

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

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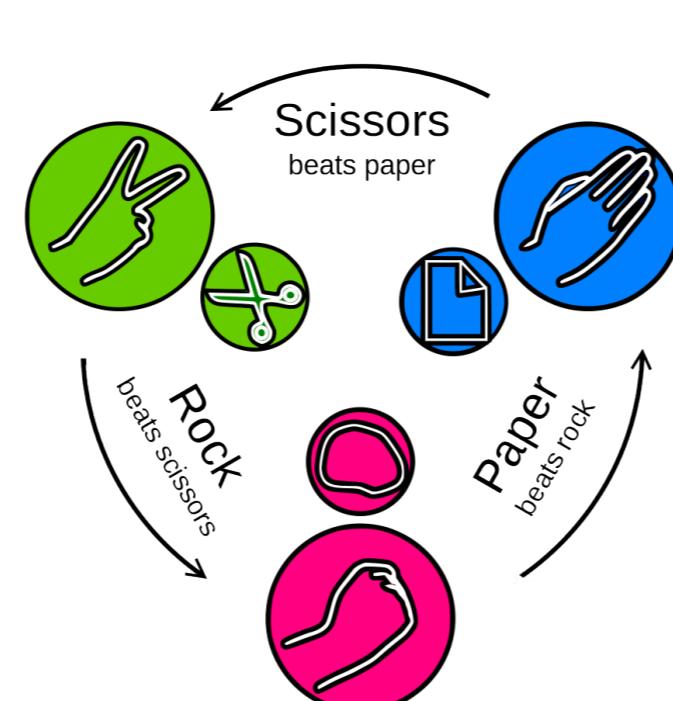
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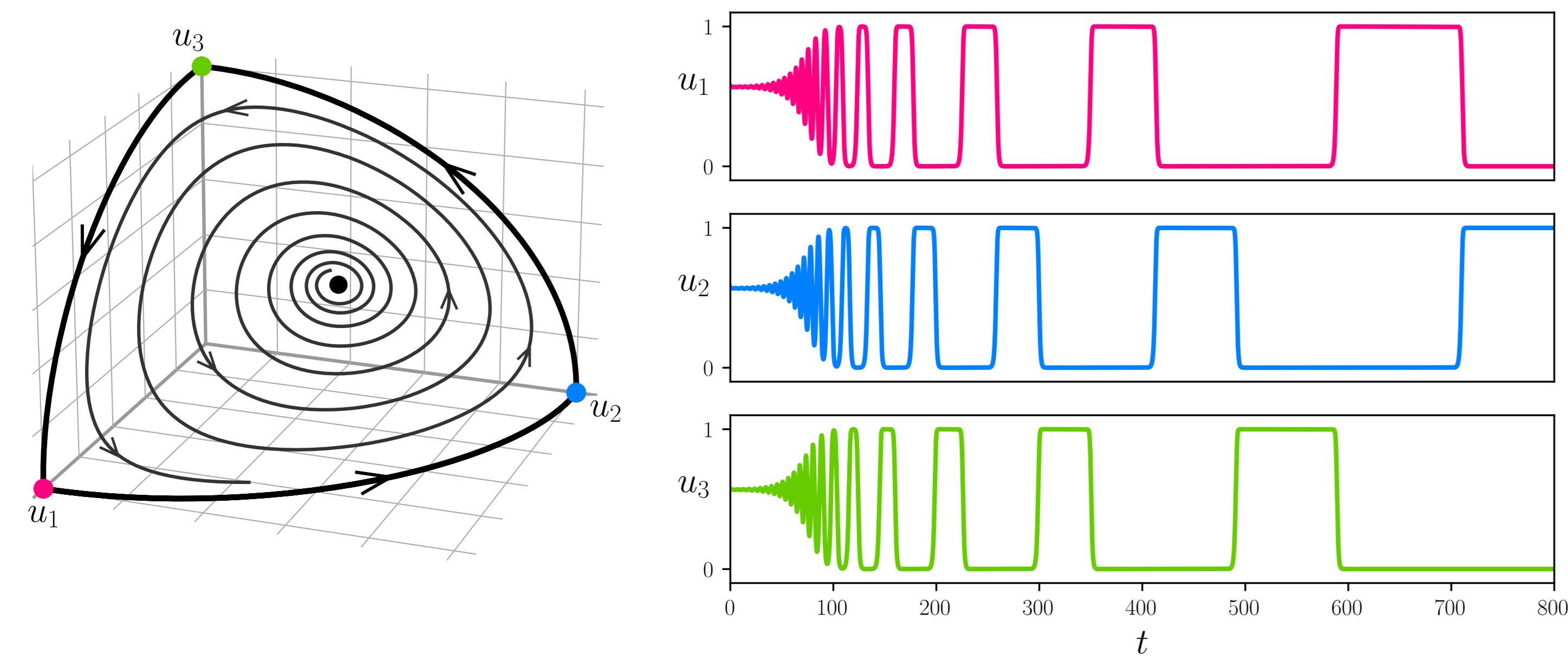
1 Heteroclinic cycles and cyclic competition

In 1975, May and Leonard [1] 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*.



Models of cyclic competition between n species have the general form of a system of n first-order ODEs for the density, u_i , of each species:

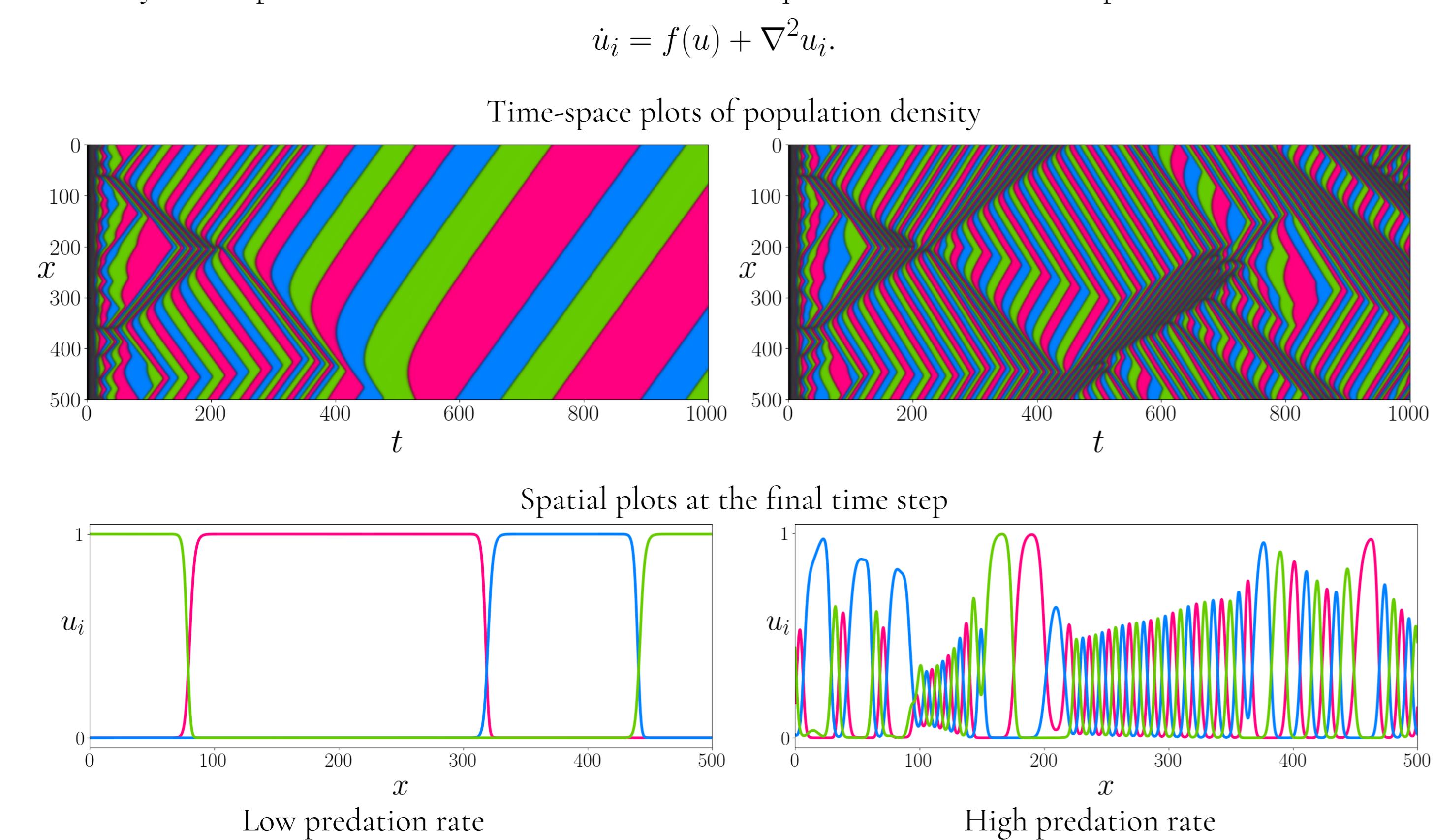
$$\dot{u}_i = f(u). \quad (1)$$



The phase space (left) and a time series (right) of the three species May–Leonard model. The solution begins near the unstable coexistence equilibrium, and then cycles between three states of being composed almost entirely of only one species. The thick black lines are *heteroclinic orbits*, solutions which connect two different equilibria.

2 Spatially-extended systems

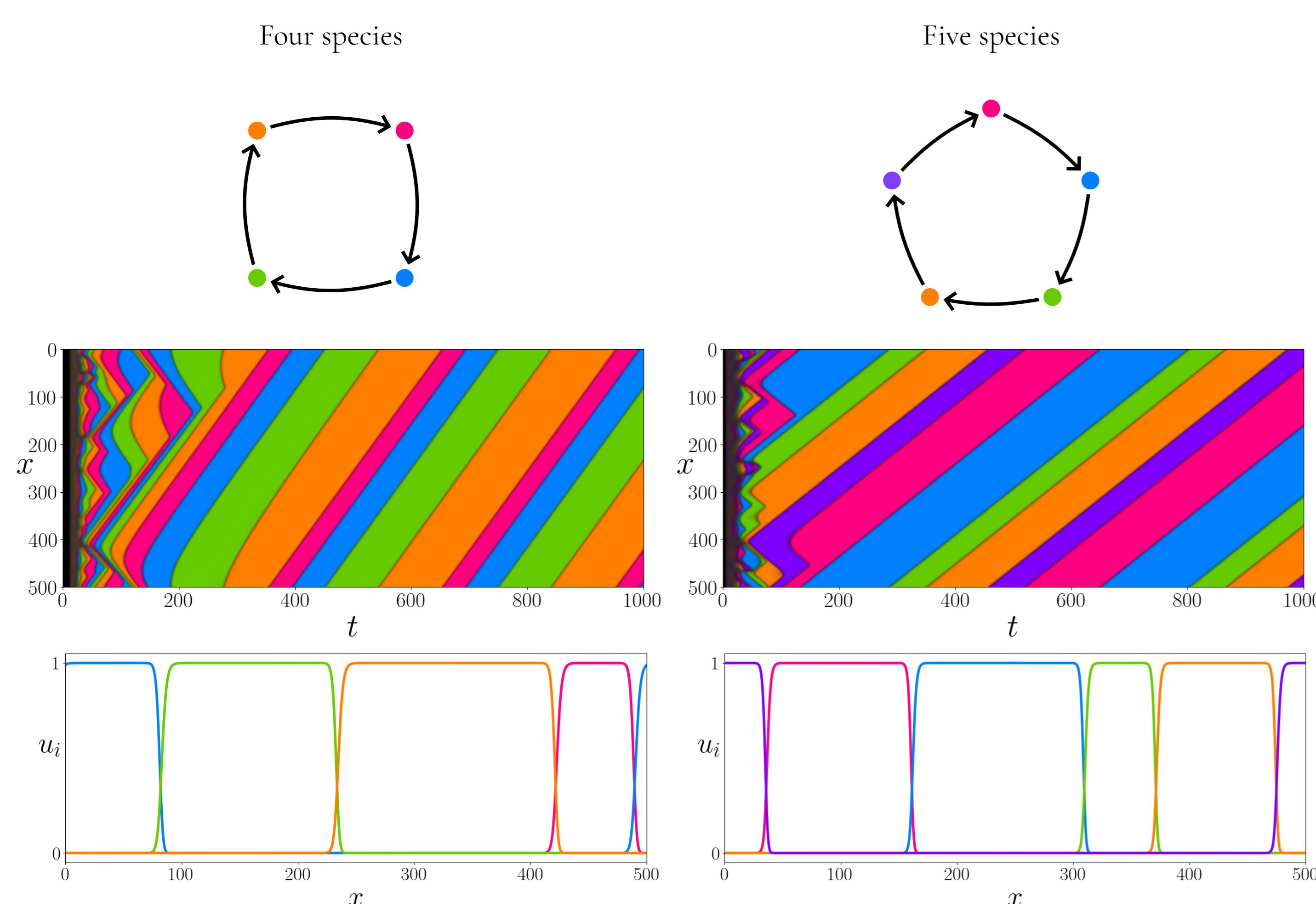
The May–Leonard model assumes the population is well-mixed, and does not consider the spatial distribution or mobility of the species. Diffusion terms can be added to eq. (1) to account for these phenomena:



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 derive n second-order ODEs in the variable z ,

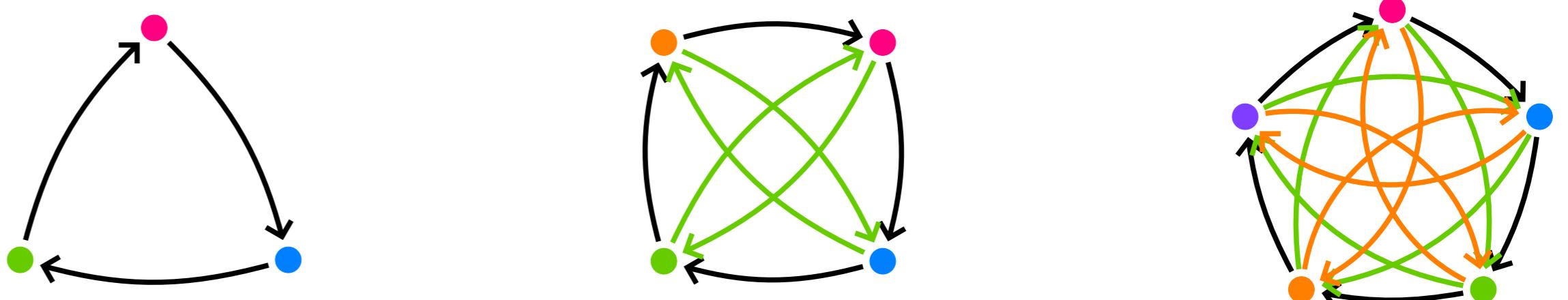
$$\frac{du_i}{dz} = f(u) + \frac{d^2u_i}{dz^2}.$$

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.



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

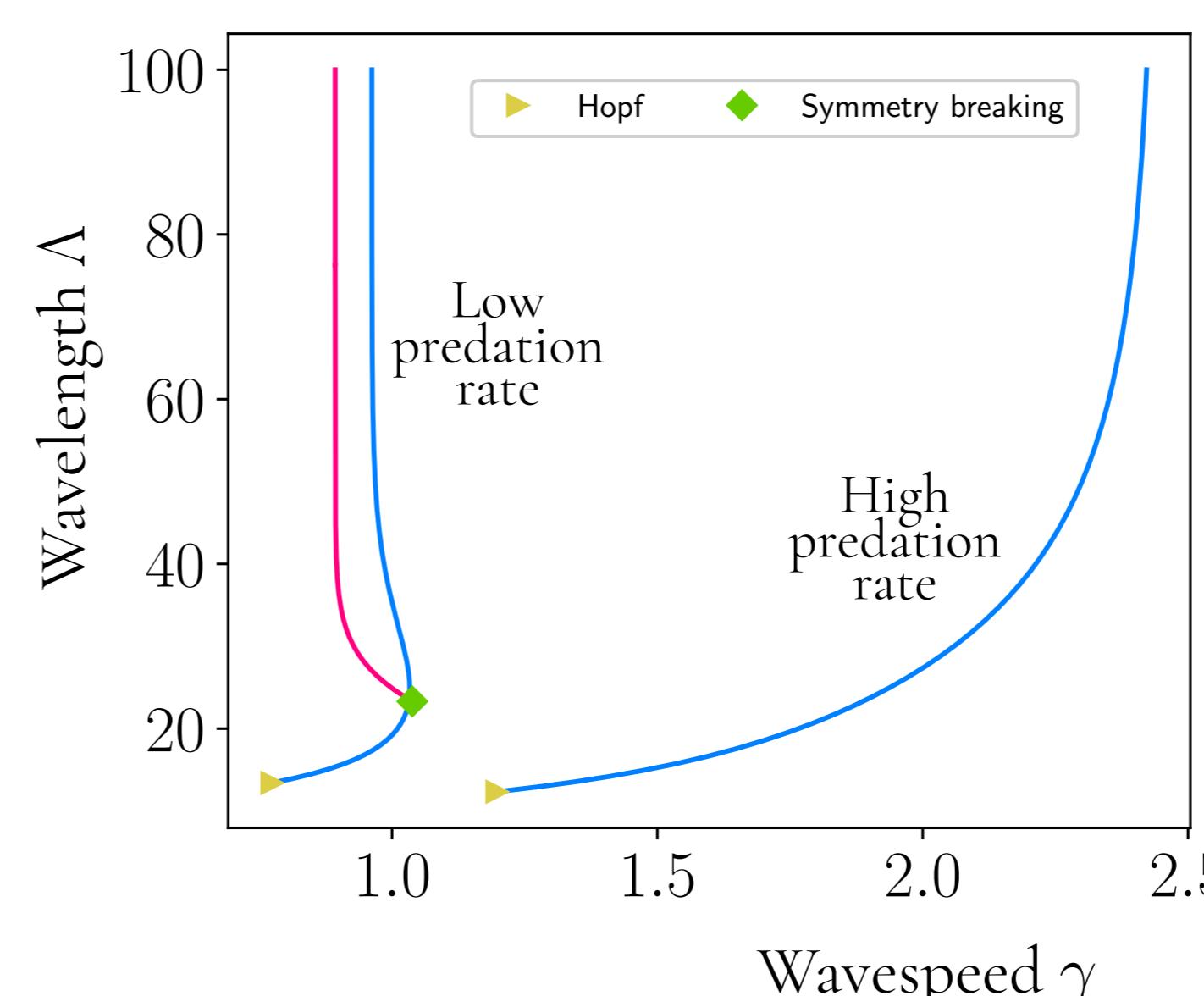
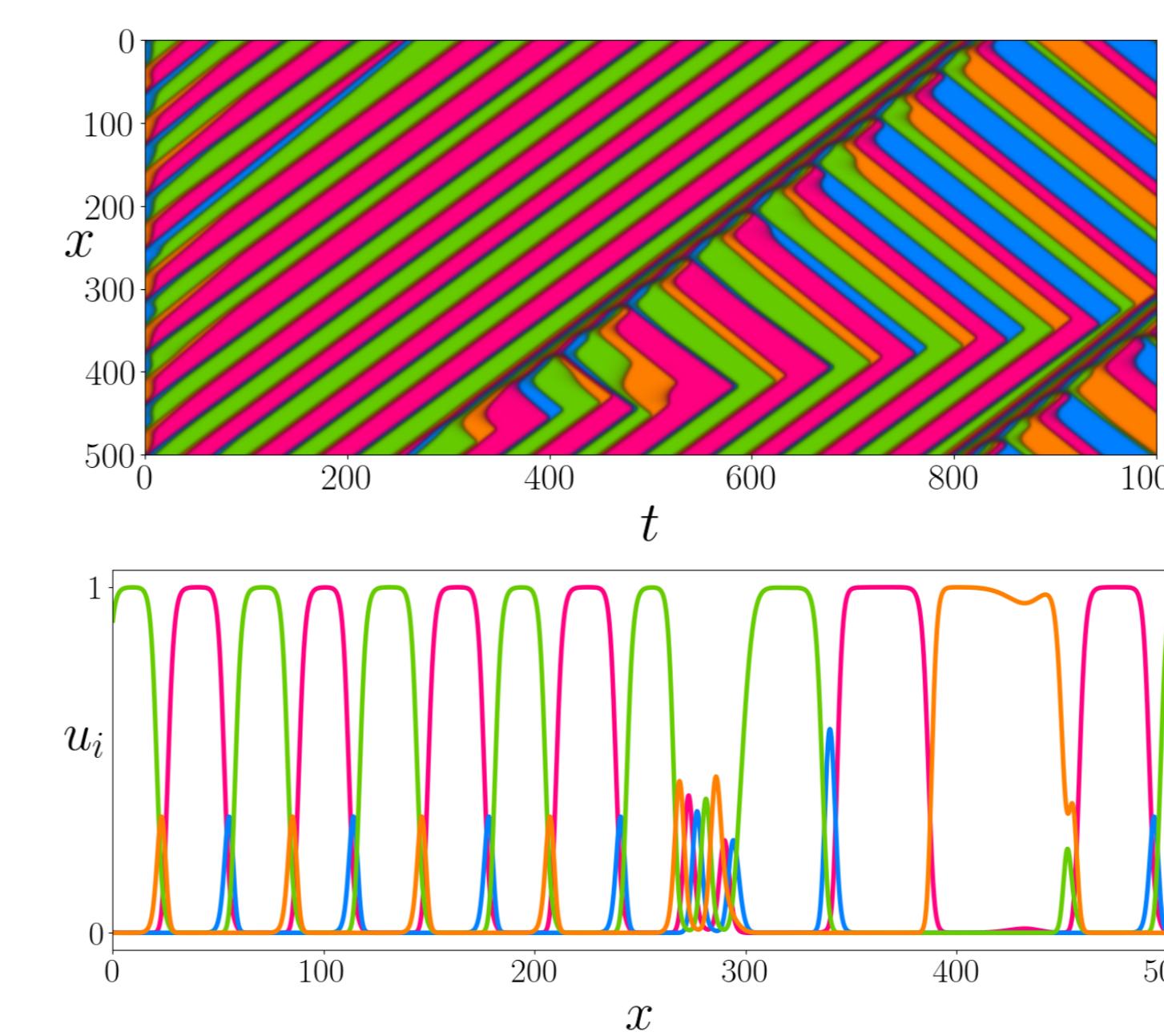
A connected union of heteroclinic cycles is called a *heteroclinic network*. In [4], we show that with four or more species in cyclic competition, the heteroclinic cycle in the well-mixed model becomes a heteroclinic *network* in the steady-state travelling frame of reference.



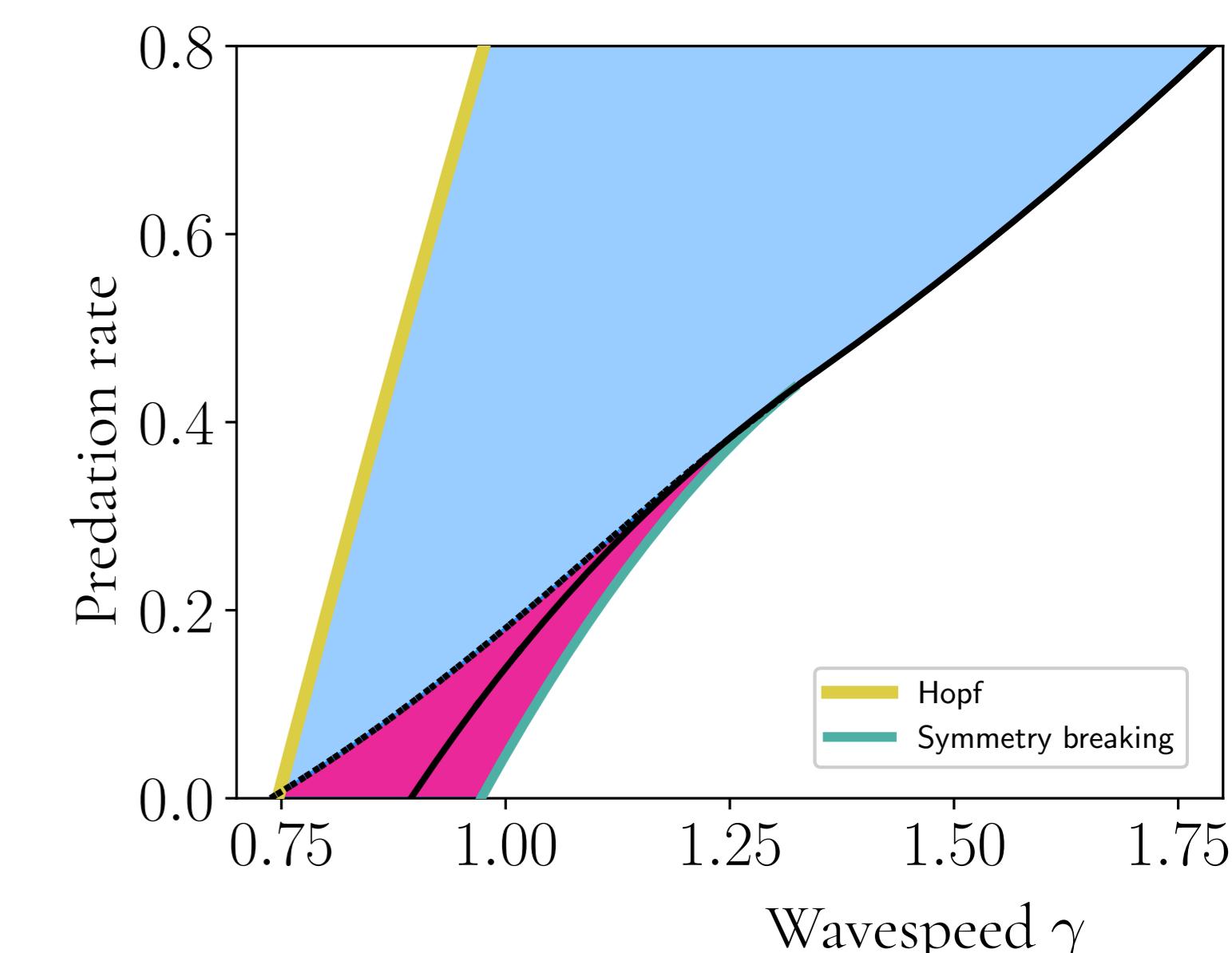
For three species, the topology of the cycle is preserved. However, for four or more species, additional heteroclinic orbits emerge between species not connected in the well-mixed model.

4 New types of travelling waves in larger systems

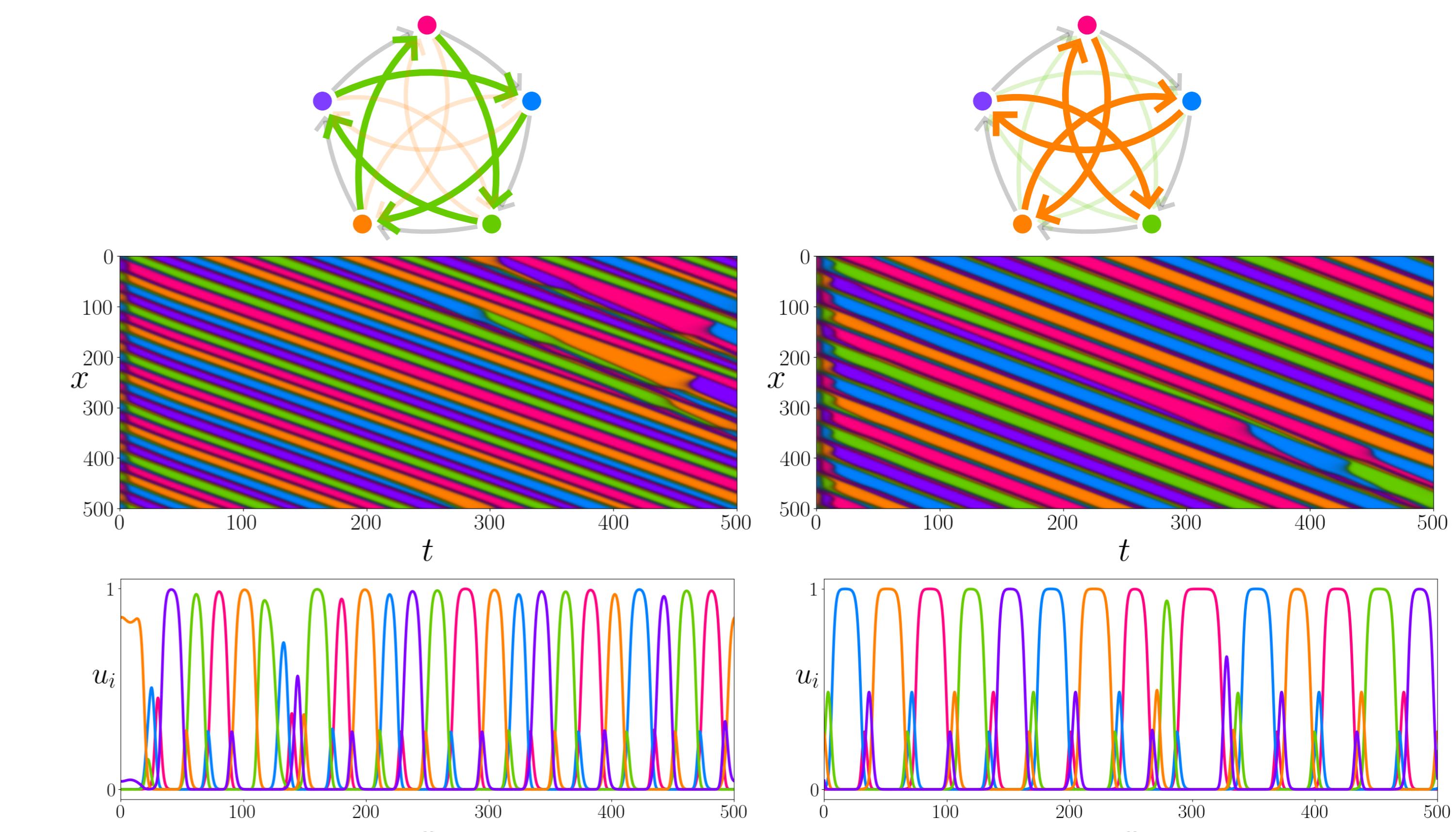
The emergence of a heteroclinic network in the steady-state travelling frame of reference allows for the formation of new travelling waves which follow orbits of the same “type”.



An example of the 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.



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



Examples of the two different new types of travelling waves which exist in the five species model. These waves are not defensive alliances, but contain an ordering of species not expected from the well-mixed model.

References

- [1] May R M and Leonard W J 1975 *SIAM J. Appl. Math.* **29** 243
- [2] Postlethwaite C M and Rucklidge A M 2017 *EPL* **117** 48006

- [3] Postlethwaite C M and Rucklidge A M 2019 *Nonlinearity* **32** 1375
- [4] Groothuizen D C and Postlethwaite C M 2023 *Nonlinearity* **36** 6546