Mutation-selection equilibrium : Kingman's house-of-cards model

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Abstract

This course deals with Kingman's house-of-cards model, introduced in 1978, and representing the dynamics of fitness distribution in a population with clonal reproduction. This dynamics is characterized by the recursive equation

$$p_{n+1}(dx) = \beta q(dx) + (1-\beta)\frac{xp_n(dx)}{\int xp_n(dx)},$$

where β and q are respectively the mutation probability and mutation law. Kingman ([9]) studies the convergence of this sequence of fitness distribution and gives conditions on the mutation law q under which a condensation phenomenon arises. Recent works by Yuan ([12, 13, 14]) and Coron & Hénard ([2], forthcoming) recently studied this deterministic discrete time model in a more general framework, including random mutation probabilities and periodic environment. These results will be presented as well as different mathematical approaches to handle the convergence of fitness distribution in this framework.

Keywords and phrases. Mutation-selection equilibrium; Kingman's House-of-cards model; quantitative genetics; fitness distribution dynamics; condensation phenomenon; deterministic dynamics of probability measures.

Contents

1 Model

The motivation of Kingman's house-of-cards model ([9]) is to study the balance between mutation and selection. This balance is a long-standing question of interest ([3]), motivated by the fact that selection tends to decrease genetic variability while mutations tend to increase this variability.

Selection is often quantified through the notion of fitness (see [3] or [5] for example). The fitness of an individual is a measure of its reproductive success. More precisely, in a non-overlapping generations model, fitness is assumed to be a number that is proportional to the mean number of child of this individual, at next generation. This number is typically a function of this individual's genotype and of the environment (possibly including other individuals), and the scaling of fitness can be such that the maximal fitness in a population is equal to 1.

In this course we will focus only on clonal reproduction, for which each individual has only one parent, and the genome of an individual can, in first approximation, be assumed to be a copy of the genome of its only parent, except for mutations. In particular, the fitness of an individual can be assumed to be equal to the fitness of its parent, in the absence of mutations.

In Kingman's house-of-cards model, mutation is assumed to be such that each new-born individual has probability $1-\beta$ to have same fitness as its parent, and probability β to have a new fitness, that has law q, where $\beta \in (0,1)$ and q is a probability measure on $[0,1]$ ($q \in \mathcal{M}([0,1])$). Note in particular that when a new-born individual is a mutant, its type is independent from the type of its parent. The article [8] suggests that this assumption which can seem quite surprising is in fact quite relevant, from a biological point of view.

These modeling assumptions lead to the following dynamics for the distribution of fitnesses. Let us denote by $p_n \in \mathcal{M}_1([0,1])$ the fitness distribution in the population at generation n. The sequence $(p_n)_{n\in\mathbb{Z}_+}$ is such that

$$p_{n+1}(dx) = \beta q(dx) + (1-\beta)\frac{x p_n(dx)}{\int x p_n(dx)}. \tag{1}$$

As mentionned previously, this model is suitable for populations with non-overlapping generations. Nevertheless, fitness distribution dynamics influenced both by selection and mutation can also be studied using more probabilistic models including birth-and-death processes for example, which will be presented in Section **??**.

This course is based on the seminal article [9], as well as the more recent articles [14], [4], and the lecture notes [11]. The review article [7] provides a thorough presentation of Kingman's recursion.

2 First properties of the model

Our main interest in this model will be the convergence of fitness distribution and a condensation phenomenon that will arise at a maximum fitness, under some conditions.

Let us denote

$$s_q = \sup\{x \in [0,1] | q([x,1]) > 0\}$$

and

$$s_{p_0} = \sup\{x \in [0,1] | p_0([x,1]) > 0\}$$

Note that without any loss of generality, one can assume that $s_{p_0} \geqslant s_q$. Indeed, if it is not the case, then $\sup\{x \in [0,1] | p_1([x,1]) > 0\} = s_q$ and one can consider the recursion (1) starting from p_1.

2.1 Simulations

Figure 1 shows that for some forms of mutation distribution q a condensation at fitness 1 (optimal fitness) occurs. One can also observe that for two mutation fitness distributions that seem quite close the model results in very different fitness distributions. This phenomenon will be our main object of interest.

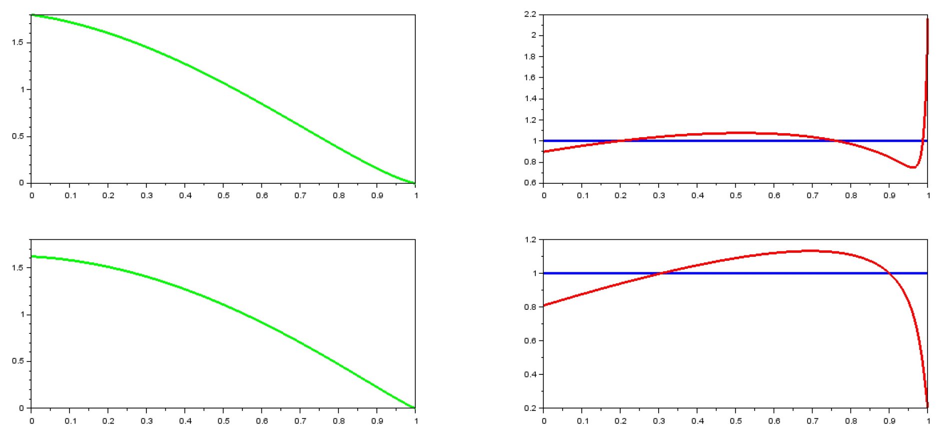

Figure 1: Each line corresponds to a different mutation law, represented in green. In both cases $q(dx) = C \times (1+x)(1-x)^{\alpha} dx$. Top: $\alpha = -1+\sqrt{5}-0.1$, bottom : $\alpha = -1+\sqrt{5}+0.1$. In blue is the initial fitness distribution (uniform distribution on $[0,1]$). In red is the fitness distribution after 100 iterations of Kingman's house-of-cards model. In both cases the mutation parameter β is equal to $1/2$.

On Figure 2 one can also see that in this previously observed configuration, the limiting fitness distribution does not seem to depend on the initial fitness distribution.

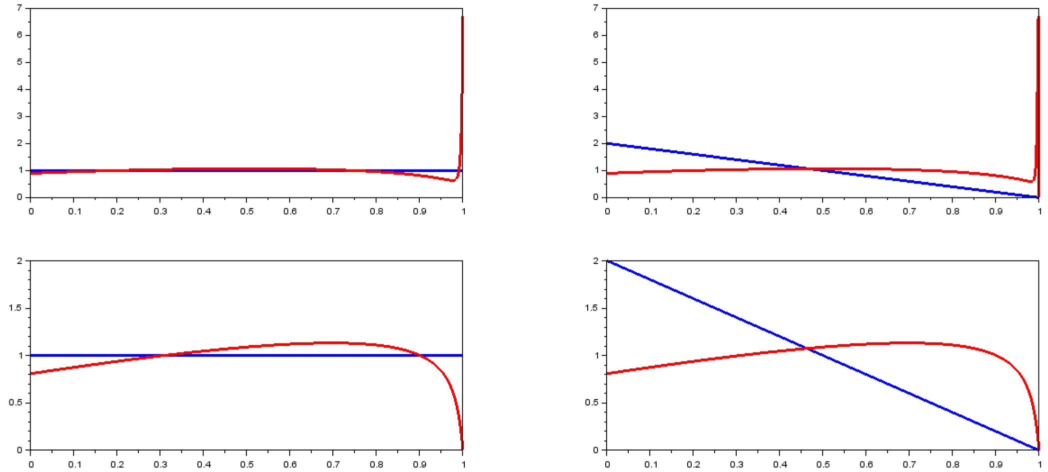

Figure 2: Initial fitness distribution and fitness distribution after a large number of time steps. Left Vs right : different fitness distributions. Up Vs down: different mutation fitness distributions.

Figure 3 shows on the contrary a situation in which p_0 has a great influence on the condensation phenomenon. We will show in the following sections that the maximum of the support of p_0 is the only element that will determine the presence or absence of condensation. We observe that in the represented case, condensation occurs only when this maximum is large enough.

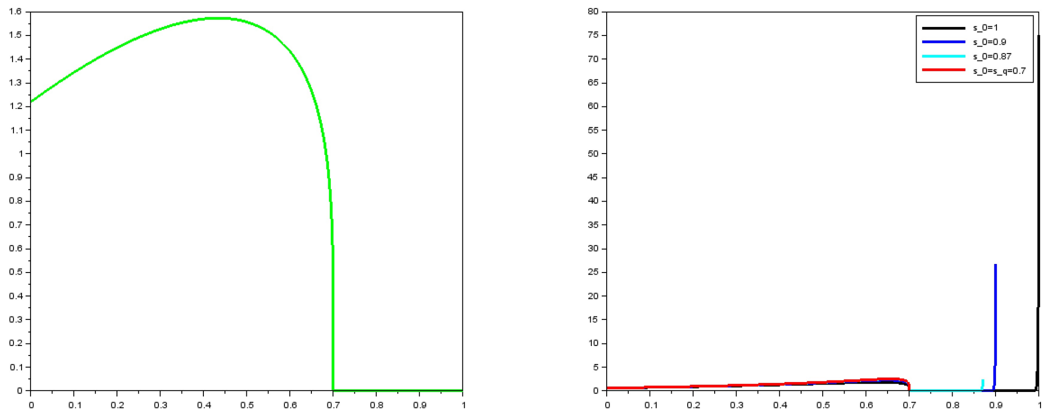

Figure 3: Left : mutation distribution q. Right: fitness distribution after 200 iterations of Kingman's House-of-cards model, starting from 4 different uniform initial fitness distributions.

2.2 Properties

This section provides several first properties of the model that give insights on its dynamics and asymptotics.

Decomposition of fitness distributions We start with a decomposition of the fitness distribution at each generation, in two parts : one that includes the initial fitness distribution p_0, and one that includes the mutation law q. A key quantity in this model will be the sequence of mean fitnesses. We denote for all $n \geqslant 0$

$$w_n = \int x p_n(dx).$$

Proposition 1 (Decomposition of fitness distributions)**.** *For each $n \in \mathbb{N}$, the fitness distribution p_n can be decomposed between mutations and initial fitness distribution :*

$$\begin{aligned} p_n(dx) &= \left(1 + \frac{(1-\beta)x}{w_{n-1}} + \frac{(1-\beta)^2 x^2}{w_{n-1}w_{n-2}} + ... + \frac{(1-\beta)^{n-1}x^{n-1}}{w_{n-1}w_{n-2}...w_1}\right)\beta q(dx) \\ &\quad + \frac{(1-\beta)^n}{w_{n-1}\dots w_0} x^n p_0(dx) \\ &= \sum_{k=0}^{n-1} \frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} x^k \beta q(dx) + \frac{(1-\beta)^n}{w_{n-1}\dots w_0} x^n p_0(dx) \qquad (2) \\ &= a_n(dx) + b_n(dx) \qquad (3) \end{aligned}$$

where a_n and b_n are two subprobability measures on $[0, 1]$.

Proof. By induction (exercise). □

This decomposition can be useful to analyze the asymptotic contributions of p_0 and q in the fitness distribution and therefore to study the balance between selection and mutation. Note however that the mean fitnesses w_k depend both on the initial condition p_0 and on the mutation law q, therefore both parts in this decomposition depend on p_0 and q. Another interpretation of this decomposition is that the term we decompose the fitness distribution p_n according to the biased fitness distributions $\frac{x^k q(dx)}{\int x^k q(dx)}$ and $\frac{x^n p_0(dx)}{\int x^n p_0(dx)}$. The coefficients before each of these distributions will then give the probability that the last mutation in the genealogy of a sampled individual of the population at time n occurred k time steps earlier.

Preservation of the order The second result is a preservation of a particular order between probability measures, through Kingman's recursion. This result can be stated using [14]. Let us define the following order between probability measures. For two probability measures p and q on $[0, 1]$, let us denote

$$p \leqslant_{1-} q \quad \text{ if } p(A) \leqslant q(A) \text{ for any Borel set } A \subset [0, 1).$$

Proposition 2 (Preservation of the order)**.** *Let p_0 and p'_0 be two probability measures on $[0,1]$ and let*

$$p_1(dx) = \beta q(dx) + (1-\beta)\frac{x p_0(dx)}{\int x p_0(dx)} \quad \text{and} \quad p'_1(dx) = \beta q(dx) + (1-\beta)\frac{x p'_0(dx)}{\int x p'_0(dx)}$$

be their respective images after one step of Kingman's recursion, using the same mutation probability β and same mutation law q. Then $p_0 \geqslant_{1-} p'_0$ implies $p_1 \geqslant_{1-} p'_1$.

Proof. First note that if $p_0 \geqslant_{1-} p'_0$ then $\int_{[0,1]} x p_0(dx) \leqslant \int_{[0,1]} x p'_0(dx)$. Indeed $\int_{[0,1]}(1-x)p_0(dx) \geqslant \int_{[0,1]}(1-x)p'_0(dx)$ since $1-x=0$ when $x=1$ and $p_0(dx) \geqslant p'_0(dx)$ elsewhere (the more general standard measure-theoretic argument is that, for any measurable $h : [0,1] \to \mathbb{R}^+$ satisfying $h(1)=0$, $\int_{[0,1]} h(x)p_0(dx) \geqslant \int_{[0,1]} h(x)p'_0(dx)$). Now

$$p_1(A) - p'_1(A) = (1-\beta)\left(\frac{\int_A x p_0(dx)}{\int_{[0,1]} x p_0(dx)} - \frac{\int_A x p'_0(dx)}{\int_{[0,1]} x p'_0(dx)}\right) \geqslant 0$$

since $\int_{[0,1]} x p_0(dx) \leqslant \int_{[0,1]} x p'_0(dx)$ and $\int_A x p_0(dx) \geqslant \int_A x p'_0(dx)$ □

Note that $p_0 \geqslant_{1-} p'_0$ implies that p_0 is stochastically bounded by p'_0, i.e. $p_0([0;x]) \geqslant p'_0([0;x])$ for any $x \in [0;1]$. This order is in fact much stronger.

A corollary of this Proposition 2 is the following

Corollary 1. *When $p_0 = \delta_1$ then the sequence of mean fitnesses $(w_n)_{n\in\mathbb{N}}$ is decreasing.*

Proof. $p_0 = \delta_1$. Therefore $p_1(dx) = \beta q(dx) + (1-\beta)\frac{x p_0(dx)}{1} \geqslant_{1-} p_0(dx)$. Therefore for all n $p_{n+1} \geqslant_{1-} p_n$, therefore for all n $w_{n+1} \leqslant w_n$. □

This result as well as the specific measure order introduced earlier is illustrated in Figure 4. One can indeed see that for each $n \geqslant 0$, $p_n \leqslant_{1-} p_{n+1}$, and the sequence of mean fitnesses $(w_n)_{n\geqslant 0}$ is decreasing.

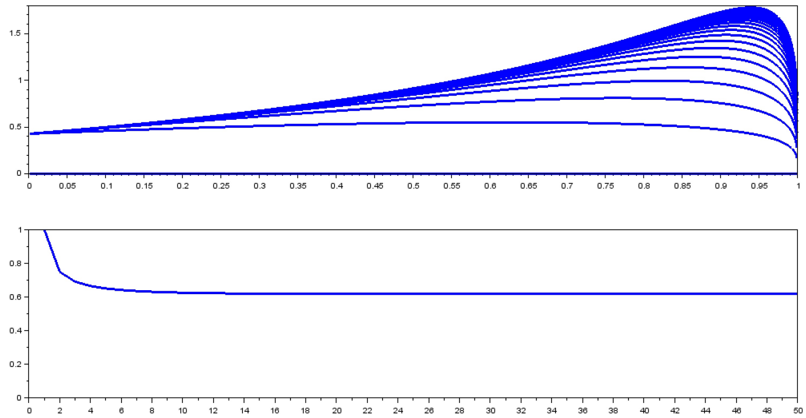

Figure 4: Starting with $p_0 = \delta_1$. Top : fitness distribution at different times. Bottom : Mean fitness as a function of time. Here we took $q(dx) = C \times (1+x)(1-x)^{\alpha} dx$ and $\alpha = -1 + \sqrt{5} - 1$.

The following result concerns the fitness distribution dynamics when the initial fitness distribution is δ_0. Note that in this case $w_0 = 0$, which is a problem to start Kingman's House-of-cards recursion (1). However we can set in this case $p_1(dx) = \beta q(dx) + (1-\beta)\delta_0$ which will start the recursion properly.

Proposition 3 (Behaviour when $p_0 = \delta_0$)**.** *If $p_0 = \delta_0$ then the sequence of mean fitnesses $w_n = \int_0^1 x p_n(dx)$ is increasing.*

Proof. By (strong) induction. Let us denote by $w_n^{(\delta_0)}$ the mean fitness at generation n when starting with fitness distribution δ_0. Now let us define the k-biased mutation distribution

$$q^{(k)}(dx) = \frac{x^k q(dx)}{\int x^k q(dx)}.$$

From Equations (1) and (4) we can write recursively that if $p_0 = \delta_0$ then for all $n \geqslant 1$,

$$p_n(dx) = \beta q(dx) + (1-\beta) \sum_{i=1}^{n-1} a_{i,n} q^{(i)}(dx) \tag{4}$$

where $\sum_{i=1}^{n-1} a_{i,n} = 1$ for all $n \geqslant 1$, and $a_{i,n+1} = (w_1/w_n) a_{i,n}$ for all $i \in \{1, ...n-1\}$. Note that $w_1 = \beta \int x q(dx) > 0 = w_0$ which initiates the recursion. Now let us assume that for all $1 \leqslant k \leqslant n-1$, $w_k > w_{k-1}$ (strong recursion assumption). Then $a_{i,n+1} < a_{i,n}$ for all $i \in \{1, ..., n-1\}$. The fact that $\int x q^{(i)}(dx) < \int x q^{(i+1)}(dx)$ for all $i \geqslant 1$ (Exercise) then gives that $w_n > w_{n-1}$ which is the needed recursion property. $\square$

The interpretation of this proof is that when $p_0 = \delta_0$, the fitness distribution p_n is a combination of the biased fitness distributions $q^{(k)}(dx)$ with $0 \leqslant k \leqslant n-1$, and as n increases, the mass in each biased distribution $q^{(k)}$ decreases, and the missing mass is reported to the fitness distribution $q^{(n)}(dx)$ that has higher mean fitness. Note that this decomposition also gives information on the time of the last mutation for an individual randomly sampled in the population at time n : β is the probability that the individual is a mutant, and next $(1-\beta)a_{i,n}$ is the probability that the last mutant in this individual's genealogy can be found i time steps before.

3 Fitness distribution convergence

We will see that some behaviours differ depending on whether $s_q = 1$ and $s_q < 1$. We start by studying the particular case where $s_q = 1$.

3.1 When $s_q = 1$

3.1.1 Invariant measures and intuitions

Let us recall Kingman's house-of-cards recursion :

$$p_{n+1}(dx) = \beta q(dx) + (1-\beta)\frac{xp_n(dx)}{\int xp_n(dx)}$$

and assume that this recursion admits an invariant measure $\pi \in \mathcal{M}_1([0,1])$. Then

$$\pi(dx) = \beta q(dx) + (1-\beta)\frac{x\pi(dx)}{\int x\pi(dx)}.$$

Therefore

$$\pi(dx)\left(1 - \frac{(1-\beta)x}{\int x\pi(dx)}\right) = \beta q(dx) \qquad \text{for all } x \in [0,1]. \tag{5}$$

Remark 1. The condition $s_q = 1$ implies that

$$w := \int x\pi(dx) \geqslant 1-\beta.$$

Indeed otherwise Equation (5) cannot be satisfied on the set $\{x \in (\frac{\int x\pi(dx)}{1-\beta}, 1], q(dx) > 0\}$ which is non empty if $s_q = 1$. (Indeed on this set the left-hand side of (5) is non positive while the right-hand side is positive).

Here two cases can be distinguished : either $w = 1-\beta$ or $w > 1-\beta$.
• If $w = \int x\pi(dx) > 1-\beta$ then

$$\pi(dx) = \frac{\beta q(dx)}{\left(1 - \frac{(1-\beta)x}{\int x\pi(dx)}\right)}$$

for all $x \in [0,1]$, which gives also that $\int x\pi(dx)$ is necessarily the only solution z to the equation

$$\int_0^1 \frac{\beta q(dx)}{\left(1 - \frac{(1-\beta)x}{z}\right)} = 1. \tag{6}$$

Note that the function $z \mapsto \int_0^1 \frac{\beta q(dx)}{\left(1-\frac{(1-\beta)x}{z}\right)}$ is strictly decreasing, which ensures that Equation (6) admits at most one solution.

• If $w = 1 - \beta$ then

$$\pi(dx) = \frac{\beta q(dx)}{1-x} \qquad \text{for all } x \in [0,1)$$

and therefore $\pi(\{1\}) = 1 - \int \frac{\beta q(dx)}{1-x}$ that must belong to $[0,1]$ for π to be a probability measure.

3.1.2 Convergence

Theorem 1 (Kingman, 1978). *Let $\beta \in (0,1)$, $q, p_0 \in \mathcal{M}_1([0,1])$, and define the sequence of fitness distributions using Kingman's house-of-cards recursion, for all $n \in \mathbb{Z}_+$:*

$$p_{n+1}(dx) = \beta q(dx) + (1-\beta)\frac{x p_n(dx)}{\int x p_n(dx)}.$$

(i) If $\int \frac{\beta}{1-x} q(dx) \geqslant 1$, then there exists a unique $z_1 \in [0,1]$ such that $\int \frac{\beta}{1-z_1 x} q(dx) = 1$ and $p_n(dx)$ converges in total variation to

$$\pi(dx) := \frac{\beta}{1 - z_1 x}\, q(dx), \tag{7}$$

and w_n converges to $\frac{1-\beta}{z_1}$.

(ii) If $\int \frac{\beta}{1-x} q(dx) < 1$, $p_n(dx)$ converges to

$$\pi(dx) := \frac{\beta}{1-x}\, q(dx) + \left(1 - \int \frac{\beta}{1-x} q(dx)\right)\delta_1, \tag{8}$$

and w_n to $1 - \beta$.

Interpreting this theorem is particularly natural when the mutation fitness distribution q has no atom in 1 (i.e. when $q(1) = 0$). Indeed in that case, an atom is present in the limiting fitness distribution (in particular it will be created if $p(1) = 0$, we can say that a condensation phenomenon occurs) if and only if $\int \frac{\beta}{1-x} q(dx) < 1$. In particular, again

when $q(\{1\}) = 0$, the limiting fitness distribution is absolutely continuous with respect to the mutation fitness distribution if and only if $\int \frac{\beta}{1-x} q(dx) \geqslant 1$.
Note also that the criterion $\int \frac{\beta q(dx)}{1-x} < 1$ can be interpreted by the fact that for condensation to occur we need that the mutant fitnesses are not too close to the optimum fitness 1. This can be explained by the fact that when the fitness of mutant can be too close to 1 then the mutant can create a competition that unfavors the optimal trait.
As mentioned previously this condensation phenomenon is quite universal and can also be found in different models, and some works have been done by [11, 1, 6].
The proof of Theorem 1 is given in [9] and also as a particular case of [14]. We give a proof close to that presented in [14]. Some elements of the proof given in [9] will be given in Subsection 3.3.
Proof of Theorem 1 following a direct approach inspired by [14] can be divided into two steps. First we prove that the sequence of mean fitnesses w_n converges towards a value that does not depend on the initial fitness distribution (Proposition 4), and then we prove that the convergence of mean fitnesses implies the convergence of fitnesses distributions (Proposition 5), towards a limit that is identified (Section 3.1.1). We now prove the convergence of the sequence of mean fitnesses.

Proposition 4. *The sequence $(w_n)_{n\in\mathbb{N}}$ converges to a value w_∞ that does not depend on the initial condition p_0.*

Proof ([14]). This proof relies on a direct analysis of Kingman's recursion (1).

• We already know that the sequence of mean fitnesses converges when $p_0 = \delta_1$ from Corollary 1. Let us denote by $w_\infty^{(\delta_1)} = \lim_{n\to\infty} w_n^{(\delta_1)}$ this limit. We must now prove that the sequence $(w_n)_{n\in\mathbb{N}}$ converges to $w_n^{(\delta_1)}$. Note that the sequence $\frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)}\dots w_0^{(\delta_1)}}$ is decreasing, therefore it converges. We distinguish two cases : either $\lim \frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)}\dots w_0^{(\delta_1)}} = 0$ or $\lim \frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)}\dots w_0^{(\delta_1)}} > 0$.

• Case (1): Let us assume that $\lim \frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)}\dots w_0^{(\delta_1)}} = 0$. Let us now recall the decomposition given in Proposition 1:

$$\begin{aligned} p_n(dx) &= \sum_{k=0}^{n-1} \frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} x^k \beta q(dx) + \frac{(1-\beta)^n}{w_{n-1}\dots w_0} x^n p_0(dx) \\ &= a_n(dx) + b_n(dx). \end{aligned}$$

From Proposition 2 we know that $w_n < w_n^{(\delta_1)}$ for all n, therefore $a_n \geqslant_{1^-} a_n^{(\delta_1)}$ for all n. Therefore $\int a_n \geqslant \int a_n^{(\delta_1)}$ for all n. Therefore $\int b_n \leqslant \int b_n^{(\delta_1)}$ for all n since $a_n + b_n$ and $a_n^{(\delta_1)} + b_n^{(\delta_1)}$ are probability measures. Finally since $w^{(\delta_1)} > 1-\beta$, $\int b_n^{(\delta_1)} \to 0$ when

n goes to infinity. Therefore $\int a_n \to 1 = \lim \int a_n^{(\delta_1)}$ and since $a_n \geqslant_{1^-} a_n^{(\delta_1)}$ one has $\int x a_n \to \lim \int x a_n^{(\delta_1)}$ and therefore $w_n \to w_\infty^{(\delta_1)}$.

• Case (2): Let us now assume that $\lim \frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)} \dots w_0^{(\delta_1)}} > 0$ (therefore $\lim w_n^{(\delta)} = 1-\beta$. Our aim is to prove that in this case w_n converges to $1-\beta$, whatever p_0. We already know from Proposition 2 that $w_n < w_n^{(\delta_1)}$ for all n. The intuition behind this convergence result is then that the fitness cannot stay too much lower than $1-\beta$ due to the recursion equation (2) describing probability measures. We first prove the result when $p_0(\{1\}) > 0$. In that case,

$$p_n(\{1\}) \geqslant \frac{(1-\beta)^n}{w_{n-1}^{(\delta_1)} \dots w_0^{(\delta_1)}} \left(\frac{1}{1-\gamma} \right)^{K_n} p_0(\{1\}).$$

where $K_n = Card(\{k \leqslant n-1 : w_k \leqslant (1-\gamma) w_k^{(\delta_1)}\}$. Since $\lim \frac{(1-\beta)^n}{w_{n-1} \dots w_0} > 0$, K_n is bounded. Therefore $w_n \to 1-\beta$.

• Case (3): Let us finally consider the case where $w_\infty^{(\delta_1)} = 1-\beta$ and $p_0(\{1\}) = 0$. For any probability measure μ on $[0,1]$, and any number $x \in [0,1]$, let us denote by $R_x(\mu)$ the probability measure defined by

$$R_x(\mu) = \mu|_{[0,x)} + \mu([x,1])\delta_x.$$

Let us define the solution p' of Kingman's house-of-cards recursion, starting from $R_{1-\epsilon}(p_0)$ and using the mutation measure $R_{1-\epsilon}(q)$. One has

$$p_n \leqslant_{1-\epsilon^-} p'_n, \qquad \text{for all } n \in \mathbb{N}$$

i.e.

$$p_n(A) \leqslant_{1-\epsilon^-} p'_n(A) \qquad \text{for all } A \subset [0, 1-\epsilon), \text{ for all } n \in \mathbb{N},$$

as illustrated in Figure 5. Therefore since $p'((1-\epsilon, 1]) = 0$, $w_n \geqslant w'_n = \int_0^1 x p'_n(dx)$ for all n.

Since $R_{1-\epsilon}(p_0)$ has an atom at the maximum of its support, the sequence $(p'_n)_{n \in \mathbb{N}}$ falls in one of the previous cases, (1) or (2). Therefore the sequence of means w'_n converges to $w' \geqslant (1-\beta)(1-\epsilon)$. Therefore

$$(1-\beta)(1-\epsilon) \leqslant \liminf w_n \leqslant \limsup w_n \leqslant 1-\beta$$

for all $\epsilon > 0$ which gives the result.

□

Finally, the proof of Theorem 1 relies on the following essential Proposition, that states that when the sequence of mean fitnesses $(w_n)_{n \in \mathbb{N}}$ converges then the sequence of fitness distribution also converges in total variation.

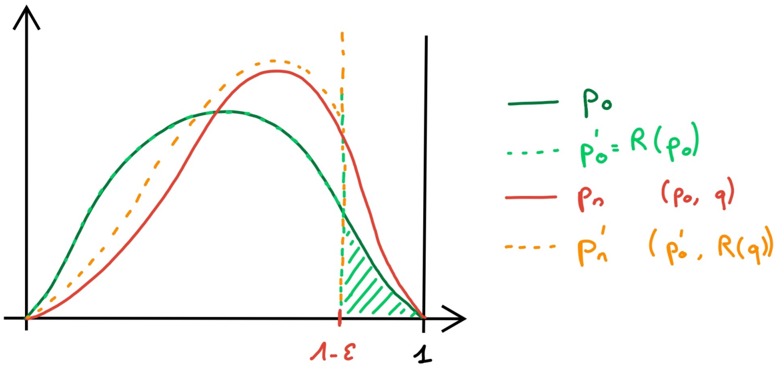

Figure 5: How the rabot works

Proposition 5 (Convergence of fitness distributions from convergence of their means)**.** *Let $(p_n)_{n\geqslant 0}$ be a sequence of probability measures satisfying Kingman's recursion with mutation probability β and mutation law q, and let $w_n = \int xp_n(dx)$ for each $n \geqslant 0$. If the sequence $(w_n)_{n\geqslant 0}$ converges towards w then the sequence $(p_n)_{n\geqslant 0}$ converges in total variation on every interval $[0,\xi]$ with $\xi < 1$ towards*

$$\pi(dx) = \frac{1}{1-\frac{(1-\beta)x}{w}}\beta q(dx) + c\delta_1$$

where $c = 1 - \int_0^1 \frac{1}{1-\frac{(1-\beta)x}{w}}\beta q(dx) \in [0,1]$.

Proof. Let $\xi < 1$. We want to compare:

$$p_n(dx) = \sum_{k=0}^{n-1} \frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} x^k \beta q(dx) + \frac{(1-\beta)^n}{w_{n-1}\dots w_0} x^n p_0(dx) \qquad =: \sum q_{n,k}(dx) + p_{0,n}(dx)$$
$$\pi(dx) := \sum_{k\geqslant 0} (\frac{1-\beta}{w})^k x^k \beta q(dx) \qquad =: \sum_{k\geqslant 0} q_{\infty,k}(dx)$$

Precisely, we prove convergence in total variation of $p_n(dx)$ towards $\pi(dx)$ on $[0,\xi]$.
First,

$$\|q_{n,k}(dx) - q_{\infty,k}(dx)\|_{TV,[0,\xi]} = \left|\frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} - \left(\frac{1-\beta}{w}\right)^k\right| \int_0^\xi x^k \beta q(dx) = \left|\frac{w^k}{w_{n-1}\dots w_{n-k}} - 1\right| q_{\infty,k}([0,\xi])$$

More generally,

$$\sum_{k=0}^{k_0-1} \|q_{n,k}(dx) - q_{\infty,k}(dx)\|_{TV,[0,\xi]} \leqslant \sum_{k=0}^{k_0-1} q_{\infty,k}([0,\xi]) \left|\frac{w^k}{w_{n-1}\dots w_{n-k}} - 1\right| \leqslant \max_{0\leqslant k\leqslant k_0} \left|\frac{w^k}{w_{n-1}\dots w_{n-k}} - 1\right| \tag{9}$$

since $\sum_{k=0}^{\infty} q_{\infty,k}([0,\xi]) \leqslant 1$, and k_0 being fixed, the last term goes to 0 as $n \to \infty$, using ou assumption that $w_n \to w$. Second,

$$\| \sum_{k \geqslant k_0} q_{\infty,k}(dx) \|_{TV,[0,\xi]} = \int_0^{\xi} \sum_{k \geqslant k_0} \left(\frac{1-\beta}{w} \right)^k x^k \beta q(dx) \leqslant C \left(\frac{(1-\beta)\xi}{w} \right)^{k_0} \tag{10}$$

for a constant $C = \int_0^{\xi} \frac{1}{1-\frac{1-\beta}{w}x} \beta q(dx) \leqslant \frac{\beta}{1-\frac{(1-\beta)\xi}{w}}$ finite, independent of n and k_0, while $\frac{(1-\beta)\xi}{w} < \frac{(1-\beta)}{w} \leqslant 1$. Third, it is possible to choose $\delta > 0$ small enough such that $\frac{(1-\beta)\xi}{(1-\delta)w} < 1$, and then choose n_0 large enough such that for $n \geqslant n_0$, $w_n \geqslant (1-\delta)w$ for $n \geqslant n_0$. Now, we split according to n_0 :

$$\left\| \sum_{k=k_0}^{n-1} q_{n,k}(dx) \right\|_{TV,[0,\xi]} = \int_0^{\xi} \sum_{k=k_0}^{n-n_0} q_{n,k}(dx) + \int_0^{\xi} \sum_{k=n-n_0+1}^{n-1} q_{n,k}(dx)$$

and the first term may be dealt with as before:

$$\int_0^{\xi} \sum_{k=k_0}^{n-n_0} \frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} x^k \beta q(dx) \leqslant \int_0^{\xi} \sum_{k=k_0}^{n-n_0} \left(\frac{1-\beta}{(1-\delta)w} \right)^k x^k \beta q(dx) \leqslant C' \left(\frac{(1-\beta)\xi}{(1-\delta)w} \right)^{k_0} \tag{11}$$

for $C' = \frac{\beta}{1-\frac{(1-\beta)\xi}{(1-\delta)w}}$ this time. For the second term, since $(w_n)_n$ is a convergent and positive sequence, there exists $\alpha > 0$ we have $w_n > \alpha w$ for every n, we use this to bound the quantities $w_0, \dots, w_{n_0}$

$$\int_0^{\xi} \sum_{k=n-n_0+1}^{n-1} \frac{(1-\beta)^k}{w_{n-1}\dots w_{n-k}} x^k \beta q(dx) \leqslant C'' \left(\frac{(1-\beta)\xi}{(1-\delta)w} \right)^{n-n_0} \tag{12}$$

choosing for instance $C'' = \sum_{k=1}^{n_0-1} \alpha^{-k}$. Fourth, the term implying p_0 is dealt with as the second term above (bounding separately the w_n, for $n \geqslant n_0$ and for $n < n_0$), this gives:

$$\left\| \frac{(1-\beta)^n}{w_{n-1}\dots w_0} x^n p_0(dx) \right\|_{TV,[0,\xi]} \leqslant \alpha^{-n_0} \left(\frac{(1-\beta)\xi}{(1-\delta)w} \right)^{n-n_0} \tag{13}$$

Now, we choose the parameters as follows : we choose k_0 large enough such that (10) and (11) are small (ie, $\leqslant \varepsilon$) and then n large enough so as to make (9), (12) and (13) small. $\square$

The proof of Theorem 1 is then complete by combining Proposition 4, Proposition 5, and the study of invariant measures of Secion 3.1.1.

Remark 2. Note that the convergence in total variation is not possible in general on $[0,1]$ due to the emergence of an atom, but in the case where $c = 0$, the convergence in total variation is also true on $[0,1]$.

Remark 3. Combining Propositions 3 and 5 gives the convergence of the sequence of fitness distributions starting from δ_0. However note that this result is not useful to prove the convergence of fitness distributions starting from another initial fitness distribution. What is more, as it will be shown in Section 4, this property is not very robust to some changes.

Remark 4. Recalling the decomposition (2), in the case where condensation occurs, the weight of the atom $1 - \int \frac{\beta}{1-x} q(dx)$ can be present only in the limiting term of a_n (if $q(1) > 0$ notably), or in both terms.

Remark 5. Figure 1 shows the fitness distribution evolution for a mutation probability equal to β, and two different mutation laws, of the form $q(dx) = C \times (1+x)(1-x)^\alpha$. For this class of mutation laws, and for $\beta = 1/2$, one can check that the condensation criteria states that condensation occurs (i.e. an atom is present in the limiting fitness distribution) if and only if $\alpha > -1 + \sqrt{5}$, which is coherent with what is presented in the two parts of Figure 1. Indeed, if $q(dx) = C \times (1+x)(1-x)^\alpha$ then

$$\beta \int \frac{1}{1-x} q(dx) = \beta \frac{\int (1+x)(1-x)^{\alpha-1} dx}{\int (1+x)(1-x)^\alpha dx},$$

and

$$\begin{aligned}
\int (1+x)(1-x)^{\alpha-1} dx &= \int (2 - (1-x))(1-x)^\alpha dx \\
&= 2\left[-\frac{-(1-x)^{\alpha+1}}{\alpha+1} \right]_0^1 - \left[-\frac{-(1-x)^{\alpha+2}}{\alpha+2} \right]_0^1 \\
&= \frac{2}{\alpha+1} - \frac{1}{\alpha+2} \\
&= \frac{\alpha+3}{(\alpha+1)(\alpha+2)}.
\end{aligned}$$

Therefore if $\beta = 1/2$, $\int \frac{\beta q(dx)}{1-x} = 1$ if and only if $\frac{(\alpha+2)^2}{\alpha(\alpha+3)} = 2$, which gives that $\alpha^2 + 2\alpha - 4 = 0$ therefore $\alpha = -1 + \sqrt{5}$.

Remark 6. Note that if we come back to the decomposition

$$p_n(dx) = \sum_{k=0}^{n-1} \frac{(1-\beta)^k}{w_{n-1} \dots w_{n-k}} x^k \beta q(dx) + \frac{(1-\beta)^n}{w_{n-1} \dots w_0} x^n p_0(dx)$$

then we now know that for each $k \geqslant 0$, the term $\int \frac{(1-\beta)^k}{w_{n-1} \dots w_{n-k}} x^k \beta q(dx)$ converges to the quantity $\beta \left(\frac{(1-\beta)}{w} \right)^k \int x^k \beta q(dx)$ that can be seen that the age of the last mutation is equal to k. Therefore condensation occurs if and only the sum of these probabilities does not converges to 1 which means that $\mathbb{P}(T = \infty) > 0$ where T is the age of the last mutation in the history of an individual.

3.2 When $s_q < 1$

3.2.1 Intuitions grabbed from invariant measures

Proposition 6. *Set*

$$x_0 = \inf \left\{ x' \in [s_q, \infty) : \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x'}} \leqslant 1 \right\}, \tag{14}$$

Then,

(i) If $x_0 \leqslant 1$, the set of invariant probability measures is

$$\left(\frac{\beta q(dx)}{1 - \frac{x}{x_1}} + \pi_1 \delta_{x_1} \right)_{x_1 \in [x_0, 1]},$$

with $\pi_1 = 1 - \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x_1}}$.

(ii) If $x_0 > 1$, the measure $\frac{\beta q(dx)}{1 - \frac{x}{x_0}}$ is the unique invariant probability measure.

Remark 7. The set of possible positions for the atom is therefore $\{s_0\} \cup [x_0, 1]$, which means that there is a gap $[s_0, x_0]$ on which no atom is possible.

Remark 8. If $x_1 = x_0$ then $\int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x_1}} = \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x_0}} = 1$ by definition of x_0, since the function $x' \mapsto \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x'}}$ is decreasing and continuous. Therefore the minimum probability of the atom is 0.

Lemma 1. *Let π be an invariant measure and let $w = \int x\pi(dx)$. Then $w \geqslant (1 - \beta)s_q$.*

Proof. Recall that

$$\pi(dx) \left(1 - \frac{(1 - \beta)x}{w} \right) = \beta q(dx).$$

Assume by contradiction that $\frac{w}{1-\beta} \leqslant s_q - \epsilon$. Therefore for $x \in [s_q - \epsilon, s_q]$, $1 - \frac{(1-\beta)x}{w} \leqslant 0$. Therefore

$$\int_{s_q - \epsilon}^{s_q} \pi(dx) \left(1 - \frac{(1 - \beta)x}{w} \right) \leqslant 0$$

while

$$\int_{s_q - \epsilon}^{s_q} q(dx) > 0$$

by definition, which is absurd. □

Proof of Proposition 6. First, on $[0, s_q)$, using that $w \geqslant (1-\beta)s_q$ from Lemma 1, we can divide and write :

$$\pi_{|[0,s_q)}(dx) = \frac{\beta q(dx)}{1 - \frac{1-\beta}{w}x}.$$

If $w > (1-\beta)s_q$ we even have the reinforcement $\pi_{|[0,s_q]}(dx) = \frac{\beta q(dx)}{1-\frac{1-\beta}{w}x}$.
Second, on $(s_q, 1]$, the equation for the invariant measure π simplifies :

$$\pi_{|(s_q,1]}(dx) = \left(\frac{1-\beta}{w}\right) x\pi_{|(s_q,1]}(dx),$$

which gives that $x = \frac{w}{1-\beta}$ if $\pi(dx) > 0$. Therefore

$$\pi_{|(s_q,1]} = \lambda\delta_{w/(1-\beta)}$$

for some $\lambda \in [0, 1]$.
As for the case $s_q = 1$, two situations can then be distinguished : either $w > (1-\beta)s_q$ or $w = (1-\beta)s_q$.

1. if $(1-\beta)s_q < w$, the invariant measure has to be of the form:

$$\frac{\beta q(dx)}{1 - \frac{1-\beta}{w}x} + C\delta_{\frac{w}{1-\beta}} = \frac{\beta q(dx)}{1 - \frac{x}{x_1}} + C\delta_{x_1}$$

   if $x_1 = \frac{w}{1-\beta} > s_q$. which is indeed an invariant measure for every $x_1 \in (s_q, 1]$ such that $\int \frac{\beta q(dx)}{1-x/x_1} \leqslant 1$, setting then $C = 1 - \int \frac{\beta q(dx)}{1-x/x_1}$.

2. if $(1-\beta)s_q = w$, the only possibility is then

$$\frac{\beta q(dx)}{1 - \frac{x}{s_q}} + C\delta_{s_q},$$

   which is indeed an invariant measure iff $\int \frac{\beta q(dx)}{1-x/s_q} \leqslant 1$, setting then $C = 1 - \int \frac{\beta q(dx)}{1-x/s_q}$.

□

3.2.2 Main result when $s_q < 1$

We know that $\max(Supp(p_n)) = s_0$ for all n. This gives the intuition for the following Theorem that can be proved using the same proof as for Theorem 1.

Theorem 2. *Set*

$$y_0 = \inf\left\{x' \in [s_0, \infty) : \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{x'}} \leqslant 1\right\}, \tag{15}$$

The sequence of probability measures $(p_n)_n$ defined by Kingman's recursion (1) converges in total variation on $[0, \xi]$ for each $\xi < s_0$ to :

$$\pi(dx) := \frac{\beta q(dx)}{1 - \frac{x}{y_0}} + \pi_0 \delta_{s_0}, \tag{16}$$

where $\pi_0 := 1 - \int_0^{s_q} \frac{\beta q(dx)}{1 - \frac{x}{y_0}}$.

The result of this theorem is illustrated in Figures 3 and 6, in which we observe that in the case where $s_q < 1$, the limiting fitness distribution depends in the initial fitness distribution, through the maximum of its support. Note also that there is a range $[s_0, y_0]$ (that can be empty) for the maximum of the support of the initial fitness distribution for which no condensation is possible, i.e. π is absolutely continuous with respect to q.

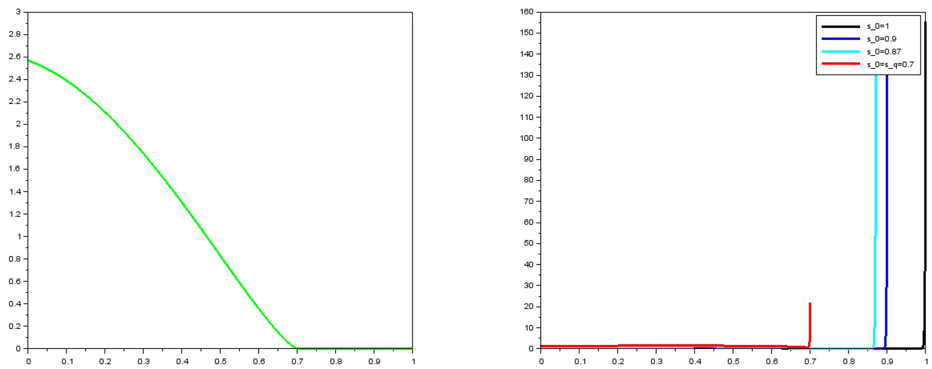

Figure 6: Impact of the support when condensation occurs

3.3 Some elements of the complex analysis approach

The convergence of the sequence of mean fitnesses given in Proposition 4 and proved using a direct analysis of solutions of the recurrence equation (1) can also be proved using a quite general complex analysis approach, which is what can be found in [9].
We give some insights of this approach here. Our aim is to prove the convergence of the sequence of mean fitnesses (w_n). We focus only on the case where $\int \frac{\beta q(dx)}{1-x} > 1$, otherwise the approach must be modified.
Let us introduce the quantities $W_n = w_0 ... w_{n-1}$ for all $n \geqslant 1$ and $W_0 = 1$.
The recursive equation (1) gives that

$$W_n p_n(dx) = \sum_{k=0}^{n-1} W_{n-k} (1-\beta)^k x^k \beta q(dx) + (1-\beta)^n x^n p_0(dx).$$

Integrating then gives that

$$W_n = \sum_{k=0}^{n-1} W_{n-k}(1-\beta)^k \int x^k \beta q(dx) + (1-\beta)^n \int x^n p_0(dx)$$

or that

$$W_n = \sum_{k=1}^{n-1} W_{n-k}(1-\beta)^{k-1} \int x^k \beta q(dx) + (1-\beta)^{n-1} \int x^n p_0(dx)$$

and the W_n are defined recursively using this equation, starting from $W_0 = 1$. Now let us introduce the function ϕ defined on $\{z \in \mathbb{C} : |z| < 1\}$ by

$$\phi(z) = z \mapsto \sum_{k=1}^{\infty} W_n z^n.$$

Then

$$\begin{aligned}
\phi(z) &= \sum_{n=1}^{\infty} W_n z^n \\
&= \sum_{n=1}^{\infty} \sum_{k=1}^{n-1} W_{n-k} z^{n-k} (1-\beta)^{k-1} \int z^k x^k \beta q(dx) + (1-\beta)^{n-1} \int z^n x^n p_0(dx) \\
&= \sum_{n=1}^{\infty} \sum_{k'=1}^{n-1} W_{k'} z^{k'} (1-\beta)^{n-k'-1} \int z^{n-k'} x^{n-k'} \beta q(dx) + (1-\beta)^{n-1} \int z^n x^n p_0(dx) \\
&= \sum_{k'=1}^{\infty} W_{k'} z^{k'} \sum_{n' \geqslant 1} (1-\beta)^{n'-1} \int z^{n'} x^{n'} \beta q(dx) + \frac{1}{1-\beta} \sum_{n \geqslant 1} \int (1-\beta)^n z^n x^n p_0(dx)
\end{aligned}$$

which gives that

$$\phi(z) = \frac{\int \frac{zx}{1-(1-\beta)zx} p_0(dx)}{1 - \int \frac{zx\beta q(dx)}{1-(1-\beta)zx}}.$$

Note that this function is analytic at least on $\{z \in \mathbb{C} : (1-\beta)|z| < 1\}$, except for singularities $z \in \mathbb{C}$ such that

$$\int \frac{zx\beta q(dx)}{1-(1-\beta)zx} = 1. \tag{17}$$

Taking the imaginary part in Equation (17) gives that singularities are attained only on real numbers. What is more the function $\int \frac{zx\beta q(dx)}{1-(1-\beta)zx}$ is strictly increasing in z on $\mathbb{R}$ so Equation (17) can have at most one solution on $\{z \in \mathbb{C} : (1-\beta)|z| < 1\}$, and it has one if and only if $\int \frac{x\beta q(dx)}{1-x} > 1$, or if $\int \frac{xq(dx)}{1-x} > 1/\beta$. What is more this zero is simple.

Therefore in the end ϕ is analytic on $\{z \in \mathbb{C} : (1-\beta)|z| < 1\}$ except for one simple pole on z_0. Standard results of complex analysis (using the developpement in power series of $\phi \times (z - z_0)$ then give that

$$\frac{W_{n+1}}{W_n} \to \frac{1}{z_0},$$

and even that

$$w_n = \frac{W_{n+1}}{W_n} = \frac{1}{z_0} + o(\Theta^n)$$

for some $\Theta < 1$, which gives that w_n converges.
Note that this approach also gives the speed of convergence of the sequence of mean fitnesses.
This approach is quite general in the sense that it aims at proving the convergence of a sequence of numbers through the study of the generating function associated to this sequence. Nevertheless it requires to be able to study this generating function which might not be possible. What is more the approach relies on the existence of a simple pole of the generating function, which is not the case anymore when $\int \frac{x\beta q(dx)}{1-x} = 1$, which therefore requires more work.
In the case where the function ϕ has no pole this approach does not work. The approach proposed by [9] then uses the theory of renewal sequences which are sequences of the form

$$u_n = \sum_{k=0}^{n-1} u_k f_{n-k}$$

(particular case of strong recurrence relation), and even the more particular case where f are moments of a probability distribution. For more results on the subject see [10].

4 Related works

Branching process Similar results can be obtained using more probabilistic models, as presented in [11]. The population starts with a single individual with a genetic fitness chosen according to q. Individuals never die, and each individual gives bith to a new individual at a rate equal to its fitness. Then a new born individual shares the fitness of its parent with probability $(1-\beta)$, otherwise its fitness is drawn according to the mutation law q. Then a condensation criterion exists, that is similar to the one for Kingman's house-of-cards model : condensation occurs if and only if

$$\int \frac{\beta q(dx)}{1-x} < 1.$$

More general models and more precisions can be found in [11].

Formation of condensation In the article [4], the authors consider the case in which condensation occurs, and focus on the form of the condensation.
More precisely they assume that

Theorem 3 ([4])**.** *Suppose that the fitness distribution q satisfies*

$$\lim_{h\to 0} \frac{q([1-h,1])}{h^\alpha} = 1,$$

where $\alpha > 1$ and that $\gamma(\beta) = 1 - \int_0^1 \frac{\beta q(dx)}{1-x} > 0$. Then for $x > 0$,

$$\lim_{p_n\to\infty} p_n \left(1 - \frac{x}{n}, 1\right) = \frac{\gamma(\beta)}{\Gamma(\alpha)} \int_0^x y^{\alpha-1} e^{-y} dy$$

This result is illustrated in Figure 7.

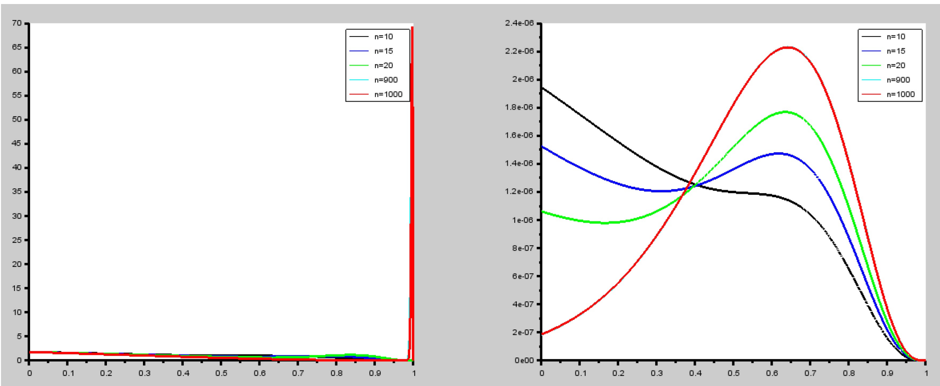

Figure 7: Zoom on the atom formation

The main element in the proof consists in proving that

$$W_n \sim cn^{-\alpha}(1-\beta)^{n-1}$$

using renewal sequences.

Random environments Some generalizations of Kingman's recursive model defined in [9] are considered in [13, 14] notably, where the case of random mutation probabilities β is considered, but no simple criterion for condensation in terms of the parameters of the model (or their law) is available. In the particular case where the mutation fitness distribution is a Dirac measure in some fitness c then there will be condensation if and only if $\mathbb{E}(\ln(h(1-\beta)/c) > 0$.

Alternating environments In [2] we consider the situation in which two environments (β_1, q_1) and (β_2, q_2) alternate deterministically. We consider the following recursion :

$$\begin{cases} p_{2n+1}(dx) & = \beta_1 q_1(x) + (1-\beta_1)\frac{xp_{2n}(dx)}{w_{2n}} \\ p_{2n+2}(dx) & = \beta_0 q_0(x) + (1-\beta_0)\frac{xp_{2n+1}(dx)}{w_{2n+1}}. \end{cases} \tag{18}$$

and consider the convergence of this sequence of fitness distributions, in the particular case where $s_0 = s_{q_1} = s_{q_2} = 1$.

Remark 9. Mean fitnesses are not (even alternatively) increasing starting from δ_0.

Let us now turn to the fundamental quantity of our study:

$$\Gamma_2 := \frac{\int \frac{\beta_0 q_0(dx)}{1+x}}{\int \frac{\beta_0 q_0(dx)}{1+x} + \int \frac{\beta_1 q_1(dx)}{1+x}} \int \frac{\beta_0 q_0(dx)}{1-x} + \frac{\int \frac{\beta_1 q_1(dx)}{1+x}}{\int \frac{\beta_0 q_0(dx)}{1+x} + \int \frac{\beta_1 q_1(dx)}{1+x}} \int \frac{\beta_1 q_1(dx)}{1-x} \in [-\infty, +\infty[.$$

To state our main result, we shall need to define the even and odd moment generating functions of the sub-probability measures $\beta_0 q_0(dx)$ and $\beta_1 q_1(dx)$ by:

$$\mu_\varepsilon^{(0)}(z) = \int \frac{\beta_\varepsilon q_\varepsilon(dx)}{1-(zx)^2} \quad \text{and} \quad \mu_\varepsilon^{(1)}(z) = \int \frac{zx\ \beta_\varepsilon q_\varepsilon(dx)}{1-(zx)^2}, \qquad \varepsilon \in \{0,1\}$$

The quantity Γ_2 rules the existence of solutions to of a key question on the generating functions of the mutation laws:

Proposition 7. *Consider the equation:*

$$\left(1-\mu_0^{(p)}(z)\right)\left(1-\mu_1^{(p)}(z)\right) - \mu_0^{(i)}(z)\mu_1^{(i)}(z) = 0, \quad z \in [0,1] \tag{$\star$}$$

We have the following dichotomy:

- *If $\Gamma_2 \geqslant 1$, the equation $(\star)$ has a unique solution z_c on $[0,1]$, and $z_c = 1$ iff $\Gamma_2 = 1$.*
- *If $\Gamma_2 < 1$, the equation $(\star)$ has no solution on $[0,1]$.*

Second, the quantity Γ_2 delimitates the condensation phase as shown in the following theorem that is our main result.

Theorem 4. *Under the assumptions just recalled,*

- *If $\Gamma_2 \geqslant 1$, the quantities z_0 and z_1 defined by $z_0 = \frac{z_c\mu_1^{(i)}(z_c)}{1-\mu_0^{(p)}(z_c)}$ and $z_1 = \frac{z_c\mu_0^{(i)}(z_c)}{1-\mu_1^{(p)}(z_c)}$ satisfy*

$$\int \frac{\beta_0 q_0(dx) + z_1 x \beta_1 q_1(dx)}{1-z_0 z_1 x^2} = 1, \qquad \int \frac{\beta_1 q_1(dx) + z_0 x \beta_0 q_0(dx)}{1-z_0 z_1 x^2} = 1$$

and $(p_{2n}(dx), p_{2n+1}(dx))$ *converges in total variation to the pair of probability measures:*

$$\left(\pi_0(dx) := \frac{\beta_0 q_0(x) + z_1 x \beta_1 q_1(dx)}{1 - z_0 z_1 x^2}, \qquad \pi_1(dx) := \frac{\beta_1 q_1(x) + z_0 x \beta_0 q_0(dx)}{1 - z_0 z_1 x^2}\right).$$

In particular the limiting distribution of both fitnesses is absolutely continuous with respect to $(q_0 + q_1)(dx)$.

- *If* $\Gamma_2 < 1$, *set*

$$z_1 = \frac{1}{z_0} = \frac{1 - \int \frac{\beta_0 q_0(dx)}{1+x}}{1 - \int \frac{\beta_1 q_1(dx)}{1+x}},$$

then $(p_{2n}(dx), p_{2n+1}(dx))$ *weakly converges to the pair of measures* (π_0, π_1) *such that*

$$\pi_0(dx) := \frac{\beta_0 q_0(x) + z_1 x \beta_1 q_1(dx)}{1 - x^2} + \gamma_0 \delta_1(dx)$$

and

$$\pi_1(dx) := \frac{\beta_1 q_1(x) + z_0 x \beta_0 q_0(dx)}{1 - x^2} + \gamma_1 \delta_1(dx)$$

where γ_0 *and* γ_1 *are such that* $\pi_0(dx)$ *and* $\pi_1(dx)$ *are probability measures on* $[0,1]$; *in particular, both limiting distributions* $\pi_0(dx)$ *and* $\pi_1(dx)$ *are singular with respect to* $(q_0 + q_1)(dx)$, *with an atom at the maximum fitness* 1 *of* $p_0(dx)$.

When considering k environments no nice formula like Γ_2 can be obtained. Nevertheless note that Equation $(\star)$ can be seen as the determinant of the matrix

$$I_2 - \begin{pmatrix} 1 - \mu_0^{(0)}(z) & -\mu_1^{(1)}(z) \\ -\mu_0^{(1)}(z) & 1 - \mu_1^{(0)}(z) \end{pmatrix}$$

The generalization of this matrix to k environments is $I_k - A(z)$ where

$$A(z) = \left(\mu_j^{([i-j])}(z)\right)_{1 \leqslant i,j \leqslant n}.$$

Equation $(\star)$ can be interpreted by the stronger condition that there exists z such that 1 is the Perron eigenvalue of the matrix $A(z)$.
Our Theorem then states that no condensation occurs if and only if there exists $z \in [0,1]$ such that the Perron eigenvalue of the matrix $A(z)$ is equal to 1. Note that the matrix A is increasing in z, so this is equivalent to the fact that the Perron eigenvalue of the matrix $A(1)$ is larger than 1.

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