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HOLLIDAY JUNCTIONS IN THE BLUME–CAPEL MODEL OF DNA

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We regard a DNA molecule as a configuration of the Blume–Capel model on paths in a Cayley tree. We study translation-invariant Gibbs measures (TIGMs) of the model on the Cayley tree of order two and show that there is a critical temperature T_c such that there exists a unique TIGM if the temperature $T > T_c$, there are two TIGMs if $T = T_c$, and there are three TIGMs if $T < T_c$. Each such measure describes a phase of the set of DNA molecules. We use these measures to study probability distributions of Holliday junctions in DNA molecules.

Keywords: Cayley tree, Blume–Capel model, Gibbs measure, Holliday junction

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1. Introduction and definitions

As is known, each DNA molecule is a double helix formed from two complementary strands of nucleotides held together by hydrogen bonds between C+G (cytosine–guanine) and A+T (adenine–thymine) base pairs. Molecules of DNA store genetic information and contain instructions for all the proteins that an organism will ever synthesize [1].

A Holliday junction [2] is a cross-shaped structure that forms during the process of genetic recombination when two double-stranded DNA molecules become separated into four strands to exchange segments of genetic information.

In [3], [4], Ising and Potts models were considered for describing DNA and studying its thermodynamics. It was shown that depending on the temperature, the number of translation-invariant Gibbs measures (TIGMs) can reach three. We note that nonuniqueness of the Gibbs measure corresponds to the coexistence of different phases in a system of DNA molecules. Holliday structures and DNA branches are studied using the theory of Markov chains (corresponding to TIGMs). Other results about the Blume–Capel model can be found in [5]–[7].

Here, we consider a set of DNA molecules that "live" on a tree graph. Let l be an edge of this graph and a function $\sigma(l)$ take a value -1, 0, or 1 (an analogue of spin values in a physical system). If $\sigma(l) = 0$, then we say that the edge l does not belong to DNA. If the edge l separates two DNA molecules, then the value $\sigma(l) = 1$ or $\sigma(l) = -1$ means that these two DNA are joined by a Holliday junction.

Following [3], [4], [8], we recall some definitions.

A Cayley tree Γ^k of order $k \geq 1$ is an infinite tree, i.e., a graph without cycles, with exactly $k+1$ edges at each vertex. Let $\Gamma^k = (V, L, i)$, where V and L are the sets of vertices and edges of the Cayley tree and i is the incidence function assigning each edge $l \in L$ its endpoints $x, y \in V$. If $i(l) = \{x, y\}$, then the vertices

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x and y are called nearest neighbors, denoted by $l = \langle x, y\rangle$. For two vertices $x, y \in V$, the distance $d(x, y)$ is the number of edges in the shortest path connecting x and y:

$$d(x,y) = \min\{d\colon \exists\, x = x_0, x_1, \dots, x_{d-1}, x_d = y \in V \text{ such that } \langle x_0, x_1\rangle, \dots, \langle x_{d-1}, x_d\rangle\}.$$

For a fixed vertex $x^0 \in V$ and $n \geq 1$, we set

$$\begin{aligned} &V_n = \{x \in V\colon d(x^0, x) \leq n\}, \qquad W_n = \{y \in V\colon d(x^0, y) = n\},\\ &\text{L}_n = \{l = \langle x, y\rangle \in L\colon x, y \in V_n\}. \end{aligned} \tag{1}$$

Let $\mathbb{Z} = \{\dots, -2, -1, 0, 1, 2 \dots\}$. It was proved in [9] that all vertices of a Cayley tree can be partitioned into equivalence classes labeled by integers and that through each vertex belonging to the mth equivalence class, there passes a unique path such that the labels of the equivalence classes to which successive vertices belong form an integer sequence $\dots, m-2, m-1, m, m+1, m+2, \dots$, which is infinite in both directions. Each such path is called a $\mathbb{Z}$-path.

We consider a function σ assigning each edge $l \in L$ values $\sigma(l) \in \{-1, 0, 1\}$ such that -1 = A+T, 1 = C+G, and $\sigma(l) = 0$ means that the edge is "free." A function $\sigma = \{\sigma(l),\, l \in L\}$ is called a configuration. The set of all configurations on L is denoted by Ω. A configuration $\sigma = \{\sigma(l),\, l \in L\}$ is said to be *admissible* if $\sigma(l) \neq 0$ for all $l \in \mathbb{Z}$-path. A restriction of an admissible configuration to a $\mathbb{Z}$-path is called a DNA molecule (because a DNA molecule can be defined as a sequence of base pairs, i.e., numbers -1 and 1). The set of admissible configurations on L or L_n is denoted by Ω^{a} or Ω^{a}_n.

We consider the following Blume–Capel model of the energy of a configuration σ of a set of DNA molecules [10]:

$$H(\sigma) = J \sum_{\langle l,t\rangle \in L\times L} (\sigma(l) - \sigma(t))^2, \tag{2}$$

where $J > 0$ is a coupling constant, $\sigma(l) \in \{-1, 0, 1\}$, and $\langle l, t\rangle$ denotes nearest neighbor edges, i.e., edges with a common vertex. We set

$$E_n = \{\langle x, y\rangle \in L\colon x \in W_{n-1}, y \in W_n\}.$$

For $l \in E_{n-1}$, we set

$$S(l) = \{t \in E_n\colon \langle l, t\rangle)\}.$$

It is easy to see that

$$S(l) \cap \mathbb{Z}\text{-path} = \begin{cases} \{l_0, l_1\} \subset L, & l \notin \mathbb{Z}\text{-path},\\ \{l_1\} \subset L, & l \in \mathbb{Z}\text{-path}. \end{cases}$$

We set

$$\begin{aligned} &S_0(l) = S(l)\backslash\{l_0, l_1\}, \quad l \notin \mathbb{Z}\text{-path},\\ &S_1(l) = S(l)\backslash\{l_1\}, \qquad l \in \mathbb{Z}\text{-path}. \end{aligned} \tag{3}$$

We can standardly reduce (see [3], [4]) the problem of studying Gibbs measures of the Blume–Capel model to the problem of solving the system of functional equations

$$\begin{aligned} z_{0,l} &= \frac{\lambda z_{l_0} + \lambda}{\lambda^4 z_{l_0} + 1} \frac{\lambda z_{l_1} + \lambda}{\lambda^4 z_{l_1} + 1} \prod_{t \in S_0(l)} \frac{\lambda z_{1,t} + \lambda + z_{0,t}}{\lambda^4 z_{1,t} + 1 + \lambda z_{0,t}}, \quad l \notin \mathbb{Z}\text{-path},\\ z_{1,l} &= \frac{z_{l_0} + \lambda^4}{\lambda^4 z_{l_0} + 1} \frac{z_{l_1} + \lambda^4}{\lambda^4 z_{l_1} + 1} \prod_{t \in S_0(l)} \frac{z_{1,t} + \lambda^4 + \lambda z_{0,t}}{\lambda^4 z_{1,t} + 1 + \lambda z_{0,t}}, \quad l \notin \mathbb{Z}\text{-path},\\ z_l &= \frac{z_l + \lambda^4}{\lambda^4 z_l + 1} \prod_{t \in S_1(l)} \frac{z_{1,t} + \lambda^4 + \lambda z_{0,t}}{\lambda^4 z_{1,t} + 1 + \lambda z_{0,t}}, \qquad\qquad l \in \mathbb{Z}\text{-path}, \end{aligned} \tag{4}$$

where $\lambda = e^{-J\beta}$.

For any set of vectors $\mathbf{z} = (z_{0,l}, z_{1,l}, z_t)$, where $l \notin \mathbb{Z}$-path and $t \in \mathbb{Z}$-path, satisfying system of functional equations (4), there exists a unique Gibbs measure μ, and vice versa. But analyzing solutions of system (4) is difficult. We present several solutions in the next section.

2. TIGMs of the DNA set

The TIGMs correspond to solutions $\mathbf{z} = (z_{0,l}, z_{1,l}, z_t)$, where $l \notin \mathbb{Z}$-path and $t \in \mathbb{Z}$-path, that are independent of l and t:

$$z_{0,l} = u, \qquad z_{1,l} = v \quad \text{for all } l \notin \mathbb{Z}\text{-path}, \qquad z_t = w \quad \text{for all } t \in \mathbb{Z}\text{-path}. \tag{5}$$

Here, u, v, and w are positive by virtue of (4) and satisfy the system of equations

$$\begin{aligned} u &= \left(\frac{\lambda v + \lambda + u}{\lambda^4 v + 1 + \lambda u}\right)^{k-2} \left(\frac{\lambda w + \lambda}{\lambda^4 w + 1}\right)^2, \\ v &= \left(\frac{v + \lambda^4 + \lambda u}{\lambda^4 v + 1 + \lambda u}\right)^{k-2} \left(\frac{w + \lambda^4}{\lambda^4 w + 1}\right)^2, \\ w &= \left(\frac{v + \lambda^4 + \lambda u}{\lambda^4 v + 1 + \lambda u}\right)^{k-1} \left(\frac{w + \lambda^4}{\lambda^4 w + 1}\right). \end{aligned} \tag{6}$$

It is clear that $v = w = 1$ satisfies this system for any $k \geq 2$ and $\lambda < 1$, and from the first equation in the system, we then obtain

$$u = \left(\frac{2\lambda + u}{\lambda^4 + \lambda u + 1}\right)^{k-2} \left(\frac{2\lambda}{\lambda^4 + 1}\right)^2. \tag{7}$$

Solving this equation is difficult for $k \geq 3$, and we therefore consider the case $k = 2$. In this case, from (7), we obtain

$$u = \left(\frac{2\lambda}{\lambda^4 + 1}\right)^2 = \left(\frac{e^{J\beta}}{\cosh(2J\beta)}\right)^2.$$

Hence, for $k = 2$ and any λ, the vector $\left((e^{-J\beta}\cosh(2J\beta)\right)^{-2}, 1, 1)$ is a solution of system (6).

To find other solutions (with $k = 2$), we substitute u and v in the third equation in system (6) and obtain

$$w = \frac{w + \lambda^4}{\lambda^4 w + 1}\left(\frac{(w + \lambda^4)^2 + \lambda^4(\lambda^4 w + 1)^2 + \lambda(\lambda w + \lambda)^2}{\lambda^4(w + \lambda^4)^2 + (\lambda^4 w + 1)^2 + \lambda(\lambda w + \lambda)^2}\right).$$

Solving this equation, we obtain three solutions: $w_1 = 1$ and

$$\begin{aligned} w_2 = w_2(\lambda) &= \frac{1 - \lambda^{12} + 3\lambda^8 - 2\lambda^7 - \lambda^4 - \sqrt{D}}{2(\lambda^{12} + \lambda^8 + \lambda^7)}, \\ w_3 = w_3(\lambda) &= \frac{1 - \lambda^{12} + 3\lambda^8 - 2\lambda^7 - \lambda^4 + \sqrt{D}}{2(\lambda^{12} + \lambda^8 + \lambda^7)}, \end{aligned}$$

where

$$D = (1 - 3\lambda^{12} - 5\lambda^8 - 4\lambda^7 - \lambda^4)(\lambda^4 - 1)^2(\lambda^4 + 1).$$

The solutions w_2 and w_3 exist if and only if

$$g(\lambda) = 3\lambda^{12} + 5\lambda^8 + 4\lambda^7 + \lambda^4 - 1 \leq 0.$$

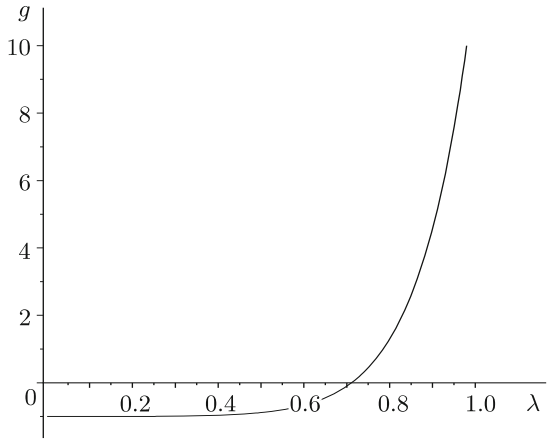

Fig. 1. Plot of the function $g(\lambda)$.

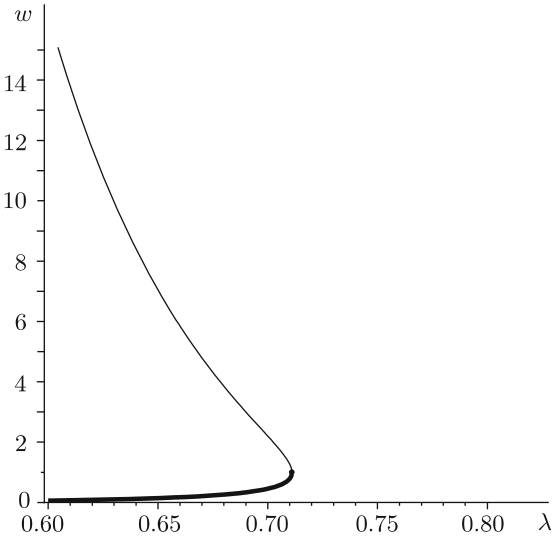

Fig. 2. Plots of the functions $w_2(\lambda)$ (bold curve) and $w_3(\lambda)$ (thin curve) for $\lambda \in (0, \lambda_*]$: the curves meet at λ_*, where $w_2(\lambda_*) = w_3(\lambda_*) = 1$.

The function $g(\lambda)$, $\lambda > 0$, increases, $g(0) = -1 < 0$, and $g(\lambda) > 0$ for $\lambda > 1$. We hence obtain $g(\lambda) < 0$ for all $\lambda < \lambda_*$, where $\lambda_* \approx 0.7110460893$ (see Fig. 1).

We note that the functions w_2 and w_3 are positive and $w_2 w_3 = 1$ (see the plots of these solutions as functions of $\lambda \in (0, \lambda_*]$ in Fig. 2).

For $k = 2$, we have thus proved the following lemma.

Lemma 1. *We have the following statements*:

- *If* $\lambda = e^{-J\beta} > \lambda_*$, *then system* (6) *has a unique solution*

$$\mathbf{z}_1 = (u_1, v_1, w_1) = \big((e^{-J\beta}\cosh(2J\beta))^{-2}, 1, 1\big).$$

- *If* $\lambda = \lambda_*$, *then system* (6) *has two solutions*

$$\mathbf{z}_1 = (u_1, v_1, w_1) = \big((e^{-J\beta}\cosh(2J\beta))^{-2}, 1, 1\big), \qquad \mathbf{z}_2 = (u_2, v_2, w_2).$$

- *If $\lambda < \lambda_*$, then system (6) has three solutions*

$$\mathbf{z}_1 = (u_1, v_1, w_1) = \big((e^{-J\beta} ch(2J\beta))^{-2}, 1, 1\big), \qquad \mathbf{z}_2 = (u_2, v_2, w_2), \qquad \mathbf{z}_3 = (u_3, v_3, w_3).$$

Here,

$$u_i = \left(\frac{\lambda w_i + \lambda}{\lambda^4 w_i + 1}\right)^2, \qquad v_i = \left(\frac{w_i + \lambda^4}{\lambda^4 w_i + 1}\right)^2, \quad i = 2, 3.$$

We let μ_i denote the Gibbs measure corresponding to the solution $\mathbf{z}_i$, $i = 1, 2, 3$. We define the critical temperature

$$T_{\rm c} = \frac{1}{\log \lambda_*^{-1}}.$$

Summarizing the results obtained above, we formulate the following theorem.

Theorem 1. *For model (2) of DNA molecules on the Cayley tree of order $k = 2$, we have the following statements*:

1. *If the temperature $T > T_{\rm c}$, then there is a unique TIGM μ_1.*
2. *If $T = T_{\rm c}$, then there are two TIGMs μ_1 and μ_2.*
3. *If $T < T_{\rm c}$, then there are three TIGMs μ_1, μ_2, and μ_3.*

3. Markov chains corresponding to TIGMs and the Holliday junction in a DNA molecule

For marginal distributions on the set of pairs of neighboring edges l and t, considering the boundary function $z_{0,l}$ and $z_{1,l}$ for $l \notin \mathbb{Z}$-path and z_t for $t \in \mathbb{Z}$-path with the normalization condition $z_{-1,l} = 1$ for -1, i.e., solutions of system (4), we obtain

$$\mu(\sigma(l) = a, \sigma(t) = b) = \frac{1}{Z} z_{a,l} e^{\beta(a-b)^2} z_{b,t}, \quad a, b = -1, 0, 1,$$

where Z is the normalizing factor. Using formulas (3) and (5) for solutions of system (6), we hence obtain three-indexed transition matrices $\mathbb{P}^{[l,t]} = (\mathbb{P}^{[l,t]}_{ij})$ of Markov chains related to Gibbs measures [11]:

$$\mathbb{P}^{[l,t]} = \mathbb{P}^{[l,t]}_{(3\to3)} = \begin{pmatrix} \dfrac{1}{1+\lambda u+\lambda^4 v} & \dfrac{\lambda u}{1+\lambda u+\lambda^4 v} & \dfrac{\lambda^4 v}{1+\lambda u+\lambda^4 v} \\ \dfrac{\lambda}{\lambda+u+\lambda v} & \dfrac{u}{\lambda+u+\lambda v} & \dfrac{\lambda v}{\lambda+u+\lambda v} \\ \dfrac{\lambda^4}{\lambda^4+\lambda u+v} & \dfrac{\lambda u}{\lambda^4+\lambda u+v} & \dfrac{v}{\lambda^4+\lambda u+v} \end{pmatrix}, \quad l, t \notin \mathbb{Z}\text{-path},$$

$$\mathbb{P}^{[l,t]} = \mathbb{P}^{[l,t]}_{(3\to2)} = \begin{pmatrix} \dfrac{1}{1+\lambda^4 w} & 0 & \dfrac{\lambda^4 w}{1+\lambda^4 w} \\ \dfrac{\lambda}{\lambda+\lambda w} & 0 & \dfrac{\lambda w}{\lambda+\lambda w} \\ \dfrac{\lambda^4}{\lambda^4+w} & 0 & \dfrac{w}{\lambda^4+w} \end{pmatrix}, \qquad l \notin \mathbb{Z}\text{-path}, \ t \in \mathbb{Z}\text{-path},$$

$$\mathbb{P}^{[l,t]} = \mathbb{P}^{[l,t]}_{(2\to2)} = \begin{pmatrix} \dfrac{1}{1+\lambda^4 w} & \dfrac{\lambda^4 w}{1+\lambda^4 w} \\ \dfrac{\lambda^4}{\lambda^4+w} & \dfrac{w}{\lambda^4+w} \end{pmatrix}, \qquad l, t \in \mathbb{Z}\text{-path}.$$

Here, the matrix element $\mathbb{P}_{ij}^{[l,t]}$ is the probability of the transition from the state i on the edge l to the state j on the neighboring edge t. We note that each matrix $\mathbb{P}_{n\to m}^{[l,t]}$, $n,m=2,3$, is homogenous on the corresponding set of neighboring edges l and t where it is defined, i.e., this matrix depends not on the pair l,t itself but on whether it belongs to a $\mathbb{Z}$-path.

For the matrix $\mathbb{P}_{(n\to m)}^{[l,t]}$ with $n=m$, it is easy to find the stationary distribution

$$\pi_{(n\to m)}=\big(\pi_{(n\to m),-1},\pi_{(n\to m),0},\pi_{(n\to m),1}\big).$$

Namely, we have

$$\pi_{(3\to 3)}=\frac{1}{N}\big(1+\lambda u+\lambda^4 v,\ (\lambda+u+\lambda v)u,\ (\lambda^4+\lambda u+v)v\big),$$

where N is the normalization factor, and

$$\pi_{(2\to 2)}=\left(\frac{1+\lambda^4 w}{w^2+2\lambda^4 w+1},\ \frac{w(\lambda^4+w)}{w^2+2\lambda^4 w+1}\right).$$

Using the ergodic theorem for stochastic matrices (see [11]) and the formulas presented above, we obtain the following statement.

Theorem 2. *In a stationary state of the DNA set for any $l\notin\mathbb{Z}$-path, a Holliday junction through the edge l does not occur with the probability (with respect to the measure μ_i, $i=1,2,3$)*

$$\pi_{(3\to 3),0}=\pi_{(3\to 3),0}^{(i)}=\frac{1}{N}(\lambda+u_i+\lambda v_i)u_i,$$

(consequently, a Holliday junction is formed with the probability $1-\pi_{(3\to 3),0}^{(i)}$), where (u_i,v_i) are defined in Lemma 1.

It can seen that $\pi_{(3\to 3),0}^{(i)}$ is a function of only i and the temperature.

We now find the limits of the stationary distribution vectors $\pi_{(3\to 3)}^{(i)}$ and $\pi_{(2\to 2)}^{(i)}$ (corresponding to the Markov chain generated by the measure μ_i) as $T\to 0$ (as $\beta\to\infty$ and $\lambda\to 0$) and as $T\to+\infty$ (as $\beta\to 0$ and $\lambda\to 1$). To find the limits, we take the dependence of u_i, v_i, and w_i, $i=1,2,3$ on $T=1/\beta$ into account.

Lemma 2. *We have the relations*

$$\lim_{T\to 0}\pi_{(3\to 3)}^{(1)}=\left(\frac{1}{2},0,\frac{1}{2}\right),\qquad \lim_{T\to 0}\pi_{(3\to 3)}^{(2)}=(1,0,0),\qquad \lim_{T\to 0}\pi_{(3\to 3)}^{(3)}=(0,0,1),$$

$$\lim_{T\to 0}\pi_{(2\to 2)}^{(1)}=\left(\frac{1}{2},\frac{1}{2}\right),\qquad \lim_{T\to 0}\pi_{(2\to 2)}^{(2)}=(1,0),\qquad \lim_{T\to 0}\pi_{(2\to 2)}^{(3)}=(0,1)$$

in the low-temperature case $T\to 0$ and

$$\lim_{T\to+\infty}\pi_{(3\to 3)}^{(1)}=\left(\frac{1}{3},\frac{1}{3},\frac{1}{3}\right),$$

$$\lim_{T\to T_c}\pi_{(3\to 3)}^{(i)}\approx(0.27773205,0.4445359,0.27773205),\quad i=1,2,3,$$

$$\lim_{T\to+\infty}\pi_{(2\to 2)}^{(1)}=\lim_{T\to T_c}\pi_{(2\to 2)}^{(i)}=\left(\frac{1}{2},\frac{1}{2}\right)$$

in the high-temperature case $T\to\infty$.

By Lemma 2, we have the following structures of the DNA set. We recall that -1 = A+T and 1 = C+G in our construction. Moreover, we assumed that A+T = T+A and similarly for G+C.

1. As $T \to 0$, the DNA set has the following stationary states (configurations).

Case μ_1. All neighboring DNA molecules are connected to each other (via Holliday junctions) with the state $\sigma(l) = -1$ for any $l \notin \mathbb{Z}$-path. The sequence of 1 in a DNA on the $\mathbb{Z}$-path is free, i.e., can be any sequence, with independent identically distributed and equiprobable (1/2) states 1 and -1.

Case μ_2. All neighboring DNA molecules are connected to each other (via Holliday junctions) with the state $\sigma(l) = -1$ for any $l \notin \mathbb{Z}$-path. The sequence of 1 in a DNA on the $\mathbb{Z}$-path is fixed, i.e., $\sigma(l) = -1$ for all $l \in \mathbb{Z}$-path. Hence, the system contains only one multiple (countable) branched DNA (which has a tree structure).

Case μ_3. All neighboring DNA molecules are connected to each other with the state $\sigma(l) = 1$ for any $l \notin \mathbb{Z}$-path. The DNA on the $\mathbb{Z}$-path is fixed, i.e., $\sigma(l) = 1$ for all $l \in \mathbb{Z}$-path. Hence, this case is similar to the case μ_2, but all -1 are replaced with 1.

2. In the case $T = T_c$, the DNA set has the following stationary states: all neighboring DNA molecules have a Holliday junction with probability 0.5554641 (more precisely, a junction via state -1 with probability 0.27773205 and a junction via state 1 with probability 0.27773205) and no junction with probability 0.4445359. The sequence of ± 1 in a DNA on the $\mathbb{Z}$-path is free with independent identically distributed and equiprobable (1/2) states 1 and -1.

3. In the case $T \to +\infty$, the DNA set has the following stationary states: all neighboring DNA molecules have a Holliday junction with probability 2/3 (more precisely, a junction via state -1 or 1 with equiprobable 1/3) and no junction with probability 1/3. The sequence of ± 1 in a DNA on the $\mathbb{Z}$-path is free similarly to the case $T = T_c$.

4. Conclusions

We have obtained the following results for the Blume–Capel DNA model on a Cayley tree.

There is a critical temperature T_c (we found its approximative value) such that

for $T > T_c$, there is a unique TIGM,

for $T = T_c$, there are two TIGMs, and

for $T < T_c$, there are three TIGMs.

Each such measure describes a phase of the DNA set. Our results related to Gibbs measures allowed studying the probability distributions of Holliday junctions. For very high and very low temperatures, we found stationary distributions and typical configurations of Holliday junctions.

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