Travelling waves and heteroclinic networks in models of spatially-extended cyclic competition

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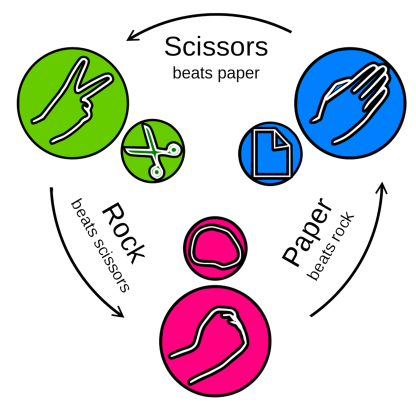
1 Heteroclinic cycles and cyclic competition



In [1], May and Leonard studied a simple Lotka-Volterra model of competition between three species, whose interaction followed the game of Rock-Paper-Scissors. In this work, they discovered the first example of a ***heteroclinic cycle***.

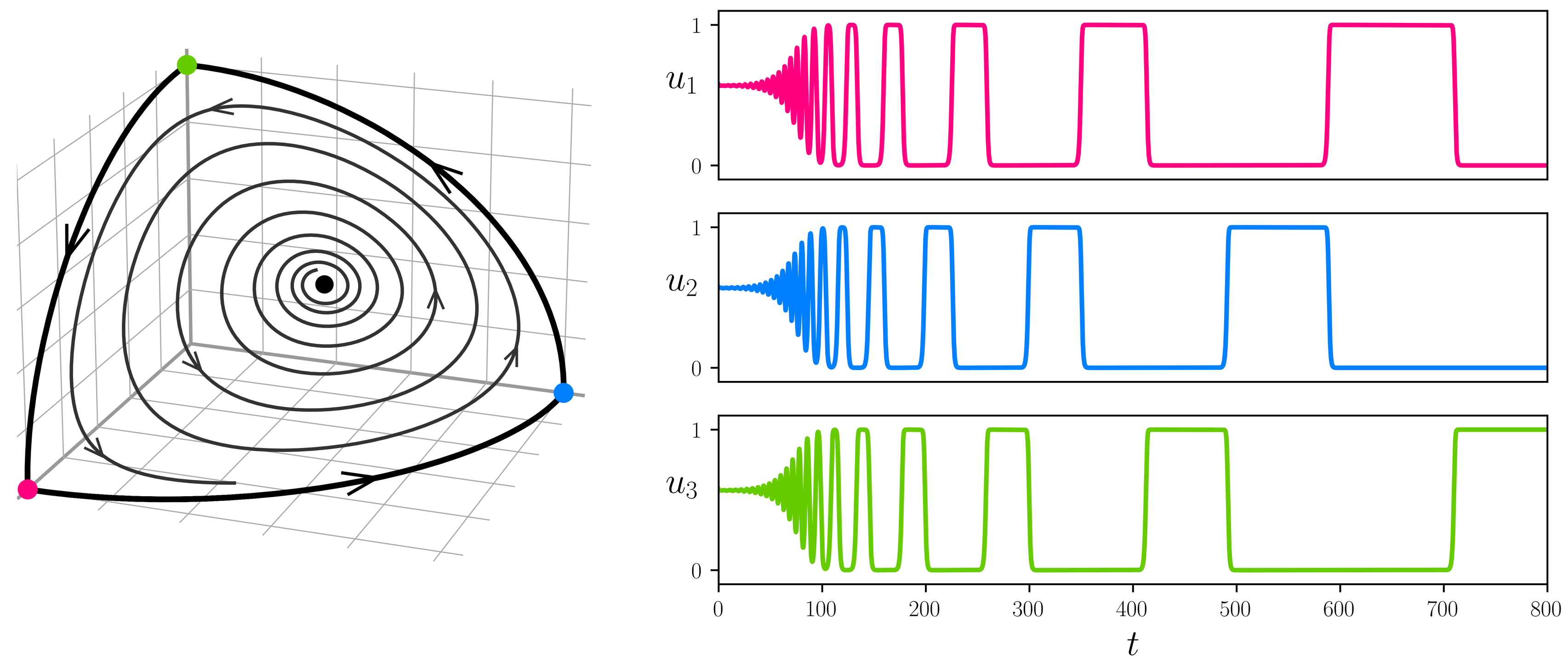


Figure 1: An example of phase space (left) and the corresponding time series (right) of the model studied by May and Leonard. The solution begins near the unstable coexistence equilibrium of all species (the black equilibrium), and then cycles between three states of being composed almost entirely of only one species (the pink, blue, and green equilibria). The thick lines are ***heteroclinic orbits***, solutions which connect two different equilibria.

2 Spatially-extended systems

The May-Leonard model assumes the population is well-mixed, and does not consider the spatial distribution or mobility of the species. Diffusion terms can be added to account for these phenomena.

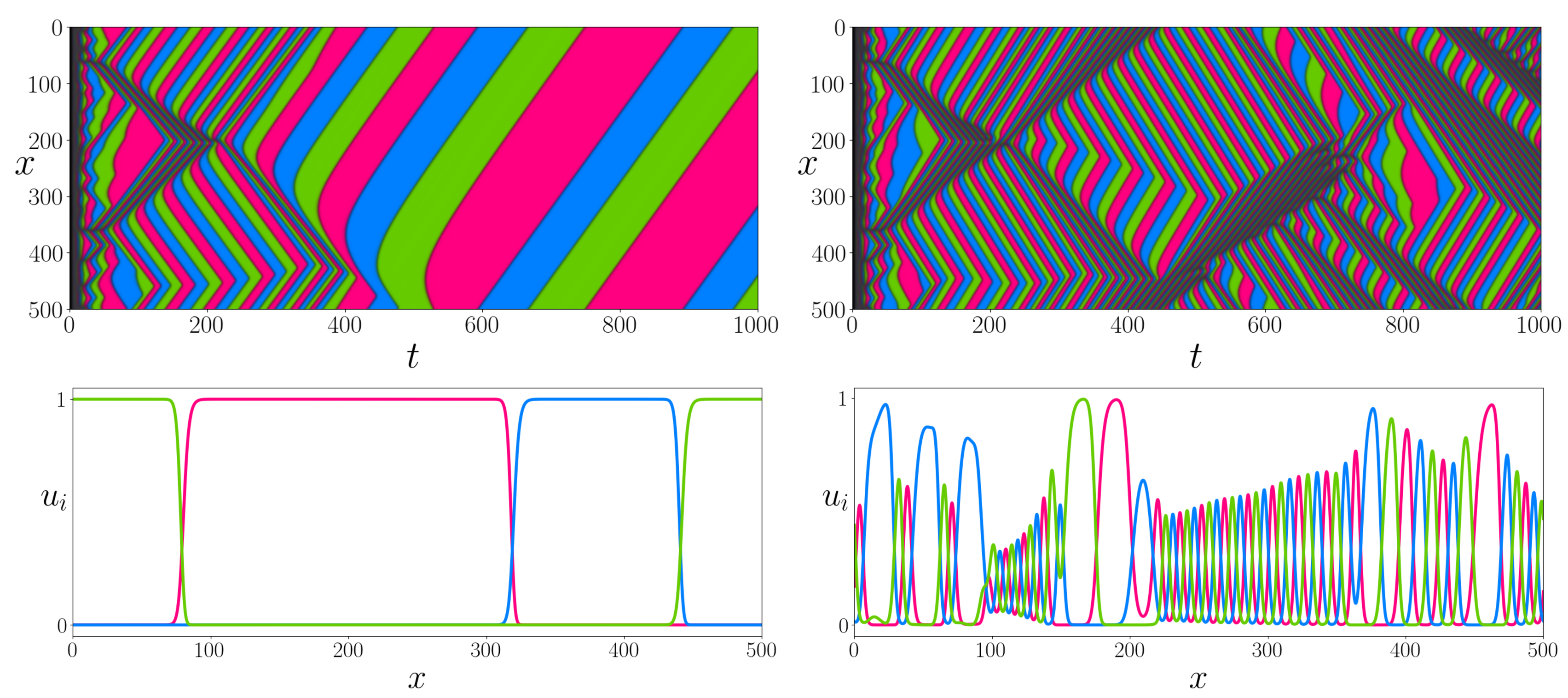


Figure 2: Simulations of the spatially-extended May-Leonard model, with random initial conditions, showing the emergence of travelling wave solutions. In the top row, we show space-time plots, coloured according to the density of each species. In the bottom row, spatial plots show the density of each species at the final timestep. The left-hand plots show a large, stable wave, whereas the right-hand plots show many interacting smaller waves.

Models of cyclic competition between n species have the general form of a system of n first-order ODEs

$$\dot{u}_i = f(u), \text{ and, with diffusion, } \dot{u}_i = f(u) + \nabla^2 u_i,$$

where u_i is the density of each species. We analyse the existence of travelling waves by moving to a steady-state travelling frame of reference with $z = x + \gamma t$, where γ is the wavespeed. We can then derive n second-orders in the variable z,

$$\gamma \frac{\mathrm{d}u_i}{\mathrm{d}z} = f(u) + \frac{\mathrm{d}^2 u_i}{\mathrm{d}z^2}.$$

Using these equations, the existence of travelling waves and the dispersion relationship between wavelength and wavespeed was analysed by Postlethwaite and Rucklidge in [2, 3] for three species in cyclic competition.

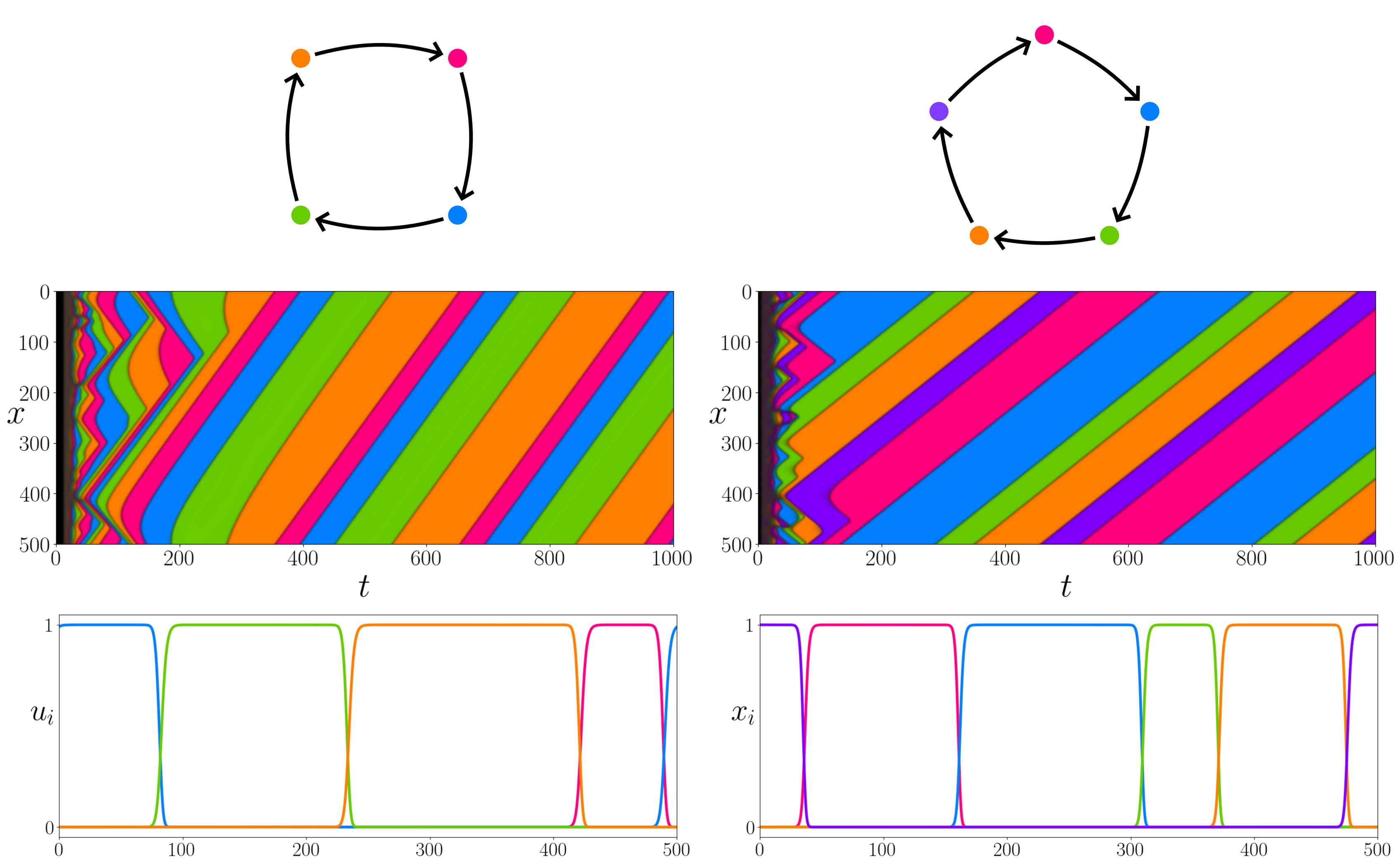


Figure 3: Time-space plots (top) and spatial plots at the final timestep (bottom) of examples of large, stable travelling waves between four (left) and five (right) species in cyclic competition, with their interaction defined by the heteroclinic cycle shown in the top row.

3 Heteroclinic networks in the steady-state travelling frame of reference

A connected union of heteroclinic cycles is called a ***heteroclinic network***. In [4], we show that with four or more species in cyclic competition, the heteroclinic cycle in the well-mixed model becomes a heteroclinic *network* in the steady-state travelling frame of reference.

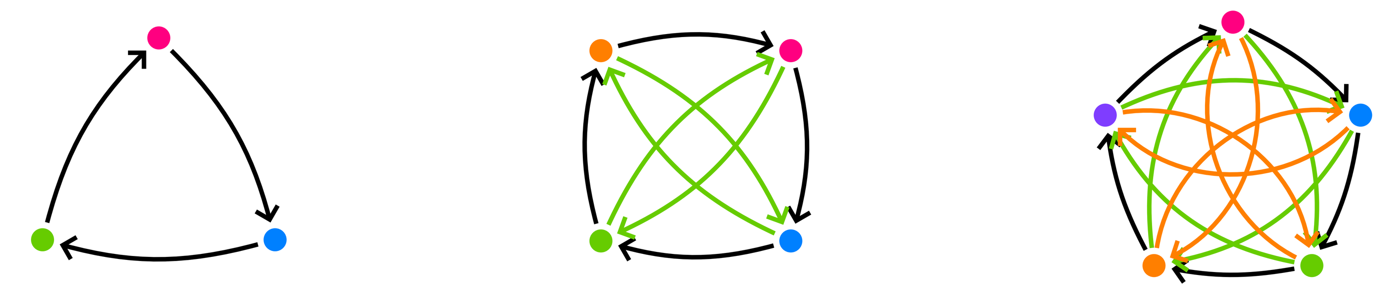
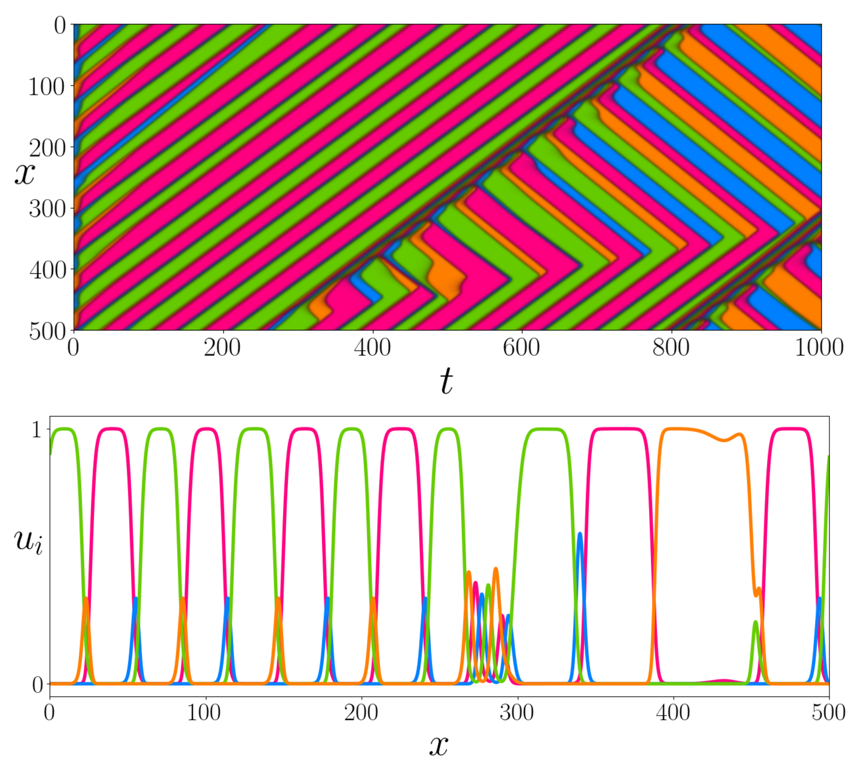


Figure 4: The heteroclinic structures that exist in the steady-state travelling frame of reference for 3, 4, and 5 species. For 3 species, the topology of the structure is preserved. However, for 4 and 5 species, additional heteroclinic orbits emerge between species not connected in the well-mixed model, forming a heteroclinic *network*.

4 New types of travelling waves in larger systems

The emergence of a heteroclinic network in the steady-state travelling frame of reference allows for the formation of new travelling waves which follow orbits of the same "type" (identified with colour in the graphs above).



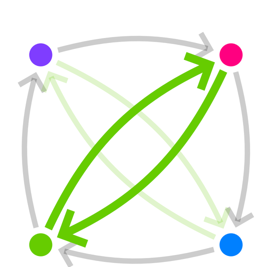


Figure 5: A simulation of a new type of travelling wave with four species, composed of bands of the first and third species, with smaller, shorter peaks of the second and fourth. This wave is known as a ***defensive alliance***, a subset of species which has coordinated to suppress the population of their respective competitors.

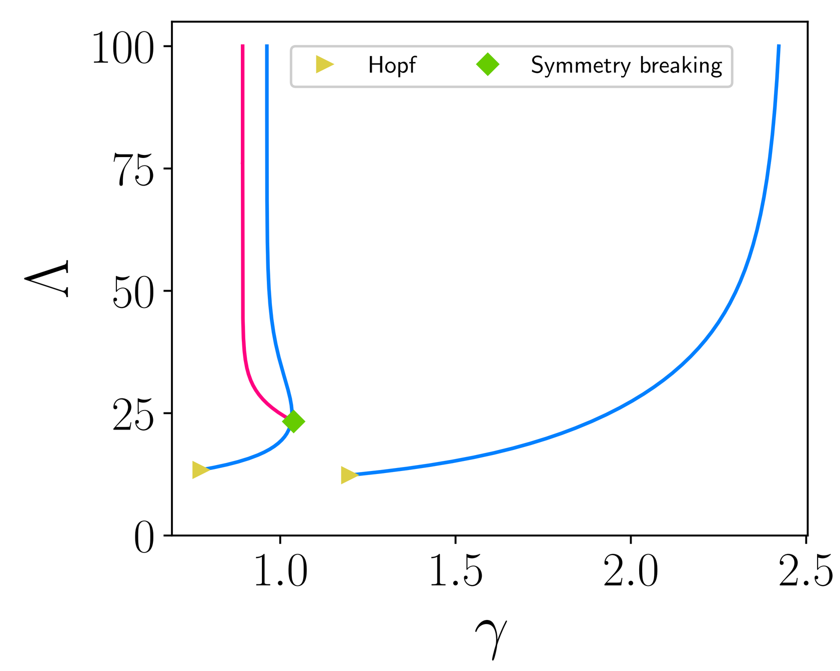


Figure 6: The dispersion relation between wavespeed γ and wavelength Λ for both the "ordinary" waves (blue), and the new type of wave (pink) in the four species model. Waves emerge from different bifurcations, as labelled, and approach a fixed γ as Λ goes to infinity.

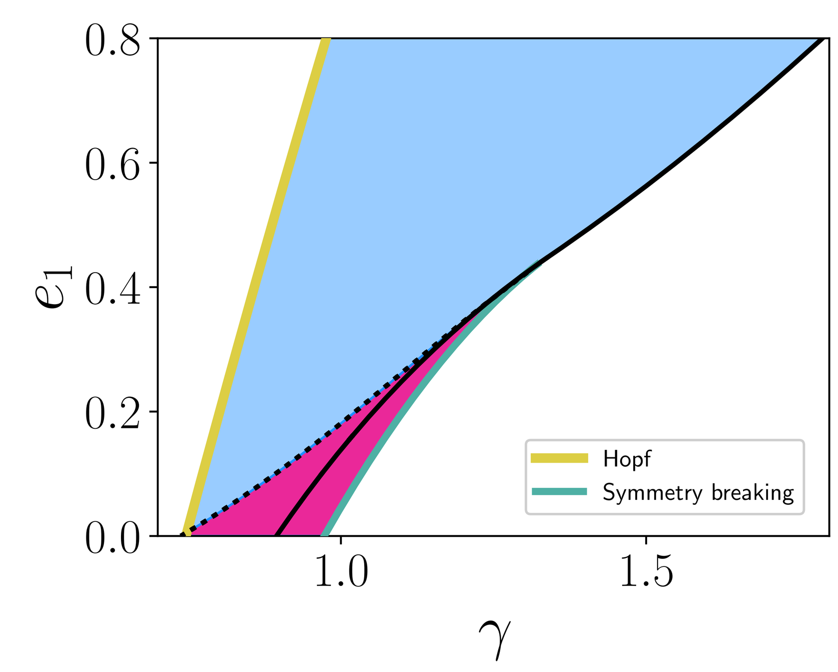


Figure 7: A bifurcation set of travelling waves in the $\gamma - e_1$ plane, where e_1 is model parameter. The new type of wave exists in the pink region. The ordinary waves exist in the pink and blue regions. The black curves gives the vale of γ approached as Λ goes to infinity.

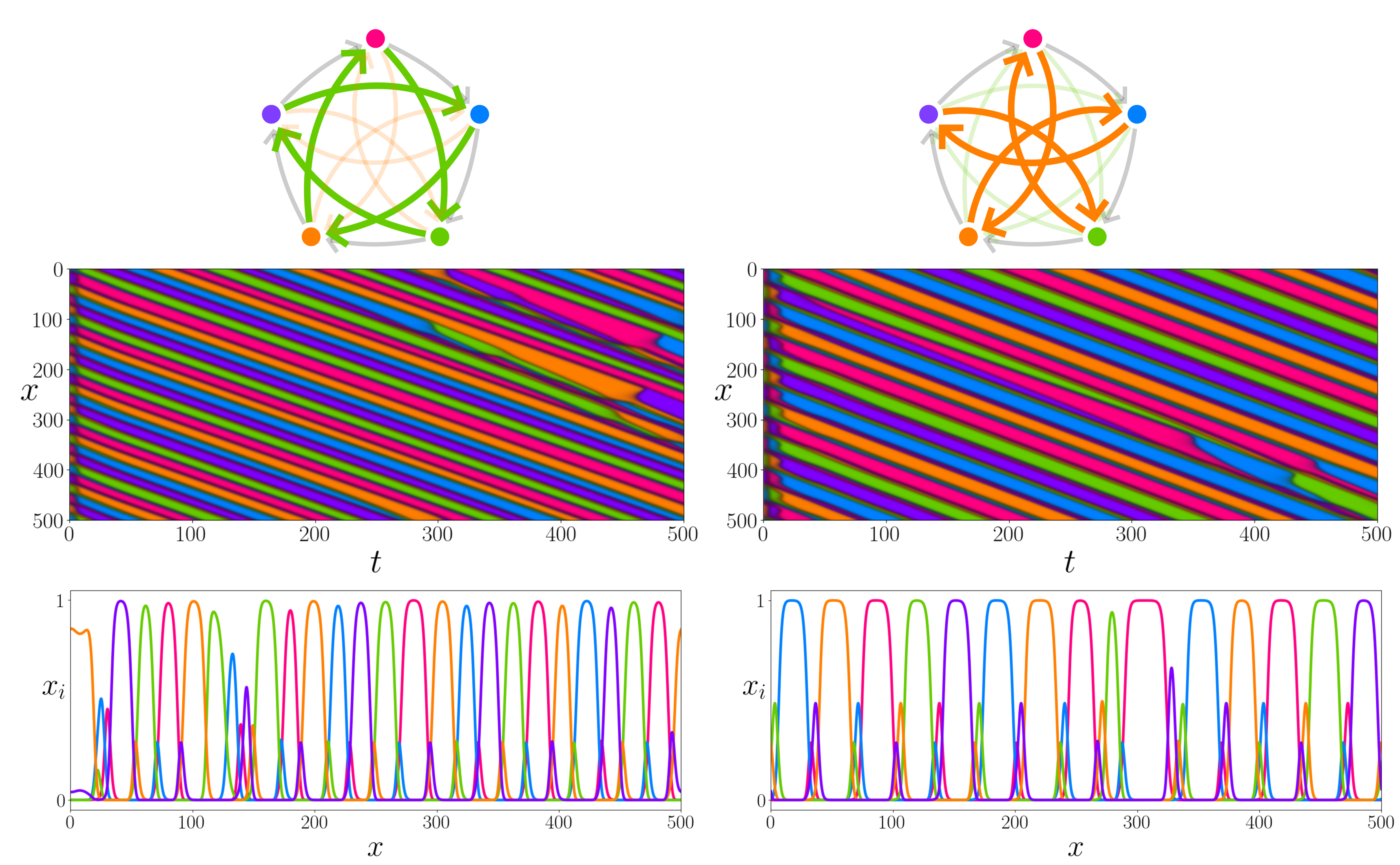


Figure 8: Simulations of the new types of travelling wave with five species, both of which follow the cycle of the network highlighted in the respective graph. As neither wave is composed of a subset of species, these waves are not defensive alliances, but still contain an ordering of species not expected from the well-mixed model.

References

[1] R. M. May, W. J. Leonard, *SIAM Journal on Applied Mathematics* **1975**, *29*, 243–253.

[2] C. M. Postlethwaite, A. M. Rucklidge, *EPL* **2017**, *117*, 48006–48012.

[3] C. M. Postlethwaite, A. M. Rucklidge, *Nonlinearity* **2019**, *32*, 1375–1407.

[4] D. C. Groothuizen Dijkema, C. M. Postlethwaite, *Submitted to Nonlinearity. arXiv:2208.05630* **2022**.