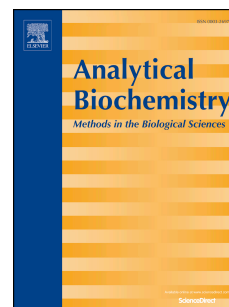# Accepted Manuscript

iRNA-Methyl: Identifying N^6-methyladenosine sites using pseudo nucleotide composition

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Subject Category: DNA Recombinant Techniques and Nucleic Acids

iRNA-Methyl: Identifying N6-methyladenosine sites using pseudo nucleotide composition

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Short Title: Identifying RNA methylation sites

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ABSTRACT

Occurring at adenine (A) with the consensus motif GAC, N^6-methyladenosine (m^6A) is one of the most abundant modifications in RNA, which plays very important roles in many biological processes. The non-uniform distribution of m^6A sites across the genome implies that, for better understanding the regulatory mechanism of m^6A, it is indispensable to characterize its sites in a genome-wide scope. Although a series of experimental technologies have been developed in this regard, they are both time-consuming and expensive. With the avalanche of RNA sequences generated in the postgenomic age, it is highly desired to develop computational method to timely identify their m^6A sites. In view of this, a predictor called "**iRNA-Methyl**" was proposed by formulating RNA sequences with the "pseudo dinucleotide composition", into which three RNA physiochemical properties were incorporated. To our best knowledge, it is the first computational predictor ever established for identifying m^6A sites in RNA. Rigorous cross validation tests have indicated that **iRNA-Methyl** holds very high potential to become a useful tool for genome analysis. For the convenience of most experimental scientists, a web server for **iRNA-Methyl** was established at http://lin.uestc.edu.cn/server/iRNA-Methyl, by which users can easily get their desired results without needing to go through the mathematical details.

I. INTRODUCTION

More than 100 kinds of post-transcriptional RNA modifications have been found in eukaryotic mRNA [1]. Among these modifications, N[6]-methyladenosine (m[6]A) is the most abundant one that is also the first RNA reversible one [2]. As shown in **Fig.1**, the modification occurs on the 6th nitrogen atom of adenine. Since it was found in 1970s, m[6]A has been identified in all three kingdoms of life [3-6] and is associated with a number of biological processes including mRNA splicing, export, stability, and immune tolerance [7-9].

With the development of high-throughput techniques such as MeRIP-Seq [10] and m[6]A-seq [11], the genome-wide distribution of m[6]A are now available for several species, such as *Saccharomyces cerevisiae* [12], *Mus musculus* [13] and *Homo sapiens* [13]. These experimental results revealed that m[6]A sites tend to occur near the stop codon, in 3' UTR, and within long internal exons [10; 13]. The nonrandom distribution of m[6]A sites across the genome is highly conserved from yeast to human, suggesting that m[6]A modification is both fundamental and important for organisms [12; 13]. The current biochemical methods are, however, both costly and time-consuming in performing genome-wide analysis. Therefore, it is in high demand to develop computational methods for analyzing the distribution and function of m[6]A, so as to help speed up the genome-wide m[6]A detection.

Unfortunately, to our best knowledge, so far there is no computational tool available whatsoever for detecting m[6]A. In view of this, the present study was initiated in an attempt to develop a new computational predictor by which one can easily identify m[6]A sites.

As demonstrated by a series of recent publications [14-22], to establish a really useful sequence-based statistical predictor for a biological system and also to make the presentation logically crystal clear, we should follow the 5-step guidelines [23]: (i) construct or select a valid benchmark dataset to train and test the predictor; (ii) formulate the biological sequence samples with an effective mathematical expression that can truly reflect their intrinsic correlation with the target to be predicted; (iii) introduce or develop a powerful algorithm (or engine) to operate the prediction; (iv) properly perform cross-validation tests to objectively evaluate the anticipated accuracy; (v) establish a user-friendly web-server for the predictor that is accessible to the public. Below, let us elaborate how to deal with these steps one-by one.

II. MATERIALS AND METHOD

II.1. Benchmark Dataset

Since the sites of m[6]A in the *S. cerevisiae* genome share a consensus motif GAC where its center base has the potential to be methylated [12], for facilitating description later, we use the following scheme to represent a RNA sample

$$\mathbf{R}_\xi(\mathbb{GAC}) = N_{-\xi}N_{-(\xi-1)} \cdots N_{-2}N_{-1}\mathbb{GAC}N_{+1}N_{+2} \cdots N_{+(\xi-1)}N_{+\xi} \tag{1}$$

where the center $\mathbb{A}$ represents "adenine", the subscript ξ is an integer, $N_{-\xi}$ represents the ξ-th upstream nucleotide from the center, the $N_{+\xi}$ the ξ-th downstream nucleotide, and so forth (**Fig.2**). The $(2\xi + 3)$-tuple RNA sample $\mathbf{R}_\xi(\mathbb{GAC})$ can be further classified into the following categories:

$$\mathbf{R}_\xi(\mathbb{GAC}) \in \begin{cases} \mathbf{R}_\xi^+(\mathbb{GAC}), & \text{if its center is a methylation site} \\ \mathbf{R}_\xi^-(\mathbb{GAC}), & \text{otherwise} \end{cases} \qquad (2)$$

where $\mathbf{R}_\xi^+(\mathbb{GAC})$ denotes a true methylation segment with adenine at its center, $\mathbf{R}_\xi^-(\mathbb{GAC})$ a false methylation segment with adenine at its center, and the symbol $\in$ means "a member of" in the set theory.

As elaborated in a comprehensive review [24], there is no need to separate a benchmark dataset into a training dataset and a testing dataset if the predictor to be developed will be tested by the jackknife test or subsampling (K-fold) cross-validation test because the outcome thus obtained is actually from a combination of many different independent dataset tests. Thus, the benchmark dataset $\mathbb{S}_\xi$ for the current study can be formulated as

$$\mathbb{S}_\xi = \mathbb{S}_\xi^+ \cup \mathbb{S}_\xi^- \qquad (3)$$

where the positive subset $\mathbb{S}_\xi^+$ only contains the samples of true methylation segments $\mathbf{R}_\xi^+(\mathbb{GAC})$, and the negative subset $\mathbb{S}_\xi^-$ only contains the samples of false methylation segments $\mathbf{R}_\xi^-(\mathbb{GAC})$ (see **Eq.2**); while $\cup$ represents the symbol for "union" in the set theory.

Because the length of RNA sample $\mathbf{R}_\xi(\mathbb{GAC})$ is $2\xi + 3$ (see **Eq.1**), the benchmark dataset with different ξ value will contain RNA segments with different number of nucleotides, as illustrated below

$$\text{The length of RNA samples in } \mathbb{S}_\xi = \begin{cases} 21 \text{ nucleotides}, & \text{if } \xi = 9 \\ 31 \text{ nucleotides}, & \text{if } \xi = 14 \\ 41 \text{ nucleotides}, & \text{if } \xi = 19 \\ 51 \text{ nucleotides}, & \text{if } \xi = 24 \\ 61 \text{ nucleotides}, & \text{if } \xi = 29 \\ \vdots & \vdots \end{cases} \qquad (4)$$

Preliminary tests had indicated, however, best prediction results were achieved when $\xi = 24$. Accordingly, hereafter we are to focus on the RNA samples with 51 nucleotides only.

The detailed procedures to construct $\mathbb{S}_{\xi=24}$ are as follows. (**1**) As done in [25], slide the $(2\xi + 3) = 51$-tuple nucleotide window along each of the RNA sequences taken from *S. cerevisiae* genome, and collected were only those RNA segments that have GAC at the center and A (adenine) or G (guanine) at the position of N_{-1} (see **Eq.1**); doing so is because the consensus motif for m6A determined by experiments for *S. cerevisiae* genome is RGAC (R=A/G) [12]. (**2**) If the upstream or downstream in an RNA was less than $\xi = 24$ or greater than $L - 24$ (L is the RNA's

length), the lacking nucleotide was filled with its mirror image (**Fig.3**). **(3)** The RNA segment samples thus obtained were put into the positive subset $\mathbb{S}_\xi^+$ if their centers have been experimentally annotated as the methylation sites; otherwise, into the negative subset $\mathbb{S}_\xi^-$. **(4)** Using the CD-HIT software [26], the aforementioned samples were further subject to a screening procedure to winnow those that were identical to any other in a same subset. (**5**) Excluded from the benchmark dataset were also those that were self-conflict; i.e., simultaneously occurring in both methylation subset $\mathbb{S}_\xi^+$ and non-methylation subset $\mathbb{S}_\xi^-$.

By following the aforementioned five steps, we first obtained a benchmark dataset consisting of 1,307 positive samples and 33,280 negative samples. It is a very imbalanced dataset, in which the size of $\mathbb{S}_\xi^-$ is overwhelmingly greater than that of $\mathbb{S}_\xi^+$. In order to minimize the underprediction or overprediction [27] caused by such a highly skewed benchmark dataset, we randomly picked out 1,307 ones from the 33,280 negative samples to form the negative dataset $\mathbb{S}_\xi^-$.

The detailed sequences for the 1,307 positive samples and 1,307 negative samples are given in <u>Online Supporting Information S1</u>. They can also be downloaded at <u>http://lin.uestc.edu.cn/server/iRNAMethy/data</u>.

II.2. Representation of RNA Samples

The RNA samples in the current benchmark dataset can be generally expressed as

$$\mathbf{R} = N_1 N_2 N_3 \cdots N_i \cdots N_{51} \tag{5}$$

where N_1 represents the 1st nucleotide at the sample sequence position 1, N_2 the 2nd nucleotide at the position 2, and so forth. They can be any of the four nucleotides; i.e.,

$$N_i \in \{A \text{ (adenine)} \quad C \text{ (cytosine)} \quad G \text{ (guanine)} \quad U \text{ (uracil)}\} \tag{6}$$

Based on the sequential model of **Eq.5**, one could directly utilize BLAST [28] to perform statistical analysis. Unfortunately, this kind of straightforward and intuitive approach failed to work when a query RNA sequence sample did not have significant similarity to any of the character-known RNA sequences.

To deal with this problem, investigators could not help but resort to the discrete or vector model. Actually, an important reason for them to do so is that all the existing machine-learning algorithms can be directly used to handle vector models but not sequences, as elaborated in [29].

The most simple vector model for an RNA sequence is its nucleic acid composition (NAC); i.e.,

$$\mathbf{R} = [f(A) \quad f(C) \quad f(G) \quad f(U)]^{\mathbf{T}} \tag{7}$$

where $f(A)$, $f(C)$, $f(T)$, and $f(U)$ are the normalized occurrence frequencies of adenine (A), cytosine (C), thymine (T), and uracil (U) in the RNA sequence, respectively; the symbol **T** is the transpose operator. As we can see from **Eq.7**, however, if using NAC to represent a RNA sample, all its sequence order information would be completely lost.

If using the k-tuple nucleotide (k-mer) composition to represent the RNA sequence, the corresponding vector will have a dimension of 4^k. With the incensement of k values, the vector's dimension will increase rapidly, leading to the so-called "high-dimension disaster" [30] or overfitting problem that will significantly reduce the deviation tolerance or cluster-tolerant capacity [31] so as to lower down the prediction success rate or stability. Therefore, the k-mer approach is useful only when the value of k is very small. In other words, it can only be used to incorporate the local or short-range sequence order or pattern information, but certainly not the global or long-range sequence order or pattern information.

To approximately cover the long-range sequence pattern information, one popular and well-known method is to use the pseudo component approach originally proposed for dealing with protein/peptide sequences [32]. Ever since introduced in 2001, the approach and its concept have been penetrating to nearly all the areas of computational proteomics (see, e.g., [33-40] as well as a long list of papers cited in a recent review article [41]. Because the pseudo component approach has been widely and increasingly used, some publicly accessible web-servers [42-44] have been established, allowing users to generate various kinds of pseudo components according their needs to study many different problems in computational proteomics. Recently, the concept of pseudo component approach was further extended to study the problems in computational genetics and genomics [18; 21; 45; 46]. Meanwhile, the corresponding web-servers have been developed accordingly for generating various kinds of pseudo components for DNA sequences [47-49] and RNA sequences [50; 51].

In order to incorporate both the local and global sequence pattern information of the RNA sequences, we adopted the approach of pseudo 2-tuple nucleotide composition or pseudo dinucleotide composition (PseDNC); i.e., represent the RNA sample of **Eq.5** with the formulation below

$$\mathbf{R} = [d_1 \quad d_2 \quad \cdots \quad d_{16} \quad d_{16+1} \quad \cdots \quad d_{16+\lambda}]^{\mathbf{T}} \tag{8}$$

where

$$d_u = \begin{cases} \dfrac{f_u}{\sum_{i=1}^{16} f_i + w \sum_{j=1}^{\lambda} \theta_j} & (1 \leq u \leq 16) \\[4mm] \dfrac{w\theta_{u-16}}{\sum_{i=1}^{16} f_i + w \sum_{j=1}^{\lambda} \theta_j} & (16 < u \leq 16 + \lambda) \end{cases} \tag{9}$$

In **Eq.9** f_u ($u = 1, 2, \cdots, 16$) is the normalized occurrence frequency of the u-th non-overlapping dinucleotides in the RNA sequence, and

$$\theta_j = \frac{1}{L - j - 1} \sum_{i=1}^{L-j-1} C_{i,i+j} \qquad (j = 1, 2, \cdots, \lambda; \ \lambda < L) \tag{10}$$

where θ_1 is called the first-tier correlation factor that reflects the sequence order correlation between all the most contiguous dinucleotide along a RNA sequence (**Fig.4a**), θ_2, the second-tier correlation factor between all the second most contiguous dinucleotide (**Fig.4b**); θ_3, the third-tier correlation factor between all the third most contiguous dinucleotide (**Fig.4c**); and so forth.

Now, it is clear that the first 16 components in **Eq.8** are used to incorporate the short-range or local sequence order information of the RNA sample, while the remaining components used for its long-range or global sequence order information. Obviously, λ can also be viewed as the number of the total pseudo components used to reflect the long-range or global sequence effect [50; 51], and w of **Eq.9** is the weight factor [32; 35]. The concrete values for λ and w will be further discussed later.

In **Eq.10** the coupling factor $C_{i,i+j}$ is given by

$$C_{i,i+j} = \frac{1}{\mu} \sum_{g=1}^{\mu} \left[P_g(D_i) - P_g(D_{i+j}) \right]^2 \tag{11}$$

where μ is the number of RNA physicochemical properties considered that is equal to 3 in the current study and will be further explained bellow.

II.3. RNA Property Parameters

Since the formation of RNA secondary structure will decrease the m[6]A methylation [52], the following three physicochemical properties, namely enthalpy [53], entropy [53] and free energy [54] that can quantify the RNA secondary structures [55-57], are used to calculate the global or long-range sequence-order effects via **Eq.10** and **Eq.11**. The concrete values of these three physicochemical properties are given in **Table 1**. Note that before substituting them into **Eq.11**, all the original values $P_g(D_i)$ ($i = 1, 2, 3$) were subjected to a standard conversion, as described by the following equation

$$P_g(D_i) \Leftarrow \frac{P_g(D_i) - \langle P_g(D_i) \rangle}{SD\{\langle P_g(D_i) \rangle\}} \tag{12}$$

where the symbol $\langle \ \rangle$ means taking the average of the quantity therein over the 16 different dinucleotides, and SD means the corresponding standard deviation. For the detailed mathematical formulation of SD, see Eq.4 of the original paper [32] or Eq.4 of the 2005 paper [35]. The advantage to do so is that the converted values obtained by **Eq.12** will have a zero mean value over the 16 different dinucleotides, and will remain unchanged if going through the same conversion procedure again [24].

II.4. Support Vector Machine (SVM)

SVM is a machine-learning algorithm based on the statistical learning theory. It has been widely used in the realm of bioinformatics (see, e.g., Min, 2013 #2932; Liu, 2014 #2934;Chen, 2014 #2975;Xiao, 2014 #3040;Xu, 2014 #2988;Qiu, 2014 #2950;Liu, 2014 #2989}). Its basic principle is to transform the input vector into a high-dimension Hilbert space and seek a separating hyperplane with the maximal margin in this space by using the following decision function

$$F(\vec{X}) = \text{sgn}\left\{\sum_{i=1}^{N} y_i \alpha_i \cdot K(\vec{X}, \vec{X}_i) + b\right\} \tag{13}$$

where α_i is the Lagrange multipliers, b the offset, $\vec{X}$ the query input vector, $\vec{X}_i$ the i-th training vector; y_i represents the type of the i-th training vector; $K(\vec{X}, \vec{X}_i)$ is a kernel function that defines an inner product in a high dimensional feature space; and sgn is the sign function. Due to its effectiveness and speed in nonlinear classification process, the radial basis kernel function (RBF) was used in the current study. For a brief formulation of SVM and how it works, see the papers [58]; for more details about SVM, see a monograph [59].

The package LIBSVM 2.84 (http://www.csie.ntu.edu.tw/~cjlin/) written by Chang and Lin was employed to perform SVM in the current study. The SVM algorithm contains two parameters: one is the regularization parameter C; the other is the kernel width parameter γ. In the current study, the two parameters were determined by an optimization procedure in which the grid search and 10-fold cross validation were performed. The final results thus obtained were $C = 32$ and $\gamma = 0.0078125$, respectively.

The predictor obtained via the above procedures is called **iRNA-Methyl**.

III. RESULTS AND DISCUSSION

III.1. Metrics Used to Evaluate the Prediction Quality

The current study is a kind of binary (two-lass) classification problem; i.e., for a given RNA sample, whether it is a positive one (belonging to the methylation segment) or negative (belonging to the non-methylation segment). For this kind of binary classification problem, the following set of metrics were often used to measure the prediction quality

$$\begin{cases} \text{Sn} = \dfrac{\text{TP}}{\text{TP} + \text{FN}} \\ \text{Sp} = \dfrac{\text{TN}}{\text{TN} + \text{FP}} \\ \text{Acc} = \dfrac{\text{TP} + \text{TN}}{\text{TP} + \text{TN} + \text{FP} + \text{FN}} \\ \text{MCC} = \dfrac{(\text{TP} \times \text{TN}) - (\text{FP} \times \text{FN})}{\sqrt{(\text{TP} + \text{FP})\,(\text{TP} + \text{FN})(\text{TN} + \text{FP})(\text{TN} + \text{FN})}} \end{cases} \tag{14}$$

where TP represents the true positive; TN, the true negative; FP, the false positive; FN, the false negative; Sn, the sensitivity; Sp, the specificity; Acc, the accuracy; MCC, the Mathew's correlation coefficient [60]. The metrics formulated in **Eq.14** is not easy-to-understand for most experimental scientists, and hence here we would prefer to use the following formulation as done by many investigators in a series of recent publications (see, e.g., [14; 22; 61-66]):

$$
\begin{cases}
\text{Sn} = 1 - \dfrac{N_-^+}{N^+} & 0 \le \text{Sn} \le 1 \\[2mm]
\text{Sp} = 1 - \dfrac{N_+^-}{N^-} & 0 \le \text{Sp} \le 1 \\[2mm]
\text{Acc} = \Lambda = 1 - \dfrac{N_-^+ + N_+^-}{N^+ + N^-} & 0 \le \text{Acc} \le 1 \\[2mm]
\text{MCC} = \dfrac{1 - \left(\dfrac{N_-^+ + N_+^-}{N^+ + N^-}\right)}{\sqrt{\left(1 + \dfrac{N_+^- - N_-^+}{N^+}\right)\left(1 + \dfrac{N_-^+ - N_+^-}{N^-}\right)}} & -1 \le \text{MCC} \le 1
\end{cases}
\tag{15}
$$

where N^+ is the total number of the positive samples or true methylation RNA segments investigated while N_-^+ the number of true methylation RNA samples incorrectly predicted to be of false methylation segment; N^- the total number of the negative samples or non-methylation RNA samples investigated while N_+^- the number of the non-methylation RNA samples incorrectly predicted to be of methylation segment. According to **Eq.15**, it is crystal clear to see the following. When $N_-^+ = 0$ meaning none of the positive sample was incorrectly predicted to be a negative one, we have the sensitivity Sn = 1. When $N_-^+ = N^+$ meaning that all the positive samples were incorrectly predicted to be the negative, we have the sensitivity Sn = 0. Likewise, when $N_+^- = 0$ meaning none of the negative samples was mispredicted, we have the specificity Sp = 1; whereas $N_+^- = N^-$ meaning that all the negative samples were incorrectly predicted as positive, we have the specificity Sp = 0. When $N_-^+ = N_+^- = 0$ meaning that none of the samples in the positive dataset and none of the samples in the negative dataset were incorrectly predicted, we have the overall accuracy Acc = 1 and MCC = 1; when $N_-^+ = N^+$ and $N_+^- = N^-$ meaning that all the samples in the positive dataset and all the samples in the negative dataset were incorrectly predicted, we have the overall accuracy Acc = 0 and MCC = −1; whereas when $N_-^+ = N^+/2$ and $N_+^- = N^-/2$ we have Acc = 0.5 and MCC = 0 meaning no better than random guess. As we can see from the above discussion, it would make the meanings of sensitivity, specificity, overall accuracy, and Mathew's correlation coefficient much more intuitive and easier-to-understand by using the formulation of **Eq.15**, particularly for the meaning of MCC.

It should be pointed out, however, the set of metrics as defined in **Eq.14** or **Eq.15** is valid only for the single-label systems. For the multi-label systems whose emergence has become more frequent in system biology [67-70] and system medicine [29; 71], a completely different set of metrics as defined in [27] is needed.

III.2. Method Used to Conduct Cross Validation

With a set of clearly defined metrics available to measure the prediction quality, the next thing is what validation method should be used to derive the metrics values. In statistical prediction, the following three cross-validation methods are often used to derive the metrics values for a predictor: independent dataset test, subsampling (or K-fold cross-validation) test, and jackknife test [72]. Of the three methods, however, the jackknife test is deemed the least arbitrary that can always yield a unique outcome for a given benchmark dataset as elucidated in [23] and demonstrated by Eqs.28-32 therein. Accordingly, the jackknife test has been widely recognized and increasingly used by investigators to examine the quality of various predictors (see, e.g., [37; 39; 40; 73-76].

Accordingly, in this study we also use the jackknife test to evaluate the accuracy of the current predictor. During the jackknife test, each of the samples in the benchmark dataset is in turn singled out as an independent test sample and all the rule-parameters are calculated without including the sample being identified. Although the jackknife test may take more computational time, it is worthwhile because it will always yield a unique outcome for a given benchmark dataset.

III.3. Parameter Determination and Anticipated Success Rates

As we can see from **Eqs.9-10**, the present model depends on the two parameters w and λ. The former is the weight factor usually within the range from 0 to 1, while the latter is the number of correlation tiers considered to reflect the global sequence pattern effect (**Fig.4**). Generally speaking, the greater the λ is, the more global sequence-pattern information the model contains. But if λ is too large, it would reduce the cluster-tolerant capacity [31] so as to lower down the cross-validation accuracy due to over-fitting or "high dimension disaster" problem [30]. Therefore, our searching for the optimal values of the two parameters was within the ranges given below

$$\begin{cases} 3 \leq \lambda \leq 6 & \text{with step } \Delta = 1 \\ 0.1 \leq w \leq 1 & \text{with step } \Delta = 0.1 \end{cases} \tag{16}$$

At this step, in order for reducing computational time, the **iRNA-Methyl** predictor was examined by the 10-fold cross validation on the benchmark dataset $\mathbb{S}$ (see **Eq.3** as well as the Online Supporting Information S1, when trained by the current benchmark dataset

Subsequently, with λ fixed at 6 and w at 0.9, the rigorous jackkni). The results thus obtained are illustrated in **Fig.5**, from which we can see that, when $\lambda = 6$ and $w = 0.9$, the predictor's accuracy (Acc) reaches its peak, indicating that the optimal λ and w values for the proposed predictor are 6 and 0.9, respectively fe tests were performed to calculate the Sn, Sp, Acc, and MCC as defined in **Eq.15** for the **iRNA-Methyl** predictor on the same benchmark dataset. The results thus obtained are listed in **Table 2.** To our best knowledge, so far no other special predictor ever developed for identifying the methylation sites in RNA, and hence **iRNA-Methyl** is the very first one in this area. Before the availability of **iRNA-Methyl**, in order to predict the methylation sites in a RNA sample, one couldn't help but use the

sequence-similarity-search-based tools (such as BLAST [28]) to search for those characters-known sequences with high similarity to the query sample. According to the BLAST approach, the query sample will be predicted as the true methylation RNA segment if it is most similar to the samples in the positive subset; otherwise, the false methylation RNA segment. Although it was quite straightforward and intuitive, unfortunately, the BLAST approach failed to work when the query sample did not have significant similarity to any of the character-known sequences as elucidated in [24]. With the availability of **iRNA-Methyl**, however, one can easily get the desired results via its web-server. The success rates obtained by **iRNA-Methyl** and the BLAST approach via the rigorous jackknife tests on the same benchmark dataset are, respectively, given in **Table 2**, from which we can see the following: (**1**) For the rates obtained by the BLAST approach, there is a big gap between Sn and Sp, indicating that the predicted results by the BLAST approach are very unstable with quite low specificity; in contrast to that, the corresponding rates obtained by **iRNA-Methyl** are much more even. (**2**) The Acc rate achieved by **iRNA-Methyl** is about 10% higher than that of BLAST approach, and the MCC rate of **iRNA-Methyl** is two times that of BLAST, indicating that **iRNA-Methyl** predictor is superior to the BLAST approach not only in overall accuracy but also in stability.

All these imply that the **iRNA-Methyl** proposed in this paper is quite promising that may become a useful high throughput tool in identifying m^{6}A sites.

III.4. Web-Server and Guide for Users

For the convenience of most experimental scientists, a publicly accessible web-server for **iRNA-Methyl** has been established. Moreover, to maximize users' convenience, a step-by-step guide on how to use it to get the desired results is given below.

Step 1. Open the web server at http://lin.uestc.edu.cn/server/iRNA-Methyl and you will see the top page of the **iRNA-Methyl** predictor on your computer screen, as shown in **Fig.6**. Click on the Read Me button to see a brief introduction about the predictor and the caveat when using it.

Step 2. Either type or copy/paste the query RNA sequences into the input box at the center of **Fig.6**. The input sequence should be in FASTA format. For the examples of RNA sequences in FASTA format, click the Example button right above the input box.

Step 3. Click on the Submit button to see the predicted result. For example, if you use the query RNA sequences in the Example window as the input, you will see the following shown on the screen of your computer. (1) RNA sequence-1 contains 5 "**GAC**" (with adenine at its middle) consensus motifs, of which only those at the sequence positions 128 is predicted to be the methylation sites or m^{6}A site, and all the others are not. (2) RNA sequence-2 contains 8 "**GAC**" consensus motifs, of which only those at the sequence positions 332 is predicted to be the methylation sites, while all the others are not. All these results are fully consistent with the experimental observations.

Step 4. Click on the <u>Data </u>button to download the datasets used to train and test the model.

Step 5. Click on the <u>Citation</u> button to find the relevant paper that document the detailed development and algorithm of **iRNA-Methyl.**

IV. CONCLUSIONS

Encouraged by the successes of pseudo amino acid composition (PseAAC) in dealing with protein/peptide sequences, a new predictor, called **iRNA-Methyl** was proposed for identifying m^{6}A sites in the *S. cerevisiae* genome by incorporating the global and long range sequence-pattern information of RNA via the PseKNC approach. This is a first computational predictor ever developed specially for identifying the methylation sites in RNA. The jackknife test on a rigorous benchmark dataset demonstrates that the **iRNA-Methyl** predictor is very promising.

Although the current **iRNA-Methyl** was trained by the benchmark dataset derived from *S. cerevisiae* genome, it can be extended to analyze the genomes of other species as well if trained by the benchmark datasets from those species, respectively.

Particularly, it has not escaped our notice that the current approach and its mathematical frame can also be used to develop different computational predictors for identifying various other modification sites in RNA.

A user-friendly a web server for **iRNA-Methyl** was established at http://lin.uestc.edu.cn/server/iRNA-Methyl, by which users can easily obtain their desired results without the need to go through the complicated mathematics involved, which were presented here just for its integrity. It is anticipated that **iRNA-Methyl** may become a useful high throughput tool for conducting genome analysis.

ACKNOWLEDGEMENTS

TABLES

Table 1. Original values of the three physicochemical properties for the 16 different dinucleotides in RNA. See the text for further explanation.

Dinucleotide	Enthalpy (Ka/mol)	Entropy (eU)	Free energy (Ka/mol)
GG	-12.2	-29.7	-3.26
GA	-13.3	-35.5	-2.35
GC	-14.2	-34.9	-3.42
GU	-10.2	-26.2	-2.24
AG	-7.6	-19.2	-2.08
AA	-6.6	-18.4	-0.93
AC	-10.2	-26.2	-2.24
AU	-5.7	-15.5	-1.10
CG	-8.0	-19.4	-2.36
CA	-10.5	-27.8	-2.11
CC	-12.2	-29.7	-3.26
CU	-7.6	-19.2	-2.08
UG	-7.6	-19.2	-2.11
UA	-8.1	-22.6	-1.33
UC	-10.2	-26.2	-2.35
UU	-6.6	-18.4	-0.93

Table 2. A comparison of iRNA-Methyl with the other method in identifying methylation sites in RNA.

Prediction method	Sn (%)	Sp (%)	Acc (%)	MCC
iRNA-Methyl[a]	70.55	60.63	65.59	0.29
BLAST approach[b]	71.76	38.79	55.27	0.11

[a]Proposed in this paper.
[b]Based on the sequence similarity principle [28].

FIGURE LEGENDS

Figure 1. An illustration to show the N^6-methylation and demethylation of adenosine. The formation of m^6A is catalyzed by N^6-adenosyl methyltransferases (MTases); while its reversible modification (demethylation) catalyzed by demethyltransferases (DMTases).

Figure 2. A schematic drawing to show how to use the flexible scaled window along a RNA sequence to collect the potential m^6A-containing segments. See **Eqs.1-5** and the relevant text for further explanation.

Figure 3. Schematic illustration to show the mirror image of (a) the 5' RNA terminal segment, and (b) the 3' RNA terminal segment. The symbol ⇔ represents a mirror, and the real RNA segment is colored in blue, while its mirror image in red.

Figure 4. A schematic illustration to show the correlations of dinucleotides along a RNA sequence. (**a**) The first-tier correlation reflects the sequence-order mode between all the most contiguous non-overlapping dinucleotide. (**b**) The second-tier correlation reflects the sequence-order mode between all the second-most contiguous non-overlapping dinucleotide. (**c**) The third-tier correlation reflects the sequence-order mode between all the third-most contiguous non-overlapping dinucleotide.

Figure 5. 3D graph to show the accuracies obtained in the 10-fold cross-validation with different values of w and λ.

Figure 6. A semi-screenshot to show the top page of the **iRNA-Methyl** web-server. Its website address is http://lin.uestc.edu.cn/server/iRNA-Methyl.

Figure 1

5' $\ldots\ldots N_{-\xi}N_{-(\xi-1)}\ldots\ldots N_{-3}N_{-2}N_{-}$ GAC $N_{+1}N_{+2}N_{+3}\ldots\ldots N_{+(\xi-1)}N_{+\xi}\ldots\ldots$ 3'

| -ξ | -(ξ-1) | | -3 | -2 | -1 | 0 | 0 | 0 | +1 | +2 | +3 | | +(ξ-1) | +ξ |
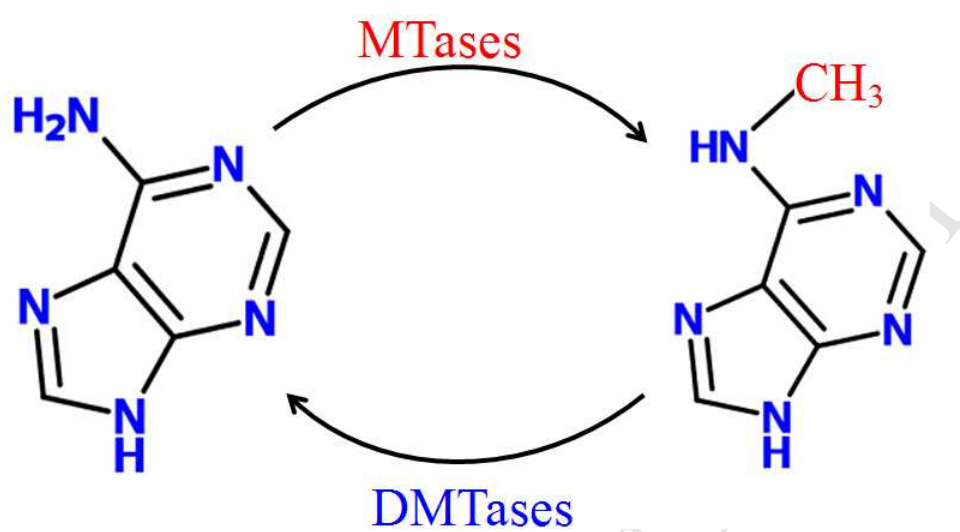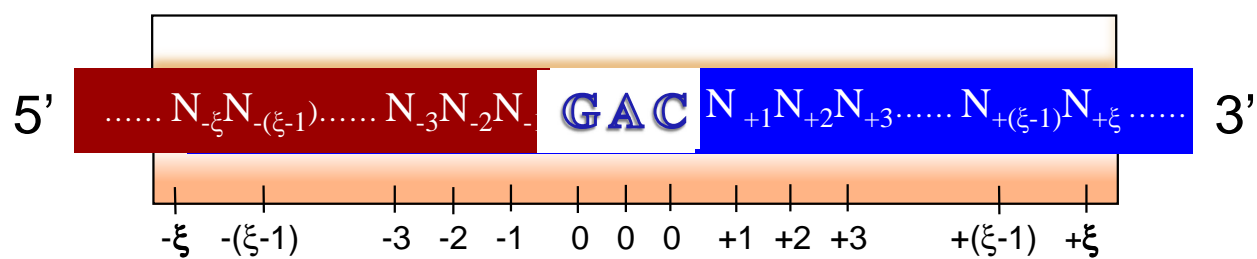
Figure 2

(a) Mirror image for 5' terminus

$$N_{-1}N_{-2} \cdots N_{-22}N_{-23} \Leftrightarrow N_{-23}N_{-22} \cdots N_{-2}N_{-1}$$

(b) Mirror image for 3' terminus

$$N_{L-23}N_{L-22} \cdots N_{L-1}N_{L} \Leftrightarrow N_{L}N_{L-1} \cdots N_{L-22}N_{L-23}$$

Figure 3
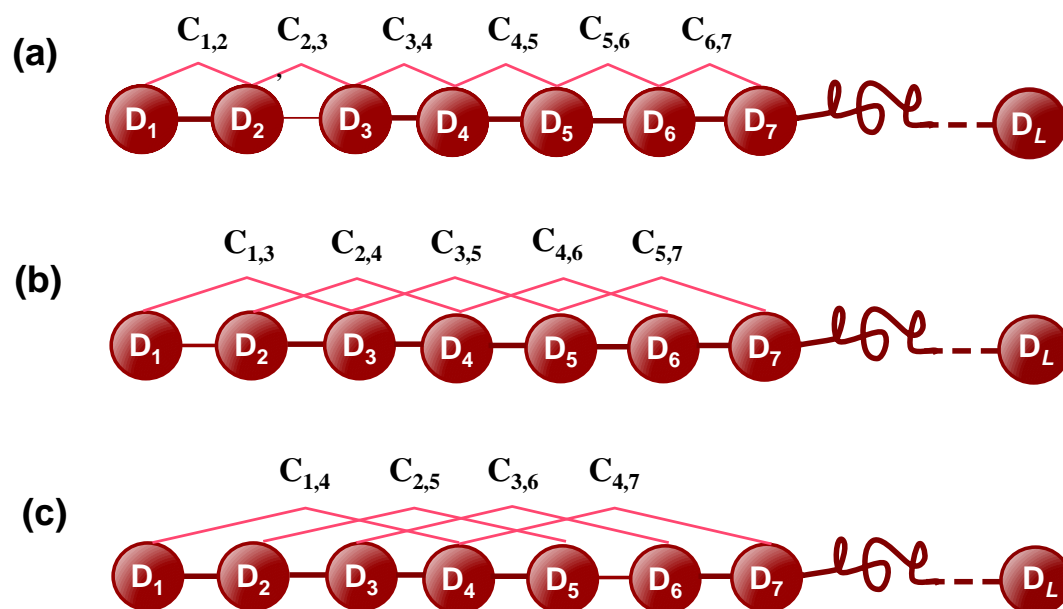
Figure 4
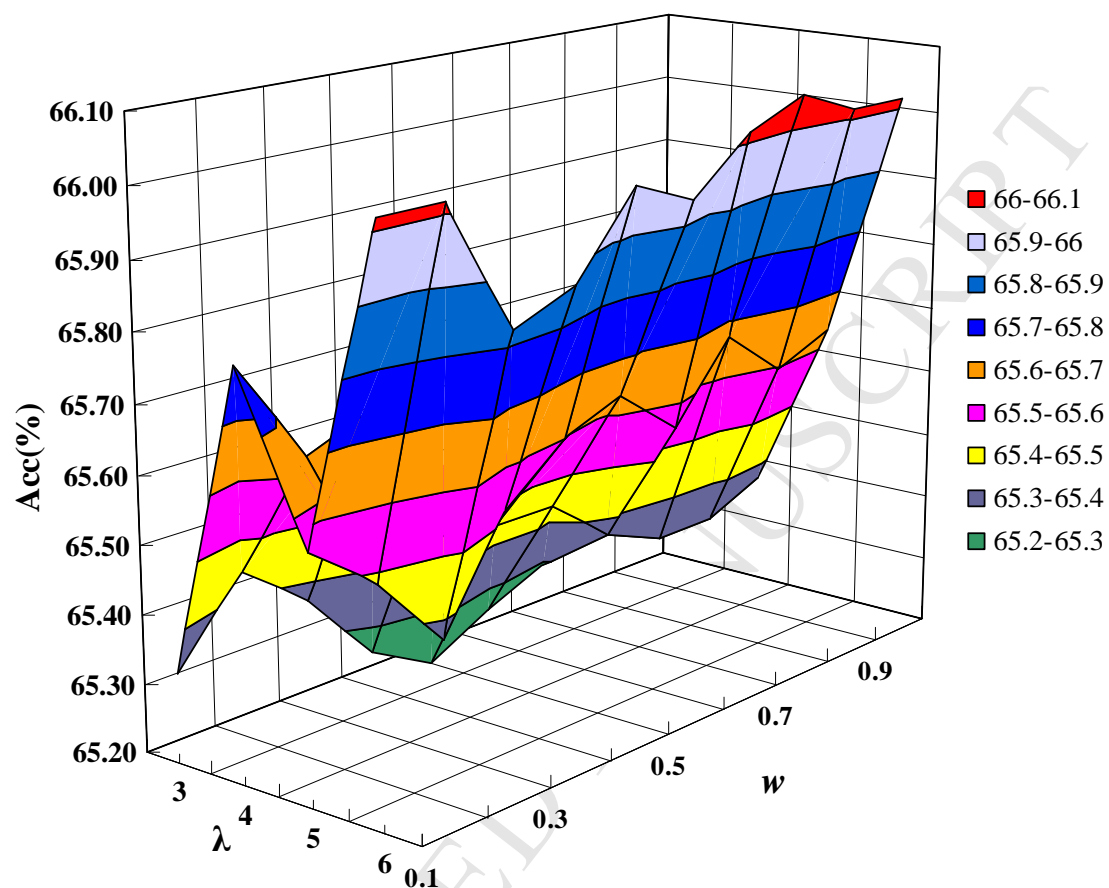
Figure 5

iRNA-Methyl: Identifying N^6-methyladenosine sites using pseudo nucleotide composition

| **Read Me** | **Data** | **Citation** |

Enter the query RNA sequences in FASTA format (**Example**):

Submit   Clear

Figure 6

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Supplementary Materials for

iRNA-Methyl: Identifying N6-methyladenosine sites using pseudo nucleotide composition

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Contents
Supporting Information S1 (pages 2-120)

Supporting Information S1. The benchmark dataset $\mathbb{S}$ contains 2,614 RNA samples (51-bp long) with a consensus motif GAC at the center. Of the 2,614 samples, 1,307 can be methylated as confirmed by experiments, while the other 1,307 cannot. The former form the positive subset, and the latter the negative subset. See the main text for further explanation.

I. List of 1,307 RNA samples in the positive subset $\mathbb{S}^+$

>P1
CAAAGGUGACCCACUUCGUUCAUGGACGUUCCCUGAAAUCAGGGACACUAU
>P2
GAUUGACAAUGACGAAGCAGAAGGGACUACAGAAUUAUUGCUGCUUGCCAU
>P3
AAUAGAGCUGACAACCAUUUCAAGGACACUUAUGGUUUCUCUAUUUUAGAC
>P4
UACCUUUGAACACAUUGCGCUAUGGACAAUUUUACAAUUGCUAGAAAGUCA
>P5
ACCGCGGCCACGCUAUUUAAAAGAGACAUUGUCACAAUGAACUUUAACAAU
>P6
AGGGUCAUUGUACCGCGAACUUUGGACCAUACAAGAAGAUCUGGAUCAUUU
>P7
ACAAUUUUAAGGGAAAUGCUAGAGGACAUUCAAUAGCUUCAUCAUUUGUUA
>P8
GCUUGCCGUAGCACAUGACAUACGGACUAUUGUGUGAGUGGUGAUGGGGUG
>P9
UUACUGGCUGACACUAGCUCUAUGGACCUCUCAGGCACGGGCGGCCAACAA
>P10
UCGCCCCAGACCCCAGCGUAUCUGGACUUUGAAGAACUUUGUAUCAAGGCA
>P11
ACGGUCCAUAGACGGAUCUAAUGGGACAUUUCAUGCUGCAGAGGAUAUUGC
>P12
AAGUAUGUGUUGAAGGACAUGAAGACAUUAGACAGGAUAGCUUGGUCAUG
>P13
GGCAAUUACAUAAAGCCCUCUCAGGACAACGUGGAUAGCAAGGACUAACCG
>P14
CCACAAGAGCUUCUGUUGAUAAUGGACUAUGUGAUAAUUCUCUACAAAUCG
>P15
AAAUUGACUUUACUGAUUAUUUAGGACCAUAACACCAUUACAAAGACAAAG
>P16
AAAAAACAUGAACGAUCUCCCUCAGACUUUAUUAUAGACUAUAGCGUGUAC
>P17
AUGUGGACAGCAUUUACACCAAUGGACAUUUUGGGAGGAUUCUGGUUAUAA
>P18
AAGGCUACUGCCAAGACAUUCACGGACAAUAAUAGGCAGAAUGUUGGCUUU
>P19

GUUUUCAUACUGGGGCCGCCGGAG**GAC**AAGAACAGUAAUAGUAACAUUAAC
>P20
GUGAAACAACUCGACGAUAUAACA**GAC**AGUAAUACAACAGAAAUUUUAACU
>P21
UUAGGAGAAAUGGCCAAAUGCCUA**GAC**AAUCCAGACCAGGGAAUAAGUGAU
>P22
ACUUUGGCGGAUCUUAUACCAGAG**GAC**AUUUGACUACCAUGAACACUUUGA
>P23
UGGUCUAGUAGCUAUUUGGAUUCG**GAC**AAUAAUCGGCGAAGGGUAUCUUCA
>P24
UUCAGCGAGGACAAUUUCAAUAAG**GAC**UAUCAGUAUAGCGAAACGAGAAAA
>P25
AACUUCAUUAAGACAAUAUUUAAG**GAC**UUUGUGUAAAGAUGCAGAGGUUUC
>P26
UGGUCAUACGACGGUAAAACAAUG**GAC**AAUUGUAUCGCUUUAAGGACUAUG
>P27
UACAAAUCGGACAGGAAAUUUAGG**GAC**AUUAUUUCCUACAACGAUAUCAUU
>P28
UGUCUACGAACACGAACACGAAAA**GAC**UUUCAUUUAAGCUCUCCAUAUCUA
>P29
AUCAAGAGCAUGGACAUGGACACG**GAC**AUUCCCAUGGCGGUAUCUUUGCCG
>P30
GGAAAAGGGGGAGUGAUAGAUUUG**GAC**AAUAGUGUUACCCAGGAAGUAUAA
>P31
UCUGCUGUUGAUAUAUUGCAAAUG**GAC**GAUAAUAAUAACAGUCUACCAACU
>P32
AAAAAUGAAAACACGGAUUUGAAA**GAC**AUUAUCCAAGGUAAUCCACUGAUG
>P33
CAAAGCUACAUUUCCAACAGAGAG**GAC**UUCAAUCAUGACAAUUUCAUUAAU
>P34
GUAUUGUAUACACUUUAACUAAUA**GAC**GAUAUGGUGAAAAAGUGGUUGCUU
>P35
GGACAAUUACCUGAGGAUGCUAAG**GAC**AUUAUUGCGAAAAGCGCCUCUAAU
>P36
UAUUACAGCAGCUGAAGGACAAUG**GAC**AUAGGGCACUUAUCUUCACACAAA
>P37
UCAAAUCAGGUUGAACAUGCAAAG**GAC**AAUGCAAAAGAUGUUUCUGUUUU
>P38
UCGGGCAAAGACUUCACGUACAUG**GAC**UAUUUAGAAAAGACACCCGAAUGG
>P39
AAGGAACUGCUUCUUGAAAUUGUG**GAC**AAUGAAAUGAGCAAAUUCGCAGAG
>P40
UUCAAUCCAAGCAGGUUCCCCAUG**GAC**GCUAUGUCGGCUGCCACAAACGAC
>P41

GUUCGUAGAGAGCGAAUAUGUUUG**GAC**ACUUAAGGAACAUACUAUGUUUAU
>P42
AGAUCACGAAAAGGACACUUAUCG**GAC**AUUAAUGGAGGAAAUUGAAUCACU
>P43
GCGAACAACGUUUUUGGCUCCAGG**GAC**UAAAUGGAUUCAAGACUGGAAAGA
>P44
UUAUUUUGUAUGGUACAUUAGCAA**GAC**AUUUACAGCAAAGUGAUGCAAGGA
>P45
ACUCUGCAGGAGGUUAAUAACGCG**GAC**GAUUAUUUUUCAUUGGGAGUGAAU
>P46
UGCUGGAACAGCAUAUACCUAAUA**GAC**UUUCGGCAGAGAGCAGACCAACUU
>P47
UGGAUUCACUUGCCAAUCAUUAAG**GAC**UUAAAGAAAGCCUGUUCUGAAGUU
>P48
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