Tutorial 2

June 7, 2017
Selected result 2: XerCD-dif recombination unlinks stepwise [SIG+13]

FtsK-dependent XerCD-dif recombination unlinks replication catenanes in a stepwise manner.

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Abstract
In Escherichia coli, complete unlinking of newly replicated sister chromosomes is required to ensure their proper segregation at cell division. Whereas replication links are removed primarily by topoisomerase IV, XerC/XerD-dif site-specific recombination can mediate sister chromosome unlinking in Topoisomerase IV-deficient cells. This reaction is activated at the division septum by the DNA translocase FtsK, which coordinates the last stages of chromosome segregation with cell division. It has been proposed that, after being activated by FtsK, XerC/XerD-dif recombination removes DNA links in a stepwise manner. Here, we provide a mathematically rigorous characterization of this topological mechanism of DNA unlinking. We show that stepwise unlinking is the only possible pathway that strictly reduces the complexity of the substrates at each step. Finally, we propose a topological mechanism for this unlinking reaction.

Keywords: DNA topology; Xer recombination; band surgery; tangle method; topology simplification

Comment in
Mathematical validation of a biological model for unlinking replication catenanes by recombination. [Proc Natl Acad Sci U S A. 2013]
Ftsk-dependent XerC/D *dif* recombination

Links are formed during replication. Topoisomerases typically perform fast and efficient unlinking via strand-passage.

In [IBBS03], it was demonstrated that a combination of recombinases (XerC/XerD) and translocase (FtsK) can also perform DNA unlinking in E. coli.

**Figure:** Process of unlinking hypothesized by [IBBS03].
In this article, the authors again study site-specific recombination modeled as a coherent band surgery.

**Figure:** Site-specific recombination by XerC/XerD-FtsK at *dif* sites in E. coli. Figure from [SIG+13].
In [SIG+13], they assume (except for last step) that recombination modeled by band surgery decreases crossing number and prove that there is a unique minimal pathway from any $T(2, m)$ torus knot or link to the unlink.

**Figure:** Unlinking pathway for the $T(2, m)$ torus knot or link.
Main technical tools

Signature, Euler characteristic and tangle calculus.

**Proposition**

*Let* \( L \) *be a nontrivial oriented knot or link. Then the following conclusions hold:*

1. \( \chi(L) \geq 2 - c(L) \) with equality if and only if \( L \) is the \( T(2, c(L)) \) torus knot or \( T(2, c(L))_p \) torus link.

2. \( |\sigma(L)| \leq 1 - \chi(L) \).

3. \( |\sigma(L)| \leq c(L) - 1 \) with equality if and only if \( L \) is the \( T(2, c(L)) \) torus knot or \( T(2, c(L))_p \) torus link.
Review: surfaces with boundary

The Euler characteristic

\[ \chi(M) := \sum (-1)^i \beta_i(M) \equiv V - E + F \]

is a number used to identify the surface.

- \( \chi(S^2) = 2 - b \)
- \( \chi(\#^g T^2) = 2 - 2g - b \)
- \( \chi(\#^k \mathbb{P}^2) = 2 - k - b \)

Here, \( b \) is the number of open disks ("punctures") removed from the surface.
1 A non-orientable surface can be deformed to (a), and is homeomorphic to (b).

2 An orientable surface can be deformed to (a), and can be made non-orientable as in (b). (Images from [AK14].)
Band Gordian distance realized by surfaces

For any knots $J$ and $K$,

$$d_b(J, K) = \min_F \{\beta_1(F)\} - 1$$

where the minimum is taken over all connected surfaces $F$ in $S^3$ spanning $J$ and $K$.

For any knots $J$ and $K$,

$$d_2(J, K) = \min_{F_N} \{\beta_1(F_N)\} - 1$$

where the minimum is taken over all connected nonorientable surfaces $F_N$ in $S^3$ spanning $J$ and $K$.

Theorem [AK14]:

$$d_b(J, K) = d_2(J, K) \text{ or } d_b(J, K) = d_2(J, K) - 1$$

$$u_b(K) = u_2(K) \text{ or } u_b(K) = u_2(K) - 1.$$
Section 6: Relationship to usual Gordian distance

Theorem ([AK14])

For knots $J$ and $K$,

$$d_b(J, K) \leq \begin{cases} 
  d(J, K) & \text{if } d(J, K) \text{ is even,} \\
  d(J, K) + 1 & \text{if } d(J, K) \text{ is odd.}
\end{cases}$$

In particular,

$$u_b(K) \leq \begin{cases} 
  u(K) & \text{if } u(K) \text{ is even,} \\
  u(K) + 1 & \text{if } u(K) \text{ is odd.}
\end{cases}$$

Also if $J$ and $K$ are unknotting number one knots then

$$d_b(J, K) \leq 2 \text{ and } u_b(J\# K) \leq 2.$$
Selected results revisited  Surfaces  Homological invariants  Polynomial invariants  Tables  Rational knots

Homological invariants

Several homological knot invariants behave predictably* under band sum:

- Linking form
- Signature
- Number of generators of $H_1$ of BDC.
- Arf invariant

*kind of
Homological invariants

Theorem ([Lic86])

Suppose $K$ can be unknotted by adding a twisted band, and let

$$
\lambda : H_1(\Sigma(K)) \times H_1(\Sigma(K)) \to \mathbb{Q}/\mathbb{Z}
$$

be the linking form. Then $H_1(\Sigma(K))$ is cyclic of order $\det(K)$ and has a generator $g$ such that $\lambda(g, g) = \pm 1/\det(K)$. 
Let $\sigma(L)$ denote the signature of an oriented link.

**Proposition (Murasugi [Mur70])**

*If $L$ and $M$ are two links related by a coherent band surgery, then $|\sigma(L) - \sigma(M)| \leq 1$.***

Let $\Sigma_p(K)$ denote the $p$-fold cyclic covering space of $S^3$ branched along $K$, and $e_p(K)$ the minimum number of generators of $H_1(\Sigma_p(K); \mathbb{Z})$.

**Proposition ([AK14])**

*If $K$ and $J$ are two knots related by an unoriented band surgery, then $|e_p(J) - e_p(K)| \leq p - 1$.***
Sometimes polynomial invariants and skein-type invariants can be used to determine band distances:

- Jones polynomial
- Alexander / Conway polynomials
- HOMFLY-PT polynomial
- Q-polynomial

Good sources for obstructions to band surgeries: [AK14], [KM09], [Kan16]
Examples of polynomial invariant obstructions

**Proposition**

If $L$ and $M$ are two links related by a band surgery (either type), their Jones polynomials are related by

$$\left| \frac{V_L(e^{i\pi/3})}{V_M(e^{i\pi/3})} \right| \in \{1, \sqrt{3}^{\pm 1}\}$$

**Proposition**

If $L$ and $M$ are two links related by a band surgery (either type), their $Q$ polynomials are related by

$$\frac{Q_L((\sqrt{5} - 1)/2)}{Q_M((\sqrt{5} - 1)/2)} \in \{\pm 1, \sqrt{5}^{\pm 1}\}$$
Table from Kanenobu-Miyazawa [KM09].

\textbf{Figure 13.} $H(2)$-unknotting number one prime knots with 9 crossings.
Table from Kanenobu [Kan16].

**Table 7.** $H(2)$-Gordian distances of knots with up to 7 crossings.

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Rational (two-bridge) knots and notation

Images and conventions here borrowed from Murasugi’s book [?]. Beware of different notation and conventions across the literature. In general: tangle $T(a_1, \cdots, a_n)$ where $a_1 \neq 0$ corresponds with

$$\frac{p}{q} = [a_n, \cdots, a_1] = a_n + \frac{1}{a_{n-1} + \cdots + \frac{1}{a_1}}$$

To build the tangle: $a_1$ is in the upper left, $a_n$ in the lower right.
Rational tangle notation

Example: \( T(2, 3, -4, 2) \) corresponds with

\[
[2, -4, 3, 2] = 2 + \frac{1}{-4 + \frac{1}{3 + \frac{1}{2}}}
\]

Figure: Exceptional tangles
Rational (2-bridge) knots

A 2-bridge knot is the denominator closure of a rational tangle, and the denominator closure of a rational tangle is a two-bridge knot.

(a) \([4, -2, 5, 1, -2] = \frac{45}{13}\)
(b) \([3, 2, 6] = \frac{45}{13}\)

Remark 1: \(C(a_1, a_2, \cdots, a_{2k+1}) \sim C(a_{2k+1}, \cdots, a_2, a_1)\).

Remark 2. \(C(a_1, \cdots, a_n)\) is of type \((\alpha, \beta)\) where \(\frac{\alpha}{\beta}\) has continued fraction \([a_1, \cdots, a_n]\).
Let $K$ and $K'$ be two-bridge knots of type $(\alpha, \beta)$ and $(\alpha', \beta')$. Then $K \simeq K'$ iff

1. $\alpha = \alpha'$ and $\beta \equiv \beta' \mod \alpha$, or

2. $\alpha = \alpha'$ and $\beta \beta' \equiv 1 \mod \alpha$

Let $K^*$ be the mirror of $K$. Then $K^*$ is of type $(\alpha, -\beta)$. If $K$ is amphichiral, $\beta^2 \equiv -1 \mod \alpha$. 
Classification of two-bridge knots and/or lens spaces

Two lens spaces $L(\alpha, \beta)$ and $L(\alpha', \beta')$ where $\alpha, \beta > 0$ are orientation preserving homeomorphic if and only if

1. $\alpha = \alpha'$ and $\beta \equiv \beta' \mod \alpha$, or
2. $\alpha = \alpha'$ and $\beta \beta' \equiv 1 \mod \alpha$

They are orientation reversing homeomorphic if and only if

1. $\alpha = \alpha'$ and $\beta \equiv -\beta' \mod \alpha$, or
2. $\alpha = \alpha'$ and $\beta \beta' \equiv -1 \mod \alpha$. 
References:

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