Quasi-stationary Distributions in Recombination

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Random Excursions with Jean Bertoin
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Some references

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Recombination

”If for a certain generation the distribution of genotypes is known and a certain law of heredity is assumed, the distribution in the next generation can be computed”. (Geiringer, 1944).

”A problem of primary importance in population genetics is that of determining the genotype frequencies in a large population of sexually reproducing organisms mating at random in non-overlapping generations with negligible mutation and selection.” (Bennett, 1954).

”Recombination is a genetic mechanism that mixes or reshuffles the genetic material of different individuals from generation to generation; it takes place in the course of sexual reproduction”. (Baake and Baake, 2020).

Recombination equation

Discrete time and non-overlapping generations.
I finite set sites, $\mathcal{A}$ finite alphabet; $\mathcal{A}^I$ set of sequences encoding genetic information in population, $\mathcal{P}_I$ set of probability measures on $\mathcal{A}^I$.

$\mu \in \mathcal{P}_I$; for $J \subseteq I$, $\mu_J \in \mathcal{P}_J$ marginal on $\mathcal{A}^J$; for δ partition of I, $\bigotimes_{J\in\delta} \mu_J$ product measure.

$\mathcal{D}$ a class of partitions of I, $\rho = (\rho_\delta > 0 : \delta \in \mathcal{D})$ probability vector, $\rho_{\{I\}} < 1$. Recombination transformation of population genetic information:

$$\Xi : \mathcal{P}_I \to \mathcal{P}_I, \quad \Xi[\mu] = \sum_{\delta\in\mathcal{D}} \rho_\delta \bigotimes_{J\in\delta} \mu_J .$$

$(\Xi^n(\mu))$ evolution of genetic information in the population.

Equation for binary partitions

For binary partitions the children sequences are derived from two parents:

$$\Xi(\mu) = \sum_{J \subseteq I} \rho_J \, \mu_J \otimes \mu_{J^c},$$

Maternal and paternal genetic information represented by two independent random elements U and V on $\mathcal{A}^I$ distributed as μ the initial distribution genetic information in population,

Genetic information Z inherited by a child is $Z_J = U_J$, $Z_{J^c} = V_{J^c}$, where $\{J, J^c\}$ random binary partition distributed according to ρ independently of U and V.
$\Xi(\mu)$ distribution of children's genetic information,

Pairs of characters

$I = \{1, 2\}$, $\mathcal{A} = \{A, a\}$. So $\mathcal{A}^I = \{AA, Aa, aA, aa\}$. (Pairs of Mendelian characters, 'A' dominant, 'a' recessive).

$p = \mu(AA)$, $\mu(Aa) = q = \mu(aA)$, $r = \mu(aa)$.

Let $\mathcal{D} = \{\delta_0\}$, $\delta_0 = \{\{1\}, \{2\}\}$, $\rho_{\delta_0} = 1$. Marginals

$$\mu_{\{1\}}(A) = p + q = \mu_{\{2\}}(A), \quad \mu_{\{1\}}(a) = q + r = \mu_{\{2\}}(a).$$

Then

$$\mu_{\{1\}} \otimes \mu_{\{2\}}(AA) = (p+q)^2,\ \mu_{\{1\}} \otimes \mu_{\{2\}}(aa) = (q+r)^2,$$

$$\mu_{\{1\}} \otimes \mu_{\{2\}}(Aa) = (p+q)(q+r)\mu_{\{1\}} \otimes \mu_{\{2\}}(aA),$$

and this is a fixed point for the iteration.

DISCUSSION AND CORRESPONDENCE

Mendelian Proportions in a Mixed Population

To The Editor of Science: I am reluctant to intrude in a discussion concerning matters of which I have no expert knowledge, and I should have expected the very simple point which I wish to make to have been familiar to biologists. However, some remarks of Mr. Udny Yule, to which Mr. R. C. Punnett has called my attention, suggest that it may still be worth making.

In the *Proceedings of the Royal Society of Medicine* (Vol I., p. 165) Mr. Yule is reported to have suggested, as a criticism of the Mendelian position, that if brachydactyly is dominant "in the course of time one would expect, in the absence of counteracting factors, to get three brachydactylous persons to one normal."

It is not difficult to prove, however, that such an expectation would be quite groundless. Suppose that *Aa* is a pair of Mendelian characters, *A* being dominant, and that in any given generation the numbers of pure dominants (*AA*), heterozygotes (*Aa*), and pure recessives (*aa*) are as $p{:}2q{:}r$. Finally, suppose that the numbers are fairly large, so that the mating may be regarded as random, that the sexes are evenly distributed among the three varieties, and that all are equally fertile. A little mathematics of the multiplication-table type is enough to show that in the next generation the numbers will be as

$$(p+q)^2 : 2(p+q)(q+r) : (q+r)^2,$$

or as $p_1{:}2q_1{:}r_1$, say.

The interesting question is – in what circumstances will this distribution be the same as that in the generation before? It is easy to see that the condition for this is $q^2 = pr$. And since $q_1^2 = p_1 r_1$, whatever the values of p, q, and r may be, the distribution will in any case continue unchanged after the second generation.

Suppose, to take a definite instance, that *A* is brachydactyly, and that we start from a population of pure brachydactylous and pure normal persons, say in the ratio of 1:10,000. Then $p = 1$, $q = 0$, $r = 10{,}000$ and $p_1 = 1$, $q_1 = 10{,}000$, $r_1 = 100{,}000{,}000$. If brachydactyly is dominant, the proportion of brachydactylous persons in the second generation is 20,001:100,020,001, or practically 2:10,000, twice that in the first generation; and this proportion will afterwards have no tendency whatever to increase. If, on the other hand, brachydactyly were recessive, the proportion in the second generation would be 1:100,020,001, or practically 1:100,000,000, and this proportion would afterwards have no tendency to decrease.

In a word, there is not the slightest foundation for the idea that a dominant character should show a tendency to spread over a whole population, or that a recessive should tend to die out.

I ought perhaps to add a few words on the effect of the small deviations from the theoretical proportions which will, of course, occur in every generation. Such a distribution as $p_1{:}2q_1{:}r_1$, which satisfies the condition $q_1^2 = p_1 r_1$, we may call a *stable* distribution. In actual fact we shall obtain in the second generation not $p_1{:}2q_1{:}r_1$ but a slightly different distribution $p{:}2q{:}r$, which is not "stable." This should, according to theory, give us in the third generation a "stable" distribution $p_2{:}2q_2{:}r_2$, also differing from $p_1{:}2q_1{:}r_1$; and so on. The sense in which the distribution $p_1{:}2q_1{:}r_1$ is "stable" is this, that if we allow for the effects of casual deviations in any subsequent generation, we should, according to theory, obtain at the next generation a new "stable" distribution differing but slightly from the original distribution.

I have, of course, considered only the very simplest hypotheses possible. Hypotheses other that [*sic*] that of purely random mating will give different results, and, of course, if, as appears to be the case sometimes, the character is not independent of that of sex, or has an influence on fertility, the whole question may be greatly complicated. But such complications seem to be irrelevant to the simple issue raised by Mr. Yule's remarks.

G. H. Hardy
Trinity College, Cambridge,
April 5, 1908

P. S. I understand from Mr. Punnett that he has submitted the substance of what I have said above to Mr. Yule, and that the latter would accept it as a satisfactory answer to the difficulty that he raised. The "stability" of the particular ratio 1:2:1 is recognized by Professor Karl Pearson (*Phil. Trans. Roy. Soc.* (A), vol. 203, p. 60).

Hardy, G. H. 1908. Mendelian proportions in a mixed population, *Science*, N. S. Vol. XXVIII: 49–50. (letter to the editor)

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Partitions and marginals

$\mathbb{D}(I)$ family of partitions of I; $\delta = \{L : L \in \delta\} \in \mathbb{D}(I)$, $L \in \delta$ atom; $|\delta|$ number of atoms.

$\delta \preceq \delta'$ notes δ' finer than δ, Finest $\{\{i\} : i \in I\}$, coarsest $\{I\}$. $\delta \vee \delta' = \{L \cap L' : L \in \delta, L' \in \delta'\}$ refinement δ, δ'.

Refinement of $J \subseteq I$ by $\delta \in \mathbb{D}(I)$ is $\delta|_J = \{J \cap L : L \in \delta\}$, partition of J.

$\mathcal{A}^I$ finite product space, $\mathcal{P}_I$ set of probability measures on it.

$\mu \in \mathcal{P}_I$, for $J \subseteq I$, $\mu_J \in \mathcal{P}_J$ marginal on $\mathcal{A}^J$, $\mu_I = \mu$, $\mu_\emptyset = 1$.

$J, K \subseteq I$, $J \cap K = \emptyset$, $\mu_J \in \mathcal{P}_J$, $\mu_K \in \mathcal{P}_K$, $\mu_J \otimes \mu_K$ product measure. $\otimes$ is stable under restriction: $J, K, M \subseteq I$, $J \cap K = \emptyset$, $M \subseteq J \cup K$:

$$(\mu_J \otimes \mu_K)_M = \mu_{J \cap M} \otimes \mu_{K \cap M}.$$

Action of partitions

$\rho = (\rho_\delta : \delta \in \mathbb{D}(I))$ probability vector on set of partitions.
$\mathcal{D} = \{d \in \mathbb{D}(I) : \rho_d > 0\}$ support of ρ (*cutting partitions*). For $\delta \in \mathbb{D}(I)$: $\mathcal{D}^\delta = \{\underline{d}^\delta = (d^\delta(K) \in \mathcal{D} : K \in \delta)\}$ set $\delta-$tuples in $\mathcal{D}$.

Partition resulting from refinement of each $K \in \delta$ with $d^\delta(K)$ is

$$\delta \vee \underline{d}^\delta = \{d^\delta(K)|_K : K \in \delta\} \in \mathbb{D}(I).$$

One has $\delta \preceq \delta \vee \underline{d}^\delta$ and

$$(\delta \vee \underline{d}(\delta)) \vee \underline{d}(\delta \vee \underline{d}(\delta)) = \delta \vee \underline{d}(\delta) \text{ with}$$
$$d^{\delta \vee \underline{d}(\delta)}(K') = d^\delta(K) \text{ for } K' \in d^\delta(K)|_K.$$

If $\underline{d}^{\delta,d_0} = (d_0, .., d_0) \in \mathcal{D}^\delta$ constant: $\delta \vee \underline{d}^{\delta,d_0} = \delta \vee d_0$.
Since $\mathcal{D}^{\{I\}} = \mathcal{D}$, $\{I\} \vee d = d$, $d \in \mathcal{D}$.

The iterated transformation

Set $\mathcal{H}^0 = \{I\}$, $\mathcal{H}^{n+1} = \{\delta \vee \underline{d}^\delta : \delta \in \mathcal{H}^n, \underline{d}^\delta \in \mathcal{D}^\delta\}$.

$\mathcal{H}^1 = \mathcal{D}$, $\mathcal{H}^n \subseteq \mathcal{H}^{n+1}$, $n \geq 1$, $(\mathcal{H}^n)$ stabilizes at finite n_0:
$\mathcal{H}_\infty = \bigcup_{n\geq 1} \mathcal{H}^n = \mathcal{H}^{n_0}$, set $\mathcal{H}_{\infty,0} = \mathcal{H}_\infty \cup \mathcal{H}^0$.

Proposition

The iterated of the recombination transformation $\Xi : \mathcal{P}_I \to \mathcal{P}_I$, $\Xi(\mu) = \sum_{d\in\mathcal{D}} \rho_d \bigotimes_{J\in d} \mu_J$ *satisfies*

$$\Xi^n(\mu) = \sum_{\delta\in\mathcal{H}^n} \rho_\delta(n) \bigotimes_{L\in\delta} \mu_L \text{ with } \rho_\delta(n) \geq 0, \sum_{\delta\in\mathcal{H}^n} \rho_\delta(n) = 1 \text{ and}$$

$$\forall \delta' \in \mathcal{H}^{n+1} : \quad \rho_{\delta'}(n+1) = \sum_{\delta\in\mathcal{H}^n} \sum_{\underline{d}^\delta \in\mathcal{D}^\delta : \delta\vee\underline{d}^\delta = \delta'} \rho_\delta(n) \prod_{J\in\delta} \rho_{d^\delta(J)}.$$

Proof

Claim: an induction argument gives,

$$\Xi^n(\mu) = \sum_{\delta\in\mathcal{H}^n} \rho_\delta(n) \bigotimes_{L\in\delta} \mu_L \text{ with } \rho_\delta(n) \geq 0, \sum_{\delta\in\mathbb{D}(I)} \rho_\delta(n) = 1.$$

If $n = 1$, $\mathcal{H}^1 = \mathcal{D}$, $\rho_\delta(1) = \rho_\delta$, so holds.

$$\begin{aligned}\Xi^{n+1}(\mu) &= \Xi^n(\Xi(\mu)) = \sum_{\delta\in\mathcal{H}^n} \rho_\delta(n) \bigotimes_{J\in\delta} (\Xi(\mu))_J \\ &= \sum_{\delta\in\mathcal{H}^n} \rho_\delta(n) \bigotimes_{J\in\delta} \left(\sum_{d\in\mathcal{D}} \rho_d \bigotimes_{L\in d} \mu_{L\cap J} \right) \\ &= \sum_{\delta\in\mathcal{H}^n} \sum_{\underline{d}^\delta\in\mathcal{D}^\delta} \rho_\delta(n) \prod_{K\in\delta} \rho_{\underline{d}^\delta(K)} \bigotimes_{M\in\delta\vee\underline{d}^\delta} \mu_M.\end{aligned}$$

By induction $\sum_{\delta\in\mathcal{H}^n} \sum_{\underline{d}^\delta\in\mathcal{D}^\delta} \rho_\delta(n) \prod_{K\in\delta} \rho_{\underline{d}^\delta(K)} = 1$ so claim.

Probabilistic elements

Let $(\Omega, \mathcal{B}, \mathbb{P})$ probability measure space,
$\Delta = (\Delta_n(i) : \Omega \to \mathcal{D} : n \geq 1, i \geq 1)$ double sequence of i.i.d. random variables with common law ρ:

$$\forall r, s \geq 1, n \leq r, i \leq s, d_n(i) \in \mathcal{D} :$$

$$\mathbb{P}(\Delta_n(i) = d_n(i) : n \leq r, i \leq s) = \prod_{n=1}^{r} \prod_{i=1}^{s} \rho_{d_n(i)}.$$

For every $\ell \geq 1$ put $\underline{\Delta}_n^\ell = (\Delta_n(i) : i = 1, .., \ell)$.

Define random variables $(Y_n : n \geq 0)$ with

$$Y_0 = \delta \in \mathcal{H}_{\infty,0}, \;\; Y_{n+1} = Y_n \vee \underline{\Delta}_{n+1}^{|Y_n|} \text{ for } n \geq 0.$$

$Y_n \vee \underline{\Delta}_{n+1}^{Y_n}$ partition whose atoms $J_i^{Y_n} \in Y_n$ refined with random partition $\Delta_{n+1}(i) \in \mathcal{D}$. So,

$$Y_{n+1} = Y_n \vee \underline{\Delta}_{n+1}^{|Y_n|} = \{\Delta_{n+1}(i)|_{J_i^{Y_n}} : i = 1, .., |Y_n|\}.$$

Markov chain and Key relation

Y_0 values in $\mathcal{H}_{\infty,0}$, Y_n values in $\mathcal{H}_\infty$ for $n \geq 1$.

$(Y_n : n \geq 0)$ Markov chain with transition matrix $P = (P_{\delta,\delta'} : \delta, \delta' \in \mathcal{H}_{\infty,0})$ given by

$$P_{\delta,\delta'} = \sum_{\underline{d}^\delta \in \mathcal{D}^\delta : \delta \vee \underline{d}^\delta = \delta'} \prod_{K \in \delta} \rho_{d^\delta(K)}.$$

$\mathbb{P}$ *law of the chain with* $Y_0 = \{I\}$ and $\mathbb{E}$ *mean expected value*.

Let $\mu^{(n)} = \bigotimes_{L \in Y_n} \mu_L$ for $n \geq 0$. So,

$$\mathbb{E}(\mu^{(n)}) = \sum_{\delta \in \mathcal{H}^n} \mathbb{P}(Y_n = \delta) \bigotimes_{L \in \delta} \mu_L.$$

Proposition

Let $Y_0 = \{I\}$. For $\mu \in \mathcal{P}_I$ one has $\Xi^n(\mu) = \mathbb{E}(\mu^{(n)})$.

Connection

$$\forall \delta, \delta' \in \mathcal{H}_{\infty,0} : \quad \delta \to \delta' \Leftrightarrow \left[\exists \underline{d}^{\delta} \in \mathcal{D}^{\delta} : \delta' = \delta \vee \underline{d}^{\delta}\right],$$

For every $\delta \in \mathcal{H}_\infty$ exists $\underline{d}^\delta \in \mathcal{D}^\delta$ such that $\delta \vee \underline{d}^\delta = \delta$, so

$$\forall \delta \in \mathcal{H}_\infty : \ \delta \to \delta. \text{ One has } \{I\} \to \delta' \Leftrightarrow \delta' \in \mathcal{D}.$$

Path $(\delta_k : k = 1, .., r)$ in $\mathcal{H}_{\infty,0}$ between $\delta \in \mathcal{H}_{\infty,0}$ and $\delta' \in \mathcal{H}_\infty$, $r \geq 2$: $\delta_1 = \delta$, $\delta_r = \delta'$, $\delta_k \to \delta_{k+1}$, $k = 1, .., r-1$. There exists path from $\{I\}$ to any $\delta \in \mathcal{H}_\infty$.

$\delta \to \delta'$ implies $\delta \preceq \delta'$. Set $\mathcal{H}_{\infty,0}$ with relation $[\delta \to \delta', \delta \neq \delta']$ has no cycles.

$P_{\delta,\delta'} > 0 \Leftrightarrow \delta \to \delta'$, so path $\delta_1 \to ... \to \delta_r$ probability > 0.

$P_{\delta,\delta'} > 0$ implies $\delta \preceq \delta'$, if (Y_n) leaves δ it does never return to it.

Loops and Hitting finest evolution partition

One has

$$P_{\delta,\delta} = \prod_{J \in \delta} \Big(\sum_{d \in \mathcal{D}: d|_J = \{J\}} \rho_d \Big).$$

So $\delta \to \delta'$, $\delta \neq \delta'$ implies $P_{\delta,\delta} < P_{\delta',\delta'}$.

$\varepsilon = \bigvee_{d \in \mathcal{D}} d$ common refinement of partitions in $\mathcal{D}$;
$\varepsilon \in \mathcal{H}_\infty$; $\forall \underline{d}^\varepsilon \in \mathcal{D}^\varepsilon$, $\varepsilon \vee \underline{d}^\varepsilon = \varepsilon$; ε finest partition in $\mathcal{H}_{\infty,0}$.
$P_{\delta,\delta} = 1$ only if $\delta = \varepsilon$, so ε absorbing state for chain (Y_n):
$P_{\varepsilon,\varepsilon} = 1$. For $\mu = \bigotimes_{L \in \varepsilon} \mu_L$, $\Xi(\mu) = \mu$.

For $\delta \in \mathcal{H}_{\infty,0}, \delta \neq \varepsilon$: $\mathbb{P}(\#\{n : Y_n = \delta\} < \infty) = 1$, $P_{\delta,\delta} \in (0, 1)$.

$\zeta = \inf\{n \geq 0 : Y_n = \varepsilon\}$: $Y_{\zeta+n} = \varepsilon$, $n \geq 0$; $\mathbb{P}(\zeta < \infty) = 1$.

Elements before absorption

If $\mathcal{D} = \{\delta^*\}$ then $\mathbb{P}(Y_n = \delta^*) = 1$. If $\mathcal{D} = \{\{I\}, \delta\}$, $\varepsilon = \delta$, $\mathbb{P}(\zeta > n, Y_n = \{I\}) = \mathbb{P}(\zeta > n) = \rho^n_{\{I\}}$.

Assume $\mathcal{D}$ contains at least two non-trivial different partitions.

$$\varepsilon^- = \{\delta \in \mathcal{H}_{\infty,0} : \delta \to \varepsilon, \delta \neq \varepsilon\}$$

set of points connected to ε different from ε and

$$\eta = \max\{P_{\delta,\delta} : \delta \in \mathcal{H}_{\infty,0}, \delta \neq \varepsilon\}, \;\; \mathcal{M} = \{\delta \in \mathcal{H}_\infty : P_{\delta,\delta} = \eta\}.$$

One has $\mathcal{H}_\infty \setminus \{\varepsilon\} \neq \emptyset$, $\mathcal{M} \neq \emptyset$, $\eta \in (0,1)$, $\varepsilon^- \neq \emptyset$.

Geometric decay and quasi-stationarity

Theorem

Let $\tau = \tau_\varepsilon$ *for* $\varepsilon = \bigvee_{\delta\in\mathcal{D}} \delta$*. Then* $\mathbb{P}(\tau < \infty) = 1$*.*

Let Let $\mathcal{H}_\infty^* = \mathcal{H}_\infty \setminus \{\varepsilon\}$*;* $\varepsilon^- = \{\delta \in \mathcal{H}_\infty : \delta \to \varepsilon, \delta \neq \varepsilon\}$*,* $\eta = \max\{P_{\delta,\delta} : \delta \in \mathcal{H}_\infty^*\}$*,* $\mathcal{M} = \{\delta \in \mathcal{H}_\infty^* : P_{\delta,\delta} = \eta\}$*. Then,* $\mathcal{M} \subseteq \varepsilon^-$ *and*

$$\begin{aligned}\lim_{n\to\infty} \eta^{-n}\mathbb{P}(\tau > n) &= \lim_{n\to\infty} \eta^{-n}\mathbb{P}(\tau > n, Y_n \in \mathcal{M}) \\ &= \mathbb{E}\left(\eta^{-\tau_\mathcal{M}}, \tau_\mathcal{M} < \infty\right) \in (0,\infty);\end{aligned}$$

$$\forall \delta \in \mathcal{M} : \lim_{n\to\infty} \mathbb{P}(Y_n = \delta \,|\, \tau > n) = \frac{\mathbb{E}\left(\eta^{-\tau_\delta}, \tau_\delta < \infty\right)}{\mathbb{E}\left(\eta^{-\tau_\mathcal{M}}, \tau_\mathcal{M} < \infty\right)},$$

and $\lim_{n\to\infty} \mathbb{P}(Y_n = \delta \,|\, \tau > n) = 0$ *when* $\delta \in \mathcal{H}_\infty^* \setminus \mathcal{M}$*.*

Proof. From hypothesis $\mathcal{H}_\infty \setminus \{\varepsilon\} \neq \emptyset$, then $\mathcal{M} \neq \emptyset$ and so $\eta \in (0,1)$. We claim

$$\forall \delta \in \mathcal{M} : \quad P_{\delta,\delta} + P_{\delta,\varepsilon} = 1.$$

In fact, let $\delta \in \mathcal{M}$ and $P_{\delta,\delta'} > 0$ for $\delta \neq \delta' \neq \varepsilon$. Then, $\eta = P_{\delta,\delta} < P_{\delta',\delta'}$ contradicting definition of η, so $P_{\delta,\delta'} = 0$ for $\delta' \notin \mathcal{M} \cup \{\varepsilon\}$. So,

$$\forall\, \delta \in \mathcal{M} \ : \quad \delta \to \delta' \Leftrightarrow \left[\, \delta' = \delta \text{ or } \delta' = \varepsilon \right].$$

Then $\mathcal{M} \subseteq \varepsilon^-$. The existence of paths from $\{I\}$ to $\mathcal{M}$ gives $\mathbb{P}(\zeta_{\mathcal{M}} < \infty) > 0$. One has

$$\forall \delta^* \in \mathcal{M},\, n \geq 0 : \ \ \mathbb{P}_{\delta^*}(Y_n = \delta^*) = \mathbb{P}_{\delta^*}(\forall j \leq n, Y_j = \delta^*) = \eta^n.$$

Let us show decay rate and quasi-limiting relations.

$$\mathbb{P}(\zeta > n) = \mathbb{P}(\zeta > n, Y_n \notin \mathcal{M}) + \mathbb{P}(\zeta > n, Y_n \in \mathcal{M}).$$

Since every $\delta \in \mathcal{H}_\infty$ attained from $\{I\}$, it exists $k_0 \geq 1$,

$$\forall\, \delta^* \in \mathcal{M} : \quad \mathbb{P}(\zeta_{\delta^*} \leq k_0) > 0.$$

Define $\alpha(\mathcal{M}) := \min\{\mathbb{P}(\zeta_{\delta^*} \leq k_0) : \delta^* \in \mathcal{M}\}$, so $\alpha(\mathcal{M}) > 0$.
From Markov property for all $\delta^* \in \mathcal{M}$,

$$\begin{aligned}
\mathbb{P}(\zeta > n) &\geq \sum_{j=1}^{k_0} \mathbb{P}(\zeta_{\delta^*} = j, \zeta > n) \\
&\geq \sum_{j=1}^{k_0} \mathbb{P}(\zeta_{\delta^*} = j)\mathbb{P}_{\delta^*}(\zeta > n - j) \\
&\geq \sum_{j=1}^{k_0} \mathbb{P}(\zeta_{\delta^*} = j)\eta^{n-j} \geq \alpha(\mathcal{M})\eta^n.
\end{aligned}$$

To analyze $\mathbb{P}(\zeta > n, Y_n \notin \mathcal{M})$ it is useful a result involving

$$\eta_1 = \max\{P_{\delta,\delta} : \delta \in \mathcal{H}_{\infty,0}, \delta \neq \varepsilon, \delta \notin \mathcal{M}\} < \eta.$$

Lemma

For $\eta_2 \in (\eta_1, \eta)$ it exists $C' = C'(\eta_2)$ such that for $n \geq 0$ one has

$$\mathbb{P}(\forall j \leq n : \ Y_j \notin \mathcal{M} \cup \{\varepsilon\}) \leq C' \, \eta_2^n.$$

This holds because the number of paths from $\{I\}$ to ε is finite. Hence,

$$\mathbb{P}(Y_n \notin \mathcal{M} \,|\, \zeta > n) \leq C'' \, (\eta_2/\eta)^n \to 0 \text{ as } n \to \infty,$$

with $C'' = C'/\alpha(\mathcal{M})$. Therefore,

$$\lim_{n\to\infty} \mathbb{P}(Y_n \in \mathcal{M} \,|\, \zeta > n) = 1.$$

Let us examine $\mathbb{P}(\zeta > n, Y_n \in \mathcal{M})$. For $\delta^* \in \mathcal{M}$ one has,

$$
\begin{aligned}
\mathbb{P}(\zeta > n, Y_n = \delta^*) &= \sum_{j=1}^{n} \mathbb{P}(\zeta > n, \zeta_{\delta^*} = j) \\
&= \sum_{j=1}^{n} \mathbb{P}(\zeta_{\delta^*} = j)\mathbb{P}_{\delta^*}(\zeta > n - j) = \sum_{j=1}^{n} \mathbb{P}(\zeta_{\delta^*} = j)\eta^{n-j} \\
&= \eta^n \left(\sum_{j=1}^{n} \eta^{-j}\mathbb{P}(\zeta_{\delta^*} = j) \right).
\end{aligned}
$$

Since $\eta_2 < \eta$ and

$$\mathbb{P}(\zeta_{\delta^*} = j) \leq \mathbb{P}(\zeta_{\mathcal{M}} = j) \leq \mathbb{P}(\forall n \leq j-1 : Y_n \notin \mathcal{M} \cup \{\varepsilon\}) \leq C' \eta_2^{j-1},$$

one gets $\sum_{j=1}^{\infty} \eta^{-j}\mathbb{P}(\zeta_{\delta^*} = j) < \infty$. Hence, for all $\delta^* \in \mathcal{M}$

$$
\begin{aligned}
\lim_{n\to\infty} \eta^{-n}\mathbb{P}(\zeta > n, Y_n = \delta^*) &= \sum_{j=1}^{\infty} \eta^{-j}\mathbb{P}(\zeta_{\delta^*} = j) \\
&= \mathbb{E}\left(\eta^{-\zeta_{\delta^*}}, \zeta_{\delta^*} < \infty\right) < \infty.
\end{aligned}
$$

For $\delta^* \in \mathcal{M}$ one has

$$\zeta_{\delta^*} < \infty \Rightarrow \left[\zeta_{\mathcal{M}} < \infty \text{ and } \forall \delta' \in \mathcal{M} \setminus \{\delta^*\}, \zeta_{\delta'} = \infty \right].$$

Then, for j finite,

$$\{\zeta_{\mathcal{M}} = j\} = \bigcup_{\delta^* \in \mathcal{M}} \{\zeta_{\delta^*} = j\}$$

and union is disjoint. So, $\eta^{-\zeta_{\mathcal{M}}} \mathbf{1}_{\zeta_{\mathcal{M}} < \infty} = \sum_{\delta^* \in \mathcal{M}} \eta^{-\zeta_{\delta^*}} \mathbf{1}_{\zeta_{\delta^*} < \infty}$.
Hence,

$$\mathbb{E}\left(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty\right) = \sum_{\delta^* \in \mathcal{M}} \mathbb{E}\left(\eta^{-\zeta_{\delta^*}}, \zeta_{\delta^*} < \infty\right) < \infty \text{ and}$$

$$\lim_{n \to \infty} \eta^{-n} \mathbb{P}(\zeta > n, Y_n \in \mathcal{M}) = \mathbb{E}\left(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty\right).$$

Therefore,

$$\begin{aligned}
&\sum_{\delta\in\mathcal{M}} \lim_{n\to\infty} \mathbb{P}(Y_n=\delta \,|\, \zeta>n) \\
= \;& \frac{1}{\mathbb{E}\left(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}}<\infty\right)} \sum_{\delta\in\mathcal{M}} \mathbb{E}\left(\eta^{-\zeta_\delta}, \zeta_\delta<\infty\right) = 1,
\end{aligned}$$

and so quasi-limiting distribution is obtained. Also,

$$\begin{aligned}
\lim_{n\to\infty} \eta^{-n}\mathbb{P}(\zeta>n) &= \lim_{n\to\infty} \eta^{-n}\mathbb{P}(\zeta>n, Y_n\in\mathcal{M}) \\
&= \mathbb{E}(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}}<\infty) \in (0,\infty).
\end{aligned}$$

This finishes proof of theorem. □

Ratio limit theorem

Recall $\mathcal{H}^*_\infty = \mathcal{H}_\infty \setminus \{\varepsilon\}$, $\mathbb{P} = \mathbb{P}_{\{I\}}$, $\mathbb{E} = \mathbb{E}_{\{I\}}$.

Proposition

The following ratio limit relation is satisfied,

$$\forall \delta \in \mathcal{H}^*_\infty : \quad \lim_{n\to\infty} \frac{\mathbb{P}_\delta(\zeta > n)}{\mathbb{P}(\zeta > n)} = \frac{\mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)}{\mathbb{E}(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)} .$$

Both ratios vanish only when $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) = 0$.

Let $P^* = (P_{\delta,\delta'} : \delta, \delta' \in \mathcal{H}^*_\infty)$. *The vector*

$$\varphi = (\varphi_\delta : \delta \in \mathcal{H}^*_\infty) \text{ given by } \varphi_\delta = \mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty),$$

right eigenvector of P^* *with eigenvalue* η *(with* $\varphi_{\{I\}} = 1$*).*

Proof. If $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) > 0$, as before one gets,

$$\lim_{n\to\infty} \eta^{-n}\mathbb{P}_\delta(\zeta > n) = \mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) \in (0,\infty),$$

If $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) = 0$ then $\mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) = 0$. So ratio limit.

If $\mathbb{P}_\delta(\zeta_{\mathcal{M}} = 0) = 1$, $\delta \in \mathcal{M}$, so $\varphi_\delta = \mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) = 1$,

$$(P^*\varphi)_\delta = \sum_{\delta':\delta'\neq\varepsilon,\delta\to\delta'} P_{\delta,\delta'}\mathbb{E}_{\delta'}(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) = P_{\delta,\delta} = \eta\,\varphi_\delta.$$

If $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) = 0$ so $\varphi_\delta = 0$. Then $P_{\delta,\delta'} > 0$ implies $\mathbb{P}_{\delta'}(\zeta_{\mathcal{M}} < \infty) = 0$ and so $(P^*\varphi)_\delta = 0 = \eta\,\varphi_\delta$.

Take $\delta \notin \mathcal{M}$ with $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) > 0$. Markov property gives,

$$\begin{aligned}\varphi_\delta &= \mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) = \sum_{\delta':\delta'\neq\varepsilon,\delta\to\delta'} \mathbb{E}_\delta(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty, Y_1 = \delta') \\ &= \sum_{\delta':\delta'\neq\varepsilon,\delta\to\delta'} P_{\delta,\delta'}\,\eta^{-1}\,\mathbb{E}_{\delta'}(\eta^{-\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty) = \eta^{-1}\,(P^*\varphi)_\delta. \square\end{aligned}$$

Q-process

Theorem

Let $\partial_{\mathcal{M}} = \{\delta \in \mathcal{H}_\infty^* : \mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) > 0\}$. *For* $\delta_i \in \mathcal{H}_\infty^*$, $i = 1,..,k$: $\lim_{n\to\infty} \mathbb{P}(Y_i = \delta_i, i = 1,..,j \,|\, \tau > n)$ *exists and vanishes if some* $\delta_i \notin \partial_{\mathcal{M}}$. *The matrix* $Q = \left(Q_{\delta,\delta'} : \delta, \delta' \in \partial_{\mathcal{M}}\right)$,

$$Q_{\delta,\delta'} = \eta^{-1}\, P_{\delta,\delta'} \frac{\mathbb{E}_{\delta'}(\eta^{\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)}{\mathbb{E}_{\delta}(\eta^{\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)} = \eta^{-1}\, P_{\delta,\delta'} \frac{\varphi_{\delta'}}{\varphi_\delta},$$

is stochastic and for all $\delta_i \in \partial_{\mathcal{M}}$, $i = 0,..,j$ *it is satisfied*

$$\lim_{n\to\infty} \mathbb{P}_{\delta_0}(Y_i = \delta_i, i = 1,..,j \,|\, \zeta > n) = \prod_{i=0}^{j-1} Q_{\delta_i,\delta_{i+1}}.$$

Q is transition matrix of Markov chain that never hits ε *and*

$$\forall \delta \in \mathcal{M} : \quad Q_{\delta,\delta} = 1 \text{ and } \forall \delta \in \partial_{\mathcal{M}} \setminus \mathcal{M} : \quad Q_{\delta,\delta} < 1.$$

Proof. One has $\varphi_\delta = 0$ if $\mathbb{P}_\delta(\zeta_{\mathcal{M}} < \infty) = 0$. Let $\delta \in \partial_{\mathcal{M}}$, so $\varphi_\delta > 0$. One has $P_{\delta,\delta'} = 0$ if $\delta \not\to \delta'$ and

$$\mathbb{P}_{\delta'}(\zeta_{\mathcal{M}} < \infty) = 0 \text{ implies } \frac{\varphi_{\delta'}}{\varphi_\delta} = \frac{\mathbb{E}_{\delta'}(\eta^{\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)}{\mathbb{E}_\delta(\eta^{\zeta_{\mathcal{M}}}, \zeta_{\mathcal{M}} < \infty)} = 0.$$

Since φ right eigenvector with eigenvalue η one gets

$$\sum_{\delta' \in \partial_{\mathcal{M}}} Q_{\delta,\delta'} = \eta^{-1} \left(\sum_{\delta' \in \partial_{\mathcal{M}}} P_{\delta,\delta'} \frac{\varphi_{\delta'}}{\varphi_\delta} \right) = \eta^{-1} \left(\frac{\eta \varphi_\delta}{\varphi_\delta} \right) = 1.$$

From Markov property, for $n > j$

$$\mathbb{P}(Y_i = \delta_i, i = 1, .., j \,|\, \zeta > n) = \mathbb{P}(Y_i = \delta_i, i = 1, .., j) \frac{\mathbb{P}_{\delta_j}(\zeta > n - j)}{\mathbb{P}(\zeta > n)}.$$

Now use ratio limit result. Limit vanishes if $\mathbb{P}_{\delta_j}(\zeta_{\mathcal{M}} < \infty) = 0$ and if $\mathbb{P}_{\delta_i}(\zeta_{\mathcal{M}} < \infty) = 0$ for some $i < j$ because $P_{\delta_i,\delta_{i+1}} > 0$ implies $\mathbb{P}_{\delta_{i+1}}(\zeta_{\mathcal{M}} < \infty) = 0$.

For $\delta_i \in \partial_{\mathcal{M}}$, $i = 0, .., j$, one has

$$
\begin{aligned}
&\lim_{n\to\infty} \mathbb{P}_{\delta_0}(Y_i = \delta_i, i = 1, .., j \,|\, \zeta > n) \\
&= \lim_{n\to\infty} \mathbb{P}_{\delta_0}(Y_i = \delta_i, i = 1, .., j) \frac{\mathbb{P}_{\delta_j}(\zeta > n - j)}{\mathbb{P}_{\delta_0}(\zeta > n)} \\
&= \mathbb{P}_{\delta_0}(Y_i = \delta_i, i = 1, .., j) \frac{\varphi_{\delta_j}}{\varphi_{\delta_0}} \eta^{-j} \\
&= \prod_{l=0}^{j-1} \left(\eta^{-1} P_{\delta_l,\delta_{l+1}} \frac{\varphi_{\delta_{l+1}}}{\varphi_{\delta_l}} \right).
\end{aligned}
$$

The diagonal terms of Q satisfy $Q_{\delta,\delta} = \eta^{-1} P_{\delta,\delta}$. Then $Q_{\delta,\delta} = 1$ for $\delta \in \mathcal{M}$ and $Q_{\delta,\delta} < 1$ when $\delta \in \partial_{\mathcal{M}} \setminus \mathcal{M}$. $\Box$.

Once the $Q-$chain hits a state in $\mathcal{M}$ it remains in it forever. So, partitions in $\mathcal{M}$ are candidates for points one observes if, after a long time has elapsed, the chain (Y_n) has not attained ε. Since $Q_{\delta,\delta'} > 0$ implies $P_{\delta,\delta'} > 0$, then

$$Q_{\delta,\delta'} > 0 \Rightarrow \delta \to \delta',$$
$$\left[\delta \to \delta', \delta \neq \delta'\right] \Rightarrow Q_{\delta,\delta} < Q_{\delta',\delta'}.$$

So, one can apply same techniques to the $Q-$chain with set of limit points $\mathcal{M}$. The geometric decay rate of the chain Q to $\mathcal{M}$ is

$$\eta' = \max\{Q_{\delta,\delta} : \delta \in \partial_{\mathcal{M}} \setminus \mathcal{M}\} = \eta^{-1} \max\{P_{\delta,\delta} : \delta \in \partial_{\mathcal{M}} \setminus \mathcal{M}\}.$$

Quasi-limiting behavior and ratio limit results stated similarly. One applies to chain Q that avoids $\mathcal{M}$ same construction as for P and $\{\varepsilon\}$, one requires $\partial_{\mathcal{M}} \setminus \mathcal{M}$ more than two points. This gives another $(Q-)$*chain* whose limit points is set of partitions δ in $\partial_{\mathcal{M}} \setminus \mathcal{M}$ maximizing $P_{\delta,\delta}$. This construction can be iterated.

Quasi-stationary distributions

Proposition

A probability measure ν on $\mathcal{H}_\infty^*$ supported on $\mathcal{M}$ satisfies $\nu' P^* = \eta\, \nu'$ and is a q.s.d.: $\mathbb{P}_\nu(Y_n = \delta \,|\, \tau > n) = \nu_\delta$ for $\delta \in \mathcal{H}_\infty^*$, $n \geq 1$. More generally if $\beta \in (0, \eta]$ satisfies

$$\mathcal{M}(\beta) = \{\delta \in \mathcal{H}_\infty^* : P_{\delta,\delta} + P_{\delta,\varepsilon} = 1,\ P_{\delta,\delta} = \beta\}.$$

So, probability measure ν supported on $\mathcal{M}(\beta)$ satisfies $\nu' P^* = \beta\, \nu'$, it is a q.s.d..

Proof. With above notation, $(\nu' P^*)_\delta = P_{\delta,\delta}\, \nu_\delta = \eta\, \nu_\delta$, so $\nu' P^* = \eta \nu'$. By iteration $\nu' P^{*n} = \eta^n\, \nu'$ which is equivalent to

$$(\nu' P^{*n})_\delta = \mathbb{P}_\nu(Y_n = \delta) = \mathbb{P}_\nu(\forall j \leq n\ Y_j = \delta) = \eta^n\, \nu'_\delta.$$

Then $\mathbb{P}_\nu(\zeta > n) = \sum_{\delta \in \mathcal{M}} (\nu' P^{*n})_\delta = \eta^n \left(\sum_{\delta \in \mathcal{M}} \nu_\delta\right) = \eta^n$. $\square$

Theorem Markov chains with no cycle

$\mathcal{K}$ finite set, $R = (R_{k,l} : k, l \in \mathcal{K})$ stochastic matrix. Graph of connections of R except by loops is $k \hookrightarrow l \Leftrightarrow \left[R_{k,l} > 0, k \neq l\right]$. If $(\mathcal{K}, \hookrightarrow)$ has no cycles and $k \hookrightarrow l$ implies $R_{k,k} < R_{l,l}$, (P on $\mathcal{H}_{\infty,0}$ satisfies them), then Theorem holds for Markov chain defined by R.
Fix $k_0 \in \mathcal{K}$ with $R_{k_0,k_0} \neq 1$. Since no cycles, for path $k_0 \hookrightarrow k_1 .. \hookrightarrow k_r$ all its points are different, so $r \leq |\mathcal{K}|$.
$U(k_0)$ set of maximal paths starting from k_0. If $k_0 \hookrightarrow k_1 .. \hookrightarrow k_r$ maximal then $R_{k_r,k_r} = 1$ so absorbing: $A(k_0)$ absorbing points attained from k_0, $\mathcal{K}(k_0)$ points attained from k_0 but not in $A(k_0)$.
As in Theorem, $\eta(k_0) = \max\{R_{k,k} : k \in \mathcal{K}(k_0)\}$ geometric decay rate of hitting time of $A(w_0)$ starting from k_0.
Quasi-limiting behavior and ratio limit formulated and proved similarly as in Theorem.

Migration-recombination equation

F. Alberti, E. Baake, I. Letter, S.M. Solving the migration-recombination equation from a genealogical point of view. To appear Journal of Mathematical Biology.

L set of locations, the population at location $\alpha \in L$ is $\mu(\alpha) \in \mathcal{P}_I$. The collection of local populations is $\mu = (\mu(\alpha) : \alpha \in L)$.

$M(\alpha, \beta)$: probability that a random individual currently living at α has migrated from β,

$$M\mu(\alpha) = \sum_{\beta \in L} M(\alpha, \beta)\mu(\beta).$$

So $\mu = M\mu$.

Recombination is the same mechanism in all locations given by $\Xi[\mu] = \sum_{\delta \in \mathcal{D}} \rho_\delta \bigotimes_{J \in \delta} \mu_J$.

The migration-recombination equation is

$$\begin{aligned}\mathcal{R}\mu(\alpha) &= \sum_{\delta\in\mathcal{D}} \rho_\delta \bigotimes_{J\in\delta} (M\mu)_J(\alpha) \\ &= \sum_{\delta\in\mathcal{D}} \rho_\delta \bigotimes_{J\in\delta} \sum_{\beta\in L} M(\alpha,\beta)\mu_J(\beta).\end{aligned}$$

Let $\delta \in \mathbb{D}$. A labelled partition with base δ is

$$\overline{\delta} = \{(J, \lambda_J^{\overline{\delta}}) : \lambda_J^{\overline{\delta}} \in L, J \in \delta\}$$

$\overline{\mathbb{D}}$ set of labelled partitions and $\overline{\mathcal{G}}$ labelled partitions with base in $\mathcal{D}$.

For $\overline{d} \in \overline{\mathcal{G}}$ define

$$\overline{\rho}_{\overline{d}}(\alpha) = \rho_d \prod_{J \in \delta} M(\alpha, \lambda_J^{\overline{\delta}})$$

One has

$$\sum_{\overline{d} \in \overline{\mathcal{G}}} \rho_{\overline{d}}(\alpha) = 1.$$

The recombination-migration evolution equation is:

$$\mathcal{R}\mu(\alpha) = \sum_{\overline{d} \in \overline{\mathcal{G}}} \overline{\rho}_{\overline{d}}(\alpha) \otimes_{J \in d} \mu_J(\lambda_J^{\overline{\delta}}).$$

This evolution is described by Markov chain $(\overline{Y}_t)$ on $\overline{\mathbb{D}}$.