# Ising quantum chain and sequence evolution

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**Abstract**

A sequence space model which describes the interplay of mutation and selection in molecular evolution is shown to be equivalent to an Ising quantum chain. Observable quantities, tailored to match the biological situation, will then be employed to treat three fitness landscapes exactly.

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## 1 Introduction

Sequence space models seek to describe biological evolution at the molecular level through mutation and selection. Well-known ones are Kauffman's adaptive walk [27] and Eigen's quasispecies model [14]. Whereas the former describes a hill-climbing process of a genetically homogeneous population in tunably rugged fitness landscapes (where the fitness values are considered as a mountain range over sequence space), the latter includes the genetic structure of the population due to the balance between mutation and selection. For equal fitness landscapes, the quasispecies model is thus more difficult to treat than the corresponding adaptive walk.

Some progress was made in [30] through the identification of the quasispecies model with a specific, anisotropic 2D Ising model: The mutation-selection matrix is equivalent to the row transfer matrix, with the mutation probability as a temperature-like parameter, and 'error thresholds' corresponding to phase transitions. This equivalence was exploited to treat simple fitness landscapes as well as spin-glass Hamiltonians with methods from statistical mechanics [31, 32, 44]. Of these results, most are approximate or numerical, and the few exact ones in [32] are restricted to the equilibrium state.

The quasispecies model assumes mutations to originate as replication errors on the occasion of reproduction events. An alternative as introduced in [2] describes mutation and selection as going on in parallel. In subsequent investigations [8, 48], this model turned out to be both more powerful and structurally simpler than the quasispecies model. Which is the more appropriate one from the biological point of view amounts to the question whether rates of molecular evolution are closer to constant per generation or constant in time – a long-standing, but still unresolved issue (see the discussion of the 'generation-time effect' in [23]). Even in the former situation, however, the parallel version is an excellent approximation. Note that both models are sequence space versions of the mutation-selection equations of classical population genetics [26].

In this article, a preliminary account of which was given in [5], we will work out that, in the same way as the quasispecies model is equivalent to the row transfer matrix of a 2D Ising model, the parallel mutation-selection model corresponds to the Hamiltonian of an Ising quantum chain. Observable quantities, tailored to match the biological situation, will then be employed to treat three simple fitness landscapes exactly (more biological implications will be dealt with elsewhere). But let us first elaborate on the evolution model and its connection to Ising quantum chains.

# 2 The evolution model

In line with the population genetic formalism (see e.g. [13]), we characterize individuals by their genotypes. For our purpose, it is sufficient to think of a gene (or even the whole genome) as a sequence in the four-letter alphabet {A(denin), C(ytosin), G(uanin), T(hymin)} of length about $10^3$ (or $10^6 - 10^9$ for a genome). In order to simplify the mathematical treatment, we assume that our sequences have fixed length $N$, and the alphabet is $\{+1, -1\}$. This binary code may be interpreted as distinguishing only between purines (G,A) and pyrimidines (C,T), as is frequently done in sequence analysis (for review, see [43]). Since we restrict ourselves to the evolution of haploid organisms (which have only one copy of every gene per cell), an individual can be characterized by, and thus identified with, a sequence $\boldsymbol{\alpha} := (\alpha_1, \alpha_2, ..., \alpha_N) \in \{+1, -1\}^N$.

A population is a collection of individuals, and is characterized by the relative frequencies $p_{\boldsymbol{\alpha}}$ of sequences $\boldsymbol{\alpha}$. We are interested in the evolution of its composition with time. In the same fashion as one describes probability distributions of spin configurations by elements of $\otimes^N \mathbb{C}^2$, a population is, at time $t$, given by the vector

$$\boldsymbol{p}(\mathrm{t}) = \sum_{\boldsymbol{\alpha} \in \{+1,-1\}^N} p_{\boldsymbol{\alpha}}(t)\, \boldsymbol{e}_{\alpha_1} \otimes ... \otimes \boldsymbol{e}_{\alpha_N}\,, \tag{2.1}$$

where $\boldsymbol{e}_{+1} := (1,0)^T$, $\boldsymbol{e}_{-1} := (0,1)^T$, and $T$ denotes transpose. Further, $p_{\boldsymbol{\alpha}}(t) \geq 0$, and $\sum_{\boldsymbol{\alpha}} p_{\boldsymbol{\alpha}}(t) = 1$. The population size is assumed infinite in the sense that the values of the $p_{\boldsymbol{\alpha}}$'s can vary continuously with time.

In our context, evolution is caused by mutation and selection. Here we choose a model where mutation and selection are decoupled, i.e. mutation is not a side effect of replication but may be caused by thermic fluctuations, mutagenic substances, or radiation at any time of the life cycle. So, at every instant, the individual $\boldsymbol{\alpha}$ reproduces at rate $R_{\boldsymbol{\alpha}}$, dies at rate $D_{\boldsymbol{\alpha}}$, and mutates to an individual of type $\boldsymbol{\beta}$ at rate $\mathcal{M}_{\boldsymbol{\beta\alpha}}$. Because reproduction and mutation are going on in parallel, we would like to call this model 'para-muse' (parallel mutation-selection) model.

The evolution of our population is then governed by the ordinary differential equation (ODE)

$$\frac{d}{dt}\boldsymbol{p}(\mathrm{t}) = (\mathcal{M}+\mathcal{R})\,\boldsymbol{p}(\mathrm{t}) \;\; - (\sum_{\boldsymbol{\alpha}} \mathcal{R}_{\boldsymbol{\alpha\alpha}}\, p_{\boldsymbol{\alpha}}\,(t)\,)\,\boldsymbol{p}(\mathrm{t}) \;\; , \tag{2.2}$$

which is the haploid version of the decoupled mutation-selection equation of population genetics (see, e.g., [13, 26]). Here, $\mathcal{M}$ is the mutation matrix with elements $\mathcal{M}_{\boldsymbol{\beta\alpha}}$, and the reproduction (or 'fitness') matrix $\mathcal{R}$ is defined as

$$\mathcal{R}_{\boldsymbol{\beta\alpha}} := (R_{\boldsymbol{\alpha}} - D_{\boldsymbol{\alpha}})\,\delta_{\boldsymbol{\beta\alpha}}\,. \tag{2.3}$$

Obviously, selection comes into operation through the tendency of 'fit' alleles to increase in number at the expense of less fit ones; mutation is expected to counteract this process. The transformation [46]

$$\boldsymbol{x}(\mathrm{t}) \;\; := \exp\left(\sum_{\boldsymbol{\alpha}} \int_0^t \mathcal{R}_{\boldsymbol{\alpha\alpha}}\, p_{\boldsymbol{\alpha}}(s)\,d\,s\right)\boldsymbol{p}(\mathrm{t}) \tag{2.4}$$

reduces the ODE (2.2) to the linear system

$$\frac{d}{dt}\,\boldsymbol{x}(\mathrm{t}) \;\; = (\mathcal{M}+\mathcal{R})\,\boldsymbol{x}(\mathrm{t}) \tag{2.5}$$

with the back-transformation

$$\boldsymbol{p}(\mathrm{t}) \;\; = \frac{\boldsymbol{x}(\mathrm{t})}{\sum_{\boldsymbol{\alpha}} x_{\boldsymbol{\alpha}}\,(t)}\,. \tag{2.6}$$

In order to specify $\mathcal{M}$, it is assumed that every single site mutates independently at rate $\mu \geq 0$, i.e.

$$\mathcal{M}_{\boldsymbol{\beta\alpha}} \; = \left\{ \begin{array}{cl} \mu & \text{if } d(\boldsymbol{\beta},\boldsymbol{\alpha}) = 1\,, \\ -N\,\mu & \text{if } \boldsymbol{\beta} = \boldsymbol{\alpha}\,, \\ 0 & \text{otherwise,} \end{array} \right. \tag{2.7}$$

where the Hamming distance $d(\boldsymbol{\beta},\boldsymbol{\alpha})$ is the number of sites where $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ differ. Thus, by using the definition

$$\sigma_k^a \; := \mathbb{1}_2 \, \otimes \ldots \otimes \mathbb{1}_2 \, \otimes \, \sigma^a \, \otimes \, \mathbb{1}_2 \, \otimes \ldots \otimes \mathbb{1}_2\,, \quad a \in \{x,y,z\} \tag{2.8}$$

with $\sigma^a$ in the $k$-th place, and Pauli's matrices

$$\sigma^x := \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}, \quad \sigma^y := \begin{pmatrix} 0 & -i \\ i & 0 \end{pmatrix}, \quad \sigma^z := \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}, \tag{2.9}$$

$\mathcal{M}$ can be written in the form

$$\mathcal{M} = \mu \sum_{k=1}^{N} (\sigma_k^x - \mathbb{1})\,. \tag{2.10}$$

The $\mathcal{R}_{\boldsymbol{\alpha}\boldsymbol{\alpha}}$ are, as yet, unspecified; their choice determines the so-called 'fitness landscape'. In contrast to $\mathcal{M}$, there is no canonical choice for $\mathcal{R}$. Since $\mathcal{R}$ is diagonal and real, $\mathcal{R}$ must be an element of the group algebra $\mathrm{span}_{\mathbb{R}} \langle \sigma_k^z, 1 \leq k \leq N \rangle$. Here, $\langle \sigma_k^z, 1 \leq k \leq N \rangle$ is the multiplicative group generated by $\{\sigma_k^z, 1 \leq k \leq N\}$, and $\mathrm{span}_{\mathbb{R}} \langle \sigma_k^z, 1 \leq k \leq N \rangle$ is the set of all linear combinations of elements in $\{\sigma_k^z, 1 \leq k \leq N\}$; i.e. $\mathrm{span}_{\mathbb{R}} \langle \sigma_k^z, 1 \leq k \leq N \rangle$ is the group algebra of $\langle \sigma_k^z, 1 \leq k \leq N \rangle$. Since the reproduction rate depends, in principle, on all levels of the genotype-to-phenotype mapping (e.g. from protein-folding to behaviour), one has to assume that $\mathcal{R}$ contains, in general, both short- and long-range interactions.

Obviously, $\mathcal{M} + \mathcal{R}$ is the Hamiltonian of an Ising quantum chain in a transverse magnetic field [35], with general interactions within the chain. For instance, the mutation-reproduction matrix of the so-called quadratic optimum model, where the fitness is proportional to $N^{-1}(N^+_{\boldsymbol{\alpha}} - N^-_{\boldsymbol{\alpha}})^2$ ($N^{\pm}_{\boldsymbol{\alpha}}$ is the number of $\pm 1$'s in $\boldsymbol{\alpha}$), is the Hamiltonian of the mean-field Ising quantum chain (cf. Section 4.3):

$$\mathcal{M} + \mathcal{R} := \mu \sum_{k=1}^{N} (\sigma_k^x - \mathbb{1}) + \frac{\gamma}{2N} \sum_{k,l=1}^{N} \sigma_k^z \sigma_l^z \,. \tag{2.11}$$

It is worth noting that Leuthäusser [30, 31, 32] found an analogous equivalence between a discrete-time version of Eigen's quasispecies model (which assumes that mutations occur only on the occasion of replication events) and the transfer matrix of a classical two-dimensional Ising model. In contrast to the para-muse model, where the time evolution is described by $\exp(t\,(\mathcal{M} + \mathcal{R}))$ according to Eq. (2.5), the time evolution of this 'coupled version' is given by $(\exp(\mathcal{M})\, \exp(\mathcal{R})\,)^M$ ($M \in \mathbb{N}$ is the number of 'generations'). Using the Trotter formula [37], one can show that the quasispecies model converges to the para-muse model if the number of generations per time unit goes to infinity.

# 3 Observable quantities

In order to characterize populations, we will now introduce observable quantities which describe the genetic structure of the population, and the structure of the population with respect to fitness. But let us start with the (unconstrained) population size,

$$P(t) := \sum_{\boldsymbol{\alpha} \in \{+1,-1\}^N} x_{\boldsymbol{\alpha}}(t) \,. \tag{3.1}$$

Since $\sum_{\boldsymbol{\alpha}} x_{\boldsymbol{\alpha}}(0) = 1$ by Eq. (2.4), $P(t)$ can be interpreted as the ratio of the population sizes at time $t$ and at time $0$. Eq. (2.5) gives

$$P(t) := 2^{N/2} \, \langle \, \Omega, e^{t\,(\mathcal{M}+\mathcal{R})} \, \boldsymbol{x}_0 \rangle. \tag{3.2}$$

Here, $\langle .,. \rangle$ is the Euclidean scalar product, $\boldsymbol{x}_0 := \boldsymbol{x}(0)$ is the initial condition, and

$$\Omega := 2^{-N/2} \sum_{\boldsymbol{\alpha} \in \{+1,-1\}^N} \boldsymbol{e}_{\alpha_1} \otimes \ldots \otimes \boldsymbol{e}_{\alpha_N} \tag{3.3}$$

(and thus $\langle \Omega, \Omega \rangle = 1$).

Eq. (3.2) implies that the population grows (or decays) exponentially (note that the ODE, Eq. (2.2), defines $\mathcal{R}$ only up to an additive constant). In experiments, populations may be prepared to grow exponentially for a certain time. But most populations, both in the laboratory and in the wild, underly some kind of population control (for example, the dilution flux in a flow reactor, or the carrying capacity of a biotope) which imposes some upper limit on the (actual) population size. It is important to note that, under quite general forms of population control, Eq. (2.2) still correctly reflects the relative frequencies of sequences in the population, even if the (actual) population size is changing. To be more precise, let the *actual* numbers of individuals with sequence $\boldsymbol{\alpha}$, $z_{\boldsymbol{\alpha}}$, behave according to

$$\frac{d}{dt}\, \boldsymbol{z}(\mathrm{t}) \;= (\mathcal{M} + \mathcal{R} - g(t)\mathbb{1})\, \boldsymbol{z}(\mathrm{t}) \;\; , \tag{3.4}$$

where $g(t)$ is some scalar (maybe nonlinear) function which describes the elimination of individuals by population control. Then Eq. (2.2) holds for $\boldsymbol{p}(t) := \boldsymbol{z}(t)/\|\boldsymbol{z}(t)\|_1$; see also [13]. In this context, $P(t)$ is the number of produced indviduals including those eliminated by population control, and their hypothetical descendants. Hence, $P(t)$ is not directly accessible to measurement.

In the sequel, the logarithm of the (unconstrained) population size will be very helpful; we will call it the population size function and label it by $F$:

$$F(t) := \log\, P(t) = \log \langle\, \Omega, e^{t\,(\mathcal{M}+\mathcal{R})}\, \boldsymbol{x}_0 \,\rangle + \frac{N}{2}\, \log\, 2\,. \tag{3.5}$$

Now, let us consider the observable quantity 'mean fitness' of the population,

$$W(t) := \sum_{\boldsymbol{\alpha}} \mathcal{R}_{\boldsymbol{\alpha}\boldsymbol{\alpha}} p_{\boldsymbol{\alpha}}(t) = \langle\, \Omega, \mathcal{R}\, \boldsymbol{p}(t)\,\rangle\,, \tag{3.6}$$

where we used Eq. (3.3) and the fact that $\mathcal{R}$ is diagonal. The other way round, this operation can be performed for all matrices which are diagonal with respect to $\{\boldsymbol{e}_{\alpha_1} \otimes \ldots \otimes \boldsymbol{e}_{\alpha_N}\,; \boldsymbol{\alpha} \in \{+1,-1\}^N\,\}$. So, by using the non-normalized vector $\boldsymbol{x}$ from Eq. (2.4) and exploiting the fact that $\sum_{\boldsymbol{\alpha}} (\mathcal{M}\boldsymbol{v}\,)_{\boldsymbol{\alpha}} \;= 0$ for all $\boldsymbol{v} \in \otimes^N \mathbb{C}^2$ (which is due to the vanishing column sums of $\mathcal{M}$), $W(t)$ can be rewritten in the form

$$W(t) = \langle\, \mathcal{M} + \mathcal{R}\,\rangle_N^t = \frac{d}{dt}\, F(t)\,, \tag{3.7}$$

where

$$\langle \mathcal{A}\,\rangle_N^t := \frac{\langle\, \Omega, \mathcal{A}\, e^{t\,(\mathcal{M}+\mathcal{R})}\, \boldsymbol{x}_0 \,\rangle}{\langle\, \Omega, e^{t\,(\mathcal{M}+\mathcal{R})}\, \boldsymbol{x}_0 \,\rangle}. \tag{3.8}$$

Thus, $W(t)$ can be interpreted as the 'growth rate' of the population, too. This implies the method of measuring the 'mean fitness' of a population by exposing a sample of the actual population to conditions under which exponential growth prevails for a certain time. This is more readily accomplished than the measurement of the (unconstrained) population size because one need not bother about the eliminated individuals. In the sequel, we will use the densities of these observables, which are defined as the observable quantities divided by $N$. They will be labelled by small letters.

It is worth noting that the connection between $P(t)$, $F(t)$, and $W(t)$ is the same as between partition function, free energy, and internal energy of an Ising quantum chain. In order to illustrate the differences between the biological and the physical quantities, let us consider the case $\boldsymbol{x}_0 = 2^{-N/2}\Omega$ (equidistribution at $t = 0$) in more detail. Then

$$P(t) = 2^{-N} \sum_{\boldsymbol{\beta},\boldsymbol{\alpha}} \langle \boldsymbol{e}_{\beta_1} \otimes ... \otimes \boldsymbol{e}_{\beta_N}, \exp(t\,(\mathcal{M} + \mathcal{R}))\, \boldsymbol{e}_{\alpha_1} \otimes ... \otimes \boldsymbol{e}_{\alpha_N} \rangle, \tag{3.9}$$

i.e. $P(t)$ is proportional to the sum over all coefficients of $\exp(t(\mathcal{M} + \mathcal{R}))$, whereas the partition function is the trace of $\exp(-\beta\mathcal{H})$. Thus, in contrast to the partition function, the population size is not invariant under similarity transformations. This reflects the fact that, for the biological system, there is one distinguished basis given by the sequences.

Let us now turn to the characterization of the genetic structure of the population. An appropriate quantity is the 'surplus', which is, up to a factor $N^{-1}$, the length $N$ minus twice the averaged number of $-1$'s in the sequences:

$$\begin{aligned} s(t) \; &:= \; \tfrac{1}{N}\,(N - 2\textstyle\sum_{\boldsymbol{\alpha}} N^-_{\boldsymbol{\alpha}}\, p_{\boldsymbol{\alpha}}\,(t)) \\ &= \; \tfrac{1}{N} \textstyle\sum_{\boldsymbol{\alpha}} (N^+_{\boldsymbol{\alpha}} - N^-_{\boldsymbol{\alpha}})\, p_{\boldsymbol{\alpha}}\,(t)\,. \end{aligned} \tag{3.10}$$

Thus, if $++...+$ or $--...-$ is the fittest sequence (which will be the case for all fitness landscapes which we will treat in the next section), the surplus is closely related to the Hamming distance from the fittest sequence. On the other hand, the surplus may be written as

$$s(t) = \langle \frac{1}{N} \sum_{k=1}^{N} \sigma^z_k \rangle^t_N\,, \tag{3.11}$$

which is the biological analogue of the magnetization of the quantum chain. Altogether, we have established a correspondence between the partition function, free energy, internal energy, and magnetization, on the one hand, and the unconstrained population size, population function, mean fitness, and surplus, on the other hand. The mathematical relationship between the thermodynamic and the population quantities is as discussed for the partition function and population size. Two other quantities will be useful, namely the two-point function $\tau_{k,k+l}$

$$\tau_{k\,l} := \tau_{k\,,l} = \langle \sigma^z_k\, \sigma^z_l \rangle^t_N\,, \tag{3.12}$$

and the variance of the surplus

$$\begin{aligned} V_s\,(t) \; &:= \; N^{-2} \sum_{\boldsymbol{\alpha}} [(N^+_{\boldsymbol{\alpha}} - N^-_{\boldsymbol{\alpha}})^2\, p_{\boldsymbol{\alpha}}\,(t)] - s^2(t) \\ &= \; N^{-2} \sum_{k,l=1}^{N} \tau_{k\,l}\,(t) - s^2(t). \end{aligned} \tag{3.13}$$

We have thus seen that mappings of the form

$$\langle\,\cdot\,\rangle^t_N : \, C_N := \mathrm{span}_{\mathbb{C}} \langle\, \sigma^z_k\,,\, 1 \le k \le N\,\rangle \to \mathbb{C};\; \mathcal{C} \mapsto \langle\, \mathcal{C}\,\rangle^t_N \tag{3.14}$$

describe the measurement of the observables of the evolution model. They correspond to the Gibbs states

$$\omega^{\beta} : A_N \to \mathbb{C};\ \mathcal{A} \mapsto \frac{\mathrm{tr}_N(\exp(-\beta\,\mathcal{H})\mathcal{A})}{\mathrm{tr}_N(\exp(-\beta\,\mathcal{H}))}\,, \tag{3.15}$$

on the Pauli algebra $A_N := \mathrm{span}_{\mathbb{C}}\langle\, \sigma_k^x,\, \sigma_k^y,\, \sigma_k^z;\, 1 \le k \le N\,\rangle$, which describe analogous measurements in quantum chains[1] [33]. An essential difference is, however, that the observables of the evolution model are elements of an Abelian algebra. This corresponds to the fact that we are not dealing with a quantum mechanical problem, but a problem of classical probability (cf. [6] and Eq. (4.53) in Section 4.3).

# 4 Examples of para-muse models

In this section, we will determine our observable quantities for three fitness landscapes. The initial condition will always be that the population at time $t = 0$ is an equidistribution of all sequences, i.e.

$$\boldsymbol{x}_0 := 2^{-N/2}\,\Omega\,, \tag{4.1}$$

which implies $\|\boldsymbol{x}_0\|_1 = 1$. This is a kind of 'worst case scenario' in the sense that the population has no genetic structure whatsoever. Note that the choice of the initial condition $\boldsymbol{x}(0)$ has no influence on the equilibrium state $\lim_{t\to\infty} \boldsymbol{p}(t)$, the Perron-Frobenius eigenvector [29] of $\mathcal{M} + \mathcal{R}$ (which exists since $\mathcal{M} + \mathcal{R}$ plus a suitable constant is irreducible).

The scaling of the quantities to be investigated is extensive. That is, the norms of $\mathcal{M}$ and $\mathcal{R}$ are proportional to $N$, which implies that the reproduction and mutation rates increase with sequence length. This is perfectly adequate as far as the molecular mutation mechanism is concerned, but may be debated for the reproduction rates. In some approaches [32, 44], $\mathcal{R}$ is chosen such that its norm is independent of $N$, whereas others [18] rely on the extensive scaling. Whereas their argument is based on the demand that the system should exhibit a phase transition, we should like to concentrate on the observable quantities. For the description of systems with fixed, finite $N$, the scaling has no immediate relevance. But we need the thermodynamic limit to extract the relevant behaviour of the systems. Under which conditions is the infinitely large system appropriate to describe a finite one? Let $\mathcal{C}$ be a fixed element of $C_N$, and $c_N : \mathbb{R} \to \mathbb{C},\ t \to \langle\, \mathcal{C}\,\rangle_N^t$. Since we are particularly interested in the dynamics of the system, we choose as our criterion that the time evolution of the observable, $(c_N(t))_{N\in\mathbb{N}}$, should converge uniformly to $c_\infty(t)$. This will be the case if the scaling of both $\mathcal{M}$ and $\mathcal{R}$ is extensive. A simple example is the surplus of the Fujiyama-landscape (cf. Eqs. (4.7) and (4.8) in Section 4.1), which does not depend on $N$. Another example is $\tau_{k,k+1}$ of Onsager's landscape (to be treated in Section 4.2, and illustrated in Fig. 7) as a function of $N$. Note that an intensively-scaled $\mathcal{R}$ cannot fulfil the criterion at the same time, of which the reader may convince himself by replacing $\gamma$ by $\gamma/N$ in the Fujiyama surplus, Eq. (4.8). Finally, we would like to remark that the intensive scaling of

[1] Note that, in order to be consistent with our calligraphic matrix notation, our symbols for the algebra and its elements are interchanged with respect to the standard literature [10].

*both* $\mathcal{M}$ and $\mathcal{R}$, as sometimes used in quantitative genetics, cannot fulfill the convergence criterion either, since the connection between the all-extensive and the all-intensive scalings is $c_N^{\mathrm{ex}}(t) = c_N^{\mathrm{in}}(Nt)$.

### 4.1 The 'Mount Fujiyama' landscape

As a warm-up exercise, let us consider the case

$$\mathcal{R}_{\boldsymbol{\alpha}\boldsymbol{\alpha}} = \gamma \sum_{k=1}^{N} \alpha_k \,. \tag{4.2}$$

This corresponds to the additive fitness scheme of population genetics (see e.g. [15]), and is similar to Kauffman's landscape of an $N$-dimensional 'Fujiyama peak' [27]. The corresponding quasispecies model has been treated in [39]. In our case, $\mathcal{M} + \mathcal{R}$ is related to an Ising quantum chain with interactions of the spins with external transversal (mutation) and longitudinal (reproduction) fields, but without spin-spin interaction:

$$\mathcal{M} + \mathcal{R} = \mu \sum_{k=1}^{N} (\sigma_k^x - \mathbb{1}) + \gamma \sum_{k=1}^{N} \sigma_k^z \,. \tag{4.3}$$

Thus, $\mathcal{M} + \mathcal{R}$ can be written as the sum of $N$ commuting angular momenta,

$$\mathcal{M} + \mathcal{R} = \sum_{k=1}^{N} (\mu\, \sigma_k^x + \gamma\, \sigma_k^z) - \mu N \mathbb{1} \,. \tag{4.4}$$

Together with $(\mu\, \sigma_k^x + \gamma\, \sigma_k^z)^2 = (\mu^2 + \gamma^2)\, \mathbb{1} =: \lambda^2 \mathbb{1}$, this results in

$$\exp(t(\mathcal{M} + \mathcal{R})) = \exp(-t\, N\, \mu) \prod_{k=1}^{N} \Big( \cosh(\lambda\, t) \mathbb{1} + \sinh(\lambda\, t) [\, \frac{\mu}{\lambda} \sigma_k^x + \frac{\gamma}{\lambda} \sigma_k^z \,] \Big) \,. \tag{4.5}$$

Let us now determine the observable quantities. The density of the population size function, $f(t)$, is given by

$$\begin{aligned} f(t) &= \frac{1}{N} \log \langle\, \Omega, e^{t\,(\mathcal{M}+\mathcal{R})}\, \Omega \,\rangle \\ &= \log(\cosh(\lambda\, t) + \frac{\mu}{\lambda} \sinh(\lambda\, t)) - \mu\, t \end{aligned} \tag{4.6}$$

(cf. Eqs. (3.5 and (4.1)). Thus, the density of the mean fitness is

$$w(t) = \frac{d}{dt} f(t) = \lambda\, \frac{\mu + \lambda\, \tanh(\lambda\, t)}{\lambda + \mu\, \tanh(\lambda\, t)} - \mu = \frac{\gamma^2\, \tanh(\lambda\, t)}{\lambda + \mu\, \tanh(\lambda\, t)}. \tag{4.7}$$

The surplus is proportional to the density of the mean fitness:

$$s(t) = \langle\, \frac{1}{N} \sum_{k=1}^{N} \sigma_k^z \,\rangle_N^t = \frac{w(t)}{\gamma} \,. \tag{4.8}$$

Figs. 1 and 2 show the surplus and the mean fitness per site for an equilibrium population, $\lim_{t\to\infty} \boldsymbol{p}(t)$. The time evolution of the surplus is depicted in Fig. 3.

Since $\mathcal{M}+\mathcal{R}$ is the sum of $N$ operators which act on the $N$ sites of the sequence, the entries are not correlated. Together with the fact that the interactions are not site-dependent, this leads to

$$\tau_{k\,l} = s^2, \qquad V_s = \frac{1}{N}(1-s^2) \tag{4.9}$$

for $k \neq l$.

We would like to remark that the same analysis is possible if we replace $\gamma$ in Eq. (4.4) with site-dependent $\gamma_k$. Then the observables are replaced by the corresponding averaged values (with the exception of $\tau_{k\,l} = \langle\sigma_k^z\rangle_N^t \langle\sigma_l^z\rangle_N^t$), which always exist in the finite system. For example,

$$s(t) = \frac{1}{N}\sum_{k=1}^{N} \frac{\gamma_k \tanh(\lambda_k\, t)}{\lambda_k + \mu \tanh(\lambda_k\, t)}\,, \tag{4.10}$$

where $\lambda_k := \sqrt{\gamma_k^2+\mu^2}$.

## 4.2 Onsager's landscape

Onsager's landscape is the fitness landscape that stems from the Ising quantum chain with nearest-neighbour interaction and periodic boundary conditions ($\sigma_{N+1}^z := \sigma_1^z$), cf. [35]. We need not worry about these boundary conditions from the biological point of view, since their influence vanishes in the thermodynamic limit. The reproduction matrix is

$$\mathcal{R} = \gamma \sum_{k=1}^{N} \sigma_k^z\, \sigma_{k+1}^z\,. \tag{4.11}$$

Thus, the reproduction rate of a sequence is proportional to $N$ minus twice the number of pairs of neighbouring sites with different entries ('domain walls'). For example:

| sequence | fitness |
|---|---|
| $++++++++$ | $\gamma\, N$ |
| $+--+++++$ | $\gamma\,(N-2\times 2)$ |
| $+--++--+$ | $\gamma\,(N-2\times 4)$ |

So, Onsager's landscape, which may be considered as a special case of Kauffman's $N2$-landscape [28], is a relatively simple one. But it has very interesting properties from the biological point of view. For instance, there are flat ridges, which means there are sequences (for example $+--+++$) from which one cannot go 'uphill' (to a fitter sequence) by a single mutational step. Put differently, for most sequences, there are neighbours in the space which are selectively equivalent, which corresponds to the idea of a 'fluctuating neutral space' (see e.g. [23]).

The corresponding Hamiltonian reads

$$\mathcal{M}+\mathcal{R} := \mu\sum_{k=1}^{N}(\sigma_k^x - \mathbb{1}) + \gamma\sum_{k=1}^{N}\sigma_k^z\,\sigma_{k+1}^z\,. \tag{4.12}$$

The aim is to find as simple as possible an expression for $\exp(t(\mathcal{M}+\mathcal{R}))$. This task being very similiar to the investigation of the transfer matrix of the 2D-Ising model with nearest-neighbour interactions, we use the methods of Schultz et. al. [40, 45]. We summarize the essential steps here since we will need them to calculate the biological observables. As a first step, we rewrite $\mathcal{M}+\mathcal{R}$ as a quadratic form in the fermionic operators

$$\begin{aligned} c_k &:= \tfrac{1}{2}\sigma_1^x \ldots \sigma_{k-1}^x (\sigma_k^z - i\,\sigma_k^y)\,, \\ c_k^\dagger &:= \tfrac{1}{2}\sigma_1^x \ldots \sigma_{k-1}^x (\sigma_k^z + i\,\sigma_k^y)\,. \end{aligned} \tag{4.13}$$

For our calculations it is essential that the vector $\Omega$ is the vacuum vector of the $c_k$'s, i.e.

$$c_k\,\Omega = \mathbf{0} \qquad \text{for all } k \in \mathbb{N}\,. \tag{4.14}$$

Using definition (4.13), one obtains

$$\mathcal{M}+\mathcal{R} = \mathcal{P}^+\,\mathcal{H}^+\,\mathcal{P}^+ + \mathcal{P}^-\,\mathcal{H}^-\,\mathcal{P}^- - N\,\mu\,\mathbb{1}\,, \tag{4.15}$$

where

$$\begin{aligned} \mathcal{H}^\pm &:= -2\,\mu \sum_{k=1}^{N} (c_k^\dagger\, c_k - \tfrac{1}{2}\mathbb{1}) + \gamma \sum_{k=1}^{N} (c_k^\dagger - c_k)(c_{k+1}^\dagger + c_{k+1})\,, \\ c_{N+1} &:= \mp c_1\,, \\ \mathcal{P}^\pm &:= \tfrac{1}{2}(\mathbb{1} \pm \mathcal{U})\,, \\ \mathcal{U} &:= \sigma_1^x \ldots \sigma_N^x = \exp(i\pi \sum_{k=1}^{N} c_k^\dagger\, c_k)\,. \end{aligned} \tag{4.16}$$

For a discussion of the relationship between the various Hamiltonians involved, see [3]. $\mathcal{U}$ distinguishes states with even and odd numbers of particles, and commutes with $\mathcal{M}+\mathcal{R}$. So, due to $c_{N+1} = \mp c_1$, the $\mathcal{P}^\pm$ can be interpreted as the projection operators on the subspaces which correspond to periodic and antiperiodic boundary conditions, respectively. In order to determine our observable quantities under the initial condition (4.1), we must evaluate terms of the form $\langle\, \Omega,\, \mathcal{C}\, \exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle$, where $\mathcal{C} \in C_N$. Due to $[\,\mathcal{P}^\pm\,,\, \mathcal{M}+\mathcal{R}\,] = 0$ and $\mathcal{P}^+\,\Omega = \Omega$, these calculations can be restricted to the image of $\mathcal{P}^+$, and we need not consider $\mathcal{H}^-$. The only exception will be the determination of $\lim_{t\to\infty} s(t)$, where we will investigate our Hamiltonian plus a small symmetry-breaking external field, where a vector in the image of $\mathcal{P}^-$ will be required. The transformation of $\mathcal{H}^-$ being very similar to that of $\mathcal{H}^+$ [40], however, we will restrict ourselves to the latter. Since $\mathcal{H}^+$ obeys antiperiodic boundary conditions with respect to the $c_k$'s (they are fermions!), it is natural to introduce the 'running wave operators'

$$\eta_{2q-1} := N^{-1/2}\, e^{i\pi/4} \sum_{k=1}^{N} e^{-i\frac{\pi}{N}k(2q-1)} c_k\ , \ 1 \le q \le N, \tag{4.17}$$

i.e. we perform a discrete Fourier transformation of the fermionic operators. Note that $\Omega$ is the vacuum state of the running wave operators, too (cf. Eq.

(4.14)). With the help of these operators, $\mathcal{H}^+$ can be decomposed into the sum

$$\mathcal{H}^+ = \sum_{q=1}^{N/2} \mathcal{H}_{2q-1}\,, \tag{4.18}$$

where here and in what follows we restrict ourselves to the case $N$ even, and

$$\begin{aligned} \mathcal{H}_{2q-1} &:= (2\gamma\,\cos(\tfrac{\pi\,(2q-1)}{N}) - 2\,\mu)\,(\eta^\dagger_{2q-1}\eta_{2q-1} + \eta^\dagger_{-2q+1}\eta_{-2q+1} - \mathbb{1}) \\ &+ 2\gamma\,\sin(\tfrac{\pi\,(2q-1)}{N})\,(\eta^\dagger_{-2q+1}\eta^\dagger_{2q-1} + \eta_{2q-1}\eta_{-2q+1}). \end{aligned} \tag{4.19}$$

Since $[\,\mathcal{H}_{2q-1}\,, \mathcal{H}_{2p-1}\,] = 0$, one obtains from Eq. (4.18) the desired simplification of $\exp(t(\mathcal{H}^+))$:

$$\exp(t\,\mathcal{H}^+) = \prod_{q=1}^{N/2} \exp(t\,\mathcal{H}_{2q-1}\,). \tag{4.20}$$

Another useful identity is [45, p. 238]

$$\begin{aligned} &(\mathcal{H}_{2q-1})^2 \\ =\;& 4\,\lambda^2_{2q-1}\,(\,\eta^\dagger_{2q-1}\eta_{2q-1}\eta^\dagger_{-2q+1}\eta_{-2q+1} + \eta_{2q-1}\eta^\dagger_{2q-1}\eta_{-2q+1}\eta^\dagger_{-2q+1}\,) \\ =:\;& 4\,\lambda^2_{2q-1}\,\mathcal{P}_{2q-1}\,, \end{aligned} \tag{4.21}$$

where $\lambda_{2q-1} := \gamma\,\sqrt{1+h^2-2\,h\,\cos(\frac{\pi}{N}(2q-1))}$ (with $h := \mu/\gamma$). Note that $\mathcal{P}_{2q-1}$ projects on the states where both corresponding fermions do or do not exist. As a direct consequence,

$$\exp(t\,\mathcal{H}^+) = \prod_{q=1}[(\mathbb{1} - \mathcal{P}_{2q-1}) + \cosh(2\,\lambda_{2q-1}\,t)\mathcal{P}_{2q-1} + \frac{\sinh(2\,\lambda_{2q-1}\,t)}{2\lambda_{2q-1}}\mathcal{H}_{2q-1}\,]. \tag{4.22}$$

Now we can determine the observable quantities, where it is essential that $\Omega$ is the vacuum vector, i.e. we are interested in vacuum expectations. The density of the population size function is:

$$\begin{aligned} f(t) &= \frac{1}{N}\,\log\langle\,\Omega, e^{t\,(\mathcal{M}+\mathcal{R})}\Omega\,\rangle \qquad (4.23) \\ &= \frac{1}{N}\sum_{q=1}^{N/2}\log(\cosh(2\,\lambda_{2q-1}\,t) + \frac{\gamma}{\lambda_{2q-1}}(h - \cos(\frac{\pi\,(2q-1)}{N})\sinh(2\,\lambda_{2q-1}\,t)) - \mu\,t. \end{aligned}$$

Consequently, the density of the mean fitness has the form

$$w(t) = \frac{2}{N}\sum_{q=1}^{N/2}\left[\lambda_{2q-1}\,\frac{\phi_{2q-1} - \chi_{2q-1}\,\exp(-4\,\lambda_{2q-1}t)}{\phi_{2q-1} + \chi_{2q-1}\,\exp(-4\,\lambda_{2q-1}t)}\right] - \mu, \tag{4.24}$$

where

$$\begin{aligned} \phi_{2q-1} &:= \sqrt{h^2+1-2\,h\,\cos(\tfrac{\pi(2q-1)}{N})} + h - \cos(\tfrac{\pi(2q-1)}{N}), \\ \chi_{2q-1} &:= \sqrt{h^2+1-2\,h\,\cos(\tfrac{\pi(2q-1)}{N})} - h + \cos(\tfrac{\pi(2q-1)}{N}). \end{aligned} \tag{4.25}$$

Let us now turn to the investigation of the genetic structure of the population by calculating the two-point function $\tau_{k,k+l} := \langle \sigma_k^z \, \sigma_{k+l}^z \rangle_N^t$. From $\sigma_k^x \, \Omega = \Omega$ and $c_k \, \Omega = \mathbf{0}$, one obtains $\langle \sigma_k^z \, \sigma_{k+l}^z \rangle_N^t = -\langle c_k \, c_{k+l} \rangle_N^t$. A transformation to the running wave operators leads to

$$\tau_{k,k+l}(t) = \frac{2}{N} \sum_{q=1}^{N/2} \frac{\sin(\frac{\pi l \, (2q-1)}{N}) \sin(\frac{\pi (2q-1)}{N})[1 - \exp(-4 \, \lambda_{2q-1} \, t)]}{\phi_{2q-1} + \chi_{2q-1} \, \exp(-4 \, \lambda_{2q-1} \, t)} \,. \tag{4.26}$$

Noting that $V_s(t) + s^2(t) = N^{-2} \sum_{k,l=1}^N \tau_{k\,l}(t)$, one gets

$$V_s(t) + s^2(t) = \frac{1}{N} + \frac{2}{N^2} \sum_{q=1}^{N/2} \frac{\cos^2(\frac{\pi (2q-1)}{2N})[1 - \exp(-4 \, \lambda_{2q-1} \, t)]}{\phi_{2q-1} \, + \chi_{2q-1} \, \exp(-4 \, \lambda_{2q-1} \, t)} \,. \tag{4.27}$$

A direct calculation of the surplus (3.11) leads to $s(t) = 0$ (as a consequence of $[\, \mathcal{U} \, , \, \mathcal{M} + \mathcal{R} \,] = 0$, $\mathcal{U} \, \Omega = \Omega$, and $\mathcal{U} \, \sigma_k^z \, \mathcal{U} = - \sigma_k^z$). But this does not necessarily describe the stable states of the system (if we regard Onsager's landscape as an idealization, where the real system contains an additional small symmetry-breaking perturbation). For the *equilibrium* state, adding a small external field ($\propto N^{-1}$) and determing the Perron-Frobenius eigenvector of the resulting Hamiltonian in first order perturbation theory according to the method by Yang [50], yields, in the limit $N \to \infty$,

$$\lim_{N \to \infty} \lim_{t \to \infty} s(t) = \begin{cases} \pm\sqrt{1-h} & \text{if } h < 1 \,, \\ 0 & \text{if } h \geq 1 \,; \end{cases} \tag{4.28}$$

see Fig. 1. For *finite* time, however, this perturbation theoretical method does not work any more. On the other hand, we can investigate $s(t)$ for finite $t$ in the limiting case $\mu = 0$ (selection only), because in this case the functional $\langle \, \cdot \, \rangle^t$ is exactly the Gibbs state (3.15) of a one-dimensional Ising model without transversal field. Then, one has to deal with $\mathcal{M} = 0$, and

$$\mathcal{R} = \gamma \sum_{k=1}^N \sigma_k^z \, \sigma_{k+1}^z + b \sum_{k=1}^N \sigma_k^z \,. \tag{4.29}$$

This gives [45, p. 127]

$$s(t) = \frac{\sinh(tb)}{\sqrt{\sinh^2(tb) + \exp(-4t\gamma)}} \; \frac{1 - x^N}{1 + x^N} \tag{4.30}$$

with

$$x = \frac{\cosh(tb) - \sqrt{\sinh^2(tb) + \exp(-4t\gamma)}}{\cosh(tb) + \sqrt{\sinh^2(tb) + \exp(-4t\gamma)}} \,.$$

It is a remarkable fact that, in contrast to the *equilibrium* state (4.28), the *time evolution* of $s(t)$ depends on the exact value of the parameter $b$, as illustrated in Fig. 4. On the other hand, for all finite $b$, the absolute value of the surplus approaches 1 in finite time (this may, however, not be a realistic biological time scale), so $s = 0$ is *unstable*. The fact that no spontaneous symmetry breaking takes place for finite temperatures gives us good reason to believe that the behaviour of the system is qualitatively the same for all $h < 1$.

Let us now consider the two-point function $\tau_{k,k+N/2}$ as an order parameter which describes the long-range order of the system (because of the periodic boundary conditions, $\tau_{k,k+N/2}$ is the two-point function of the spins with maximum distance). Evaluating the leading term in $N$ (see Appendix A.1), one obtains

$$\tau_{k,k+N/2} \approx \begin{cases} \dfrac{(1-h)\,(1-e^{-4t(\gamma-\mu)})}{\cosh(N\,(1-h)\,e^{-2\,(\gamma-\mu)t})}\,, & h < 1\,, \\ 0\,, & h \geq 1\,; \end{cases} \tag{4.31}$$

see Fig. 8. It is worth noting that

$$\lim_{t\to\infty} \tau_{k,k+N/2}\,(t) = 1 - h = \lim_{t\to\infty} s^2(t)\,, \tag{4.32}$$

where $s$ is the surplus of the *perturbed* system, cf. Eq. (4.28). This corresponds to the result of Potts and Ward [34, 36] who found that the magnetization of the two-dimensional Ising model can be determined as the square root of a two-spin correlation. The time evolution of $\tau_{k,k+N/2}$ is illustrated in Fig. 5.

As a consequence of Eq. (4.31), $\tau_{k,k+N/2}$ has critical exponent 1 at $h = 1$ for all $t > 0$. So, using $\tau_{k,k+N/2}$ as an order parameter, we call the point $h = 1$ an error threshold, in correspondence with the notion of a phase transition in physics. Here, the action of selection is overcome by the randomizing effect of mutation, and the population loses its genetic structure.

Determing the leading term of the right-hand side of Eq. (4.27) (cf. Appendix A.1) and using the identity $s(t) = 0$ (here, the *unperturbed* quantity is required) results in

$$V_s\,(t) = \begin{cases} \frac{1}{N}(1 + \sinh(2\,(\gamma-\mu)t)\,\tanh(N\,(1-h)\,e^{-2\,(\gamma-\mu)t}))\,, & h < 1 \\ \frac{1}{N}\left(1 + \frac{1}{\pi}\displaystyle\int_0^\pi \frac{\cos^2(x/2)\,[1-\exp(-4\lambda(x)t)]}{\phi(x)+\chi(x)\,\exp(-4\lambda(x)t)}\,dx\right)\,, & h \geq 1. \end{cases} \tag{4.33}$$

Here, $\phi(x)$, $\chi(x)$ and $\lambda(x)$ are the functions $\phi(\frac{\pi\,(2q-1)}{N}) := \phi_{2q-1}$, $\chi(\frac{\pi\,(2q-1)}{N}) := \chi_{2q-1}$ , and $\lambda(\frac{\pi\,(2q-1)}{N}) := \lambda_{2q-1}$. It is worth noting that

$$\lim_{t\to\infty} V_s(t) = \lim_{t\to\infty} \tau_{k,k+N/2}(t) = \lim_{t\to\infty} s^2(t) \tag{4.34}$$

for $h < 1$. Here, $s$ is the surplus of the perturbed system again, see Eq. (4.28); but we should like to emphasize that $V_s$ belongs to the *un*perturbed situation where the population 'splits' into the two stable branches (within each branch, the variance vanishes). The essential point of the time evolution of the 'long-range correlation' $\tau_{k,k+N/2}$ and of the variance of the surplus is that they are determined by $N\,\exp(-2\,(\gamma-\mu)t)$. Hence, the time scale is of the order of $\log N$, which implies that the corresponding equilibrium values are reached (approximately) in a realistic time, at least if $h \not\approx 1$. In the limit $h \nearrow 1$, the time required to reach the equilibrium diverges ('critical slowing down' with critical exponent 1). Another direct consequence of the fact that Eqs. (4.31) and (4.33) depend on $N$ is that a performance of the thermodynamic limit $N \to \infty$ for

$\tau_{k,k+N/2}$ and $V_s$ (for $h < 1$) would lead us to results which do not correctly reflect the system's behaviour. In contrast, the values of the 'short-range correlation' $\tau_{k,k+1}$, and the growth rate converge for all $t$ to the value of the thermodynamic limit, which are given by the corresponding integral,

$$\tau_{k,k+1}(t) = \frac{w(t)}{\gamma} = \frac{1}{\pi} \int_0^\pi \frac{\sin^2(x)[1 - \exp(-4\,\lambda(x)\,t)]}{\phi(x) + \chi(x)\,\exp(-4\,\lambda(x)\,t)}\,d\,x\,, \tag{4.35}$$

as illustrated in Fig. 6. As a direct consequence, the time scale of the time evolution of these quantities does not depend on system size. In the limit $t \to \infty$, one gets

$$\tau_{k,k+1} = \frac{2}{\pi}(1+h)\,E(\frac{\pi}{2},\theta) - h, \tag{4.36}$$

which is illustrated in Fig. 2. Here, $\theta^2 = \frac{4\,h}{(1+h)^2}$, and $E(\frac{\pi}{2},\theta)$ is the complete elliptic integral of the second kind [1, 17.2.8]. In particular, for all $t > 0$, $\lim_{N\to\infty}(\lim_{h\to 1}\frac{d^2}{d\,h^2}\,w(t))$ diverges logarithmically (cf. Fig. 8). We thus observe three different phenoma which are typical of second-order phase transitions, namely long-range order, critical slowing down, and non-analyticity of $w$, at the 'error threshold'.

## 4.3 The mean-field landscape

Onsager's landscape is a landscape with ridges and neutrality, but it should not be taken too literally as a model of biological interaction. In contrast to the simple nearest-neighbour interaction in this model, true fitness values depend on all levels of the genotype-phenotype mapping, thus giving rise to interactions that are long-range and very complicated in the sequence picture. Examples are the genetic determination of quantitative traits, or the fact that DNA strings serve as templates for proteins, which then fold in three dimensions.

Let us therefore consider the following mutation-reproduction matrix as a representative model with long-range interactions:

$$\mathcal{M} + \mathcal{R} := \mu \sum_{k=1}^{N}(\sigma_k^x - \mathbb{1}) + \frac{\gamma}{2N}(\sum_{k=1}^{N}\sigma_k^z)^2\,. \tag{4.37}$$

This corresponds to the Hamiltonian of an Ising quantum chain with homogeneous mean-field interactions within the row. In the context of evolution, this is a realistic example of fitness landscapes that are invariant under permutation of sites, which are also relevant for the multi-locus theory of population genetics (see, e.g., [7]). For $\gamma < 0$ ($\gamma > 0$), the fitness landscape is a concave (convex) function of the number of sites with identical entries. The case of $\gamma < 0$ is related to the quadratic optimum model as used in quantitative genetics (but note the different scaling of the mutation rates and fitness values as discussed in Section 3). It is worth emphasizing that, in contrast to the situation in physics, where interactions are inherently local and a mean-field Hamiltonian is an approximation, Eq. (4.37) is a model as such in the evolutionary context.

Let us begin the investigation of the mean-field landscape by briefly discussing how one can treat the mean-field Ising quantum chain by operator algebraic methods [10, 11], and which results of statistical mechanics carry over to the evolution model. This method seems to be attractive since it works for all permutation invariant models [16, 21, 38] and thus in principle allows generalization to a four-state model (after all, the genetic code is a four-letter alphabet). So we will use this relatively simple model to introduce the method which we hope will be helpful in more complicated (and realistic) cases.

Consider the Pauli algebra $A_N := \mathrm{span}_{\mathbb{C}}\langle\, \sigma_k^a;\ a \in \{x,y,z\},\ 1 \le k \le \mathbb{N}\rangle$ (cf. Eq. (3.15)) as a $C^*$-algebra on the Hilbert space $H_N := (\otimes^N \mathbb{C}^2, \langle\,.\,,\,.\,\rangle)$, where $\mathcal{A}^*$ is the canonical adjoint matrix of $\mathcal{A}$ for all $\mathcal{A} \in A_N$. The scalar product of $H_N$ (the canonical scalar product on $\otimes^N \mathbb{C}^2$) induces the norm on $A_N$.

Let $A_N^*$ be the set of all continuous linear functionals on $A_N$. In the finite case $N < \infty$, there exists some $\varrho_N^\omega \in A_N$ such that $\omega_N(\mathcal{A}) = \mathrm{tr}_N(\varrho_N^\omega\, \mathcal{A})$. $\omega_N \in A_N^*$ corresponds to a state on $A_N$ (i.e. $\omega_N(\mathcal{A}^*\mathcal{A}) \ge 0$, $\omega_N(\mathbb{1}) = 1$) if and only if $\varrho_N^\omega$ is a density matrix (i.e. if $\varrho_N^\omega$ is self-adjoint with positive spectrum, and $\mathrm{tr}(\varrho_N^\omega) = 1$). An example is the Gibbs state $\omega_N^\beta$ (of the Ising quantum chain) at the inverse temperature $\beta$, given by the density matrix

$$\varrho_N^\beta := \exp(-\beta\, \mathcal{H}_N)/\mathrm{tr}_N(\exp(-\beta\, \mathcal{H}_N)) \tag{4.38}$$

with the Hamiltonian

$$\mathcal{H}_N := -\mu \sum_{k=1}^{N} (\sigma_k^x - \mathbb{1}) - \frac{\gamma}{2N} (\sum_{k=1}^{N} \sigma_k^z)^2 \tag{4.39}$$

corresponding to the mutation-reproduction matrix (4.37).

It is a well-known result from statistical mechanics [11, 24] that the Gibbs state $\omega_N^\beta$ is the unique minimizer of the free energy (density) functional

$$\omega \to f_N^\beta(\omega) = \frac{1}{N}(\mathrm{tr}_N(\varrho_N^\omega\, \mathcal{H}_N) + \frac{1}{\beta}\mathrm{tr}_N(\varrho_N^\omega\, \log(\varrho_N^\omega))) \tag{4.40}$$

on the states on $A_N$.

Another essential point is that $\omega_N^\beta$ is invariant with respect to the permutation of sites. In more detail: Let the representation of the symmetric group $S_N$ be given by the following definition of the transposition $t_{kl}$ of sites $k$ and $l$:

$$t_{kl} := \frac{1}{2}(\mathbb{1} + \sigma_k^x\, \sigma_l^x + \sigma_k^y\, \sigma_l^y + \sigma_k^z\, \sigma_l^z), \qquad 1 \le k,l \le N,\ k \ne l\,. \tag{4.41}$$

Then for all $\mathcal{A} \in A_N$, $\mathcal{G} \in S_N := \langle t_{kl}\,,\ 1 \le k,l \le N\rangle$:

$$\omega_N^\beta(\mathcal{A}) = \omega_N^\beta(\mathcal{G}\,\mathcal{A}\,\mathcal{G}^{-1})\,. \tag{4.42}$$

The inversion of all spins is another symmetry of $\omega_N^\beta$:

$$\omega_N^\beta(\mathcal{A}) = \omega_N^\beta(\mathcal{U}\mathcal{A}\mathcal{U})\,, \tag{4.43}$$

where $\mathcal{U} := \sigma_1^x ... \sigma_N^x$.

In the thermodynamic limit, there are many results available on the set of equilibrium states of the infinite chain. Therefore we consider $A_N$ naturally embedded in the 'quasilocal algebra' $A$ (for details, see [10]) such that $A := \overline{\bigcup_{N\in\mathbb{N}} A_N}^{\|\cdot\|}$.

This can be interpreted as considering every finite system as a subsystem of an infinitely large one. In particular, every state $\omega_N$ on $A_N$ can be considered as a state $\hat{\omega}_N$ on $A$ (the extension is not unique, but the ambiguity has no relevance for Gibbs states $\omega_N^\beta$ in the limit $N \to \infty$). For example, we can choose $\hat{\omega}_N$ such that

$$\omega_N^\beta(\mathcal{A}_{N'}) = \mathrm{tr}_{\max\{N,N'\}}(\varrho_N \mathcal{A}_{N'}) \tag{4.44}$$

(this is the continuation of $\varrho_N$ with the trace state on $A$ for $\mathcal{A}_{N'} \in A_{N'}$ if $N' \geq N$).

The thermodynamic limit of $\hat{\omega}_N^\beta$ ($N \in \mathbb{N}$) is performed in the weak$^*$-topology, i.e. we are looking for the limiting Gibbs state $\omega^\beta$ which is defined by $\lim_{N\to\infty} \hat{\omega}_N^\beta(\mathcal{A}) = \omega^\beta(\mathcal{A})$ for every $\mathcal{A} \in A$, if it exists at all.

Every accumulation point of the sequence $(\hat{\omega}_N^\beta)_{N\in\mathbb{N}}$ must be permutation invariant, i.e. $\omega^\beta(\mathcal{A}) = \omega^\beta(\mathcal{G}\,\mathcal{A}\,\mathcal{G}^{-1})$ for all $\mathcal{A} \in A$, $\mathcal{G} \in \bigcup_{N\in\mathbb{N}} S_N$. It follows from the permutation invariance of $\omega^\beta$, cf. [41, 42] that this state can be decomposed into homogeneous product states denoted by $\otimes^\infty\phi$ with $\phi$ a state on the one-point algebra of all $2 \times 2$-matrices $M_2 := \mathrm{span}_{\mathbb{C}}\langle\, \sigma^x, \sigma^y, \sigma^z \,\rangle$ (this is even the central decomposition of $\omega^\beta$ [10]). With the invariance of $\omega^\beta$ under the inversion of all spins, we find ([22, 20]):

$$\omega^\beta(\mathcal{A}) = \int_{\hat{B}_1} [\frac{1}{2}(\otimes^\infty\phi(x,y,z))(\mathcal{A}) + \frac{1}{2}(\otimes^\infty\phi(x,y,-z))(\mathcal{A}))]\, d\theta_\beta(x,y,z)\,. \tag{4.45}$$

$\hat{B}_1$ denotes the set $\{x^2+y^2+z^2 \leq 1; z \geq 0\}$ which parametrizes the spin-inversion invariant states on $M_2$ (the one-point algebra). For $x^2+y^2+z^2 \leq 1$, in particular, the set of all density matrices in $M_2$ is given by $\{\varrho^{\phi(x,y,z)} := \frac{1}{2}(\mathbb{1}_2 + x\,\sigma^x + y\,\sigma^y + z\,\sigma^z)\,\}$. $\theta$ is a uniquely determined probability measure on $\hat{B}_1$.

Furthermore, one can show [21, 38] that $\omega^\beta$ minimizes the limiting free energy density functional. Since this functional is an affine function on the simplex of permutation invariant states, it is sufficient to investigate the boundary of that simplex which is given by the set of product states $\{\otimes^\infty\phi\}$. This leads to the following formula for $f^\beta$:

$$f^\beta(\otimes^\infty\phi) = -\mu\,\mathrm{tr}(\varrho^\phi\,\sigma^x) + \mu\,\mathrm{tr}(\varrho^\phi\,\mathbb{1}) - \frac{\gamma}{2}\mathrm{tr}^2(\varrho^\phi\,\sigma^z) + \frac{1}{\beta}\mathrm{tr}(\varrho^\phi \log\varrho^\phi). \tag{4.46}$$

Every minimizer $\phi$ of Eq. (4.46) is a solution of a self-consistency equation (but not vice versa! see below), which allows the determination of all limiting Gibbs states as

$$\omega^\beta(\mathcal{A}) = \frac{1}{2}\mathrm{tr}(\otimes^\infty\varrho_+^\beta\mathcal{A}) + \frac{1}{2}\mathrm{tr}(\otimes^\infty\varrho_-^\beta\mathcal{A}), \tag{4.47}$$

where

$$\varrho_\pm^\beta := \frac{\exp(\beta(\mu\,\sigma^x \pm \gamma\,m\,\sigma^z))}{\mathrm{tr}(\exp(\beta(\mu\,\sigma^x \pm \gamma\,m\,\sigma^z)))}\,, \tag{4.48}$$

and $m(\beta) := \mathrm{tr}(\varrho^\beta\sigma^z)$ fulfils the self-consistency equation

$$m = m\gamma\,\tanh(\beta\sqrt{\mu^2+(\gamma\,m)^2})/\sqrt{\mu^2+(\gamma\,m)^2}\,. \tag{4.49}$$

The $\otimes^\infty \varrho^\beta_\pm$ ($\varrho^\beta_\pm$ considered as states on $M_2$) minimize the limiting free energy density if $m$ is a solution of $\sqrt{\mu^2+(\gamma m)^2} = \gamma \tanh(\beta\sqrt{\mu^2+(\gamma m)^2})$, or $m=0$ if this equation has no solution. In particular, one obtains the following formula for the ground state energy density[2] ($h := \mu/\gamma$):

$$\lim_{\beta\to\infty}\lim_{N\to\infty} \omega^\beta_N(N^{-1}\mathcal{H}_N) = \begin{cases} -\frac{\gamma}{2}(1-h)^2\,, & \text{if } h<1\,, \\ 0\,, & \text{if } h\geq 1\,. \end{cases} \tag{4.50}$$

What do these results for the quantum chain mean for the observables of the corresponding para-muse model? As mentioned in Section 3 (cf. Eq. (3.14)),

$$\langle\,\cdot\,\rangle^t_N = \frac{\langle\,\Omega,\,\cdot\,\exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle}{\langle\,\Omega, \exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle} \tag{4.51}$$

plays the same role for the para-muse model as the Gibbs-state in statistical mechanics. An essential difference is that $\langle\,\cdot\,\rangle^t_N$ is not a state on $A_N$. To see this, let us rewrite Eq. (4.51) as

$$\langle\,\cdot\,\rangle^t_N = \mathrm{tr}_N(\,\cdot\,\varrho^t_N\,)\,, \tag{4.52}$$

where

$$\varrho^t_N := \frac{\exp(t(\mathcal{M}+\mathcal{R}))\,\prod_{k=1}^N(\mathbb{1}+\sigma^x_k)}{\mathrm{tr}_N(\,\exp(t(\mathcal{M}+\mathcal{R}))\,\prod_{k=1}^N(\mathbb{1}+\sigma^x_k))}\,. \tag{4.53}$$

Note that $\varrho^t_N$ is not self-adjoint and hence no density matrix. So $\langle\,\cdot\,\rangle^t_N$ is not a state on $A_N$. But on the other hand, since $p_{\boldsymbol{\alpha}}(t)\geq 0$, $\sum_{\boldsymbol{\alpha}} p_{\boldsymbol{\alpha}}(t) = 1$, $\langle\,\cdot\,\rangle^t_N$ is a state on the Abelian $C^*$-algebra $C_N := \mathrm{span}_{\mathbb{C}}\langle \sigma^z_k, 1\leq k\leq N\,\rangle$. Embedding $C_N$ into the corresponding 'quasi-local algebra' $C$ (with the same embedding scheme as in the case of the $A_N$), one looks for the limiting state $\langle\,\cdot\,\rangle^t_\infty := \lim_{N\to\infty}\langle\,\cdot\,\rangle^t_N$ in the weak$^*$-topology. Because $\langle\,\cdot\,\rangle^t_N$ has the same symmetries as $\omega^\beta_N$, each accumulation point of $(\langle\,\cdot\,\rangle^t_N)_{N\in\mathbb{N}}$ must be of the form

$$\langle\,\mathcal{C}\,\rangle^t_\infty = \int_0^1 \frac{1}{2}[(\otimes^\infty\phi(z))(\mathcal{C}) + (\otimes^\infty\phi(-z))(\mathcal{C})]\,d\theta_t(z)\,,\ \mathcal{C}\in C\,, \tag{4.54}$$

where $\{\varrho^{\phi(z)} := \frac{1}{2}(\mathbb{1}_2 + z\sigma^z);\ z^2\leq 1\}$ is the set of all states on the one-point algebra $\mathrm{span}_{\mathbb{C}}\langle\,\sigma^z\,\rangle$, and $\theta$ is a probability measure on the interval $[0,1]$. Note that the restriction to the Abelian algebra results in an identification of all linear functionals of $\mathcal{A}$ which differs only in the $\sigma^x$- or $\sigma^y$-component. Hence one can characterize each state of the one-point algebra by $z := \phi(\sigma^z)$. As in the physical situation, a *direct* determination of the state in the thermodynamic limit seems to be impossible. Unlike the situation in physics, however, there is no remedy in the form of an extremal principle for the muse model.

Let us continue to exploit our knowledge in terms of the biological observables. Because of the inverted sign of the Hamiltonian (cf. Eqs. (4.37) and (4.38)), the Perron-Frobenius eigenvector of $\mathcal{M}+\mathcal{R}$ is exactly the energy ground state of $\mathcal{H}_N$ (up to normalization). Thus

$$\lim_{t\to\infty}\langle\,\frac{1}{N}(\mathcal{M}+\mathcal{R})\,\rangle^t_N = -\lim_{\beta\to\infty}\omega^\beta_N(\frac{1}{N}\mathcal{H}_N)\,, \tag{4.55}$$

[2] Since $\omega^\beta_M(N_1^{-1}\mathcal{H}_{N_1}) + \frac{\gamma}{2}N_1^{-1} = \omega^\beta_M(N_2^{-1}\mathcal{H}_{N_2}) + \frac{\gamma}{2}N_2^{-1}$ for all $N_1, N_2\leq M$, the limit $\lim_{N\to\infty}\omega^\beta_N(N^{-1}\mathcal{H}_N)$ coincides with $\lim_{N\to\infty}\lim_{M\to\infty}\omega^\beta_M(N^{-1}\mathcal{H}_N)$.

i.e. the density of the mean fitness of the equilibrium state is the density of the ground state energy of the Ising quantum chain, up to a minus sign. Thus, one obtains, from Eq. (4.50), the maximum eigenvalue of $N^{-1}(\mathcal{M}+\mathcal{R})$ in the limit $N \to \infty$ (see Fig. 2). It is worth emphasizing that, in principle, there can be a problem in the determination of the ground state energy of the quantum chain if the two limiting processes $\beta \to \infty$ and $N \to \infty$ do not commute. But in the case of the mean-field para-muse model both successions lead to the same result. Note that Eq. (4.50) is a first hint that there is an error threshold at $h = 1$.

It can be shown (cf. Appendix A.2) that the equilibrium state is given by

$$\lim_{N\to\infty} \lim_{t\to\infty} \langle\, \mathcal{C}\, \rangle_N^t = \begin{cases} \frac{1}{2}(\otimes^\infty \phi(1-h))(\mathcal{C}) + \frac{1}{2}(\otimes^\infty \phi(h-1))(\mathcal{C})\,, & h < 1 \\ (\otimes^\infty \phi(0))(\mathcal{C})\,, & h \geq 1\,. \end{cases} \tag{4.56}$$

So the limiting state undergoes a transition from two branches with opposite nontrivial order parameter $s$ to a phase with vanishing surplus; see Fig. 1. It is this bifurcation that makes us identify $h = 1$ with an error threshold.

Now, let us consider the time-evolution of this model. As mentioned above, we cannot determine the limiting state $\lim_{N\to\infty}\langle \cdot \rangle_N^t$ for arbitrary $t$ because we do not have an extremal principle for this purpose. But since the time evolution of a population is a highly relevant issue, we don't want to finish without a conjecture about the time-evolution in the thermodynamic limit. But let us first consider the limiting case $\mu = 0$. In this case,

$$\langle\, \mathcal{C}\, \rangle_N^t = \omega_N^t(\mathcal{C}) \quad \text{for all } \mathcal{C} \in C_N\,. \tag{4.57}$$

In particular, the surplus coincides with the physical magnetization for all $N \in \mathbb{N}$. As a consequence of Eqs. (4.48) and (4.49), the para-muse model without mutation can be described in the thermodynamic limit by

$$\langle\, \mathcal{C}\, \rangle_\infty^t = \frac{1}{2}(\otimes^\infty\, \phi_+^t)(\mathcal{C}) + \frac{1}{2}(\otimes^\infty\, \phi_-^t)(\mathcal{C})\,, \tag{4.58}$$

where

$$\varrho_\pm^t := \frac{\exp(\pm t\,\gamma\, s\, \sigma^z)\,(\mathbb{1}+\sigma^x)}{\operatorname{tr}(\exp(\pm t\,\gamma\, s\, \sigma^z)\,(\mathbb{1}+\sigma^x))}\,, \tag{4.59}$$

and $s := |\operatorname{tr}(\sigma^z\, \varrho_\pm^t)|$ is the positive solution of $s = \tanh(t\,\gamma\, s)$ if this solution exists, and $s = 0$ otherwise. Note that in this case we cannot distinguish between $\varrho_\pm^t$ and the density matrix of the corresponding quantum chain. Our conjecture is that, for all $\mu$, the mean-field para-muse model may be described as a particle in an 'effective field'. The possibility which seems to be the most natural one, namely $\varrho_\pm^t := \exp(t(\mu\sigma^x \pm \gamma\, s\, \sigma^z))\,(\mathbb{1}+\sigma^x)/\operatorname{tr}(\exp(t(\mu\sigma^x \pm \gamma\, s\, \sigma^z))\,(\mathbb{1}+\sigma^x))$, is not a suitable candidate, however, because it would imply $\lim_{t\to\infty} s(t) = 1-2h$ in contradiction with Eq. (4.56). We thus have to look for a 'deformed effective field'.

As an ansatz we choose

$$\varrho^t = \frac{\exp(t(\mu\sigma^x + \gamma\, f(s)\, \sigma^z)\,(\mathbb{1}+\sigma^x)}{\operatorname{tr}(\exp(t(\mu\sigma^x + \gamma\, f(s)\, \sigma^z)\,(\mathbb{1}+\sigma^x))}\,, \tag{4.60}$$

where $f(s)$ is some function of $s$. This leads to the 'self-consistency equation' for $s(t)$:

$$s(t) = \langle \sigma_k^z \rangle = \mathrm{tr}(\sigma^z \varrho^t) = \frac{\gamma f(s) \tanh(\lambda t)}{\lambda + \mu \tanh(\lambda t)} \tag{4.61}$$

with $\lambda := \sqrt{f^2 + \mu^2}$. In order to determine the possible choices for $f(s)$, we investigate the limit $t \to \infty$:

$$s = \frac{f(s)}{\sqrt{f^2(s) + h^2} + h}, \tag{4.62}$$

which has the solutions

$$f(s) = 0 \quad \text{and} \quad f(s) = \frac{2\,h\,s}{1 - s^2}. \tag{4.63}$$

Let us consider the non-trivial solution in more detail. It is required that, in the limiting case $\mu = 0$, Eq. (4.58) is reproduced for all $t$. Furthermore, we know that $\lim_{t\to\infty} s(t) = \pm(1-h)$ for $h < 1$. We thus replace $1 - s^2$ by $2h - h^2$, which leads to $f(s) = 2s/(2-h)$. Our conjecture then takes the form

$$\varrho^t_\pm = \frac{\exp(t(\mu\sigma^x \pm (2s\gamma)/(2-h)\,\sigma^z))\,(\mathbb{1} + \sigma^x)}{\mathrm{tr}(\exp(t(\mu\sigma^x \pm (2s\gamma)/(2-h)\,\sigma^z))\,(\mathbb{1} + \sigma^x))}, \tag{4.64}$$

where $s(t)$, according to Eq. (4.61), is given by the positive solution of

$$s = \frac{2-h}{2\gamma}\sqrt{\lambda^2 - \mu^2} \quad \text{with} \quad \lambda = \gamma \frac{2 - h + h^2}{2-h} \tanh(\lambda t) \tag{4.65}$$

if this solution exists, and $s = 0$ otherwise. At equilibrium, Eq. (4.65) reduces to

$$\lim_{t\to\infty} s(t) = \begin{cases} 1-h, & h < 1, \\ 0, & h \geq 1, \end{cases} \tag{4.66}$$

in agreement with Eq. (4.56).

Our solution is certainly not a rigorous one. So one has to check numerically whether $\langle\cdot\rangle_t^N$ corresponds with the state we have conjectured. One ambiguity should be taken into account: The equidistribution of all sequences and the population which consists only of sequences with $N/2$ 'up-spins' and $N/2$ 'down-spins' converge to the same product state in the thermodynamic limit, namely $\otimes^\infty \phi(0)$. We thus use (mixtures of) both initial conditions of the finite system to test our conjecture. Fig. 9 demonstrates that we may be quite confident about it.

It is worth noting that our solution implies a threshold behaviour in the time evolution for $h < 1$. The reason seems to be that the neighbourhood of the minimum of the fitness landscape is so flat that evolution can only find its way uphill after an initial 'spreading' phase.

# 5 Discussion

The correspondence between muse models in sequence space and two-dimensional Ising models, as first described by Leuthäusser a decade ago, did not find its way into many applications; the work of Tarazona [44] and Franz et al. [18] are notable exceptions. It may have been felt that, despite the attractive formalism, transfer matrices are hard to treat explicitly except in favourable cases, especially since one has to bother about surface phenomena here [44, 18]. Also, the anisotropy of the interactions (nearest-neighbour between rows but long-range within rows) leads to hard problems in the construction of solvable examples; competing interactions like those treated in [17] cannot be accomodated in this picture. Very recently, however, a new 'radiation' of (mainly approximate) statistical mechanics methods as applied to sequence space models has taken place. Among these, there are moment equations [49], stochastic differential equations [51], spin glass theory [18], and methods from random polymers [19]. Naturally, interest has centered on the error threshold phenomenon, although there has been considerable disagreement on how to interpret it as a phase transition (cf. [18]).

The relationship between the para-muse model and the Ising quantum chain, which we have made precise in this paper, serves a two-fold purpose in this context. Firstly, quantum chain Hamiltonians are more tractable than the corresponding transfer matrices and may be dealt with rigorously, at least for representative examples. This becomes particularly clear for the permutation-invariant fitness landscapes. In the transfer matrix picture, this is a difficult situation, since the mean-field interaction is restricted to *within* the rows, whereas nearest-neighbour interaction prevails *between* the rows. One must therefore rely on heuristic arguments and approximations with their typical ambiguities [32, 44]. In sharp contrast, the mean-field Hamiltonian of the corresponding quantum chain is tailored to the biological situation and lends itself to rigorous treatment.

Care must be exercised, however, in defining (and evaluating) suitable observables. Since one has to deal with classical probabilities instead of quantum-mechanical ones, the quantum-mechanical formalism may not be taken too far. Whereas it does carry over to the calculation of the mean fitness ('ground state energy'), the biological 'surplus' differs decisively from the physical magnetization and requires special methods for its evaluation; see also [6]. In general, great care must be exercised when converting quantum mechanical states to classical probabilities, as was already noted in a different genetic context [12].

These observables have also led us to make precise the notion of an error threshold. The equivalence between the *size*, *size function*, *mean fitness*, and *surplus* of a population, and the *partition function*, *free energy*, *internal energy*, and *magnetization* of the quantum chain allows us to lean heavily on the physical concepts here. On the one hand, the phase transition was described via the vanishing of the two-point correlation function for long-range order. On the other hand, the bifurcation of symmetric states could also be used to characterize an error threshold.

It is worth emphasizing, however, that the biological interest is by no means in critical points (and critical exponents) alone. The availability of quantum chain methods for muse models should help us to learn more about the full distribution of mutants, and individual fitness, for sub-critical mutation rates–and for more realistic fitness landscapes.

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# A Appendix

## A.1 Onsager's landscape: the determination of $\tau_{k,k+N/2}$ and $V_s$ in the large system limit

Let us first assume that $0 < h < 1$. The essential problem is that, since $\sin(\frac{\pi(2q-1)}{N}) = (-1)^{q+1}$ and $\lim_{N\to\infty} \phi_1 = 0$ for $h < 1$, the right-hand side of Eq. (4.26) does not converge to an integral.

Using $\phi_{2q-1}\,\chi_{2q-1} = \sin^2(\frac{\pi\,(2q-1)}{N})$, one obtains

$$\tau_{k,k+N/2}(t) = \frac{2}{N}\sum_{q=1}^{N/2} \frac{(-1)^{q+1}\,\sin(\frac{\pi\,(2q-1)}{N})\,\chi_{2q-1}(1-e^{-4\lambda_{2q-1}t})}{\sin^2(\frac{\pi\,(2q-1)}{N}) + \chi^2_{2q-1}\,e^{-4\lambda_{2q-1}t}}\,. \qquad \text{(A.1)}$$

Choosing an arbitrary, but small and fixed $x_0 > 0$ and defining $q_0 := \sup\{q \in \{1,...,N/2\}, \frac{\pi(2q-1)}{N} \leq x_o\}$ leads to

$$\tau_{k,k+N/2} := I_1 \,+ I_2\,, \qquad \text{(A.2)}$$

where $I_1$ ($I_2$) is the rhs of Eq. (A.1) with the sum running from $q = 1$ to $q = q_0$ ($q = q_0 + 1$ to $q = N/2$).

Let us first consider $I_2$. The alternating sign in the sum together with the mean value theorem gives that $I_2$ (up to a term of order $N^{-2}$) is proportional to $N^{-1}$ times an approximation of the integral

$$\int_{x_0}^{\pi} \frac{d}{d\,x} f(x)\;d\,x = -f(x_0), \qquad \text{(A.3)}$$

where

$$f(x) = \frac{\sin(x)\,\chi(x)(1-e^{-4\lambda(x)t})}{\sin^2(x) + \chi^2(x)\,e^{-4\lambda(x)t}}\,; \qquad \text{(A.4)}$$

note that $f(\pi) = 0$, by de l'Hospital's rule. Thus, since $\frac{d}{d\,x}f(x)$ is an integrable function on $[x_0, \pi]$, $I_2$ is a term of order $N^{-1}$ and may hence be neglected, i.e. $\tau_{k,k+N/2} \approx I_1$.

Let us now turn to $I_1$, where we replace every term by approximations separately (recall that $\frac{\pi\,(2q-1)}{N} \leq x_o$):

$$\begin{array}{rcl} \sin(\frac{\pi\,(2q-1)}{N}) & \approx & \frac{\pi\,(2q_1)}{N}\,, \\ \lambda_{2q-1} & \approx & \gamma-\mu\,, \\ \chi_{2q-1} & \approx & 2\,(1-h)\,, \\ \chi_{2q-1}+\phi_{2q-1} & \approx & 2\,(1-h)\,. \end{array} \qquad \text{(A.5)}$$

These approximations result in:

$$I_1 \approx z\sum_{q=1}^{q_0} \frac{(-1)^{q+1}(2q-1)}{(2q-1)^2\,x^2+y^2}, \qquad \text{(A.6)}$$

where $x := \pi/N$, $y := 2\,(1-h)\,\exp(-2(\gamma-\mu)t)$, and $z := 4\pi\,(1-h)\;(1-\exp(-4(\gamma-\mu)t))/N^2$. Replacing the finite sums in Eq. (A.6) by the corresponding series results in [25, (6.1.62)]:

$$\tau_{k,k+N/2} \approx I_1 \approx \frac{(1-h)(1-\exp(-4(\gamma-\mu)t))}{\cosh(N\,(1-h)\exp(-2(\gamma-\mu)t))} \text{ for } h<1. \tag{A.7}$$

Fig. 7 shows that this is an appropriate approximation of $\tau_{k,k+N/2}$.

Now let $h>1$. Since $\lim_{N\to\infty}\phi_1 = 2\,(h-1)$, one finds (in the same manner as for $I_2$) that $\tau_{k,k+N/2}$ is proportional to $N^{-1}$ times an approximation of the integral

$$\int_0^\pi \frac{d}{d\,x}\,f(x)\;d\,x = f(\pi)-f(0) = 0\,, \tag{A.8}$$

i.e. $\tau_{k,k+N/2}$ is a term of order smaller than $N^{-1}$ for $h>1$.

The variance of the surplus can be determined in much the same fashion (the mean-value theorem is not required, and formula [25, (6.1.41)] may be used directly).

## A.2 Mean-field landscape: The determination of the equilibrium state $\lim_{t\to\infty} p(t)$

Let us consider the state

$$\langle\,\cdot\,\rangle_N^t = \frac{\langle\,\Omega\,,\cdot\exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle}{\langle\,\Omega\,,\exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle}\,. \tag{A.9}$$

Since $\mathcal{G}\,\Omega = \Omega$ and $[\mathcal{G},\mathcal{M}+\mathcal{R}] = 0$ for each $\mathcal{G}\in S_N$, one can rewrite $\langle\,\cdot\,\rangle_N^t$ in the form

$$\langle\,\cdot\,\rangle_N^t = \frac{\langle\,\Omega\,,\mathcal{P}\,\cdot\,\mathcal{P}\exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle}{\langle\,\Omega\,,\mathcal{P}\exp(t(\mathcal{M}+\mathcal{R}))\,\Omega\,\rangle}\,, \tag{A.10}$$

where $\mathcal{P} = (N!)^{-1}\sum_{\mathcal{G}\in S_N}\mathcal{G}$. In particular, the equilibrium state of the paramuse model is given by

$$\lim_{t\to\infty}\langle\,\cdot\,\rangle_N^t = \langle\,\Omega\,,\mathcal{P}\,\cdot\,\mathcal{P}\boldsymbol{y}\,\rangle\,, \tag{A.11}$$

where $\boldsymbol{y}$ is the Perron-Frobenius eigenvector and $\sum_{\boldsymbol{\alpha}} y_{\boldsymbol{\alpha}} = 1$. As a consequence, $\boldsymbol{y}$ is an element of the $(N+1)$-dimensional vector space (in order to simplify the notation we restrict ourselves to the case $N$ even)

$$V := \mathrm{span}_{\mathbb{C}}\{\boldsymbol{f}_m := \mathcal{P}\,\underbrace{\boldsymbol{e}_{+1}\otimes\ldots\otimes\boldsymbol{e}_{+1}}_{N/2+m}\otimes\underbrace{\boldsymbol{e}_{-1}\otimes\ldots\otimes\boldsymbol{e}_{-1}}_{N/2-m},\ -N/2\le m\le N/2\}\,. \tag{A.12}$$

Note that

$$\boldsymbol{f}_m = \binom{N}{N/2+m}^{1/2}\,|\,N/2,m\,\rangle\,, \tag{A.13}$$

where $\{ |N/2, m\rangle, -N/2 \leq m \leq N/2\}$ is the common eigenbasis of the angular momenta operators $(J_x)^2 + (J_y)^2 + (J_z)^2$ and $J_z$ ($J_a := \frac{1}{2} \sum_{k=1}^N \sigma_k^a$), all well-known from quantum mechanics ($\langle N/2, m \mid N/2, m\rangle = 1$). The coefficients in Eq. (A.13) are caused by the condition that the sum of the vector coefficients in the $2^N$-dimensional vectorspace is the same as the sum restricted to $V$:

$$\sum_{\boldsymbol{\alpha} \in \{+1,-1\}^N} y_{\boldsymbol{\alpha}} = \sum_{m=-N/2}^{N/2} \tilde{y}_m = 1 \, , \tag{A.14}$$

where

$$\boldsymbol{y} = \sum_{\boldsymbol{\alpha} \in \{+1,-1\}^N} y_{\boldsymbol{\alpha}} \, \boldsymbol{e}_{\alpha_1} \otimes \ldots \otimes \boldsymbol{e}_{\alpha_N} = \sum_{m=-N/2}^{N/2} \tilde{y}_m \, \boldsymbol{f}_m \, . \tag{A.15}$$

On the other hand, $\mathcal{M} + \mathcal{R}$ can be written in terms of angular momentum operators

$$\mathcal{M} + \mathcal{R} = 2\,\mu\,(J_x - \frac{N}{2}\mathbb{1}) + 2\,\frac{\gamma}{N}\,(J_z)^2 \, . \tag{A.16}$$

Thus, up to the similarity transformation defined in Eq. (A.13), $\mathcal{M} + \mathcal{R}$ restricted to $V$ is given by the coefficients of the angular momentum operators in quantum mechanics which belong to the irreducible representation of $su(2, \mathbb{C})$ of dimension $N+1$. As a result, $N^{-1}(\mathcal{M} + \mathcal{R})$ restricted to $V$ obeys the eigenvalue equation:

$$-\mu\,\tilde{y}_m + \mu(\frac{1}{2} + \frac{2m+2}{N})\,\tilde{y}_{m+1} + \mu(\frac{1}{2} - \frac{2m-2}{N})\,\tilde{y}_{m-1} + \frac{\gamma}{2}\,(\frac{2m}{N})^2\,\tilde{y}_m = \lambda\,\tilde{y}_m \, . \tag{A.17}$$

Now, $\lim_{t\to\infty}\langle\,\cdot\,\rangle_N^t = \langle\,\Omega\,,\,\mathcal{P}\,\cdot\,\mathcal{P}\,\boldsymbol{y}\,\rangle$ can be identified with the probability measure $f_N := \sum_{m=-N/2}^{N/2} \tilde{y}_m \, \delta_{2m/N}$ on the spectrum of $N^{-1} \sum_{k=1}^N \sigma_k^z$. We would like to remark that this is the 'permutation invariant version' of the usual formulation of $\langle\,\cdot\,\rangle_N^t$ as used in, e.g., [12]. Thus, one obtains the following equation for the measure of the equilibrium state:

$$\begin{aligned} -\mu\,(\textstyle\sum_{m=-N/2}^{N/2} \tilde{y}_m\,\delta_{2m/N}) + \mu\,(\textstyle\sum_{m=-N/2}^{N/2-1} \tilde{y}_{m+1}\,\delta_{(2m+2)/N}) \\ +\mu\,(\textstyle\sum_{m=-N/2+1}^{N/2} \tilde{y}_{m-1}\,\delta_{(2m-2)/N}) + \frac{\gamma}{2}\,(\textstyle\sum_{m=-N/2}^{N/2}(\frac{2m}{N})^2\,\tilde{y}_m\,\delta_{2m/N}) \\ = \lambda_{max}^N\,(\textstyle\sum_{m=-N/2}^{N/2} \tilde{y}_m\,\delta_{2m/N}\,). \end{aligned} \tag{A.18}$$

The Fourier transform of $f_N$ is defined as

$$\hat{f}(k) = \int_{\mathbb{R}} e^{-i\,k\,x}\,df(x) = \sum_{m=-N/2}^{N/2} \tilde{y}_m\,e^{-2\,i\,k\,\frac{m}{N}} \, , \tag{A.19}$$

cf. [9]. Thus, an application of the Fourier transformation to Eq. (A.18) results in:

$$-\frac{\gamma}{2}\frac{d^2}{d\,k^2}\,\hat{f}_N - \mu\,\sin(2\,k\,N^{-1})\frac{d}{d\,k}\,\hat{f}_N + \mu\,(\cos(2\,k\,N^{-1}) - 1)\,\hat{f}_N = \lambda_{max}^N\,\hat{f}_N \, . \tag{A.20}$$

The initial conditions of this ODE are:

$$\hat{f}_N(0) = \sum_{m=-N/2}^{N/2} \tilde{y}_m = 1, \qquad \frac{d}{d\,k}\,\hat{f}(k)\bigg|_{k=0} = 0\,. \tag{A.21}$$

The second equation is a consequence of the symmetry of $f$: Since $f$ is invariant with respect to the inversion of the spins, there must be $\tilde{y}_m = \tilde{y}_{-m}$ for all $-N/2 \le m \le N/2$. Thus, $\hat{f}(k) = \hat{f}(-k)$ for all $k \in \mathbb{R}$, which leads to the second initial condition.

Since the coefficients of Eq. (A.20) are continuous functions of $N^{-1}$, $\hat{f}_N(k)$ is a continuous function of both $N$ and $k$ [47, p.124] and will thus converge to $\hat{f}_\infty(k)$ for all $k \in \mathbb{R}$, where $\hat{f}_\infty(k)$ is the solution of the ODE

$$-\frac{\gamma}{2}\frac{d^2}{d\,k^2}\,\hat{f}_\infty = (\lim_{N\to\infty}\lambda_{max}^N)\,\hat{f}_\infty = \begin{cases} \frac{\gamma}{2}\,(1-h)^2\,\hat{f}_\infty\,, & h < 1, \\ 0\,, & h \ge 1 \end{cases} \tag{A.22}$$

where we used formula (4.50) for the energy ground state of the Ising quantum chain. Taking into account the initial conditions (A.21) one gets

$$\hat{f}_\infty(k) = \begin{cases} \frac{1}{2}e^{i\,k\,(1-h)} + \frac{1}{2}e^{-i\,k\,(1-h)}\,, & h < 1 \\ 1\,, & h \ge 1. \end{cases} \tag{A.23}$$

The fact that $\lim_{N\to\infty}\hat{f}_N(k) = \hat{f}_\infty(k)$ for all $k \in \mathbb{R}$ together with Levy's Continuity Theorem [9] results in

$$\lim_{N\to\infty} f_N = \begin{cases} \frac{1}{2}\delta(x-(1-h)) + \frac{1}{2}\delta(x+(1-h))\,, & h < 1 \\ \delta(x)\,, & h \ge 1 \end{cases} \tag{A.24}$$

in the weak topology. As a result, $h = 1$ is an error threshold of this model.

Remember that the only difference between the determination of the Perron-Frobenius eigenvector of the para-muse model and the calculation of the energy ground state of the quantum chain is the similarity transformation defined in Eq. (A.13). But in the thermodynamic limit the energy ground state (represented as a vector) is given by

$$\lim_{N\to\infty} g_N = \begin{cases} \frac{1}{2}\delta(x-(\frac{1}{2}(1-\sqrt{1-h^2})) + \frac{1}{2}\delta(x+(\frac{1}{2}(1-\sqrt{1-h^2}))\,, & h < 1 \\ \delta(x)\,, & h \ge 1 \end{cases} \tag{A.25}$$

in contrast to Eq. (A.24); cf. [6]. Obviously, the thermodynamic limit does not commute with the similarity transformation.

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# Figure Captions

Figure 1:
Average surplus of sites with value +1 ($s$) at equilibrium, in the thermodynamic limit. Dotted: Fujiyama landscape (with $\alpha_j \equiv \alpha = 1$); dashed: Onsager landscape(with $\gamma = 1$); solid line: mean-field landscape(with $\gamma = 2$).

Figure 2:
Mean fitness per spin ($w$) at equilibrium, in the thermodynamic limit. Dotted: Fujiyama landscape; dashed: Onsager landscape; solid line: mean-field landscape. Parameters as in Fig. 1.

Figure 3:
Fujiyama landscape: Time evolution of the surplus in the case $\mu = 0.5$, $\gamma = 1$. Solid line: Time evolution according to Eq. (4.8). Dashed line: surplus in the limit $t \to \infty$, cf. Fig. 1.

Figure 4:
Onsager's landscape: Time evolution of the surplus according to Eq. (4.30) in the case $\mu = 0$ and $\gamma = 1$. Dotted line: $b = 0.01$; dashed line: $b = 0.0033$; solid line: $b = 0.001$.

Figure 5:
Onsager's landscape: Time evolution of $\tau_{k,k+N/2}$ for $N = 100$, $\gamma = 1$, as given by the approximate formula (4.31). Dotted line: $\mu = 0.1$; dashed line: $\mu = 0.5$; solid line: $\mu = 0.9$.

Figure 6:
Onsager's landscape: Time evolution of $\tau_{k,k+1}$ for $\gamma = 1$, as given by formula (4.35). Dotted line: $N = 10$; dashed line: $N = 100$; solid line: $N = 1000$.

Figure 7:
Onsager's landscape: Time-evolution of $\tau_{k,k+N/2}$. Solid lines: exact solutions (A.1) for $N = 50$. Dashed lines: approximations in the large system limit according to Eq. (4.31).

Figure 8:
Onsager's landscape: Second derivative of $w$ with respect to $h$, cf. Eq. (4.35). Solid line: $N = 100$. Dotted line: $N = 1000$.

Figure 9:
Mean-field landscape: time evolution of the surplus. Dotted line: Numerical solution for $N = 150$, with the initial condition $\boldsymbol{x}_0 = 2^{-N/2}\Omega$. Dashed line: Numerical solution for $N = 150$, with the initial condition $\boldsymbol{x}_0 = \frac{2^{-N/2}}{10}\Omega + \frac{9}{10}(0, \ldots, 0, 1, 0, \ldots, 0)^T$, with 1 in the $N/2$-th place. Solid line: Conjectured solution in the thermodynamic limit, according to Eq. (4.61).

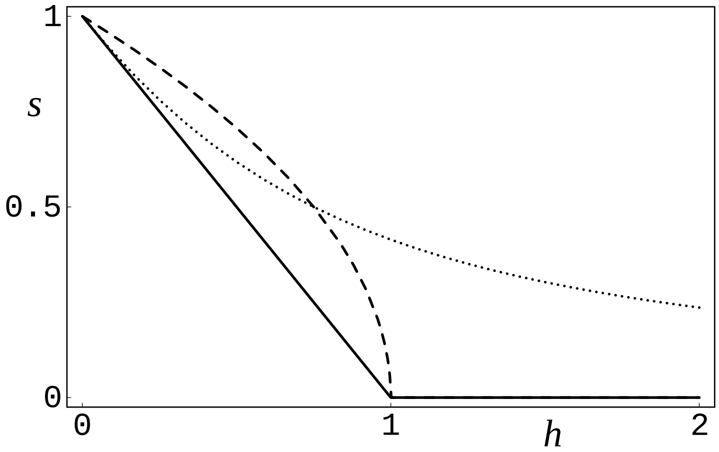



Figure 1:

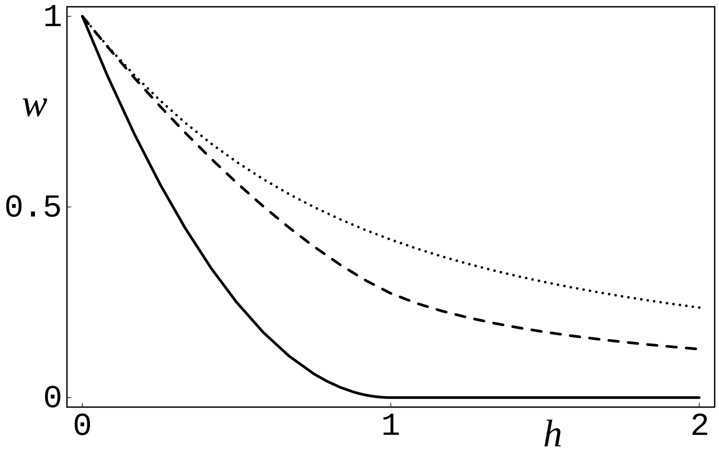
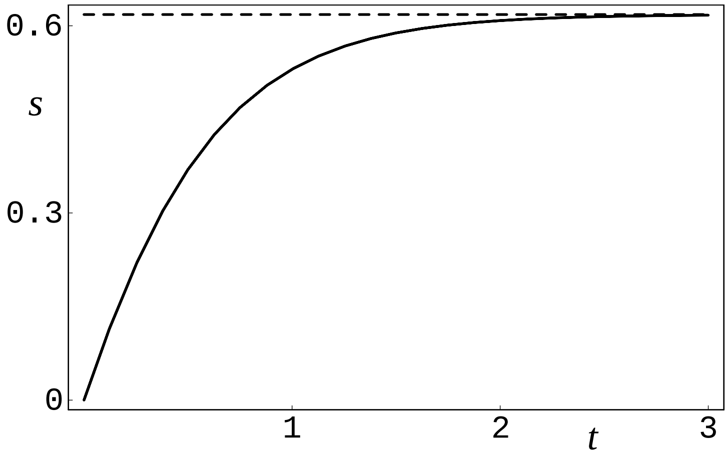



Figure 2:

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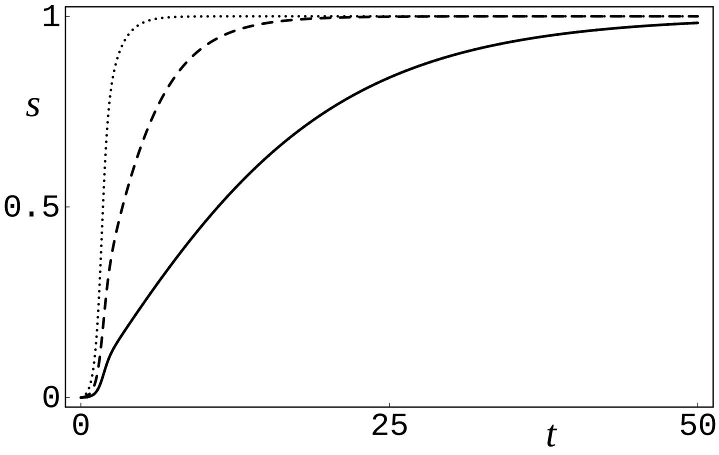


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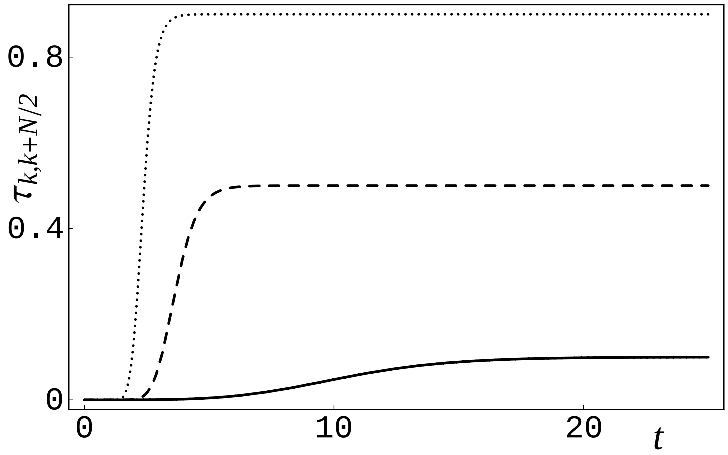


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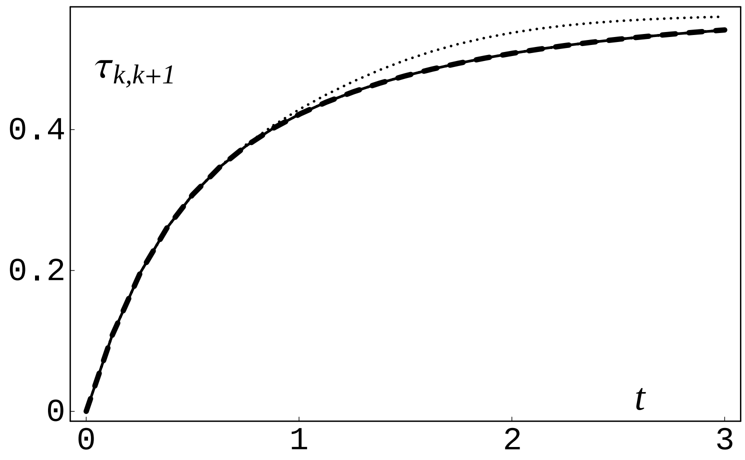


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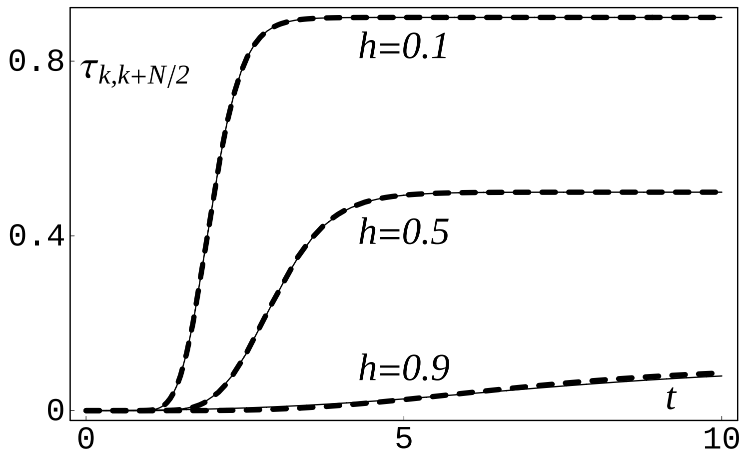


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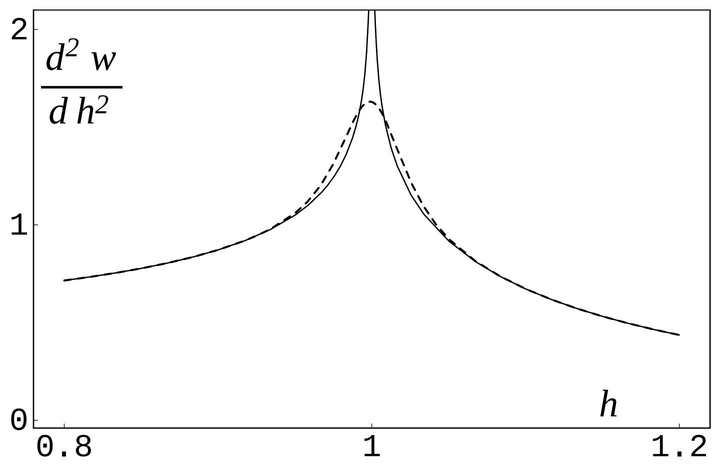


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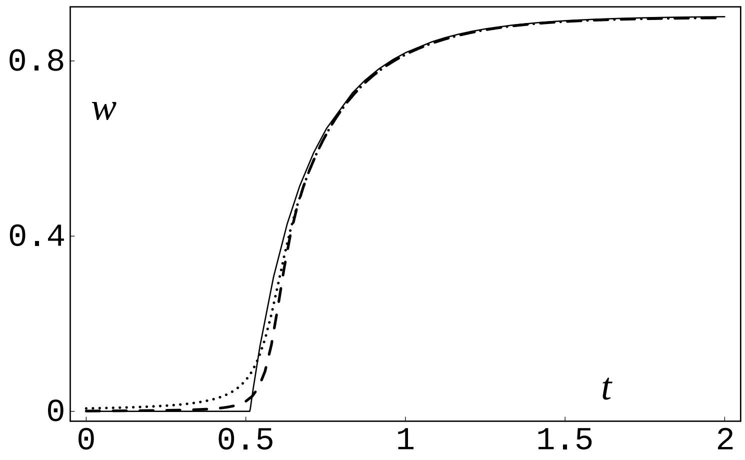


Figure 9: