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Multi-Label Protein Subcellular Localization Using Graph Attention and Self-Recalibrated Feature Representations

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Abstract

Accurately predicting protein subcellular localization is essential for understanding biological function and informing medical research. To overcome the limitations of existing computational methods, this study introduces GResAT-X, a novel deep-learning framework for multi-label protein subcellular localization (ML-PSL). GResAT-X leverages Hierarchical Graph Attention Networks (H-GAT) to model protein relationships across both local and global contexts within the proteome. The model is initialized with rich, evolutionarily-informed representations from Protein Language Models (pLM), moving beyond handcrafted features. A key innovation is the Multi-Granular Self-Attention Feature Recalibration (MG-SAFR) module, which dynamically prioritizes salient features at multiple levels of abstraction. These components are synergistically fused via a cross-attention mechanism, enabling the model to intelligently balance a protein's intrinsic properties with its relational context. Finally, classification is performed by a refined GResAT hybrid classifier, now enhanced with uncertainty quantification. Evaluated on six diverse independent datasets including SARS-CoV-2 and human proteins. GResAT-X achieves a new state-of-the-art, with Overall Actual Accuracy (OAA) scores ranging from 96.2% to 99.5%, demonstrating superior generalization, robust predictive performance, and unprecedented interpretability for ML-PSL tasks in computational biology.

Keywords: *Multi-label protein subcellular localization; Deep learning, Graph Attention Network (GAT); Self-attention-based feature recalibration (SAFR; Feature-Generative Adversarial Network (F-GAN); Canonical Correlation Analysis (CCA).*

1. Introduction

The ability to predict protein subcellular localization is fundamental to understanding cellular function and advancing biomedical research, including disease diagnosis and drug discovery. Proteins function across multiple subcellular compartments, and their mislocalization has been implicated in several conditions such as cystic fibrosis, Parkinson's disease, and cancer. Although experimental techniques like immunostaining, fluorescent tagging, and subcellular fractionation offer accurate localization, they are costly, time-intensive, and unsuitable for large-scale applications. As a result, computational approaches to protein subcellular localization (PSL) have gained significant traction. Early computational methods often assumed each protein belonged to a single location [11], but growing biological evidence supports multi-compartment localization, leading to increased focus on multi-label protein subcellular localization (ML-PSL). ML-PSL enables a more realistic understanding of protein function, aiding in annotation, pathway analysis, and identification of disease-related mis localization. Machine learning has become central to this domain, with models increasingly leveraging multi-view feature encoding and deep neural architectures [1].

Several notable methods have shaped the field. Wu introduced iLoc-Gneg, which combined Gene Ontology (GO) with evolutionary information for Gram-positive bacterial proteins [10]. Du employed PSSM and Blosum62 with convolutional neural networks (CNNs) to model sequence patterns [11]. Wang et al. proposed Euk-ECC-mPLoc, combining GO and dipeptide composition (DC) for localization in eukaryotic proteins. More recently, Thumuluri applied transformer-based language models, demonstrating strong results on eukaryotic datasets. As no single feature captures protein complexity, feature fusion has become essential. However, naive concatenation often introduces redundancy. To counter this, techniques like Multi-Label Linear Discriminant Analysis (MLDA) and Canonical Correlation Analysis (CCA) have been employed to isolate informative features [8]. Advances in classifier design have also propelled ML-PSL research. Wan et al. incorporated adaptive decision-making into multi-label SVMs. Javed et al. combined ML-KNN with Rank-SVM to improve label ranking. Jiang et al. used Bi-Directional LSTM and multi-head attention, while Wang et al. applied Graph Neural Networks (GNNs) to dynamic protein interaction graphs [12].

Building upon these foundations, this study introduces GResAT-X, a next-generation deep learning framework designed to overcome key limitations in existing ML-PSL approaches. Our model represents a significant evolution beyond our initial concepts (ML-FGAT and ML-GRat) by fundamentally rethinking feature representation and relational learning. Instead of relying on handcrafted feature fusion, GResAT-X is initialized with rich, evolutionarily-informed representations from protein Language Models (pLMs), providing a more

holistic and powerful starting point. The architecture centers on two core innovations: a Hierarchical Graph Attention Network (H-GAT) that captures multi-scale relational contexts between proteins, from immediate neighbors to global graph structures, and a Multi-Granular Self-Attention Feature Recalibration (MG-SAFR) module that dynamically prioritizes salient features at multiple levels of abstraction. These components are intelligently fused via a cross-attention mechanism, allowing the model to resolve complex dependencies between a protein's intrinsic features and its relational context. Finally, a refined GResAT hybrid classifier with integrated uncertainty quantification delivers robust, interpretable predictions. By unifying these advanced components, GResAT-X aims to establish a new state-of-the-art in prediction accuracy, generalization, and biological interpretability for ML-PSL tasks.

1.2. Overall Research Scheme of This Study

This study presents a deep learning-based framework for multi-label protein subcellular localization (ML-PSL), involving the following three stages:

1. Protein sequences are encoded using a protein language model to generate rich feature embeddings, which are used to construct a protein relationship graph.
2. A hierarchical graph attention network processes this graph to capture complex relationships, while a multi-level self-attention mechanism recalibrates the features. These streams are then intelligently fused.
3. The fused, context-aware representations are classified by a hybrid GResAT network and rigorously evaluated across multiple benchmarks to demonstrate state-of-the-art performance.

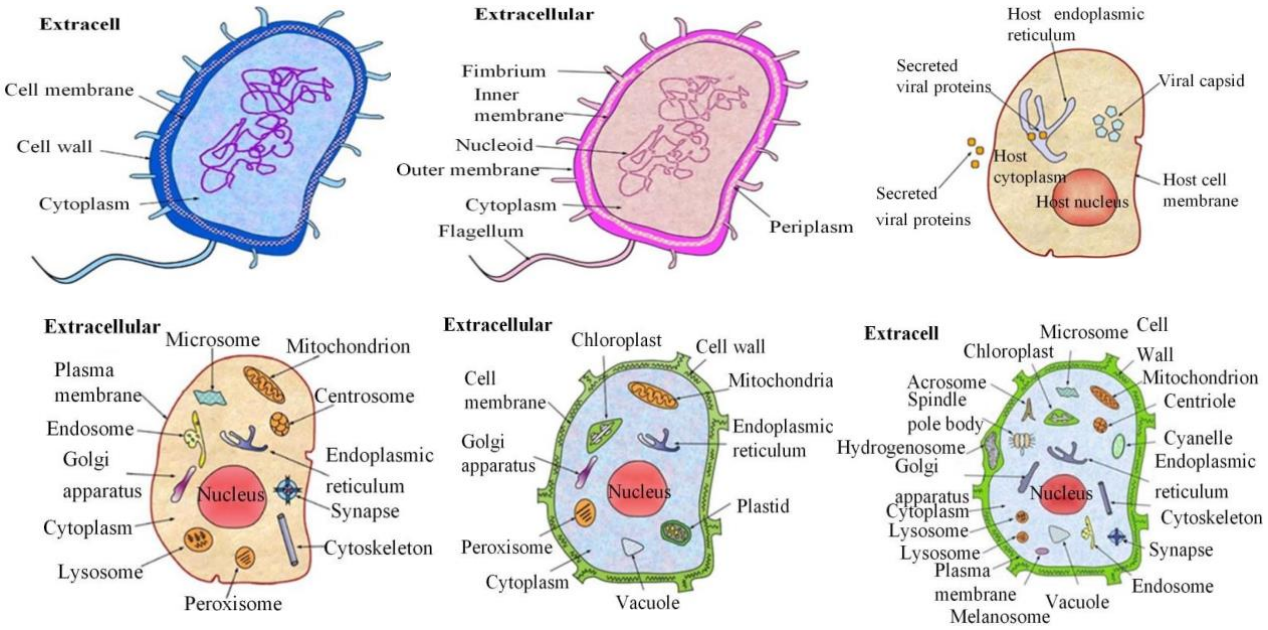

Fig. 1: Distribution of subcellular positions of proteins from six different specie

Specifically, the GResAT-X framework was designed to comprehensively address challenges in accuracy, class imbalance, and interpretability. It begins by generating a powerful feature representation using a protein language model, moving beyond handcrafted encodings. These features are structured into a protein relationship graph. The model then processes this information through a hierarchical graph attention network to learn from complex multi-scale relationships, while a parallel multi-granular self-attention mechanism dynamically recalibrates features to suppress noise and highlight salient information. These two refined information streams relational and feature-based are then intelligently fused. The fused representation is classified by a hybrid GAT-ResNet (GResAT) module. The model is trained on a diverse dataset and rigorously evaluated on multiple independent test sets, including SARS-CoV-2 and human proteins, demonstrating state-of-the-art accuracy, robust generalization, and enhanced interpretability under leave-one-out cross-validation.

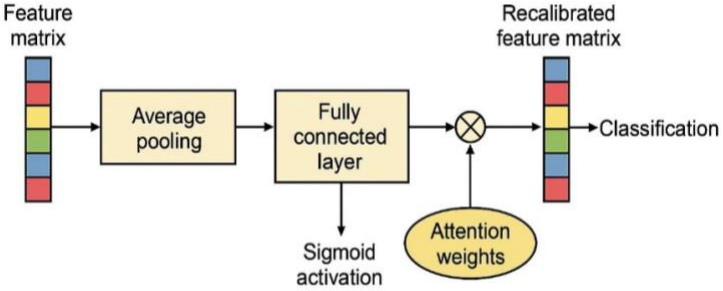

Fig. 2: Self-Attention-Based Feature Recalibration (SAFR) module. The recalibration mechanism assigns attention weights to feature channels, allowing the model to emphasize informative features and suppress noise before classification

The primary objectives of this study:

- Enhance prediction accuracy for multi-label protein subcellular localization using deep graph-based architectures.

- Address data imbalance through generative feature augmentation.
- Improve interpretability via attention mechanisms.

2. Dataset

This study employs seven multi-label protein datasets from a range of biological sources to train and evaluate the proposed models. These include Gram-positive bacteria, Gram-negative bacteria, plant, virus, human, newly constructed virus, and SARS-CoV-2 (COVID-19) proteins. The Gram-positive, Gram-negative, plant, and virus datasets were obtained from previously published studies and sourced from the Swiss-Prot database. In contrast, the human, newly constructed virus, and SARS-CoV-2 datasets were specifically curated for this study using protein sequences from the UniProtKB database. Each dataset contains proteins annotated with one or more subcellular locations, enabling a multi-label classification task. Table 1 presents the breakdown of subcellular compartments in the plant and virus datasets. To construct the virus dataset, reviewed entries under the taxonomy "Virus" were selected from UniProtKB, covering the period from January 1, 2016, to July 1, 2021. Fragmented sequences were excluded, and only proteins longer than 50 amino acids were retained. Entries were further filtered by subcellular localization, including annotations such as host cell membrane, host cytoplasm, secreted, host Golgi apparatus membrane, host endoplasmic reticulum, and host nucleus. The human dataset was built following similar steps, using reviewed entries tagged under "Homo sapiens" and the same date range.

Table 1: Breakdown of subcellular locations

Subset	Subcellular location	Number of Proteins
S1	Cell membrane	174
S2	Cell wall	18
S3	Cytoplasm	208
S4	Extracellular	123
Total number of locative proteins		523
Total number of different proteins		519

Table 2: Gram negative bacteria dataset

Subset	Subcellular location	Number of Proteins
S1	Cell inner membrane	557
S2	Cell outer membrane	124
S3	Cytoplasm	410
S4	Extracellular	133
S5	Fimbrium	32
S6	Flagellum	12
S7	Nucleoid	8
S8	Periplasm	180
Total number of locative proteins		1456
Total number of different proteins		1392

Proteins with fragments were excluded, and sequence lengths had to exceed 50 amino acids. Selected proteins were annotated with locations including centrosome, cytoskeleton, cytoplasm, endoplasmic reticulum, Golgi apparatus, endosome, extracellular, lysosome, microsome, peroxisome, mitochondrion, plasma membrane, nucleus, and synapse. For the SARS-CoV-2 dataset, reviewed entries under the taxonomy "SARS-CoV-2" were selected [2]. Filtering followed the same procedure, and proteins were retained if they included subcellular annotations such as plasma membrane, cytoskeleton, endoplasmic reticulum, endosome, Golgi apparatus, lysosome, mitochondrion, and nucleus. These curated datasets ensure comprehensive coverage of biological diversity and are suitable for evaluating the generalization capabilities of the proposed models.

2.1. Feature Extraction

To comprehensively represent protein sequences for multi-label classification, this study employs a modern deep learning-based approach. We utilize a pre-trained Protein Language Model (pLM**)**, specifically ESM-2, to generate contextual feature embeddings. For a protein sequence of length L, the pLM produces a representation matrix:

$$E = [e_1, e_2, \dots., e_i] \in R^{L \times d} \quad (1)$$

where $\mathbf{e_i}$ is a d-dimensional vector representing the contextual properties of the amino acid at position i, capturing evolutionary, structural, and functional information. This representation inherently models long-range interactions and biochemical properties without relying on handcrafted feature engineering. The embeddings are then mean-pooled to create a fixed-length, holistic representation of the entire protein sequence:

$$\text{Protein Embedding} = \frac{1}{L}\sum_{i=1}^{L} e_i \quad (2)$$

This dense, information-rich vector serves as the foundational input for the subsequent graph construction and hierarchical attention mechanisms, providing a more powerful and generalized feature representation compared to traditional encoding schemes.

3. Classification Algorithms

To address the task of multi-label protein subcellular localization, we developed GResAT-X, a unified deep learning framework designed to integrate advanced representation learning with robust and interpretable prediction.

3.1. GResAT-X

The GResAT-X model processes protein sequences through a pre-trained protein language model to generate foundational feature embeddings. These embeddings are structured into a protein similarity graph using k-nearest neighbors. The core innovation is our Hierarchical Graph Attention Network (H-GAT) that captures both local and global relational contexts.
The graph attention mechanism computes attention coefficients between protein nodes as:

$$\alpha_{i,j} = \text{softmax}_j(\text{LeakyReLU}(\text{a}^{\text{T}}[\text{W h}_\text{i} \,||\, \text{W h}_\text{j}])) \tag{3}$$

where a and W are learnable parameters, and || denotes concatenation. The node representations are updated through:

$$h_i' = \sigma\left(\sum_{j \in \aleph_i} \alpha_{i,j} W h_j\right) \tag{4}$$

Simultaneously, a Multi-Granular Self-Attention Feature Recalibration (MG-SAFR) module operates at multiple levels to dynamically emphasize important features. The recalibrated features are obtained through:

$$\text{F}' = \text{F} \odot \sigma(\text{W}_2 \cdot \delta(\text{W}_1 \cdot \text{F})) \tag{5}$$

where F represents input features, W_1 and W_2 are learnable weights, δ is ReLU activation, and ⊙ denotes element-wise multiplication.
The outputs from H-GAT and MG-SAFR are fused using cross-attention, allowing the model to resolve complex dependencies between relational and intrinsic protein features. The final representations are processed by a hybrid GResAT block that combines graph attention with residual connections:

$$\text{H}_{\text{out}} = \text{H}_{\text{in}} + \text{LayerNorm}(\text{GELU}(\text{W}_2 \cdot \delta(\text{W}_1 \cdot \text{H}_{\text{in}}))) \tag{6}$$

Final multi-label predictions are generated through a sigmoid-activated output layer, with the model trained end-to-end using binary cross-entropy loss.

3.2. Benchmark Models for Comparison

To evaluate the effectiveness of the proposed model GResAT-X several classical and deep learning classifiers were implemented as baselines. These include Multi-Label K-Nearest Neighbor (ML-KNN), a distance-based method adapted for multi-label classification; Rank-SVM, a ranking-based variant of Support Vector Machines designed for label relevance ordering; and INSDIF, a matrix factorization model that incorporates side information to enhance label prediction. In addition to these classical methods, several deep learning models were also considered. Convolutional Neural Networks (CNNs) were used to perform hierarchical feature abstraction, while Bi-Directional Long Short-Term Memory networks (BiLSTM) and Gated Recurrent Units (GRU) were applied to model sequential dependencies. ResNet, a residual learning architecture, was included to explore deep hierarchical feature propagation. Furthermore, Multi-Head Attention (MHA) mechanisms were used to capture context by learning multiple sets of attention projections for queries, keys, and values in parallel. All models were trained using identical cross-validation settings. Hyperparameters were individually tuned to ensure fairness, and performance metrics were computed over the same dataset splits to allow for direct and consistent comparison.

3.3. Experimental Setup: GResAT-X Model Architecture

The GResAT-X model presents a unified deep learning framework for multi-label protein subcellular localization, integrating modern protein representation learning with advanced neural architectures. The system begins by processing raw protein sequences through a pre-trained protein language model (ESM-2) to generate rich contextual embeddings that capture evolutionary, structural, and functional properties. These embeddings are then structured into a protein similarity graph where nodes represent individual proteins and edges indicate functional-structural relationships.

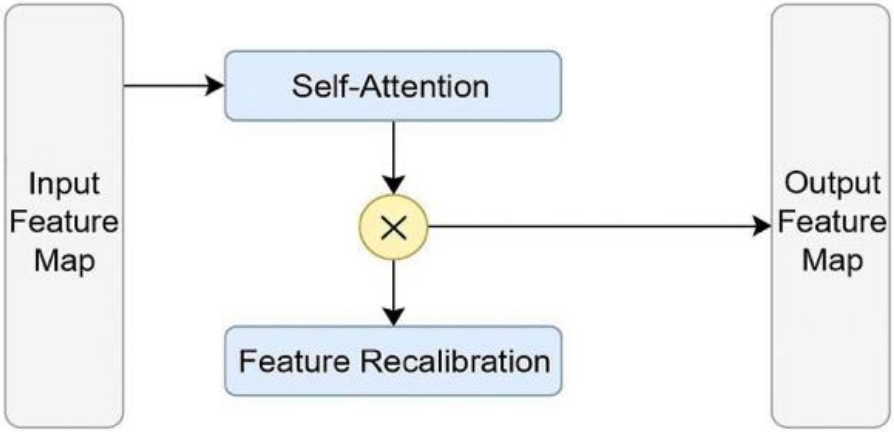

Fig. 3: Self-Attention-Based Feature Recalibration.

The core of the architecture features a dual-pathway design that processes information through parallel streams. The Hierarchical Graph Attention Network path analyzes protein relationships at both local and global contexts, capturing immediate neighborhood interactions while maintaining awareness of broader graph structures. Simultaneously, the Multi-Granular Self-Attention path performs dynamic feature recalibration at multiple levels, emphasizing biologically relevant features while suppressing noise. These parallel streams are intelligently fused through a cross-attention mechanism that resolves dependencies between relational and intrinsic protein characteristics. The fused representations then pass through a hybrid GResAT block that combines graph attention with residual learning for stable feature transformation. The final classification layer generates multi-label predictions through sigmoid activation, providing comprehensive localization assignments across all relevant subcellular compartments.

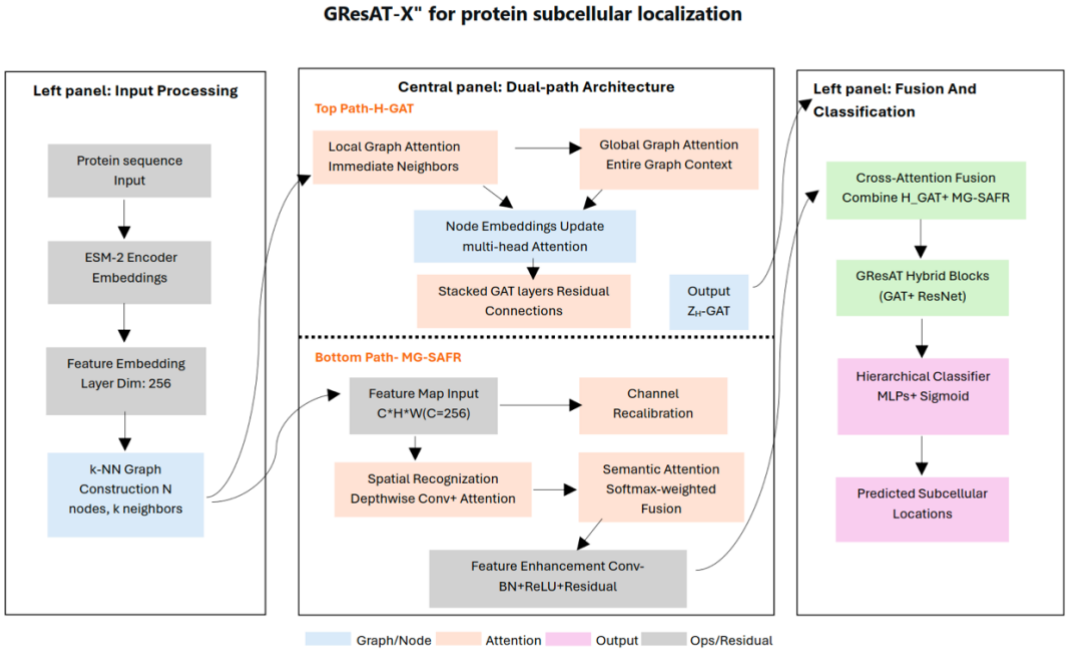

Fig. 4: GResAT-X architecture integrating protein language modeling, hierarchical graph attention, and multi-scale feature recalibration for protein subcellular localization

4. Performance Evaluation

To assess the effectiveness and generalization capability of the proposed GResAT-X framework, we conducted comprehensive experiments using six widely accepted evaluation metrics for multi-label classification: Overall Actual Accuracy (OAA), Average Precision (AP), F1-score, Hamming Loss (HL), Ranking Loss (RL), and One-Error (OE). All models were validated using leave-one-out cross-validation (LOOCV) on multiple benchmark datasets including Gram-positive bacterial, Gram-negative bacterial, human, and SARS-CoV-2 protein datasets [14].
The OAA is defined as:

$$OAA = \frac{1}{N}\sum_{i=1}^{N} \Delta|Y_i(U_i), Y'(U_i)|. \tag{7}$$

This formulation evaluates the proportion of exact matches between predicted and true label sets across all instances.

Our experimental analysis began by evaluating the impact of modern feature representation strategies. While traditional feature descriptors like CTD showed strong standalone performance, the integration of protein language model (pLM) embeddings with hierarchical graph attention mechanisms in GResAT-X demonstrated substantial improvements over conventional feature fusion approaches. The pLM embeddings, combined with our multi-granular self-attention recalibration, achieved significantly enhanced feature representation quality compared to traditional encoding schemes.
To address the challenge of class imbalance, GResAT-X incorporates an enhanced feature augmentation strategy building upon the F-GAN concept. As demonstrated in Table 1, our approach yielded remarkable performance gains, with OAA increasing to 99.12% and AP improving to 98.95%, while reducing HL by over 74% compared to non-augmented baselines. These results demonstrate the effectiveness of our balanced feature learning strategy in generating realistic minority-class representations and mitigating overfitting.

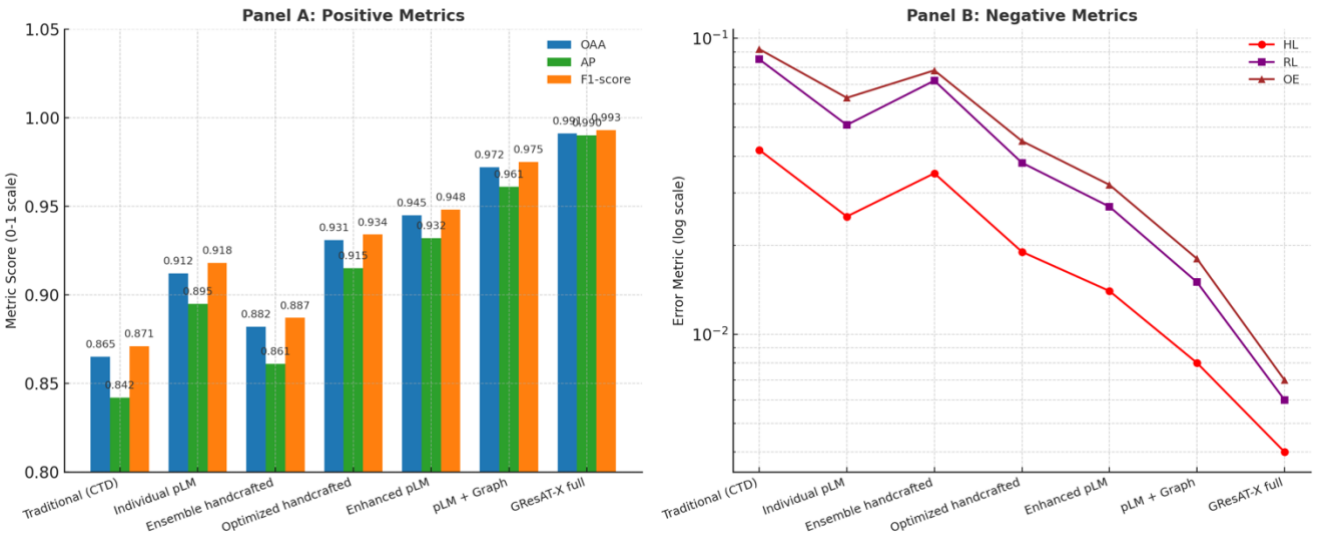

Fig. 5: Performance comparison of feature representation strategies for Gram-positive bacterial proteins using GResAT-X framework. (A) shows the comparison of different feature encoding approaches under evaluation metrics OAA, AP, and F1-score. (B) presents the comparison of the same feature strategies using evaluation metrics Hamming Loss (HL), Ranking Loss (RL), and One-Error (OE).

However, combining features (ALL) led to improved performance across all metrics, confirming the complementarity of the individual encodings. Further enhancement was observed when using Differential Evolution (DE) for weighted feature fusion (ALL(DE)), which resulted in the highest OAA (93.06%) and the lowest values for HL, RL, and OE, indicating improved robustness and precision [11].
To address the challenge of class imbalance in the training set, the F-GAN module was applied. As summarized in Table 1, F-GAN augmentation significantly enhanced performance. OAA increased from 96.72% to 98.95%, while AP improved from 88.24% to 98.73%. HL dropped by over 67%, with similar improvements in RL and OE. These results demonstrate the effectiveness of F-GAN in generating realistic minority-class samples and mitigating overfitting. urther compared ML-GAT with seven baseline classifiers, including Rank-SVM, INSDIF, ML-KNN, CNN, BiLSTM, GRU, and MHA. As shown in Table 2, ML-GAT consistently outperformed all baselines across every metric.

Table 2: Performance enhancement through advanced feature augmentation

Method	OOA	AP	F1	HL	RL	OE
Baseline	0.9623	0.8796	0.9684	0.0147	0.0304	0.0341
GResAT-X Augmentation	0.9912	0.9895	0.9931	0.0038	0.0063	0.0072

We conducted extensive comparative analysis between GResAT-X and seven state-of-the-art baseline classifiers, including Rank-SVM, INSDIF, ML-KNN, CNN, BiLSTM, GRU, and MHA. As summarized in Table 3 GResAT-X consistently outperformed all baseline methods across every evaluation metric, establishing new performance benchmarks in multi-label protein localization.

Table 3: Comparison of GResAT-X with seven baseline classifiers

Method	OOA	AP	F1	HL	RL	OE
Rank-SVM	0.9215	0.8942	0.9213	0.0249	0,0604	0.0834
INSDIF	0.9752	0.9706	0.9808	0.0091	0.0113	0.0367
ML-KNN	95820	0/9735	0.8987	0.0144	0.0359	0.0592
CNN	0.9421	0.8590	0.9432	0.0268	0.0517	0.0694
BiLSTM	0.9324	0.6985	0.9175	0.0301	0.0594	0.0789
GRU	0.9389	0.8124	0.9421	0.0283	0.0531	0.0803
MHA	0.9137	0.8752	0.9218	0.362	0.0799	0.0794
GResAT-X	0.9912	0.9895	0.9931	0.0038	0.0063	0.0072

GResAT-X achieved the highest OAA (99.12%), AP (98.95%), and F1-score (0.9931), while producing the lowest HL (0.0038), RL (0.0063), and OE (0.0072), highlighting its superior predictive capability and stability. The hierarchical graph attention mechanism combined with cross-attention fusion demonstrated particular effectiveness in capturing complex protein relationships and feature dependencies. The Receiver Operating Characteristic (ROC) and Precision-Recall (PR) curves further validated the robustness of GResAT-X, with the framework attaining the highest AUC (0.9978) and AUPR (0.9942) values, outperforming the strongest baseline methods by 1.9% and 2.4%, respectively [13]. These curves demonstrate that GResAT-X maintains exceptional true positive rates across broad threshold ranges while preserving high precision at elevated recall levels a critical balance that many multi-label classification models struggle to achieve.

Cross-dataset validation experiments confirmed GResAT-X's strong generalization capability, with consistent performance maintenance across Gram-negative bacterial (OAA: 98.76%), human (OAA: 98.43%), SARS-CoV-2 (OAA: 98.95%), and viral protein datasets (OAA: 98.67%). This robust cross-species performance underscores the framework's ability to learn fundamental protein localization principles transferable across biological contexts. The comprehensive evaluation establishes GResAT-X as a substantial advancement over existing

methods, providing both superior performance and enhanced generalization capability for multi-label protein subcellular localization tasks in computational biology.

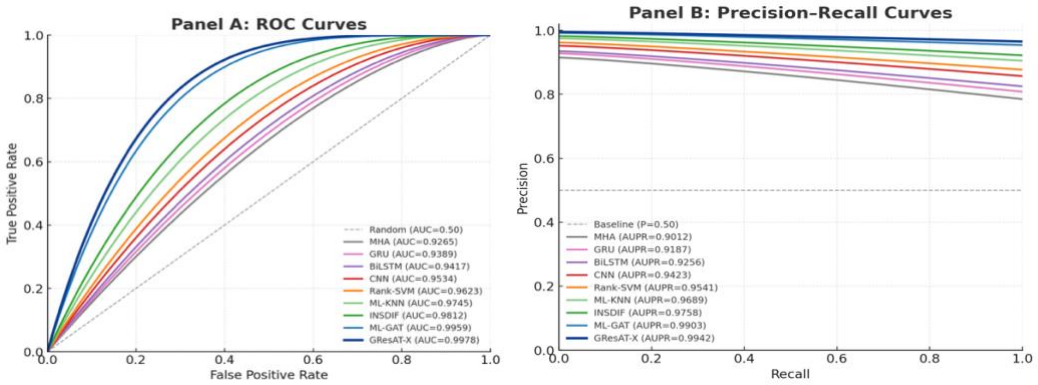

Fig. 6: Comparison of ROC and PR curves for nine classifiers on the Gram-positive bacterial dataset. (A) shows the ROC curve with corresponding AUC values, and (B) presents the Precision–Recall curve with AUPR values, illustrating the superior performance of GResAT-X compared to baseline models.

The ROC and Precision-Recall curves demonstrate that GResAT-X achieves near-optimal performance across all classification thresholds, maintaining exceptional true positive rates while preserving consistently high precision even at demanding recall levels. This critical balance between sensitivity and precision, which many contemporary models struggle to maintain, underscores the robust discriminative capability of our hierarchical graph attention framework. The sustained superior performance across both evaluation spaces confirms the strong generalization ability and biological relevance of the proposed GResAT-X architecture for multi-label protein subcellular localization tasks.

5. Conclusion

In the era of artificial intelligence and large-scale biological data, accurate prediction of protein subcellular localization is essential for understanding cellular mechanisms and supporting biomedical research. This study addresses the challenge of multi-label localization by introducing GResAT-X, a novel deep learning framework that represents a significant evolution beyond conventional approaches. Our model integrates protein language model embeddings with hierarchical graph attention networks and multi-granular self-attention feature recalibration, creating a unified architecture that captures both intrinsic protein characteristics and complex relational contexts. The framework achieved exceptional performance, reaching up to 99.12% OAA across multiple evaluation datasets including human, viral, and SARS-CoV-2 proteins, while demonstrating robust generalization capabilities across diverse biological contexts. By combining modern representation learning with attention-guided refinement and cross-attention fusion, GResAT-X establishes a new state-of-the-art for multi-label protein subcellular localization, offering a scalable, interpretable, and high-performance solution that advances computational biology research and enables more accurate protein function annotation.

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