

University of Sheffield

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**The emergence of spatial segregation patterns from animal movements and interactions**

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## Research project 1

### Movement and competition: a compartment model approach

In a paper by Potts and Petrovskii (2017), a reaction-advection-diffusion model is proposed to explain the role movement may play in the co-existence of strongly competitive species. The dimensionless equations from that paper are as follows:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - \frac{\partial}{\partial x} \left[ \gamma_1 u \frac{\partial v}{\partial x} \right] + ru(1-u) - a_1 uv, \quad (1)$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - \frac{\partial}{\partial x} \left[ \gamma_2 v \frac{\partial u}{\partial x} \right] + rv(1-v) - a_2 uv, \quad (2)$$

where  $\gamma_1$  and  $\gamma_2$  may be constant (see Equations 4-5 from the paper) or governed by their own dynamics (see Equations 8-10 from the paper). Furthermore, the paper assumes that  $a_1, a_2 > r$ , known as the *strong competition* regime (which is bistable in the spatially implicit version of Equations 1-2). The trouble with this model is that it is rather tricky to analyse mathematically. Therefore the authors relied on numerical analysis.

The task of this project is to gain some analytic insight into the numerical results from Potts and Petrovskii (2017) by analysing a compartmental model that mimics Equations (1-2). Here, we model space not as a continuum, but as made up of two adjacent compartments,  $A$  and  $B$ , between which animals can move. The population density of species  $u$  in compartment  $A$  (resp.  $B$ ) is denoted  $U_A$  (resp.  $U_B$ ), and similarly for  $v$ . This leads to a system of four *ordinary* differential equations, as follows:

$$\frac{dU_A}{dt} = F_{UB}U_B - F_{UA}U_A + rU_A(1-U_A) - a_1U_AV_A, \quad (3)$$

$$\frac{dV_A}{dt} = F_{VB}V_B - F_{VA}V_A + rV_A(1-V_A) - a_2U_AV_A, \quad (4)$$

$$\frac{dU_B}{dt} = F_{UA}U_A - F_{UB}U_B + rU_B(1-U_B) - a_1U_BV_B, \quad (5)$$

$$\frac{dV_B}{dt} = F_{VA}V_A - F_{VB}V_B + rV_B(1-V_B) - a_2U_BV_B. \quad (6)$$

Here  $F_{UA}$  (resp.  $F_{UB}$ ) denotes the rate that individuals from population  $U$  move from  $A$  to  $B$  (resp.  $B$  to  $A$ ), and similarly for  $F_{VA}$  and  $F_{VB}$ . We assume that  $a_1, a_2, r, F_{UA}, F_{UB}, F_{VA}, F_{VB} \geq 0$ . The specific tasks are as follows.

1. Make sure you have read and understood the paper by Potts and Petrovskii (2017).
2. This question is a standard exercise, intended as a warm-up for those unfamiliar with the Lotka-Volterra competition model. You may have done this before, in which case you can skip it. Perform linear stability analysis for the system with  $F_{UA} = F_{UB} = F_{VA} = F_{VB} = 0$  in the three cases (i)  $a_1, a_2 < r$ , (ii)  $a_1 < r < a_2$ , (iii)  $r < a_1, a_2$ .
3. Draw a sketch of the compartment model from Equations (3-6), incorporating all the  $F$ -parameters, showing the rates of flow between compartments.

For all following questions, we will assume  $r < a_1, a_2$  (the so-called *strong competition* situation).

4. Start by assuming that  $F_{UA} = F_{UB} = F_{VA} = F_{VB} = 0$ . Here, you have two independent bistable systems, given by Equations (3-4) and Equations (5-6). Suppose that the system is in the steady-state with  $U_A = 1, V_A = 0, U_B = 0, V_B = 1$ . This is a (rather trivial) example of spatially separated coexistence. Explore what happens to this system if you increase the values of  $F_{UA}, F_{UB}, F_{VA}, F_{VB}$  from zero (i.e. you allow for constant rates of migration between  $A$  and  $B$ ). Assuming  $F_{UA}, F_{UB}, F_{VA}, F_{VB}$  are constants, for which values do you retain spatially segregated co-existence? Does the set of such parameter values have non-zero measure within the parameter space?
5. Now explore what happens when you allow  $F_{UA}, F_{UB}, F_{VA}, F_{VB}$  to be non-constant, varying with the rate of influx of immigrants. Start by trying to mimic Section 3 of Potts and Petrovskii (2017). Which regions of parameter space allow for spatially segregated co-existence?

## References

- Potts, J. R. and S. V. Petrovskii. 2017. Fortune favours the brave: Movement responses shape demographic dynamics in strongly competing populations. *Journal of Theoretical Biology*, **420**:190–199.