselective genetics are isotopes of the algebras for particularly simple systems of inheritance. Moreover, interesting aspects of the structure are preserved under the relevant isotopies.

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1. Introduction: genetic algebras and isotopes

THE OBJECT of this paper is to show that the algebras corresponding to certain important families of genetic mechanisms are *isotopic*, and to examine the reasons for, and consequences of, this relation.

In genetic algebras the symbols $a_0, a_1, \ldots, a_n$ represent the different genetic types (e.g. gametes or zygotes). We study the algebra of linear forms $a = \sum_i x_i a_i$ over the complex numbers, with multiplication table

$$a_i a_j = \sum_k \gamma_{ijk} a_k, \tag{1.1}$$

where γ_{ijk} is the probability that a union of a type i and a type j produces a type k. Here and in the following, $\sum$ denotes summation from 0 to n. Thus, $\gamma_{ijk} \geq 0$ and $\sum_k \gamma_{ijk} = 1$ for every pair (i, j). If $\omega(a) = \sum_i x_i$, we see that

$$\omega(\theta a) = \theta\omega(a), \qquad \omega(a + b) = \omega(a) + \omega(b), \qquad \omega(ab) = \omega(a)\omega(b).$$

An algebra that admits such a homomorphism to its base field is said to be *baric*. The function ω is called the weight function, and its kernel, the set of elements of weight 0, is denoted by $\mathcal{K}$. In many genetic algebras, it is found that there is a strictly descending chain of ideals $\mathcal{K}_0 = \mathcal{A}$ (the given algebra), $\mathcal{K}_1 = \mathcal{K}$, and $\mathcal{K}_2, \ldots, \mathcal{K}_d = \{0\}$, with $\mathcal{K}_{i+1} \subset K_i$, obeying the multiplicative condition $\mathcal{K}_1\mathcal{K}_i \subseteq \mathcal{K}_{i+1}$. In this case, $\mathcal{A}$ is called a *Schafer algebra*. If we can find a chain satisfying the above conditions, with $\dim(\mathcal{K}_i/\mathcal{K}_{i+1}) = 1$ for $i = 1, \ldots, d-1$, then $\mathcal{A}$ is called a *Gonshor algebra*. In the latter case, we can show that the algebra is

isomorphic to an algebra of linear forms $\sum_j y_j c_j$ with multiplication table

$$c_i c_j = \sum_k \lambda_{ijk} c_k, \qquad \lambda_{000} = 1, \tag{1.2}$$

$$\lambda_{ijk} = 0 \quad \text{if either } i = 0 \text{ and } k < j \text{ or } i \geq 1 \text{ and } k \leq j.$$

We have $\omega(\sum_j y_j c_j) = y_0$, and the triangular/supertriangular form of the multiplication table (1.2) reveals the properties of the algebra and facilitates calculation. If the principal powers $\mathcal{H}^i$ of $\mathcal{H}$ form a chain satisfying the above condition, $\mathcal{A}$ is called a *special train algebra.*

Isomorphic algebraic entities are mathematically the same. Their elements may have different names or representations, but all additive and multiplicative relations between the objects map faithfully from one entity to another. This is useful in applications, because it allows us to work with a member of an isomorphic class the form of which makes calculation simple or makes the algebraic structure particularly clear.

Isotopy is a much weaker relation than isomorphism and is of importance when we deal with less highly structured algebraic entities such as semigroups, near rings, and nonassociative systems. Let two algebras $\mathcal{A}^\circ$ and $\mathcal{A}^*$ be defined on the same vector space, multiplication being indicated by a circle ($\circ$) and a star ($*$), respectively. If there exist three fixed nonsingular linear transformations P, Q, and S, such that

$$a \circ b = [(aP) * (bQ)]S, \tag{1.3}$$

then $\mathcal{A}^\circ$ and $\mathcal{A}^*$ are said to be *isotopes*. In comparison, isomorphism requires that the two multiplication rules should be linked by a single nonsingular linear transform T such that $a \circ b = [(aT) * (bT)]T^{-1}$. In particular, $\mathcal{A}^\circ$ is isomorphic to an algebra with product rule $[(aP)T * (bQ)T]ST^{-1}$. We can choose $T = S$ and note that every isotope of $\mathcal{A}^*$ is isomorphic to a *principal isotope*, defined by a relation (1.3) with $S = I$.

However, the fact that one algebra arising in genetics is an isotope of another is usually not sufficient. If we begin with, for example, a baric or a Gonshor algebra, it is highly desirable that the property should be preserved on passing from one member of the isotopic class of interest to another.

Further details of the theory of genetic algebras can be obtained from the monograph by Wörz-Busekros (1980). Isotopy and its role in nonassociative algebras is discussed by Albert (1942).

2. Mutation algebras

The 'natural' basis of the $n+1$ allelic, diploid gametic algebra at a single locus consists of the symbols $a_0, a_1, \ldots, a_n$ denoting the alleles. In the absence of mutation, the multiplication table is

$$a_i * a_j = \tfrac{1}{2}(a_i + a_j). \tag{2.1}$$

(The output of a zygote formed by the union of a type i and a type j will produce

these gametes with equal probabilities.) Thus, ω is defined by $\omega(a_i) = 1$, the kernal $\mathcal{K}$ is spanned by the elements $c_i = a_0 - a_i$ $(i = 1, \ldots, n)$, and $c_i * c_j = 0$ if $i,j \geq 1$, and hence $\mathcal{K} * \mathcal{K} = 0$. We set $c_0 = a_0$.

We introduce the mutation algebra by supposing that, before participating in the formation of a zygote, the allele a_i may undergo a spontaneous change to an a_j, with probability m_{ij}. (The probability that it remains unchanged is m_{ii}.) We write $a_iM = \sum_j m_{ij}a_j$, and note that $m_{ij} \geq 0$, and for every i, $\sum_j m_{ij} = 1$. The mutation algebra is the symmetric principal isotope of (2.1), defined by

$$a_i \circ a_j = a_iM * a_jM \tag{2.2}$$

LEMMA 1 *The weight function ω of the algebra* (2.1), *and hence the kernel $\mathcal{K}$, is invariant under M.*

We have $\omega(a_iM) = \omega(\sum_j m_{ij}a_j) = \sum_j m_{ij} = 1 = \omega(a_i)$, and extend the result by linearity. It follows that $\mathcal{K} \circ \mathcal{K} = \mathcal{K} * \mathcal{K}$. Thus, the ideal structure of the mutation algebra is the same as that of the algebra without mutation.

We next consider polyploidy. In $2m$-ploid individuals, each gamete contains m genes. If there are $n+1$ alleles $a_0, a_1, \ldots, a_n$, the gametes can be written $a_0^{p_0}a_1^{p_1} \cdots a_n^{p_n}$ with $\sum_i p_i = m$. The vector space of linear forms in these monomials is the symmetric tensor mth power of the space for diploidy. In the absence of mutation, the product of the above elements and $a_0^{q_0}a_1^{q_1} \cdots a_n^{q_n}$ is obtained by combining them to form a zygote $a_0^{p_0+q_0}a_1^{p_1+q_1} \cdots a_n^{p_n+q_n}$, then selecting m of its genes at random. Hence,

$$(a_0^{p_0}a_1^{p_1} \cdots a_n^{p_n})(a_0^{q_0}a_1^{q_1} \cdots a_n^{q_n})$$

$$= \binom{2m}{m}^{-1} \sum_{r_0+\cdots+r_n=m} \binom{p_0+q_0}{r_0}\binom{p_1+q_1}{r_1} \cdots \binom{p_n+q_n}{r_n} a_0^{r_0}a_1^{r_1} \cdots a_n^{r_n}. \tag{2.3}$$

As in the diploid case, we write $c_0 = a_0$ and $c_i = a_0 - a_i$ for $i \geq 1$. Then, the set of linear forms in the gametic symbols, obtained by multiplying out the symbols $c_0^{p_0}c_1^{p_1} \cdots c_n^{p_n}$, with $\sum_i p_i = m$, forms a basis for the polyploid algebra. The multiplication rule can be obtained without calculation by noting that the 'union' of this gametic form and $c_0^{q_0}c_1^{q_1} \cdots c_n^{q_n}$ is the zygotic form $c_0^{p_0+q_0}c_1^{p_1+q_1} \cdots c_n^{p_n+q_n}$. The gametic output is then obtained by applying the operation of choosing m out of $2m$ gametes to each term in the linear zygotic form, when expanded in terms of the natural basis. The number of ways of choosing r_i copies of the a_i gene is the same whether in the context of the $2m$ genes of the zygote or the m genes of the gamete. Since this determines the factor involving $a_0 - a_i = c_i$, the product will contain a factor $c_1^{p_1+q_1} \cdots c_n^{p_n+q_n}$. The remaining symbolic factor c_0 must then be raised to a power $m - \sum_i' p_i - \sum_i' q_i$ $(= p_0 + q_0 - m)$, where $\sum_i'$ denotes summation from 1 to n. The numerator of the numerical multiplier is the number of ways this number of a_0 genes can be chosen from the $p_0 + q_0$ (which is equal to $2m - \sum_i' p_i - \sum_i' q_i$) that are left after the factors $a_0 - a_i$ have been included. This is

$$\binom{p_0+q_0}{p_0+q_0-m} = \binom{p_0+q_0}{m}.$$

The denominator is the number of ways of choosing m genes from $2m$. Thus,

$$(c_0^{p_0}c_1^{p_1}\cdots c_n^{p_n})(c_0^{q_0}c_1^{q_1}\cdots c_n^{q_n}) = \binom{2m}{m}^{-1}\binom{p_0+q_0}{m}c_0^{p_0+q_0}c_1^{p_1+q_n}\cdots c_n^{p_n+q_n}. \quad (2.4)$$

The product is zero if $p_0+q_0<m$, that is, if $\sum_i' p_i+\sum_i' q_i>m$. We define a function ω by $\omega(c_0^m)=1$, $\omega=0$ if $p_i>0$ for any $i=1,\ldots,n$. This is easily seen to be a weight function. We now define $\mathcal{K}_j$ to be the space spanned by the canonical basis elements $c_0^{p_0}c_1^{p_1}\cdots c_n^{p_n}$ with $\sum_i' p_i \geqslant j$. Equation (2.4) shows that each $\mathcal{K}_j$ is an ideal and that the strictly descending sequence $\mathcal{K}_0=\mathcal{A}$, $\mathcal{K}_1=\mathcal{K}$, $\mathcal{K}_2,\ldots$ satisfies the condition for a Schafer algebra. In fact, $\mathcal{K}_j=\mathcal{K}^j$ and consists of linear sums of terms each containing j factors from $\mathcal{K}$. The canonical multiplication in polyploid algebras has been derived in several ways using direct computation (e.g. Holgate, 1966; Abraham, 1980, for two alleles; Gonshor, 1971, for several).

We now extend the mutation mapping to the symmetric tensor power space. Thus,

$$(a_0^{p_0}a_1^{p_1}\cdots a_n^{p_n})M = \prod_{i=0}^{n}\left(\sum_j m_{ij}a_j\right)^{p_i}.$$

Since M leaves invariant the set of forms $\sum_i x_i a_i$ satisfying $\sum_i x_i=0$, it also leaves $\mathcal{K}$ invariant, and hence leaves invariant each power $\mathcal{K}^{*j}$ (which is equal to $\mathcal{K}_j$).

A mutation algebra for multiallelic polyploids can now be defined as a symmetric principal isotope of that without mutation by setting

$$(a_0^{p_0}a_1^{p_1}\cdots a_n^{p_n})\circ(a_0^{q_0}a_1^{q_1}\cdots a_n^{q_n}) = [(a_0^{p_0}a_1^{p_1}\cdots a_n^{p_n})M][a_0^{q_0}a_1^{q_1}\cdots a_n^{q_n})M]. \quad (2.5)$$

The above results can be summarized in the following theorem.

THEOREM 1 *The genetic algebras for a single locus with multiple alleles, with all possible nonsingular mutation matrices M, are isotopic. They admit a common weight function ω, and the principal powers of $\mathcal{K}=\ker\omega$ are identical in every member of the isotopic class. In each case, the powers of $\mathcal{K}$ are ideals and $\mathcal{K}$ is nilpotent, and hence all algebras of the isotopic class are special train algebras.*

3. Modes of segregation

The mechanism described by equation (2.3) is *chromosome segregation*. If this is replaced by

$$(a_0^{p_0}a_1^{p_1}\cdots a_n^{p_n})(a_0^{q_0}a_1^{q_1}\cdots a_n^{q_n})$$

$$=\binom{2ms}{m}^{-1}\sum_{r_0+\cdots+r_n=m}\binom{s(p_0+q_0)}{r_0}\binom{s(p_1+q_1)}{r_1}\cdots\binom{s(p_n+q_n)}{r_n}a_0^{r_0}a_1^{r_1}\cdots a_n^{r_n}, \quad (3.1)$$

with $s=2$, we have *chromatid segregation*. The phenomenon of double reduction

can be modelled by supposing that (2.3) or (3.1) occur with specified probabilities θ and $1-\theta$. It has been shown (Holgate, 1966) that the algebras for these types of segregation, for all values of θ, are *special* isotopes. That is, they satisfy (1.3) with $P = Q = I$. All mixtures of algebras of the type (3.1) for $s = 1, 2, \ldots$ are also special isotopes of (2.3) and (3.1), although those with $s > 2$ have no genetic significance.

An alternative proof, which shows the reason for the result in biological terms, is given below. The algebras $\mathscr{A}^*$ and $\mathscr{A}^\circ$ are special isotopes if, for all i and j,

$$\sum_k \lambda_{ijk} a_k = a_i \circ a_j = (a_i * a_j)S = \sum_l \sum_k \gamma_{ijl} s_{lk} a_k.$$

That is, if

$$\lambda_{ijk} = \sum_l \gamma_{ijl} s_{lk}.$$

If λ_{ijk} and γ_{ijk} both depend on i and j only through $i+j$, we can write

$$\lambda_{ijk} = \lambda_{i+j,k}, \qquad \gamma_{ijk} = \gamma_{i+j,k}, \qquad \lambda_{pk} = \sum_l \gamma_{pl} s_{lk}.$$

Then, writing $\Gamma = [\gamma_{ij}]$ and $\Lambda = [\lambda_{ij}]$, we have $S = \Lambda\Gamma^{-1}$. This leads to the following result.

LEMMA 2 *Let $\mathscr{C}$ be the class of all commutative algebras that admit a basis $\{a_i\}$ and multiplication table $a_i a_j = \sum_j \lambda_{ijk} a_k$ such that* (i) *λ_{ijk} depends on i and j only through $i+j$ and* (ii) *for which, if $a_i a_j = \sum_k \lambda_{i+j,k} a_k$, the matrix $[\lambda_{i+j,k}]$ is nonsingular. Then, all members of $\mathscr{C}$ are specially isotopic.*

In polyploid inheritance, with any mode of segregation, the gametic output of the union of two gametes depends only on the total number of alleles of each kind contained in the union. Hence, the condition (i) for special isotopy is satisfied, and we have the following theorem.

THEOREM 2 *The algebras defined by* (3.1), *and in particular the polyploid gametic algebras for chromosome segregation, chromatid segregation, and mixtures of them, are special isotopes. The powers of $\mathscr{H}$ are the same for all algebras of the class, they are ideals, and $\mathscr{H}$ is nilpotent. Hence, all algebras of the isotopic class are special train algebras.*

4. Recombination isotopes

A chromosome may be classified according to the alleles present at each of k loci, indexed by the set of integers $\{1, 2, \ldots, k\} = K$. For simplicity and without real loss of generality, we suppose that there are just two alleles, A_i and B_i, at locus i, and hence 2^k kinds of chromosome. For every $I \subseteq K$, the gametic type with A_i at locus i, if $i \in I$, and B_i, if $i \in \bar{I}$ ($\bar{I} = K \backslash I$), will be denoted by $a(I)$. A zygote carrying the unordered pair of gametes $\{a(I), a(J)\}$ will be denoted by $a(I, J)$.

In the absence of recombination, the system is equivalent to that of a single locus with 2^k alleles. We could take a canonical basis: $c(\varnothing) = a(\varnothing)$ and $c(I) = a(\varnothing) - a(I)$ $(I \neq \varnothing)$. Then we would obtain the star multiplication table

$$d(\varnothing) * d(\varnothing) = d(\varnothing), \qquad d(\varnothing) * d(I) = \tfrac{1}{2}d(I) \quad (I \neq \varnothing),$$
$$d(I) * d(J) = 0 \quad (I,J \neq \varnothing). \tag{4.1}$$

We shall see below that it is preferable to choose the canonical basis

$$c(I) = \sum_{J \subseteq I} (-1)^j a(J), \qquad a(I) = \sum_{J \subseteq I} (-1)^j c(J). \tag{4.2}$$

Since $c(I) = \sum_{\varnothing \neq J \subseteq I} (-1)^j d(J)$, or by direct calculation, we see that the multiplication table for this basis is the same as (4.1), namely,

$$c(\varnothing) * c(\varnothing) = c(\varnothing), \qquad c(\varnothing) * c(I) = \tfrac{1}{2}c(I) \quad (I \neq \varnothing),$$
$$c(I) * c(J) = 0 \quad (I,J \neq \varnothing). \tag{4.3}$$

The multiplication of the zygotic symbols is given by the standard rules of duplication:

$$a(I, J) * a(L, M) = \big(a(I) * a(J),\ a(L) * a(M)\big)$$
$$= \tfrac{1}{4}[a(I, L) + a(I, M) + a(J, L) + a(J, M)].$$

Transformation (4.2) is extended to the zygotic symbols by the formulae

$$c(I, J) = \sum_{L \subseteq I} \sum_{M \subseteq J} (-1)^{l+m} a(L, M), \qquad a(I, J) = \sum_{L \subseteq I} \sum_{M \subseteq J} (-1)^{l+m} (L, M). \tag{4.4}$$

The canonical table for star multiplication in the zygotic algebra is

$$\left.\begin{aligned} &c(\varnothing, \varnothing) * c(\varnothing, \varnothing) = c(\varnothing, \varnothing),\ c(\varnothing, \varnothing) * c(\varnothing, I) = \tfrac{1}{2}c(\varnothing, I) \quad (I \neq \varnothing), \\ &\qquad c(\varnothing, I) * c(\varnothing, J) = \tfrac{1}{4}c(I, J) \quad (I,J \neq \varnothing), \\ &\quad * \text{ products involving } c(I, J) \text{ are zero for } I,J \neq \varnothing. \end{aligned}\right\} \tag{4.5}$$

However, the effect of recombination is that an $a(I, J)$ individual does not only pass on $a(I)$ or $a(J)$ gametes to the next generation. For every subset $U \subseteq K$, there is the probability that the loci of U on one chromosome will recombine with those of $\bar{U}$ from the other, the complementary sets also combining, and that one of the recombinant gametes will be passed on.

We define the recombination operator $R(U)$ acting on the natural zygotic symbols $a(I, J)$ by

$$a(I, J)R(U) = a(I \cap U + J \cap \bar{U},\ I \cap \bar{J} + J \cap U).$$

The effect of $R(U)$ on the elements of the canonical basis (4.4) is

$$c(I, J)R(U) = \sum_{L \subseteq I} \sum_{M \subseteq J} (-1)^{l+m} \sum_{S \subseteq L \cap U + M \cap \bar{U}} \sum_{T \subseteq L \cap \bar{U} + M \cap U} (-1)^{s+t} c(S, T).$$

If S and T are held constant, the powers of (-1) will add to zero except in the

case where $S = I \cap U + J \cap \bar{U}$ and $T = I \cap \bar{U} + J \cap U$. Hence,

$$c(I, J)R(U) = (-1)^{i+j-|I \cap J|}\, c(I \cap U + J \cap \bar{U},\ I \cap \bar{U} + J \cap U). \tag{4.6}$$

In general, we consider a probability distribution $\{\lambda(U)\}$ over the subsets U of K corresponding to the possible modes of recombination, and define the recombination operator

$$R = \sum_{U \subseteq K} \lambda(U)R(U).$$

If we introduce a circle multiplication by the rule

$$a \circ b = (a * b)R, \tag{4.7}$$

it represents inheritance at k-linked loci with recombination according to the probability distribution $\{\lambda(U)\}$. The genetic algebra of inheritance with recombination is thus a special isotope of that for inheritance without recombination.

Now consider the subspace Id L in the zygotic algebra, spanned by all $c(I, J)$ with $I + J \supseteq L$. In view of (4.5), Id L is an ideal in the star multiplication algebra, which corresponds to inheritance without recombination. However, the union of the argument sets on the right-hand side of equation (4.6) is $I + J$, independently of U, so that even the general recombination operator R leaves invariant each subspace Id L. This shows that the subspaces Id L are ideals for every circle multiplication introduced by (4.7). Let us now define

$$\mathrm{Id}_s = \bigcup_{|L|=s} \mathrm{Id}\, L.$$

Then, $\mathcal{K} = \mathrm{Id}_1$, $\mathcal{K}^s = \mathrm{Id}_s$, $\mathcal{K}$ is nilpotent, and every power is an ideal, in all the circle recombination algebras. This establishes that they are all special train algebras. The results are summarized in the following theorem.

THEOREM 3 *The zygotic algebras for inheritance at k loci, with arbitrary crossover distribution, are specially isotopic. The subspaces* Id L *are ideals in all algebras of the class,* $\mathcal{K} = \mathrm{Id}_s$ *is nilpotent, all its powers are ideals, and hence all algebras of the class are special train algebras.*

Linkage and recombination at k loci have been studied via genetic algebras in other ways (e.g. Holgate, 1979, and references therein).

5. Selection isotopes

If the viability of the zygote a_{ij} carrying gametes a_i and a_j is v_{ij}, and $*$ denotes multiplication in the nonselective algebra, then circle multiplication, defined by $a \circ b = (a * b)V$ and $a_{ij}V = v_{ij}a_{ij}$, defines a special isotope which corresponds to inheritance with selection. Unfortunately, a general set of constants v_{ij} destroys the ideal structure, including the property of being baric.

6. Discussion

In Sections 2–4, it has been shown that all the genetic algebras for mutation (among polyploids), for different modes of segregation, and for recombination

among zygotic pairs of chromosomes can be *defined* as special or symmetric principal isotopes of the algebras for inheritance without mutation, with chromosome segregation, and without recombination, respectively. Population genetics involves an essentially quadratic interaction between the parts of the population playing male and female roles. The isotopies show that we can restrict the analysis of the quadratic aspects of the very small number of cases, and obtain the full range of modes of inheritance (mutation, partial double reduction, and recombination) by linear applications after each generation.

The algebraically striking feature is that these linear applications preserve the ideal $\mathcal{K}$ of codimension 1 in the genetic algebra, and its sequence of principal powers $\mathcal{K}^t$. Since, in the elementary case of each set, these powers satisfy the conditions necessary for the algebra to be special train, the same is true for all algebras of each isotopic class. This is equivalent to the assertion that mutation, complex modes of segregation, and recombination affect only the details of the algebraic structure of inheritance, without changing its basic framework. Moreover, although it has not been done here because of the heavy notation that would be involved, a class of polyploid zygotic algebras with mutation, partial double reduction, and recombination can be constructed, every member of which is isotopic to the zygotic polyploid algebra with no mutation or recombination, and chromosome segregation.

In his study of isotopy, Albert (1942: §12 ff.) shows that, among isotopic classes each member of which contains a multiplicative identity, it is often possible to choose one which satisfies specified desirable conditions. The absence of a multiplicative identity is an essential feature of genetic algebras. The present study shows that even so, in a field of application, certain isotopic relations preserve important aspects of structure, while enabling us to work with a simple member of the isotopic class.

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