PSEUDOKNOT RNA STRUCTURES WITH ARC-LENGTH ≥ 4

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Abstract. In this paper we study k-noncrossing RNA structures with minimum arc-length 4 and at most $k-1$ mutually crossing bonds. Let $\mathsf{T}_k^{[4]}(n)$ denote the number of k-noncrossing RNA structures with arc-length ≥ 4 over n vertices. We prove (a) a functional equation for the generating function $\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n$ and (b) derive for $k\leq 9$ the asymptotic formula $\mathsf{T}_k^{[4]}(n)\sim c_k\, n^{-((k-1)^2+(k-1)/2)}\,\gamma_k^{-n}$. Furthermore we explicitly compute the exponential growth rates γ_k^{-1} and asymptotic formulas for $4\leq k\leq 9$.

1. Introduction

RNA pseudoknot structures [2, 28] are a reality. They occur in functional RNA (RNAseP [19]), ribosomal RNA [18] and are conserved in the catalytic core of group I introns. Due to the crossings of arcs their theory differs considerably from RNA secondary structures. In particular the standard folding routine does not work. Recently the concept of k-noncrossing RNA structures has been introduced [14]. Here the idea is that the complexity of the structure is tantamount to an inherently "local" property: the maximal number of mutually crossing bonds. A structure is k-noncrossing, if there exists no k-set of mutually crossings arcs. The locality is in fact of central importance: at present time, the generating function of Stadler's "bisecondary structures" [12], which correspond to *planar* 3-noncrossing structures [14], is not known.

A very intuitive approach to the k-noncrossing property of RNA molecules is their diagram representation [12]. We draw the nucleotide-labels $1,\dots,n$ in increasing order in a horizontal line and draw arc-labels (i,j) in the upper half-plane, if and only if i and j are paired in the structure, see Figure 1. We call a diagram k-noncrossing, if it does not contain k mutually crossing arcs. The

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length of an arc (i, j) is given by $\lambda = j - i$ and a stack of length σ is a sequence of "parallel" arcs of the form $((i, j), (i + 1, j - 1), \ldots, (i + (\sigma - 1), j - (\sigma - 1)))$.

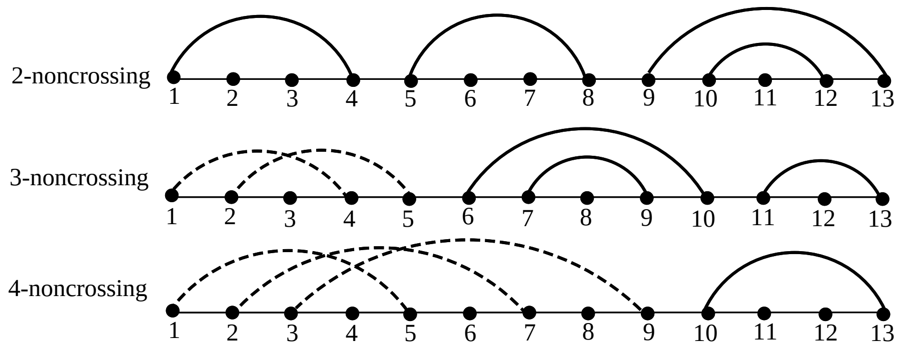

FIGURE 1. k-noncrossing structures: 2- 3- and 4-noncrossing structures (top to bottom). Maximal set of mutually crossing arcs are drawn dashed, respectively.

A k-noncrossing RNA structure is a k-noncrossing diagram over $[n]$ having minimum arc-length $\lambda > 1$. These structures have been studied in [14, 15, 16] via a bijection into vaccillating tableaux in the context of tangled diagrams [4]. For the enumeration of structures with crossing arcs the tableaux-interpretation is non-optional. There is, at present time, no way to inductively construct k-noncrossing structures, despite the fact that they are D-finite.

For RNA secondary structures (2-noncrossing RNA structures), certain combinatorial restrictions, for instance minimum arc-length or stack-size are relatively straightforward to deal with. The combinatorics of RNA secondary structures has been pioneered by Waterman *et.al.* in a series of excellent papers [21, 26, 25, 27, 10]. He proved for the number of RNA secondary structures of length n (arc-length ≥ 2), $\mathsf{T}_2^{[2]}(n)$, the fundamental recursion

$$\mathsf{T}_2^{[2]}(n) = \mathsf{T}_2^{[2]}(n-1) + \sum_{s=0}^{n-3} \mathsf{T}_2^{[2]}(n-2-s)\mathsf{T}_2^{[2]}(s) \ , \tag{1.1}$$

where $\mathsf{T}_2^{[2]}(0) = \mathsf{T}_2^{[2]}(1) = \mathsf{T}_2^{[2]}(2) = 1$. Eq. (1.1) is an immediate consequence considering secondary structures as peak-free Motzkin-paths, i.e., peak-free paths with *up*, *down* and *horizontal* steps that stay in the upper halfplane, starting at the origin and end on the x-axis. The recursion is in particular the key for all asymptotic results since it immediately implies a functional equation for the corresponding generating function. This allows the application of Darboux-type theorems [11, 24]. For the number of secondary structures with minimum arc-length λ, $\mathsf{T}_2^{[\lambda]}(n)$ it is straightforward to derive

$$\mathsf{T}_2^{[\lambda]}(n) = \mathsf{T}_2^{[\lambda]}(n-1) + \sum_{s=0}^{n-(\lambda+1)} \mathsf{T}_2^{[\lambda]}(n-2-s)\mathsf{T}_2^{[\lambda]}(s)\ . \tag{1.2}$$

All asymptotic formulae for secondary structures are of the same type: a square root. In other words, the asymptotic behavior is determined by an algebraic branch singularity with the subexponential factor $n^{-\frac{3}{2}}$.

The situation changes for k-noncrossing RNA structures. A different approach has to be made, since in lack of functional equations Darboux-type theorems [24], cannot be employed. The idea is to analyze the dominant singularities directly, using Hankel contours. This type of singularity analysis has been developed by Flajolet [7]. Basically, the "singular-analogue" of a Taylor-expansion is constructed. It can be shown that, under certain conditions, there exists an approximation, which is locally of the same order as the original function. The particular, local approximation allows then to derive the asymptotic form of the coefficients. In contrast to the subtraction of singularities-principle [20] the only contributions to the contour integral come from segments close to the singularity. In our situation all conditions for singularity analysis are satisfied since all our functions are D-finite [22, 30] and D-finite functions have an analytic continuation into any simply-connected domain containing zero. The above strategy works also for tangled diagrams [5]. The particular singularity-type of the generating function of k-noncrossing RNA structures depends solely on the crossing number [15, 17]. Furthermore an interesting feature is the appearance of logarithms for $k \equiv 1 \mod 2$ in the singular expansion for k-noncrossing RNA structures.

Due to biophysical constraints a minimum arc-length of four can be assumed for minimum free energy RNA structures. The key objective of this paper is to derive and analyze the generating function for k-noncrossing RNA structures with minimum arc-length 4, see Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\mathsf{T}_k^{[4]}(n)$	1	1	1	1	2	5	15	51	179	647	2397	9081	35181	139307	563218

TABLE 1. The first 15 numbers of 4-noncrossing RNA structures with arc-length ≥ 4

Based on our results the next step is to compute the subset of stable structures, i.e. the subset of structures with arc-length ≥ 4, having no isolated arcs. While it is straightforward to obtain eq. (1.2) from eq. (1.1) considerable complication arises, considering k-noncrossing structures with arc-length > 3. To understand why, one observes that the number of ways to place 3-arcs satisfies

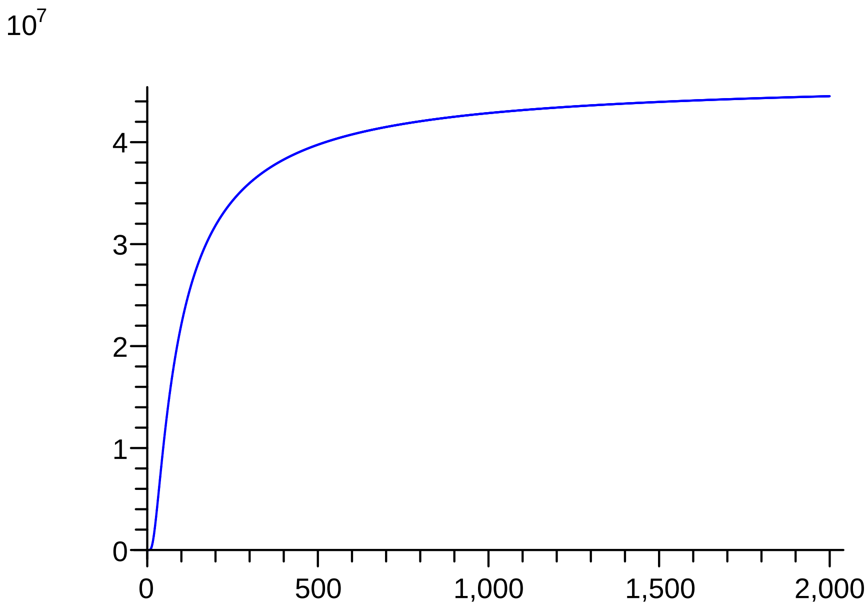

FIGURE 2. The ratio $r(n) = \mathsf{T}_4^{[4]}/(n^{-21/2}\gamma_4^{-n})$ as a function of n. The curve shows that the asymptotic approximation is valid as $r(n) \sim c_4 \approx 4.450939000 \times 10^7$

a new type of recursion, see eq. (3.6). As a result and in contrast to k-noncrossing structures with minimum arc-length $\lambda \le 3$ the generating function $\sum_{n\ge 0} \mathsf{T}_k^{[4]}(n)\, z^n$ turns out to be a sum of two power series (Theorem 2). The exponential growth rate can easily be computed via the formula given in Theorem 3, see Table 2 and Figure 2.

k	4	5	6	7	8
γ_k^{-1}	6.52900	8.64830	10.71759	12.76349	14.79631
$\mathsf{T}_k^{[4]}(n)$	$c_4 n^{-\frac{21}{2}}(\gamma_4^{-1})^n$	$c_5 n^{-18}(\gamma_5^{-1})^n$	$c_6 n^{-\frac{55}{2}}(\gamma_6^{-1})^n$	$c_7 n^{-39}(\gamma_7^{-1})^n$	$c_8 n^{-\frac{105}{2}}(\gamma_8^{-1})^n$

TABLE 2. Exponential growth rates and asymptotic formulas for k-noncrossing RNA structures with minimum arc-length ≥ 4.

The paper is organized as follows: in Section 2 we provide the background on the methods used in this paper. In Section 3 we prove a functional equation relating RNA structures to k-noncrossing matchings. We then study the singularity of the generating function and obtain the asymptotic formula in Section 4.

2. Preliminaries

In this Section we provide some background on the generating functions of k-noncrossing matchings [3, 13] and k-noncrossing RNA structures [14, 15, 16]. We denote the numbers of k-noncrossing matchings and RNA structures with arc-length $\geq \lambda$ by $f_k(2n)$ and $\mathsf{T}_k^{[\lambda]}(n)$, respectively. The former corresponds to k-noncrossing diagrams without isolated points and the latter to k-noncrossing diagrams with arc-length $\geq \lambda$. Furthermore let $\mathsf{T}_k^{[\lambda]}(n,h)$ denote the number of k-noncrossing RNA structures wit arc-length $\geq \lambda$ having exactly h arcs and $\mathsf{M}_k(n)$ denotes the number of partial matchings, or equivalently the number of k-noncrossing diagrams over $[n]$ (i.e. with isolated points and minimum arc-length 1). Pringsheim's Theorem [23] guarantees the existence of a positive real, dominant singularity of $\sum_{n\geq 0} \mathsf{M}_k(n)\, z^{2n}$ which we denote by μ_k. In order to get some intuition about the various types of diagrams involved, see Figure 3.

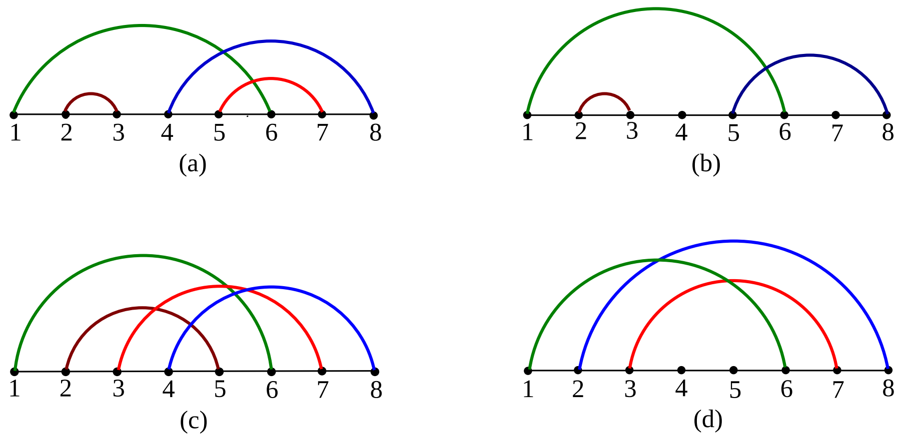

FIGURE 3. Basic diagram types: (a) 3-noncrossing matching (no isolated points), (b) 4-noncrossing partial matching (isolated points 4 and 7), (c) 4-noncrossing RNA structure with arc-length ≥ 3, (d) 3-noncrossing RNA structure with arc-length ≥ 4.

2.1. **k-noncrossing matchings.** Our main objective is to discuss some basic properties of $f_k(2n)$ and to give an asymptotic formula. Let us recall that a power series $u(x)$ is called D-finite if $\dim_{K(x)}\{u, u', \dots\} < \infty$ [22]. The generating function of k-noncrossing matchings satisfies the following identity due to Grabiner *et.al.* [9]

$$\sum_{n\geq 0} f_k(2n)\cdot \frac{z^{2n}}{(2n)!} \quad = \quad \det[I_{i-j}(2z) - I_{i+j}(2z)]|_{i,j=1}^{k-1} \tag{2.1}$$

where

$$I_r(2z) = \sum_{j\geq 0} \frac{z^{2j+r}}{j!(r+j)!} \tag{2.2}$$

denotes the hyperbolic Bessel function of the first kind of order r. Eq. (2.1) allows to conclude that

$$F_k(z) = \sum_{n\geq 0} f_k(2n) z^{2n} \tag{2.3}$$

is D-finite. Indeed, the hyperbolic Bessel function[9] itself is D-finite and D-finite functions form an algebra closed under taking Hadamard products [22]. Therefore D-finiteness of $F_k(z)$ follows from eq. (2.1). However, beyond the cases $k = 2$ and $k = 3$, eq. (2.1) does not give directly explicit formulas for $f_k(2n)$ or $F_k(z)$. For small k-values asymptotic formulas can be obtained using the approximation of the Bessel function

$$I_m(z) = \frac{e^z}{\sqrt{2\pi z}} \left(\sum_{h=0}^{H-1} \frac{(-1)^h}{h!8^h} \prod_{t=1}^{h} (4m^2 - (2t-1)^2) z^{-h} + O(|z|^{-H}) \right) \tag{2.4}$$

which holds for $-\frac{\pi}{2} < \arg(z) < \frac{\pi}{2}$ [1]. For arbitrary k, systematic analysis of the determinant $\det[I_{i-j}(2x) - I_{i+j}(2x)]|_{i,j=1}^{k-1}$ [13] shows for arbitrary k

$$f_k(n) \sim c_k\, n^{-((k-1)^2+(k-1)/2)}\, (2(k-1))^n, \qquad c_k > 0\ . \tag{2.5}$$

In the following we shall denote the dominant singularity of $F_k(z)$ by $\rho_k = \frac{1}{2(k-1)}$.

2.2. **k-noncrossing RNA structures.** k-noncrossing RNA structures are k-noncrossing diagrams satisfying specific arc-length conditions. The latter induce asymmetries which prohibit enumeration using the reflection-principle [8] directly (the reflection, for instance, implies eq (2.1)). For any $k \geq 2$ the numbers of k-noncrossing RNA structures with minimum arc-length ≥ 2 are given by [14]

$$\mathsf{T}_k^{[2]}(n) \quad = \quad \sum_{b=0}^{\lfloor n/2 \rfloor} (-1)^b \binom{n-b}{b} \mathsf{M}_k(n-2b) \ . \tag{2.6}$$

and we have [15]

$$\mathsf{T}_k^{[2]}(n) \quad \sim \quad c_k^{[2]}\, n^{-((k-1)^2+(k-1)/2)}\, (\gamma_k^{[2]})^{-n}, \qquad c_k^{[2]} > 0 \ , \tag{2.7}$$

where $\gamma_k^{[2]}$ is the unique, solution of minimal modulus of $\frac{z}{z^2-z+1} = \rho_k$. For k-noncrossing RNA structures with arc-length ≥ 3 we have according to [14]

$$\forall\, k > 2; \qquad \mathsf{T}_k^{[3]}(n) \quad = \quad \sum_{b \leq \lfloor \frac{n}{2} \rfloor} (-1)^b \lambda(n,b)\, \mathsf{M}_k(n-2b) \ , \tag{2.8}$$

where $\lambda(n,b)$ denotes the number of way selecting b arcs of length ≤ 2 over n vertices. Fortunately, the nonexplicit terms $\lambda(n,b)$ vanish in the functional equation [16]

$$\sum_{n\geq 0} \mathsf{T}_k^{[3]}(n)\, z^n = \frac{1}{1-z+z^2+z^3-z^4} \sum_{n \geq 0} f_k(2n) \left(\frac{z-z^3}{1-z+z^2+z^3-z^4} \right)^{2n} \ . \tag{2.9}$$

Singularity analysis based on eq. (2.9) eventually allows to derive the asymptotic formula

$$\mathsf{T}_k^{[3]}(n) \quad \sim \quad c_k^{[3]}\, n^{-((k-1)^2+(k-1)/2)}\, (\gamma_k^{[3]})^{-n}, \qquad c_k^{[3]} > 0 \ , \tag{2.10}$$

where $\gamma_k^{[3]}$ denotes the unique, minimal positive real solution of $\frac{z-z^3}{1-z+z^2+z^3-z^4} = \rho_k$.

2.3. **Singularity Analysis.** Pringsheim's Theorem [23] guarantees that each power series with positive coefficients has a positive real dominant singularity. This singularity plays a key role for the asymptotics of the coefficients. In the proof of Theorem 3 it will be important to deduce relations between the coefficients from functional equations of generating functions. The class of theorems that deal with such deductions are called transfer-theorems [7]. One key ingredient in this framework is a specific domain in which the functions in question are analytic, which is "slightly" bigger than their respective radius of convergence. It is tailored for extracting the coefficients via Cauchy's integral formula. Details on the method can be found in [22, 7]. In case of D-finite functions we have analytic continuation in any simply connected domain containing zero [29] and all prerequisits of singularity analysis are met. We use the notation

$$\{f(z) = O\left(g(z)\right) \text{ as } z \to \rho\} \quad \Longleftrightarrow \quad \left\{ \frac{f(z)}{g(z)} \text{ is bounded as } z \to \rho \right\} \tag{2.11}$$

The key result used in Theorem 3 is

Theorem 1. [7] *Let $f(z), g(z)$ be D-finite functions with unique dominant singularity ρ and suppose*

$$f(z) = O(g(z)) \quad as \;\; z \to \rho \; . \tag{2.12}$$

Then we have

$$[z^n]f(z) = C\left(1 - O(\frac{1}{n})\right)[z^n]g(z) \tag{2.13}$$

where C is a constant and $[z^n]h(z)$ denotes the n-th coefficient of the power series $h(z)$ at $z = 0$.

3. The functional equation

In this Section we prove a functional relation for the generating function of $\mathsf{T}_k^{[4]}(n)$, the number of k-noncrossing RNA structures with arc-length ≥ 4. Our first result is a technical lemma which is instrumental in the proof of Theorem 2 below. The proof of the lemma given below is new and uses integral representations[6] instead of dealing with the combinatorial coefficients directly. Contour integration is a powerful method to prove combinatorial identities straightforwardly.

Lemma 1. [16] *Let z be an indeterminate over $\mathbb{C}$. Then we have the identity of power series*

$$\forall\, |z| < \mu_k; \qquad \sum_{n\geq 0} \mathsf{M}_k(n)\, z^n = \left(\frac{1}{1-z}\right)\sum_{n\geq 0} f_k(2n)\left(\frac{z}{1-z}\right)^{2n} \quad . \tag{3.1}$$

Proof. Expressing the combinatorial terms by contour integrals [6] we obtain

$$\binom{n}{2m} = \frac{1}{2\pi i}\oint_{|u|=\alpha}(1+u)^n u^{-2m-1}du \qquad f_k(2m) = \frac{1}{2\pi i}\oint_{|v|=\beta} F_k(v)v^{-2m-1}dv \tag{3.2}$$

where α, β are arbitrary small positive numbers. We derive

$$\begin{aligned}
\mathsf{M}_k(n) &= \frac{1}{(2\pi i)^2}\sum_m \oint_{|u|=\alpha,|v|=\beta}(1+u)^n u^{-2m-1}F_k(v)v^{-2m-1}dudv \\
&= \frac{1}{(2\pi i)^2}\oint_{|u|=\alpha,|v|=\beta}(1+u)^n \frac{uv}{(uv)^2-1}F_k(v)dudv \\
&= \frac{1}{(2\pi i)^2}\oint_{|v|=\beta}F_k(v)v^{-1}\left[\oint_{|u|=\alpha}\frac{(1+u)^n u}{(u+\frac{1}{v})(u-\frac{1}{v})}du\right]dv
\end{aligned}$$

Since $u = \frac{1}{v}$ and $u = -\frac{1}{v}$ are the only singularities (poles) enclosed by the particular contour, eq. (3.1) implies

$$\begin{aligned}\oint_{|u|=\alpha} \frac{(1+u)^n u}{(u+\frac{1}{v})(u-\frac{1}{v})} du &= 2\pi i \left[\frac{(1+u)^n u}{u-\frac{1}{v}}|_{u=-\frac{1}{v}} + \frac{(1+u)^n u}{u+\frac{1}{v}}|_{u=\frac{1}{v}} \right] \\ &= \pi i \left(\left[1-\frac{1}{v}\right]^n + \left[1+\frac{1}{v}\right]^n \right),\end{aligned}$$

Therefore, for $|z| < \mu_k$

$$\begin{aligned}\sum_{n\geq 0} \mathsf{M}_k(n) z^n &= \frac{1}{4\pi i} \sum_{n\geq 0} \oint_{|v|=\beta} F_k(v) v^{-1} \left(\left[1-\frac{1}{v}\right]^n + \left[1+\frac{1}{v}\right]^n \right) z^n dv \\ &= \frac{1}{4\pi i} \oint_{|v|=\beta} F_k(v) \frac{1}{v-(v-1)z} dv + \frac{1}{4\pi i} \oint_{|v|=\beta} F_k(v) \frac{1}{v-(v+1)z} dv \ .\end{aligned}$$

The first integrand has its unique pole at $v = -\frac{z}{1-z}$ and the second at $v = \frac{z}{1-z}$, respectively:

$$\frac{1}{v-(v-1)z} = \frac{1}{v+\frac{z}{1-z}} \frac{1}{1-z} \quad \text{and} \quad \frac{1}{v-(v+1)z} = \frac{1}{v-\frac{z}{1-z}} \frac{1}{1-z} \ .$$

In view of $F_k(z) = F_k(-z)$ we derive

$$\sum_{n\geq 0} \mathsf{M}_k(n) z^n = \frac{1}{1-z} \left[\frac{1}{2} F_k\left(-\frac{z}{1-z}\right) + \frac{1}{2} F_k\left(\frac{z}{1-z}\right) \right] = \frac{1}{1-z} F_k\left(\frac{z}{1-z}\right)$$

whence the lemma. □

Before we state the main result of this section, let us introduce some notation. We set

$$u(z) = \sqrt{1+4z-4z^2-6z^3+4z^4+z^6} \tag{3.3}$$

$$f_j(z) = -\frac{-2z^2+z^3-1+(-1)^j\, u(z)}{2(1-2z-z^2+z^4)} \ . \tag{3.4}$$

Note that $f_j(z)$ is an algebraic function over the function field $K(z)$, i.e. there exists a polynomial with coefficients being polynomials in z for which $f(z)$ is a root.

Theorem 2. *Let k be a positive integer, $k > 3$ and $f_1(z)$ and $f_2(z)$ be given by eq.(3.4). Then we have the functional equation*

$$\begin{aligned}\sum_{n\geq 0} \mathsf{T}_k^{[4]}(n)\, z^n &= \frac{F_1(-z^2)}{1-zf_1(-z^2)} \sum_{n\geq 0} f_k(2n) \left(\frac{z\, f_1(-z^2)}{1-zf_1(-z^2)} \right)^{2n} + \\ &\quad \frac{F_2(-z^2)}{1-zf_2(-z^2)} \sum_{n\geq 0} f_k(2n) \left(\frac{z\, f_2(-z^2)}{1-zf_2(-z^2)} \right)^{2n} \ .\end{aligned}$$

Proof. Let $\lambda(n,b)$ denote the number of ways to place b arcs of length ≤ 4 over $[n]$. Then we have *Claim* 1.

$$\mathsf{T}_k^{[4]}(n) \quad = \quad \sum_{b\leq\lfloor\frac{n}{2}\rfloor}(-1)^b\lambda(n,b)\mathsf{M}_k(n-2b) \tag{3.5}$$

and $\lambda(n,b)$ satisfies the recursion

$$\begin{aligned}&\lambda(n+2b,b)=\\&\lambda(n+2b-1,b)+\lambda(n+2b-4,b-2)+\lambda(n+2b-5,b-2)+\lambda(n+2b-6,b-3)\\&+\sum_{i=1}^{b}[\lambda(n+2b-2i,b-i)+2\lambda(n+2b-2i-1,b-i)+\lambda(n+2b-2i-2,b-i)]\\&-\lambda(n+2b-3,b-1)\end{aligned} \tag{3.6}$$

where $\lambda(n,0)=1$, $\lambda(n,1)=3n-6$ and $n\geq 2b$.

The proof of eq. (3.5) and eq. (3.6) are analogous to the proof of Theorem 5 in [14]. In order to keep the paper selfcontained we present it in Section 5. The idea is now to relate $\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)\,z^n$ to the power series $\sum_{n\geq 0}\mathsf{M}_k(n)\,z^n$. For this purpose we compute

$$\begin{aligned}\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n &= \sum_{n\geq 0}\sum_{2b\leq n}(-1)^b\lambda(n,b)\sum_{m=2b}^{n}\binom{n-2b}{m-2b}f_k(m-2b,0)\,z^n\\&=\sum_{b\geq 0}(-1)^b z^{2b}\sum_{n\geq 2b}\lambda(n,b)\,\mathsf{M}_k(n-2b)z^{n-2b}\\&=\sum_{b\geq 0}(-1)^b z^{2b}\sum_{n\geq 0}\lambda(n+2b,b)\,\mathsf{M}_k(n)\,z^n\ .\end{aligned}$$

Interchanging the summations w.r.t. b and n we arrive at

$$\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n=\sum_{n\geq 0}\left[\sum_{b\geq 0}(-1)^b x^{2b}\lambda(n+2b,b)\right]\mathsf{M}_k(n)\,z^n\ . \tag{3.7}$$

Now we use the recursion formula for $\lambda(n,b)$. Let

$$\varphi_n(z)=\sum_{b\geq 0}\lambda(n+2b,b)z^b\ . \tag{3.8}$$

Multiplying with z^b and taking the summation over all b ranging from 0 to $\lfloor n/2\rfloor$ implies for $\varphi_n(z)$, $n=1,2\ldots$

$$\left(1-z^2-z^3-\frac{z}{1-z}\right)\varphi_n(z)=\left(z^2+\frac{z^2+1}{1-z}\right)\varphi_{n-1}(z)+\left(\frac{z}{1-z}\right)\varphi_{n-2}(z)\ . \tag{3.9}$$

We now make the Ansatz

$$f(x,y) = \sum_{n\geq 0}\sum_{j\leq \frac{n}{2}} \lambda(n,j)x^j \, \frac{y^n}{n!} = \sum_{n\geq 0} \varphi_n(x)\, \frac{y^n}{n!} \ . \tag{3.10}$$

Multiplying with $\frac{y^n}{n!}$ and taking the summation over all $n \geq 0$ leads to the partial differential equation

$$\left(1-x^2-x^3-\frac{x}{1-x}\right)\frac{\partial^2 f(x,y)}{\partial y^2} = \left(x^2+\frac{x^2+1}{1-x}\right)\frac{\partial f(x,y)}{\partial y} + \left(\frac{x}{1-x}\right) f(x,y) \ . \tag{3.11}$$

The general solution of eq. (3.11) can be computed by MAPLE and is given by

$$\begin{aligned} f(x,y) &= F_1(x)\exp(f_1(x)\cdot y) + F_2(x)\exp(f_2(x)\cdot y) \\ &= \sum_{n\geq 0} \left[F_1(x)\, f_1(x)^n + F_2(x)\, f_2(x)^n\right] \frac{y^n}{n!} \ , \end{aligned}$$

where $F_1(x)$, $F_2(x)$ are arbitrary functions and

$$f_1(x) = \frac{2x^2-x^3+1+u(x)}{2(1-2x-x^2+x^4)}, \quad f_2(x) = \frac{2x^2-x^3+1-u(x)}{2(1-2x-x^2+x^4)} \ . \tag{3.12}$$

By definition we have $f(x,y) = \sum_{n\geq 0}\varphi_n(x)\cdot \frac{y^n}{n!}$ and

$$\varphi_n(x) = F_1(x)(f_1(x))^n + F_2(x)(f_2(x))^n \ . \tag{3.13}$$

In order to solve eq. (3.13) it remains to compute $F_1(x)$ and $F_2(x)$. The key information lies in the initial conditions for $f(x,y)$ and $\varphi_n(x)$. Explicitly we have $f(x,0) = 1$ and $\varphi_1(x) = \lambda(1,0)\,x^0 = 1$, which implies

$$\begin{aligned} F_1(x) + F_2(x) &= 1 \\ F_1(x)f_1(x) + F_2(x)f_2(x) &= 1 \ . \end{aligned}$$

Accordingly we obtain

$$F_1(x) = \frac{f_2(x)-1}{f_2(x)-f_1(x)} \quad \text{and} \quad F_2(x) = \frac{f_1(x)-1}{f_1(x)-f_2(x)} \ . \tag{3.14}$$

In view of $\varphi_n(-z^2) = \sum_{b\geq 0}\lambda(n+2b,b)(-1)^b z^{2b}$ we can express $\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n$ as follows:

$$\begin{aligned} \sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n &= \sum_{n\geq 0}\varphi_n(-z^2)\,\mathsf{M}_k(n)\,z^n \\ &= F_1(-z^2)\sum_{n\geq 0}\mathsf{M}_k(n)\,\left(f_1(-z^2)z\right)^n + F_1(-z^2)\sum_{n\geq 0}\mathsf{M}_k(n)\,\left(f_2(-z^2)z\right)^n \ . \end{aligned}$$

Now we use Lemma 1:

$$\sum_{n\geq 0}\mathsf{M}_k(n)\,z^n=\left(\frac{1}{1-z}\right)\sum_{n\geq 0}f_k(2n)\,\left(\frac{z}{1-z}\right)^{2n}\quad ,$$

which allows to express $\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)z^n$ via $\sum_{n\geq 0}f_k(2n)\,z^{2n}$

$$\begin{aligned}\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)\,z^n=&\frac{F_1(-z^2)}{1-zf_1(-z^2)}\sum_{n\geq 0}f_k(2n)\left(\frac{zf_1(-z^2)}{1-zf_1(-z^2)}\right)^{2n}+\\&\frac{F_2(-z^2)}{1-zf_2(-z^2)}\sum_{n\geq 0}f_k(2n)\left(\frac{zf_2(-z^2)}{1-zf_2(-z^2)}\right)^{2n}\quad .\end{aligned}$$

□

4. Asymptotics of RNA pseudoknot structures with arc-length ≥ 4

We set

$$\vartheta_1(z)\quad=\quad\frac{z\,f_1(-z^2)}{1-zf_1(-z^2)}\tag{4.1}$$

$$\vartheta_2(z)\quad=\quad\frac{z\,f_2(-z^2)}{1-zf_2(-z^2)}\;.\tag{4.2}$$

Note that $\vartheta_1(z)$ and $\vartheta_2(z)$ are algebraic functions over the function field $K(z)$.

Theorem 3. *Let $k>3$ be a positive integer and ρ_k,γ_k denote the positive real singularities of $F_k(z)=\sum_{n\geq 0}f_k(2n)z^{2n}$ and $\sum_{n\geq 0}\mathsf{T}_k^{[4]}(n)\,z^n$, respectively. Then the number of k-noncrossing RNA structures with arc-length ≥ 4 is for $k\leq 9$ asymptotically given by*

$$\mathsf{T}_k^{[4]}(n)\sim c_k\,n^{-((k-1)^2+(k-1)/2)}\,\left(\gamma_k^{-1}\right)^n\quad ,\tag{4.3}$$

where γ_k is the unique positive, real solution of $\vartheta_1(\gamma_k)=\rho_k$.

Proof. Setting

$$F_k(\vartheta_1(z))=\sum_{n\geq 0}f_k(2n)\left(\frac{z\,f_1(-z^2)}{1-zf_1(-z^2)}\right)^{2n}\quad\text{and}\quad F_k(\vartheta_2(z))=\sum_{n\geq 0}f_k(2n)\left(\frac{z\,f_2(-z^2)}{1-zf_2(-z^2)}\right)^{2n}$$

According to Theorem 2 we have the functional equation

$$\sum_{n\geq 0} \mathsf{T}_k^{[4]}(n)\, z^n \quad = \quad \frac{F_1(-z^2)}{1-zf_1(-z^2)}\, F_k(\vartheta_1(z)) + \frac{F_2(-z^2)}{1-zf_2(-z^2)}\, F_k(\vartheta_2(z)) \ .$$

We consider the functions $\vartheta_1(z)$, $\vartheta_2(z)$ given by eq. (4.1) and eq. (4.2). The mappings $x \mapsto \vartheta_1(x)$ and $x \mapsto \vartheta_2(x)$ are strictly monotone and $\vartheta_1(x) > \vartheta_2(x)$ for $\vartheta_1(x) \in]0, \frac{1}{5}]$. Furthermore we have $\rho_k < \rho_4 = \frac{1}{6}$, for $k > 4$. We can conclude from this that the real, positive dominant singularity, γ_k, of $\sum_{n\geq 0} \mathsf{T}_k^{[4]}(n)\, z^n$, whose existence is guaranteed by Pringsheim's Theorem [23], satisfies

$$\vartheta_1(\gamma_k) = \rho_k \ . \tag{4.4}$$

Being a determinant of Bessel functions [9], $F_k(z)$ is D-finite and $\vartheta_1(z)$ and $\vartheta_2(z)$ are algebraic over $K(z)$ and satisfy $\vartheta_1(0) = 0 = \vartheta_2(z)$. Therefore the composition $F_k(\vartheta_i(z))$, $i = 1, 2$, is D-finite [22] and $F_k(\vartheta_1(z))$ and $F_k(\vartheta_2(z))$ have singular expansions, respectively. We further observe that neither $\frac{F_1(-z^2)}{1-zf_1(-z^2)}$ nor $\frac{F_2(-z^2)}{1-zf_2(-z^2)}$ have a singularity ζ with $|\zeta| \leq \gamma_k$. Hence if ζ is a dominant singularity of $\sum_n \mathsf{T}_k^{[4]}(n)\, z^n$ then it is necessarily a singularity of $F_k(\vartheta_1(z))$ or $F_k(\vartheta_2(z))$. As for singularities of $F_k(\vartheta_1(z))$ and $F_k(\vartheta_2(z))$, we consider for $k \leq 9$ the ODE satisfied by $F_k(z)$:

$$q_{0,k}(z)\frac{d^e}{dz^e}F_k(z) + q_{1,k}(z)\frac{d^{e-1}}{dz^{e-1}}F_k(z) + q_{e,k}(z)F_k(z) = 0 \ , \tag{4.5}$$

where $q_{j,k}(z)$ are polynomials. The key point is now that any dominant singularity of $F_k(z)$ is contained in the set of roots of $q_{0,k}(z)$ [22]. Computing the ODEs for $4 \leq k \leq 9$ we can therefore conclude that $F_k(z)$ has only the two dominant singularities ρ_k and $-\rho_k$. Let $S = \{\zeta \mid \vartheta_1(\zeta) = \rho_k \text{ or } \vartheta_2(\zeta) = -\rho_k\}$. Then γ_k is the unique S-element of minimal modulus. We can draw two conclusions: first

$$[z^n]\, \mathsf{T}_k^{[4]}(z) \ \sim \ c_k\, [z^n]\, F_k(\vartheta_1(z)) \quad \text{for some } c_k > 0 \tag{4.6}$$

and secondly, γ_k is the unique dominant singularity of $\sum_n \mathsf{T}_k^{[4]}(n)\, z^n$. In view of eq. (4.6) it thus remains to analyze the subexponential factors of the singular expansion of $F_k(\vartheta_1(z))$ at $z = \gamma_k$. Since $\vartheta_1(z)$ is regular at γ_k we are given the supercritical case of singularity analysis [7]. In the supercritical case the subexponential factors of the compositum, $F_k(\vartheta_1(z))$ coincide with those of the outer function, $F_k(z)$. According to [13] we have for arbitrary k

$$f_k(2n)(n) \sim n^{-((k-1)^2 + \frac{k-1}{2})} \left({\rho_k}^{-1}\right)^n \tag{4.7}$$

and therefore

$$\mathsf{T}_k^{[4]}(n) \sim c_k\, n^{-((k-1)^2 + \frac{k-1}{2})} \left({\gamma_k}^{-1}\right)^n \ . \tag{4.8}$$

proving the theorem. $\square$

5. Proof of Claim 1

We recall that the numbers of k-noncrossing matchings and RNA structures with arc-length $\geq \lambda$ are denoted by $f_k(2n)$ and $\mathsf{T}_k^{[\lambda]}(n)$, respectively. Furthermore, let $\mathsf{T}_k^{[\lambda]}(n,\ell)$ denote the number of k-noncrossing RNA structures with arc-length $\geq \lambda$ having exactly ℓ arcs, and let $f_k(m,\ell)$ denote the number of k-noncrossing diagrams with ℓ isolated points over m vertices. Let $\mathscr{G}_{n,k}(\ell, j_1, j_2, j_3)$ be the set of all k-noncrossing diagrams having exactly ℓ isolated points and exactly j_1 1-arc, j_2 2-arcs and j_3 3-arcs. We set $G_k(n,\ell,j_1,j_2,j_3) = |\mathscr{G}_{n,k}(\ell,j_1,j_2,j_3)|$. In particular, we have $G_k(n,\ell,0,0,0) = \mathsf{T}_k^{[4]}(n,\ell)$. We observe that eq. (3.5) is implied (taking the sum over all ℓ) by

$$\mathsf{T}_k^{[4]}(n,\ell) \quad = \sum_{b\leq\lfloor\frac{n}{2}\rfloor} (-1)^b \lambda(n,b)\, f_k(n-2b,\ell)\ , \tag{5.1}$$

where $\lambda(n,b)$ satisfies the recursion

$$\begin{aligned}\lambda(n,b) = {} & \lambda(n-1,b) + \lambda(n-4,b-2) + \lambda(n-5,b-2) + \lambda(n-6,b-3) \\ & + \sum_{i=1}^{b} [\lambda(n-2i,b-i) + 2\lambda(n-2i-1,b-i) + \lambda(n-2i-2,b-i)] \\ & - \lambda(n-3,b-1)\end{aligned}$$

with the initial conditions $\lambda(n,0)=1$, $\lambda(n,1)=3n-6$ and $n\geq 2b$. We shall proceed by proving eq. (5.1). For this purpose, let $\lambda(n,b_1,b_2,b_3)$ denote the number of ways to select exactly b_1 1-arcs, b_2 2-arcs and b_3 3-arcs over $1,\dots,n$ vertices.

Claim A.

$$\sum_{j_1\geq b_1, j_2\geq b_2, j_3\geq b_3} \binom{j_1}{b_1}\binom{j_2}{b_2}\binom{j_3}{b_3} G_k(n,l,j_1,j_2,j_3) = \lambda(n,b_1,b_1,b_3) f_k(n-(b_1+b_2+b_3),l). \tag{5.2}$$

The idea is to construct a family $\mathcal{F}$ of $\mathscr{G}_{n,k}$-diagrams, having ℓ isolated points and *at least* b_1 1-arcs and b_2 2-arcs and b_3 3-arcs, respectively. We then express $|\mathcal{F}|$ via the numbers $G_k(n,\ell,j_1,j_2,j_3)$. We select (a) b_1 1-arcs and b_2 2-arcs and b_3 3-arcs and (b) an arbitrary k-noncrossing diagram over the remaining $n-2(b_1+b_2+b_3)$ vertices with exactly ℓ isolated points. Let $\mathcal{F}$ be the family of diagrams obtained in this way. It is straightforward to show that $\lambda(n,b_1,b_2,b_3)$ satisfies the recursion:

$$\begin{aligned}
&\lambda(n,b_1,b_2,b_3)\\
&=\lambda(n-1,b_1,b_2,b_3)+\lambda(n-2,b_1-1,b_2,b_3)+\lambda(n-4,b_1-1,b_2,b_3-1)\\
&+\lambda(n-5,b_1,b_2,b_3-2)+\lambda(n-6,b_1,b_2,b_3-3)-\lambda(n-3,b_1,b_2-1,b_3)\\
&+\sum_{i=1}^{b}[2\lambda(n-2i-1,b_1,b_2-1,b_3-(i-1))+\lambda(n-2i-2,b_1,b_2,b_3-i)]\\
&\sum_{i=2}^{b}[\lambda(n-2i,b_1,b_2-2,b_3-(i-2))]
\end{aligned}$$

with the initial conditions $\lambda(n,0,0,0)=1$, $\lambda(n,1,0,0)=n-1$, $\lambda(n,0,1,0)=n-2$, $\lambda(n,0,0,1)=n-3$, $n\geq 2b$.

Clearly, each element $\theta\in\mathcal{F}$ is contained in $\mathscr{G}_{n,k}(\ell,j_1,j_2,j_3)$ for some $j_1\geq b_1$ and $j_2\geq b_2$ and $j_3\geq b_3$. Indeed, any 1-arc or 2-arc or 3-arc can only cross at most two other arcs. Therefore 1-arcs and 2-arcs and 3-arcs cannot be contained in a set of more than 3-mutually crossing arcs. As a result, for $k>3$ the construction generates k-noncrossing diagrams. Clearly, θ has exactly ℓ isolated vertices and in step (b) we potentially derive additional 1-arcs and 2-arcs and 3-arcs, whence $j_1\geq b_1$ and $j_2\geq b_2$ and $j_3\geq b_3$, respectively. Next we observe that we have by construction

$$|\mathcal{F}|=\lambda(n,b_1,b_2,b_3)\,f_k(n-2(b_1+b_2+b_3),\ell)\ .$$

Since any of the k-noncrossing diagrams over $n-2(b_1+b_2+b_3)$ vertices can generate additional 1-arcs or 2-arcs or 3-arcs, we consider

$$\mathcal{F}(j_1,j_2,j_3)=\{\theta\in\mathcal{F}\mid\theta\text{ has exactly }j_1\text{ 1-arcs, }j_2\text{ 2-arcs and }j_3\text{ 3-arcs}\}\ .$$

Obviously, we then have the partition $\mathcal{F}=\dot\cup_{j_1\geq b_1,j_2\geq b_2,j_3\geq b_3}\mathcal{F}(j_1,j_2,j_3)$. Suppose $\theta\in\mathcal{F}(j_1,j_2,j_3)$, then $\theta\in\mathscr{G}_{n,k}(\ell,j_1,j_2,j_3)$ and furthermore θ occurs with multiplicity $\binom{j_1}{b_1}\binom{j_2}{b_2}\binom{j_3}{b_3}$ in $\mathcal{F}$ since by construction any b_1-element subset of the j_1 1-arcs and b_2-element subset of the j_2 2-arcs and b_3-element subset of the j_3 3-arcs is counted respectively in $\mathcal{F}$. Therefore we have

$$|\mathcal{F}(j_1,j_2,j_3)|=\binom{j_1}{b_1}\binom{j_2}{b_2}\binom{j_3}{b_3}G_k(n,\ell,j_1,j_2,j_3) \tag{5.3}$$

and

$$\sum_{j_1\geq b_1,j_2\geq b_2,j_3\geq b_3}|\mathcal{F}(j_1,j_2,j_3)|=\lambda(n,b_1,b_2,b_3)f_k(n-2(b_1+b_2+b_3),\ell)$$

proving Claim A. We next set

$$F_k(x,y,z)=\sum_{j_1\geq 0}\sum_{j_2\geq 0}\sum_{j_3\geq 0} G_k(n,\ell,j_1,j_2,j_3)x^{j_1}y^{j_2}z^{j_3}\ .$$

Taking derivatives we obtain

$$\begin{aligned}
&\frac{1}{b_1!}\frac{1}{b_2!}\frac{1}{b_3!}F_k^{b_1,b_2,b_3}(1)\\
&=\sum_{j_1\geq b_1,j_2\geq b_2,j_3\geq b_3}\binom{j_1}{b_1}\binom{j_2}{b_2}\binom{j_3}{b_3}G_k(n,\ell,j_1,j_2,j_3)1^{j_1-b_1}1^{j_2-b_2}1^{j_3-b_3}
\end{aligned}$$

and accordingly

$$\begin{aligned}
&\sum_{j_1\geq 0,j_2\geq 0,j_3\geq 0} G_k(n,\ell,j_1,j_2,j_3)x^{j_1}y^{j_2}z^{j_3}\\
&=\sum_{b_1\geq 0,b_2\geq 0,b_3\geq 0}\left[\sum_{j_1\geq b_1,j_2\geq b_2,j_3\geq b_3}\binom{j_1}{b_1}\binom{j_2}{b_2}\binom{j_3}{b_3}G_k(n,\ell,j_1,j_2,j_3)\right]\\
&(x-1)^{b_1}(y-1)^{b_2}(z-1)^{b_3}\\
&=\sum_{b_1\geq 0,b_2\geq 0,b_3\geq 0}\lambda(n,b_1,b_2,b_3)f_k(n-2(b_1+b_2+b_3),\ell)(x-1)^{b_1}(y-1)^{b_2}(z-1)^{b_3}\ .
\end{aligned}$$

By construction $G(n,\ell,0,0,0)$ is the constant term of the $F_k(x,y,z)$. That is, the number of k-noncrossing RNA structures with ℓ isolated vertices and no 1-arcs 2-arcs and 3-arcs is given by

$$G(n,\ell,0,0,0)=\sum_{b_1\geq 0,b_2\geq 0,b_3\geq 0}(-1)^{b_1+b_2+b_3}\lambda(n,b_1,b_2,b_3)f_k(n-2(b_1+b_2+b_3),\ell)\ . \tag{5.4}$$

We take the sum over all ℓ and derive

$$\begin{aligned}
&\mathsf{T}_k^{[4]}(n)=\\
&\sum_{b_1\geq 0,b_2\geq 0,b_3\geq 0}^{\lfloor\frac{n}{2}\rfloor}(-1)^{b_1+b+2+b_3}\lambda(n,b_1,b_2,b_3)\left[\sum_{\ell=0}^{n-2(b_1+b_2+b_3)}f_k(n-2(b_1+b_2+b_3),\ell)\right]\ .
\end{aligned} \tag{5.5}$$

Setting

$$\lambda(n,b)=\sum_{b_1+b_2+b_3=b}\lambda(n,b_1,b_2,b_3)$$

we conclude first

$$\mathsf{T}_k^{[4]}(n)\quad=\quad\sum_{b\leq\lfloor\frac{n}{2}\rfloor}(-1)^b\lambda(n,b)\,\mathsf{M}_k(n-2b)$$

and secondly eq. (5.2), completing the proof of Claim 1.

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