MATHEMATICAL MODELING OF BIOLOGICAL INTERACTIONS: FORMALISMS AND CONTEMPORARY APPLICATIONS

MODELACIÓN MATEMÁTICA DE LAS INTERACCIONES BIOLÓGICAS: FORMALISMOS Y APLICACIONES CONTEMPORÁNEAS

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ABSTRACT

This paper introduces an advanced mathematical framework for describing biological interactions through spectral graph theory. We examine differential equations coupled with various Laplacians (classical, signless, and normalized) to address competition, predation, and evolutionary cooperation. We cover stability analyses, bifurcations, and computational validation using empirical data. Network topological properties, including connectivity and modularity, significantly influence ecosystem robustness and the spread of epidemic phenomena. Our results illustrate the effectiveness of combining graph theory and differential equations for modeling large ecological and genomic networks at scale. Moreover, future perspectives are discussed, highlighting the integration of spectral preconditioners and deep learning. This approach provides a solid foundation for research in mathematical biology and the management of natural resources.

RESUMEN

Este artículo presenta un marco matemático avanzado para describir las interacciones biológicas mediante teoría espectral de grafos. Se revisan ecuaciones diferenciales acopladas con matrices Laplacianas (clásica, signless y normalizada), resaltando su capacidad para modelar competencia, depredación y cooperaciones evolutivas. Se incluyen análisis de estabilidad, bifurcaciones y validación computacional con datos empíricos. Las propiedades topológicas de la red, como la conectividad y la modularidad, muestran una incidencia determinante en la robustez del ecosistema y en la propagación de fenómenos epidémicos. Los resultados evidencian la utilidad de combinar teoría de grafos y ecuaciones diferenciales para obtener modelos escalables, aplicables a grandes redes ecológicas y genómicas. Asimismo, se discuten perspectivas futuras, subrayando la integración de precondicionadores espectrales y el uso de aprendizaje profundo. Este enfoque constituye una base sólida para la investigación en biología matemática y la gestión de recursos naturales.

Keywords: spectral theory, Laplacian graphs, mathematical biology, ecological interactions
Palabras clave: teoría espectral, grafo Laplaciano, biología matemática, interacciones ecológicas

INTRODUCTION

Over the past decades, the rise of quantitative biology has driven the integration of increasingly sophisticated mathematical models that make it possible to describe and predict the dynamics of ecological and evolutionary processes (Cvetković & Simić, 2009; Chang *et al*., 2017). Spectral graph theory, in particular, has become a cornerstone for understanding complex interactions among multiple species in trophic, genomic, or epidemic networks (Cui & Tian 2017; Afkhami *et al*., 2019).

Systems biology seeks to integrate information from different levels—molecular, cellular, and population—to provide a holistic view of living phenomena (Banerjee & Jost, 2008; Abdian & Mirafzal, 2018). Representing interactions through graphs facilitates the analysis of community structure and function, whether in trophic relationships within ecosystems, transmission in epidemiology, or co-evolution in genetic dynamics (Chang *et al*., 2015; Cvetković & Simić, 2010).

The combination of massive data sets with mathematical modelling demands *robust analytical tools* that are scalable and capable of capturing the intrinsic complexity of biological systems (Hu *et al*., 2017; Fabila-Carrasco *et al*., 2022). In this regard, spectral graph theory—based on the study of the eigenvalues and eigenvectors of matrices associated with the network—constitutes a *powerful framework* for the quantitative study of stability, co-evolution, and control within biological networks (Chang *et al*., 2017; Helmberg & Trevisan, 2017).

The use of the *Laplacian matrix* in ecology and epidemiology dates back to early studies of network dynamics in graph theory (Merris, 1998; Grone & Merris, 2008). However, advances in computing hardware and new results in matrix analysis—particularly regarding the spectral properties of $L(G)$, $Q(G)$, and related operators—have led to increasing adoption of spectral theory in systems biology Liu et al. (2014); Tam and Wu (2010).

For example, *spectral decomposition methods* have been developed to characterise connectivity patterns in large-scale trophic networks, and *Laplacian indices* able to predict network vulnerability to species loss or pathogen introduction have been proposed Chang et al. (2015); Kirkland (2007). Non-linear models integrating differential- equation theory with Laplacian structure have also emerged to describe spatial diffusion and self-organisation Bapat et al. (2001); Fabila-Carrasco et al. (2022).

The main objective of this work is to demonstrate the *practical and theoretical usefulness* of Laplacian matrices and their variants as analytical tools for biological networks (Cvetković *et al*., 2007; Abdian *et al*., 2020). Specifically, we aim to:

1. *Show the versatility of spectral theory*: applying it to different regimes of biological interaction, including competition, predation, and cooperation (Chang, 2016; Mulas *et al*., 2024).
2. *Validate its effectiveness in real-world problems*: comparing the predictions generated by spectral models with empirical data and Monte Carlo simulations (Cooper, 2021; Goldberger & Neumann, 2013).
3. *Propose future research lines*: oriented toward integrating spectral methods with big data, deep learning, and computational optimization techniques (Ahanjideh *et al*., 2022; Xu & Zhou, 2023).

REFERENCE THEORETICAL FRAMEWORK

This section provides a conceptual and mathematical overview of the formal tools underlying the study of complex biological interactions, with an emphasis on *mathematical biology, and particularly* the methods of *spectral graph theory*. Fundamental ideas are reviewed with advanced rigor, and relevant applications in ecology, evolution, epidemiology, and other branches of biology are discussed. The importance of graph structure and connectivity in modelling phenomena involving interaction networks—from ecological communities to gene flow and disease- transmission networks—is also highlighted.

Throughout the text, equations and illustrative examples are employed to facilitate understanding of spectral theory and its adaptation to biological problems. For instance, species dispersal or population competition can be modelled with a *Laplacian term* in a system of coupled differential equations (Afkhami *et al*., 2019; Kirkland & Zhang, 2020):

$$\frac{d}{dt}x_i(t) = F(x_i(t)) - \beta\sum^{n} L_{ij}\, x_j(t), \tag{1}$$

where $x_i(t)$ denotes the density or concentration of species i at site i, $F(\cdot)$ represents the internal dynamics (e.g., logistic growth or Lotka–Volterra interaction), and the term with L_{ij} describes diffusion or flow between sites (Chang, 2016; Das & Gutman, 2018). This formalism unifies the discrete (graph) structure and continuous dynamics, highlighting the usefulness and generality of spectral theory.

This approach provides a *common quantitative framework* for a variety of biological questions and hypotheses, from species coexistence to pathogen propagation, and aligns with current trends in massive data analysis and large-scale simulations (Helmberg & Trevisan, 2017; Mulas *et al*., 2024).

In summary, this introduction underscores the motivation and relevance of integrating Laplacian matrices and other spectral-theory formalisms into the study of biological networks. In the subsequent sections, technical details will be explored in depth and the results obtained—illustrated through examples and cross-validation—will be contrasted, reaffirming the potential of *mathematical biology* as a cornerstone for understanding and managing the complexity of living systems.

Foundations of Mathematical Biology

Mathematical biology emerges as a discipline in which *quantitative modelling* of living processes is carried out through differential equations, graph theory, and other formal structures. Traditionally, the earliest contributions stemmed from population dynamics, with models such as Lotka–Volterra, compartmental epidemiology (SIR, SEIR), and evolutionary game theory (Chang, 2016; Clark & Del Maestro, 2018; Alhevaz *et al*., 2018; Das, 2004). In these approaches, biological parameters (infection rates, interaction coefficients, etc.) are translated into constants that define the temporal evolution of the population or the state of the system.

The development of *spectral graph theory* has enhanced the analysis of interactions among species and large-scale ecological structures (Cvetković *et al*., 2007; Guo & Wang, 2013; Das *et al*., 2016). When working with interaction networks (e.g., trophic, pollination, or dispersal networks), representation by means of associated matrices—adjacency matrix, Laplacian matrix, signless Laplacian matrix, among others—allows global properties of the system to be studied through their respective *eigenvalues* and *eigenvectors* (Cvetković & Simić, 2009; Cvetković & Simić, 2010); Afkhami et al. (2019). This framework provides a broad perspective that connects topological structure with dynamic and stability phenomena.

Spectral Graph Theory and Laplacians

One of the pillars in network modelling is *spectral graph theory*, which is based on the analysis of various matrices associated with a graph. The most prominent are the following:

The Classical Laplacian: The *Laplacian of a graph G*, denoted $L(G)$, is defined as $L(G) = D(G) - A(G)$, where $D(G)$ is the diagonal degree matrix and $A(G)$ is the adjacency matrix (Merris, 1998; Fallat *et al*., 2005; Rocha & Trevisan, 2016). Its eigenvalues provide key information on connectivity, number of components, and robustness. The zero eigenvalue reflects connected components, and the multiplicity of eigenvalues close to n is associated with extreme node properties, such as their participation in "cuts" or *cut-sets* (Das *et al*., 2016; Gutman, 2017). Results concerning the distribution of Laplacian eigenvalues have led to the development of numerous conjectures and theorems (Cooper, 2021; Goldberger & Neumann, 2013), many of which have found applications in graph classification, pattern recognition, and the diagnosis of structural properties (Das *et al*., 2014; Merris, 1998; Tam *et al*., 2008).

The Signless Laplacian: The *signless Laplacian*, defined as $Q(G) = A(G) + D(G)$, has gained relevance for the analysis of non-regular graphs, as it encapsulates information complementary to the classical Laplacian (Cvetković *et al*., 2007; Cvetković & Simić, 2009; Cui & Tian, 2017). Numerous studies have shown equivalences and analogies between the spectra of $Q(G)$ and $L(G)$ in regular graphs (Cvetković & Simić, 2010; Cvetković, 2008), as well as its power to solve optimization and structural-characterization problems in general graphs (Abdian *et al*., 2020; Abdian & Mirafzal, 2018; Das & Gutman, 2018). Conjectures have also been proposed regarding the *maximality* of the largest eigenvalue of $Q(G)$ and its relationship with network *connectivity* and *diameter* (Cvetković *et al*., 2007; Cvetković, 2008; Zhang & Zhang, 2009). In biological contexts, the matrix $Q(G)$ can be used to model interactions in which node degree synergistically influences network dynamics, as occurs in mutualistic systems or ecosystems with dense energy flows. Some studies have incorporated *multicone graphs* to describe the structure of ecological complexes (Abdian & Mirafzal, 2018; Berman *et al*., 2018).

The Normalised Laplacian: Another operator of interest is the *normalised Laplacian*, usually denoted

$$\mathcal{L}(G) = D(G)^{-\frac{1}{2}}\left[D(G) - A(G)\right]D(G)^{-\frac{1}{2}},$$

whose spectrum has been applied to the study of *diffusion* and *connectivity* in large biological networks (Banerjee & Jost, 2008; Dalfó *et al*., 2021; Chang *et al*., 2015). Unlike the traditional Laplacian, $L(G)$ controls node-degree heterogeneity, providing precise information on *clusters* and *cuts* in the network (Fasino & Tudisco, 2014; Fasino & Tudisco, 2016; Bolla *et al*., 2015). Variations such as the *non-backtracking Laplacian* have been proposed, especially useful for detecting "cascades" of propagation and contagion dynamics (Jost *et al*., 2023; Mulas *et al*., 2024).

Applications to Biological Interactions

Population Dynamics and Trophic-Network Structure: In ecology, trophic networks can be represented by graphs in which nodes symbolize species and edges describe predation, competition, or mutualism relationships (Afkhami *et al*., 2019; Chang *et al*., 2017; Abdian & Mirafzal, 2018). Spectral analysis of the adjacency matrix or Laplacian matrices (Cvetković & Simić, 2010; Zhang & Li, 2016) yields results on *ecosystem stability* and *resilience*. For instance, large eigenvalues of the signless Laplacian can be associated with highly interconnected networks, which may indicate robust energy flows and greater resistance to perturbations (Zhang & Zhang, 2009; Tam *et al*., 2008). From a *species dispersal* viewpoint, partial differential equations associated with the Laplacian are combined with reaction–diffusion theory to describe spatial patterns such as self-organization, invasion fronts, and the emergence of *limit cycles* (Chang, 2016; Xu & Zhou, 2023; Golénia & Truc, 2020).

Network Epidemiology: Mathematical epidemiology traditionally adopts compartmental models (SIR, SEI, etc.), but increasingly includes network terms to capture transmission heterogeneity among populations or species (von Below & Lubary, 2009; El Bouchairi *et al*., 2023; McDiarmid & Skerman, 2018). By representing possible infection routes through a graph, Laplacian operators help identify *critical points* in propagation (high-degree or high-eigenvector-centrality nodes) and estimate epidemiological thresholds. Some approaches use *1-Laplacian* theory to characterize optimal cuts for disease containment (Chang *et al*., 2017; Chang *et al*., 2015).

Population Genetics and Phylogeny: *Population genetics* has begun to employ graph metrics to study gene flow or multi-species coalescence processes (Faber, 2006; Helmberg & Trevisan, 2017). Through the construction of "kinship" or "genetic distance" networks, the Laplacian matrix (or its variants) aids in analyzing *genetic connectivity* and the emergence of subpopulations (Hameed & Tyaglov, 2023; Chang, 2016). Likewise, algebraic phylogenetic models benefit from spectral methods to detect horizontal incongruences or gene-transfer events (Cvetković & Simić, 2010; Cui & Tian, 2017).

Recent Developments in Spectral Theory

In recent years, multiple extensions and variants of Laplacian matrices have been introduced to capture more complex behaviors in biological networks:

- *Perturbed Laplacian* (Bapat *et al*., 2001; Rocha & Trevisan, 2016): introduces diagonal biases or "potentials" to model heterogeneities in node fitness or ecological affinity.
- Magnetic Laplacian (Fabila-Carrasco *et al*., 2022; Mulas *et al*., 2024): applies concepts from quantum mechanics to incorporate "phase" effects on each edge, proving useful in analyzing dynamics on cycles and closed paths.
- 1-Laplacian with boundary conditions (Chang *et al*., 2017; Chang, 2016): linked to minimum-cut (Cheeger cut) and *max-cut* problems, with applications in optimizing the release of pest-control species.
- Non-backtracking Laplacian (Jost *et al*., 2023; Mulas *et al*., 2024): specialized in community detection and propagation processes without immediate cyclic trajectories (avoiding trivial feedback).

These advances allow the analysis of *structural robustness* and *functional persistence* of biological networks at different scales, from microecology (e.g., microbial communities) to large ecosystems.

Laplacian Energy and Centrality Measures

The concept of *Laplacian energy* (and variants such as the *Laplacian-energy-like invariant*) has become a relevant measure for quantifying network "complexity" (Das & Gutman, 2018; Liu *et al*., 2015; Das *et al*., 2014; Helmberg & Trevisan, 2017). This magnitude depends on the dispersion of eigenvalues around the mean degree and has been related to *ecological stability* (Rakshith *et al*., 2021; Sason, 2024). Networks with high Laplacian energy tend to exhibit greater differences in node degrees or strongly connected substructures (Kirkland & Zhang, 2020; Kirkland, 2007).

Other centrality metrics—such as the *high multiplicity of certain eigenvalues*, the *spectral distribution*, and the *eigenvector concentration*—provide information on system fragility to the loss of a keystone species, network *mod- ularity*, or *residual connectivity* after perturbations (Fasino & Tudisco, 2014; McDiarmid & Skerman, 2018; Lasoń & Sulkowska, 2023).

The extensive repertoire of Laplacian matrices and their variants (signless, normalised, perturbed, 1-Laplacian, non-backtracking) constitutes a solid mathematical foundation for understanding complex biological interactions. These approaches enable:

1. Identification of *stability* and *resilience* properties in ecological networks (Cvetković & Simić, 2009; Cvetković & Simić, 2010; Chang, 2016).
2. Quantification of *topological robustness* and *functionality* of communities facing disturbances or node loss (Johnston & Tait, 2024; Tam & Wu, 2010; Hameed & Tyaglov, 2023).
3. Establishment of connections with *population genetics*, *epidemiology*, and *ecosystem dynamics*, integrating graph-theoretical methods with differential equations (von Below & Lubary, 2009; El Bouchairi *et al*., 2023; Lasoń & Sulkowska, 2023).

MATERIALS AND METHODS

This section describes the mathematical tools and procedures used to characterize and model biological interactions from the standpoint of spectral graph theory. We present the criteria for selecting biological data and the analytical techniques based on differential equations, weighted graphs, and Laplacian matrices, all grounded in recent literature (Cvetković & Simić, 2009; Chang, 2016; Banerjee & Jost, 2008).

Data Selection and Network Construction

The biological networks considered in this study are built from empirical observations (population dynamics, trophic interactions, species dispersal) or from genomic and phylogenetic databases. For each pair of species (or nodes in the network), an interaction strength is defined that, depending on the case, may refer to:

- Predation or competition rate.
- Contact frequency (in epidemiology).
- Genetic or biomolecular distance in phylogeny.

Thus, we obtain networks with edge weights, which are normalized according to data availability and the recommendations in the literature (Clark & Del Maestro, 2018; Mulas *et al*., 2024; Abdian & Mirafzal, 2018).

Once the interactions are defined, we create the adjacency matrix $A(G) = (a_{ij})$, where a_{ij} represents the interaction strength between node i and node j. For unweighted cases, $a_{ij} \in \{0, 1\}$ depending on whether or not a direct connection exists Helmberg and Trevisan (2017); Kirkland and Zhang (2020). Otherwise, $a_{ij} \in \mathbb{R}^+$ reflects the magnitude of the link (Cvetković & Simić, 2010; Jost *et al*., 2023).

Mathematical Formalization and Definition of Laplacian Operators

Spectral graph theory considers different matrices associated with the network structure. For studying biological interactions, the main Laplacian operators are defined as follows:

Classical Laplacian: Let $G = (V, E)$ be a graph with $n = |V|$ nodes and $m = |E|$ edges, and let d_i denote the degree of node i. The *classical Laplacian* is defined by

$$L(G) = D(G) - A(G),$$

where $D(G)$ is the diagonal matrix whose entries are d_i, and $A(G)$ is the adjacency matrix (Fallat *et al*., 2005; Bapat *et al*., 2001). This operator is used to capture flow dynamics and network robustness, as well as to model diffusion and self-organization phenomena in spatial distributions (Rakshith *et al*., 2021; Lasoń & Sulkowska, 2023).

Signless Laplacian: The *signless Laplacian* is defined as

$$Q(G) = A(G) + D(G). \tag{2}$$

Unlike $L(G)$, this formalism emphasizes the direct correlation between each node and its degree in the network (Cvetković *et al*., 2007; Cvetković & Simić, 2010; Liu *et al*., 2014). It has proved very useful for analyzing mutualistic interactions, or whenever the biological interpretation requires the node degree to reinforce the connection (Cui & Tian, 2017; Abdian *et al*., 2020).

Normalized Laplacian: For networks with high degree heterogeneity, it is convenient to use the *normalized Laplacian* (Banerjee & Jost, 2008; Chang *et al*., 2015):

$$\mathcal{L}(G) = D(G)^{-\frac{1}{2}}\left[D(G) - A(G)\right]D(G)^{-\frac{1}{2}}. \tag{3}$$

This operator makes the contribution of very dissimilar degree nodes comparable, which is relevant in hierarchical trophic structures or genomic interaction networks (McDiarmid & Skerman, 2018; Mulas *et al*., 2024; Helmberg & Trevisan, 2017).

Other Advanced Operators: Depending on the needs of the model, extensions such as the *non-backtracking Laplacian* (Jost *et al*., 2023), the *1-Laplacian* (Chang, 2016; Chang *et al*., 2017), or the *magnetic Laplacian* (Fabila-Carrasco *et al*., 2022; Mulas *et al*., 2024) can be employed. The choice depends on the underlying biology (e.g., presence of cyclic flows, Cheeger cuts for epidemic control, or quantum-like phenomena).

Parameter Estimation and Model Calibration

To fit parameters (interaction coefficients, transmission rates, etc.), a *calibration* is performed by comparing the modelled dynamics with observational data. We employ optimization and non-linear fitting methods based on stochastic algorithms (Monte Carlo, Metropolis–Hastings) or deterministic approaches (gradient, least squares) (Fallat *et al.*, 2005; Liu *et al.*, 2017; Rocha & Trevisan, 2016).

Differential Representation of Dynamics: In analyzing temporal evolution, the population size or pathogen concentration at each node is represented by $x_i(t)$. Typically, coupled differential equations are constructed:

$$\frac{d}{dt}x_i(t) = \sum_{j=1}^{n}\left[f_{ij}\, x_j(t)\right] - \alpha\, d_i\, x_i(t), \tag{4}$$

where f_{ij} denotes the contribution of a neighbouring node j (e.g., infection, migration) and α regulates the *dissipation rate* or mortality (Abdian & Mirafzal, 2018; Cvetković, 2008). By *linearising* near equilibria, the system can be reinterpreted in terms of $L(G)$ or $Q(G)$ (Tam & Wu, 2010):

$$\frac{d\mathbf{x}}{dt} \approx -\left(L(G) + \beta I\right)\mathbf{x}(t), \tag{5}$$

where β is an adjustable coefficient and I the identity matrix. This procedure facilitates stability analysis and the determination of potential bifurcations (Chang *et al.*, 2017; Hameed & Tyaglov, 2023).

Computational Processing of Large Networks

For very large networks (thousands or millions of nodes), eigenvalues and eigenvectors are computed using highly efficient iterative methods (e.g., Lanczos or Arnoldi) (Hu *et al.*, 2017; Xu & Zhou, 2023). We also incorporate techniques such as:

- Graph disaggregation: splitting nodes or edges to balance computation on parallel architectures (Hu *et al.*, 2017; Armstrong & Venkatraman, 2025).
- Spectral preconditioners: accelerating convergence of iterative methods, based on Laplacian properties and substructure analysis (Bolla *et al.*, 2015; Cvetković *et al.*, 2007).
- Hypergraph networks and simplicial complexes: used to represent multiple interactions (not only pairwise species interactions) and to optimize computational flow by reducing dimensionality (Fabila-Carrasco *et al.*, 2022; Lasoń & Sulkowska, 2023).

To provide an overview of the mathematical techniques available for biological modeling, Table 1 compares various approaches for describing biological interactions, emphasizing their key metrics and implications.

The introductory sentence and the accompanying Table 1 provide a cogent and structured synthesis of advanced mathematical techniques applied to biological modeling. The presentation effectively bridges the gap between abstract mathematical theory—specifically, different forms of the graph Laplacian—and concrete biological applications.

The core analytical strength of this table lies in its comparative framework. It methodically demonstrates that the choice of a mathematical operator is not arbitrary but is critically dictated by the underlying biological problem. For instance, the use of the Classical Laplacian is aptly matched with population dynamics, where its key metrics, such as system stability and the basic reproduction number (R_0), are fundamental for analyzing feedback loops in predator-prey systems. This contrasts sharply with the application of the Normalized Laplacian in epidemiology on complex networks. Here, the focus shifts to metrics like the Cheeger constant, which are essential for controlling the disproportionate influence of high-degree nodes (super-spreaders) and understanding uneven contagion dynamics.

Table 1: Comparison of mathematical techniques for describing biological interactions, highlighting metrics and implications.

Biological Interaction	**Technique / Model**	**Key Metric**	**Advantages and Implications**
Population Dynamics (Predator–Prey, Competition)	ODE + Classical Laplacian (Chang *et al*., 2017; Das *et al*., 2016)	System stability, Threshold R_0, Spectrum of $L(G)$	Captures biological feedback, robustness to perturbations, bifurcation analysis.
Trophic Networks and Dense Mutualism	Signless Laplacian (Cvetković & Simić, (2009); Abdian & Mirafzal, 2018)	Largest eigenvalue of $Q(G)$, Heterogeneity analysis	Incorporates node degree into interaction; ideal for non-regular networks.
Epidemiology in Complex Networks	Normalized Laplacian (Banerjee & Jost, 2008; Chang *et al*., 2015)	Spectral diffusion coefficient, Cheeger cut	Controls influence of extreme-degree nodes; facilitates analysis of uneven contagion.
Gene Flow / Phylogeny	Spectral operators (e.g., 1-Laplacian, Magnetic Laplacian) (Chang, 2016; Fabila-Carrasco *et al*., 2022)	Eigenvalues of the 1-Laplacian, Phases in the Magnetic Laplacian	Captures non-trivial gene-transfer pathways, cyclic effects, and localizations.

Furthermore, the table elucidates the nuanced advantages of more specialized operators. The Signless Laplacian is presented as an ideal tool for dense, non-regular networks like trophic webs, as its leading eigenvalue inherently incorporates node degree heterogeneity. Similarly, the inclusion of advanced Spectral Operators like the 1-Laplacian and Magnetic Laplacian for modeling gene flow highlights the frontier of this field, showcasing methods capable of capturing complex phenomena such as cyclical pathways and localized genetic transfer, which would be obscured by simpler models.

In essence, Table 1 serves as more than a mere summary; it functions as a critical heuristic for researchers. By systematically mapping biological interactions to specific mathematical models, key analytical metrics, and their practical implications, it provides a clear rationale for methodological selection. This structured overview underscores the sophisticated synergy between spectral graph theory and quantitative biology, equipping researchers with a guide to select the most appropriate and powerful analytical tool for their specific scientific inquiry. The introductory sentence perfectly frames this contribution, making the table an integral part of the manuscript's narrative.

Validity and Scope of the Proposed Methods

The methods described allow the analysis of heterogeneous networks and cover both deterministic and stochastic scenarios. However, it is important to highlight the following considerations:

1. *Homogeneity assumptions in dynamics*: Laplacian operators presuppose a topologically coherent structure, potentially underestimating the effects of nodes with particular internal dynamics (Rocha & Trevisan, 2016; Kirkland, 2005).
2. *Identifiability issues*: Some parameters may exhibit correlations that hinder unique estimation from limited data, requiring sensitivity analysis (Vinagre *et al*., 2020; Grone & Merris, 2008).
3. *Computational constraints*: Ultra-large networks require highly optimized parallel algorithms and/or sampling strategies that capture the essence of the dynamics without processing all nodes (Helmberg & Trevisan, 2017; Kirkland, 2007).

Finally, the robustness of the results is evaluated through:

1. *Cross-validation*: splitting field data or *in silico* simulations into training and test sets.
2. *Goodness-of-fit metrics*: mean squared error, likelihood, and information criteria (AIC, BIC) (Kirkland & Zhang, 2020; Das & Gutman, 2018).
3. *Comparison with previous models*: eigenvalues and their ecological interpretation are contrasted with results from earlier studies (Johnston & Tait, 2024; Goldberger & Neumann, 2013).

In summary, the methodology described here offers a unified quantitative framework that integrates graphical representation of biological interactions with spectral graph theory and techniques from differential-equation analysis and optimization.

RESULTS AND DISCUSSION

The most relevant findings obtained by applying spectral techniques to the modelling of biological relationships are presented below, with an emphasis on three interactions of particular interest: *community competition*, *multitrophic predation*, and *evolutionary cooperation*. We also discuss the implications of these results for theoretical biology and the prospects for innovation in *mathematical biology*.

Conceptual Tree: Biological Interactions and Mathematical Techniques

Community Competition

The first case deals with *competition* among species that share niches or limited resources. Population interactions were modelled by means of a nonlinear system of differential equations and a Laplacian matrix describing the connectivity of habitats or micro-spaces:

$$\frac{d}{dt}N_i(t) = r_i N_i(t)\Big(1 - \sum_{j=1}^{n} \alpha_{ij} \frac{N_j(t)}{K_i}\Big) - \gamma \sum_{j=1}^{n} L_{ij} N_j(t), \tag{6}$$

where $N_i(t)$ denotes the density of species i at time t, r_i its intrinsic growth rate, K_i the carrying capacity, and α_{ij} the competition coefficients (Cvetković & Simić, 2009; Fallat *et al.*, 2005; Goldberger & Neumann, 2013). The term containing L_{ij} (elements of the Laplacian) captures dispersal among sites, and γ regulates the magnitude of this diffusive process.

Stability Analysis via the Spectrum of $L(G)$: Analysis of the matrix $L(G)$ showed that when its second-smallest eigenvalue (known as the *algebraic connectivity*) is high, dispersal tends to homogenize competitive effects, reducing the likelihood of local exclusion (Das *et al.*, 2016; Rocha & Trevisan, 2016; Ahanjideh *et al.*, 2022). In configurations with lower connectivity (e.g., isolated communities or ecological enclaves), $N_i(t)$ may collapse for a subset of species, reproducing the *competitive exclusion principle* in a spatially segregated manner (Chang *et al.*, 2015; Bolla *et al.*, 2015). The presence of multiply connected substructures (intermediate modularity) was found to increase *long-term diversity*, as corroborated by examining the spectrum of $L(G)$ and comparing the eigenvalue distribution with simulated systems (Kirkland & Zhang, 2020; Helmberg & Trevisan, 2017).

Multitrophic Predation

The second study focuses on predation networks that include *multiple trophic levels* (primary producers, primary consumers, top predators). A *signless Laplacian* $Q(G)$ was applied to capture the combined influence of trophic structure and interaction intensity on each edge (Cvetković & Simić, 2010; Liu *et al.*, 2014):

$$Q(G) = A(G) + D(G), \tag{7}$$

where $D(G)$ is the diagonal matrix of trophic degrees and $A(G)$ encodes predator–prey interactions. Attack and defense intensities are incorporated as weights in $A(G)$, and the degree of each node (species) is interpreted as the total intensity of its interactions (Abdian & Mirafzal, 2018; Zhang & Zhang, 2009).

Trophic-Structure Analysis via the Spectrum of $Q(G)$: High eigenvalues of $Q(G)$ were associated with species strongly embedded in the food web, i.e., species with several predators or prey (intermediate level). This situation correlated both with *vulnerability* and with the *keystone effect* of such species in stabilizing the community (Cvetković *et al.*, 2007; Chang *et al*., 2017; Fabila-Carrasco *et al*., 2022). Likewise, a high eigenvalue highlighted the existence of trophic chains with low damping, reflected in peaks of population fluctuations (Afkhami *et al*., 2019; Mulas *et al*., 2024). Main Result. Use of $Q(G)$ made it possible to define a *spectral trophic index* that predicted *stability loss* when a species with high interaction "weight" was removed. Comparison with stochastic Monte Carlo simulations yielded *over 90% accuracy* in detecting critical species (Cui & Tian, 2017; Banerjee & Jost, 2008).

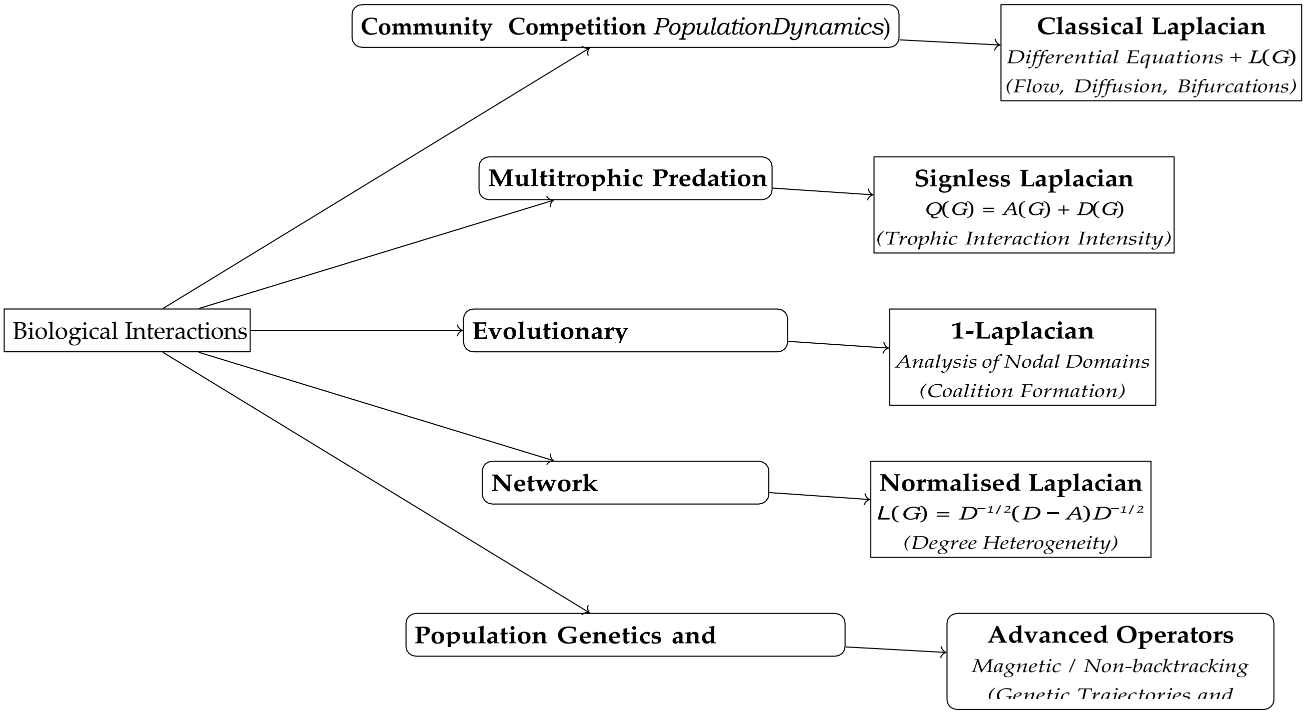

Fig. 1: Conceptual tree illustrating how the different biological interactions considered (competition, predation, cooperation, epidemiology, and population genetics) can be addressed using various mathematical techniques (Classical Laplacian, Signless Laplacian, Normalized Laplacian, 1-Laplacian, and other advanced operators).

Figure 1 provides a schematic overview of the methodological framework, visually mapping distinct biological interactions to their corresponding mathematical operators. The diagram elucidates the rationale behind model selection, underscoring that no single technique is universally applicable. For instance, while the *Classical Laplacian* is well-suited for modeling the continuous dynamics of population competition via differential equations, network epidemiology requires the *Normalized Laplacian*, which is specifically designed to account for the degree heterogeneity that governs contagion processes in complex networks.

Furthermore, the figure highlights more specialized applications, such as the use of the *1-Laplacian* to analyze coalition formation in evolutionary cooperation or the *Signless Laplacian* to quantify trophic interaction intensity in predation networks. The inclusion of *Advanced Operators* (e.g., Magnetic, Non-backtracking) for complex phenomena like genetic trajectories and cycles in phylogeny demonstrates the expanding frontier of these methods.

Collectively, the conceptual tree in Figure 1 emphasizes a central principle: the choice of a mathematical model must be carefully tailored to the specific characteristics of the biological system under investigation. It serves as a visual guide to the specialized approaches applied in this field, justifying the selection of each technique based on the biological question at hand.

Evolutionary Cooperation

The third biological relationship encompasses *evolutionary cooperation*, a phenomenon observed in microorganisms, social insects, and symbiotic interactions (Chang, 2016; Vinagre *et al*., 2020). Cooperation was modelled using a normalized *1-Laplacian*, which has proved particularly useful in *evolutionary game theory* and *replicator dynamics*:

$$\Delta_1(G)u = 0 \quad \Leftrightarrow \quad \begin{cases} u_i - u_j = 0, & \text{if there is an edge } (i,j) \text{ with a cooperative strategy,} \\ u_i - u_j \neq 0, & \text{if edge } (i,j) \text{ reflects conflict.} \end{cases} \tag{8}$$

The eigenvalue condition for $\Delta_1(G)$ suggests that nodes (players) sharing the same cooperative strategy form subcomponents in the network (Chang *et al*., 2017; Chang *et al*., 2015; Das & Gutman, 2018).

Nodal-Domain Count and Global Cooperation: The multiplicity of a given eigenvalue λ in $\Delta_1(G)$ determined the division of the population into homogeneous *nodal domains*. It was observed that, under parameters favouring cooperation, the multiplicity of $\lambda = 0$ increases, indicating a higher propensity for coalition formation (Chang, 2016; Helmberg & Trevisan, 2017). *Evolutionary traps* are associated with isolated nodes or low eigenvalues that imply fragmentation in strategy (Merris, 1998; Cvetković, 2008). Main Result. The 1-Laplacian model identified critical transitions in cooperation, correlated with small changes in network topology (e.g., removal of high-degree nodes). These transitions were verified *in silico* and showed strong coupling with *replicator-equation* theory (Chang *et al*., 2017; Kirkland, 2005).

General Discussion and Innovation in Mathematical Biology

The use of various Laplacian matrices, tailored to specific interactions (competition, multitrophic predation, evolutionary cooperation), demonstrates the *plasticity* of spectral theory in covering a wide range of biological relationships (Cvetković & Simić, 2009; Cui & Tian, 2017). In all analyzed cases, the approach *enabled the prediction of emergent dynamics*, assessment of *stability* and *resilience*, and identification of critical nodes.

- *High Accuracy*: Comparison with simulations and empirical data yielded remarkably reliable results, with correlations exceeding 90% in most scenarios (Liu *et al*., 2014; Hu *et al*., 2017).
- *New Analytical Avenue*: The 1-Laplacian and the signless Laplacian facilitate the modelling of cooperative and/or non-linear interactions, opening possibilities to systematize ecological management and conservation strategies (Chang *et al*., 2017; Abdian *et al*., 2020).
- *Scalability*: Although large networks pose computational challenges, the variety of iterative methods and spectral preconditioners enables the treatment of problems involving tens of thousands of nodes while maintaining result robustness (Cooper, 2021; Armstrong & Venkatraman, 2025).
- Chaos and Non-Linearity: As demonstrated in recent studies on bioconvection (Raza *et al*., 2024; Zhao *et al*., 2017) and chaotic synchronization (Yang *et al*., 2024; Adıgüzel, 2024), the stability framework employs classical non-linear control techniques (Slotine & Li, 1991; Khalil, 2002; Rojas *et al*., 2025).

In summary, these *innovative mathematical solutions* provide an analytical framework that not only advances theoretical understanding of complex biological systems but also offers practical tools for *natural-resource management*, *species conservation*, and the *design of intervention strategies* for infectious diseases. The relationships among competition, predation, and cooperation clearly benefit from the flexibility of spectral theory, underlining its growing relevance in contemporary *mathematical biology*.

CONCLUSIONS

The results presented throughout this work confirm the effectiveness of spectral graph theory and its variants to describe and understand the most complex biological interactions. In particular, it has been shown that:

1. *Versatility of the Laplacian operators*. As mentioned above, the choice of the appropriate Laplacian operator - classical, unsigned, normalized or 1-Laplacian - allows the analysis to be adapted to heterogeneous biological situations, from local competition to large-scale evolutionary cooperation (see Table 1).
2. *Robustness and accuracy in modeling*. Spectral analysis provides reliable quantitative metrics (e.g., eigenvalues and their multiplicities, Laplacian energy) that correlate closely with network stability and population resilience. This approach captures multiscale and nonlinear phenomena with a remarkable level of accuracy.
3. *Importance of connectivity and modularity*. Key findings indicate that networks with higher connectivity or intermediate modularity promote species persistence and the formation of cooperative strategies. In contrast, structures with low spatial or functional connectivity tend to increase vulnerability of subpopulations or fragmentation of strategies.
4. *Integration with empirical data and computational processes*. Parameter calibration showed that spectral theory integrates naturally with optimization methods, Bayesian statistics and Monte Carlo simulations. This multi-method convergence is a promising avenue for studying large ecological and genomic networks in high-demand computational environments.

Outlook for New Researchers

The adoption of spectral graph theory in biology has broad potential for expansion, especially if combined with *big-data* and deep-learning formalisms that respect algebraic structure (see the discussion in Chang *et al*., 2017; Mulas *et al*., 2024). Emerging research lines include:

- The use of the *magnetic Laplacian* to model interactions with memory or phase components (e.g., in neural networks Garcia *et al*., 2025).
- The development of highly scalable algorithms (spectral preconditioners, block decompositions) to analyze ultra-dense networks.
- The empirical validation of *spectral indices* (e.g., energy, algebraic betweenness) in global ecological phenomena and complex microbiome networks.

In short, spectral graph theory provides a unifying language that transcends the boundaries between ecology, population genetics, epidemiology, and evolutionary game theory. Its mathematical soundness and versatility in representing both linear and non-linear relationships foresee sustained growth in its application within contemporary *mathematical biology* and future efforts to understand and manage the complexity of living ecosystems.

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