Uncovering Temporal Patterns in *Saccharomyces cerevisiae* Gene Co-expression Networks through Dynamic Community Detection

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1 Background of the Study

1.1 Network Biology and Biological Networks

Biological systems are inherently complex—molecules such as genes, proteins, and metabolites intricately interact with each other to perform essential functions that regulate cellular processes. Barabási and Oltvai (2004) highlight that traditional reductionist approaches in examining biological functions is insufficient, since such methods only focus on individual cellular components. In reality, biological characteristics are seen as a product from complex interactions between multiple molecules, such as proteins, DNA, and small molecules (Barabási and Oltvai, 2004). This shift in perspective gave way for network biology: an interdisciplinary domain which integrates the computational field of network theory with biological sciences.

Girvan and Newman (2002) emphasize that many networks in different domains of study exhibit community structures, where nodes cluster into tightly connected groups. In particular, this phenomenon is prevalent in biological systems, where such community structures may pertain to functional modules—a group of genes, proteins or other biological entities that work in conjunction to perform a specific biological role. Biological networks, such as gene regulatory networks (GRNs), protein-protein interaction networks (PPIs) and metabolic pathways, are compelling topics for research as it can uncover how certain molecules are grouped within cells (Yu et al., 2013).

Dorogovtsev and Mendes (2002) explained that a crucial aspect of biological networks is that they are not static—they evolve over time, adapting to changing internal and external conditions. This dynamic nature is especially evident in gene co-expression networks, where gene interactions fluctuate throughout different stages of biological processes. Thus, studying the dynamic community structure within these networks can provide insights into how biological functions are regulated, and how brief interactions between genes may arise and disappear during key cellular events. This evolving nature of biological networks makes

dynamic community detection a critical tool for revealing how these molecular interactions change over time.

1.2 Dynamic Community Detection in Networks

Building on this understanding of dynamic biological networks, dynamic community detection has emerged as a key approach for analyzing networks across different domains, including social networks and biological systems. Much of the existing research regarding community detection begins with a strict assumption that real-world phenomena are represented using static networks which are fixed and unchanging over time. However, this assumption does not align with the evolutionary world around us.

Complex networks such as gene regulatory networks are generated at a blistering pace, which spawns the problem of the difficulty of modeling these networks as static relations. Time is an important component in studying the evolution of connectivity and patterns. The dynamic nature of these real-world networks further complicates the task of community detection as the structure of these communities evolve along with the networks themselves. The need to integrate the knowledge from the temporal dimension has led to the emergence of a new field of study: dynamic network analysis (Rossetti and Cazabet, 2018; Sattar et al., 2023).

Dynamic community detection is one of the key problems under this field. Over time, nodes and edges in a dynamic network can appear and disappear, causing significant shifts in its structure. Communities, which are the fundamental building blocks of this complex network, are heavily influenced by these local changes. While the objective of traditional community detection algorithms is to reveal hidden substructures, the goal of dynamic approaches is to monitor these local topological changes and their transformations over time (Rossetti and Cazabet, 2018). Understanding how community structures in complex networks evolve over time are vital in gaining valuable insights. The insights can be used to understand the structural dynamicity of the network. There is also great potential in the medical domain for analyzing disease progression (Redekar and Varma, 2022).

1.3 Gene Co-expression Networks and their Dynamic Nature

Gene co-expression networks (GCNs) are widely used to model interaction between genes based on their expression levels across different biological conditions or datasets, and across varying time points (Ovens et al., 2021; Lau et al., 2020). In GCNs, nodes represent genes, and edges signify co-expression relationships, where the strength of an edge correlates with the similarity in gene expression.

That said, GCNs will be the focus of this paper because of their temporal and dynamic properties. A study done by Lau et al. (2020) show the need to capture the temporal dynamics of GCNs, as gene co-expression patterns fluctuate significantly over time. Consequently, the community structure of GCNs will

also fluctuate, with different clusters of genes forming or dissipating at different timepoints. These changes highlight the importance of dynamic community detection techniques in capturing the evolving structure of GCNs (Ovens et al., 2021), which can reveal crucial insights on their functional grouping.

2 Preliminaries

2.1 Gene Co-expression Networks (GCNs)

A graph-based representation of genes, where nodes represent individual genes and edges represent co-expression relationships based on their expression patterns across multiple conditions or time points. Co-expression relationship refers to the correlation between the expression levels of two or more genes across different conditions (Stuart et al., 2003). Expression levels refer to the amount of mRNA produced by a gene in a cell at a given time. To put it simply, co-expression relationship is when two or more genes show similar patterns of activity (expression levels) across different conditions or samples. If their activity goes up or down together, they are said to be co-expressed, which often means they might work together or be controlled by the same regulatory processes (Ovens et al., 2021).

2.2 Community Detection

The process of identifying clusters of groups of nodes in a network that are more densely connected internally than with nodes outside the group. There are several community detection techniques (Redekar and Varma, 2022), depending on the nature of the network, whether static or dynamic.

2.2.1 Static Community Detection. Static community detection assumes that the network is fixed across different time points. From there, communities are identified based on a single snapshot of the network. This method is well-suited for networks where relationships between nodes are stable and predictable, if not unchanging. Techniques such as Louvain or Girvan-Newman are prime examples of static community detection algorithms, where it can reveal hierarchical structures in the network (Redekar and Varma, 2022).

2.2.2 Dynamic Community Detection. Dynamic community detection is designed for networks that evolve over time. It is able to detect communities and how they vary at each time step, tracking the evolution, merging and splitting of nodes and edges as the network changes (Dorogovtsev and Mendes, 2002). Capturing these temporal changes are crucial for understanding time-dependent phenomena, such as gene interactions that change during biological processes.

For the purposes of this paper, dynamic community detection is employed, as the study focuses on the evolving structure of gene co-expression networks across different phases of the cell cycle in *Saccharomyces cerevisiae*.

2.3 *Saccharomyces cerevisiae*

According to Parapouli et al. (2020), *Saccharomyces cerevisiae* is a unicellular fungus that is hailed as model organism—extensively used in biological research due to its well-annotated genome. In the field of bioinformatics, *Saccharomyces cerevisiae* contains around 6,000 documented genes which allows for in-depth research on cellular processes that is shared with higher-level eukaryotes. This includes gene regulation, cell cycle control, and metabolic functions. Due to its accessibility and applications, the gene expression data of this fungus is an ideal candidate for constructing a GCN through Dynamic Community Detection techniques.

For brevity, *Saccharomyces cerevisiae* is succinctly referred to as *S. cerevisiae*, or simply just *yeast* in this paper.

3 Review of Related Literature

3.1 Time-Series Gene Expression Data of *S. cerevisiae*

Cho et al. (1998) conducted a time-series laboratory experiment on *S. cerevisiae* across the different phases of the mitotic cell cycle. Of the original 6220 documented genes from the yeast, it was determined that 416 genes were actively involved in 17 different time points. These genes were functionally grouped according to their activity during the different phases of the cell cycle:

1. Early G1 Phase
2. Late G1 Phase
3. Synthesis Phase
4. G2 Phase
5. Mitosis
6. Multi-phase (occurring in different phases)

This grouping according to the cell cycle phase is denoted as the *Level 1* classification within the dataset. Another classification occurs within the dataset, denoted as *Level 2*, which represents a more specific subcategory or function within the broader classification in *Level 1*. For example, within the Early G1 Phase in *Level 1*, it can be further branched in to specific cellular processes in *Level 2*, such as Cell Cycle Regulation, Directional Growth, DNA Replication, and more. As such, one may observe the hierarchical structure of the data, where categories and subcategories form across the 17 different time points.

The resulting data from Cho et al. (1998) laid the foundation for Yeung et al. (2001), where they further processed the data for clustering analysis. Notably, they dropped the sixth functional grouping (multi-phase) so that the dataset only shows genes that peak in only one phase. This leaves with a gene expression data of 384 genes across 17 different time points.

Though this dataset is comprehensive, it is possibly outdated, especially with the rise of modern biotechnologies. Calderon et al. (2024) attempted to reconcile the Cho-Yeung dataset with the more precise and updated groupings from the

Kyoto Encyclopedia of Genes and Genomes (KEGG) (Kanehisa et al., 2022). Calderon et al. (2024) undertook a detailed comparison of the gene classifications. Their goal was to align the functional groupings from the time-series data of Cho with KEGG's established pathways and gene groupings, which are based on more modern genomic studies.

The KEGG *S. cerevisiae* dataset contains three levels of classification, as opposed to the Cho et al. (1998) of two levels. To reconcile the three levels of classification from KEGG with the two levels in Cho's dataset, they performed a detailed comparison using the Adjusted Rand Index (ARI) to measure the similarity between the groupings at different levels. First, the KEGG data was filtered to include only the genes that had both complete classification information in KEGG and were present in the Cho dataset. As a result, the 384 genes was reduced down to 149 genes. They then compared the classifications at each level of KEGG (*Levels 1, 2* and *3*) with each of the two levels from Cho's dataset (*Level 1* and *Level 2*).

The ARI was calculated for every possible combination of levels between KEGG and Cho, as shown in the table below.

Table 1. Relationship between KEGG and CHO classifications with ARI Calderon et al., 2024

KEGG Level	CHO Level	ARI
1	1	0.022699
1	2	0.083272
2	1	0.057357
2	2	0.118445
3	1	0.043423
3	2	0.156492

The highest ARI score was found between KEGG Level 3 and Cho Level 2, indicating the strongest correlation between these more detailed levels of classification.

3.2 Hierarchical Community Detection on GCNs

The study conducted by Calderon et al. (2024) provides a foundational exploration of hierarchical community detection on gene co-expression networks using the dataset from Cho et al. (1998) obtained from Yeung et al. (2001). Their research paper sought to explore the functional organization of gene communities within the *S. cerevisiae* cell-cycle dataset using hierarchical clustering techniques to uncover the existing substructures of co-expressed genes. In particular, they conducted a performance analysis on three hierarchical community detection algorithms: Girvan-Newman (GN), Paris, and Local Optimization Function Model (LFM).

Hierarchical community detection is appropriate for GCNs due to their hierarchical nature; genes may form smaller functional modules that integrate into larger biological processes. This is evident in the gene dataset they utilized, where there are levels of categorization. Calderon et al. (2024) applied the three community detection algorithms which can reveal modular and nested structures that govern gene regulation in *S. cerevisiae*.

However, while their hierarchical approach provided significant insights into the static structure of the GCN, it did not account for the dynamic nature of gene interactions, as mentioned by Calderon et al. (2024) in their recommendations—it is an open problem left by their research. This static focus on hierarchical organization is what this present study aims to address; by shifting to a dynamic community detection approach, this paper will explore how gene communities evolve across different cell cycle phases, thereby capturing temporal changes.

3.3 Dynamic Community Detection Algorithms

Dynamic community detection (DCD) algorithms not only uncover communities in complex networks but also the evolution of these networks over time. Several studies have probed into the performance of various DCD algorithms on both real-world and synthetic datasets (Ma and Dong, 2017; Seifikar et al., 2020; Singh et al., 2020; Redekar and Varma, 2022; Sattar et al., 2023; Calderon et al., 2024). We will be taking a look on a selection of noteworthy algorithms from previous studies, which all offer unique methods in discovering relevant communities in dynamic networks.

3.3.1 C-Blondel Algorithm. The C-Blondel algorithm is a DCD algorithm proposed by Seifikar et al. (2020) that is built upon the Louvain algorithm. It is an algorithm that leverages the historical information of network which improves its execution time. It applies the Louvain method over a compressed graph generated from the previous network snapshot. It runs faster than the Louvain algorithm by working with a smaller and more efficient compressed graph. This graph consists of supernodes that represent the previously detected communities, and superedges which connect these supernodes. It is important to note that there are no destructive nodes inside of these communities. Destructive nodes are defined to be the nodes in a community wherein the lack of them causes a corresponding community to break up into smaller subcommunities. To recognize these nodes, a degree centrality heuristic is employed. A node is considered destructive if its degree centrality is higher than the community average. The C-Blondel algorithm accounts for all changes in the network which are handled by the removal of a node. The remaining communities and subcommunities are transformed into supernodes, and their links become superedges, forming the new compressed graph.

The study compared C-Blondel with other DCD algorithms, particularly S-Blondel (Greene et al., 2010) and D-Blondel (He et al., 2017), on three real-world datasets. They concluded that it outperformed the selected algorithms, while remaining comparable in terms of the modularity metric (Seifikar et al., 2020).

3.3.2 Semi-supervised ENMF (sE-NMF) Algorithm. The sE-NMF algorithm is an algorithm proposed by Ma and Dong (2017). This algorithm combines evolutionary nonnegative matrix factorization (ENMF) frameworks for dynamic community detection, and spectral clustering. The aim of ENMF is to balance the trade-off between maximizing clustering accuracy at a given time step and maintaining the consistency of the clusters across time steps. A key difference of sE-NMF from classical semi-supervised algorithms is the integration of a priori information to its primary function. It is advantageous because it enables the algorithm to avoid local optima without affecting the run time complexity (Ma and Dong, 2017).

The group evaluated the performance of the sE-NMF algorithm against three well-known algorithms (FacetNet, Kim-Han, DYNMOGA) on three artificial and two real-world dynamic networks. One of the real-world networks is of particular interest, which modeled breast cancer progression based on the gene-expression data. It was found out that sE-NMF performs better than the other algorithms in both the specificity and sensitivity metrics, which is a great indicator of its ability to discover biological dynamic communities. It is also a great tool for assessing temporal networks of disease progression (Ma and Dong, 2017).

3.3.3 TILES Algorithm TILES is an algorithm that detects and tracks the evolution of overlapping communities in dynamic social networks. Its approach is similar to that of a fall of a domino tile. Every time a new interaction (edge) is introduced to the network, it first updates the local communities before propagating the changes to the surrounding nodes which in turn affects their community memberships. The algorithm characterizes two types of community memberships for the nodes: *peripheral* membership and *core* membership. A node is a *core* node if it is part of a triangle within the same community. Meanwhile, it is classified as a *peripheral* node if it is connected to a *core* node but not part of that any triangle within the *core* node's community. Only *core* nodes are allowed to propagate community membership to their neighboring nodes. Therefore, the TILES algorithm generates overlapping communities, where a node can belong to different communities at the same time which is identical to real-world networks (Rossetti et al., 2017).

The online nature of this algorithm is advantageous. The updating process is expedited because the computation of network substructures is localized and involves a minimal number of nodes and communities. Two evolutionary behaviors can also be observed due to this algorithm: (1) the persistence of individuals' ties to the communities, and (2) the gradual evolution of communities through interactions. Compositionality is an interesting property of TILES, which makes its execution parallelizable, thus allowing for faster computations of communities (Rossetti et al., 2017).

Rossetti et al. (2017) evaluated the performance of TILES versus other CD algorithms (DEMON, CFinder, and iLCD) both on synthetic and real-world networks, which included social media and call network data. The results showed that TILES had faster execution times and was more accurate with ground truth

communities. It was also able to identify significant lifecycle events which affected the structure of these communities, which provided great insights into the dynamics of these networks. TILES could also be adapted to gene co-expression networks because they are dynamic in nature as well.

3.3.4 InfoMap Algorithm InfoMap is an algorithm that utilizes a map equation to detect community structures in networks. It views community detection as a coding problem and applies the minimum description length (MDL) in computing the optimal partition. In this algorithm, the description length of a random walker in the network is expressed by the map equation. A partition with a good modular structure is usually emphasized by a smaller description length, and it is incorporated in the objective function in uncovering better network partitions. A partition's description length can be compressed if a random walker tends to stay longer within it, so those with greater community structure will yield minimum description length. This approach groups nodes through a collective process, initially treating each node as a separate module. Then, it randomly selects nodes to combine together, which leads to a significant decrease in the map equation. In the succeeding steps, previously formed modules are treated as nodes and the process is repeated until a decrease in the map equation is no longer possible. A fundamental element of this algorithm is the utilization of flows in the graph. It is robust as long as clusters inside it flow well, which indicates the tendency of staying inside the same cluster when doing random walks. Otherwise, it fails if there is a lack of flow or if it mostly results to deadlocks (Held et al., 2016; Chejara and Godfrey, 2017; Sun et al., 2019).

3.4 Statistical Analysis of Dynamic Community Detection

3.4.1 Internal Criteria Internal criteria are used to assess the clustering results of the CD algorithms without using external information such as ground-truth data, and it only utilizes information that are inherent to the data (Liu et al., 2020).

One of the widely used metrics that we will employ in this study is Modularity, which is used to assess the quality of a network community structure. High modularity is an indication that vertices within the same community have denser connections compared to vertices across different communities which have sparser connections. It is particularly useful in assessing the strength of an algorithm in dividing a given network into communities (Zhuang et al., 2021).

Another metric that we will consider applying is Closeness Centrality. It is used to quantify the speed at which information gets transmitted to a node from all other nodes in a given network. This metric is a good measure of the overall accessibility of a node in the network and their capability to obtain information rapidly (Kherad et al., 2024).

By applying these internal criteria — modularity and closeness central — we aim to evaluate the effectiveness of DCD algorithms both in the strength and cohesion of detected communities but also the accessibility and influence

of individual nodes as the network structure changes over time. It can give us valuable biological insights into the temporal nature of the *S. cerevisiae* gene co-expression network.

3.4.2 External Criteria On the other hand, external criteria are used to evaluate the similarity of the clustering results of the CD algorithms against a "ground truth" generated by prior experiments.

The Adjusted Rand Index (ARI) is a key metric in assessing the similarity between two communities. To understand it, we must first understand the Rand Index (RI). RI considers every pair of nodes and determine whether they belong in the same community. If so, it compares these pairs against another graph. For a given node pair, it gets a score of 1 if it is either in the same community for both graphs or not in the same community for both graphs. Otherwise, it gets a 0 which indicates the difference between the community structure of the graphs. The result of dividing the sum of the scores of all node pairs and the number of pairs is between 0 and 1, where the result is directly proportional to the similarity of two graph's community structures (Bakker et al., 2018). With that in mind, ARI is simply an extension of RI where chance is taken into account. The equation for ARI is as follows:

$$\text{ARI} = \frac{RI - ExpectedRI}{MaxRI - ExpectedRI} \tag{1}$$

An ARI value of 1 indicates the identicality between the predicted and actual clustering, while a negative value implies that the cluster agreement is lower than expected by chance (Clemente et al., 2022).

Another metric that is commonly used when ground-truth information is present is Normalized Mutual Information (NMI). A confusion matrix N is defined, where the rows are the ground truth class labels, and the columns are the communities generated by a CD algorithm. An element N_{ij} is the number of nodes with class label i that are in community j. The NMI is defined as follows:

$$\text{NMI}(A, C) = \frac{-2 \sum_{i=1}^{n_A} \sum_{j=1}^{n_C} N_{ij} \log\left(\frac{N_{ij} N}{N_{i.} N_{.j}}\right)}{\sum_{i=1}^{n_A} N_{i.} \log\left(\frac{N_{i.}}{N}\right) + \sum_{j=1}^{n_C} N_{.j} \log\left(\frac{N_{.j}}{N}\right)} \tag{2}$$

where A is the ground-truth partition C is the CD algorithm partition, n_A is the number of ground-truth communities, n_C is the number of communities detected by the CD algorithm, $N_{i.}$ is the number of nodes with class label i, and $N_{.j}$ is the number of nodes in community j. NMI is 1 if the partitions are equal, and 0 otherwise (Márquez and Weber, 2023).

By employing these external criteria — ARI and NMI — we will be able to understand the accuracy of DCD algorithms when tested with real-world data, particularly biological data.

4 Statement of the Problem

The study of gene co-expression networks (GCNs) in *S. cerevisiae* has provided significant insights into the modular and hierarchical structure of gene interactions, particularly as they relate to the cell cycle. However, the absence of a dynamic approach leaves an open problem: how do gene communities in *S. cerevisiae* evolve throughout the cell cycle, and what are the implications of these temporal changes for gene regulation? Addressing this question requires the application of dynamic community detection techniques, which can track the formation, dissolution, and transformation of gene communities over time.

Therefore, this study aims to fill the gap by applying dynamic community detection to the same dataset used by Calderon et al. (2024). The objectives of this research paper is as follows:

1. **Discovering Temporal Changes:** Identify how the gene communities of *S. cerevisiae* across different phases of the cell cycle, revealing time-dependent co-expression patterns.
2. **Provide a Dynamic Map of Gene Regulatory Networks**: Construct a time-resolved map of gene regulatory interactions in *S. cerevisiae*, offering a comprehensive view of how gene interactions evolve over time.
3. **Supplement Existing Knowledge on *S. cerevisiae***: Contribute to the open problem posed by Calderon et al. (2024) by applying dynamic community detection to their dataset, expanding our understanding of temporal dynamics within gene co-expression networks of *S. cerevisiae*.

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