Minicourse: Multiscale behaviour in selection-mutation systems

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Part 4: Special form of the duality for finitely many types

1. Duals for mutation: Set-valued duals
2. Modified selection dual: finitely manly types
3. Ordered and tableau-valued duals
4. The dual - branching mesostate dynamics and malthusian parameter

Mutation

On *finite* type space

$$\mathbb{I} = \{1, \dots, K\}. \tag{0.1}$$

allows a modified dynamic of the function-valued process $\mathcal{F}_t^+, \mathcal{G}_t^+$ (later on called $\mathcal{F}_t^{++}, \mathcal{G}_t^{++}$)

Observation: Suffices to study indicator functions.

Definition (Set-valued mutation jumps)

This transition from type i to type j occurs at rate

$$m \cdot m_{i,j}\ ; i,j \in \{1,2,\cdots,K\} \tag{0.2}$$

and results in a jump (depending on whether $\ell \in \{i,j\}$ or not):

$$\begin{aligned} 1_{\{j\}} &\longrightarrow 1_{\{i\}\cup\{j\}} \\ 1_{\{i\}} &\longrightarrow 0 \\ 1_{\{\ell\}} &\longleftrightarrow 1_{\{\ell\}}\ \ell \notin \{i,j\} \end{aligned} \tag{0.3}$$

for $i,j \in \{1,2,\cdots,K\}$ and $j \neq i$. □

State space

$$\mathbb{F}_k := \{f = \sum_{i=1}^{n} \prod_{j=1}^{k_i} 1_{B_{i,j}}(u_j), B_{i,j} \subseteq \{1, 2, \cdots, K\}, n \in \mathbb{N}, k = \max_{i=1,\ldots,n} k_i\}, \quad (0.4)$$

$$\text{with} \quad \int_{\mathbb{I}^k} f d\mu^{\otimes k} \leq 1. \quad (0.5)$$

$$\text{Set:} \quad \mathbb{F} := \bigcup_{k=1}^{\infty} \mathbb{F}_k \quad (0.6)$$

Next extend this to $\mathbb{F}$. For this purpose let $B \subseteq \{1, \cdots, K\}$ and consider the indicator $1_B(u)$. Since this indicator can be written as

$$1_B(u) = \sum_{k \in B} 1_{\{k\}}(u), \tag{0.7}$$

we continue the transition in (0.3) as a linear map acting on the indicators $f = 1_{\{\ell\}}(\cdot)$, with $\ell \in \{1, \ldots, K\}$.

More generally proceed as follows. The transition $f \to \tilde{f}$ associated with the parameter (i,j) is obtained by applying to f the matrix $\bar{M}$ (in (k,ℓ)) which we define as

$$\bar{M}(i,j)[k,\ell] = \begin{cases} 1 & (k,\ell) = (i,j),\ k = i \neq \ell \\ 0 & \text{otherwise.} \end{cases} \tag{0.8}$$

This specifies the transition occurring in one of the several variables of f.

Assume that there are ℓ fitness levels reaching from 0 to 1 and denote them by

$$0 = e_1 < e_2 < \cdots < e_\ell = 1 \tag{0.9}$$

We refine the selection dynamic:

Births occur at total rate s but now when a birth occurs the *type of birth* $\in \{2, \cdots, \ell\}$) is chosen i.i.d. for this event with probabilities

$$(e_i - e_{i-1})_{i=2,\cdots,\ell}. \tag{0.10}$$

Define therefore for each level of fitness i,

$$A_i := \{j \in \mathbb{I} : \chi(j) \geq e_i\}. \tag{0.11}$$

$$\psi_C f := \sum_{m=1}^{k} [1_C(u_m) f(u_1, \ldots, u_k) + f(u_1, \ldots, u_k)(1 - 1_C(u_{k+1}))] \quad (0.12)$$

Observe that $(\psi_C - 1d)$ is the generator of a rate 1 jump process on $\mathbb{F}$. Namely denote $1_C^\ell = 1_C(u_\ell)$ and introduce for $f \in \mathbb{F}_k$ for every variable $u_j, j = 1, \cdots, k$ at rate 1 transitions:

$$f \longrightarrow 1_C^j f + f \otimes (1 - 1_C^j), \; j = 1, \cdots, k. \quad (0.13)$$

Then each jump from some f in $\mathbb{F}_k$ ends in $\mathbb{F}_{k+1}$.

We apply this to our context with C replaced by the sets defined in 0.11, we use the notation

$$\chi_i^j = 1_{A_i}(u_j) \quad (0.14)$$

Set for $f \in \mathbb{F}_k$,

$$(\psi_i^{j,k} f)(u_1, \cdots, u_{k+1}) = ((\chi_i^j f) \otimes 1_{\mathbb{I}}^{k+1}) + (1 - \chi_i^j) \otimes f))(u_1, \cdots, u_{k+1}). \tag{0.15}$$

Again we can define an alternative transition as follows

$$\begin{aligned}(\widehat{\psi}_i^{j,k} f)(u_1, \cdots, u_{k+1}) &= \chi_i^j(u_i) f(u_1, \cdots, u_n) 1(u_{k+1}) \\ &\quad + (1 - \chi_i^j(u_i)) f(u_1, \cdots, u_{i-1}, u_{k+1}, u_{i+1}, \cdots, u_k).\end{aligned} \tag{0.16}$$

Definition (Selection jump)

Introduce transitions for a process $\mathcal{F}^{++}$(jumps in $\mathbb{F}$) for the function-valued part of the form:

$$f \longrightarrow \psi_i^{j,k} f \text{ from } \mathbb{F}_k \to \mathbb{F}_{k+1}, \tag{0.17}$$

whenever a *birth of type i* due to partition element j in η occurred. (Recall here i is chosen with probability $(e_i - e_{i-1})$). This will replace the transition we had in $\mathcal{F}_t^+$ before. For $\mathcal{G}_t^{++}$ we use $\widehat{\psi}_i^{j,k}$. □

The state of the process $\mathcal{F}^{++}, \mathcal{G}^{++}$ is a sum of

$$2^{\overline{N}_t} - \text{summands}\ , \overline{N}_t = N + \#\ \text{birth till time}\ t \tag{0.18}$$

$$\mathcal{F}_t^{++} = \sum_{k \in \tau} \prod_{i=1}^{\overline{N}_t} g_i^k, \tag{0.19}$$

$\tau =$ leaves on a binary tree, g_i^k indicator on $\mathbb{I}$.

How can we describe the array of summands and its evolution?

How should we order the factors in a summand to exploit cancellations effects?

Idea: Describe summands and ordered factors as tableaus of rows and columns of functions.

We can perform calculations by expressing the dual expectation in terms of a suitably chosen population of factors, which gives the dynamic of the $(g_i^k)_{i,k}$. In particular we now *consider the population of summands and the dynamic of the products in each summand.* However we can give a more refined description by noting that whenever a birth event in η occurs and the selection operator acts on $\mathcal{F}_t^{++}$, we can get new summands. We can therefore record the information on the order at which variables appeared in the expression and we can also order the summands by splitting at each selection event a summand in two (ordered) summands getting a matrix with entries among $\{g_i^k, i, k\}$. After the first step starting with f_1 we get the tableau :

$$\begin{matrix} f_1 1_A & 1 \\ f_1 & 1 - 1_A, \end{matrix} \tag{0.20}$$

The basic idea: passing to tableaus

The key trick is to order factors and introduce factors 1. This is based on the following observation. We can also keep track of some historical information in order to deal with the sum on the r.h.s. of (0.19). In particular we introduce an *ordering of the factors* that allows us to *associate factors in different summands.*
First note that a product of indicators can change into a *sum* of products of indicators only by the selection mechanism and all other transitions preserve the product structure of the indicators of a summand in the $\mathcal{F}_t^{++}$ respectively $\mathcal{G}_t^{++}$ dynamic.

Recall next that selection operates by $1_A \cdot f + (1 - 1_A) \otimes f$ with $1 - 1_A$ corresponding to a new variable. *Observe first that we can write without changing integrals but having the same number of variables for both summands as*

$$f \to 1_A \cdot f \otimes 1 + f \otimes (1 - 1_A). \tag{0.21}$$

Then it is useful to place the new factors 1 and $(1 - 1_A)$ not at the end of the product but next to the factor giving birth.

From (0.21) we see that we get a sum of two terms now involving a new variable corresponding to the particle added by the birth event in the dual particle system. As time goes on this produces a *binary tree* and each path in this tree starting from the root and ending in a leaf corresponds uniquely to a summand which consists of an ordered product of factors. In general and more precisely we make the resulting two summands comparable in the sense that they have the same number of variables in both summands in (0.21), but without changing the value. To do this we write this action of the selection operator as follows.

Take a function $f = f^3 \otimes f^1 \otimes f^2$, where f^1 is a function of *one* variable, the one on which selection acts and f^2, f^3 of the remaining variables ordered in the order of the corresponding partition elements in the ordered particle system. Write:

$$f \to f^3 \otimes (1_A \cdot f^1) \otimes 1 \otimes f^2 + f^3 \otimes f^1 \otimes (1 - 1_A) \otimes f^2, \qquad (0.22)$$

where 1 stands for (111), in general $(11 \cdots 1)$ with M ones, which integrates to 1 for any probability measure.
This means that we have inserted a new variable in *both* summands. This allows us then to associate factors in the two summands after the selection jump one to one starting from the initial factor and ending with the last born variable.

To formalize the above ideas we need two changes.

(1) We want to view the function $\mathcal{F}_t^{++}$ not just as a function but to add as part of its description some additional information on its *form*. Namely, we want to consider a sum of *products of indicators* where each factor is associated with a particular particle in η and the particles are ordered in a certain way related to their appearance as selection acts. Note that this involves **historical information** on the evolution of the dual $(\eta, \mathcal{F}^{++})$.

(2) This means we can enrich the F_t^{++} to a marked *tableau* whose rows correspond to summands and columns to factors (which are indicators) each of which is a function of one variable.

For this purpose we need to *order the factors* and to introduce *new factors of* 1 where necessary in order that all the summands in the expression for $\mathcal{F}_t^{++}$ consist of an equal number of factors. This leads to a collection of factors which are ordered, carry a location and are organized in summands. This object we will call $\mathcal{F}_t^{++,<}$.

Definition (Order relation among factors, ranks, transition under selection)

(a) We start with giving rank $1, \cdots, N_0$ to the N_0 initial particles and the associated factors. New factors are created by the selection operator as follows.
Suppose there is a birth by selection operating on the $j-$th particle in η and the corresponding factor is in the ℓ-th rank and m denotes the current number of partition elements. That is, selection hits the factor with rank ℓ and produces the transition of $f^1 \otimes \cdots \otimes f^m$ to:

$$\begin{aligned} f^1 \otimes \cdots f^{\ell-1} \quad \otimes \quad & (f^\ell 1_A) \otimes 1 \otimes f^{\ell+1} \otimes \cdots \otimes f^m \\ & + f^1 \otimes \cdots f^{\ell-1} \otimes f^\ell \otimes (1 - 1_A) \otimes f^{\ell+1} \otimes \cdots \otimes f^m. \end{aligned} \tag{0.23}$$

Definition

In order to work with an ordered object we use the rule that

- the additional factor 1 is placed at the $(\ell + 1)$-th position directly to the right of the factor on which the operator is acting producing $f^{\ell} 1_A$ on the ℓ-th position,
- the remaining factors are shifted one unit to the right
- the factor 1 and $1 - 1_A$is put at the $(\ell + 1)$-th position.

Definition

(b) We denote this *order* of factors of one variable by

$$<, \text{ that is, } f^1 < f^2 \tag{0.24}$$

means that the factor f^1 lies to the left of the factor f^2 in this order.

(c) We shall relabel all factors counting left to right and we assign the factors the

$$\text{ranks } 1, 2, 3, \cdots \tag{0.25}$$

with the natural order on $\mathbb{N}$. □

Definition (State description of the enriched ordered dual$(\eta', \mathcal{F}_t^{++,<})$)

(a) The state of the ordered dual has the form of an *enriched ordered particle system* together with a *collection of maps defined on the particle system*, where the collection of maps is given by

$$\{\varphi_i(k)(t); \quad i = 1, \cdots, \tilde{N}_t; \quad k = 1, \cdots, N_t\}, \tag{0.26}$$

$$\varphi_i : \qquad \{1, \cdots, N_t\} \longrightarrow \mathbb{F} \times \{1, \cdots, N\} \times \mathbb{N}, \tag{0.27}$$

where *rows corresponding to the index i represent summands, and columns corresponding to the index k represent the factors of a given rank* in different summands. Furthermore by the φ_i every column is assigned the **type of factor** in position (i, k) in the array as well as a **location** in $\{1, \cdots, N\}$ and assigning the **rank** to dual particles corresponding to columns.

Definition

A row of the tableau can be split into a product of a set of sub-products of factors, one sub-product for each occupied location.
We denote (a factor is a function $\mathbb{I} \to \mathbb{R}^+$)

$$\mathbb{F}^* = \text{ the set of possible factors.} \tag{0.28}$$

Definition

(b) Then the state at time t can be uniquely described by a collection of

$$\tilde{N}_t \text{ summands (rows) of } N_t \text{ factors of one variable (columns)} \tag{0.29}$$

and the state is denoted

$$\{\varphi_i, \quad i \in \{1, \cdots, \tilde{N}_t\}\} \tag{0.30}$$

where each summand is associated to a map $\varphi_i (= \varphi_i(t))$, specifying separately for each summand for each factor the *type* of the factor, the *location* in geographic space and finally *rank* in the order called $<$.

Definition

We write

$$\varphi_i(k)(t) = (f_k^i(t), j_k(t), \ell_k(t)) \quad , \quad k = 1, \cdots, N_t, \tag{0.31}$$

with the constraints that

$$f_k^i = f_{k'}^i \text{ and } j_k = j_{k'} \text{ if } \ell_k = \ell_{k'}. \tag{0.32}$$

We set

$$\mathcal{F}_t^{++,<} = \{f_k^i(t) : k = 1, \cdots, N_t, i = 1, \ldots, \tilde{N}_t\}. \tag{0.33}$$

Definition

(c) At time 0 we set $\tilde{N}_0 = 1$ and the individuals $\{1, \ldots, N_0\}$ are assigned an initial index and the particles $\{1, \ldots, N_t - N_0\}$ are indexed in order of their birth times, the first birth assigned index $N_0 + 1$, etc. In contrast to the index the rank assigned to a particle changes dynamically due to coalescence or other births (recall also (0.23)) to be described by the dynamics below after (0.40).

Definition

(d) The set of particles assigned the same rank corresponds to the partition elements defined in *Subsection 5.1*. As in *Subsection 5.1* the set of partition elements at time t is denoted

$$\pi_t = (\pi_t(1), \cdots, \pi_t(\mid \pi_t \mid)) \tag{0.34}$$

and the partition elements have the form

$$\pi_t(\ell) = \{k : j_k = j, \ell_k = \ell\}, \quad \ell = 1, \ldots, \mid \pi_t \mid . \tag{0.35}$$

This defines a mapping

$$\xi_t : \{1, \ldots, \mid \pi_t \mid\} \to \{1, \ldots, N\}, \tag{0.36}$$

such that the partition element corresponding to rank ℓ is located at site

$$\xi_t(\ell) = j. \tag{0.37}$$

Definition

Then π_t defines a mapping

$$\pi_t : \{1, \dots, N_t\} \to \{1, \dots, |\pi_t|\}, \tag{0.38}$$

where the partition elements are now *indexed* by the smallest index of the particles they contain and ξ_t defines a mapping $(\pi_t(1), \cdots, \pi_t(|\pi|)) \to \Omega$ (giving the locations of partition elements). We define the enriched (from η) particle system

$$\eta'_t = (N_t, \pi_t, \xi_t, \Re_t), \tag{0.39}$$

that is, η'_t is given by the set of particles $\{1, \cdots, N_t\}$, their partition structure π_t, locations ξ_t together with the list of current ranks $\Re_t$ of partition elements. $\square$

The dual evolution can be described as follows. First the particle system η.

- Starting with N_0 initial dual particles each located at one of the sites in $\{1, \dots, N\}$ at time 0, new particles are created by a pure birth process with birth rate sk when the current number of dual particles is k. More precisely, independently each particle gives birth at rate s.
- Each particle is located at one of the points in $\{1, \dots, N\}$and is assigned in addition a *rank*.
  Then the enriched evolution with the transitions by (1) coalescence, (2) mutation and (3) birth (selection) is as follows.

(1) *Coalescence* (two particles at the same location) *effectively* decreases the number of factors even though here we keep formally the number of factors and introduce an additional factor 1. We make the convention that upon coalescence of two factors we replace the one with lower rank by the product of the two factors and the one with upper rank becomes $(\cdots)$ (this is the analogue of the well known look-down process). In formulas, at the coalescence of individuals i' and k' in the particle system η which corresponds in a particular summand to factors with ranks i and k (in the labeling (0.25)) we get for the function-valued part the transition given by

$$f^1 \otimes \cdots \otimes f^i \otimes \cdots \otimes f^k \otimes \cdots \longrightarrow f^1 \otimes \cdots \otimes (f^i f^k) \otimes \cdots \otimes 1 \otimes \cdots , \tag{0.40}$$

with each factor we associate a rank and the new factor 1 gets the same rank which introduces then a new order by rank. The rank is defined as in a selection operation the newly created factor.

(2) Mutations act as before on factors corresponding to each variable independently and we note that in particular acting on $(\underline{1})$ or $(\underline{0})$ mutation has no effect.

(3) Selection creates a new particle in the dual particle system η and at the same time the transition given in (0.21) occurs. *Ranks* change at the same time as follows. The offspring of a particle of rank k is assigned the rank $k+1$ and the ranks of all particles with ranks $\ell \geq k+1$ are reassigned rank $\ell+1$. We denote the resulting number of particles in the dual system η_t at time t by N_t where $N_t - N_0$ denotes the number of births. Moreover at a birth time the offspring of a particle is located at the same site as the parent.

To complete the description of the dual we must define the corresponding function $\mathcal{F}_t^{++,<}$ which is a function of N_t variables but has the form of a sum of *ordered* products of factors. The transitions of $\mathcal{F}_t^{++,<}$ are as listed above.

Lemma (Representation via enriched process)

Consider the dual process $(\eta'_t, \mathcal{F}_t^{++,<})_{t \geq 0}$. *Let pr denote the map* $(N_t, \pi_t, \zeta_t, \Re_t) \to (N_t, \pi_t, \xi_t)$ *associating with* η' *the triple* η *arising by ignoring the rank. Given the collection of maps associated with* $(\eta', \mathcal{F}^{++}, <)$ *as* $f_k^i, : k \leq N, i = 1, \dots, \tilde{N}\}$, *we define for this state the pair:*

$$(\eta, \mathcal{F}^{++}) = \left(pr(\eta'), \sum_{i=1}^{\tilde{N}} \prod_{j \in S} \prod_{\ell=1}^{|\pi|} \left(1_{\xi(\ell)=j}(f_\ell^i(u_\ell))\right) \right). \qquad (0.41)$$

Then we obtain a version of $(\eta_t, \mathcal{F}_t^{++})_{t \geq 0}$ *on the probability space of* $(\eta', \mathcal{F}^{++,<})$. □

Definition (Ordering the rows)

(a) In order to keep track of the summands and produce a convenient visualization as a tableau we adopt the following convention for ordering the summands. Starting with a single factor f operated on by selection as in (ref 7.4) we produce the ordered rows

$$\begin{array}{cc} \chi_A \cdot f & 1 \\ f & (1-\chi_A). \end{array} \tag{0.42}$$

In general

- The operation of selection at a rank is applied successively to each row starting at the top and then moving down to each original row. When selection acts on the rank at a row it produces an additional row immediately below the row on which it acts. If selection produces a row with a zero factor this row is removed.
- Also mutation and coalescence can produce a row with a zero factor which is then removed but otherwise they do not change the order of the rows.

Definition

(b) This means that we want to think of the

$$\text{state of } (\eta', \mathcal{F}^{++,<}) \text{ as a } \textit{tableau} \tag{0.43}$$

where *rows* are ordered dynamically according to (a) and correspond to summands and *columns* to variables and *marks* on the entries indicate the location of the factor.

Definition

(c) For convenience we denote the tableau of ordered rows and columns of indicator functions (of one variable in each column) associated to the particle system η'_t and to the object $\mathcal{F}_t^{++,<}$ as

$$t((\eta'_t, \mathcal{F}_t^{++\cdot<})), \tag{0.44}$$

where a *column* corresponds to a *variable* which are ordered according to the rank in the tableau from left to right and a *row* to a particular *summand* which we order according to the convention in (0.42). □

Definition (Tableau-valued process)

The evolution of the Markov jump process $(\eta'_t, \mathcal{F}_t^{++,<})_{t\geq 0}$ induces a *marked tableau-valued* pure jump process driven by an autonomous particle process η'_t:

$$(t((\eta'_t, \mathcal{F}_t^{++,<})))_{t\geq 0}. \quad \square \tag{0.45}$$

COMMENT ON $(t((\eta'_t, G_t^{++,<})))_{t\geq 0}$. In this case the rows in the tableau correspond to disjoint subsets and we have the set-valued dual.

Tableau and set-valued dual: $\mathcal{G} = \mathcal{G}^{++,<}$

Example: $M_1 + M_2 = K$ types. We identify the indicator function of a set $A \subset \mathbb{I} = \{1, \ldots, K\}$ with the set.

Notation: Given set $A \subset \mathbb{I}$, the indicator function is denoted

$$1_A = (a_1, \ldots, a_K) \quad \text{where } a_j = 1 \text{ if } j \in A, \text{ otherwise } a_j = 0$$

e.g. $K = 3$, $1_1 = (100)$

Modified duality under exchangeability of X_0

Recall: The dual $\mathcal{G} = \mathcal{G}^{++,<}$ is obtained from $\mathcal{F}^{++,<}$ by coupling the transitions in the summands. It produces a set-valued dual with countable state space $((2^{\mathbb{I}})^{\mathbb{N}})^{S}$ with $S = \{1, \ldots, N\}$ or $\mathbb{N}$ (and with only finitely many factors not equal to $\mathbb{I}$).

Dual dynamics with $M_1 = 2$, $M_2 = 1$ and $\chi(2) = \chi(3) = 1$

$\mathcal{G}_0 = (110)_1 = (110)_1 \otimes (111)_1^{\mathbb{N}}$, subscript = geographic site in S:

Selection: $(110)_1 \to (010)_1 \otimes (111)_1 + (100)_1 \otimes (110)_1$.

Coalescence

$$1_A \otimes 1_B \to 1_{A \cap B}.$$

Mutation:

$$\text{rate } m_{21} : (100) \to (110) \quad \text{rate } m_{12} : (100) \to (000).$$

$(110) \to (010)$(rare mutation) , $(010) \to (000)$ level 1 mutation.

Example

Single site with $M_1 = 2,\ M_2 = 1,\ e_1 = 0\ e_2 = e_3 = 1.$

$\mathcal{G}_0 = (110)_1 = (110)_1 \otimes (111)^{\mathbb{N}}$, indicator functions, subscript = geographic site:
Then four (011) selection operations, $f \to f \cdot 1_{\{23\}} \otimes 1_{\{123\}} + 1_{\{1\}} \otimes f$

$$\mathcal{G}_1(\tau_4) = \begin{pmatrix} (010)_1 & & & & \\ (100)_1 & (010)_1 & & & \\ (100)_1 & (100)_1 & (010)_1 & & \\ (100)_1 & (100)_1 & (100)_1 & (010)_1 & \\ (100)_1 & (100)_1 & (100)_1 & (100)_1 & (010)_1 \end{pmatrix}$$

where we omit factors of the form $1_{\mathbb{I}} = (111)$.

Migration:

A rank at a site $i \in \{1, \ldots, N\}$ can migrate to j with rate $\frac{c}{N}$.
The location of a rank determines the set of possible coalescence events – only ranks at the same site can coalesce.

Start with $(110)_1$, 4 selection operations and then 3rd rank migrates

$$
\begin{array}{llllll}
 & (010)_1 & & & & \\
 & (100)_1 & (010)_1 & & & \\
(110)_1 \rightarrow & (100)_1 & (100)_1 & (010)_2 & & \\
 & (100)_1 & (100)_1 & (100)_2 & (010)_1 & \\
 & (100)_1 & (100)_1 & (100)_2 & (100)_1 & (110)_1
\end{array}
$$

then 2 selection operations at site 2:

$$
\begin{array}{llllllll}
 & (010)_1 & & & & & & \\
 & (100)_1 & (010)_1 & & & & & \\
 & (100)_1 & (100)_1 & (010)_2 & & & & \\
\rightarrow & (100)_1 & (100)_1 & (100)_2 & (010)_2 & & & \\
 & (100)_1 & (100)_1 & (100)_2 & (100)_2 & (010)_2 & & \\
 & (100)_1 & (100)_1 & (100)_2 & (100)_2 & (100)_2 & (010)_1 & \\
 & (100)_1 & (100)_1 & (100)_2 & (100)_2 & (100)_2 & (100)_1 & (110)_1
\end{array}
$$

Decoupling - resolution

If a mutation $1 \to 2$ occurs in either column 1 or column 2, then the new site 2 is removed, i.e. becomes (111) and therefore inactive.

On the other hand if the mutation $2 \to 1$ occurs in both column 1 and column 2, and the last two columns coalesce with one of the first two columns, then we have

$$\begin{array}{lllll} & & (010)_2 & & \\ (110)_1 & \otimes & (100)_2 & (010)_2 & \\ & & (100)_2 & (100)_2 & (010)_2 \end{array}$$

We then say that site 1 has resolved and the new site 2 is active and is decoupled from the parent site.

Population of metafactors

Starting with $(110)_1$, the action of selection, mutation and coalescence, before resolution, produces an irreducible multisite tableau.

At its eventual resolution it can produce a number of resulting offspring multisite tableau each identified as an element of the countable set of mesostates.

This results in a branching population of metafactors each with internal dynamics given by a process on the set of mesostates. Mesostate internal dynamics - multitype birth death process with catastrophes.

The detailed analysis of emergence requires information on the **distribution and structure of this population of metafactors**.

Exponential rare mutant growth in the case $m_1 \geq 2$

Role of deleterious mutation: Type 3 has a selective advantage only in sites with significant type 1 present! If m_{21} is small then there can be large sets of spatial sites with high concentration of type 2 mass. Then the growth of rare mutant excursions occur in a sparse set of sites having significant proportion of type 1.

Emergence time depends on the population of mesostates.

Parameter regimes

Case 1: "mutation dominant case"
Depends on malthusian parameter of finitely many type CMJ.

Case 2: "selection dominant case"
Depends on malthusian parameter of countably many type CMJ.

Additional reference for duality:

D.A. Dawson and T.G. Kurtz (1982). Applications of duality to measure-valued diffusions, Springer Lecture Notes in Control and Inf. Sci. 42, 177-191.