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# EXPLICIT SOLUTION OF THE EVOLUTIONARY EQUATIONS FOR SINGLE LOCUS AUTOSOMAL POLYPLOID POPULATIONS

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In the note [KiL74] the first two authors suggested a general evolutionary equation for a panmictic multilocus multiallele population under common action of principal hereditary factors: any polyploid type, any sexual structure (with an arbitrary numbers of sexes), recombination, mutation and migration. In the selection free case all trajectories converge if and only if the spectrum of the mutation-migration matrix lies in the set $\{\lambda \in \mathbf{C} : |\lambda| < 1 \text{ or } \lambda = 1\}$. This result covers a series of limit theorems for the selection free populations under action of a single factor [H], [G47, G49], [R60], [E65], [Ke70], [L71], [Ki73], see also [M62] and [L92]. Moreover, though evolutionary equations are nonlinear they were can be explicitly solved in some diploid situations [L71], [Ki93], [L92], see also [B01] for a recent development. The goal of the present work is to explicitly solve the evolutionary equations for a single locus autosomal polyploid population. We apply the method originated from [L71] and developed in [Ki74], see also [L92, Chapter 6].However, this can be done only after a conceptual elaboration we will start with.

Let us assume that there are $l$ different alleles and that each gamete is $N$-ploid. Such a *gamete* $g$ can be formally defined as an arbitrary mapping from the set $\mathfrak{N} = \{1, 2, ..., N\}$ of chromosomes into the set $\mathfrak{L} = \{1, 2, ..., l\}$ of alleles. More generally, we define a *partial gamete* $\gamma$ as a partial mapping $\gamma\colon \mathfrak{N} \to \mathfrak{L}$, i.e. a mapping from a subset of $\mathfrak{N}$ into $\mathfrak{L}$. This subset is called the *support* of $\gamma$ and denoted by supp($\gamma$). It may happen that supp($\gamma$)=$\emptyset$. In this case we will write $\gamma = \emptyset$.

Let $U$ be a partial mapping $\mathfrak{N} \to \mathfrak{N}$, i.e. a mapping from a subset $D_U \subset \mathfrak{N}$ into $\mathfrak{N}$. Let $\gamma$ be a partial gamete. Then the sequence $\mathfrak{N} \xrightarrow{U} \mathfrak{N} \xrightarrow{\gamma} \mathfrak{L}$ determines the composition (product) $\gamma U : \mathfrak{N} \to \mathfrak{L}$ which is a partial gamete again. We denote by $\Delta_U$ the mapping defined as $\Delta_U \gamma = \gamma U$, $\Delta_U$ maps the set of all partial gametes into itself but so that $\mathrm{supp}(\gamma U) \subset D_U$. In more detail, $\mathrm{supp}(\gamma U)$ is the set of those chromosomes from $D_U$ the $U$-images of which are contained in $\mathrm{supp}(\gamma)$. The allele from $i$-th chromosome of $\gamma U$ is the same as the allele from $U(i)$-th chromosome of $\gamma$. Note that $\Delta_\emptyset \gamma = \emptyset$ for all $\gamma$ and

$$\Delta_U \Delta_V = \Delta_{VU} \tag{1}$$

A *state of the population* in generation is a formal linear combination

$$G = \sum_g p(g) g \tag{2}$$

where the coefficients $p(g)$ are the probabilities of gametes in a generation. In this context we consider the real linear space $R^{|\mathfrak{G}|}$ where $\mathfrak{G}$ is the set of gametes. The latter is a natural basis in $R^{|\mathfrak{G}|}$, the set of states is just the coordinate simplex.

To describe the evolution in our terms we consider the unordered pairs $U|V$ of partial mappings $\mathfrak{N} \mapsto \mathfrak{N}$ which are *complementary* in the sense that $D_U \cap D_V = \emptyset$ and $D_U \cup D_V = \mathfrak{N}$ (i.e.$D_U|D_V$ is a partition of $\mathfrak{N}$). For each complementary pair $U|V$ and each two gametes $g$ and $h$ we have the partial gametes $\Delta_U g = gU$ and $\Delta_V h = hV$ whose supports are $D_U$ and $D_V$ respectively. This allows us to introduce the gamete $f = (\Delta_U g)(\Delta_V h)$ as the *contamination* of the partial mappings $\Delta_U g$ and $\Delta_V h$. Namely, if $i \in \mathfrak{N}$ then

$$f(i) = \begin{cases} (gU)(i), & i \in D_U,\ U(i) \in \mathrm{supp}(g) \\ (hV)(i), & i \in D_V,\ V(i) \in \mathrm{supp}(h). \end{cases}$$

Biologically, $g$ and $h$ are parental gametes, $f$ is one of possible offspring gametes, namely, the chromosomes the numbers of which belong to $\Delta_U$ go to $f$ from $g$ according to the mapping $gU$; similarly, the mapping $V$ determines the transition of genes from $h$. For example, let $N$=4 and let the alleles are $A$ and $a$. For the mappings $U, V$ such that $U(1) = 3$, $U(2) = 3$, $U(3) = 4$, $U(4) = 1$ the gene transition is that of Fig.1.

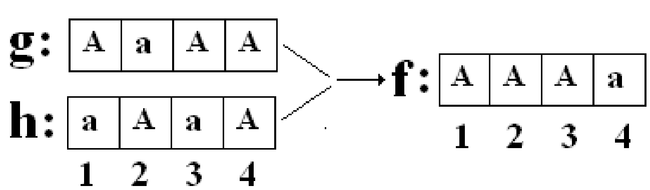


Fig. 1. Gametegenesis: a typical case.

Formally, a *meiotic distribution* is a probability distribution $\rho(U|V)$ on the set of all complementary pairs $U|V$. The probability $\rho(U|V)$ corresponds to a random appearing of the offspring gamete $(\Delta_U g)(\Delta_V h)$ in the meiosis when the parental gametes are $g$ and $h$. Then the state of the offspring population created by the pair $g$, $h$ is

$$g \times h = \sum_{U|V} \rho(U|V)(\Delta_U g)(\Delta_V h). \tag{3}$$

Formula (3) can be treated as a multiplication table for the basis vectors in $R^{|\mathfrak{G}|}$. This multiplication is commutative. We can extend it by linearity to the whole space $R^{|\mathfrak{G}|}$:

$$G \times H = \sum_{U|V} \rho(U|V)(\Delta_U G)(\Delta_V H). \tag{4}$$

This is the one-locus polyploid *gamete algebra*, cf. e.g. [4, Section 6.2]. Now the evolutionary equation (in a vector form) is

$$G' = G \times G \equiv G^2 \tag{5}$$

where $G$ is the state of the population in a generation and $G'$ is the state in the next generation under panmixia. In more detail,

$$G' = \sum_{U|V} \rho(U|V)(\Delta_U G)(\Delta_V G). \tag{6}$$

By iteration of this mapping in the coordinate simplex we obtain the trajectories $\{G_t\}_0^\infty$ the behavior of which we are going to study. Every trajectory $\{G_t\}_0^\infty$ is the solution to the evolutionary equation

$$G_{t+1} = \sum_{U|V} \rho(U|V)(\Delta_U G_t)(\Delta_V G_t) \tag{7}$$

where $t = 0, 1, 2, \ldots$, and $G_0$ is an arbitrary initial state.

The evolutionary operator $G \mapsto G'$ is quadratic but some terms in (6) are linear. It is important to separate the linear part of (6) from the purely quadratic one, namely,

$$G' = \sum_{U:D_U=\mathfrak{N}} \rho(U|\emptyset)(\Delta_U G) + \sum_{V:D_V=\mathfrak{N}} \rho(\emptyset|V)(\Delta_V G) + \sum_{U|V\neq\emptyset} \rho(U|V)(\Delta_U G)(\Delta_V G) \tag{8}$$

where $U|V \neq \emptyset$ means that $U \neq \emptyset$ and $V \neq \emptyset$.

`Now we introduce the following symmetry condition for the meiotic distribution:`

$$\rho(\sigma U \omega | \tau V \omega) = \rho(U|V) \tag{9}$$

for all $\sigma$, $\tau$, $\omega \in \mathfrak{P}(\mathfrak{N})$ where $\mathfrak{P}(\mathfrak{N})$ is the set of permutations of $\mathfrak{N}$. This means that $\rho(U|V)$ depends only on the combinatorial structure of the mappings $U$, $V$. Namely, denote by $\nu_k(U)$ the number of those elements in the image of a mapping $U$, whose preimages consist of $k$ elements, so that

$$\sum_k k\nu_k(U) = |D_U|.$$

We call the sequence $\nu(U) = (\nu_k(U))_{k=1}^N$ the *characteristic* of $U$. An equivalent form of assumption (9) is:

$$\rho(U'|V') = \rho(U|V) \tag{10}$$

if $(\nu(U') = \nu(U))$ & $(\nu(V') = \nu(V))$ or $(\nu(U') = \nu(V))$ & $(\nu(V') = \nu(U))$. In particular,

$$\rho(U^\sigma|V^\sigma) = \rho(U|V) \tag{11}$$

where $U^\sigma = \sigma U \sigma^{-1}$, $V^\sigma = \sigma V \sigma^{-1}$.

A state $G$ of a population is said to be *symmetric* if any reordering of chromosomes does not affect it. In notation (2) this means that

$$p(g) = p(g^\sigma),\ g^\sigma = g\sigma^{-1} \tag{12}$$

for all gametes $g$ and all permutations $\sigma$.

***Lemma 1.*** *If a state $G$ is symmetric then such is $G'$.*

**Proof.** Let

$$G' = \sum_g p'(g)g. \tag{13}$$

Then

$$p'(g) = \sum_{U|V,h_1,h_2} \{\rho(U|V)p(h_1)p(h_2) : (\Delta_U h_1)(\Delta_V h_2) = g\}.$$

After a permutation $\sigma$ each gamete $g$ becomes $g^\sigma = g\sigma^{-1}$. Hence,

$$p'(g^{\sigma^{-1}}) = \sum_{U|V,h_1,h_2} \{\rho(U|V)p(h_1)p(h_2) : ((\Delta_U h_1)(\Delta_V h_2))^\sigma = g\}.$$

However,

$$((\Delta_U h_1)(\Delta_V h_2))^\sigma = ((h_1 U)(h_2 V))\sigma^{-1} =$$

$$(h_1 U \sigma^{-1})(h_2 V \sigma^{-1}) = (h_1^\sigma U^\sigma)(h_2^\sigma V^\sigma) = (\Delta_{U^\sigma} h_1^\sigma)(\Delta_{V^\sigma} h_2^\sigma)$$

On the other hand, we have (11) and $p(h_1^\sigma) = p(h_1)$, $p(h_2^\sigma) = p(h_2)$. By substitutions $U^\sigma \rightsquigarrow U$, $V^\sigma \rightsquigarrow V$ we obtain for $p(g^{\sigma^{-1}})$ the same expression as for $p(g)$. Hence, $p(g^{\sigma^{-1}}) = p(g)$ or, equivalently, $p(g^\sigma) = p(g)$ for all $g$ and $\sigma$. □

Later on all states under consideration are supposed to be symmetric.

Recall that a system $\mathfrak{C} = \{C_1, ..., C_r\}$ of sets is called disjunctive if so are any two $C_i, C_k$ with $i \neq k$, i.e. $C_i \bigcap C_k = \emptyset$. For two disjunctive systems $\mathfrak{A} = \{A_1, ..., A_p\}$ and $\mathfrak{B} = \{B_1, ..., B_q\}$ of subsets of $\mathfrak{N}$ we will write $\{A_1, ..., A_p\} \succeq \{B_1, ..., B_q\}$ if every $B_i$ is the union of some $A_j's$. Obviously if $\mathfrak{A} \succeq \mathfrak{B}$ and $\mathfrak{B} \succeq \mathfrak{A}$ then $p = q$ and the systems $\mathfrak{A}$ and $\mathfrak{B}$ are some permutations each of other.

We provide the set of partial mappings $\mathfrak{N} \to \mathfrak{N}$ with a quasiorder, namely,

$$U \succeq W \Leftrightarrow \{U^{-1}(t)\}_{t \in \mathrm{Im}(U)} \succeq \{W^{-1}(s)\}_{s \in \mathrm{Im}(W)}. \tag{14}$$

where $U^{-1}(t)$ and $W^{-1}(s)$ mean the preimages. Obviously, if $U, V$ is a complementary pair then $U^{-1}(t) \bigcap W^{-1}(s) = \emptyset$ hence, neither $U \succeq V$ nor $V \succeq U$.

***Lemma 2.*** *The relation $U \succeq V$ is valid if and only if there exists a partial mapping $Z : \mathfrak{N} \to \mathfrak{N}$ such that $W = ZU$.*

**Proof.** Let $W = ZU$. Then for any $s \in \mathrm{Im}(ZU)$ we have

$$W^{-1}(s) = (ZU)^{-1}(s) = U^{-1}(Z^{-1}(s)) = \cup\{U^{-1}(t) : t \in Z^{-1}(s)\},$$

i.e. $U \succeq W$.

Conversely, we define Z with $D_Z = UD_W$ by setting $Z(i) = W(j)$ whenever $i = U(j)$ and $j \in D_W$. This definition would be correct if $W(j_1) = W(j_2)$ for any pair $j_1, j_2 \in D_W$ such that $U(j_1) = U(j_2)$. Suppose to the contrary that $W(j_1) = t_1, W(j_2) = t_2$ and $t_1 \neq t_2$. The $W^{-1}(t_1) \cap W^{-1}(t_2) = \emptyset$. On the other hand, since $U \succeq V$, there are $s_1, s_1 \in D_U$ such that $U(j_1) = s_1$ and $U(j_2) = s_2$. Hence, $s_1 = s_2$ and their common $U$-preimage belongs to $W^{-1}(t_1)$ and $W^{-1}(t_2)$, a contradiction. □

The partial mappings $U$ and $W$ are called *equivalent*, $U \sim W$, if $U \succeq W$ and $W \succeq U$, in other words, if

$$\{U^{-1}(t)\}_{t \in \mathrm{Im}U} = \{W^{-1}(s)\}_{s \in \mathrm{Im}W}. \tag{15}$$

In particular,

$$(U \sim W) \Rightarrow (D_U = D_W). \tag{16}$$

We will write $U \succ W$ when $U \succeq W$ and $U$ and $W$ are not equivalent.

***Corollary 1.*** *$U \sim W$ if and only if there exists $\sigma \in \mathfrak{P}(\mathfrak{N})$ such that $U = \sigma W$ (and then $W = \sigma^{-1}U$).*

**Proof.** By Lemma 2 we have $U \succeq W$ if $U = \sigma W$ and $W \succeq U$ since $W = \sigma^{-1}U$. Finally, $U \sim W$.

Conversely, let $U \sim W$. By Lemma 2 again, $U = Z_1W$ and $W = Z_2U$. Hence, $D_U = D_W$ and $U = (Z_1Z_2)U$ so, $Z_1Z_2 = \mathrm{id}|\mathrm{Im}U$. Similarly, $Z_2Z_1 = \mathrm{id}|\mathrm{Im}W$. Thus, $Z_1$ determines a bijection $\mathrm{Im}W \to \mathrm{Im}U$ and $Z_1$ is the inverse bijection. Hence, $U = \sigma W$ where $\sigma \in \mathfrak{P}(\mathfrak{N}), \sigma|\mathrm{Im}W = Z_1$. □

***Corollary 2.*** *If $U \sim W$ then $UV \sim WV$ for all $V$.*

We call two pairs $U|V$ and $U'|V'$ *equivalent* if $U \sim U'$ & $V \sim V'$ or $U \sim V'$ & $V \sim U'$. Obviously, two cases of the latter alternative are uncompatible.

***Corollary 3.*** *If $U|V \sim U'|V'$ then*

$$\rho(U'|V') = \rho(U|V). \tag{17}$$

**Proof.** This follows from (10) since the equivalent mappings have the same characteristics. □

***Lemma 3.*** *If $U \sim W$ then $\Delta_U G = \Delta_W G$.*

**Proof.** By Corollary 1, $U = \sigma W$ for some $\sigma \in \mathfrak{P}(\mathfrak{N})$. Applying $\Delta_U$ to (2) we obtain

$$\Delta_U G = \sum_g p(g)\Delta_U g = \sum_g p(g)(gU) = \sum_g p(g\sigma)(g\sigma W)$$

since $G$ is symmetric. Setting $g\sigma = \gamma$ we obtain

$$\Delta_U G = \sum_\gamma p(\gamma)(\gamma W) = \sum_\gamma p(\gamma)\Delta_W \gamma = \Delta_W G.$$ □

Now we fix an arbitrary partial mapping $W : \mathfrak{N} \to \mathfrak{N}$ and apply the operator $\Delta_W$ to both parts of (6). This yields

$$\Delta_W G' = \sum_{U|V} \rho(U|V)(\Delta_{UW} G)(\Delta_{VW} G). \tag{18}$$

since

$$\Delta_W((\Delta_U g)(\Delta_V h)) = ((\Delta_W \Delta_U)g)((\Delta_W \Delta_V)h) = (\Delta_{UW} g)(\Delta_{VW} h). \tag{19}$$

Let us stress that *the pair $UW|VW$ is complementary with respect to $D_W$* (instead of $\mathfrak{N}$), i.e. $D_U W$ and $D_V W$ constitute a partition of $D_W$. In general, we will use the notation $u|v$ for the complementary pair of partial mappings $D_W \to \mathfrak{N}$, so that

$$D_u \cup D_v = D_W, \quad D_u \cap D_v = \emptyset. \tag{20}$$

In (18) many summands can be brought together because of the equalities of shape $(\Delta_{U'W} G)(\Delta_{V'W} G) = (\Delta_{UW} G)(\Delta_{VW} G)$.

Using Lemma 3 we obtain

$$\Delta_W G' = \sum_{u|v} \rho_W(u|v)(\Delta_u G)(\Delta_v G\ ) \tag{21}$$

where the summation is taken over a complete system of pairwise non-equivalent $u|v$ and

$$\rho_W(u|v) = \sum_{\tilde{u}|\tilde{v}} \{\tilde{\rho}_W(\tilde{u}|\tilde{v}) : \tilde{u}|\tilde{v} \sim u|v\}, \tag{22}$$

and, in its turn,

$$\tilde{\rho}_W(\tilde{u}|\tilde{v}) = \sum_{U|V}\{\rho(U|V) : UW = \tilde{u}, VW = \tilde{v} \text{ or } UW = \tilde{v}, VW = \tilde{u}\}, \tag{23}$$

Here $\rho_W(u|v) = 0$ if $u|v$ is not of shape $UW|VW$.

In particular, we use $W|\emptyset$ as a representative of the corresponding equivalence class, so that

$$\rho_W(W) = \rho_W(W|\emptyset) = \sum_{\tilde{u}\sim W} \tilde{\rho}_W(\tilde{u}|\emptyset) \tag{24}$$

where

$$\tilde{\rho}_W(\tilde{u}|\emptyset) = \sum_{U|V}\{\rho(U|V) : UW = \tilde{u}, VW = \emptyset \text{ or } UW = \emptyset, VW = \tilde{u}\}. \tag{25}$$

Note that if $\tilde{u} \sim W$ and $U|V$ is such that $UW = \tilde{u}$ then $VW = \emptyset$. Indeed, in this case $\tilde{u} = \omega W$ where $\omega \in \mathfrak{P}(\mathfrak{N})$. Thus, $D_{UW} = D_{\tilde{u}} = D_{\omega W} = D_W$. Hence, $\mathrm{Im}W \subset D_U$ and then $\mathrm{Im}W \bigcap D_V = \emptyset$.

Formula (21) can be rewritten as

$$\Delta_W G' = \rho_W(W)\Delta_W G + \sum_{u|v\neq\emptyset} \rho_W(u|v)(\Delta_u G)(\Delta_v G), \tag{26}$$

where $\rho_W(u|v)$ is well-defined as a function of the equivalence class of $u|v$. Moreover, we have

***Lemma 4.*** *The probabilities $\rho_W(u|v)$ depend only on the equivalence classes of $W$ and $u|v$.*

**Proof.** . Let $W_1 \sim W$ so, $W_1 = \omega W$ where $\omega \in \mathfrak{P}(\mathfrak{N}$. By (23) we have

$$\tilde{\rho}_{W_1}(\tilde{u}|\tilde{v}) = \sum_{U|V}\{\rho(U|V) : UW_1 = \tilde{u}, VW_1 = \tilde{v} \text{ or } UW_1 = \tilde{v}, VW_1 = \tilde{u}\} =$$

$$\sum_{U|V}\{\rho(U|V) : U\omega W = \tilde{u}, V\omega W = \tilde{v} \text{ or } U\omega W = \tilde{v}, V\omega W = \tilde{u}\}.$$

Passing to the summation over $U\omega|V\omega$ and taking (9) into account we obtain that $\tilde{\rho}_{W_1}(\tilde{u}|\tilde{v}) = \tilde{\rho}_W(\tilde{u}|\tilde{v})$. By (22) we have $\rho_{W_1}(u|v) = \rho_W(u|v)$.

Now if $u_1|v_1 \sim u|v$ then (22) shows that $\rho(u_1|v_1) = \rho(u|v)$ since $(\tilde{u}|\tilde{v} \sim u_1|v_1) \Leftrightarrow (\tilde{u}|\tilde{v} \sim u|v)$. □

In particular, $\rho_W(W)$ depends only on the equivalence class $\Gamma$ of $W$. Moreover, we have

***Lemma 5.*** *The probabilities $\rho_W(W)$ depend only on $|\mathrm{Im}W|$.*

**Proof.** If follows from (24) and (25) that

$$\rho_W(W) = \sum_{\tilde{u}\sim W}\sum_{U|V}\{\rho(U|V) : UW = \tilde{u} \text{ or } VW = \tilde{u}\}$$

Obviously, $UW = u \sim W$ if and only if $U|\mathrm{Im}W \in \mathfrak{P}(\mathrm{Im}W)$. Hence,

$$\rho_W(W) = \sum_{\omega\in\mathfrak{P}(\mathrm{Im}W)} \sum_{U|V} \{\rho(U|V) : U|\mathrm{Im}W = \omega \text{ or } V|\mathrm{Im}W = \omega\} \tag{27}$$

If $|\mathrm{Im}W_1| = |\mathrm{Im}W|$ then there exists a bijection $\sigma : \mathfrak{N} \to \mathfrak{N}$ such that $\mathrm{Im}W = \sigma(\mathrm{Im}W_1)$. After transformations $\omega \mapsto \sigma^{-1}\omega\sigma$, $U \mapsto U^\sigma$, $V \mapsto V^\sigma$ the sum (27) turns into the similar sum for $\rho_{W_1}(W_1)$. □

Since $D_W$ is the same for all equivalent $W$, one can introduce the notation $D_\Gamma$ for any equivalence class $\Gamma$. We say that two equivalence classes $K$ and $Q$ constitute a *partition* $K|Q$ *of the class* $\Gamma$ if

$$D_\Gamma = D_K \cup D_Q,\ \ D_K \cap D_Q = \emptyset. \tag{28}$$

We denote the set of all partition of $\Gamma$ by $\mathfrak{S}(\Gamma)$. It follows from Lemma 4 that the values $\rho_\Gamma(K|Q)$ are well-defined. Moreover, Lemma 5 allows us to set

$$\rho(n_\Gamma) = \rho_W(W) \tag{29}$$

for $W \in \Gamma$ and $n_\Gamma = |\mathrm{ImW}|$. For any equivalence class $\Gamma^0$ which is minimal with respect to the order " $\prec$ " we have $\left|\mathrm{Im}(\Gamma^0)\right| = 1$, i.e. $\rho(1) = 1$.

By Lemma 3 we can introduce $\Delta_\Gamma G$ as $\Delta_W G$, the same for all $W \in \Gamma$. Similarly, we have the well-defined $\Delta_K G$ and $\Delta_Q G$ for any partition $K|Q$ of $\Gamma$. As a result, formula (26) can be translated into the language of classes,

$$\Delta_\Gamma G' = \rho(n_\Gamma)\Delta_\Gamma G + \sum\{\rho_\Gamma(K|Q)(\Delta_K G)(\Delta_Q G) : K|Q \in \mathfrak{S}(\Gamma),\ K|Q \neq \emptyset\}. \tag{30}$$

Accordingly, the evolutionary equation (7) reduces to

$$\Delta_\Gamma G_{t+1} = \rho(n_\Gamma)\Delta_\Gamma G_t + \sum\{\rho_\Gamma(K|Q)(\Delta_K G_t)(\Delta_Q G_t) : K|Q \in \mathfrak{S}(\Gamma),\ K|Q \neq \emptyset\}. \tag{31}$$

Note that for any minimal class $\Gamma^0$ we have $\Delta_{\Gamma^0} G_t = \Delta_{\Gamma^0} G_0$ for all $t$. This is a base for the inductive assumption in the proof of convergence of trajectories. The induction is conducted with respect to ordering of the classes like [4,Section 6.3],moreover, in this way we obtain the Convergence Theorem.

***Theorem 1.*** *The limit states* $\Delta_\Gamma G_\infty$ *are*

$$\Delta_\Gamma G_\infty = \sum_{K_1|\ldots|K_q} \beta_{K_1|\ldots|K_q}(\Gamma) \prod_{i=1}^{q} \Delta_{K_i} G_0, \tag{32}$$

*where* $\beta_{K_1|\ldots|K_q}(\Gamma)$ *are some coefficients, the sum is taken over all partitions* $K_1|\ldots|K_q$ *of class* $\Gamma$ *such that* $K_i$ *are minimal classes,* $K_i \prec \Gamma$.

The coefficients $\beta_{K_1|\ldots|K_q}(\Gamma)$ can be presented explicitly. It follows from (26) and Lemmas 4, 5 that

$$\Delta_\Gamma G_\infty = (1 - \rho(n_\Gamma))^{-1} \sum_{u|v} \rho_\Gamma(u|v)(\Delta_u G_\infty)(\Delta_v G_\infty). \tag{33}$$

If $n_u \neq 1$ (or $n_v \neq 1$), then the same equations can be written for $\Delta_u G_\infty$ ( or $\Delta_v G_\infty$ respectively). For each partition $K_1|...|K_q$ mentioned in Theorem 1 we consider the set $\omega = \{1, 2, ..., q\}$ and realize the following dichotomic process: $\omega$ splits into two subsets $\omega_1$ and $\omega_2$, after that each of $\omega_1$, $\omega_2$ splits into two subsets, etc. Each implementation of this process determines a tree $T^\Gamma_{K_1|\ldots|K_q}$ with the root $\Gamma$ and with the minimal classes (singletons) as the end vertices. Let

$$z \in (T^\Gamma_{K_1|\ldots|K_q})',$$

where prime means that the end vertices are removed. Denote by $x, y$ the classes appearing by splitting of $z$ and let

$$K_x = \bigcup_{i \in x} K_i,\ \ K_y = \bigcup_{i \in y} K_i,\ \ K_z = \bigcup_{i \in z} K_i = K_x \cup K_y.$$

The above mentioned explicit formula is

$$\beta_{K_1|\ldots|K_q}(\Gamma) = \sum_{T^\Gamma_{K_1|\ldots|K_q}} \prod_{z \in (T^\Gamma_{K_1|\ldots|K_q})'} \gamma(z) \tag{34}$$

where

$$\gamma(z) = \frac{\rho_{K_z}(K_x|K_y)}{1 - \rho(n_{K_z})}, \tag{35}$$

cf. [4,(6.5.15)].

For the polyploids the following Linearization Theorem is quite similar to Theorem 6.4.1 from [4].

***Theorem 2.*** *For each class $\Gamma$ there exists a univariate polynomial $\Phi_\Gamma(\lambda)$ such that all trajectories $\{\Delta_\Gamma G_t\}_{t=0}^\infty$ satisfy the equation*

$$[\Phi_\Gamma(T)\Delta_\Gamma G_t] = 0 \ (t = 0, 1, 2, ...), \tag{36}$$

*where $T$ is the shift operator, $T(\Delta_\Gamma G_t) = \Delta_\Gamma G_{t+1}$.*

This polynomial is uniquely determined by the inductive construction

$$\Phi_\Gamma(\lambda) = (... \vee [\Phi_K(\lambda)\diamondsuit\Phi_Q(\lambda)] \vee ...) \vee (\lambda - \rho(n_\Gamma)) \tag{37}$$

where $K|Q$ runs over the set of partitions of $\Gamma$, $\Phi_K(\lambda)\diamondsuit\Phi_Q(\lambda)$ is the quasitensor product of $\Phi_K$ and $\Phi_Q$, the symbol "$\vee$" means the least common multiple. (In the case when $\rho(n_\Gamma)$ coincides with a root of some $\Phi_K(\lambda)\diamondsuit\Phi_Q(\lambda)$, the factor $\lambda - \rho(n_\Gamma)$ must be replaced by $(\lambda - \rho(n_\Gamma))^\nu$ with some $\nu$.)

The leading coefficient in $\Phi_\Gamma(\lambda)$ is equal to 1 if as long as this condition is fulfilled for the minimal classes. This $\Phi_\Gamma(\lambda)$ is called the *evolutionary polynomial*, its roots are called the *evolutionary roots* and they constitute the *evolutionary spectrum* $W(\Gamma)$.The construction (37) leads to

***Theorem 3.*** $1 \in W(\Gamma) \subset [0, 1]$.

**Proof.** $W(\Gamma^0) = \{1\}$ for every minimal $\Gamma^0$ and

$$W(\Gamma) = \{\rho(n_\Gamma)\} \bigcup \bigcup_{K|Q \neq \emptyset} W(K)W(Q) \tag{38}$$

by induction based on (37). □

***Theorem 4.*** *The evolutionary spectrum $W(\Gamma)$ consists of all products*

$$\lambda_{n_1|\dots|n_m} = \prod_{i=1}^{m} \rho(n_i) \tag{39}$$

*where $n_i$ satisfy the condition*

$$n_i \geq 2, \ \sum_{i=1}^{m} n_i \leq |\mathrm{Im}(\Gamma)| \tag{40}$$

*and $\lambda_\emptyset = 1$.*

**Proof.** The root $\lambda_{n_\Gamma} = \rho(n_\Gamma)$ is already presented in (39). According to (38), all other roots of $\Phi_\Gamma(\lambda)$ are some products of roots of $W(K)$ and $W(Q)$ where $K|Q$ runs over nontrivial partitions of $\Gamma$. Therefore, if (39) is true for $K$ and $Q$ separately then it is true for $\Gamma$. (Recall that the roots of $\Phi \diamondsuit \Psi$ are the products of two factors, one of which runs over roots of $\Phi$ and the second runs over the roots of $\Psi$.)

Conversely, $\lambda_{n_1|\dots|n_m} \in W(\Gamma)$ under condition (40). Indeed, if $m = 1$ then either $n_1 = n_\Gamma$ or $n_1 < n_\Gamma$ and we can take $K|Q$ with $n_K = n_1$ ($1 \in W(K)$ because of Theorem 3). Let $m \geq 2$. By induction, $K|Q$ can be chosen so that $n_K = n_1$ and $\lambda_{n_2|\dots|n_m} \in W(Q)$ because of $n_2 + ... + n_m \ \leq \ |\mathrm{Im}(Q)| = |\mathrm{Im}(\Gamma)| - |\mathrm{Im}(K)|$. □

Also, by induction one can prove the following

***Theorem 5.*** *An evolutionary polynomial $\Phi_\Gamma(\lambda)$ does not have multiple roots if and only if the inequality*

$$\rho(n) \neq \prod_{i=1}^{m} \rho(n_i), \ \sum_{i=1}^{m} \rho_i \leq n, \ n_i < n \tag{41}$$

*is true for all $n, \ 1 < n \leq n_\Gamma$.*

Further we assume (41) to hold true (a condition of no "resonances"). Then, given $G_0$, the corresponding solution to the linear difference equation (36) is a linear combination of exponents $(\lambda_{n_1|\dots|n_m})^t$ with some vector coefficients depending on $G_0$. Thus,

$$\Delta_\Gamma G_t = C_\emptyset(\Delta_\Gamma G_0) + \sum_{n_1|\dots|n_m} C_{n_1|\dots|n_m}(\Delta_\Gamma G_0)(\prod_{i=1}^{m} \rho(n_i))^t \tag{42}$$

where the summation on the right-hand side is taken over all sets $\{n_i\}_1^m$ satisfying (40). In particular,

$$G_t = \Delta_I G_t = C_\emptyset(G_0) + \sum_{n_1|\dots|n_m} C_{n_1|\dots|n_m}(G_0)(\prod_{i=1}^{m} \rho(n_i))^t, \tag{43}$$

$$n_i \geq 2,\ \sum_{i=1}^{m} n_i \leq N \tag{44}$$

As long as the coefficients $C_{n_1|\ldots|n_m}(G_0)$ in (43) are presented explicitly, this formula turns into that we want.

Without loss of generality, we can assume that

$$\lambda_{n_1|\ldots|n_m} \neq \lambda_{k_1|\ldots|k_l} \tag{45}$$

if the unordered sets $\{n_1, ..., n_m\}$ and $\{k_1, ..., k_l\}$ are different.

Since all roots $\lambda_{n_1|\ldots|n_m}$ are less than 1, we get from (42)

$$\Delta_\Gamma G_\infty = C_\emptyset(\Delta_\Gamma G_0) \tag{46}$$

For all trajectories of form (42) to be in accordance with (21), it is necessary and sufficient that all $C_{n_1|\ldots|n_m}(\Delta_\Gamma G_0)$ satisfy the initial condition

$$\Delta_\Gamma G_0 = C_\emptyset(\Delta_\Gamma G_0) + \sum_{n_1|\ldots|n_m} C_{n_1|\ldots|n_m}(\Delta_\Gamma G_0) \tag{47}$$

and the recurrent equation

$$C_\emptyset(\Delta_\Gamma G_0) + \sum C_{n_1|\ldots|n_m}(\Delta_\Gamma G_0)(\prod_{i=1}^{m} \rho(n_i))^{t+1} =$$

$$\rho(n_\Gamma)[C_\emptyset(\Delta_\Gamma G_0) + \sum C_{n_1|\ldots|n_m}(\Delta_\Gamma G_0)(\prod_{i=1}^{m} \rho(n_i))^{t}]+$$

$$\sum_{K|Q} \rho_\Gamma(K|Q)[C_\emptyset(\Delta_K G_0) + \sum C_{n_1|\ldots|n_m}(\Delta_K G_0)(\prod_{i=1}^{m} \rho(n_i))^{t}]\times$$

$$[C_\emptyset(\Delta_Q G_0) + \sum C_{n_1|\ldots|n_m}(\Delta_Q G_0)(\prod_{i=1}^{m} \rho(n_i))^{t}], \tag{48}$$

where $\{n_i\}$ satisfy (40) and $K|Q$ are partitions of $\Gamma$. In its turn, (48) is true for all $t$ if the coefficients at the corresponding roots are the same on both sides of it. By assumption (45) this condition is also necessary. Now the induction yields

$$C_{n_1|\ldots|n_m}(\Delta_\Gamma G_0) =$$

$$[\prod_{i=1}^{m} \rho(n_i) - \rho(n_\Gamma)]^{-1} \sum_{K|Q} \rho_\Gamma(K|Q) \sum C_{n_1^K|\ldots|n_m^K}(\Delta_K G_0) C_{n_1^Q|\ldots|n_m^Q}(\Delta_Q G_0) \tag{49}$$

where the exterior sum is taken over all $K|Q$ such that there exist $\lambda_{n_1^K|\ldots|n_m^K} \in W(K)$ and $\lambda_{n_1^Q|\ldots|n_m^Q} \in W(Q)$ such that

$$\lambda_{n_1^K|\ldots|n_m^K} \lambda_{n_1^Q|\ldots|n_m^Q} = \lambda_{n_1|\ldots|n_m};$$

the interior sum, corresponds to all possible partitions of $\{n_i\}$ into $\{n_i^K\}$ and $\{n_i^Q\}$. If there exists $\lambda_{n_1|...|n_m} \in W(K)$, then $\lambda_\emptyset$ is chosen from $W(Q)$ and, accordingly, one of summands in (49) equals $C_{n_1|...|n_m}(\Delta_K G_0) C_\emptyset(\Delta_Q G_0)$. Of course, $\lambda_{n_1|...|n_m} \in W(Q)$ are handled similarly. Note that the formula (49) makes no sense for $m = 1$ and $n_1 = n_\Gamma$.

Let us rewrite (47) as

$$C_{n_\Gamma}(\Delta_\Gamma G_0) = \Delta_\Gamma(G_0 - G_\infty) - \sum_{n_1|...|n_m}{}' C_{n_1|...|n_m}(\Delta_\Gamma G_0) \tag{50}$$

where prime means that the terms $C_\emptyset(\Delta_\Gamma G_0) = \Delta_\Gamma G_\infty$ and $C_{n_\Gamma}(\Delta_\Gamma G_0)$ are omitted. Thus, $C_{n_\Gamma}(\Delta_\Gamma G_0)$ have to satisfy (50).

Let us determine for $C_{n_1|...|n_m}(\Delta_\Gamma G_0)$ in the shape

$$C_{n_1|...|n_m}(\Delta_\Gamma G_0) = \sum_{\Gamma_1|...|\Gamma_m} C_{\Gamma_1|...|\Gamma_m}(\Delta_\Gamma G_0) \tag{51}$$

where $\Gamma_i$ are the equivalence classes such that

$$\Gamma_i \prec \Gamma, \;\; D_{\Gamma_i} \cap D_{\Gamma_j} = \emptyset \;\, (i \neq j), \;\; n_{\Gamma_i} = n_i. \tag{52}$$

The sets $\Gamma_1|...|\Gamma_m$ and $n_1|...|n_m$ are unordered but $C_{\Gamma_1|...|\Gamma_m}(\Delta_\Gamma G_0)$ is uniquely determined. Inserting (51) in to (49) we get

$$\sum_{\Gamma_1|...|\Gamma_m} C_{\Gamma_1|...|\Gamma_m}(\Delta_\Gamma G_0) = [\prod_{i=1}^m \rho(n_i) - \rho(n_\Gamma)]^{-1} \sum_{K|Q} \rho_\Gamma(K|Q)$$

$$\sum_{k_1|...|k_l|k_{l+1}|...|k_m \preceq K|Q} C_{k_1|...|k_l}(\Delta_K G_0) \times C_{k_{l+1}|...|k_m}(\Delta_Q G_0), \tag{53}$$

$k_i \preceq K \;\, (i = 1, ..., l), \;\, k_i \preceq Q \;\, (i = l+1, ..., m),$

$$D_{k_i} \cap D_{k_j} = \emptyset, \{n_{k_i}\}_1^l \cup \{n_{k_i}\}_{l+1}^m = \{n_{\Gamma_i}\}_1^m.$$

(If $l = 0$ or if $l = m$ then one of the sets is empty.) Each system $\{k_i\}_1^l \cup \{k_i\}_{l+1}^m$ corresponds to a set $\{\Gamma_i\}_1^m = \{k_i\}_1^m$ of subclasses of $\Gamma$. Vice versa, each set $\{\Gamma_i\}$ from $\Gamma$ corresponds to a $K|Q \succeq \Gamma_1|...|\Gamma_m$ with sets $\{\Gamma_i^K\}_1^m$ and $\{\Gamma_i^Q\}_1^m$. Hence, for the equality (49) to be true, the following equality is sufficient:

$$C_{\Gamma_1|...|\Gamma_m}(\Delta_\Gamma G_0) = [\prod_{i=1}^m \rho(n_{\Gamma_i}) - \rho(n_\Gamma)]^{-1}$$

$$\sum_{K|Q \succeq \Gamma_1|...|\Gamma_m} \rho_\Gamma(K|Q) C_{\Gamma_1^K|...|\Gamma_m^K}(\Delta_K G_0) C_{\Gamma_1^Q|...|\Gamma_m^Q}(\Delta_Q G_0) \tag{54}$$

for all $\Gamma_1|...|\Gamma_m$ satisfying (52). In the case when all $\Gamma_i \preceq K$ we take $C_\emptyset(\Delta_Q G_0)$ and, similarly, for all $\Gamma_i \preceq Q$. Since $C_{n_\Gamma}(\Delta_\Gamma G_0) = C_\Gamma(\Delta_\Gamma G_0)$ ($n_K < n_\Gamma$ for any subclass $K \prec \Gamma$), it follows from (50) and (51) that

$$C_\Gamma(\Delta_\Gamma G_0) = \Delta_\Gamma(G_0 - G_\infty) - \sum_{\Gamma_1|...|\Gamma_m}{}' C_{\Gamma_1|...|\Gamma_m}(\Delta_\Gamma G_0) \tag{55}$$

where $\Gamma_1|...|\Gamma_m$ satisfy (52) with any $\{n_i\}$ admissible in (40) except $n = n_\Gamma$. The following theorem is a consequence of (54) and (55),

***Theorem 6.*** *If coefficients $C_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)$ satisfy (54) and (55) then they can be represented as*

$$C_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0) = \sum_{Q_1|\ldots|Q_q} B^{Q_1|\ldots|Q_q}_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0) \prod_{i=1}^{q} \Delta_{Q_i}(G_0 - G_\infty) \tag{56}$$

*where $Q_1|\ldots|Q_q$ runs over all partitions such that*

$$a) D_{Q_i} \cap D_{Q_j} = \emptyset \ (i \neq j) \text{ and } n_{Q_j} \geq 2;$$

$$b) \text{ for each } Q_i \text{ there is a } \Gamma_j,\ Q_i \prec \Gamma_j;$$

$$c) \text{ for each } \Gamma_j \text{ there is a } Q_i,\ \Gamma_j \succ Q_i; \tag{57}$$

*The values $B^{Q_1|\ldots|Q_q}_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)$ depend only on the initial state $\Delta_\Gamma G_0$ and on meiotic distribution.*

It follows from (57c) that $q \geq m$. The products $\prod_{i=1}^{q} \Delta_{Q_i}(G_0 - G_\infty)$ express "how far" the initial state is from the final state and are called the *measures of disequilibrium* for $Q_1|\ldots|Q_q$. The number $q$ is called the *degree* of the measure of disequilibrium.

Theorem 6 gives a necessary condition on the coefficients $C_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)$ and gives a hint to construct them. The next problem is to find $B^{Q_1|\ldots|Q_q}_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)$ such that $C_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)$ defined by (56) do satisfy (54) and (55).

The equality (54) is true if

$$B^{Q_1|\ldots|Q_q}_{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0) = [\prod_{i=1}^{m} \rho(n_{\Gamma_i}) - \rho(n_\Gamma)]^{-1}$$

$$\sum_{K|Q \succeq \Gamma_1|\ldots|\Gamma_m} \rho_\Gamma(K|Q) B^{Q_1^Q|\ldots|Q_q^Q}_{\Gamma_1^K|\ldots|\Gamma_m^K}(\Delta_K G_0) B^{Q_1^Q|\ldots|Q_q^Q}_{\Gamma_1^Q|\ldots|\Gamma_m^Q}(\Delta_Q G_0) \tag{58}$$

for all $\Gamma,\ \Gamma_1|\ldots|\Gamma_m$ with $n_{\Gamma_i} \neq n_\Gamma$. The systems $Q_1^K|\ldots|Q_q^K$ ($Q_1^Q|\ldots|Q_q^Q$) satisfy (57) for $\Gamma_1^K|\ldots|\Gamma_m^K$ (for $\Gamma_1^Q|\ldots|\Gamma_m^Q$ respectively). In addition, $B_\emptyset(\Delta_K G_0) = C_\emptyset(\Delta_K G_0) = \Delta_K G_\infty$.

Let us consider the following process: a class $\Gamma$ is divided into two subclasses $K, Q$ ($K \prec \Gamma,\ Q \prec \Gamma$) in a way such that for any $i$ either $K \succeq \Gamma_i$ or $Q \succeq \Gamma_i$. If $K \neq \Gamma_i$ for all $i$ and there exists a $\Gamma_j$ such that $K \succeq \Gamma_j$, then $K$, in its turn, falls into two parts consistently with $\Gamma_i^K$.(For $Q$, instead of $K$, the above procedure is similar.) The process must be continued up to a natural halt. Each its realization yields some tree $T \in \Im_\Gamma^{\Gamma_1|\ldots|\Gamma_m}$, whose set of terminating vertices consists of $\Gamma_i$'s and of the equivalence classes which constitute a partition of $\Gamma \setminus \bigcup_{i=1}^{m} \Gamma_i$.

A union $\bigcup_i \Gamma_i$ of classes $\Gamma_i$ where $D_{\Gamma_i} \cap D_{\Gamma_j} = \emptyset$ for all $\Gamma_i, \Gamma_j,\ i \neq j$, is a class $\Gamma' = \bigcup_i \Gamma_i$ such that the system of sets $\{u^{-1}(t)\}_{t \in \mathrm{Im}(u)}$ ($u \in \Gamma'$) equals to the union of systems $\{u_i^{-1}(t)\}_{t \in \mathrm{Im}(u_i)}$ ($u_i \in \Gamma_i$) with $i$ from 1 to $m$. Let $K|Q$ be a partition of $\Gamma$, $K|Q \succeq \Gamma_1|...|\Gamma_m$. Let us associate with a pair of trees $T_1 \in \Im_K^{\Gamma_1^K|...|\Gamma_m^K}$ and $T_2 \in \Im_Q^{\Gamma_1^Q|...|\Gamma_m^Q}$ another tree $T_1 \cdot T_2 \in \Im_\Gamma^{\Gamma_1|...|\Gamma_m}$.Namely, the root of $T_1 \cdot T_2$ branches into $K$ and $Q$ and the nodes that follow $K$, $Q$ correspond to the nodes of trees $T_1$ and $T_2$.

For each nonterminating node $z \in T'$ let us define a function $\Theta(z)$:

$$\Theta(z) = [\prod_{i,\ \Gamma_i \prec z} \rho(n_{\Gamma_i^z}) - \rho(n_z)]^{-1} \rho_z(x|y)\delta(x)\delta(y) \tag{59}$$

where $x$, $y$ are the classes in which class $z$ is divided into, $\Gamma_i^z$ are those $\Gamma_i$ for which $z \succ \Gamma_i$, and $\delta(x) = \Delta_x G_\infty$ when $x \not\succeq \Gamma_i$ $(i = 1, 2, ..., m)$ but $\delta(x) = 1$ when $x \succeq \Gamma_i$. The equality (58) is true if and only if

$$B_{\Gamma_1|...|\Gamma_m}^{Q_1|...|Q_q}(\Delta_\Gamma G_0) = [\sum_{T \in \Im_\Gamma^{\Gamma_1|...|\Gamma_m}} \prod_{z \in T'} \Theta(z)] \prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|...|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i} G_0). \tag{60}$$

To prove the statement above it is sufficient to note that (60) can be derived from (58) by consecutive applying of the latter. If all $B_{\Gamma_1|...|\Gamma_m}^{Q_1|...|Q_q}(\Delta_\Gamma G_0)$ can be represented in the form (60) then

$$[\prod_{i=1}^m \rho(n_{\Gamma_i}) - \rho(n_\Gamma)]^{-1} \sum_{K|Q \succ \Gamma_1|...|\Gamma_m} \rho_\Gamma(K|Q) B_{\Gamma_1^K|...|\Gamma_m^K}^{Q_1^K|...|Q_q^K}(\Delta_K G_0) B_{\Gamma_1^Q|...|\Gamma_m^Q}^{Q_1^Q|...|Q_q^Q}(\Delta_Q G_0) =$$

$$[\prod_{i=1}^m \rho(n_{\Gamma_i}) - \rho(n_\Gamma)]^{-1} [\sum_{K|Q,\ K \succeq \bigcup_1^m \Gamma_i} \rho_\Gamma(K|Q) \Delta_Q G_\infty ( \sum_{T \in \Im_K^{\Gamma_1|...|\Gamma_m}} \prod_{z \in T'} \Theta(z)) \times$$

$$\prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|...|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i} G_0) + \sum_{K|Q,\ Q \succeq \bigcup_1^m \Gamma_i} \rho_\Gamma(K|Q) \Delta_K G_\infty ( \sum_{T \in \Im_Q^{\Gamma_1|...|\Gamma_m}} \prod_{z \in T'} \Theta(z)) \times$$

$$\prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|...|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i} G_0) + \sum_{K|Q,\ K=\Gamma_j,\ j=1,...,m} \rho_\Gamma(K|Q) B_{\Gamma_j}^{Q_1^{\Gamma_j}|...|Q_q^{\Gamma_j}}(\Delta_{\Gamma_j} G_0) \times$$

$$( \sum_{T \in \Im_Q^{\Gamma_1^Q|...|\Gamma_m^Q}} \prod_{z \in T'} \Theta(z))$$

$$\prod_{i \neq j} B_{\Gamma_i}^{Q_1^{\Gamma_i}|...|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i} G_0) + \sum_{K|Q,\ Q=\Gamma_j,\ j=1,...,m} \rho_\Gamma(K|Q) B_{\Gamma_j}^{Q_1^{\Gamma_j}|...|Q_q^{\Gamma_j}}(\Delta_{\Gamma_j} G_0) \times$$

$$( \sum_{T \in \Im_K^{\Gamma_1^K|...|\Gamma_m^K}} \prod_{z \in T'} \Theta(z)) \prod_{i \neq j} B_{\Gamma_i}^{Q_1^{\Gamma_i}|...|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i} G_0) +$$

$$\sum_{K|Q\succ\Gamma_1|\ldots|\Gamma_m}\rho_\Gamma(K|Q)(\sum_{T_1\in\Im_K^{\Gamma_1^K|\ldots|\Gamma_m^K}}\prod_{z\in T_1'}\Theta(z))\times$$

$$(\sum_{T_2\in\Im_Q^{\Gamma_1^Q|\ldots|\Gamma_m^Q}}\prod_{z\in T_2'}\Theta(z))\prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|\ldots|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i}G_0)=$$

$$(\sum_{T\in\Im_\Gamma^{\Gamma_1|\ldots|\Gamma_m}}\prod_{z\in T'}\Theta(z))\prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|\ldots|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i}G_0)=B_{\Gamma_1|\ldots|\Gamma_m}^{Q_1|\ldots|Q_q}(\Delta_\Gamma G_0).$$

In order to provide (55) we need

$$B_\Gamma^\Gamma(\Delta_\Gamma G_0)=1, \tag{61}$$

then

$$B_{\Gamma_1|\ldots|\Gamma_m}^{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)=\sum_{T\in\Im_\Gamma^{\Gamma_1|\ldots|\Gamma_m}}\prod_{z\in T'}\Theta(z). \tag{62}$$

Now the formula (60) can be rewritten as

$$B_{\Gamma_1|\ldots|\Gamma_m}^{Q_1|\ldots|Q_q}(\Delta_\Gamma G_0)=B_{\Gamma_1|\ldots|\Gamma_m}^{\Gamma_1|\ldots|\Gamma_m}(\Delta_\Gamma G_0)\prod_{i=1}^m B_{\Gamma_i}^{Q_1^{\Gamma_i}|\ldots|Q_q^{\Gamma_i}}(\Delta_{\Gamma_i}G_0). \tag{63}$$

To our goal it is sufficient to have both (61) and

$$B_\Gamma^{Q_1|\ldots|Q_q}(\Delta_\Gamma G_0)=-\sum_{\bigcup Q_i\preceq K\preceq\Gamma}B_{K_1|\ldots|K_p}^{Q_1|\ldots|Q_q}(\Delta_\Gamma G_0), \tag{64}$$

where $K=\bigcup_{i=1}^p K_i$. For $\{K_i\}$, (57b,c) is true with respect to $Q_1|...|Q_q$, the sum on the right is taken over all possible $K_1|...|K_p$ except $K_1=\Gamma$. Thus, for (54) and (55) to be true it is sufficient to find such $B_{\ldots}^{\ldots}$ that satisfy (60), (61) and (64) (or (61)-(64)).

Formula (64) drastically reduced if $q=1$. In this case

$$B_\Gamma^Q(\Delta_\Gamma G_0)=-\sum_{Q\preceq K\prec\Gamma}B_K^Q(\Delta_\Gamma G_0)=-\sum_{Q\preceq K\prec\Gamma}B_K^Q(\Delta_K G_0)[\sum_{T\in\Im_\Gamma^K}\prod_{z\in T'}\Theta(z)]=$$

$$-\sum_{Q\preceq K\prec\Gamma}B_K^Q(\Delta_K G_0)B_K^K(\Delta_\Gamma G_0). \tag{65}$$

The values $B_K^K(\Delta_\Gamma G_0)$ can be found explicitly using (62).

Let us consider a chain $\Gamma=K_0\succ K_1\succ K_2\succ\ldots\succ K_n=Q$. A tree $T\in\Re_\Gamma^Q$ corresponds to every chain of such a form, $n=|T'|$ is the height of the tree. The equality (65) is equivalent to

$$B_\Gamma^Q(\Delta_\Gamma G_0)=\sum_{T\in\Re_\Gamma^Q}(-1)^{|T'|}\prod_{i=1}^{|T'|}B_{K_i}^{K_i}(\Delta_{K_{i-1}}G_0), \tag{66}$$

where the sum is taken over all trees $T$ of the form described above. The proof of equivalence of (65) and (66) is similar to the proof of (58) and (60).

Let $q \neq 1$ in (64). Let us consider partitions $K_1|...|K_p$ of a class $K$, $\bigcup Q_i \preceq K \preceq \Gamma$ which satisfy (57b, c) (with respect to $Q_1|...|Q_q$). If the partition consists of a single class $K_1 = K$ then it is required that $K \prec \Gamma$. A similar partition has to be done for some subclasses $\tilde{K}_i$ ($\tilde{K}_i \succeq \bigcup Q_j^{K_i}$) of every class $K_i$ which is not equal to any $Q_j$, and so on, up to appearing of $Q_j$. Each realization of such a process yields a tree $T$ out of the set $\Re_\Gamma^{Q_1|...|Q_q}$ of all the trees of this type. According to (63), the formula (64) can be rewritten as

$$B_\Gamma^{Q_1|...|Q_q}(\Delta_\Gamma G_0) = -{\sum}'_{\bigcup Q_i \preceq K \preceq \Gamma} B_{K_1|...|K_p}^{K_1|...|K_p}(\Delta_\Gamma G_0) \prod_{i=1}^{p} B_{K_i}^{Q_1^{K_i}|...|Q_q^{K_i}}(\Delta_{K_i} G_0), \quad (67)$$

By considerations stated prove, (67) can be rewritten as

$$B_\Gamma^{Q_1|...|Q_q}(\Delta_\Gamma G_0) = \sum_{T \in \Re_\Gamma^{Q_1|...|Q_q}} (-1)^{|T'|} \prod_{J \in T'} B_{J_1|...|J_l}^{J_1|...|J_l}(\Delta_J G_0), \quad (68)$$

where $J_1|...|J_l$ is the partition of the subclass of a node $J$ that corresponds to $T$; $|T'|$ is the number of nonterminating nodes of the tree $T$. The equality (66) is a special case (68).

Combining (32), (13), (42), (46), (51), (56), (61), (62), (63) and (68) **we obtain the explicit evolution formula for $\Delta_\Gamma G$ and, when $\Gamma = I$, for $G$ in its own.**

Since the coefficients $C_{n_1|...|n_m}(G_0)$ depend on the initial state $G_0$ continuously, the spectrum for $G$ lies on the $[0, 1]$. The explicit evolution formula implies that *all trajectories are stable in Lyapunov's sence*, i.e. they continuously depend on the initial state.

In conclusion let us illustrate our general theory by the following simple example, when $\mathfrak{N} = \{1, 2\}$. Then there exist exactly eight partial mappings $\mathfrak{N} \to \mathfrak{N}$:

Tab.1

| $\emptyset$ | $u_1$ | $u_2$ | $u_3$ | $u_4$ | $u_5$ | | $u_6$ | | $u_7$ | | $u_8$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $\emptyset$ | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| $\emptyset$ | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1 |

Accordingly, we have the following table of characteristics:

Tab. 2

| | $\emptyset$ | $u_1$ | $u_2$ | $u_3$ | $u_4$ | $u_5$ | $u_6$ | $u_7$ | $u_8$ |
|---|---|---|---|---|---|---|---|---|---|
| $\nu_0$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $\nu_1$ | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 2 |
| $\nu_2$ | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |

Thus, we have 4 characteristic vectors

$$\chi_0 = [0, 0, 0],\ \chi_1 = [0, 1, 0],\ \chi_2 = [0, 0, 1],\ \chi_3 = [0, 2, 0],$$

so that

$$\begin{aligned}
&\nu(u_0) = \chi_0\\
&\nu(u_1) = \nu(u_2) = \nu(u_3) = \nu(u_4) = \chi_1\\
&\nu(u_5) = \nu(u_6) = \chi_2\\
&\nu(u_7) = \nu(u_8) = \chi_3
\end{aligned}$$

The complementary pairs $U|V$ are

$$u_1|u_3,\ u_1|u_4,\ u_2|u_3,\ u_2|u_4,\ u_5|\emptyset,\ u_6|\emptyset\ u_7|\emptyset,\ u_8|\emptyset$$

respectively. By the symmetry condition (9) we have

$$\left.\begin{aligned}
&\rho(u_1|u_3) = \rho(u_1|u_4) = \rho(u_2|u_3) = \rho(u_2|u_4) = \alpha_1,\\
&\rho(u_5|\emptyset) = \rho(u_6|\emptyset) = \alpha_2,\\
&\rho(u_7|\emptyset) = \rho(u_8|\emptyset) = \alpha_3.
\end{aligned}\right\} \tag{69}$$

This meiotic distribution satisfies all required assumption, and, obviously

$$8\alpha_1 + 4\alpha_2 + 4\alpha_3 = 1. \tag{70}$$

As a consecuence,

$$0 \le \alpha_1 \le 1/8,\ 0 \le \alpha_2 \le 1/4,\ 0 \le \alpha_3 \le 1/4. \tag{71}$$

If an initial state is symmetric then by (69) we obtain the evolutionary equation

$$G_{n+1} = 4\alpha_3\Delta_{u_7}G_n + 4\alpha_2\Delta_{u_5}G_n + 8\alpha_1(\Delta_{u_1}G_n)(\Delta_{u_3}G_n). \tag{72}$$

In order to apply $\Delta_{u_k}(k = 1, 3, 5, 7)$ to (72) we need the following multiplication table containig the product $u_iu_k$ at the intersection of $u_i$-th row and $u_k$-th column:

Tabl. 3

| | $u_1$ | $u_3$ | $u_5$ | $u_7$ |
|---|---|---|---|---|
| $u_1$ | $u_1$ | $u_3$ | $u_5$ | $u_1$ |
| $u_3$ | $\emptyset$ | $\emptyset$ | $\emptyset$ | $u_3$ |
| $u_5$ | $u_1$ | $u_3$ | $u_5$ | $u_5$ |
| $u_7$ | $u_1$ | $u_3$ | $u_5$ | $u_7$ |

By the rule (1) we have

$$\Delta_{u_1}G_{n+1} = 4\alpha_3\Delta_{u_7u_1}G_n + 4\alpha_2\Delta_{u_5u_1}G_n + 8\alpha_1(\Delta_{u_1u_1}G_n)(\Delta_{u_3u_1}G_n),$$

and then, according to Table 3,

$$\Delta_{u_1}G_{n+1} = 4\alpha_3\Delta_{u_1}G_n + 4\alpha_2\Delta_{u_1}G_n + 8\alpha_1(\Delta_{u_1}G_n)(\Delta_{\emptyset}G_n) = (8\alpha_1 + 4\alpha_2 + 4\alpha_3)\Delta_{u_1}G_n$$

since the factor $\Delta_{\emptyset}G_n$ must be canceled. Finally,

$$\Delta_{u_1}G_{n+1} = \Delta_{u_1}G_n \tag{73}$$

because of (70).

Similarly,

$$\Delta_{u_3} G_{n+1} = \Delta_{u_3} G_n,\ \ \Delta_{u_5} G_{n+1} = \Delta_{u_5} G_n, \tag{74}$$

and

$$\Delta_{u_7} G_{n+1} = 4\alpha_3 \Delta_{u_7} G_n + 4\alpha_2 \Delta_{u_5} G_n + 8\alpha_1 (\Delta_{u_1} G_n)(\Delta_{u_3} G_n) \tag{75}$$

Since $u_7$ is the identity mapping we have

$$G_{n+1} = 4\alpha_3 G_n + 4\alpha_2 \Delta_{u_5} G_n + 8\alpha_1 (\Delta_{u_1} G_n)(\Delta_{u_3} G_n).$$

However,

$$\Delta_{u_1} G_n = \Delta_{u_1} G_0,\ \ \Delta_{u_3} G_n = \Delta_{u_3} G_0,\ \ \Delta_{u_5} G_n = \Delta_{u_5} G_0, \tag{76}$$

so that

$$G_{n+1} = 4\alpha_3 G_n + H, \tag{77}$$

$$H = 4\alpha_2 \Delta_{u_5} G_0 + 8\alpha_1 (\Delta_{u_1} G_0)(\Delta_{u_3} G_0). \tag{78}$$

Assume $\alpha_3 < 1/4$. Then the general solution of the difference equation (77) is

$$G_n = C(4\alpha_3)^n + \frac{H}{1-4\alpha_3}, \tag{79}$$

where $C$=const. In fact,

$$C = G_0 - \frac{H}{1-4\alpha_3}. \tag{80}$$

Thus,

$$G_n = (G_0 - \frac{H}{1-4\alpha_3})(4\alpha_3)^n + \frac{H}{1-4\alpha_3}. \tag{81}$$

Passing to the limit as $n \to \infty$ we obtain

$$G_\infty = \frac{H}{1-4\alpha_3} = \frac{4\alpha_2 \Delta_{u_5} G_0 + 8\alpha_1 (\Delta_{u_1} G_0)(\Delta_{u_3} G_0)}{1-4\alpha_3}, \tag{82}$$

therefore,

$$G_n = G_\infty + (4\alpha_3)^n (G_0 - G_\infty). \tag{83}$$

We see that the evolutionary spectrum consist of $\lambda_\emptyset = 1$ and $\lambda_2 = 4\alpha_3$. The exact rate of convergence is $O((4\alpha_3)^n)$. Note that the value $\alpha_3$ can be arbitrarily small.

In the extremal case $\alpha_3 = 1/4$ we have $\alpha_1 = \alpha_2 = 0$ as follows from (70) for $\alpha_1 \geq 0,\ \alpha_2 \geq 0$. Then $H = 0$ by (78) and $G_{n+1} = G_n$ by (77). Hence, $G_n$ =const, so $G_n = G_\infty$ in this case.

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