Exornata: A Web-based Tool for the Visualization and Editing of RNA Secondary Structures ☆

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Abstract

RNA secondary structures serve as bridges between RNA sequences and often-unknown three-dimensional structures, offering insights into base pairing, structural motifs, and the overall organization of RNA molecules. To support efficient visualization and editing of these structures, we present Exornata, a modern, web-based tool designed to facilitate generation of detailed and standardized RNA secondary structure modeling. Exornata is an expanded successor to the original XRNA software and is implemented using React and JavaScript/TypeScript technologies to ensure flexibility, interactivity, and high-quality rendering. Users can load, edit, and export RNA structures in multiple supported formats, ranging from conventional SVG to an advanced, in-house–developed JSON schema designed for interoperability with other resources such as R2DT, Traveler, and RiboVision2. The application supports multiple constraint-based editing modes (*e.g.,* nucleotide, strand, helix, and domain) allowing precise and hierarchical manipulation of RNA elements. Exornata supports detailed, interactive visualization of canonical and non-canonical base pairs. It enables researchers to format and annotate structures, and to integrate them into broader bioinformatics pipelines. The tool is open-source, freely available at https://exornata.chemistry.gatech.edu/ and is accompanied by a user guide.

Introduction

Elizabeth Keller's tRNA cloverleaf [1], the first RNA secondary structure [2], was a conceptual breakthrough that ultimately enabled systematic visualization [3], analysis, and comparison of RNAs across disease states and the tree of life [4]. Secondary structures depict elements of RNA architecture including canonical and non-canonical base pairs, helices, loops, bulges, and junctions, and encode interactions that govern folding and function.

Secondary structures provide interpretable and adaptable scaffolds for integrating and comparing diverse biochemical and structural observations [5]. RNA secondary structures have become a foundational tool that have advanced both the teaching and the science of RNA biochemistry and biology, providing quantitative grammar that can be used to interpret hierarchies of RNA folding and evolution. They link sequence, tertiary structure,

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chemistry, and biology. Secondary structure can be readily annotated with chemical modifications, metal ion interactions, and cleavage frequencies. Data from transcriptomes, x-ray diffraction, cryo-EM, chemical probing, and other experimental approaches are represented, integrated, and understood within the frameworks of RNA secondary structures.

However, until recently, RNA secondary structural formats have been poorly standardized and remain idiosyncratic. A given RNA is commonly depicted in a variety secondary structures differing in helix linearity, interhelical angles, inclusion of canonical versus non-canonical base pairs, criteria for defining secondary and tertiary interactions, relative weighting of those interactions, methods used to represent tertiary contacts, and the degree to which historically inherited but inaccurate features are retained.

A given RNA family [6,7], such as ribosomal RNA, RNase P RNA, or viral genomic RNA, is commonly represented in multiple formats. This variability reduces utility. The lack of standardization makes integration, visualization and comparison of data difficult or even impossible. Recently, the R2DT pipeline [8,9] was developed in part to address this problem. The pipeline uses existing RNA templates in standard orientations for various RNA families and generates new secondary structure layouts using a template-based approach. However, even with this pipeline, researchers still need the ability to (a) create *de novo* templates for new families and subfamilies of RNA molecules and (b) adjust the automatically generated layouts for precise, accurate, and esthetically pleasing representations of various RNA elements.

Here we present Exornata (*lat.* ornamented), a web-based tool that creates RNA secondary structures from pre-existing templates. This application enables standardization of RNA secondary structures and bulk transformations between formats. In addition, Exornata can *de novo* create RNA secondary structures for new RNA families. It enables precision manual editing and formatting of RNA of secondary structures.

Exornata has been integrated with other essential components of the R2DT pipeline such as Traveler [10] and, RNAcanvas [11] (also supporting some of their formats). The tool aims to establish and expand standardized representations of RNA molecules that can serve as templates for many RNAs from the same family [5].

Exornata is an expanded and upgraded version of the XRNA software developed by Harry Noller [12]. The current editor facilitates detailed and accurate RNA secondary structure editing, supporting a wide range of editing and visualization tasks commonly needed in RNA modeling, bioinformatics, and comparative biology. Implemented as a web application, the editor is freely available at https://exornata.chemistry.gatech.edu/. Exornata enables users to import and export 2D structures in multiple supported formats, select and format elements within 2D layouts, constrain editing to specific secondary structure elements, and edit structures within a selected constraint mode, offering comprehensive features for RNA editing and visualization.

The ultimate goal of the Exornata webserver is creation of 2D RNA layouts for a variety of RNA molecules representing different families in the standardized layouts, so that the RNAs can be compared and shared among the community as high quality images.

Results

Overview of Exornata capabilities

Basic features. Interface. The functionalities of Exornata are accessed via a modern interface containing three modules: the Navigation panel, Canvas and the Properties panel (Figure 1A–C). The Navigation panel provides an ability to manipulate the secondary structure, enabling editing, formatting, and labeling capabilities. The Naviagtion panel is divided into four sections: (i) Import/Export bar; (ii) RNA Constraint Modes selection, (iii) Specialized Tools for Editing, Formatting, and Labeling the RNA molecules, and (iv) Utilities. The Canvas represents a workspace exemplified here by a secondary structure layout of the P4–P6 domain of the *Tetrahymena thermophila* intron (Figure 1D).

The Canvas represents a scalable workspace with scalable auxiliary elements (grid box and cycles) to facilitate the alignment and precise positioning of various RNA objects. The Canvas offers a complete suite of tools, allowing users to create *de novo* RNA layouts or customize existing layouts (*e.g.,* imported from R2DT).

The Navigation panel provides extensive Editing and Visualization options that vary among RNA elements (and are defined by a specific constraint mode). The Properties panel is accessed via right-clicking on any nucleotide according to the behavior of the currently active selection constraint.

Users are presented with a customizable grid and background that enable precise control for aligning a structure to their own layout preference. Following the guidelines in WCAG 2.2, we added the ability to further finetune the color of the background, grid and any text present in the canvas. We also support a diverse set of fonts that can be simply pasted in the text box and applied to either the whole or part of the structure.

Constraints. Exornata partially inherits the hierarchical philosophy of XRNA and provides users with an ability to manipulate various sub-structures within RNA molecules. Thus, within

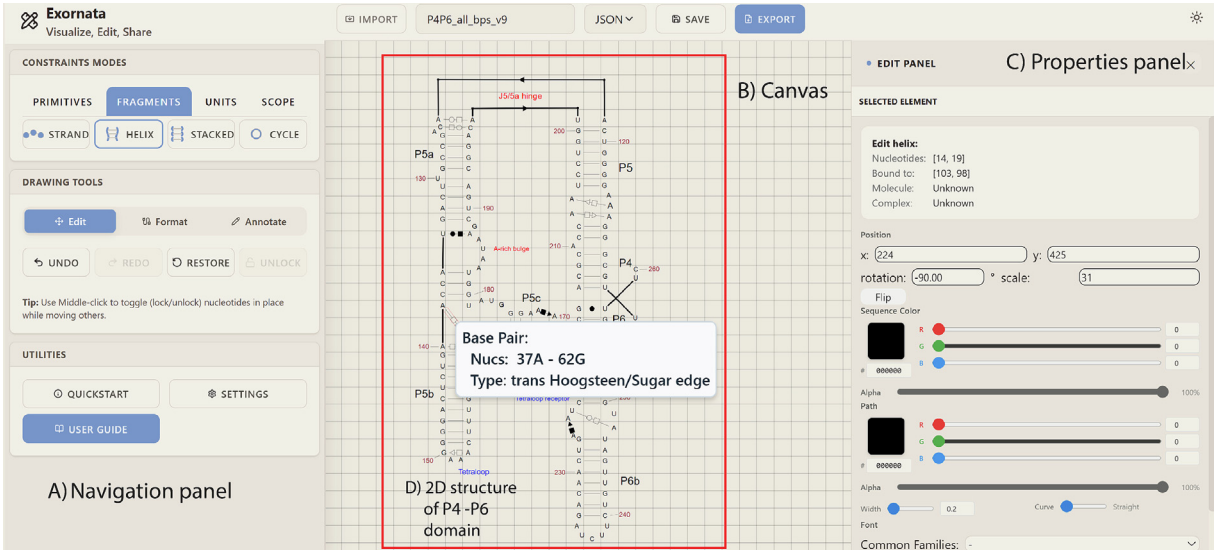

Figure 1. Exornata interface. The interface of Exornata contains three major areas: (A) Navigation panel; (B) Canvas, and (C) Properties panel. The Properties panel is invoked by selecting (right clicking) a specific object on the Canvas, and contains a set of properties unique to that object. (D) A secondary structure layout of the P4–P6 domain of the *Tetrahymena thermophila* intron with visualization of all base pairs extracted from the crystal structure (PDB ID: 1GID [13] using FR3D [14,15]. The tooltip is invoked by hovering a mouse on a specific RNA object (a nucleotide or a base pair and contains all the information related to that object). The non-canonical base pairs are depicted for visualization purposes only and are ignored during editing and formatting.

each editing or formatting mode (described below) the user is expected to choose a constraint (a set of pre-defined substructure-selection rules that describe how a specific element can be treated). The constraints account for the difference in the base pairing state (single nucleotide, single base pair, single strand, helix), as well as for the more complex hierarchy of elements within an RNA molecule (stacked helix, cycle, sub-domain, RNA molecule). For users' convenience, the constraints are organized in four tabs (Primitives, Fragments, Units, and Scope) in the Navigation panel.

For example, when the "single nucleotide" constraint is selected, click-and-drag will reposition only the clicked-on nucleotide. In contrast, if the "RNA molecule" constraint were active instead, all nucleotides within the parent molecule would be dragged along with the clicked-on nucleotide. XRNA-React also supports manipulation of multiple RNA molecules (independent or crosslinked with each other via base-pairing). While the individual elements of these molecules can be manipulated as previously described, multiple RNA molecules depicted on the canvas can be simultaneously transformed using the "RNA Complex" constraint.

Edit Tool. The Edit Tool enables users to manipulate the topology of an RNA molecule by arranging its nucleotides on the canvas via translation or rotation, individually or cooperatively, depending on the selected constraint regime. Single nucleotides can be moved individually to a new position. Nucleotides within single-stranded regions can be aligned as equally spaced straight lines or arcs of a given circumference, determined by the positions of anchor points. By default, the anchors are assigned as the nearest base-paired nucleotides capping the single-stranded regions. The anchors can be manually adjusted to any pair of nucleotides within the desired single-stranded region via a locking mechanism (a middle-mouse click). The "Cycle" constraint enables the arrangement of a selected junction (two or more helices separated from each other by single-stranded nucleotides) into regularly shaped cycles of a desired circumference, in which the nucleotides within each single-stranded region are aligned along the circumference and are equally spaced, and the helices are arranged along radial lines from the center of the cycle pointing outward. Constraints that contain fragments capped with a base pair (single base pair, helix, or RNA domain), or the entire RNA molecule, can be rotated, translated or flipped on the canvas as rigid objects.

Format Tool. The Format Tool enables users to set, delete, or modify the base pairs of a given RNA molecule or complex and thus alter its topology. Once the topology is altered, Exornata automatically reassigns the constraint mode of the selected fragments (*e.g.*, two single nucleotides become a base pair, two single-stranded regions become a helix or vice versa) and adjusts its geometry to default parameters, unless the user

specifies to keep the positions of nucleotides frozen. Exornata supports dynamic formatting of base paired nucleotides and helices. Base pairs can be created or deleted directly on the canvas, and the helices can be dynamically realigned using keyboard shortcuts.

Exornata provides an ability to depict non-canonical base pairing according to Leontis-Westhof notation [16]. Advanced manipulations of RNA topology are achieved within the base pair editor (described in the Advanced Features section).

Supported file formats.

Input

Exornata supports multiple input-file formats and output-file formats; some formats are supported both as input files and output files. The most well-supported and portable format is JSON [9] (a detailed description of JSON format is given in a separate section below). Exornata also supports XRNA legacy files for the sake of backward compatibility, FASTA files (with optional dot bracket notation of the secondary structure) as well as CT and BPSEQ files. For the last three options, coordinates of nucleotides are generated automatically by aligning a provided nucleotide sequence along circumference of a circle. Exornata also provides an ability to export base pairing from the existing 3D structures using FR3D API.

Output

Exornata supports several output formats. JSON is the default output format, which enables cross compatibility of all features provided by Exornata with other platforms. Details of the JSON format are described below. Other formats include XRNA legacy format, BPSeq, and Traveler [10], limited to supporting canonical base pairs. Our tool also generates vector images in SVG format that are suitable for publication. The SVG files contain a hierarchical structure, where different objects are partitioned across separate layers, and can be further post-processed in graphical packages such as Adobe Illustrator.

Advanced features. Non-canonical base pairing. Exornata features a built-in algorithm for detecting base pair types when their type is not explicitly specified. The default options are Canonical for C-G, G-C, A-U, and U-A base pairs; Wobble for G-U pairs; and Mismatch for all other combinations. Canonical base pairs are graphically represented as "—", Wobbles are depicted by "●", and Mismatches are "○".

In addition to the default base pair assignments, Exornata contains functionality to define and visualize base pairing according to the schema proposed by Leontis and Westhof [16], which uses the orientation of the bases (W, Watson-Crick; H, Hoogsteen; and S, sugar) and the orientation of the glycosidic bonds with respect to each other (cis or trans). Exornata uses the conventional graphical formalism proposed by Leontis and Westhof to depict non-canonical base pairing. For example, cWW represents a canonical Watson-Crick interaction and is depicted by "—", while tWH represents a non-canonical trans Watson-Crick-Hoogsteen interaction.

Note that some base pair symbols contain directional information. The standard Leontis-Westhof notation prioritizes the order of the base pairing (W > H > S) over the nucleotide index number. While users have the flexibility to define such base pairs as either G72 A104, tSH or A104 G72, tHS in the base pair editor or input file, the output will be written according to the 12 standard representations in the output JSON file (*e.g.,* A104 G72, tHS) [16]. Detailed information about nucleotides and base pairs is provided in the tooltip, which is automatically invoked by hovering a mouse over a specific object (Figure 1D).

Base pair editor. One of the advanced features of Exornata is an ability for users to supply or alter the topology (base pairing state) of an RNA molecule laid out on the Canvas at any moment. In addition to intuitive formatting steps performed with the mouse, users can also specify and manipulate the base pairing state in the text format using a built-in base-pair editor. The base-pair editor (Figure 2) is toggled by activating the Format Tool and right clicking on a nucleotide or a base pair. The editor will appear in the bottom part of the Canvas and its vertical size can be modified by dragging the mouse at the window's edge.

The editor consists of a pairwise list of nucleotides involved in base pairing, including specification of the respective RNA molecules (if more than one molecule is shown on canvas). The editor also automatically detects and auto-populates the base pairing type, with an ability to edit and modify the base pairing to non-canonical interactions according to the Leontis-Westhof schema [16]. When the "Treat non-canonical base pairs as unpaired nucleotides" setting is enabled, non-canonical base pairs are displayed for visualization purposes only. They are excluded from helix formatting properties and do not appear in the formatting editor's listings.

The editor supports two independent pairs of display modes. The first pair consists of "Base Pairs" versus "Helices" modes: under "Base Pairs" mode, individual base pairs may be edited or deleted, while "Helices" mode displays contiguous base pairs in a compact form without editing features. The second pair consist of "Constrained" versus "Global" modes: under "Constrained"

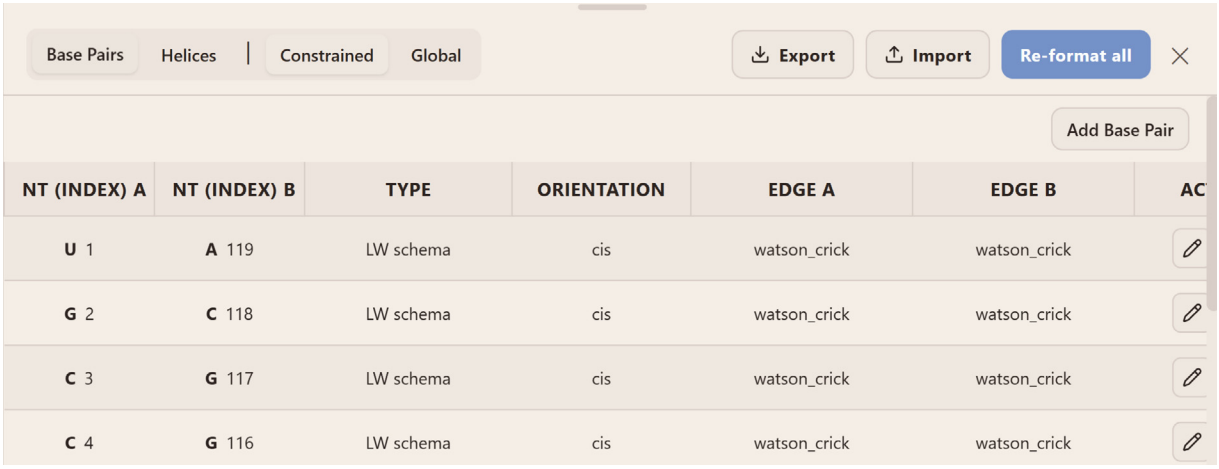

Figure 2. The base pair editor interface for specifying and manipulating RNA topology. The editor displays base pairs in either individual or helical format with Constrained or Global viewing modes, automatically detects base pairing types according to the Leontis-Westhof schema, and provides tools to create, delete, reformat, and import/export base pairing topology as csv files.

mode, the displayed set of base pairs or helices is limited according to the selection detected by the active constraint as a function of the clicked-on nucleotide or base pair, whereas "Global" mode displays all helices in the scene.

The editor further contains buttons that allow users to apply, update or delete the base-pairing topology, reflecting changes on the Canvas. Users can alter the topology of an RNA molecule or apply simultaneous reformatting of affected regions. When "Re-format All" is pressed, all basepair/helix elements displayed in the editor (and only these elements) will be repositioned along their helix axis; this feature may be utilized to re-align newly added base pairs to their parent helix. Finally, users have an ability to upload or download the base pair list as a csv file.

Support of multiple RNA molecules. Exornata supports the simultaneous visualization, editing, and formatting of multiple RNA molecules on a single canvas. These molecules can exist as isolated structures with only intramolecular base pairing, or they can be cross-linked through intermolecular base pairs. Each RNA molecule is treated independently unless molecules share common helical regions. Additional RNA molecules can be added to canvas via input interface at any stage of editing.

For example, the large subunit (LSU) rRNA of eukaryotes (Figure 3) comprises multiple chains (including 5.8S and 28S rRNAs) that are interconnected through intermolecular base pairs. For intermolecular interactions, nucleotides involved in base pairing are annotated to indicate their corresponding partner molecules within the complex. Exornata enables simultaneous yet independent editing, formatting, and labeling of each molecular component within such complexes.

Annotate Tool: Labeling, coloring and altering representation. Exornata contains Annotate Tool that provides users with the ability to label nucleotides. Users have an ability to (i) select any range of the residues within the molecule, (ii) set the incremental value for labels; and (iii) shift the displayed nucleotide indices within the molecule to any arbitrary integer. As a specific example, annotations are automatically laid out as angles tangent to the curve that the nucleotide sequence implicitly forms. Angular interpolation enables intuitive-looking annotations without requiring manual correction of annotation angles and positions.

Exornata provides an interactive editor for coloring nucleotides, labels, and label lines. It also enables users to alter representation of RNA into a more coarse-grained contour line path, with options to adjust line thickness and capping curvature of the individual segments.

Finally, the Annotate Tool contains an additional set of automated and manual features that enhance representation of RNA secondary structures. Exornata provides users with an ability to automatically generate connecting lines between disjoint elements within a 2D layout when they exceed a specified distance threshold. These connector lines (solid, dashed, or dotted) can further be customized: users can modify their color and style, subdivide them into multiple segments, or convert them into curved paths. Individual line segments can be decorated with

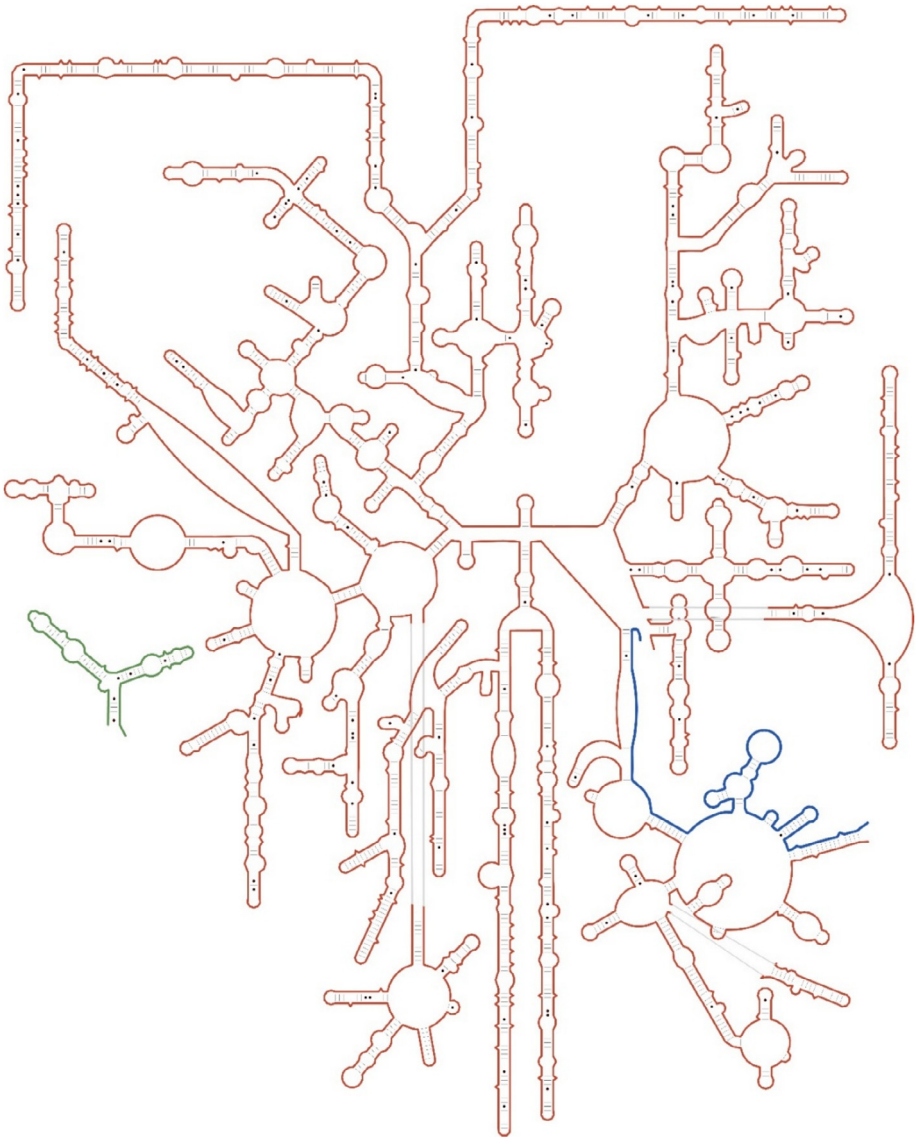

Figure 3. The secondary structure of the LSU rRNA of *H. sapiens, which* consists of three RNAs: 5.8S rRNA (blue), 28S rRNA (red), and 5S rRNA (green), in contour line representation output by Exornata.

various symbols such as arrows or triangles, and text annotations can be added throughout the structure.

Coding and Technical Details

Implementation and technical details. Exornata is a web application implemented in React.js and TypeScript, enabling visualization and interactive manipulation of RNA secondary structures. Using capabilities of React, Exornata supports a highly interactive suite of tools facilitating an intuitive user experience. The underlying data model is structured hierarchically: RNA complexes contain one or more RNA molecules composed of nucleotide sequences. Nucleotides may form intramolecular or intermolecular base pairs.

Exornata leverages linear algebra to implement intuitive features: automatic label re-orientation and repositioning. Application performance is optimized via React memorization hooks to achieve smooth real-time interactions, even with large RNA structures. Upon user-driven input-file upload of a particular file format (*e.g.,* JSON), the output format dynamically updates to match (when supported). Likewise, SVG visualization enables resolution-independent rendering of nucleotides and their base pairs.

Description of JSON format. The Exornata JSON format is an in-house designed schema (https://github.com/LDWLab/RNA2D-data-schema) for encoding RNA secondary structure layouts. JSON represents a modern mechanism of sharing

the 2D RNA layouts with different properties across multiple platforms like R2DT [8,9], Traveler [10], RNAcanvas [11],and RiboVision2 [17]. For, example, a predicted secondary structure from R2DT can be directly accessed and further edited via. https://exornata.chemistry.gatech.edu/?source_url=https://www.ebi.ac.uk/Tools/services/rest/r2dt/result/r2dt-{r2dt_job_id}/json.

The hierarchical data model aims to capture overall organization of RNA layouts. It defines RNA layouts as RNA complexes with various attributes, which contain one or more RNA molecules (requiring "name", "sequence", basePairs", and "labels" properties). Each nucleotide in the "sequence" array must specify "residueIndex" (integer), "residueName" (string), and coordinate properties "x" and "y" (floating-point numbers). Base pairs are defined through "basePairs" arrays at either the complex or molecule level, requiring "residueIndex1" and "residueIndex2" (plus "rnaMoleculeName1" and "rnaMoleculeName2" for intermolecular pairs), with optional "basePairType" that supports classifications including "canonical", "wobble", "mismatch", and Leontis-Westhof notation types like "cWW" or "tHS".

Labels are defined through objects in the "labels" array, each requiring a "residueIndex" to anchor them to specific nucleotides. Labels can contain "labelContent" objects (with required "label" text and "x", "y" coordinates) and "labelLine" objects (with a "points" array of coordinate objects for drawing leader polylines). All visual elements—nucleotides, base pairs, labels, and their components—can reference style "classes" by name or specify individual styling properties.

Such combination of explicit structural attributes and flexible styling makes the JSON schema a precise blueprint for representing RNA secondary structures in various pipelines of structural and computational biology. This standardized format enables researchers to produce, edit, and share RNA layouts across different platforms in the research community.

Discussion and Summary

RNA secondary structures serve as essential bridges between sequence and biological function. They provide an intermediate level of organization that connects the linear sequence of nucleotides to the three-dimensional architecture and ultimate biological activity of RNA molecules. These structures link sequence, tertiary structure, chemistry, and biology in ways that are accessible to both computational analysis and human interpretation.

RNA secondary structures can be determined from sequences [18–21] and can be extracted from three-dimensional structures [14,22–24]. A number of packages aimed at drawing, manipulating, and visualizing RNA secondary structures are available, including VARNA [25], R2R [26], RNAVis2 [27], RNAstructure [28], Forna [29], and RNAscape [23]. Many of these tools automate layout, producing visual representations of base-pairing patterns, with some programs implementing algorithms that automatically determine feasible layouts of RNA molecules [9,30,31].

Despite these advances, most RNA drawing software lacks the capability to easily represent non-Watson-Crick base pairs, even though some tools can extract these interactions [16] from three-dimensional structures [14,22,24]. This creates a disconnect between what researchers can analyze and what they can effectively visualize [32]. More recent tools like RNA2Drawer [33] and its web-based successor RNAcanvas [11] were developed specifically to address these limitations by allowing graphical structure editing while maintaining geometric consistency throughout structural changes. RNAcanvas provides enhanced functionality including motif search capabilities, support for Leontis-Westhof notation for non-canonical base pairs, and optimization for editing large structures. RNArtist [34] offers additional modern approaches to RNA structure visualization. These recent tools bridge the gap between sophisticated RNA structure representation and user accessibility, combining manual editing capabilities with extensive interactive features and publication-quality output.

Beyond visualization, the standardization of RNA secondary structural layouts has proven essential for researchers in structural and evolutionary biology. Expert-curated layouts serve as reference frameworks that consistently position conserved structural elements in recognizable locations, making it immediately apparent where sequences differ and where they maintain structural conservation. This need for standardization led to recent joint efforts by multiple teams to develop the R2DT pipeline [8,9], which uses a template-based approach that integrates powerful tools for detecting specific RNA families and automatically adapting available templates to the features of specific sequences.

Exornata extends these capabilities by providing users with a modern, web-based platform that facilitates highly interactive, dynamic editing and reformatting of RNA secondary structure diagrams. In contrast to legacy desktop applications, Exornata is designed to be used directly in the browser, improving accessibility and eliminating setup and installation requirements. The software was designed with intuitive use in mind, implementing several quality-of-life features such as dynamic repositioning and realignment of annotations when underlying structures are edited or annotated.

The integration of Exornata into the R2DT pipeline represents a significant step toward establishing libraries of standardized RNA layouts.

By supporting formats from complementary tools including Traveler and RNAcanvas, and enabling representation of non-Watson-Crick base pairs, Exornata bridges the gap between structural analysis and visualization. This interoperability ensures that researchers can leverage automated template-based generation while maintaining the option for manual refinement when needed.

The web-based implementation of Exornata democratizes access to sophisticated RNA editing capabilities, eliminating installation barriers and enabling collaborative development of standardized layouts. As the field continues to discover novel RNA families and refine structural models of known RNAs, the availability of user-friendly tools for creating publication-quality, standardized diagrams becomes increasingly important.

Future developments may include enhanced support for three-dimensional structure integration with RiboVision2, expanded motif libraries, and collaborative editing features within the R2DT community. The ultimate goal remains the establishment of a comprehensive, community-curated repository of standardized RNA secondary structure layouts that accelerate comparative analysis and deepen our understanding of RNA structure–function relationships across all domains of life.

In summary, Exornata modernizes RNA secondary structure editing, providing an intuitive tool set implemented in popular web technologies like React and TypeScript. These features make Exornata a user-friendly alternative to traditional RNA editing applications.

CRediT authorship contribution statement

Caeden D. Meade: Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Formal analysis. **Biswajit Banerjee:** Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Data curation. **Yuzheng Yang:** Writing – original draft, Visualization, Validation, Formal analysis. **Arsh Suri:** Resources, Software, Validation. **David Hoksza:** Writing – review & editing, Methodology, Data curation. **Loren Dean Williams:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition. **Anton S. Petrov:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

DATA AVAILABILITY

No data was used for the research described in the article.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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