

Nonlinear Patterns and Waves in Biological Systems Special Session A10

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As widely observed in different fields, self-organisation in several fields of applications often leads to the emergence of patterned and travelling wave solutions. A few examples include the formation of spots and travelling vegetation bands in water-limited regions, the firing patterns of neurons, and the emergence of inflammatory aggregates related to immune responses. These relevant phenomena are mostly modelled from the mathematical viewpoint via reaction/advection/cross-diffusion equations. As these models aim to incorporate relevant real-life features, such as complex spatial domains and space/time-dependent parameters, their complexity has steadily increased in the last few years. In turn, an increasing effort of the scientific community has been devoted to advancing the analytical and numerical tools to analyse the emerging solutions and predict their long-time evolution.

The aim of this Special Session is to provide an overview of some of the most recent developments in the investigation of patterned and travelling wave solutions arising in a wide variety of mathematical models. Bringing together experts from the US and the European communities will allow the interactions and the exchange between different techniques and foster new collaborations.

For more information visit <https://sites.google.com/view/ams-umi-special-session-a10/home>.

Schedule and Abstracts

July 23, 2024

11:00–11:40 Coherent structures in an IntraGuild predation reaction-diffusion model with anti-predator behavior

Maria Carmela Lombardo (University of Palermo, ITALY)

Abstract. This study introduces the following cross-diffusion model defined on the spatial domain $\Omega \subset \mathbb{R}$:

$$(1) \quad \begin{cases} \frac{\partial N_1}{\partial \tau} = D_1 \Delta N_1 + N_1 (B - a_{11} N_1 - a_{12} N_2 - a_{13} N_3), & \text{on } \mathbb{R}_+ \times \Omega, \\ \frac{\partial N_2}{\partial \tau} = D_2 \Delta N_2 + D \nabla \cdot (N_2 \nabla N_3) + N_2 (-M_2 + a_{21} N_1 - a_{23} N_3), & \text{on } \mathbb{R}_+ \times \Omega, \\ \frac{\partial N_3}{\partial \tau} = D_3 \Delta N_3 + N_3 (-M_3 + a_{31} N_1 + a_{32} N_2), & \text{on } \mathbb{R}_+ \times \Omega, \end{cases}$$

where $N_1(\tau, X)$, $N_2(\tau, X)$, $N_3(\tau, X)$, represent the densities of a basal resource, an intermediate consumer (the IGPrey) and an omnivorous predator (the IGPredator), respectively. The model describes the dynamics of intraguild predation communities, where predators and prey also compete for shared resources within an ecological guild. It incorporates IntraGuild Prey exhibiting anti-predator behavior, dispersing along local gradients in predator density, while local dynamics are described by the Lotka-Volterra functional form [1].

Beginning with an overview of existing results concerning the existence and stability of the steady state of homogeneous coexistence, we demonstrate that the local dynamics support the

bistability of the spatially homogeneous equilibrium with oscillations due to a subcritical Hopf bifurcation.

We prove that the predator avoidance strategy described by cross-diffusion is crucial for pattern formation in the reaction-diffusion system and characterize the cross-diffusion-driven Turing bifurcation. Using the formalism of amplitude equations, we derive the asymptotic profiles of the stationary solutions, revealing that anti-predator behavior can account for segregation patterns between IntraGuild Prey and IntraGuild Predator observed in field studies. Through a combination of analytical and numerical tools, we demonstrate that the predator avoidance strategy serves as a mechanism that stabilizes coexistence states in Intraguild Predation communities beyond the conditions imposed by the corresponding spatially homogeneous model.

We shall also prove that the system is able to reproduce spatially non-homogeneous periodic-in time species distribution, in the neighborhood of the codimension-2 Turing-Hopf bifurcation point, where the stationary and temporal instability coexist.

In the latter part of the presentation, we address the issue of localized pattern. We demonstrate the existence of stationary spikes, namely far-from-equilibrium highly localized patterns that are singularly perturbed solutions of the model system. Using asymptotic techniques, we shall derive explicit conditions for the existence of the spike patterns and construct their asymptotic profile.

Finally, we identify multiple bifurcating branches of localized states organized in a characteristic snakes-and-ladders structure, termed *homoclinic snaking*. Adopting the spatial dynamics description, we show that the origin of the spatially localized patterns is due to a reversible 1 : 1 resonance (Hamilton-Hopf bifurcation), whose normal form gives the explicit form of the small-amplitude branch of homoclinic solutions.

References

- [1] F. Farivar, G. Gambino, V. Giunta, M.C. Lombardo, M. Sammartino, *Intraguild predation communities with anti-predator behavior*, SIAM J.Appl.Dyn.Sys., (2024), *in press*.

11:50–12:30 Emergence of Vascular Networks

Pedro Aceves-Sanchez (University of Arizona, USA)

Abstract. The emergence of vascular networks is a long-standing problem which has been the subject of intense research in the past decades. One of the main reasons being the widespread applications that it has in tissue regeneration, wound healing, cancer treatment, etc. The mechanisms involved in the formation of vascular networks are complex and despite the vast amount of research devoted to it, there are still many mechanisms involved which are poorly understood. Our aim is to bring insight into the study of vascular networks by defining heuristic rules, as simple as possible, and to simulate them numerically to test their relevance in the vascularization process. We will present a hybrid agent-based/continuum model that couples blood flow, oxygen flow, capillary network dynamics, and tissue dynamics. And we will show simulations that demonstrate the ability of our model to capture the main features of vascular networks. This is joint work with P. Degond, B. Aymard, L. Castella, A. Lorisgnol, P. Kennel, F. Plouraboue, and D. Peurichard.

References

- [1] P. Aceves-Sanchez, B. Aymard, D. Peurichard, P. Kennel, A. Lorisgnol, F. Plouraboue, L. Casteilla & P. Degond, *A new model for the emergence of blood capillary networks*, Networks and Heterogeneous Media 16(1), (2021).

14:30–15:10 Competing effects in fourth-order aggregation-diffusion PDEs: a variational approach

Antonio Esposito (University of Oxford, UK)

Abstract. The talk concerns the analysis of fourth-order aggregation-diffusion equations using an optimal transport approach. These models have been recently obtained as approximation of nonlocal systems of PDEs describing cell-cell adhesion. This is a crucial mechanisms regulating collective cell migration during tissue development, homeostasis and repair, allowing cell populations to self-organise and form and maintain complex tissue shapes. In a recent work, we use

the 2-Wasserstein gradient flow structure of such equations to give sharp conditions for global in time existence of weak solutions, in any dimension and for general initial data. The energy involved presents two competing effects: the Dirichlet energy and the power-law internal energy. Homogeneity of the functionals reveals critical regimes that we analyse. In addition, we study a system of two Cahn-Hilliard-type equations exhibiting an analogous gradient flow structure. This is based on a joint work with J. A. Carrillo, C. Falcó, and A. Fernández-Jiménez in Oxford.

References

- [1] J. A. Carrillo, A. Esposito, C. Falcó, A. Fernández-Jiménez, *Competing effects in fourth-order aggregation-diffusion equations*, preprint arXiv:2307.14706 (2023).

15:20–16:00 The role of boundary constraints in simulating biological systems with nonlocal dispersal

Gabriela Jaramillo (University of Houston, USA)

Abstract. Population and vegetation models often use nonlocal forms of dispersal to describe the spread of individuals and plants. When these long-range effects are modeled by spatially extended convolution kernels, the mathematical analysis of solutions can be simplified by posing the relevant equations on unbounded domains. However, in order to numerically validate these results, these same equations then need to be restricted to bounded sets. Thus, it becomes important to understand what effects, if any, do the different boundary constraints have on the solution. To address this question we present a quadrature method valid for convolution kernels with finite second moments. This scheme is designed to approximate at the same time the convolution operator together with the prescribed nonlocal boundary constraints, which can be Dirichlet, Neumann, or what we refer to as free boundary constraints. We then apply this scheme to study pulse solutions of an abstract 1-d nonlocal Gray-Scott model as a case study. We consider convolution kernels with exponential and with algebraic decay.

References

- [1] Jaramillo, Gabriela, Loic Cappanera, and Cory Ward. "Numerical methods for a diffusive class of nonlocal operators." *Journal of Scientific Computing* 88.1 (2021): 30.

17:00–17:40 A nodal ghost method based on variational formulation and regular square grid for elliptic problems on arbitrary domains and applications to biological network formation

Clarissa Astuto (University of Catania, ITALY)

Abstract. This talk focuses on the numerical solution of elliptic partial differential equations (PDEs), specifically addressing the challenges arising from irregular domains. Both finite element method (FEM) and finite difference method (FDM) face difficulties in dealing with arbitrary domains. We introduce a novel nodal symmetric ghost method based on a variational formulation approach, which combines the advantages of FEM and FDM. The method employs bilinear finite elements on a structured mesh and provides a detailed implementation description. The convergence rates are validated with many numerical experiments, in both one and two space dimensions. At the end, we show an application to biological network formation in a leaf-shaped domain, computing the solution of a reaction-diffusion equation for the conductivity tensor, coupled with a Poisson equation for the pressure of the fluid.

References

- [1] C. Astuto, D. Boffi, G. Russo and U. Zerbinati, *A nodal ghost method based on variational formulation and regular square grid for elliptic problems on arbitrary domains in two space dimensions* arXiv 2402.04048, 2024
- [2] C. Astuto, J. Haskovec, P. Markowich and S. Portaro, *Self-regulated biological transportation structures with general entropy dissipations, part I: The 1D case*, *Journal of Dynamics and Games*, 2023

- [3] C. Astuto, P. Markowich, S. Portaro and G. Russo *Self-regulated biological transportation structures with general entropy dissipation, part 2: The 2D case and leaf-shaped domain*, in preparation

July 24, 2024

11:30–12:10 Stopping waves: Geometric analysis of coupled bursters

Iulia Martina Bulai (University of Sassari, ITALY)

Abstract. Bursting is a type of electrical activity seen in many neurons and endocrine cells where episodes of action potential firing are interspersed by silent phases. In [1] we investigate partial synchrony and wave propagation in a population of square-wave bursters. In particular, by using a prototypical polynomial bursting model and slow/fast bifurcation analysis, we study why electrically coupled model bursters typically synchronize very easily, as reflected in the tendency for simulated excitation waves to propagate far into the region of silent cells when an excitation gradient is imposed. Such simulation are inspired by, but do not reproduce, experimentally observed Ca^{2+} waves in pancreatic islets exposed to a glucose gradient. Our analyses indicate a possible modification of the model so that the excitation waves stop at the border between “active” and “silent” cells. We verify this property by simulations using such a modified model for a chain, and for a cubic cluster, of coupled cells. Furthermore, we show how our one- and two-parameter bifurcation analyses allow us to predict where the simulated waves stop, for both the original model and the modified version.

References

- [1] I.M. Bulai, M.G. Pedersen, *Stopping waves: geometric analysis of coupled bursters in an asymmetric excitation field*. *Nonlinear Dyn* 96, 1927–1937, 2019.

12:15–12:55 Pattern formation and stability for a kinetic model of ants

Oscar de Wit (University of Cambridge, UK)

Abstract. We present an interacting particle system to model the behaviour of collectives of ants. The particles are modelled as Active Brownian Particles interacting only via chemical pheromones. The particles also have an antenna by which they sense the pheromones. The particles form typical Keller–Segel collapse clusters or, depending on the length of the antenna, travelling clusters. We study the formal mean field limit PDE model to substantiate these particle behaviours. We show analytical and numerical results for the PDE. We begin by demonstrating analytical well-posedness and uniform boundedness globally in time. Using a convergent scheme we are also able to obtain the linear instability curve in the parameter space. In the linearly unstable regime finite volume simulations demonstrate that there is pattern formation reflecting either the Keller–Segel collapse or lane formation, depending on the length of the antenna and the interaction strength. The patterning is also explained by the shape of the growing eigenfunctions associated to the linear theory. We also show there is a region of bistability where Keller–Segel collapse and lane formation compete.

References

- [1] M. Bruna, M. Burger and O. de Wit, *Lane formation and aggregation spots in a model for ants*, preprint, (2024), <https://arxiv.org/abs/2401.15046>

14:30–15:10 Topics on the complex spatio-temporal dynamics of spatially heterogeneous biological systems

Jonathan Touboul (Brandeis University, ITALY)

Abstract. From the development of plants and animals to large-scale vegetation organization, biological systems are often characterized by the emergence of patterns in heterogeneous environments. In particular, vegetation and animal population distributions adjust to varying levels of precipitation, sun, and soil quality, and generate patterns according to both nonlinear interactions with each other, but also their fitness at different locations in space. In embryonic development, particularly in the development of brain areas, ample experimental evidence established the importance of morphogen gradients interaction with nonlinear competitions between

gene expression. These motivate the fine understanding of pattern formation in spatially heterogeneous domains. In his seminal paper [1], Alan Turing immediately made the observation that: “most of an organism, most of the time, is developing from one pattern to another, rather than from homogeneity into a pattern”. Despite this importance, little remains known mathematically about pattern formation in heterogeneous environments. Indeed, most mathematical works on pattern formation deal with homogeneous systems or include gradients of parameters crossing bistable regimes, and we are still lacking a systematic understanding of the phenomenon of crossing transiently regions of parameters associated with multiple bifurcations. Recent investigations of these problems uncovered an astounding complexity of phenomena.

In this talk, I will review recent works and ongoing explorations around the problem of pattern formation in heterogeneous environments and will outline a few open problems. In particular, I will present some recent techniques developed to account for the remarkable reliability of brain area formation and will argue that homeoprotein diffusion, a phenomenon associated with extremely local diffusion of transcription factors, could in fact have far-reaching consequences on the formation and stabilization of sharp boundaries between developing brain region [2]. Mathematically, I will show that this phenomenon could be related to the behavior of general reaction-diffusion systems in competition with external cues. In these systems, typically exhibiting a bistable regime between two states, I will show that small diffusion leads to the emergence of two domains with a sharp transition between them using asymptotic methods involving Wentzel–Kramers–Brillouin expansions (or Hopf–Cole transforms) and viscosity solutions [2]. Contrasting with this paradigm, new data showed that genetic mutations can shatter the transition into multiple ectopic domains. I will show that these can be related to the crossing of multiple Turing instabilities and that the shape of the gradient will strongly impact the presence and nature of the patterns observed [3]. More generally, complex, possibly chaotic phenomena arise at the crossing of branches of periodic orbits that I will also review in this talk [4].

These topics cover collaborations with C. Quiñinao, A. Prochiantz, S-J Chou’s laboratory, D. Patterson, S. Levin and others.

References

- [1] Alan Mathison Turing, *The chemical basis of morphogenesis*, Phil. Trans. R. Soc. Lond. B23737–72 (1952)
- [2] Quiñinao, Perthame and Touboul, *Competition and boundary formation in heterogeneous media: Application to neuronal differentiation* M3AS 25 (13) 2477–2502 (2015)
- [3] Feng et al, *COUP-TFI specifies the medial entorhinal cortex identity and induces differential cell adhesion to determine the integrity of its boundary with neocortex*. Science Advances, 7(27), p.eabf6808 (2021).
- [4] Patterson, Staver, Levin, Touboul, *Spatial Dynamics with Heterogeneity*, SIAM Applied Math, S225-S248 (2023).

15:20–16:00 Noise-induced patterns in biological systems

Francesca Di Patti (University of Perugia, ITALY)

Abstract. Patterns across various scales in time and space are pervasive in nature. However, for many of these systems, deterministic descriptions often require fine-tuning of parameters to facilitate pattern formation, a process at odds with their observed natural robustness. Moreover, intrinsic stochasticity, such as fluctuations in small copy numbers of interacting basic variables, can significantly impact these systems. This necessitates characterizing their microscopic dynamics through master equations, which provide the probability of observing a system in a given state at a given time. The application of van Kampen’s system size expansion to approximate analytically solutions of these master equations reveals how demographic noise emerges perturbatively and how intrinsic stochasticity can self-consistently amplify, yielding nearly regular oscillations in space and time.

In this talk, we will explore two natural systems where demographic noise plays a crucial role, demanding an inherently stochastic, individual-based description. Firstly, we will examine a stochastic one-dimensional model of coupled clock cores and their phosphorylation states in

Anabaena, a multicellular filamentous cyanobacterium [1]. This model demonstrates that demographic noise can instigate stochastic oscillations, termed quasi-cycles, beyond the region where deterministic limit cycles with circadian periods occur. Additionally, it reproduces the observed spatio-temporal coherence along filaments, indicating that noise can paradoxically organize into regular quasi-periodic orbits, fostering macroscopic order from microscopic disorder. Secondly, we will investigate the development of trichome patterns on the epidermis of wild-type *Arabidopsis thaliana* leaves [2]. The statistical characterization of these patterns reveals power spectra with fat tails, a signature indicative of noise-driven stochastic Turing patterns, absent in patterns driven by deterministic instabilities. We will present a theoretical model incorporating demographic noise arising from birth-death processes of genetic regulators, which we analyze both analytically and through stochastic simulations. This model successfully captures the observed experimental features of trichome patterns.

References

- [1] R. Goren, V. Buonfiglio, F. Di Patti, S. Camargo, A. Zhitnitsky, A. Valladares, E. Flores, A. Herrero, D. Fanelli and J. Stavans, *Robust, coherent, and synchronized circadian clock-controlled oscillations along Anabaena filaments*, eLife, 10 (2021), e64348.
- [2] F. Di Patti, Y. Ugartechea Chirino, R. Goren, T. Sharon, A. Castillo, E. Alvarez-Buylla, D. Fanelli and J. Stavans, *Stochastic Turing patterns of trichomes in Arabidopsis leaves*, PNAS, 120 (2023), e2309616120.