

# Multi-scale modularity in self-organized biological and artificial systems

## 1. Introduction

A common feature of many complex systems is that they are organized as a hierarchy of modules that structures their interactions and processes. Basic building blocks combine into more complex structures, which serve as modules that can in turn organize into structures at the next level (see Figure 1), a process that can repeat multiple times and span many spatiotemporal scales. Such multi-scale modular and hierarchical (MSMH) organization is particularly ubiquitous in living systems, where it is often observed in biological interaction networks such as genetic networks, metabolic networks, neural networks, or ecological networks. As technological systems become increasingly complex, decentralized, and interconnected; their organization into MSMH structures is also becoming more common, resulting from modular design principles, bio-inspired solutions, or self-organization. The networks underlying complex machines, distributed computations, or even manufacturing processes seem to favor such structures to be manageable and effective.

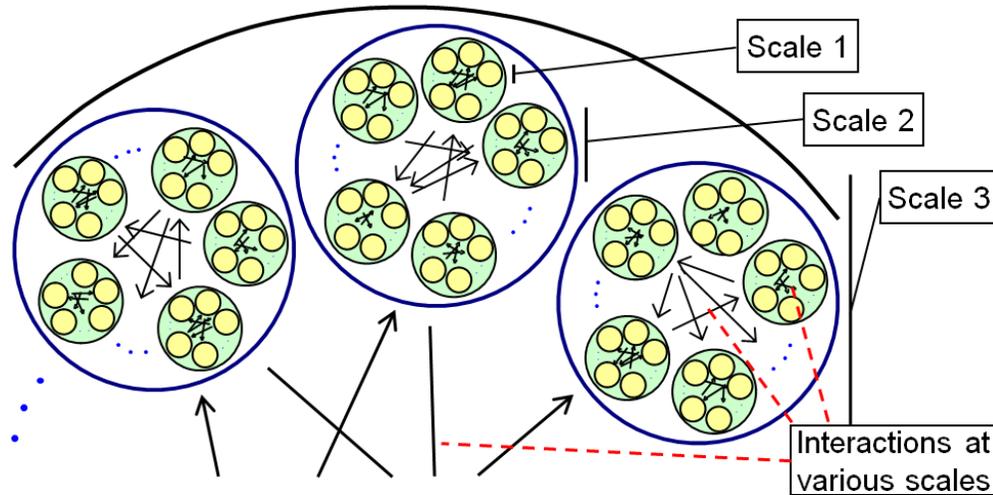
Despite the ubiquity of MSMH structures in biological and artificial systems, we still have only a few formal tools to characterize them and a limited understanding of their dynamics and emergence. They have received little attention from the perspective of Physics, where self-similarity and scaling arguments are common but traditional systems do not exhibit the level of emergent organization required to develop complex MSMH features. This opens the tantalizing opportunity of exploring the properties of MSMH systems with the type of minimal, general, and hopefully universal descriptions often used in Physics.

In statistical physics, the analysis of idealized approaches such as the Ising model and kinetic theory has been essential for understanding the properties of a number of systems, which extend far beyond the ferromagnetic materials and ideal gases for which they were originally designed. As more and more information on MSMH systems is gathered, a similar approach (albeit using new models and techniques) appears timely and necessary to understand more deeply the origins and dynamics of these structures.

## 2. Fundamental Questions

The proposed research program aims to understand MSMH systems from a fundamental theoretical viewpoint by combining approaches from complex networks, non-equilibrium dynamics, and statistical physics with insights from biology and robotics. We will be guided by the following central, overarching, and open questions:

- What types of dynamics are supported by MSMH structures?
- What conditions are required for MSMH structures emerge and evolve?



**Figure 1:** Schematic representation of a multi-scale modular hierarchical structure (displaying here three scales). Interacting modules organize in a hierarchy of levels or scales. Small yellow discs are modules that interact (through the smallest arrows) to produce the dynamics of the embedding green discs (modules at the next scale). These interact in turn within the embedding blue modules to produce dynamics at the next scale.

We will directly address the fundamental properties that can lead to, and result from, MSMH structures. This ambitious, novel and distinct research program will be informed by other investigations that we are concurrently performing in collaboration with diverse theoretical and experimental groups, whose range of expertise span synthetic biology, collective behavior, evolutionary dynamics, network theory, active matter, and swarm robotics.

By implementing and analyzing simple and generic network-based and agent-based computer models specifically designed to study MSMH systems and by developing analytical descriptions when possible, we hope to carry out foundational work that will help us understand the self-organization, performance, and evolution of this broad class of complex systems.

### 3. Current Knowledge on MSMH Structures

We will describe here some of the elements of current knowledge, coming from different fields, that will serve as starting point for our research program. To date, much of the work involving MSMH systems has focused on: (i) developing network analysis tools to study the degree of hierarchy and modularity in real networks, (ii) implementing network growth models that produce MSMH topologies, and (iii) investigating examples of the dynamics supported by them.

MSMH structures are believed to be an essential part of biological organization, related to the many levels and types of functional and structural heterogeneity in living systems<sup>[1-3]</sup>. At least three MSMH features have been found experimentally in biological networks: motifs, modules, and hierarchical

organization. For example, genetic regulatory networks contain a small set of recurring patterns (motifs) with similar regulation functions<sup>[4]</sup>, which can be viewed as low-level modules. Specific definitions of modules and hierarchies, together with ways to quantify their presence in networks, are still being developed. A module can be defined as a part of a system that integrates a set of processes and operates comparatively autonomously with respect to other modules<sup>[1,5]</sup>. While approaches for identifying multi-level hierarchies in network data are still being investigated<sup>[6-10]</sup>, these structures appear to be recurrent in biological networks<sup>[11-14]</sup>. We will build on this knowledge involving real MSMH structures to mimic and quantify them in our models.

Theoretical studies have considered the question of how to generate network architectures that are consistent with the MSMH organization observed in nature. The properties of the metabolic networks of 43 distinct organisms were shown to be compatible with a hierarchy of highly connected modules, combined into successively larger and less connected structures<sup>[15,16]</sup>. Networks with such architecture are called hierarchical networks and are organized as MSMH systems. Various deterministic algorithms for constructing these networks have been introduced<sup>[15,17-19]</sup>, which we will use to build MSMH structures for our research.

A cornerstone of our research program is to study the evolution of idealized MSMH systems. Evolution is a strong unifying principle in biology and an essential component for the development of living systems at all scales, from basic genetic processes to complex interactions between species. Despite its apparent universality and simple conceptual basis, the role and mechanisms of natural selection at different levels of MSMH structures is still the subject of intense debate<sup>[20,21]</sup>. Various models have been developed to try to reproduce the essential properties of evolving systems, including: minimal models based on cellular automata<sup>[22]</sup> and Boolean networks<sup>[23]</sup>, models based on game theory<sup>[24]</sup> and graph theory<sup>[25]</sup>, and sophisticated genetic algorithms<sup>[26]</sup> and artificial life programs<sup>[27]</sup>. However, none of these were designed to explore evolution at multiple scales and seem to lack the necessary degrees of freedom or selective pressures to sustain MSMH structures. We plan to combine algorithms that generate MSMH structures with evolutionary dynamics simulations to study their emergence and stability. Our initial steps will be guided by recent work suggesting that modular structures naturally emerge in systems that evolve under alternating fitness criteria<sup>[28-30]</sup>. This allows them to rapidly access different functions by activating different modules when selection pressures change.

## **4. Research Program**

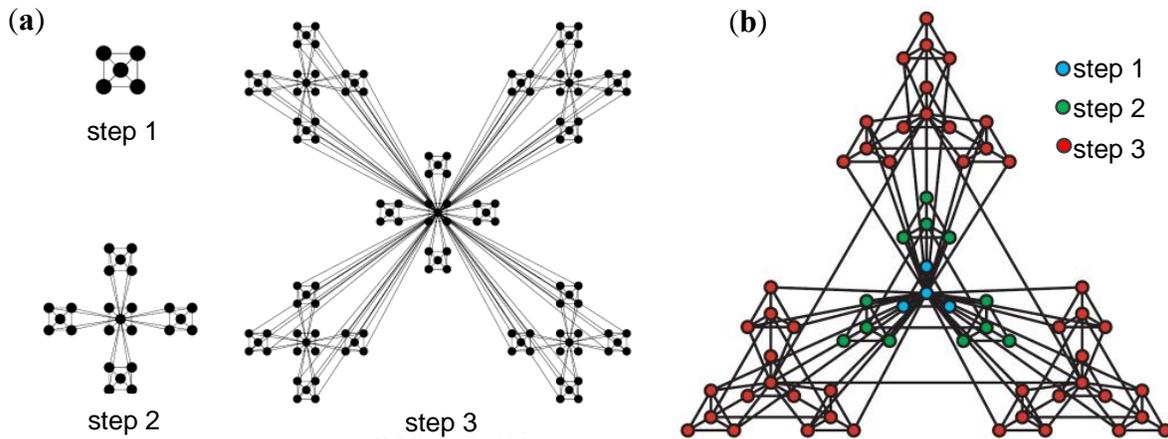
### **4.1 Overview**

The proposed research program aims to advance our understanding of MSMH systems by investigating their dynamical consequences and evolutionary origins. More specifically, we will use simple, generic models to study: (i) the relationship between different MSMH interaction structures and the dynamics that they can support; (ii) growth and evolutionary algorithms that produce MSMH structures, including artificial life simulations; and (iii) the robustness and evolvability of MSMH systems.

We aim to establish and analyze archetypical minimal models that capture the conceptual origin and possible behaviors of the MSMH organization observed in a diversity of complex systems, testing their universality in our work. This goal is similar to the development of the aforementioned Ising or kinetic theory approaches, which have led to numerous conceptual advances, simulations, analytical developments, and extensions to other fields. Our models will specifically focus on capturing nonequilibrium emerging features that are evolutionary-based and fundamentally multi-scale.

Our current research places us in a unique position to pursue this ambitious and innovative research program. Indeed, such an abstract approach could easily lose focus or relevance if it was not strongly motivated by experiments and applications. We have established a network of fruitful collaborations with experimental, applied, and theoretical groups that led us to develop this program, and will continue to inform it. In a different collaborative project with Prof. Joshua Leonard (Northwestern University), we plan to study the dynamics, evolvability, and adaptability of modular hierarchical bacterial toxin-antitoxin networks created in synthetic biology experiments his lab. In collaboration with Prof. Ali-Emre Turgut and Dr. Eliseo Ferrante (KU-Leuven), we developed the AEM model described below based on a decentralized control algorithm that they implemented on swarming autonomous robots, which we continue to study in the context of active matter. In a recent project with Prof. Iain Couzin (Princeton University), we studied how individual interactions produce emerging collective structures in fully controlled fish schooling experiments performed in his lab. In collaboration with Prof. Dirk Brockmann (Humboldt University and Robert Koch Institute, Berlin), we are combining the analysis of diffusive processes and modular structures. In continuing efforts with Prof. Thilo Gross (University of Bristol), we have developed approaches to model collective motion in space using non-spatial adaptive networks. Through our participation in these parallel investigations, we have direct access to complementary models and analysis techniques, and to concrete systems that should be captured by our general approach.

We describe below the two modeling frameworks that will be used in our research program. The first one considers non-spatial network-based interactions, and can describe a broad range of complex interacting systems. It will allow us to establish parallels with the diverse and rapidly growing datasets on the interactions and dynamics of real MSMH networks (biological, social, technological), and to apply the current knowledge on MSMH topologies described in Section 3. The second framework considers simple spatial interactions that have been shown to be generic in active, self-propelled systems and to generate collective dynamics. It is not restricted to physical space, and could also describe dynamics in abstract spaces such as fitness landscapes, which greatly expands its applicability. It will allow us to relate, within a concrete and intuitive mechanical representation, the connectivity, dynamics, and evolution of MSMH systems. It also relates our work to spatially-based MSMH processes (e.g. morphogenesis) and has technological applications<sup>[31,32]</sup> (e.g. the deployment of robot swarms). These two modeling frameworks will be developed in parallel, addressing the types of questions listed in Section 5.



**Figure 2:** Examples of published duplication-based algorithms that generate hierarchical networks<sup>[15,18]</sup>. The generating steps are displayed separately (a) or labeled by color (b). At each step the current structure is duplicated (here 4 or 3 times, respectively) and linked in specific ways to produce MSMH topologies.

## 4.2 The Complex Network Approach

This approach is based on a family of network models that implement MSMH systems by growing or evolving specific interaction topologies and by stipulating dynamical rules for the node states. These structures will also serve as the basis for simple artificial-life simulations where the evolving topology is recoupled to its supported dynamics.

MSMH network topologies can be generated using various recently proposed algorithms. These can be categorized into: duplication based, subdivision based, and adaptive-network based. Duplication based algorithms grow the network by making copies of the current network and wiring these to produce a larger network<sup>[15,17-19,33]</sup>. Subdivision based algorithms, instead, repeatedly replace individual nodes of the current network by sub-networks, following a given protocol<sup>[34-36]</sup>. Adaptive-network based algorithms evolve the connectivity according to the node state dynamics supported by the network or to emergent properties of its topology<sup>[28-30, 37-42]</sup>.

MSMH dynamics will be studied by implementing Boolean-based or ODE-based dynamics on the generated networks. In both cases, the state of each node state is updated as a function of the states of the nodes linked to it. Boolean-based dynamics assign a True or False state to each node and are determined by truth tables. They allow the systematic analysis of all possible dynamics supported by a given topology, an approach first developed in the context of genetic networks<sup>[43-45]</sup>. ODE-based dynamics assign a continuous variable to each node and are determined by ordinary differential equations. They provide a closer match to real systems.

The family of models considered will be based on a generalized algorithm that provides a common framework and will allow the use of a single computer code (with modular subroutines) in our studies. It iterates all or some of the following steps: (i) A seeding or initialization step where simple network

structures are defined as initial condition; (ii) a multiplication step where modules are duplicated; (iii) a linking or unlinking step that connects or disconnects modules; and (iv) a selection step where nodes, links, or structures are selected based on their emerging dynamical or topological properties.

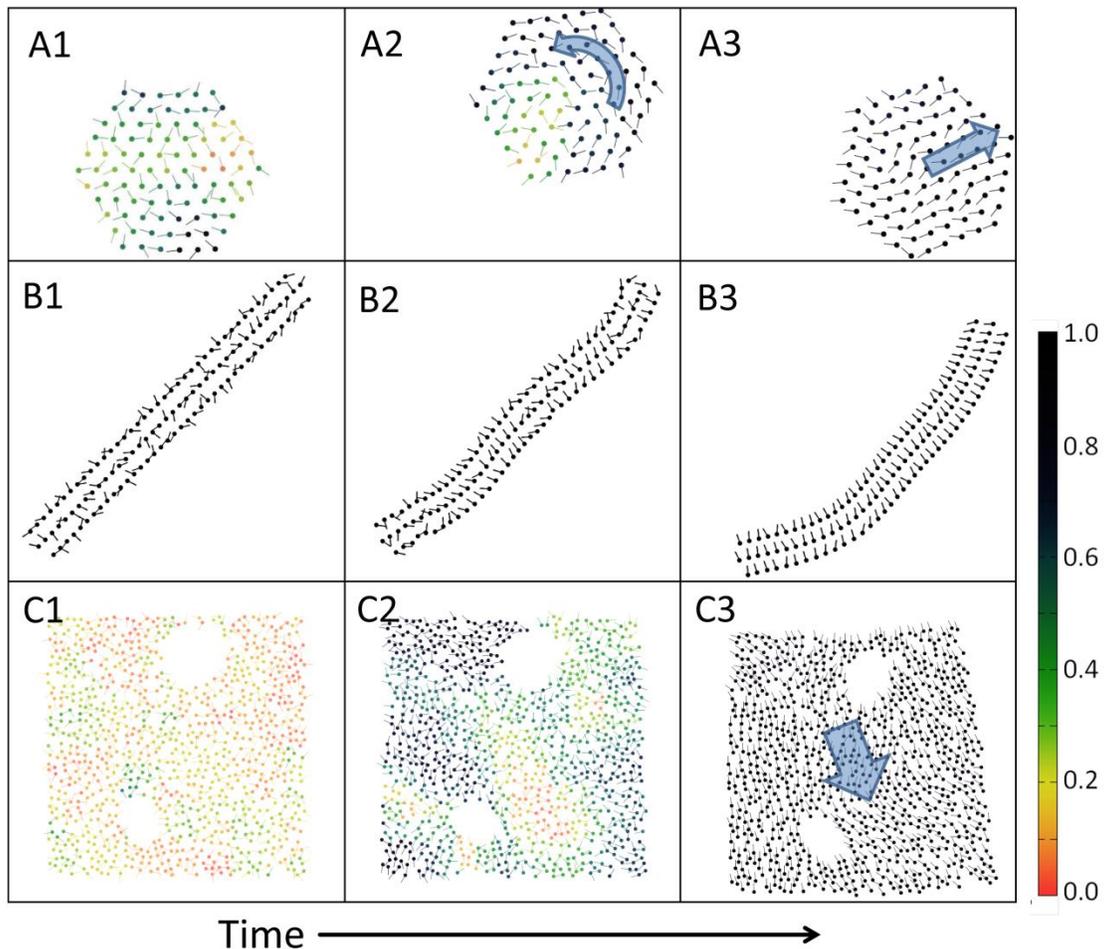
Figure 2 displays a simple network growth algorithm that results from implementing steps (i)-(iii) with rules that generate MSMH topologies that have properties found in biological networks<sup>[15,18]</sup>. By adding mutations to step (ii) and including step (iv), the algorithm becomes an idealized developmental or evolutionary dynamics. To complete the analogy, selective pressures can be imposed on the fitness of the resulting structures, defined through the properties of the corresponding Boolean- or ODE-based dynamics of network states, which serve here as a proxy for the system's function.

### **4.3 The Active Matter Approach**

The Active Matter Approach will be based on a family of models of self-propelled agents or other active agents connected through spring-like interactions. Mechanical analogies have a long tradition in physics as prototypical systems that are reasonably simple, have practical realizations, and help build intuition and explore classes of solutions. A relatively recent example is the double-pendulum system in the study of chaotic dynamics. We will focus below on a specific type of active matter model, but envision also implementing other variations.

The Active Elastic Membrane (AEM) model was recently introduced to describe groups of self-propelled agents permanently connected by virtual springs<sup>[46,47]</sup>. Under certain conditions, individual velocities self-organize into growing regions of coherent motion through a mechanism based on standard elasticity, eventually reaching collective rotation or translation (Fig. 3). This decentralized motion coordination is achieved without agents exchanging information on their velocities (which correspond here to their states). Instead, interactions are based on positions (i.e. an integral of their states). Self-organization results from the cascading of energy to larger scales through the selection of collective elastic modes. The system thus naturally contains a physics-based self-organizing mechanism at the module level, which we will also compare to consensus achieved through the direct coupling of velocity states.

Agents can be linked into structures with any shape, activity, or mechanical properties. We will simulate physical representations of MSMH structures by replacing on the MSMH networks on Fig. 2, and others, nodes by self-propelled agents and links by springs. This will generate MSMH dynamics on a system whose only phenotypic trait is motion in physical space. Modules become internally self-organized and then interact with other modules to achieve coherent motion at the next hierarchical level. This captures an essential feature of biological systems: the need to self-organize the energy produced at the individual component level before it can effectively do work, and power the next hierarchical level. The MSMH-AEM model will thus allow us to study in a concrete nonequilibrium physical framework the self-organization and evolution of MSMH structures.



**Figure 3:** Simulations of three active elastic structures produced with the AEM model<sup>[46,47]</sup>. Nearby agents are linked by virtual springs. Collective motion and coherent deformation spontaneously emerges from initially randomly oriented self-propelled components. The color scale indicates degree of local alignment. Larger AEM systems, containing hierarchies of modular structures, will be used to study MSMH dynamics.

The dynamics of various MSMH-AEM systems composed of up to thousands of agents will be simulated. We will make them compete for resources on a virtual arena to implement simple artificial life systems. The design of these structures will determine their self-organized motion, which in turn conditions their ability to reach resources effectively. By introducing mutations and selective pressures, we can thus study the emergence and evolution of MSMH structures. We will develop a crowdsourcing experiment based on these ideas, implementing an online game on existing platforms (such as Amazon’s Mechanical Turk) where participants will be challenged to design AEM structures that compete with others (either user-designed or evolved) for resources. Given the complexity and diversity of AEM-based “machines” that can be engineered using thousands of springs and agents with different properties, modular design at different scales will be encouraged, thus leading to MSMH structures<sup>[48,49]</sup>. This unique game-based crowdsourcing experiment will allow a fascinating comparison between evolved and engineered solutions to the same problems. It will involve the public in our research and could generate widespread interest.

## 5. Specific Questions

The approaches described above will allow us to investigate in two simple and generic models specific questions such as those listed below.

We will develop a framework for generating and characterizing MSMH structures, and ask: Which algorithms produce MSMH systems similar to those in biological and engineered networks? How sensitive are different MSMH structures to perturbations of the interactions and rules?

We will investigate the relationship between MSMH structures and dynamics, asking: What characterizes MSMH dynamical processes and their response to external influences? Are the dynamics of the modules different at different hierarchical levels? Is there a time-scale separation that emerges directly from MSMH interaction topologies (as claimed in ref.<sup>[50]</sup>)? How do perturbations propagate between hierarchical levels? Does averaging within modules make MSMH dynamics more robust? Do we observe energy cascades like those in fluid turbulence<sup>[51,52]</sup>?

We will explore the evolvability and adaptability of MSMH structures, asking: What selection mechanisms enhance modularity? Is there a relationship between modularity and adaptability to changing conditions? How do selective pressures and mutations propagate between hierarchical levels? Can MSMH structures spontaneously evolve and are they stable? Do “symbiotic” or “collaborative” structures emerge as a higher hierarchy of modular organization?

## 6. Broader Impacts

The proposed research program could lead to breakthroughs in our knowledge and management of biological systems, our ability to engineer complexity, and our fundamental understanding of complex systems and self-organization.

This research could have a variety of possible impacts in biology, such as clarifying design constraints in synthetic biology approaches; helping identify critical structures in human or pathogen physiology to correct genetic, physiological or neurological disorders; and improving our ability to control ecological systems. Furthermore, understanding how evolution has shaped biological MSMH structures to achieve desirable properties could help design systems with similar features, including robotic, computational, and technological systems. Finally, the new approaches developed will extend the reach of nonlinear, statistical, and non-equilibrium physics further into the realm of complex systems.

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