ON DISCRETE EVOLUTIONARY DYNAMICS DRIVEN BY QUADRATIC INTERACTIONS

N. GROSJEAN, TH. HUILLET, G. ROLLET

Abstract. After an introduction to the general topic of models for a given locus of a diploid population whose quadratic dynamics is determined by a fitness landscape, we consider more specifically the models that can be treated using genetic (or train) algebras. In this setup, any quadratic offspring interaction can produce any type of offspring and after the use of specific changes of basis, we study the evolution and possible stability of some examples. We also consider some examples that cannot be treated using the framework of genetic algebras. Among these are bistochastic matrices.

Keywords: Evolutionary dynamics, quadratic interactions, genetic algebras, polymorphism, bistochastic interaction.

1. Introduction

In Section 2, we briefly revisit the basics of the deterministic dynamics arising in discrete-time asexual multiallelic evolutionary genetics driven only by fitness, in the diploid case with $K$ alleles. In this setup, there is a deterministic updating dynamics of the full array of the genotype frequencies involving the fitness matrix attached to the genotypes. When mating is random so that the Hardy-Weinberg law applies, one may limit oneself to the induced marginal allelic frequencies dynamics. Assuming non-overlapping generations, the updating dynamics on the simplex involves the ratio of marginal fitnesses (as affine functions in the frequencies) and the mean fitness as a quadratic form in the current frequencies. We will also consider an alternative updating mechanism of allelic frequencies over the simplex, namely the Mendelian segregating mechanism: here the fitness matrix is based on skew-symmetric matrices and the fitness landscape will be said flat. In the latter flat fitness model, the offspring can only repeat the genotype of any one of its parents as is the case in a (fair or unfair) Mendelian inheritance framework.

In Section 3, we will consider more general quadratic interaction models for which any pair-wise interaction can produce any type of offspring, thereby generalizing the latter flat fitness model: recombination is allowed. Under some stochasticity condition on the interactions, the framework of such models is the one of genetic algebras formalism that we introduce and develop in some details, largely inspired by the fundamental treatises \[28, 23\]. In some ("Gonshor-linearizable") cases, such dynamics are amenable to linear ones but in higher dimension. We give five examples for which detailed computations of the linearization procedure and the precise corresponding equilibria sets are supplied: the hypergeometric polyploidy model, the binomial Fisher-Wright model, the Hilbert matrix model, the shift model and the unbalanced Mendelian model with crossover. The equilibria sets are shown,
depending on the examples, to be either a point, or a curve or a surface. This concerns Subsection 3.1.

While using negatively the algebraic criteria that ensures the Gonshor-linearizability, we give, in Subsection 3.2, some important examples where linearizability fails: this includes permutation and more generally bistochastic models, together with the unbalanced Mendelian inheritance model (without crossover). The simple $K = 2$ dimensional case will be given a full detailed analysis in this respect.

2. Single locus: diploid population with $K$ alleles driven by fitness

For this approach on fitness, we refer to the general treatises \([9]\) and \([21]\).

2.1. Joint and marginal allelic dynamics (fitness). Consider $K$ alleles $A_k, k \in \{1, ..., K\}$ attached to a single locus. Let $W = (W_{k,l} \geq 0 : k, l \in \{1, ..., K\}^2)$ where $W_{k,l}$ stands for the absolute fitness of the genotypes $A_k A_l$ attached to a single locus. Since $W_{k,l}$ is proportional to the probability of an $A_k A_l$ surviving to maturity, it is natural to assume that $W$ is symmetric. Let $X = (x_{k,l} : k, l \in \{1, ..., K\}^2)$ be the current frequency distribution at (integral) time $t$ of the genotypes $A_k A_l$, so with $x_{k,l} \geq 0$ and $\sum_{k,l} x_{k,l} = 1$. Assuming Hardy-Weinberg proportions, the frequency distribution at time $t$ of the genotypes $A_k A_l$ is given by: $x_{k,l} = x_{k,l} W_{k,l}$ where $x_{k,l} = \sum_l x_{k,l}$ is the marginal frequency of allele $A_k$. The whole frequency information is now enclosed within $x = X 1^T$, where $1' = (1, ..., 1)$ is the 1-row vector of dimension $K$. And $x := (x_k : k \in \{1, ..., K\})$ belongs to the $K$-simplex $S_K = \{x_k : k = 1, ..., K\} \in \mathbb{R}^K : x \succeq 0, |x| = 1$.

Define the frequency-dependent marginal fitness of $A_k$ by $w_k(x) = (Wx)_k := \sum_l W_{k,l} x_l$. For some vector $x$, denote by $D_x \equiv \text{diag}(x_k : k \in \{1, ..., K\})$ the associated diagonal matrix. Assuming non-overlapping generations, the marginal mapping $p : S_K \rightarrow S_K$ of the dynamics of $x$ when driven by viability selection is given by:

$$x(t + 1) = p(x(t)), \text{ where } p(x) = \frac{1}{\omega(x)} D_x W x = \frac{1}{\omega(x)} D_W x x.$$

It involves a multiplicative quadratic interaction between $x_k$ and $(Wx)_k$, the $k$th entry of the image $Wx$ of $x$ by $W$ and a normalization by the mean fitness quadratic form $\omega(x) = x' W x$.

**Recombination.** Genetic recombination is the production of offspring with combinations of traits that can differ from those found in either parent. The model \([1]\) is a particular case of the following more general one displaying recombination effects. \([5], [23]\): let $\Gamma_k, k = 1, ..., K$ be $K$ nonnegative matrices with entries $\Gamma_k (i, j)$ representing the propensities for an interacting pair of alleles of type-$(i, j)$ to produce a type-$k$ allele. Let $\Gamma = \sum_{k=1}^K \Gamma_k$. Consider the dynamics $p$ on $S_K$:

$$x_k(t + 1) = p_k(x(t)), \text{ where } p_k(x) = \frac{x \Gamma_k x}{x \Gamma x}, k = 1, ..., K.$$
In such generalized models, it requires a pair of alleles to produce offsprings and any pair can in principle produce any type of offspring. The updating mechanism \( p \) is a fractional transformation with numerator and denominator both homogeneous of degree two as in (1). Clearly, the mapping \( x \rightarrow p(x) \) is \( k \)-Lipschitzian for \( 0 < k < \infty \), so uniformly continuous on \( S_{K} \), so if \( x(t) \rightarrow x_{eq}, \) \( x_{eq} \) has to be a fixed point of \( p \). This fixed point is unique if \( k < 1 \) but its stability condition is then open. For some very particular choices of \( \Gamma_{k} \), the situation turns out to be simpler. Let for instance \( \gamma_{k} = \Gamma_{k}1 \) and substitute \( P_{k} := D_{\gamma_{k}}^{-1} \Gamma_{k} \) to \( \Gamma_{k} \) in (2), namely consider the normalized dynamics on \( S_{K} \):

\[
x_{k}(t + 1) = p_{k}(x(t)), \quad \text{where } p_{k}(x) = \frac{x' P_{k} x}{x' P x}, \quad k = 1, ..., K.
\]

Then \( P_{k}1 = 1, \) \( k = 1, ..., K, \) so all \( P_{k} \) are stochastic matrices, not symmetric. And the barycenter \( x_{eq} = K^{-1}1 \) is an equiprobable equilibrium state of (3). Similarly, if \( \| \Gamma_{k} \|_{1} := \sum_{i,j} \Gamma_{k}(i,j) = \text{Cte}, \) for all \( k = 1, ..., K \) (all \( \Gamma_{k} \) matrices share the same matrix 1-norm), then \( x_{eq} = K^{-1}1 \) is an equilibrium state as well.

Let us now see under what conditions the generalized model (2) boils down to (1). Let \( I_{k} \) be the matrix whose entries are all zero except for the entry in position \((k,k)\), which is 1. Suppose \( \Gamma_{k} = I_{k}W \) where \( W \) is the symmetric fitness matrix in (1). Then \( \sum_{k=1}^{K} \Gamma_{k} = \Gamma = W \) is symmetric, \( \Gamma_{k}x = (Wx)_{k} e_{k} \) where \( e_{k} \) is the \( k \)-th unit vector of \( S_{K} \) and (2) matches with (1). If \( \Gamma_{k} = I_{k}W \), the propensities for a pair of individuals of type-(\( i,j \)) to produce a type-\( k \)-individual is zero unless \( i = k \): a model of Mendelian inheritance. A stochastic version of a similar model, coined the Fisher-Wright-Haldane model, was studied in [19] and [20]. A general dynamical theory of selection in multiallelic locus and even of additive selection in multiallelic multilocus system is developed in [23], Chapter 9.

2.2. The flat fitness model. We now address the so-called flat fitness model. Let \( A \) be some real skew-symmetric matrix, so obeying \( A' = -A \). Let \( J := 11' \) be the all-ones matrix and let \( \sigma > 0 \). Consider the evolutionary dynamics of the form (1) but now when \( W \) is of the form \( W = J + \sigma A \geq 0 \) with \( A' = -A \) and such that \( |A_{k,l}| \leq 1/\sigma \). The mean fitness function \( \omega(x) \) appearing in (1) is a constant \( \omega(x) = x' W x = 1 \), and in this sense the fitness matrix \( W \) is called flat. Because \( W_{k,l} + W_{l,k} = 2 \), these models correspond to constant-sum games in which each pair of two players has opposed interest or to evolution under the effect of segregation distortion in population genetics; See [27], [18] and [14]. The dynamics (1) for this particular form of \( W \) boils down to

\[
x(t + 1) = p(x(t)), \quad \text{where } p(x) = \frac{1}{\omega(x)} D_{x} W x = x + \sigma D_{x} A x.
\]

Let \( \Gamma_{k}, \) \( k = 1, ..., K \) be \( K \) nonnegative symmetric matrices with \( [0,1] \)-valued entries \( \Gamma_{k}(i,j) \) representing the probabilities for a pair of alleles of type-(\( i,j \)) to produce a type-\( k \) allele. Let \( \Gamma = \sum_{k=1}^{K} \Gamma_{k} \) and suppose \( \Gamma = J \). Consider the dynamics on \( S_{K} \) generalizing (1):

\[
x_{k}(t + 1) = p_{k}(x(t)), \quad \text{where } p_{k}(x) = \frac{x' \Gamma_{k} x}{x' \Gamma x} = x' \Gamma_{k} x, \quad k = 1, ..., K.
\]
Here $x'\Gamma x = 1$ and the fitness landscape is flat as in [11]. If in addition $\Gamma_k \mathbf{1} = \mathbf{1}$, $k = 1, ..., K$ (all $\Gamma_k$ are symmetric bistochastic matrices [25]), or if $\sum_{i,j} \Gamma_k (i,j) = Cte$ for all $k = 1, ..., K$, then $x_{eq} = K^{-1} \cdot \mathbf{1}$ is an unstable polymorphic equilibrium state of [11], the barycenter of $S_K$.

If $\Gamma_k (i,j) = 0$ unless $i = k$ or $j = k$ (the offspring can only repeat the genotype of any one of its parents as in a Mendelian model), then (5) is of the form (4) with $A (k,l) = 2\Gamma_k (k,l) - 1$ for $k \neq l$ and $A (l,k) = -A (k,l)$. $|A (k,l)| \leq 1$, (resulting from $\Gamma_k (k,l) + \Gamma_l (l,k) = 1$), corresponding to a fitness matrix $W = J + \sigma A \succeq \mathbf{0}$ with $\sigma = 1$. Therefore [41] is a very particular case of [25].

3. Genetic algebras

In this Section, we will consider the general model (5) under the flat fitness condition $x'\Gamma x = 1$ which can be dealt with through genetic algebras ideas, [28], [26].

Let $(e_1, ..., e_K)$ be the natural basis of $A = \mathbb{R}^K$ representing the extremal states of the simplex $S_K$. With $x (t) \in S_K$, we have

\begin{equation}
(6) \quad x (t) = \sum_{k=1}^{K} x_k (t) e_k,
\end{equation}

the species frequency vector in the simplex. Suppose a $K-$dimensional algebra $A$ over the field $\mathbb{R}$ with natural multiplication table

\begin{equation}
(7) \quad e_i e_j = \sum_{k=1}^{K} \gamma_{ijk} e_k,
\end{equation}

where $\gamma_{ijk} \in [0,1]$ constitute the structure constants, obeying the property $\sum_{k=1}^{K} \gamma_{ijk} = 1$ for all $i, j, k = 1, ..., K$. $A$ can be equipped with a weight homomorphism $\varpi : A \rightarrow \mathbb{R}$ obeying $\varpi (xy) = \varpi (x) \varpi (y)$ and for which $\forall i, \varpi (e_i) = 1$. And then $S_K = \varpi^{-1} (1) \cap \{ x \succeq \mathbf{0} \}$. Consider the dynamics $x (t+1) = x (t)^2$ (the second-order principal power of $x (t)$ in the algebra). Identifying $\gamma_{ijk} = \Gamma_k (i,j)$ and observing $x'\Gamma x = 1$ as a result of $\Gamma = J$, we obtain (5) evolving in $S_K$. Note that, without loss of generality for the dynamics above, $\gamma_{ijk} = \gamma_{jik}$, a commutativity property $(e_i e_j = e_j e_i)$. And because in general $(e_i e_j) e_k \neq e_i (e_j e_k)$, $A$ is commutative but not associative; such an algebra is called algebra with genetic realization in [28], [26], or stochastic algebra in [11]. Note also $x (t + m) =: x (t)^{m+1} = x (t)^{2m}$ with $x^{[m]} = x^{[m-1]} x^{[m-1]} = x^{[1]} = x$, defining the plenary powers of $x$ in $A$, not to be confused with the principal powers of $x$ in $A$, namely $x^m = xx^{m-1}, x^1 = x$.

Defining $\hat{e}_j$ to be the multiplication of $x \in A$ by $e_j$; $x \xrightarrow{\hat{e}_j} e_j x$, we get that its corresponding linear $K \times K$ transformation matrix acting to the left on column vectors is the matrix $E_i$ with entries $E_i (k,j) = \gamma_{ijk}$. The matrices $E_i$ are all column stochastic ($\forall i, j, \sum_k E_i (k,j) = 1$) and they do not commute in general.

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2Symmetric bistochastic matrices is the convex hull of extremal matrices of the form $(P + P') / 2$ where $P$ is any permutation matrix.
Let \((c_1, \ldots, c_K)\) denote some canonical basis in which \(x(t) = \sum_{k=1}^{K} y_k(t) c_k\). Suppose the multiplication table of the \(c_k\)s is given by

\[c_i c_j = \sum_{k=1}^{K} \lambda_{ijk} c_k,\]

where the canonical structure constants \(\lambda_{ijk}\) satisfy the Gonshor conditions [12]

\[
\begin{align*}
\lambda_{111} &= 1 \\
\lambda_{1jk} &= \lambda_{j1k} = 0 \text{ if } j > k \\
\lambda_{ijk} &= 0 \text{ if } i, j > 1 \text{ and } i \lor j \geq k.
\end{align*}
\]

If there is a change of basis \(e \rightarrow c\) so that the latter Gonshor conditions holds, then \(\mathcal{A}\) is called a genetic algebra. For genetic algebras, it holds that \(\varpi(c_i) = 1\) and \(\varpi(c_i) = 0, \ i = 2, \ldots, K\) so that \(I := \varpi^{-1}(0) = \ker \varpi\) is an ideal of \(\mathcal{A}\) \((\mathcal{A} \subseteq I)\) and \(I = \text{Span}(\{c_2, \ldots, c_K\}) = \langle c_2, \ldots, c_K \rangle\) is nilpotent \((I^n = \{0\} \text{ for some integer } n, \text{ the degree of nilpotency})\). For a genetic algebra to be a special train algebra, the following additional condition is required, [12], [26]:

All principal power subalgebras \(I^m\) of \(\mathcal{A}\) are ideals of \(\mathcal{A}\) \(\Rightarrow \mathcal{A} \supset I \supset \cdots \supset I^r \supset I^{r+1} = \{0\}\) and the sequence of ideals terminates after \(r\) steps called the rank of the special train algebra.

Special train algebras constitute a subclass of train algebras. For train algebras, the weaker nilpotency condition holds: every element of \(I = \ker \varpi\) is nilpotent of index less or equal \(r\). Consequently, if \(\mathcal{A}\) is a train algebra, for each \(x \in \mathcal{A}\), \(r(x) := x(x - \lambda_1) \cdots (x - \lambda_{r-1}) = 0\) and for each \(x \in \ker \varpi, x^r = 0\); \(r(x)\) is the rank polynomial of \(\mathcal{A}\) and the \(\lambda_i\) are the principal train roots of \(\mathcal{A}\). When \(\mathcal{A}\) is moreover a genetic algebra, the right train roots of \(\mathcal{A}\) are \(\lambda_{1ii}, i = 1, \ldots, K\), and the principal train roots of \(\mathcal{A}\), as a train algebra, is a subset of the right train roots of \(\mathcal{A}\) (one of which being 1), possibly including multiplicities. Apart from \(\lambda_{111} = 1\), all train roots \(\lambda_{1ii}\) of a genetic algebra obey \(|\lambda_{1ii}| \leq 1/2\) ([29], Coroll. 5). In this context, we recall the following general useful result stated in ([23], theorem 7.2.6): “suppose all the train roots of a genetic algebra are real. All trajectories converge if and only if all train roots different from 1/2 lie in the open circle of radius 1/2 and the dimension of the manifold of non-zero idempotents is the same as the number of train roots equal to 1/2.”

All genetic algebras are train algebras but not necessarily special train algebras, [12], [13], [26]. For an example of a (Bernstein) genetic algebra which is not special train and a sufficient condition for a genetic algebra to be a special train algebra, see Ex. 12 and Th. 13 of [10]. See also the Remark of [3], page 14.

For genetic algebras, we can define the matrices \(\Lambda_k(i, j) = \lambda_{ijk}\), with \(\Lambda_k\) having zero entries for those \((i, j)\) obeying the above constraints. Some of the \(\lambda_{ijk}\) which are non-zero from the above Gonshor constraints can occasionally be zero in some examples, thereby defining special classes of genetic algebras.
Defining \( \hat{c}_i \) to be the left-multiplication of \( x \in \mathcal{A} \) by \( c_i \): \( x \xrightarrow{\hat{c}_i} c_i x \), we get for its left linear \( K \times K \) transformation matrices

\[
C_i = \begin{bmatrix}
0 & \ldots & \lambda_{ii} & \ldots & 0 \\
\vdots & \ddots & \vdots & \ddots & \vdots \\
0 & \lambda_{i(i+1)} & \ldots & \lambda_{ii(i+1)} & 0 \\
\vdots & \vdots & \ddots & \ddots & \vdots \\
\lambda_{iK} & \ldots & \lambda_{iK} & \ldots & \lambda_{i(K-1)K} & 0
\end{bmatrix}
\]

if \( i = 2, \ldots, K \)

\[
C_1 = \begin{bmatrix}
\lambda_{111} & \lambda_{122} \\
\lambda_{112} & \lambda_{122} \\
\vdots & \ddots \\
\lambda_{11i} & \ldots & \lambda_{11i} \\
\lambda_{11K} & \ldots & \lambda_{11K} \\
\lambda_{1K} & \ldots & \lambda_{1K}
\end{bmatrix}
\]

if \( i = 1 \).

The right train roots \( \lambda_{ii} \) of \( \mathcal{A} \) are read on the diagonal of \( C_1 \) (they are the characteristic roots of the operator which is multiplication by \( c_1 \)), whereas the left train roots \( \lambda_{ii} \) of \( \mathcal{A} \) are read on the \((i, 1)\)—entry of \( C_i \). They are the values which were underlined.

We note that with \( \{ \omega_{i,k}, i = 2, \ldots, K, k > i \} \) the column \( K \)—vectors with entries \( \omega_{i,k} (j) = \lambda_{ijk}, j = 1, \ldots, k-1, = 0 \) if \( j = k, \ldots, K \), so that \( \omega_{i,k}^t e_l = 0 \) for all \( l = k, \ldots, K \), then

\[
C_i = \lambda_{ii} e_i e_i^t + \sum_{k=i+1}^{K} e_k \omega_{i,k}^t, \quad i = 2, \ldots, K.
\]

This decomposition into projectors together with the property \( \omega_{i,k}^t e_l = 0 \) is enough to ensure the nilpotency of the latter matrices \( C_i \) and it gives their orders of nilpotency.

From the shape of the \( C_i \)s, it also holds that \( \forall i = 2, \ldots, K : C_i (c_K) = (0) \) (all \( C_i \), \( i = 2, \ldots, K \) share \( c_K \) as a common eigenvector associated to the eigenvalue 0) and, with \( (c_k+1, \ldots, c_K) \subset (c_k, \ldots, c_K), k = 1, \ldots, K-1 \),

\[
\begin{align*}
C_i (c_k, \ldots, c_K) & \subseteq (c_{i+1}, \ldots, c_K), \text{ for all } i = 2, \ldots, K \text{ and } k = 2, \ldots, i \\
C_i (c_k, \ldots, c_K) & \subseteq (c_{k+1}, \ldots, c_K), \text{ for all } i = 2, \ldots, K \text{ and } k = i, \ldots, K \\
C_i (c_k, \ldots, c_K) & \subseteq (c_k, \ldots, c_K) \text{ if } i = 1 \text{ and } k = 1, \ldots, K.
\end{align*}
\]

If \( x = \sum_j y_j c_j \), where the \( y_j \)s are the coordinates of \( x \in S_K \) in the canonical basis (with \( y_1 = 1 \)), the matrix associated to the left multiplication \( \hat{x} \) by \( x \) is \( C_x = \sum_j y_j C_j \), which is lower-left triangular with \( \text{diag}(C_x) = \text{diag}(\lambda_{ii}) \). Therefore,

\[
\sum_{j=1}^{K} y_j C_j x = \sum_{j,k=1}^{K} y_j y_k C_j c_k
\]
are the coordinates of \( x^2 \in S_K \) in the canonical basis.

Suppose \( c_i = \sum_{j=1}^K B(i,j) e_j \) so with (non-singular) matrix \( B \) defining the change of basis. Then \( e_i = \sum_{j=1}^K B^{-1}(i,j) c_j = c_1 + \sum_{j=2}^K B^{-1}(i,j) c_j \) with \( B^{-1}(i,1) = 1 \) so as to ensure the compatibility of \( \forall i, \varpi(e_i) = 1 \) and \( \varpi(c_i) = \delta_{i,1} \).

In the sequel, we shall use

\[
B_1 = \begin{bmatrix}
1 & 1 \\
-1 & 0 \\
& \\
& \\
& \\
& \\
& \\
1 & 0 & 1
\end{bmatrix}
\quad \text{with } B_1^{-1} = \begin{bmatrix}
1 & 0 & 1 \\
1 & 0 & 1 \\
0 & 1 & 0
\end{bmatrix},
\]

and \( B_2(i,j) = (-1)^{j-1} \binom{i-1}{j-1} \), with \( B_2^{-1}(i,j) = B_2(i,j) \). In the latter case, we shall also use \( B_3 = B_2 P \) where \( P \) is the permutation matrix \( P(i,j) = \delta_{i,K+1-j} \) so with \( B_3(i,j) = (-1)^{K-j} \binom{i-1}{K-j} \).

Write \( b_{ij} := B(i,j) \). Then (using Einstein notations while summing over repeated indices): \( \lambda_{ijk} = b_{iv} b_{jv} \gamma_{i'j'k} b_{k'k}^{-1} \) gives the way the natural structure constants are deformed into the canonical ones of Gonshor, with the obvious inverse transformation, would the algebra be genetic. Note that this also means \( C_i = B^{i-1}(\sum_{i'} b_{ii'} E_{i'}) B' \) where \( B' \) is the transpose of \( B \), together with

\[
E_i = B' \left( \sum_{i'} b_{ii'}^{-1} C_{i'} \right) B'^{-1} = B' \left( C_1 + \sum_{i' \neq 1} b_{ii'}^{-1} C_{i'} \right) B'^{-1}.
\]

The latter identity shows that for genetic algebras, the \( E_i \)s must be mutually similar to triangular matrices (non-commutative in general and simultaneously triangularizable by the same similarity matrix \( B' \)). Because \( \forall i, b_{i1}^{-1} = 1 \), for every \( i, j \),

\[
E_i - E_j = B' \left( \sum_{i' \neq 1} \left( b_{ii'}^{-1} - b_{j1}^{-1} \right) C_{i'} \right) B'^{-1},
\]

with the matrix inside the parenthesis strictly lower-triangular. Thus \( E_i - E_j \) must also be similar to a nilpotent matrix, so nilpotent itself.

Given \( \lambda_{ijk} \) and \( b_{ij} \) it is not always satisfied that \( \gamma_{ijk} \) are \([0,1]\) valued with the property \( \sum_k \gamma_{ijk} = 1 \) for all \( i, j \). With \( \Gamma = (\Gamma_k, K = 1, ..., K), \Lambda = (\Lambda_k, k = 1, ..., K) \) and \( B \), we shall say that the triple \((\Gamma, \Lambda, B)\) is Gonshor-compatible if the \( \Gamma_k \) are \([0,1]\)-valued matrices with \( \sum_k \Gamma_k = J \). In this case, the model \( \Gamma \) is linearizable in a higher dimensional state-space whose rapidly growing dimension is given in Proposition 2 of Abraham [1] (would there be no other zero \( \lambda_{ijk} \) but the ones given from the Gonshor constraints, the dimension of the embedding linear space grows like \( \sqrt{2^{K^2}} \)).

3.1. **Examples of models akin to a genetic algebra.** Let us give some examples of genetic algebras. *In case the genetic algebras under study are train algebras, our examples will serve as an illustration of ([1], theorem 7.2.6) discussed above, characterizing the dimension of the equilibria sets.*
• **Pascal change of basis:** Suppose the hypergeometric model $\Gamma$ with

$$
\gamma_{ijk} = \binom{2(K - 1)}{K - 1}^{-1} \binom{i + j - 2}{k - 1} \binom{2K - (i + j)}{K - k}, \quad i,j,k = 1,\ldots,K.
$$

$\gamma_{ijk}$ (as the probability that an $i,j$ interaction produces $k$) is the probability that $k-1$ successes occur in a $K-1$ draw without replacement from a population of size $2(K - 1)$ containing $i + j - 2$ successes and $2K - (i + j)$ failures, $2 \leq i + j \leq 2K$. Clearly, $\gamma_{ijk}$ are $[0,1]$-valued as probabilities with $\sum_k \gamma_{ijk} = 1$ as a result of the Vandermonde convolution identity. Then using the change of basis $B_3(i,j) = (-1)^{K-j}\binom{i-1}{K-j}$, we get the Gonshor-like structure constants

$$
\lambda_{ijk} = \binom{2(K-1)}{i+j-2}^{-1}\binom{(K-1)}{i_{i+j-2}}, \quad \text{if } k = i + j - 1,
$$

$$
= 0 \quad \text{if not}
$$

and using $B_2(i,j) = (-1)^{j-1}\binom{j-1}{i-1}$, with $S_{ijk} := \sum_{l=0}^{i+j-2} (-1)^l \binom{i+j-2}{l} \binom{j-1}{k-l}$

$$
\lambda_{ijk} = \binom{2(K-1)}{K-1}^{-1}\binom{2K-k-1}{K-k}(-1)^{k-1}S_{ijk}, \quad i+j \leq k + 1.
$$

which are Gonshor-like structure constants. More precisely, because here $S_{ijk} = (-1)^{k-1}$ if $i + j = k + 1 = 0$ if $i + j \neq k + 1$

$$
\lambda_{ijk} = \begin{cases} 
\binom{2(K-1)}{K-1}^{-1}\binom{2K-(i+j)}{K-(i+j-1)}, & \text{if } i+j = k + 1 \\
= 0, & \text{if } i+j \neq k + 1.
\end{cases}
$$

For the hypergeometric model $\Gamma$, $(\Gamma, \Lambda, B)$ is Gonshor-compatible for $B = B_2$ and $B = B_3$. The latter models are models of polyploidy of degree 1. In the polyploidy of degree 1 examples, the $\Lambda_k$s are zero except on the anti-diagonals $i + j = k + 1$. The genetic polyploidy algebra is a special train algebra with train roots $\lambda_{111} = \binom{2(K-1)}{K-1}^{-1}\binom{(2K-1)-(i-1)}{K-i}$ verifying $\lambda_{111} = 1, \lambda_{122} = 1/2, \lambda_{1(i+1)(i+1)} < \lambda_{1ii}$, [12]. Because $\lambda_{122} = 1/2$ is a train root with multiplicity 1, we expect an equilibrium curve, ([12], [23], theorem 7.2.6).

Building from this example the column stochastic matrices $E_i$ with entries $E_i(k,j) = \gamma_{ijk}$, they can be seen to be simultaneously triangularizable and the matrices $E_i - E_j$ are all nilpotent.

**Example:** Let $K = 4$ and consider the Gonshor multiplication table in this low-dimensional case ($\lambda_{111} = 1$) using $B_3$. We have

$$
c_1^2 = \lambda_{111}c_1 = c_1
$$

$$
c_1c_2 = \lambda_{122}c_2, \quad c_1c_3 = \lambda_{133}c_3
$$

$$
c_1c_4 = \lambda_{144}c_4, \quad c_2^2 = \lambda_{222}c_3, \quad c_2c_3 = \lambda_{234}c_4
$$

$$
c_2c_4 = c_3^2 = c_3c_4 = c_4^2 = 0
$$

---

3It can indeed be checked here that $I^2 = \langle c_3,\ldots,c_K \rangle, I^3 = \langle c_4,\ldots,c_K \rangle$,...and $\mathcal{A}I^2 \subseteq I^3, \mathcal{A}I^3 \subseteq I^3,$...
where $\lambda_{j(i+j-1)} = \binom{i+j-2}{i-1}^{-1} \binom{3}{i-1}$ and so $\lambda_{122} = 1/2$, $\lambda_{133} = 1/5$, $\lambda_{144} = 1/20$, $\lambda_{223} = 1/5$ and $\lambda_{234} = 1/20$. Considering the time evolution $x(t+1) = x(t)^2$ in the Gonshor basis where $x(t) = c_1 + y_2(t)c_2 + y_3(t)c_4 + y_4(t)c_4$, we get

$$x(t+1) = c_1^2 + y_2^2(t)c_2^2 + 2y_2(t)c_1c_2 + 2y_3(t)c_1c_3 + 2y_4(t)c_1c_4 + 2y_2(t)y_3(t)c_2c_3$$

$$= c_1 + 2y_2(t)\lambda_{122}c_2 + (y_2^2(t)\lambda_{223} + 2y_3(t)\lambda_{133})c_3 + 2(y_4(t)\lambda_{144} + y_2(t)y_3(t)\lambda_{234})c_4$$

$$= y_1(t+1)c_1 + y_2(t+1)c_2 + y_3(t+1)c_3 + y_4(t+1)c_4.$$ 

To get a finite recursion, we need to generate the evolution of the additional states $y_2^3(t)$, $y_2(t)y_3(t)$ and $y_3^2(t)$ one of which is cubic. We get

$$y_2^3(t+1) = 4y_2^3(t)\lambda_{122}$$

$$y_2(t+1)y_3(t+1) = 2y_2^3(t)\lambda_{122}\lambda_{223} + 4y_2(t)y_3(t)\lambda_{122}\lambda_{133}$$

$$y_3^2(t+1) = 8y_3^2(t)\lambda_{122}^2$$

There are three additional states to generate here and we obtain the closed 7-dimensional (triangular) evolution

$$\begin{bmatrix}
y_1(t+1) \\
y_2(t+1) \\
y_2^3(t+1) \\
y_2^2(t+1) \\
y_2y_3(t+1) \\
y_3(t+1) \\
y_4(t+1)
\end{bmatrix} = \begin{bmatrix}
1 & 2\lambda_{122} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 4\lambda_{122} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 8\lambda_{122} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 2\lambda_{122}\lambda_{223} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \lambda_{133} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 2\lambda_{144} \\
0 & 0 & 0 & 0 & 0 & 0 & 0
\end{bmatrix} \begin{bmatrix}
y_1(t) \\
y_2(t) \\
y_2^3(t) \\
y_2^2(t) \\
y_2y_3(t) \\
y_3(t) \\
y_4(t)
\end{bmatrix}.$$ 

The transition matrix of this dynamics has 1 as a dominant eigenvalue with multiplicity 4 (because $\lambda_{122} = 1/2$), the corresponding eigenvector being, up to an indeterminate constant $y_2 : (1, y_2, y_2^2, y_2^3, y_2^3/3, y_2^3/3, y_2^3/27)$.

Recalling the correspondence between the $x$s and the $y$s, namely $x_k = \sum_{j=1}^4 y_jB_3(j,k) = (−1)^k\sum_{j=5−k}^4 y_j\binom{j−1}{k}$, in view of $y'_s = (1, y_2, y_2^2, y_2^3, y_2^3/3, y_2^3/3, y_2^3/27)$, leads to equilibrium states $x_{eq}$ of the $x$ dynamics in the simplex given by

$$x_{eq'} = (-y_2^3/27, y_2^2/3 + y_2^3/9; -y_2 + 2y_2^2/3 + y_2^3/9 ≤ 1 + y_2 + y_2^2/3 + y_2^3/27),$$

with normalizing constant 1 and for those values of $−3 ≤ y_2 ≤ 0$ for which $x_{eq}$ belongs to the simplex. This equilibrium curve, parameterized by $y_2$, is cubic and skew; it is stable and the rate at which the dynamics moves to $\{x_{eq}\}$ is geometric with parameter $2(\lambda_{133} \lor \lambda_{144}) = 2/5 < 1$. Note $x_{eq'} = (1; 0; 0; 0)$ if $y_2 = −3$ and $x_{eq} = (0; 0; 0; 1)$ if $y_2 = 0$; they are the extreme points of the cubics on the simplex.

**Polyplody of degree $d$:** Let $d ≥ 2$ be some integer, with $2d$ measuring the degree of polyplody (the case $d = 1$ being the previous case). Suppose the extended hypergeometric model $\Gamma$ with

$$\gamma_{ijk} = \binom{2d(K−1)}{K−1}^{-1} \binom{d(i+j−2)}{k−1} \binom{d(2K−(i+j))}{K−k}, \ i,j,k = 1,\ldots,K.$$ 

$\gamma_{ijk}$ is the probability that $k−1$ successes occur in a $K−1$ draw without replacement from a population of size $2d(K−1)$ containing $d(i+j−2)$ successes and
For $d (2K - (i + j))$ failures, $2 \leq i + j \leq 2K$. Then, using the change of basis $B_3$, with $S_{ijk} (d) := \sum_{l=0}^{i+j-2} (-1)^l \binom{i+j-2}{l} \binom{d_l}{k-1}$, we get the Gonshor-like structure constants
\begin{equation}
\lambda_{ijk} = \binom{2d (K - 1) - (i + j - 2)}{K - k} (K - i + j - 1), \quad i + j \leq k + 1.
\end{equation}
and using the change of basis $B_2$
\begin{equation}
\lambda_{ij} = \binom{2d (K - 1)}{K - 1} \binom{2d (K - 1) - (i + j - 2)}{K - k} (K - i + j - 1), \quad i + j \leq k + 1.
\end{equation}

In both cases, $S_{ijk} (d)$ is such that $S_{ijk} (d) \neq 0$ if $i + j \leq k + 1$, $= 0$ if $i + j > k + 1$.

Although more complex, this is also a Gonshor-like set of structure constants. In particular, in the latter $B_2$ case, when $i + j - 1$ varies from $1$ to $K$, in view of $(k = i + j - 1)$ $S_{ijk} (d) = (d_i+j-2)$
\begin{equation}
\lambda_{ij(i+j-1)} = \binom{2d (K - 1)}{K - 1} \binom{2d (K - 1) - (i + j - 2)}{K - (i + j - 1)} d_i+j-2,
\end{equation}
defining the train roots (right and left train roots being respectively
\begin{equation}
\lambda_{1j} = \binom{2d (K - 1)}{K - 1} \binom{2d (K - 1) - (j - 1)}{K - j} d_j-1 and \lambda_{ii} = \lambda_{1i},
\end{equation}
with $\lambda_{111} = 1$, $\lambda_{122} = 1/2$, $\lambda_{1(i+1)(i+1)} < \lambda_{1ii})$. In the polyploidy of degree $d > 1$ examples, the $\Lambda_k$ are upper-left triangular (a special class of genetic algebras known as special train genetic algebra with train roots $\lambda_{ij(i+j-1)}$). Like in the polyploidy model of degree $d = 1$, in both $B_3$ and $B_2$ cases, the equilibrium set is a curve because $\lambda_{122} = 1/2$ is a train root with multiplicity 1, (HEM, 23, theorem 7.2.6.)

**Fisher-Wright model.** Let $\alpha > 0, 1 > \beta > 0$ obeying $\alpha < 2 (K - 1) (1 - \beta)$.

Suppose the Fisher-Wright model $\Gamma$ for which $i, j, k = 1, \ldots, K$
\begin{equation}
\gamma_{ijk} = \frac{\binom{K - 1}{k - 1} (\alpha + \beta (i + j - 2))^{k-1} (2 (K - 1) - \alpha - \beta (i + j - 2))^{K-k}}{(2 (K - 1))^{K-k}}.
\end{equation}

$\gamma_{ijk}$ is a binomial-like probability system obeying $\sum_{k=1}^{K} \gamma_{ijk} = 1$. Using the change of basis $B_2$, whenever $i + j \leq k + 1$, we easily get
\begin{equation}
\lambda_{ijk} = (-1)^{k-1} \frac{\binom{K - 1}{k - 1}}{(2 (K - 1))^{k-1}} \sum_{l=0}^{i+j-2} (-1)^{l} \binom{i + j - 2}{l} (\alpha + \beta l)^{k-1},
\end{equation}
which are Gonshor-like structure constants with $\lambda_{ij1} = 0$ ($ij \neq 1$) and $\lambda_{ijk} = 0$ if $i + j > k + 1$, $\lambda_{ijk}$ depending only on $i + j$.

The last point can be checked while observing $\sum_{l=0}^{n} (-1)^l \binom{n}{l} x^l = 0$ for all $0 \leq k \leq n - 1$: consider indeed the degree-$n$ polynomial $P_n(x) = (x - 1)^n$ and with $D_k = (x \partial_x)^k$ consider then the degree-$n$ polynomial $D_k P_n(x)$. We have $D_k P_n(1) = \sum_{l=0}^{n} (-1)^l \binom{n}{l} x^l = 0$, for all $0 \leq k \leq n - 1$ and $D_n P_n(1) = \sum_{l=0}^{n} (-1)^l \binom{n}{l} l^n = n!$.

Note that with $i + j \leq k + 1$,
\begin{equation}
\lambda_{ijk} = \frac{K - 1}{K - 1} \left( \frac{-\alpha}{2 (K - 1)} \right)^{k-1} \sum_{l=i+j-2}^{k-1} \binom{k-1}{l} (\beta / \alpha)^l D_l P_{i+j-2} (1).
\end{equation}
For the Fisher-Wright model $\Gamma$, $(\Gamma, A, B_2)$ is Gonshor-compatible and this model defines a special train algebra with right (and left) train roots (when $\beta < 1$)

$$
\lambda_{1j} = \frac{(-1)^{j-1}}{(2 \cdot (K-1))^{(j-1)}} (K-1) \sum_{l=0}^{j-1} (-1)^l \binom{j-1}{l} (\alpha + \beta l)^{j-1} = \frac{(K-1)(j-1)!\beta^{j-1}}{(2 \cdot (K-1))^{(j-1)}},
$$

obeying $\lambda_{1(j+1)/(j+1)/1j} = \beta (K-j)/(2 \cdot (K-1)) < 1$. In particular, $\lambda_{122} = \beta/2 < 1/2$, $\lambda_{133} = (K-2)(\beta/2)^2/(K-1) < (\beta/2)^2 < 1/4,...$

**Example:** Let $K = 3$ and consider the Gonshor multiplication table in this low-dimensional case ($\lambda_{111} = 1$)

$$
\begin{align*}
\lambda_{11}^2 &= \lambda_{111} c_1 + \lambda_{112} c_2 + \lambda_{113} c_3 \\
\lambda_{12} c_2 &= \lambda_{122} c_2 + \lambda_{123} c_3 \\
\lambda_{13} c_3 &= \lambda_{133} c_3, c_2^2 = \lambda_{223} c_3 \\
c_2 c_3 &= c_3^2 = 0.
\end{align*}
$$

Here, $\lambda_{112} = -\alpha/2$, $\lambda_{122} = \beta/2$, $\alpha_{113} = \alpha^2/16$, $\alpha_{123} = -\beta (2\alpha + \beta)/16$ and $\alpha_{133} = \lambda_{223} = \beta^2/8$. Considering the time evolution $x(t) = x(t)^2$ in the Gonshor basis where $x(t) = c_1 + y_2(t) c_2 + y_3(t) c_3$, we get

$$
x(t+1) = c_1^2 + y_2^2(t) c_2^2 + 2y_2(t) c_1 c_2 + 2y_3(t) c_1 c_3
= c_1 + (\lambda_{112} + 2y_2(t) \lambda_{122}) c_2 + (\lambda_{113} + 2y_2(t) \lambda_{123} + y_2^2(t) \lambda_{223} + 2y_3(t) \lambda_{133}) c_3
= : y_1(t+1) c_1 + y_2(t+1) c_2 + y_3(t+1) c_3.
$$

The additional state $y_2^2(t)$ should be generated here with $y_2^2(t+1) = (\lambda_{112} + 2y_2(t) \lambda_{122})^2 = \lambda_{112}^2 + 4y_2(t) \lambda_{112} \lambda_{122} + 4y_2^2(t) \lambda_{122}^2$. We obtain the closed 4-dimensional evolution

$$
\begin{bmatrix}
y_1(t+1) \\
y_2(t+1) \\
y_2^2(t+1) \\
y_3(t+1)
\end{bmatrix} =
\begin{bmatrix}
1 & 0 & 0 & 0 \\
\lambda_{112} & 2\lambda_{122} & 0 & 0 \\
\lambda_{113} & 2\lambda_{123} & \lambda_{223} & 2\lambda_{133} \\
122 & 113 & 2123 & 2133
\end{bmatrix}
\begin{bmatrix}
y_1(t) \\
y_2(t) \\
y_2^2(t) \\
y_3(t)
\end{bmatrix}.
$$

The transition matrix of the $y_2$ dynamics has 1 as a dominant eigenvalue, the corresponding eigenvector being (recalling $2\lambda_{122} = \beta < 1$ and observing $\lambda_{133} = \beta^2/8 < 1/8$), up to a multiplicative constant

$$
y' = \left(\frac{1}{1-2\lambda_{133}} \left( \lambda_{113} + \frac{2\lambda_{112} \lambda_{122} + \lambda_{223} + 4\lambda_{112} \lambda_{122}}{1-2\lambda_{122}} \right) \right) y.
$$

Recalling the correspondence between the $x$s and the $y$s, namely $x_k = \sum_{j=1}^3 y_j B_2(j, k) = (-1)^{k-1} \sum_{j=k}^3 y_j (\lambda_j^{-1})$, gives the equilibrium state $x_{eq}$ of the $x$s dynamics in the simplex $x_{eq} = (1 + y_2 + y_3; -y_2 - 2y_3; y_3)$, with normalizing constant 1. For each $\alpha > 0$, $0 < \beta < 1$, this equilibrium point is stable because the eigenvalue 1 is simple and dominant. The rate at which the dynamics moves to $x_{eq}$ is geometric with parameter $2\lambda_{122} < 1$.

In the boundary cases for $(\alpha, \beta)$ for which $\alpha = 0$ and $\beta = 1$, $\lambda_{112} = \lambda_{113} = 0$, $\lambda_{122} = 1/2$, $\lambda_{123} = -1/16$ and $\lambda_{133} = \lambda_{223} = 1/8$, the transition matrix of the
$y_k$s dynamics has $1$ as a dominant eigenvalue with multiplicity $4$. This leads to an 
equilibrium quadratic skew curve of equation

$$\begin{align*}
x'_{eq} &= (y_1 + y_2 + y_3; -y_2 - 2y_3; y_3), \text{ where} \\
y_1 &= 1; \ y_3 = (y_2^2 - y_2)/6.
\end{align*}$$

This curve is parameterized by $-2 \leq y_2 \leq 0$; it passes through the extreme points of the simplex $(0; 0; 1)$ and $(1; 0; 0)$ if respectively $y_2 = -2$ or $y_2 = 0$ and also through the barycenter $(1/3; 1/3; 1/3)$ if $y_2 = -1$. The rate at which the dynamics moves to the equilibrium curve $\{x_{eq}\}$ is geometric with parameter $2\lambda_{133} = 1/4$.

\* Hilbert matrices model. With $i, j, k \geq 1$, suppose

$$\gamma_{ijk} = \frac{1}{i + j - 1}, \text{ if } k = 1, \ldots, i + j - 1; = 0 \text{ else.}$$

Note here $i, j, k$ are not bounded above by some $K$ (the model has infinitely many species). If this is so, $\sum_{k \geq 1} \gamma_{ijk} = 1$ for all $i, j \geq 1$.

Using the change of basis $B_2$, with $b(i, j) = (-1)^{j-1} \binom{j-1}{i-1} = b^{-1}(i, j)$ and $m = i' + j' + 2$, we easily get that

$$\lambda_{ijk} = b_{i'i''}b_{j'j''}b_{k'k''}^{-1} = \sum_{i', j', k'=1}^{i,j,k} (-1)^{i'+j'+k' - 2} \binom{i-1}{i'-1} \binom{j-1}{j'-1} \binom{k-1}{k'-1} \sum_{k''=k}^{i+j+k} (-1)^{k''} \binom{k'-1}{k''-1} \binom{k''}{k'}$$

$$= (-1)^{k-1} \sum_{m=k-1}^{i+j-2} (-1)^m \frac{m+1}{m+1} \sum_{l=k-1}^{m} \binom{l}{k-1}.$$  

$\lambda_{ijk}$ depends only on $i + j$ and is $0$ if $i + j < k + 1$ and also if $i + j > k + 1$. Indeed, using the identity

$$\sum_{l=k-1}^{m} \binom{l}{k-1} = \frac{m + 1 - (k-1)(m+1)}{k} (m+1),$$

$$\lambda_{ijk} = \frac{(-1)^{k-1}}{k} \sum_{m=k-1}^{i+j-2} (-1)^m \binom{i+j-2}{m} \binom{m}{k-1}$$

$$= \frac{1}{k} \binom{i+j-2}{k-1} \sum_{l=0}^{i+j-k-1} (-1)^l \binom{i+j-k-1}{l}$$

$$= 0 \text{ except if } k = i + j - 1.$$  

Thus $\lambda_{ijk}$ reduces to $\lambda_{ij(i+j-1)} = 1/(i + j - 1)$ and $\Lambda_k$ is reduced to the antidiagonal $i + j = k + 1$. With $x(t) = \sum_{k \geq 1} y_k(t) c_k$, we have

$$\begin{align*}
x(t+1) &= x(t)^2 = \sum_{k \geq 1} y_k^2(t) c_k^2 + 2 \sum_{1 \leq k < l} y_k(t) y_l(t) c_k c_l \\
&= \sum_{k \geq 1} \frac{y_k^2(t)}{2k-1} c_{2k-1} + 2 \sum_{1 \leq k < l} \frac{y_k(t) y_l(t)}{k+l-1} c_{k+l-1} \\
&= \sum_{j \geq 1} \sum_{k,l \geq 1: k+l-1=j} y_k(t) y_l(t) =: \sum_{j \geq 1} y_j((t+1)^2) c_j.
\end{align*}$$
so with \( y_j (t + 1) = \frac{1}{t} \sum_{k=1}^{l} \gamma_{ij} y_k (t) y_j (t) \). To produce a triangular infinite-dimensional linear system, we need to generate all the additional states \( y_k (t) y_l (t), 1 < k < l \). For an account on such infinite-dimensional genetic algebras, see [17].

**The shift change of basis.**

We start with an example. Let \( K = 3 \) and consider the Gonshor multiplication table in this low-dimensional case (\( \lambda_{111} = 1 \))

\[
\begin{align*}
c_1^2 &= \lambda_{111} c_1 + \lambda_{112} c_2 + \lambda_{113} c_3 \\
c_1 c_2 &= \lambda_{121} c_2 + \lambda_{123} c_3 \\
c_1 c_3 &= \lambda_{133} c_3 \\
c_2^2 &= \lambda_{223} c_3 \\
c_2 c_3 &= c_3^2 = 0
\end{align*}
\]

Assume \( \lambda_{ijk} > 0 \) and let \( x (t) = \sum_{k=1}^{3} x_k (t) e_k \). Then, with \( c_1 = e_1, c_2 = e_2 - e_1, c_3 = e_3 - e_1, (c_k = \sum B_1 (k, j) e_j), x (t) = y_1 (t) c_1 + y_2 (t) c_2 + y_3 (t) c_3 \) where \( y_1 (t) = 1, y_2 (t) = x_2 (t) \) and \( y_3 (t) = x_3 (t) \). This change of basis (of type \( B_1 \)) can be inverted to give \( e_1 = c_1, e_2 = c_2 + c_1, e_3 = c_3 + c_1 \). Hence, \( x_k (t) = \sum_j y_j (t) B_1 (j, k) \). Considering the time evolution \( x (t + 1) = x (t)^2 \) in the Gonshor canonical basis, we get

\[
x (t + 1) = c_1^2 + y_2^2 (t) c_2^2 + 2 y_2 (t) c_1 c_2 + 2 y_3 (t) c_1 c_3 \\
= c_1 + (\lambda_{112} + 2 y_2 (t) \lambda_{121}) c_2 + (\lambda_{113} + \lambda_{223} y_2^2 (t) + 2 y_2 (t) \lambda_{123} + 2 y_3 (t) \lambda_{133}) c_3 \\
= y_1 (t + 1) c_1 + y_2 (t + 1) c_2 + y_3 (t + 1) c_3
\]

To get a finite recursion if ever, we need to generate the evolution of the additional state \( y_2^2 (t) \). We get

\[
y_2^2 (t + 1) = \lambda_{112}^2 + 4 y_2^2 (t) \lambda_{112} \lambda_{121} + 4 y_2^2 (t) \lambda_{121}^2
\]

Therefore, we obtain the closed finite-dimensional evolution

\[
\begin{bmatrix}
y_1 (t + 1) \\
y_2 (t + 1) \\
y_2^2 (t + 1) \\
y_3 (t + 1)
\end{bmatrix} =
\begin{bmatrix}
1 & 0 & 0 & 0 \\
\lambda_{112} & 2 \lambda_{121} & 0 & 0 \\
\lambda_{112}^2 & 4 \lambda_{112} \lambda_{121} & 4 \lambda_{121}^2 & 0 \\
\lambda_{113} & 2 \lambda_{123} & 2 \lambda_{223} & 2 \lambda_{133}
\end{bmatrix}
\begin{bmatrix}
y_1 (t) \\
y_2 (t) \\
y_2^2 (t) \\
y_3 (t)
\end{bmatrix}.
\]

The corresponding matrices \( \Gamma_k \) given by \( \gamma_{ijk} = \Gamma_k (i, j) \) giving the evolution of the \( x_k \)s, are obtained while considering the products \( e_i e_j \) expressed in the Gonshor basis, making use of its multiplication table and then coming back to the natural basis. They are symmetric matrices with

\[
\Gamma_2 =
\begin{bmatrix}
\lambda_{112} & \lambda_{112} + \lambda_{121} & \lambda_{121} \\
\lambda_{112} + 2 \lambda_{121} & \lambda_{112} + \lambda_{121} \\
\lambda_{112} & \lambda_{112} + \lambda_{121}
\end{bmatrix}
\]

\[
\Gamma_3 =
\begin{bmatrix}
\lambda_{113} & \lambda_{113} + \lambda_{123} & \lambda_{113} + \lambda_{133} \\
\lambda_{113} + \lambda_{123} + \lambda_{223} & \lambda_{113} + \lambda_{123} + \lambda_{133} \\
\lambda_{113} + \lambda_{133} & \lambda_{113} + 2 \lambda_{133}
\end{bmatrix}
\]

\[
\Gamma_1 = J - (\Gamma_2 + \Gamma_3)
\]
The entries of these matrices should be $[0, 1]$-valued. The compatibility conditions ensuring this (besides $\lambda_{ijk} > 0$) are found to be by inspection of the $\Gamma_k$s

$$\max (2\lambda_{121} + \lambda_{123} + \lambda_{223}, \lambda_{121} + \lambda_{123} + \lambda_{133}, 2\lambda_{133}) \leq 1 - (\lambda_{112} + \lambda_{113})$$

$$\lambda_{112} + \lambda_{113} \leq 1.$$  

If these constraints are fulfilled (a sufficient condition being $\lambda_{112} + \lambda_{113} + 2\lambda_{121} + 2\lambda_{123} + 2\lambda_{133} + \lambda_{223} \leq 1$), then the quadratic model with the above $\Gamma_k$s is Haldane linearizable along the dynamics of the $y_k$s. Under the above conditions on the Gonshor structure constants, $(\Gamma, \Lambda, B_1)$ is Gonshor-compatible.

The transition matrix of the $y_k$s dynamics has 1 as a dominant eigenvalue, the corresponding eigenvector being (observing $\lambda_{121} < 1/2$ and assuming $\lambda_{133} < 1/2$), up to a multiplicative constant

$$y' = \left(1, \frac{\lambda_{112}}{1 - 2\lambda_{121}}, -\frac{\lambda_{112}}{1 - 2\lambda_{121}}\right)^2, \frac{\lambda_{113} (1 - 2\lambda_{121})^2 + 2\lambda_{112} \lambda_{123} (1 - 2\lambda_{121}) + \lambda_{112}^2 \lambda_{223}}{(1 - 2\lambda_{121})^2 (1 - 2\lambda_{133})} \right) = : (1; y_2; y_3).$$

Recalling the correspondence between the $x$s and the $y$s, namely $x_k = \sum_j y_j B_1 (j, k)$, we get the equilibrium state of the $x$s dynamics in the simplex $x'_{eq} = (1 - y_2 - y_3; y_2; y_3)$, with normalizing constant 1. This equilibrium point is stable because the eigenvalue 1 is simple and dominant.

Note that in the extremal case $\lambda_{112} = \lambda_{113} = 0$, $\lambda_{133} = 1/2$, provided

$$\max (2\lambda_{121} + \lambda_{123} + \lambda_{223}, \lambda_{121} + \lambda_{123} + \lambda_{133}) \leq 1,$$

1 is a double eigenvalue of the transition matrix for the $y_k$s and the equilibrium point is $x'_{eq} = (1; 0; 0)$, at the boundary of the simplex.

- Gametic algebra with recombination (28, Ex.1.3).

Let $K = 4$ and with $\theta \in (0, 1)$ and for all $i, j = 1, \ldots, 4$, let

$$e_i e_j = \frac{1}{2} (e_i + e_j) + (-1)^{i+j} - \frac{\theta}{2} (e_1 + e_4 - e_2 - e_3) 1_{(i+j=5)}$$

defining the $\gamma_{ijk}$s as a perturbed version of the fair Mendelian inheritance model involving crossovers. $\theta$ is the recombination rate, here the probability that zygote (1,4) undergoes a transition to zygote (2,3) and conversely. In this example, with $\overline{\theta} := 1 - \theta$

$$\Gamma_1 = \begin{bmatrix} 1 & 1/2 & 1/2 & \overline{\theta}/2 \\ 1/2 & 0 & \theta/2 & 0 \\ \overline{\theta}/2 & \theta/2 & 0 & 0 \\ \theta/2 & 0 & 0 & 0 \end{bmatrix}, \quad \Gamma_2 = \begin{bmatrix} 0 & 1/2 & 0 & \theta/2 \\ 1/2 & 1 & \overline{\theta}/2 & 1/2 \\ 0 & \overline{\theta}/2 & 0 & 0 \\ \theta/2 & 1/2 & 0 & 0 \end{bmatrix},$$

$$\Gamma_3 = \begin{bmatrix} 0 & 0 & 1/2 & \theta/2 \\ 0 & 0 & \overline{\theta}/2 & 0 \\ 1/2 & \overline{\theta}/2 & 1 & 1/2 \\ \theta/2 & 0 & 1/2 & 0 \end{bmatrix}, \quad \Gamma_4 = \begin{bmatrix} 0 & 0 & 0 & \overline{\theta}/2 \\ 0 & 0 & \theta/2 & 1/2 \\ 0 & \theta/2 & 0 & 1/2 \\ \overline{\theta}/2 & 1/2 & 1/2 & 1 \end{bmatrix}.$$
with $\Gamma_1 + \Gamma_2 + \Gamma_3 + \Gamma_4 = J$. And

$$E_1 = \begin{bmatrix} 1 & 1/2 & 1/2 & \theta/2 \\ 1/2 & 1 & 0 & \theta/2 \\ 0 & 0 & 1/2 & \theta/2 \\ 0 & 0 & 0 & \theta/2 \end{bmatrix}, \quad E_2 = \begin{bmatrix} 1/2 & 0 & \theta/2 & 0 \\ 1/2 & 1 & \theta/2 & 0 \\ 0 & 0 & \theta/2 & 1/2 \\ 0 & 0 & \theta/2 & 1/2 \end{bmatrix},$$

$$E_3 = \begin{bmatrix} 1/2 & \theta/2 & 0 & 0 \\ \theta/2 & 1 & 0 & 0 \\ 0 & \theta/2 & 1 & 1/2 \\ 0 & \theta/2 & 0 & 1/2 \end{bmatrix}, \quad E_4 = \begin{bmatrix} \theta/2 & 0 & 0 & 0 \\ \theta/2 & 1/2 & 0 & 0 \\ \theta/2 & 0 & 1/2 & 0 \\ \theta/2 & 1/2 & 1/2 & 1 \end{bmatrix}.$$  

Using,

$$B_4 := \begin{bmatrix} 1 & 1 & -1 & -1 \\ 1 & 0 & -1 & -1 \\ 1 & 1 & -1 & 1 \end{bmatrix},$$

with $B_4^{-1} = B_4$, we get

$$c_1^2 = \lambda_{111} c_1 = c_1,$$

$$c_{12} = c_{2}/2, \quad c_{13} = c_{3}/2,$$

$$c_{14} = (1 - \theta) c_{4}/2, \quad c_2^2 = 0, \quad c_{23} = \theta c_{4}/2,$$

$$c_{24} = c_3 c_4 = c_4^2 = 0,$$

which is Gonshor-like with right train roots $\lambda_{111} = 1, \lambda_{122} = \lambda_{133} = 1/2, \lambda_{144} = (1 - \theta)/2$. Because $\lambda_{122} = 1/2$ is a train root with multiplicity 2, we expect an equilibrium surface for this model, ([13], [23], theorem 7.2.6). Considering indeed the time evolution $x(t+1) = x(t)^2$ in the Gonshor basis where $x(t) =: c_1 + y_2(t) c_2 + y_3(t) c_3 + y_4(t) c_4$, we get

$$x(t+1) = c_1 + y_2(t) c_2 + y_3(t) c_3 + ((1 - \theta) y_4(t) + \theta y_2(t) y_3(t)) c_4$$

$$=: y_1(t+1) c_1 + y_2(t+1) c_2 + y_3(t+1) c_3 + y_4(t+1) c_4.$$

To get a finite recursion, we need to generate the evolution of one additional state, namely $y_2(t) y_3(t)$. We simply get

$$y_2(t+1) y_3(t+1) = y_2(t) y_3(t).$$

We obtain the closed finite-dimensional evolution

$$\begin{bmatrix} y_1(t+1) \\ y_2(t+1) \\ y_3(t+1) \\ y_2 y_3(t+1) \\ y_4(t+1) \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & \theta & 1 - \theta \\ 0 & 0 & 0 & \theta & 1 - \theta \end{bmatrix} \begin{bmatrix} y_1(t) \\ y_2(t) \\ y_3(t) \\ y_2 y_3(t) \\ y_4(t) \end{bmatrix}.$$

The transition matrix of this dynamics has 1 as a dominant eigenvalue with multiplicity 4, the corresponding eigenvector being, up to two indeterminate constants $y_2, y_3$: $(1, y_2, y_3, y_2 y_3, y_2 y y_3)$. 

Recalling the correspondence between the $x$s and the $y$s, namely $x_k = \sum_{j=1}^4 y_j B_4(j, k)$, in view of $y_\ast = (1, y_2, y_3, y_2 y_3)$, leads to equilibrium states $x_{eq}$ of the $x$s dynamics in the simplex given by $x_{eq} = (1 + y_2 + y_3 + y_2 y_3; -y_2 - y_2 y_3; -y_3 - y_2 y_3; y_2 y_3)$, with normalizing constant 1 and for those values of $-1 \leq y_2, y_3 \leq 0$ for which $x_{eq}$

\footnote{Because this model is Gonshor-compatible, the Lie algebra generated by $\{E_1, \ldots, E_4\}$ is solvable, see below. And all $E_i - E_j$ are nilpotent.}
belongs to the simplex. This equilibrium hypervolume, parameterized by \(y_2, y_3\), is skew; the equilibrium surface is defined as the intersection of the simplex \(S_4\) with the latter hypervolume which is seen to be of equation \(x_2x_3 = x_1x_4\). It is stable and the rate at which the dynamics moves to the equilibrium surface \(\{x_{eq}\}\) is geometric with parameter \(1-\theta < 1\). Note that \(\{x_{eq}\}\) contains the faces of the simplex: \((0; 1 + y_3; 0; -y_3)\) and \((0; 0; 1 + y_2; -y_2)\) obtained respectively when \(y_2 = -1\) and \(y_3 = -1\), together with the barycenter of the simplex obtained when \(y_2 = y_3 = -1/2\). Coming back to the natural basis, it can be checked in addition that in this example

\[
x(t + 1) - x(t) = \theta (x_2(t) x_3(t) - x_1(t) x_4(t)) u,
\]

where \(u' = (1, -1, -1, 1)\). So \(x(t)\) moves in the direction of \(u\), starting from \(x(0)\), before hitting the set \(\{x_{eq}\}\): the domain of attraction of a point in \(\{x_{eq}\}\) is included in a line pointing to \(\{x_{eq}\}\) from \(x(0)\) in the direction of \(u\).

3.2. Models not in the class of genetic algebras. So far, we gave some examples of symmetric matrices \(\Gamma_k\) (obeying \(\forall \ i, j, \sum_k \Gamma_k (i, j) = 1\)) leading to genetic algebras which are linearizable in higher dimension. We now give some examples which are not. From the previous arguments, the necessary and sufficient conditions under which a choice of \(\Gamma\) leads to genetic algebras is that:

1/ The matrices \(E_i\) with \(E_i (k, j) = \Gamma_k (i, j) = \gamma_{ijk}\) should be simultaneously triangularizable (ST) and
2/ \(\forall i < j, E_i - E_j\) should be nilpotent matrices.

A particular stochastic model \(\{\Gamma\}\) may fail to be Gonshor-compatible if condition 1/ or 2/ or both fail.

Concerning condition 1/: Quasi-commutative matrices are matrices commuting with their commutators (with commuting matrices being quasi-commutative). If \(\forall i < j, \forall k, [E_k; E_i, E_j] = 0\), then the set of matrices \(E_i\) are said to be quasi-commutative and in this case the \(E_i\) are simultaneously triangularizable (ST) in the extension \(\mathbb{C}\) of \(\mathbb{R}\) [24]. Commuting matrices are even simultaneously diagonalizable.

If quasi-commutativity is a ST sufficient condition, it is not necessary. In [25], the necessary and sufficient condition for ST was shown to be: \(\forall i < j, P(E_1, ..., E_K)[E_i, E_j]\) are nilpotent matrices for any polynomial \(P\) in the possibly non-commutative variables \(\{E_1, ..., E_K\}\). By Theorem 3 in [25], this condition is equivalent to the solvability of the Lie algebra \(L := \langle E_1, ..., E_K \rangle_{LA}\) spanned by \(\{E_1, ..., E_K\}\), closing the linear space generated by the \(E_i\) with respect to the commutator operation (the solvability of \(L\) means that its derived series terminates in the zero subalgebra [5]). \(L\) has \(d (K \leq \dim(L) = d \leq K^2)\) linearly independent basis matrices \(\{E_1, ..., E_d\}\), with \(\{E_1, ..., E_K\} \subseteq \{E_1, ..., E_d\}\), and \([E_i, E_j] = \sum_{k=1}^d e_{ijk} E_k\) where \(e_{ijk}\) are the structure constants of \(L\) obeying \(e_{ijk} = -e_{jik}\) and the Jacobi identity. The matrix \(K\) associated to the Killing form of \(L\) is \(K := [k_{i,j}]\), where

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5This means that for all examples designed in Section 3.1, the Lie algebras generated by the \(\{E_i\}\) which can be built from the \(\{\Gamma_i\}\) we started from, were solvable and that all \(E_i - E_j\) were nilpotent.
$k_{i,j} = \sum_{k,l} e_{ilk} e_{jkl}$. Its non-degeneracy is a signature of the semi-simplicity of $L$, with semi-simplicity $\Rightarrow$ non-solvability (the reciprocal being false in general).

A constructive (although prohibitive even for small $K$) test for pair-wise ST of $\{E_1, \ldots, E_K\}$ is that of Theorem 6 of [4]: for every $k \in \{1, K^2 - 1\}$, $\forall i < j$, with $U_l \in \{E_i, E_j\}$, $l = 1, ..., k$, each matrix of the form $U_1 \cdots U_k [E_i, E_j]$ has zero trace. ST of $\{E_1, \ldots, E_K\}$ condition is: for every $k \in \{1, K^K - 1\}$, $\forall i < j$, with $U_l \in \{E_1, \ldots, E_K\}$, $l = 1, ..., k$, each matrix of the form $U_1 \cdots U_k [E_i, E_j]$ has zero trace.

The conditions 1/ and 2/ can be used to show that special important families of $\Gamma_k$ do not lead to genetic algebras.

- **Permutations.**

  (i) Suppose
  \[
  \Gamma_1 = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}, \quad \Gamma_2 = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}.
  \]
  Then $E_1 = \Gamma_1$ and $E_2 = \Gamma_2$ are commuting matrices so simultaneously triangularizable (in fact diagonalizable). However $E_1 - E_2 = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}$ with trace $-2$ is not nilpotent.

  (ii) Suppose
  \[
  \Gamma_1 = \begin{bmatrix} 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix}, \quad \Gamma_2 = \begin{bmatrix} 0 & 0 & 1 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \end{bmatrix}, \quad \Gamma_3 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 1 & 0 \end{bmatrix}.
  \]
  Then
  \[
  E_1 = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}, \quad E_2 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}, \quad E_3 = \begin{bmatrix} 0 & 0 & 1 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \end{bmatrix}
  \]
  which are commuting permutation matrices so simultaneously triangularizable (in fact diagonalizable with a unitary matrix). However $E_1 - E_2 = \begin{bmatrix} -1 & 1 & 1 \\ 0 & -1 & 1 \\ 1 & 0 & -1 \end{bmatrix}$ with trace $-3$ is not nilpotent.

  (iii) Suppose
  \[
  \Gamma_1 = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}, \quad \Gamma_2 = \begin{bmatrix} 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix},
  \]
  \[
  \Gamma_3 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix}, \quad \Gamma_4 = \begin{bmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}.
  \]
with $\Gamma_1 + \Gamma_2 + \Gamma_3 + \Gamma_4 = J$. Then

$$E_1 = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}, \quad E_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix},$$

$$E_3 = \begin{bmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix}, \quad E_4 = \begin{bmatrix} 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix},$$

are also permutation (non-symmetric) matrices which are not even quasi-commuting. Note $E_1 + E_2 + E_3 + E_4 = J$. We have for instance

$$E_2 E_3 [E_1, E_2] = \begin{bmatrix} -1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & -1 \end{bmatrix}$$

with trace $-3$, so not nilpotent. Moreover,

$$E_1 - E_2 = \begin{bmatrix} -1 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 1 & 0 & 0 & -1 \\ 0 & 0 & -1 & 1 \end{bmatrix},$$

with trace $-1$, is not nilpotent. The (non-solvable) Lie algebra $L$ generated by the $E_i$, $i = 1, \ldots, 4$, has dimension $d = 10$, with basis

$$\{E_1; E_2; E_3; E_4; E_5 = [E_1, E_2]; E_6 = [E_1, E_3]; E_7 = [E_1, E_5]; E_8 = [E_1, E_6]; E_9 = [E_1, E_8]; E_{10} = [E_2, E_5]\}.$$

The associated structure constants can be computed, together with the associated Killing matrix $K$ which is found to be of rank 8, so degenerate. The Lie algebra $L$ is neither solvable nor semisimple.

$(iii')$ Suppose

$$\Gamma_1 = I, \quad \Gamma_2 = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}, \quad \Gamma_3 = \begin{bmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix}, \quad \Gamma_4 = \begin{bmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix},$$

with $\Gamma_1 + \Gamma_2 + \Gamma_3 + \Gamma_4 = J$. Then $E_i = \Gamma_i$, $i = 1, \ldots, 4$ are also permutation (symmetric) matrices which are commuting (the Lie algebra $L$ generated by the $E_i$ is solvable of order 1). However,

$$E_1 - E_2 = \begin{bmatrix} 1 & -1 & 0 & 0 \\ -1 & 1 & 1 & 0 \\ 1 & 0 & 1 & -1 \\ 0 & 0 & -1 & 1 \end{bmatrix},$$

with trace 4, is not nilpotent.

These examples suggest that, would $\Gamma_k$ be symmetric (involutive) permutation matrices, such models should not lead to genetic algebras in general (Recall though
that the fixed equilibrium point of such dynamics is always the barycenter $x_B$ of the simplex $S_K$. This suggestion is not reduced to symmetric permutation matrices. Suppose

$$\Gamma_1 = \begin{bmatrix} 0 & 1/2 & 1/2 \\ 1/2 & 0 & 1/2 \\ 1/2 & 1/2 & 0 \end{bmatrix} = \Gamma_2, \Gamma_3 = I,$$

the symmetrized version of the non-symmetric permutation matrices

$$P_1 = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}, P_2 = \begin{bmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}, P_3 = I.$$

Then

$$E_1 = \begin{bmatrix} 0 & 1/2 & 1/2 \\ 0 & 1/2 & 1/2 \\ 1 & 0 & 0 \end{bmatrix}, E_2 = \begin{bmatrix} 1/2 & 0 & 1/2 \\ 1/2 & 0 & 1/2 \\ 0 & 1 & 0 \end{bmatrix}, E_3 = \begin{bmatrix} 1/2 & 1/2 & 0 \\ -1/2 & 0 & 1/2 \\ 1 & 0 & -1 \end{bmatrix},$$

which are non-quasi-commuting bistochastic matrices, however with $E_1 [E_1, E_2]$ nilpotent for instance. But $E_1 - E_3 = \begin{bmatrix} -1/2 & 0 & 1/2 \\ -1/2 & 0 & 1/2 \\ 1 & 0 & -1 \end{bmatrix}$ with trace $-3/2$ is not nilpotent. The Lie algebra $L$ generated by the $E_i, i = 1, ..., 3$, has dimension $d = 3$, with basis $\{E_1; E_2; E_3\}$. The associated structure constants can be computed, together with the associated Killing matrix $K$ which is found to be of rank 1, so degenerate. The Lie algebra $L$ is solvable of order 2 (the brackets $[E_i, E_j], i < j$ being proportional to the same matrix $E_1 - E_2$) and not semisimple.

- **The general 2–dimensional stochastic case, including the bistochastic matrices case.**

(iv) With $\alpha, \beta, \gamma \in (0, 1)$ and $\overline{\alpha} = 1 - \alpha, \overline{\beta} = 1 - \beta, \overline{\gamma} = 1 - \gamma$, suppose

$$\Gamma_1 = \begin{bmatrix} \alpha & \beta & \gamma \\ \beta & \gamma & \overline{\beta} \end{bmatrix}, \Gamma_2 = \begin{bmatrix} \overline{\alpha} & \overline{\beta} & \overline{\gamma} \\ \beta & \gamma & \overline{\beta} \end{bmatrix},$$

the general 2–dimensional stochastic problem. Then

$$E_1 = \begin{bmatrix} \alpha & \beta & \gamma \\ \overline{\alpha} & \overline{\beta} & \overline{\gamma} \end{bmatrix}, E_2 = \begin{bmatrix} \beta & \gamma & \overline{\beta} \\ \beta & \gamma & \overline{\beta} \end{bmatrix},$$

which do not commute in general (unless $\beta \overline{\beta} = \gamma \overline{\gamma}$). The Lie algebra $L$ generated by $\{E_1, E_2\}$ has dimension $d = 3$ with basis $\{E_1, E_2, E_3 = [E_1, E_2]\}$ if $\alpha + \gamma \neq 2\beta$ and dimension $d = 2$ if $\alpha + \gamma = 2\beta$. It is solvable in both cases because, by Cartan solvability criterion, the Killing form $K$ satisfies $K(E, E') = \text{Trace}(E, E') = 0$ for all $E$ in $L$ and $E'$ in $[L, L]$. However here, $E_1 - E_2 = \begin{bmatrix} \alpha - \beta & \beta - \gamma \\ \overline{\alpha} - \overline{\beta} & \overline{\beta} - \overline{\gamma} \end{bmatrix}$, with trace $\alpha - \beta + \overline{\beta} - \overline{\gamma}$. It is not nilpotent unless $\alpha + \gamma = 2\beta$. Although $L$ is solvable, the general 2–dimensional stochastic problem is not Gonshor-linearizable unless $\alpha + \gamma = 2\beta$.

If $\alpha + \gamma = 2\beta$, the evolutionary dynamics $x(t + 1) = x(t)^2$ reads

$$x_1(t + 1) = (x_1(t), 1 - x_1(t)) \Gamma_1 (x_1(t), 1 - x_1(t)) = 2(\beta - \gamma) x_1(t) + \gamma,$$

$$x_2(t + 1) = 2(\beta - \gamma) x_2(t) + \overline{\alpha}.$$
It is indeed linear with fixed point $x_{eq} = (\gamma / (\gamma + \alpha), \alpha / (\gamma + \alpha))^T$, in the simplex. So, except in this particular case, the general 2-dimensional problem is not amenable to a linear problem and when it is, there is no additional state to generate.

However, because of the very low dimension ($K = 2$) of the problem, the analysis of the model with $\{\Gamma_1, \Gamma_2\}$ defined above is possible. We find that for any $\alpha, \beta, \gamma \in (0, 1)$, the 2-dimensional dynamics $x_k(t + 1) = x^T \Gamma_k x$, $k = 1, \ldots, 2$ always has a fixed point in the simplex. Defining $\varepsilon = (\alpha + \gamma) / 2 - \beta$, the dynamics is

$$x_1(t + 1) = 2\varepsilon x_1(t)^2 + (\alpha - \gamma - 2\varepsilon)x_1(t) + \gamma =: f(x_1(t)),$$

with a quadratic $f$. With $\Delta = (2\beta - 1)^2 + 4\gamma \varepsilon > 0$, the fixed point in the simplex therefore is

$$(\alpha, \beta, \gamma) = \frac{\gamma - \alpha + 2\varepsilon + 1 - \sqrt{\Delta}}{4\varepsilon}, x_{eq} = 1 - x_{1,eq}.$$\

With $\Delta > 1 \Leftrightarrow \beta \bar{\beta} < \gamma \bar{\alpha}$, we have $f'(x_{1,eq}) = 1 - \sqrt{\Delta}$ with $|f'(x_{1,eq})| < 1$ if $\Delta \leq 1$ or $1 < \Delta \leq 4$. So $x_{1,eq}$ is asymptotically stable if and only if $\Delta \leq 4$. If $\Delta > 4$, $x_1(t)$ oscillates between two limiting values in the simplex around $x_{1,eq}$, as a center fixed and unstable point: we have two period-two equilibrium points (obeying $f(f'(x)) = x$). If $4 > \Delta > 1$, $x_1(t)$ tends to $x_{1,eq}$ while oscillating around $x_{1,eq}$, as a fixed stable equilibrium point. Else, if $\Delta < 1$, $x_1(t)$ tends to $x_{1,eq}$ from below or from above (depending on the initial condition) without over-crossing its limiting value more than once.

If $\beta = \alpha = \gamma$ then $\beta \bar{\beta} = \gamma \bar{\alpha}$, $\Gamma_1$ and $\Gamma_2$ are bistochastic and $[E_1, E_2] = 0$. In this case, $E_1 - E_2 = \left[\begin{array}{cc} 2\alpha - 1 & -2\alpha \\ 2\alpha - 1 & 2\alpha - 1 \end{array}\right]$ with zero trace. This matrix is not nilpotent unless $\alpha = \beta = \gamma = 1/2$, a trivial case. In dimension $K = 2$, bistochastic models are not Gonshor-linearizable in general either.

**Unbalanced Mendelian inheritance model.**

(v) With $a_1 + a_2 = 1$, $b_1 + b_2 = 1$, $b_2 + a_3 = 1$, suppose $(\Gamma_1 + \Gamma_2 + \Gamma_3 = J)$

$$\Gamma_1 = \left[\begin{array}{ccc} 1 & a_1 & b_1 \\ a_1 & 0 & 0 \\ b_1 & 0 & 0 \end{array}\right], \quad \Gamma_2 = \left[\begin{array}{ccc} 0 & a_2 & 0 \\ a_2 & 1 & b_2 \\ 0 & b_2 & 0 \end{array}\right], \quad \Gamma_3 = \left[\begin{array}{ccc} 0 & 0 & b_3 \\ 0 & 0 & a_3 \\ b_3 & a_3 & 1 \end{array}\right].$$

This is a model with Mendelian segregation for which only interactions $(k, j)$ or $(i, k)$ can produce type-$k$ offspring. Here $x(t + 1) = x(t)^2$ where $x(t) = \sum_i x_i(t) e_i$ and multiplication table given by $e_i e_j = \Gamma_i (i, j) e_i + \Gamma_j (i, j) e_j$, where $\Gamma_i (i, j) + \Gamma_j (i, j) = 1$. As observed previously in Section 2, the dynamics of species frequencies is also $x_k(t + 1) = x^T \Gamma_k x$, $k = 1, \ldots, 3$. It can alternatively be written in vector form as

$$x(t + 1) = x(t) + D_{x(t)} Ax(t),$$

$$x(t + 1) = x(t) + D_{x(t)} A x(t),$$
where \( A := \begin{bmatrix} 0 & 2a_1 - 1 & 2b_1 - 1 \\ 2a_2 - 1 & 0 & 2b_2 - 1 \\ 2b_3 - 1 & 2a_3 - 1 & 0 \end{bmatrix} \) is a skew-symmetric matrix. In such a case, 
\[
E_1 = \begin{bmatrix} 1 & a_1 & b_1 \\ 0 & a_2 & 0 \\ 0 & 0 & b_3 \end{bmatrix}, \quad E_2 = \begin{bmatrix} a_1 & 0 & 0 \\ a_2 & 1 & b_2 \\ 0 & 0 & a_3 \end{bmatrix}, \quad E_3 = \begin{bmatrix} b_1 & 0 & 0 \\ 0 & b_2 & 0 \\ b_3 & a_3 & 1 \end{bmatrix}
\]
which are non-commuting column stochastic matrices with \( E_1 [E_1, E_2], E_2 [E_1, E_2], E_1 E_2 [E_1, E_2], \ldots \), nilpotent matrices.

However \( E_1 - E_2 = \begin{bmatrix} 1 - a_1 & a_1 & b_1 \\ -a_2 & a_2 - 1 & -b_2 \\ 0 & 0 & b_3 - a_3 \end{bmatrix} \) with trace \( a_2 - a_1 + b_3 - a_3 \) is not nilpotent unless \( a_1 = a_2 = 1/2, \ b_3 = a_3 \) and \( b_1 = b_2 \). Similarly, \( E_2 - E_3 = \begin{bmatrix} a_1 - b_1 & 0 & 0 \\ a_2 & 1 - b_2 & b_2 \\ -b_3 & -a_3 & a_3 - 1 \end{bmatrix} \) with trace \( a_1 - b_1 + a_3 - b_2 \) is not nilpotent unless \( a_3 = b_2 = 1/2, \ b_1 = a_1, \) and \( a_2 = b_3 \) and \( E_1 - E_3 = \begin{bmatrix} 1 - b_1 & a_1 & b_1 \\ 0 & a_2 - b_2 & 0 \\ -b_3 & -a_3 & b_3 - 1 \end{bmatrix} \) is not nilpotent unless \( a_2 = b_2, \ b_1 = b_3 = 1/2, \) and \( a_1 = a_3 \). This shows that the only case when \( E_i - E_j \) are all nilpotent is the trivial balanced (fair) Mendelian case when \( a_1 = a_2 = a_3 = b_1 = b_2 = b_3 = 1/2, \) corresponding to \( A = 0 \) with \( x(t + 1) = x(t) \), its linear but uninteresting corresponding dynamics. This suggests that unbalanced Mendelian segregation dynamics should not be Gonshor-linearizable in general.

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LABORATOIRE DE PHYSIQUE THÉORIQUE ET MODÉLISATION, CNRS-UMR 8089 ET UNIVERSITÉ DE CERGY-PONTOISE, 2 AVENUE ADOLPHE CHAUVIN, F-95302, CERGY-PONTOISE, FRANCE, E-MAIL: NICOLAS.GROSJEAN@U-CERGY.FR, THIERRY.HUILLET@U-CERGY.FR, GENEVIEVE.ROLLET@U-CERGY.FR