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A random matrix approach to RNA folding with interaction

I GARG and N DEO*
Department of Physics & Astrophysics, University of Delhi, Delhi 110 007, India
*Corresponding author. E-mail: ndeo@physics.du.ac.in

Abstract. In the matrix model of RNA [G Vernizzi, H Orland and A Zee, *Phys. Rev. Lett.* **94**, 168103 (2005)] we introduce external interactions on n bases in the action of the partition function where $n \leq L$ and L is the length of the polymer chain. The RNA structures found in the model can be separated into two regimes: (i) $0 \leq \alpha \leq 1$, $n < L$ and $0 \leq \alpha < 1$, $n = L$ where unpaired and paired base structures exist and (ii) $\alpha = 1$, $n = L$ with only completely paired base structures. Figures for the genus distribution functions show differences at small lengths. We consider the situation when the strength of external perturbation is different on different bases in the polymer chain.

Keywords. RNA folding; random matrix model; external perturbation.

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1. Introduction

Random matrix models have played an important role in understanding complex systems like the nucleus, quantum chaos, disordered condensed matter systems, quantum chromodynamics, quantum gravity and string theory [1–3]. A random matrix model of RNA which captures the topological character of RNA has been studied in [4]. The partition function of the RNA polymer chain in the model has contributions from the tertiary in addition to the planar structures (primary and secondary). The approach is based on the observation made by G 't Hooft [5] which relates the topology of the Feynman graph with the powers of $1/N^2$ (N being the dimension of the matrix in the theory). N in the model is analogous to the role played by chemicals/ions in a cell such as Na^+ and Mg^{2+} which help in the separation of secondary and tertiary structures [6]. A tractable random matrix model of RNA is obtained by making the following simplifications in [4]: (i) all base pairings are allowed (not just complementary base pairings: Watson–Crick (A–U, G–C) and Wobble (G–U)), (ii) all base pairings come with the same probability v and (iii) the chain is considered to be infinitely flexible, i.e., the stiffness and rigidity of the chain are neglected [7]. This model counts all the possible types of structures (primary, secondary and tertiary) that can exist for any length L of the polymer chain (length given by the number of bases in the chain). Though the model does not take into consideration the effects such as base stacking and

finite flexibility of the polymer chain, it captures the topological properties of RNA which are essential for understanding the folding of RNA. For example, the average genus of a structure for a given length L of the chain in [7] is found to be $\leq L/4$ which is a result observed for the real RNA sequences [8]. The total number of structures counted by the matrix model [7] are large if we compare them with the structures that have been discovered. A change in the RNA structure can occur due to contact with cell walls, ions and other organelles, during transcription and translation among other genetically important processes. These changes are of interest in order to study and completely understand different types of RNA structures and their functions. Thus we study the effect of interactions which are added in the action of the partition function of the model of RNA in [7]. As a first step, we consider a simple interaction so that the basic structure of the model is retained. The next important steps are to consider non-linear interactions and to study their effects.

In §2, we study the matrix model of RNA folding with an external interaction introduced on $n \leq L$ bases in the action of the partition function of the polymer chain. The general form of the partition function for the polymer chain is found which gives the Feynman diagram representation of the model with interaction and we discuss the genus distribution functions for the case $n = L$. Section 3 presents a general method to consider the effect of external interactions when the strength of interaction is different on the bases of the polymer chain.

2. Matrix model of RNA with an external interaction on $n \leq L$ nucleotides

The matrix models of RNA [4,7] are non-trivial due to the presence of a complicated observable along with the Gaussian potential [6]. The complexity with the addition of external interactions makes computations in these models very difficult. We add a perturbation, $U(\phi_i)$, in the action of the partition function of the random matrix model of [7] (which is a simplification of [4]) and study the effect of external interaction when it acts on different nucleotides. The partition function of the matrix model with perturbation is

$$Z_{L,\alpha}(N) = \frac{1}{A_L(N)} \int \prod_{i=1}^{L} \mathrm{d}\phi_i \mathrm{e}^{-\frac{N}{2}\sum_{i,j=1}^{L}(V^{-1})_{i,j}\mathrm{Tr}\phi_i\phi_j} \times \mathrm{e}^{-N\mathrm{Tr}U(\phi)} \frac{1}{N}\mathrm{Tr}\prod_{i=1}^{L}(1+\phi_i). \tag{1}$$

We discuss the addition of linear external interaction on $n \leq L$ bases in the action of the partition function of the polymer chain. Adding a linear interaction in these matrix models is an important step [9,10]. The partition function is given by

$$Z_{L,\alpha}(N) = \frac{1}{A_L(N)} \int \prod_{i=1}^{L} \mathrm{d}\phi_i \mathrm{e}^{-\frac{N}{2}\sum_{i,j=1}^{L}(V^{-1})_{i,j}\mathrm{Tr}\phi_i\phi_j} \times \mathrm{e}^{-N\sum_{i=1}^{n}(W^{-1})_i\mathrm{Tr}\phi_i} \frac{1}{N}\mathrm{Tr}\prod_{i=1}^{L}(1+\phi_i), \tag{2}$$

where ϕ_i are $(i = 1, ..., L)$ independent $(N \times N)$ Hermitian matrices, $V_{i,j}$ are the elements of a $(L \times L)$ interaction matrix giving interactions between the bases at positions i and j and the observable $\prod_i(1 + \phi_i)$ is an ordered product over ϕ_i that ensure self-pairing of bases is not allowed. The interaction term is $\mathrm{e}^{-N\sum_{i=1}^{n}(W_i)^{-1}\mathrm{Tr}\phi_i}$ where $W_i = w$ gives the strength of the external perturbation and $i = 1, ..., n$ in the sum of the interaction term [11]. $A_L(N)$ is the normalization constant, $A_L(N) = \int\prod_{i=1}^{L}\mathrm{d}\phi_i\mathrm{e}^{-\frac{N}{2}\sum_{i,j=1}^{L}(V^{-1})_{i,j}\mathrm{Tr}\phi_i\phi_j}\mathrm{e}^{(-N)\sum_{i=1}^{n}(W^{-1})_i\mathrm{Tr}\phi_i}$ which can be rewritten as $A_L(N) = \mathrm{e}^{\frac{N}{2}\mathrm{Tr}(\frac{n^2v}{L^2w^2})}\int\prod_{i=1}^{L}\mathrm{d}\Phi_i\mathrm{e}^{-\frac{N}{2}\mathrm{Tr}[\Phi_i(V^{-1})_{i,j}\Phi_j]}$ where Φ is defined as $\Phi_i = (\phi_i + V_{i,j}W_j^{-1})$.

Considering $V_{i,j} = v$ and performing a series of Hubbard–Stratonovich transformations on the multi-matrix integral in eq. (2) (keeping all the assumptions the same as in [7]), we get the partition function

$$Z_{L,\alpha}(N) = \frac{X}{R_L(N)}\int\mathrm{d}\sigma\mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}(\sigma)^2}\int\prod_{i=1}^{L}\mathrm{d}\psi_i\mathrm{d}\phi_i\mathrm{e}^{i\mathrm{Tr}[\phi_i\sum_i\psi_i-\sigma\sum_i\psi_i]} \times\mathrm{e}^{\frac{-N}{Lw}\sum_{i=1}^{n}\mathrm{Tr}\phi_i}\frac{1}{N}\mathrm{Tr}\prod_{i=1}^{L}(1+\phi_i), \tag{3}$$

where $X^{-1} = \mathrm{e}^{\frac{N}{2}\mathrm{Tr}(\frac{n^2v}{L^2w^2})}$ and $R_L(N) = \int\mathrm{d}\sigma\mathrm{e}^{\frac{-N}{2v}\mathrm{Tr}(\sigma)^2}$ is the normalization constant. In eq. (3), sum over the perturbation term runs up to n. The integral over ψ_i is a delta function, $\int\prod_{i=1}^{L}\mathrm{d}\psi_i\mathrm{e}^{i\mathrm{Tr}[\phi_i\sum_i\psi_i-\sigma\sum_i\psi_i]} = \prod_{i=1}^{L}\delta(\phi_i-\sigma)$, which will replace each of the n ϕ_is with σ. Partition function in eq. (3) using the definition of delta function is

$$Z_{L,\alpha}(N) = \frac{X}{R_L(N)}\int\mathrm{d}\sigma\mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}(\sigma)^2}\mathrm{e}^{\frac{-Nn}{Lw}\mathrm{Tr}\sigma}\frac{1}{N}\mathrm{Tr}(1+\sigma)^L, \tag{4}$$

where the multi-matrix integral has been reduced to an integral over a single $(N\times N)$ matrix σ and the linear term has a coefficient Nn/Lw as n different ϕ have been replaced by $n\sigma$. The partition function of eq. (4) after completing the square in the exponent (which cancels the X in eq. (4) is

$$Z_{L,\alpha}(N) = \frac{1}{R_L(N)}\int\mathrm{d}\sigma\mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}(\sigma+\frac{nv}{Lw})^2}\frac{1}{N}\mathrm{Tr}(1+\sigma)^L. \tag{5}$$

Redefining: $\sigma' = (\sigma + \frac{nv}{Lw}) = (\sigma + \frac{n\alpha}{L})$ where $\alpha = v/w$ is the ratio of the strength of interaction between the bases v, to the strength of the perturbation w, the partition function becomes

$$Z_{L,\alpha}(N) = \frac{1}{R_L(N)}\int\mathrm{d}\sigma'\mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}(\sigma')^2}\frac{1}{N}\mathrm{Tr}\left(1+\sigma'-\frac{n\alpha}{L}\right)^L. \tag{6}$$

The integral in eq. (6) is a Gaussian matrix integral with a complicated observable $\frac{1}{N}\mathrm{Tr}(1+\sigma'-\frac{n\alpha}{L})^L$. We define the exponential generating function $G(t, N, \alpha)$ of the partition function $Z_{L,\alpha}(N)$ as

Table 1. The partition functions $Z_{L,\alpha}(N)$ for lengths up to $L = 7$ of the polymer chain are listed when the external perturbation is on $n \leq L$ bases.

L	$Z_{L,\alpha}(N)$
1	$1 - \frac{n\alpha}{L}$
2	$1 + v + (\frac{n\alpha}{L})^2 - 2(\frac{n\alpha}{L})$
3	$1 + 3v - (\frac{n\alpha}{L})^3 + 3(\frac{n\alpha}{L})^2 - 3(\frac{n\alpha}{L}) - 3v(\frac{n\alpha}{L})$
4	$1 + 6v + 2v^2 + v^2/N^2 + (\frac{n\alpha}{L})^4 - 4(\frac{n\alpha}{L})^3 + 6(\frac{n\alpha}{L})^2 + 6v(\frac{n\alpha}{L})^2 - 4(\frac{n\alpha}{L}) - 12v(\frac{n\alpha}{L})$
5	$1 - (\frac{n\alpha}{L})^5 + 5(\frac{n\alpha}{L})^4 - 10(\frac{n\alpha}{L})^3 + 10(\frac{n\alpha}{L})^2 - 5(\frac{n\alpha}{L}) + 10v + 10v^2 + 5v^2/N^2 - 10v(\frac{n\alpha}{L})^3$ $+30v(\frac{n\alpha}{L})^2 - 30v(\frac{n\alpha}{L}) - 10v^2(\frac{n\alpha}{L}) - 5v^2(\frac{n\alpha}{L})/N^2$
6	$1 + (\frac{n\alpha}{L})^6 - 6(\frac{n\alpha}{L})^5 + 15(\frac{n\alpha}{L})^4 - 20(\frac{n\alpha}{L})^3 + 15(\frac{n\alpha}{L})^2 - 6(\frac{n\alpha}{L}) + 15v + 30v^2 + 15v^2/N^2$ $+5v^3 + 10v^3/N^2 + 15v(\frac{n\alpha}{L})^4 - 60v(\frac{n\alpha}{L})^3 + 90v(\frac{n\alpha}{L})^2 + 30v^2(\frac{n\alpha}{L})^2 + 15v^2(\frac{n\alpha}{L})^2/N^2$ $-60v(\frac{n\alpha}{L}) - 60v^2(\frac{n\alpha}{L}) - 30v^2(\frac{n\alpha}{L})/N^2$
7	$1 - (\frac{n\alpha}{L})^7 + 7(\frac{n\alpha}{L})^6 - 21(\frac{n\alpha}{L})^5 + 35(\frac{n\alpha}{L})^4 - 35(\frac{n\alpha}{L})^3 + 21(\frac{n\alpha}{L})^2 - 7(\frac{n\alpha}{L}) + 21v + 70v^2$ $+35v^2/N^2 + 35v^3 + 70v^3/N^2 - 21v(\frac{n\alpha}{L})^5 + 105v(\frac{n\alpha}{L})^4 - 210v(\frac{n\alpha}{L})^3 - 70v^2(\frac{n\alpha}{L})^3$ $-35v^2(\frac{n\alpha}{L})^3/N^2 + 210v(\frac{n\alpha}{L})^2 + 210v^2(\frac{n\alpha}{L})^2 + 105v^2(\frac{n\alpha}{L})^2/N^2 - 105v(\frac{n\alpha}{L})$ $-210v^2(\frac{n\alpha}{L}) - 105v^2(\frac{n\alpha}{L})/N^2 - 35v^3(\frac{n\alpha}{L}) - 70v^3(\frac{n\alpha}{L})/N^2$

$$G(t, N, \alpha) = \sum_{L=0}^{\infty} Z_{L,\alpha}(N) \frac{t^L}{L!}. \tag{7}$$

Using $Z_{L,\alpha}(N)$ from eq. (6), we get the generating function

$$G(t, N, \alpha) = \mathrm{e}^{\frac{vt^2}{2N} + t(1 - \frac{n\alpha}{L})} \left[\frac{1}{N} \sum_{k=0}^{N-1} \binom{N}{k+1} \frac{(t^2 v)^k}{k! N^k} \right]. \tag{8}$$

The partition functions $Z_{L,\alpha}(N)$ for different L, α and n can be found exactly from the exponential generating function (eq. (8)) by equating the coefficients of powers of t on both sides of the equation (listed in table 1 upto $L = 7$). It is important to note that the term $\mathrm{e}^{t(1-\frac{n\alpha}{L})}$ arises from the observable (see eq. (6)) in the generating function. The general form of the partition function (with the re-written $A_L(N)$ in terms of Φ) can be obtained from eq. (2) using the Wick theorem and is found to be (table 1)

$$Z_{L,\alpha}(N) = \left(1 - \frac{n\alpha}{L}\right)^L + \left(1 - \frac{n\alpha}{L}\right)^{(L-2)} \sum_{i<j} V_{i,j} + \left(1 - \frac{n\alpha}{L}\right)^{(L-4)} \sum_{i<j<k<l} V_{i,j} V_{k,l}$$

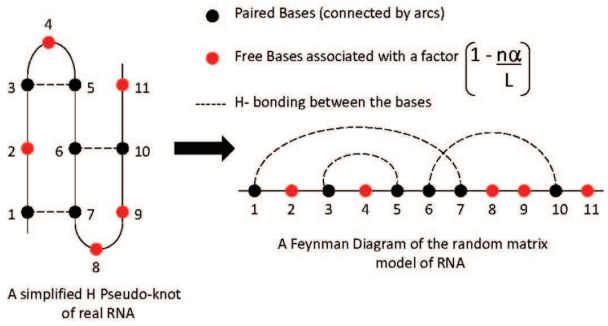

Figure 1. Schematic representation of a simplified H pseudoknot from a real RNA and its corresponding Feynman diagram are shown. The paired bases (black dots) are connected by dashed lines (representing H bonds between the bases) and each unpaired base (red dots) is weighted by the factor $(1-\frac{n\alpha}{L})$.

$$+\left(1-\frac{n\alpha}{L}\right)^{(L-4)}\sum_{i<j<k<l}V_{i,l}V_{j,k}$$
$$+\left(\frac{1}{N}\right)^{2}\left(1-\frac{n\alpha}{L}\right)^{(L-4)}\sum_{i<j<k<l}V_{i,k}V_{j,l}$$
$$+\cdots. \tag{9}$$

The multiplicative factor of powers of $(1-\frac{n\alpha}{L})$ on each term in the general partition function, shows that the effect of interaction is on all the free bases in the polymer chain which are weighted by $(1-\frac{n\alpha}{L})$ whereas paired bases are weighted 1. One such term in the partition function is shown in figure 1. In the partition function, the power of v gives the number of arcs in the corresponding Feynman diagram, the coefficient of v gives the total number of diagrams with those many arcs and the power of $1/N$ distinguishes between the planar structures ($(1/N)^0$, genus $=0$) and the non-planar structures ($(1/N)^{2k}$, where $k \geq 1$, i.e., non-zero genus). The power of $(1-\frac{n\alpha}{L})$ gives the number of unpaired bases in the diagram, each of which is weighted by $(1-\frac{n\alpha}{L})$ and paired bases with 1. The structures/diagrams in the model can be divided into two regimes: (a) $0 \leq \alpha \leq 1$, $n < L$ and $0 \leq \alpha < 1$, $n = L$ where we have structures with unpaired and paired bases and (b) $\alpha = 1$, $n = L$ where completely paired base structures exist.

The genus distribution functions of the model can be found from eq. (8) for (a) the weighted total number of diagrams at a given length L, n and α independent of genus, $\mathcal{N}_\alpha$ (defined as $\mathcal{N}_\alpha = Z_{L,\alpha}(N=1)$) and (b) the weighted number of diagrams at a fixed length L, genus g, n and α, $a_{L,g,\alpha}$ (defined through $Z_{L,\alpha}(N) = \sum_{g=0}^{\infty} a_{L,g,\alpha}\frac{1}{N^{2g}}$). For $n = L$ [12] these are plotted as functions of genus (figures 2 and 3) and length (figure 4) for different α values. The differences in the genus distribution functions arise in the number of normalized diagrams $a_{L,g,\alpha}/\mathcal{N}_\alpha$, the shapes of the distribution functions as α approaches 1 and in an even–odd length behaviour for these distributions at small lengths (figure 4).

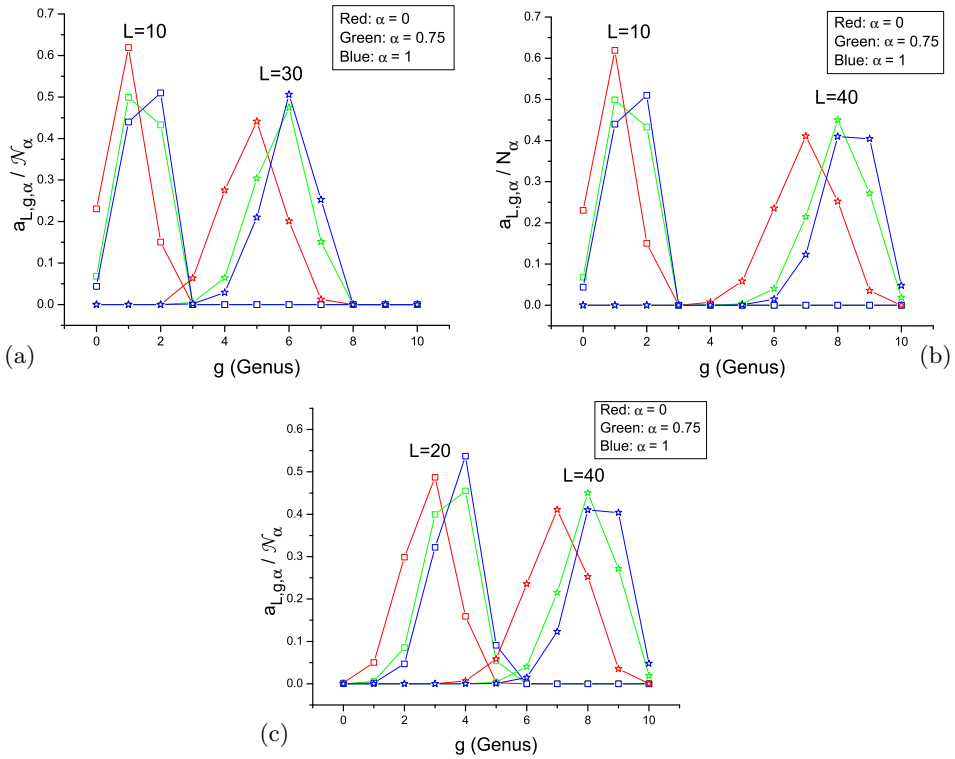

Figure 2. Genus distributions for different pairs of even lengths for a set of three α values, $\alpha = 0, 0.75, 1$: (**a**) $L = 10$ and 30, (**b**) $L = 10$ and 40 and (**c**) $L = 20$ and 40.

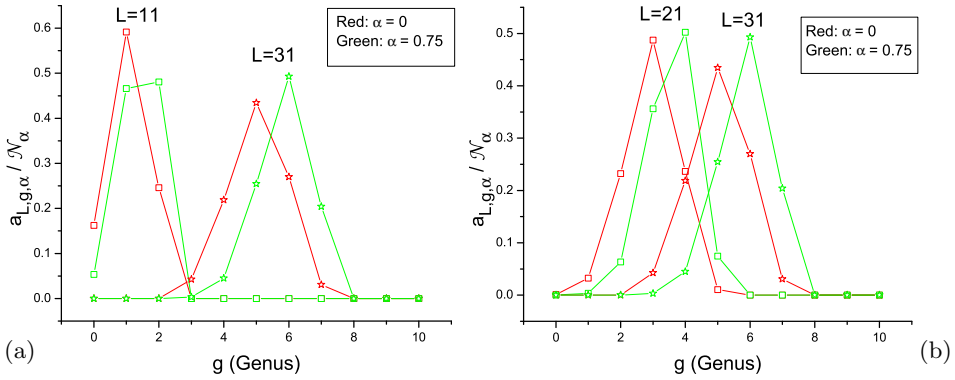

Figure 3. Genus distributions for the following pairs of odd lengths (**a**) $L = 11$ and 31 and (**b**) $L = 21$ and 31 for $\alpha = 0, 0.75, 1$ are shown in these figures. Note, the $\alpha = 1$ distribution (blue curve in the even length plots of figure 2) is absent.

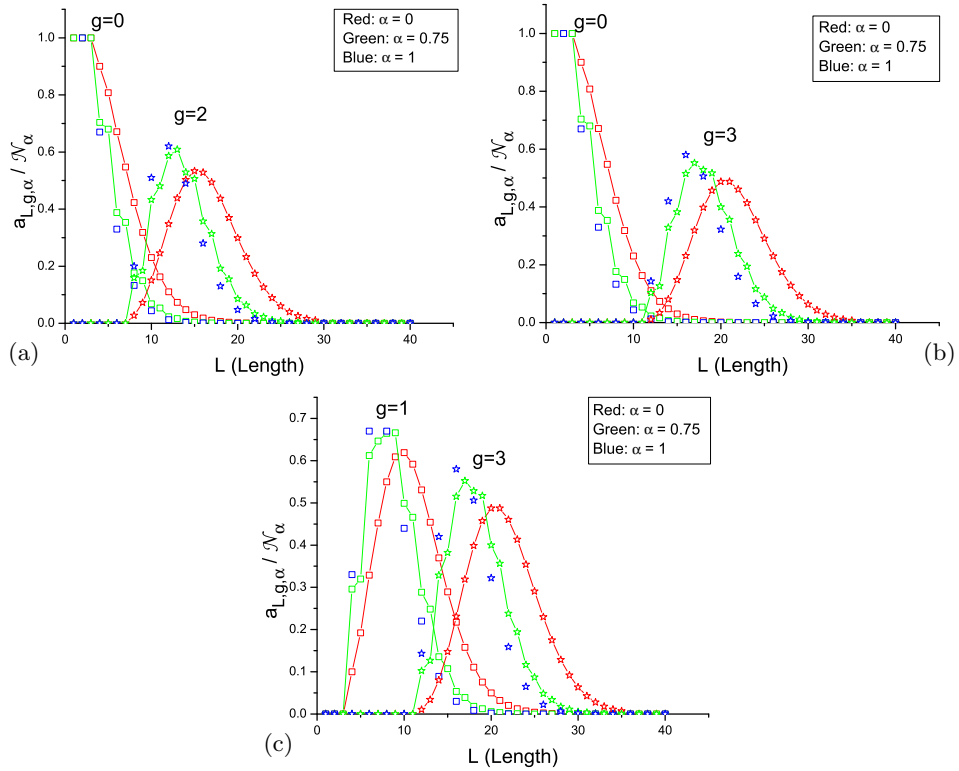

Figure 4. Genus distributions for three pairs of genii (**a**) $g = 0$ and 2, (**b**) $g = 0$ and 3 and (**c**) $g = 1$ and 3 for $\alpha = 0, 0.75, 1$ are shown in these figures.

3. External interaction with different strengths on different bases

We discuss here the case when we consider the strength of the external interaction to be different on different bases. We start with the partition function equation (2) in §2 where we take the sum in the interaction term to be $i = 1, ..., n$ with $W_1 = w_1$ and $W_2 = W_3 = \cdots W_L = w$, i.e., the strength of perturbation on base 1 is w_1 and is w on rest of the bases in the polymer chain. If we carry out a series of Hubbard–Stratonovich transformations and use the delta function equation, $\int \prod_{i=1}^{L} \mathrm{d}\psi_i \mathrm{e}^{i\mathrm{Tr}[\phi_i \sum_i \psi_i - \sigma \sum_i \psi_i]} = \prod_{i=1}^{L} \delta(\phi_i - \sigma)$, the partition function becomes

$$Z_{L,\alpha}(N) = \frac{1}{D_L(N)} \int \mathrm{d}\sigma \mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}(\sigma)^2} \mathrm{e}^{-N[\frac{1}{w}+\frac{1}{L}(\frac{w-w_1}{ww_1})]\mathrm{Tr}\sigma} \frac{1}{N}\mathrm{Tr}(1+\sigma)^L, \tag{10}$$

which can be simplified to

$$Z_{L,\alpha}(N) = \frac{1}{D'_L(N)} \int \mathrm{d}\sigma \mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}[\sigma+vC]^2} \mathrm{e}^{\frac{N}{2v}\mathrm{Tr}(vC)^2} \frac{1}{N}\mathrm{Tr}(1+\sigma)^L, \tag{11}$$

where $D'_L(N) = \int \mathrm{d}\sigma \mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}[\sigma+vC]^2} \mathrm{e}^{\frac{N}{2v}\mathrm{Tr}(vC)^2}$ and $C = (\frac{Lw_1+w-w_1}{Lww_1})$. Re-defining $\sigma' = [\sigma + vC]$, we can write the partition function as

$$Z_{L,\alpha}(N) = \frac{1}{D'_L(N)} \int \mathrm{d}\sigma' \mathrm{e}^{-\frac{N}{2v}\mathrm{Tr}[\sigma']^2} \frac{1}{N} \mathrm{Tr}(1 + \sigma' - vC)^L. \tag{12}$$

In a similar way, if we now consider that $W_1 = w_1$, $W_2 = w_2$ and $W_3 = W_4 = \cdots W_L = w$, i.e., the strength of perturbation on base 1 is w_1, on base 2 is w_2 and is w on rest of the bases in the polymer chain, then the partition function is the same as eq. (12) but with a much more complex C which is, $C = (\frac{Lw_1w_2+ww_1+ww_2-2w_1w_2}{Lww_1w_2})$. From the point of view of application to the pulling experiments, it is of relevance to see what happens when the perturbation acts on one base or two bases at a time. This can be found from eq. (12) by putting $w = 0$. In this case, C will be just $C = 1/Lw_1$ for perturbation on a single base and $C = (\frac{1}{Lw_1} + \frac{1}{Lw_2})$ for perturbation on two bases. The linear interaction introduced in the action of the partition function can have applications to experiments with RNA such as RNA pulling experiments and RNA interacting with ions.

4. Conclusion

A linear perturbation which acts on $n(\leq L)$ bases in the action of the partition function is studied. The general form of the partition function $Z_{L,\alpha}(N)$ (eq. (9)) consists of multiplicative factors of powers of $(1 - \frac{n\alpha}{L})$ with each term. There are two regimes: (i) $0 \leq \alpha \leq 1$ with $n < L$ and $0 \leq \alpha < 1$ with $n = L$ which consists of unpaired and paired base structures with each free base weighted by $(1-\frac{n\alpha}{L})$ and (ii) $\alpha = 1$ and $n = L$ comprising of completely paired base structures only. The genus distributions for $n = L$ are shown in figures 2–4 which show an interesting odd–even length behaviour at small lengths. We outlined a general method to consider interactions of varying strengths on different bases of the polymer chain in these matrix models of interacting RNA. In the application of these matrix models to a particular experiment, the calculation of physically relevant correlation functions is an important future research direction.

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