CHARACTERISATIONS OF GENETIC ALGEBRAS

P. HOLGATE

1. Introduction

This paper is concerned with the non-associative algebras which arise in theoretical population genetics, an introductory account of which is given by Etherington in [2]. Let $\mathfrak{A}$ be an algebra of dimension $n+1$, commutative but not necessarily associative, over an algebraically closed field $\mathfrak{F}$ of characteristic zero. If $\mathfrak{A}$ admits a representation $x \rightarrow \beta(x)$ on $\mathfrak{F}$, of degree one, it is called a baric algebra. I will call $\beta(.)$ the baric function of $\mathfrak{A}$, and $\beta(x)$ the baric value of $x$. The terms weight and weight function have been used hitherto, but may cause confusion because of the different use of these terms in the theory of Lie algebras. It is clear that the set $\mathfrak{N}(\mathfrak{A})$ of elements of $\mathfrak{A}$ having baric value 0 constitutes an ideal, the nil ideal of $\mathfrak{A}$.

Let $R_x$ be the matrix of the transformation $y \rightarrow yx$, relative to some basis, and denote by $\mathfrak{R}(\mathfrak{A})$ the matrix algebra generated by the $R_x$, $x \in \mathfrak{A}$, and $I$ the unit matrix of order $n+1$. Thus a typical element of $\mathfrak{R}(\mathfrak{A})$ is

$$T = \alpha I + f(R_{x_0}, R_{x_1}, ..., R_{x_m}),$$

where $\alpha \in \mathfrak{F}$ and $f$ is a matrix polynomial. Schafer [7] introduced the idea of a genetic algebra, defining a baric algebra $\mathfrak{A}$ to be genetic if the characteristic polynomial of $T$ given by (1) depended on the elements $x_0$, $x_1$, ..., $x_m$ only through their baric values. More precisely, if $T^*$ is another element of $\mathfrak{R}(\mathfrak{A})$ given by

$$T^* = \alpha I + f(R_{y_0}, R_{y_1}, ..., R_{y_m}),$$

with $\beta(y_0) = \beta(x_0)$, $\beta(y_1) = \beta(x_1)$, ..., $\beta(y_m) = \beta(x_m)$, then it must have the same characteristic polynomial as $T$. This definition was inspired by the need to find some class of baric algebras sufficiently wide to include all those arising in the genetics of symmetric inheritance, in the absence of selection, differential viability or assortative mating, yet sufficiently narrow for the structure of its members to be elucidated. In particular, the first of these requirements means that the class must be closed under the duplication of algebras.

The commutative duplicate of an algebra $\mathfrak{A}$, which will be denoted here by $\mathfrak{A}^D$, consists of unordered pairs of its elements with the multiplication rule

$$(x, y)(u, v) = (xy, uv).$$

Its genetic relevance is discussed in [2], and its algebraic properties are studied in [3].

Schafer commented [7; p. 121] that "our interest in these algebras is entirely in the algebraic formalism, and we can give no indication beyond Etherington's own remarks of their possible contribution to the study of genetics". My object in this paper is to present alternative characterisations of Schafer's genetic algebras which are susceptible to interpretation in terms of properties of the genetic situation.

The class of train algebras introduced by Etherington (e.g. [2; p. 245]) which is wider than that of Schafer's genetic algebras, does involve a genetically meaningful
property. Suppose that in a baric algebra $\mathcal{A}$ the sequence of principal powers of $x$ is defined by $x^2 = xx$, $x^{n+1} = x^n x$, and that the rank equation

$$\sum_{i=0}^{n+1} \lambda_i x^{i+1} = 0$$

depends on $x$ only through its baric value, then $\mathcal{A}$ is said to be a train algebra. The fact that a genetic algebra, as he defined it, is necessarily a train algebra, was proved by Schafer [7; Theorem 1]. The genetic interpretation is that a fixed recurrence relation exists between the probability distributions of genetic types for a line of descendants produced by a process of backcrossing [2; p. 247].

2. Main theorems

Let $\mathfrak{L}(\mathcal{A})$ denote the Lie algebra generated by the matrices $R_x$, $x \in A$, with the commutator product $[R_x, R_y] = R_x R_y - R_y R_x$. Let $a_0, a_1, \ldots, a_n$ be a basis for the baric algebra $\mathcal{A}$, all of whose members have baric value one. In an algebra arising in genetics, the $a_i$ could for instance correspond to populations which are entirely of type $i$. Every element of $\mathfrak{L}(\mathcal{A})$ can be expressed in at least one way as

$$T = \alpha I + f(R_{a_0}, R_{a_1}, \ldots, R_{a_n}).$$

Now let $\mathfrak{S}(\mathcal{A})$ denote the subset of those elements of $\mathfrak{L}(\mathcal{A})$ which can be written in at least one way in the form

$$h(R_{a_0}, R_{a_1}, \ldots, R_{a_n}),$$

where $h$ is a matrix polynomial having the property that the sum of the coefficients of the terms of degree $d$ is zero, for $d = 1, 2, \ldots$. $\mathfrak{S}(\mathcal{A})$ is clearly an ideal in $\mathfrak{L}(\mathcal{A})$, and moreover the first derived algebra $\mathfrak{L}'(\mathcal{A})$ of the Lie algebra $\mathfrak{L}(\mathcal{A})$ satisfies $\mathfrak{L}'(\mathcal{A}) \subseteq \mathfrak{S}(\mathcal{A})$. An element $x$ of the non-associative algebra will be said to be nilpotent if the principal power $x^s$ is zero for all sufficiently large integers $s$.

**Theorem 1.** A baric algebra $\mathcal{A}$ is a Schafer genetic algebra if and only if

1. $\mathfrak{L}(\mathcal{A})$ is solvable, and
2. every element in $\mathfrak{S}(\mathcal{A})$ is nilpotent.

**Proof.** Suppose that the conditions are satisfied. In view of (i) it follows from Lie's theorem [5; p. 50] that it is possible to choose a basis in $\mathcal{A}$ such that all the matrices in $\mathfrak{S}(\mathcal{A})$ are upper triangular. If $R_x$ is upper triangular, nilpotency implies that its diagonal elements must be zero, or in Jacobson's terminology [5; p. 34] that it is nil triangular. Then if $\beta(u) = \beta(v)$, $R_u - R_v = R_{u-v}$, which is the multiplication matrix of an element of weight zero and hence is nilpotent by (ii), must be nil triangular. Thus $R_u$ and $R_v$ must have identical diagonals. The defining property of a Schafer genetic algebra is an immediate consequence.

On the other hand, suppose that $\mathcal{A}$ is a Schafer genetic algebra and that $h(R_{a_0}, R_{a_1}, \ldots, R_{a_n}) \in H(A)$, where as before $a_0, a_1, \ldots, a_n$ is a basis in which

$$\beta(a_0) = \beta(a_1) = \ldots = \beta(a_n) = 1.$$ 

The element

$$\alpha I + h(R_{a_0}, R_{a_1}, \ldots, R_{a_n})$$
has the same characteristic polynomial as

$$\alpha I + h(R_{ao}, R_{ao}, \ldots, R_{ao}).$$

This latter element is simply $\alpha I$ in view of the definition of $S(\mathfrak{A})$, and its characteristic polynomial is $(\lambda - \alpha)^n$. Thus $h(R_{ao}, R_{ao}, \ldots, R_{ao})$ is nilpotent. In particular, every matrix in $\mathcal{L}(\mathfrak{A})$ is nilpotent, which implies that $\mathcal{L}(\mathfrak{A})$ is nilpotent as a Lie algebra, and hence that $\mathcal{L}(\mathfrak{A})$ itself is solvable. In a Schafer genetic algebra, moreover, every element of $\mathfrak{N}(\mathfrak{A})$ is nilpotent, since this is already true for a train algebra [7; p. 126].

Condition (i) is equivalent to the requirement that $\mathfrak{N}(\mathfrak{A})$ does not admit an irreducible representation on $\mathfrak{A}$ of degree exceeding one [6; Theorems 1 and 3]. Condition (ii) is satisfied whenever it is known that $\mathfrak{N}$ is a train algebra, and thus the solvability of $\mathcal{L}(\mathfrak{A})$ can be looked on as being a sufficient additional requirement needed to ensure that a train algebra is a Schafer genetic algebra.

Suppose that $\mathfrak{N}$ has a baric function $\beta(.)$. Let $\mathfrak{A}^*$ be a non-zero subalgebra of $\mathfrak{N}$, (possibly identical with $\mathfrak{N}$) which is also baric with baric function $\beta^*(.)$. I propose to call $\beta^*(.)$ a partial baric function for $\mathfrak{N}$, and to call two partial baric functions $\beta^*(.)$ and $\beta^{**}(.)$ essentially different if there is an $x$ for which both are defined and for which $\beta^*(x) \neq \beta^{**}(x)$. Thus two partial baric functions may be different but not essentially different if they have different domains of definition but coincide on the intersection of these domains. The following result, which is of independent interest, prepares the way for an alternative characterisation of genetic algebras.

**Lemma 1.** Let $\mathfrak{N}$ be a baric algebra with baric function $\beta(.)$, and nil ideal $\mathfrak{N}$. If every element of $\mathfrak{N}$ is nilpotent, there is no other essentially different partial baric function on $\mathfrak{N}$.

**Proof.** Suppose that $\beta^*(.)$ is another partial baric function, and that $x$ belongs to its domain of definition. If $\beta(x) = 0$ then $x$ is nilpotent, which implies that $\beta^*(x) = 0$. If $\beta(x) \neq 0$, then $\beta(x^2/\beta(x) - x) = 0$ and the above argument then implies that $\beta^*(x^2/\beta(x) - x) = 0$, which in turn implies that either $\beta^*(x) = 0$ or $\beta^*(x) = \beta(x)$. Now since the difference algebra $\mathfrak{N}/\mathfrak{N}$ is one-dimensional, any element $z \in \mathfrak{N}$ can be represented in the form $z = \alpha x + d$ with $\alpha \in \mathfrak{A}$, $d \in \mathfrak{N}$ and thus if the first alternative were true it would imply that $\beta^*(z) = 0$ for all $z \in \mathfrak{N}$, so that $\beta^*(.)$ would be trivial. Thus $\beta^*(x) = \beta(x)$ for all $x$ for which both are defined.

In the case where $\mathcal{L}(\mathfrak{N})$ is solvable, let $\{c_0, c_1, \ldots, c_n\}$ be a basis for $\mathfrak{N}$ relative to which all matrices in $\mathfrak{N}(\mathfrak{N})$ are upper triangular. Let $\mathfrak{N}_k$ denote the subspace spanned by $\{c_k, \ldots, c_n\}$. Each space $\mathfrak{N}_k$ is thus invariant for every matrix in $\mathfrak{N}(\mathfrak{N})$.

**Theorem 2.** A baric algebra $\mathfrak{N}$ is a Schafer genetic algebra if and only if

(i) $\mathcal{L}(\mathfrak{N})$ is solvable, and

(ii) $\mathfrak{N}$ does not admit more than one essentially different partial baric function.

**Proof.** If $\mathfrak{N}$ is a Schafer genetic algebra, Lemma 1 enables condition (ii) of the theorem to be deduced from condition (ii) of Theorem 1.
On the other hand, suppose that $\mathfrak{L}(\mathfrak{U})$ is solvable but that $\mathfrak{U}$ is not a Schafer genetic algebra. Then by Theorem 1 there must be some element in $\mathfrak{H}(\mathfrak{U})$ which is not nilpotent. If the one-dimensional ideal $\mathfrak{U}_n$ is not nilpotent, it contains an idempotent element $x$. Then $\beta^*(x) = 1$ is a partial baric function on the subalgebra $\mathfrak{U}_n$ which is essentially different from $\beta(x)$. If $\mathfrak{U}_n$ is nilpotent, let $k$ be the largest integer such that $\mathfrak{U}_k$ is not nilpotent, but $\mathfrak{U}_{k+1}$ is nilpotent. Then $\mathfrak{U}_{k+1}$ is an ideal in $\mathfrak{U}_k$ of dimension one less than that of $\mathfrak{U}_k$. Hence [7; p. 123] $\mathfrak{U}_k$ is a baric subalgebra of $\mathfrak{U}$, entirely contained in $\mathfrak{H}(\mathfrak{U})$ and thus its baric function is a partial baric function for $\mathfrak{U}$, essentially different from $\beta(x)$.

3. Interpretations of the conditions

An algebra can be defined corresponding to any panmictic genetic system. The basis elements $a_0, a_1, \ldots, a_n$ correspond to the genetic types, and the multiplication table is defined by

$$a_i a_j = \sum_{k=0}^{n} \gamma_{ijk} a_k,$$

where $\gamma_{ijk}$ is proportional to the expected number of individuals of type $k$ which are produced by a mating between individuals of types $i$ and $j$, and survive to form part of the next generation. In the absence of differential fertility or viability, the $\gamma_{ijk}$ may be taken as the probabilities that a mating between individuals of types $i$ and $j$ produces an individual of type $k$. In this case $\sum_{k=0}^{n} \gamma_{ijk} = 1$ for every pair $i, j$. It follows immediately that the correspondence $a_i \to 1, i = 0, 1, \ldots, n$ defines a homomorphism of $\mathfrak{U}$ on $\mathfrak{S}$.

The relevance of the solvability conditions in Theorems 1 and 2 arises from the high degree of symmetry present in simple genetic systems. It is elucidated by a result of Borel and Serre [1], which was proved in a slightly different way by Jacobson [4], and which asserts that a Lie algebra is nilpotent if it admits an automorphism of prime order which leaves no non-zero element fixed. Examination of the proofs shows that this condition can be weakened at the expense of elegance.

**Theorem 3 (Borel–Serre).** A Lie algebra is nilpotent if the quotient algebra with respect to the ideal of absolute divisors of zero admits an automorphism with respect to which no non-zero element is fixed.

If the genetic types $i$ and $j$ play a symmetric role in the breeding structure of the population, $i$ and $j$ may be interchanged throughout the multiplication table of the algebra, thus producing an automorphism of $\mathfrak{U}$. This in turn induces automorphisms of $\mathfrak{H}(\mathfrak{U})$ and $\mathfrak{L}(\mathfrak{U})$, the size of the automorphism group being a measure of the genetic symmetry. Now the solvability of a finite-dimensional Lie algebra $\mathfrak{L}(\mathfrak{U})$ is equivalent to the nilpotency of its first derived algebra $\mathfrak{L}'(\mathfrak{U})$ [5; p. 51]. Thus, to show in a particular case that $\mathfrak{L}(\mathfrak{U})$ is solvable it is sufficient to show that, for every matrix polynomial in $\mathfrak{L}'(\mathfrak{U})$, it is either an absolute divisor of zero, or that there is an automorphism of $\mathfrak{L}'(\mathfrak{U})$ with respect to which it is not fixed. Since $\mathfrak{L}'(\mathfrak{U}) \subseteq \mathfrak{S}(\mathfrak{U})$ it is sufficient to verify this for polynomials homogeneous in $R_{a0}, R_{a1}, \ldots, R_{an}$ the sum of whose coefficients is zero. Some specific examples are now considered.
(i) The gametic algebra for a diploid population at a single locus with \( n + 1 \) alleles, for which the multiplication table is

\[
a_i \cdot a_j = \frac{1}{2}(a_i + a_j).
\]

The automorphism group contains as a subgroup the symmetric group on the elements \( \{a_0, a_1, \ldots, a_n\} \). The only polynomials in \( R_{a_0}, R_{a_1}, \ldots, R_{a_n} \) which are invariant under this group are symmetric polynomials, and since the sum of their coefficients is non-zero they lie outside \( \mathcal{L}'(\mathcal{A}) \).

(ii) The zygotic algebra for a diploid population at a single locus with two alleles. If in the previous example \( n = 1 \), the basis of the zygotic algebra may be taken as \( (a_0, a_0), (a_0, a_1), (a_1, a_1) \) exhibiting it as the duplicate \( \mathcal{A}^\mathcal{D} \) of the gametic algebra \( \mathcal{A} \). In this case the element

\[
R_{(a_0, a_0)} + R_{(a_1, a_1)} - 2R_{(a_0, a_1)};
\]

which belongs to \( \mathcal{H}(\mathcal{A}^\mathcal{D}) \) is invariant under the symmetric group on \( \{a_0, a_1\} \). It is, however, the multiplication matrix of the element \( (a_0, a_0) + (a_1, a_1) - 2(a_0, a_1) \) in \( \mathcal{A}^\mathcal{D} \), which is, in the terminology of duplicate algebras, a homomorph of zero. Hence it, and the corresponding multiplication matrix, are absolute divisors of zero. In genetic terms an element like this represents the difference between two populations which, while zygotically distinct, have the same gametic outputs.

Conditions under which a genetic algebra arising in practice is baric have been outlined in the first paragraph of this section. The uniqueness of the baric function is assured if there is sufficient symmetry. An element representing a population in which every allele is the same may be called pure (e.g. \( a_i \) in example (i) above, and \( (a_0, a_i) \) in example (ii)), \( D_0 \) and \( D_n \) in the diallelic polyploid gametic algebra with chromosome segregation, whose multiplication table is

\[
D_i \cdot D_j = \left( \begin{array}{c} 2n \\ n \end{array} \right)^{-1} \sum_{s=0}^n \binom{i+j}{s} \binom{2n-i-j}{n-s} D_s,
\]

and \( (D_0, D_0) \) and \( (D_n, D_n) \) in its duplicate the corresponding zygotic algebra. From genetic considerations a pure element must be idempotent, if mutation is excluded, and hence it must have baric value 0 or 1. If a permutation of the symbols representing the alleles induces an automorphism, then all pure elements must have the same value with respect to any baric function. But genetic considerations applying in practice imply that the pure elements form a generating set for the algebra. This excludes the possibility of all pure elements having baric value zero, and assures the uniqueness of the baric function.

Ramifications of the arguments used in this section appear to provide ways of demonstrating through Theorem 2 that algebras arising naturally in genetics will be "genetic" in Schafer's sense, provided that there is sufficient symmetry. It is satisfying to find that their relationship to the relevant genetic factors is visible.

4. Duplication

Finally, the characterisations of genetic algebras contained in Theorems 1 and 2 provide easy proofs of the closure of the class of Schafer genetic algebras under duplication.
Theorem 4. Each of the following statements about $\mathfrak{A}$ implies the same statement about $\mathfrak{A}^2$ and the same statement about $\mathfrak{A}^3$;

(i) $\mathfrak{L}(\mathfrak{A})$ is solvable;
(ii) the elements of baric value zero in $\mathfrak{A}$ are all nilpotent;
(iii) $\mathfrak{A}$ admits (does not admit) more than one essentially different baric function.

Proof. For the first part of the theorem, (i) $\mathfrak{L}(\mathfrak{A}^2)$ is a sub-Lie algebra of $\mathfrak{L}(\mathfrak{A})$, and hence is solvable, (ii) the elements of baric value zero in $\mathfrak{A}^2$ are a subset of those in $\mathfrak{A}$, and (iii) if $\beta(x) \neq \pm \gamma(x)$ then $\beta(x^2) \neq \gamma(x^2)$, with $x^2 \in \mathfrak{A}^2$, while the existence of essentially different partial baric functions on $\mathfrak{A}^2$ implies their existence on $\mathfrak{A}$, by definition.

For the second part, it is shown in [3] that $\mathfrak{A}^3$ is a direct sum of an ideal $\mathfrak{O}$ consisting of absolute divisors of zero, and an algebra isomorphic to $\mathfrak{A}^2$. The addition of $\mathfrak{O}$ clearly does not affect the three conditions. Since, by Lemma 1, condition (ii) implies the uniqueness of the baric function, there is no ambiguity in the interpretation of the theorem.

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References


Birkbeck College,
University of London.