Literature Review: Citation Landscape

Mariia Zhokhova

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1 Literature Review

To contextualize the field, Table 1 summarizes the key articles collected in our bibliography, their approximate citation counts (as of September 2025), and notes on their importance.
Some entries in the bibliography have ambiguous titles (e.g., "M et al.," "Zhao et al.," "DeepFGRN," "Hegde et al.") and could not be matched to precise counts without full citation details. These should be clarified in the final bibliography.

2 Before the review - main articles

Core Surveys & Overviews

Wu et al. 2021 - A Comprehensive Survey on Graph Neural Networks, the most cited GNN survey (>13k citations), cornerstone for theory.

Zhang et al. 2021 — GNNs in Bioinformatics → key survey focused on biomedicine (your thesis domain).

Ata et al. 2021 — Network-based methods for disease gene prediction → survey bridging GRNs and disease applications.

Classical GRN Foundation Karlebach Shamir 2008 — Modelling and Analysis of Gene Regulatory Networks → foundational review, highly cited.

Chan et al. 2017 — PIDC (GRN inference from single-cell data) → one of the first widely used single-cell GRN methods.

Liu et al. 2016 — Bayesian GRN inference → probabilistic baseline.

Core GNN Architectures

Kipf Welling 2017 — Graph Convolutional Networks (GCN) → GNN model, cited a lot. Hamilton et al. 2017 — GraphSAGE → inductive learning on graphs.

Veličković et al. 2018 — Graph Attention Networks (GAT) → attention applied to graphs.

Key Biomedical GNN Applications

Singh Lio 2019 — Probabilistic generative GNNs for disease–gene prediction → early application of GNNs in your exact domain.

Chatzianastasis et al. 2023 — Explainable Multilayer GNN (EMGNN) → explainable approach.

Mastropietro et al. 2023 — XGDAG → explainability + positive–unlabeled learning.

Gu et al. 2022 — REDDA: drug–disease prediction with heterogeneous GNNs → highly relevant for translational applications.

Article	Citations	Notes / Importance
MuSe-GNN: Learning Unified Gene Representation From Multimodal Biological Graph Data (2023)	∼31	Multimodal integration; relevant for unified representations.
Modelling and Analysis of Gene Regulatory Networks (Karlebach & Shamir, 2008)	∼1650	Highly influential review; foundation for GRN modeling.
Detection of Gene Communities in Multi-Networks Reveals Cancer Drivers (Cantini et al., 2015)	∼138	Multi-network approach; links to cancer driver discovery.
Constrained Community-Based GRN Inference (Fioretto et al., 2015)	∼6	Niche method; constrained optimization in GRN inference.
Inference of GRN via Local Bayesian Networks (Liu et al., 2016)	∼176	Strong probabilistic baseline for GRN inference.
PIDC: GRN Inference from Single-Cell Data (Chan et al., 2017)	∼615	Widely used single-cell GRN method.
Towards Probabilistic Generative Models Harnessing GNNs for Disease–Gene Prediction (Singh & Lio', 2019)	∼20	Early work combining GNNs with generative models.
Recent Advances in Network-Based Methods for Disease Gene Prediction (Ata et al., 2021)	∼91	Survey of network-based methods; useful context.
Weighted Patient Networks for Chronic Disease Prediction (Lu & Uddin, 2021)	∼101	Applies GNNs to patient networks; good for clinical angle.
Disease Prediction via GNNs (Sun et al., 2021)	∼77	GNNs applied to medical concept + EMR graphs.
ComHub: Community Predictions of Hub Genes (Åkesson et al., 2021)	∼15	Benchmarking hub predictions across GRN methods.
A Comprehensive Survey on GNNs (Wu et al., 2021)	>13,000	The most cited GNN survey; essential for theoretical grounding.
Graph Neural Networks and Their Current Applications in Bioinformatics (Zhang et al., 2021)	∼481	Bioinformatics-specific survey; high relevance to thesis.
Computing Graph Neural Networks: Algorithms to Accelerators (Abadal et al., 2021)	∼345	Systems/computing view; good for scalability discussion.
REDDA: Relations-Enhanced Drug–Disease Association Prediction (Gu et al., 2022)	∼58	Heterogeneous GNN with attention; drug repurposing focus.
HGNNLDA: Heterogeneous GNN for lncRNA–Disease Prediction (Shi et al., 2022)	∼19	Type-aware GNN for non-coding RNA.
GCNAT for Metabolite–Disease Associations (Sun et al., 2022)	∼234	Strong results with attention; metabolite-focused.
PDMDA: Predicting Deep-Level miRNA–Disease Associations (Yan et al., 2022)	∼31	Extends GNNs to miRNA–disease links.
Explainable Multilayer GNN for Cancer Gene Prediction (EMGNN, Chatzianastasis et al., 2023)	∼27	Explainability + multilayer networks; very relevant.
Identifying Candidate Disease–Gene Associations via GNNs (Cinaglia & Cannataro, 2023)	(counts vary)	Applied GNNs on BioSNAP/DisGeNET datasets.
XGDAG: Explainable Disease–Gene Associations (Mastropietro et al., 2023)	∼13	Explainable PU-learning framework; important direction.

Table 1: Approximate citation counts for key articles (Google Scholar/Semantic Scholar, Sept 2025).

Sun et al. 2022 — GCNAT for metabolite–disease → one of the more cited association models beyond genes.

Top 10

Wu 2021 (GNN survey)
Zhang 2021 (Bioinformatics GNN survey)
Karlebach Shamir 2008 (GRN foundation)
Chan 2017 (PIDC, scRNA-seq GRN inference)
Kipf Welling 2017 (GCN)
Hamilton 2017 (GraphSAGE)
Veličković 2018 (GAT)
Singh Lio 2019 (first GNN for disease–gene prediction)
Chatzianastasis 2023 (EMGNN, explainable cancer gene prediction)
Gu 2022 (REDDA, drug–disease associations)

3 Introduction

The identification of disease–gene associations, the repurposing of existing drugs, and the integration of large-scale omics data represent some of the most pressing challenges in contemporary biomedical research. Understanding how genetic and molecular factors contribute to disease not only advances basic biological knowledge but also enables the discovery of new therapeutic strategies. However, the rapidly growing volume and complexity of biomedical data, ranging from high-throughput sequencing to electronic medical records, makes manual curation and traditional analysis approaches insufficient.

Over the past two decades, computational methods have played an increasingly central role in addressing these challenges. Early approaches relied heavily on classical statistical models and feature engineering techniques, which were often limited by their dependence on handcrafted features and their inability to capture nonlinear dependencies in high-dimensional data. With the advent of machine learning, particularly ensemble methods such as random forests, more powerful predictive models emerged that were able to exploit large-scale molecular and clinical datasets.

The subsequent rise of deep learning further transformed the field, offering end-to-end learning pipelines capable of automatically extracting hierarchical representations from raw biological data. Yet, despite their success, conventional deep learning models typically operate on grid-like data structures (e.g., sequences or images) and fail to fully capture the relational nature of biological systems, where entities such as genes, proteins, metabolites, and diseases are interconnected in complex networks.

Graph neural networks (GNNs) have recently emerged as a powerful paradigm to bridge this gap. By extending deep learning to graph-structured data, GNNs provide a natural framework for modeling the heterogeneous and relational structure of biological networks. This has led to rapid growth in their application to tasks such as disease–gene prioritization, biomarker discovery, drug repurposing, and patient-level disease prediction. Comprehensive surveys illustrate both the theoretical foundations and practical applications of GNNs: Wu et al. [18], with over 13,000 citations, presents one of the most influential reviews of GNN models across domains, while Zhang et al. [20] provides a bioinformatics-specific survey that highlights their applications to disease prediction, drug discovery, and biomedical imaging. Together, these works underscore the increasing relevance of GNN-based methods in computational biology and set the stage for the

studies reviewed in this chapter.

4 Background on Gene Regulatory Networks

A central concept in systems biology is the *gene regulatory network* (GRN), which captures the complex regulatory relationships between transcription factors, genes, and other molecular components. GRNs provide a natural abstraction for understanding how cellular processes are controlled, how perturbations propagate through molecular systems, and how genetic variation contributes to disease. The importance of GRNs lies in their ability to connect genotype to phenotype, offering a framework to explain how molecular-level interactions influence higher-level biological outcomes.

One of the most influential early reviews of GRN modeling is provided by Karlebach and Shamir [8], which comprehensively surveyed mathematical and computational approaches for representing and analyzing regulatory networks. With over 1,600 citations, their work remains a cornerstone reference that highlights the diversity of available methodologies, ranging from Boolean and Bayesian models to systems of differential equations. This review set the stage for more specialized methods aimed at improving inference accuracy and scalability in the face of increasingly complex data.

As high-throughput technologies matured, single-cell RNA sequencing (scRNA-seq) created new opportunities and challenges for GRN inference. Chan, Stumpf, and Babtie [3] addressed this with the PIDC framework, which applied information-theoretic measures to infer regulatory relationships from scRNA-seq data. With more than 600 citations, PIDC remains a widely adopted baseline for single-cell network reconstruction, illustrating both the potential and the limitations of information-based methods in handling the sparsity and noise inherent in single-cell measurements.

Subsequent research expanded GRN inference with probabilistic and constraint-based approaches. Liu et al. [9] proposed a local Bayesian network method, emphasizing modular inference to improve scalability while retaining interpretability. This Bayesian perspective provided a principled framework for handling uncertainty in network structure, earning considerable attention in the literature. In parallel, Fioretto, Dovier, and Pontelli [6] introduced a constrained optimization formulation for GRN inference, exploring the integration of prior biological knowledge into the learning process. While less widely cited, this line of work illustrates how domain-specific constraints can guide more biologically plausible network reconstructions.

Recent surveys have synthesized these diverse approaches and assessed their performance in modern omics contexts. Ata et al. [2] reviewed network-based methods for disease gene prediction, providing a bridge between GRN inference and translational applications. Similarly, Nguyen et al. [12, 13] offered comprehensive surveys of GRN inference from scRNA-seq data, systematically comparing methodological classes and benchmarking their relative strengths and weaknesses. These surveys emphasize the need for robust, interpretable, and scalable approaches as GRN inference continues to evolve in the era of single-cell and multi-omics data.

5 Graph Neural Networks in Bioinformatics

While classical approaches to network inference and disease–gene prediction have achieved important advances, they often struggle with scalability, noise, and the integration of het-

erogeneous biological data. Traditional statistical and machine learning models typically rely on handcrafted features or assume simplified network structures, limiting their ability to capture the full complexity of molecular interactions. Deep learning methods improved upon these approaches by learning data-driven representations, yet conventional architectures such as convolutional or recurrent neural networks are not inherently designed to handle graph-structured data, where entities and their relationships form irregular, non-Euclidean topologies.

Graph neural networks (GNNs) extend deep learning to graph-structured domains by incorporating neighborhood information into node and edge embeddings through iterative message passing. This makes them particularly well suited for biological problems, where genes, proteins, RNAs, metabolites, drugs, and diseases are naturally represented as interconnected networks. Through architectures such as graph convolutional networks (GCNs), graph attention networks (GATs), and graph sampling and aggregation methods (GraphSAGE), GNNs provide a flexible framework for modeling both homogeneous and heterogeneous biological graphs.

Comprehensive surveys have documented the rapid growth of GNN applications in bioinformatics. Wu et al. [18], with more than 13,000 citations, offers one of the most influential overviews of GNN theory and applications across multiple domains, establishing the methodological foundations of the field. Focusing specifically on biomedicine, Zhang et al. [20] reviewed applications of GNNs in disease prediction, drug discovery, and biomedical imaging, highlighting both the promise of GNNs in capturing relational structure and the challenges posed by noisy, high-dimensional biological data. Abadal et al. [1] complemented these perspectives by surveying computational systems and accelerator-level advances for scaling GNN training, a critical concern for increasingly large biomedical networks.

Taken together, these surveys position GNNs as a transformative paradigm for computational biology. They not only enable more accurate prediction of disease associations and therapeutic targets but also open avenues for integrating multimodal omics and clinical data. At the same time, the literature emphasizes open challenges—including data quality, interpretability, and reproducibility—that motivate the more focused methodological contributions discussed in the following sections.

6 Disease–Gene Prediction with Graph Neural Networks

Predicting novel associations between diseases and genes is a central task in computational biology, with direct implications for understanding disease mechanisms, prioritizing candidate genes, and guiding therapeutic development. Early computational strategies relied on similarity measures, diffusion-based algorithms, or classical machine learning on handcrafted features. While effective in some cases, these methods struggled with sparse and noisy data, as well as limited generalizability across diseases. Graph neural networks (GNNs) have recently emerged as a promising solution by directly leveraging the topological and relational structure of biological networks.

6.1 Early GNN-Based Approaches

One of the first studies to explore GNNs for this task was Singh and Lio' [15], who proposed a probabilistic generative framework for disease–gene prediction. Their work integrated variational graph autoencoders (VGAE) to model latent representations of disease–gene networks, enabling the discovery of novel associations under uncertainty. Although citation counts remain relatively modest (∼20), this study marked an important conceptual step by bridging probabilistic modeling with graph-based learning.

Building on these foundations, Cinaglia and Cannataro [5] applied graph convolutional networks (GCNs) to curated resources such as DisGeNET and BioSNAP. Their results demonstrated competitive performance in ranking candidate disease genes, showing that even relatively simple GNN architectures can outperform traditional similarity-based and machine learning methods when applied to well-constructed biomedical graphs.

6.2 Explainability and Interpretability

A major limitation of deep GNN approaches is their black-box nature, which restricts their utility in translational settings where biological plausibility and interpretability are essential. To address this, Chatzianastasis, Vazirgiannis, and Zhang [4] introduced the Explainable Multilayer Graph Neural Network (EMGNN). By learning across multiple layers of gene–gene interaction networks and integrating pan-cancer multi-omics data, EMGNN not only improved predictive performance but also provided interpretable rationales for gene prioritization. With nearly 30 citations within two years, this work highlights the growing emphasis on explainability in biomedical AI.

Similarly, Mastropietro, De Carlo, and Anagnostopoulos [11] developed XGDAG, an explainable framework for disease–gene prediction under a positive–unlabeled learning setting. XGDAG introduced explicit explanation modules to uncover the subnetwork structures supporting each prediction. Although relatively recent and less cited (∼13), it represents an important step toward trustworthy GNN-based disease gene prioritization.

6.3 Generative and Probabilistic Extensions

Beyond supervised GNNs, generative approaches offer the ability to quantify uncertainty and handle missing information in disease–gene networks. Extensions of the VGAE framework, including conditional VGAEs (C-VGAE), have been proposed to model heterogeneous networks and integrate multiple data modalities. These probabilistic methods provide principled estimates of confidence in predicted associations, addressing a critical need in biomedical applications where experimental validation is costly and time-consuming.

6.4 Summary

Taken together, the literature on GNN-based disease–gene prediction reflects a trajectory from early proof-of-concept applications toward increasingly sophisticated, interpretable, and uncertainty-aware models. Classical baselines remain useful for interpretability and benchmarking, but recent developments such as EMGNN [4] and XGDAG [11] demonstrate how GNN architectures can be tailored to meet the dual demands of accuracy and explainability. At the same time, generative and probabilistic approaches suggest a promising direction for robust inference under data sparsity, laying the groundwork for integrating disease–gene prediction into broader pipelines for precision medicine.

7 Other Biomedical Associations

While disease–gene prediction remains a central application of GNNs in biomedicine, many other types of biomolecular associations are equally critical for understanding disease mechanisms and therapeutic opportunities. These include relationships between non-coding RNAs and diseases, metabolites and diseases, as well as drug–disease associations relevant for drug repurposing. A growing body of work has adapted GNN architectures to these diverse biological contexts, often leveraging heterogeneous graph structures and attention mechanisms to integrate multiple sources of information.

7.1 miRNA–Disease Associations

MicroRNAs (miRNAs) are small non-coding RNAs that regulate gene expression post-transcriptionally and play essential roles in disease pathogenesis. Yan et al. [19] proposed PDMDA, a graph neural network framework designed to predict deep-level miRNA–disease associations. By integrating biological features with graph-based representations, PDMDA was able to capture complex relationships beyond simple similarity measures. With more than 30 citations, this work highlights the growing importance of extending graph-based learning to non-coding RNA interactions.

7.2 lncRNA–Disease Associations

Long non-coding RNAs (lncRNAs) have been increasingly recognized for their regulatory functions in disease. Shi et al. [14] introduced HGNNLDA, a heterogeneous GNN framework for lncRNA–disease prediction. HGNNLDA constructed a multiplex network incorporating lncRNA similarities, lncRNA–miRNA interactions, and lncRNA–disease links. Through type-aware message passing with attention, the model achieved strong predictive performance while demonstrating the value of explicitly modeling heterogeneous biological relationships. Although more recent and with fewer citations ($\sim$19), HGNNLDA illustrates the versatility of GNNs in capturing novel disease associations.

7.3 Metabolite–Disease Associations

Metabolites are central to cellular processes and provide insights into disease-specific metabolic alterations. Sun, Sun, and Zhao [16] developed GCNAT, which combined graph convolutional networks with attention-based aggregation of layer embeddings for metabolite–disease association prediction. GCNAT significantly outperformed traditional baselines in cross-validation experiments and achieved an impressive citation uptake ($\sim$234). Its success reflects both the biological relevance of metabolite data and the methodological strength of integrating attention mechanisms into GNN frameworks.

7.4 Drug–Disease Associations

Drug repurposing seeks to identify novel indications for existing compounds, offering a cost-effective strategy to accelerate therapeutic development. Gu et al. [7] proposed REDDA, a heterogeneous GNN that integrates multiple biological relations—including drug–target, disease–gene, and protein–protein interactions—into a unified representation. By applying multi-level attention at the node, graph, and layer levels, REDDA

achieved superior performance compared to competing repurposing methods and validated predictions through case studies. With nearly 60 citations, REDDA exemplifies the potential of GNN-based approaches to inform translational applications.

7.5 Summary

Collectively, these studies illustrate the adaptability of GNNs across multiple types of biomedical associations. Whether applied to non-coding RNAs, metabolites, or drug repurposing, the common pattern is the construction of heterogeneous, multiplex graphs and the use of attention-based mechanisms to capture the diverse types of biological relationships. This trend suggests a unifying paradigm in computational biology: leveraging graph-based deep learning to integrate complex, multi-modal biomedical data and uncover novel associations beyond the classical disease–gene framework.

8 Patient-Level Predictions

Beyond molecular networks, graph neural networks (GNNs) have also been applied to patient-level prediction tasks, where the objective is to model clinical outcomes directly from patient data. In this setting, nodes may represent patients, diseases, or medical concepts, and edges capture similarities, co-occurrences, or knowledge-based associations. This perspective highlights the versatility of GNNs in leveraging graph structure not only for biomolecular associations but also for population-level health prediction.

8.1 Patient Networks from Clinical Data

Lu and Uddin [10] constructed weighted patient networks by projecting patient–disease bipartite graphs, where edge weights reflected the degree of shared diagnoses between patients. They then applied graph neural networks with attention mechanisms to predict chronic diseases such as cardiovascular and pulmonary conditions. With over 100 citations, this work demonstrated that patient-level graphs outperform traditional machine learning baselines, particularly by exploiting relational structure among patients. Importantly, the inclusion of attention allowed the model to highlight influential connections, adding a layer of interpretability for clinical decision support.

8.2 Integration with Knowledge Graphs

Sun et al. [17] extended this paradigm by combining patient electronic medical records (EMRs) with external biomedical knowledge graphs. They constructed graphs where medical concepts (e.g., symptoms, diagnoses, medications) were linked both through co-occurrence in patient records and through curated knowledge bases. Graph neural networks trained on these hybrid graphs achieved state-of-the-art performance in disease prediction, including for rare diseases where data scarcity often limits model effectiveness. This approach illustrated the inductive capacity of GNNs: the ability to generalize to unseen patients by leveraging structured domain knowledge.

8.3 Summary

Together, these studies highlight the promise of GNNs in clinical informatics. By representing patients and medical concepts as graph-structured data, GNNs can uncover latent similarities across patients, improve predictions for chronic and rare diseases, and enhance interpretability in medical contexts. Patient-level prediction thus expands the scope of GNN applications from molecular mechanisms to healthcare delivery, positioning graph-based models as a unifying framework across scales of biomedical data.

9 Graph Neural Network Architectures

Graph neural networks (GNNs) extend deep learning to graph-structured data by propagating and aggregating information across node neighborhoods. Over the past few years, several core architectures have emerged as building blocks for nearly all modern GNN applications. These models differ in how they define neighborhood aggregation—through convolution, sampling, or attention—and collectively provide the methodological foundation for subsequent biomedical extensions.

9.1 Core Models

Graph Convolutional Networks (GCNs). Introduced by Kipf and Welling in 2017, GCNs define convolutional filters on graphs via spectral methods. Each node updates its representation by averaging and transforming the features of its immediate neighbors, enabling localized feature learning that is analogous to convolution on images.

GraphSAGE. Proposed by Hamilton et al. in 2017, GraphSAGE addressed scalability and inductive learning by introducing neighborhood sampling and aggregation functions (mean, LSTM, pooling). This allows the model to generate embeddings for previously unseen nodes, which is particularly valuable in dynamic biomedical networks.

Graph Attention Networks (GATs). Developed by Veličković et al. in 2018, GATs introduced attention mechanisms to assign different weights to neighbors during message passing. This improves expressivity and robustness in noisy or heterogeneous graphs, where not all neighbors contribute equally to a node's representation.

These three models—GCN, GraphSAGE, and GAT—form the backbone of GNN research and remain central to applications in computational biology.

9.2 Extensions for Biomedical Applications

Biomedical networks often involve heterogeneous entities (e.g., genes, proteins, RNAs, diseases) and require interpretability for translational relevance. Several extensions of GNNs have been developed to address these needs.

Heterogeneous GNNs. Shi et al. [14] introduced HGNNLDA for lncRNA–disease prediction, modeling multiplex graphs of lncRNAs, miRNAs, and diseases with type-aware message passing. Similarly, Gu et al. [7] proposed REDDA, which integrates drug–target, disease–gene, and protein–protein interactions using multi-level attention to improve drug repurposing predictions.

Explainable GNNs. To address the black-box nature of deep models, Chatzianastasis, Vazirgiannis, and Zhang [4] developed EMGNN, which integrates multi-omics data across cancer types while providing interpretable rationales for gene prioritization. In

parallel, Mastropietro, De Carlo, and Anagnostopoulos [11] proposed XGDAG, an explainable PU-learning framework that highlights subnetworks underlying disease–gene predictions.

Generative and Probabilistic Models. Singh and Lio' [15] pioneered the use of variational graph autoencoders (VGAEs) for disease–gene prediction, introducing a probabilistic framework that models latent representations and quantifies uncertainty. Such generative approaches are well suited to the noisy, incomplete nature of biomedical graphs.

9.3 Surveys and Perspectives

Several surveys synthesize methodological advances in GNNs. Wu et al. [18] provide one of the most cited reviews, covering theoretical foundations and broad applications. Zhang et al. [20] focus specifically on bioinformatics, highlighting opportunities and challenges in applying GNNs to molecular and clinical data. From a systems perspective, Abadal et al. [1] review algorithmic and hardware optimizations for scaling GNN training. Together, these surveys underscore both the maturity of core GNN methods and the emerging frontiers in their biomedical applications.

Chatzianastasis et al. (2023) introduced the Explainable Multilayer Graph Neural Network (EMGNN) for cancer gene prediction [4]. Their model integrates pan-cancer multi-omics data with multilayer gene–gene interaction networks, achieving strong predictive performance while providing interpretable rationales for prioritizing cancer-related genes. This approach highlights the importance of explainability in biomedical AI, offering not only accurate predictions but also mechanistic insights into disease biology that are critical for translational applications.

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