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The potential impact of complex dynamics resulting from species interactions on the resilience of systems under stress

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Introduction

Species interactions in population models may lead to complex dynamics. Also in coupled individual-based models (IBMs) such complexity may emerge. To understand emerging complex behaviour and to be able to predict it, it will be useful to study simpler models containing essentially the same processes. It might be that some of the tools for analysis of simple (ordinary differential equation) models can be adapted to work for IBMs as well.

We used a simple competition model to help explain the behaviour and stability properties of a 2-species IBM, and to predict the consequences of chronic stress and of a pulsed stress event (both affecting survival) on this behaviour. The coupled IBMs are not only an example of 2-species models with (simple) competitive interactions, but also of model systems with potentially alternative stable states (ASS). The impact of stress in the presence of ASS is an issue that deserves further attention in the context of chemical risk assessment, in particular when the ambition is to move beyond the single-species approach.

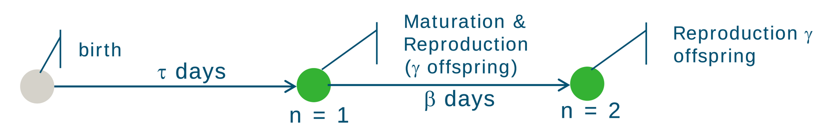
Material & Methods

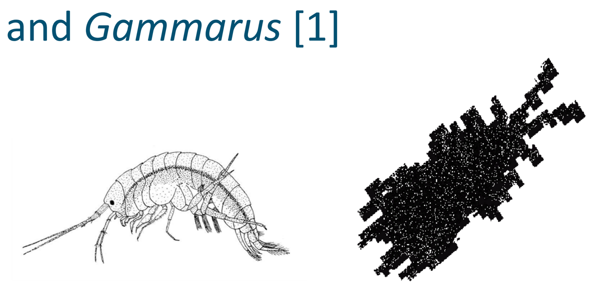
General approach

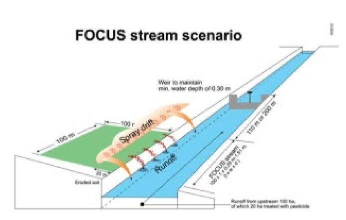
- Find and use a simple, deterministic, non-spatial model to obtain a search image of the potential 'complex' dynamics and stability properties of the IBM
- Apply analysis methods available for deterministic ODE-based models, e.g. graphical analysis, bifurcation analysis.
- Where possible adjust and apply these methods also for IBM
- Predict from the simple models the possible impact of chronic stress and of a pulsed stress event, on dynamics and stability
- Test predictions in IBMs

Individual-based Model (IBM)

Relatively simple, stochastic, IBMs for *Asellus* and *Gammarus* [1]







Movement within a simple 1D or 2D system (edge-of-field scale)

Competition between the species defined as additional density-dependent mortality, with intensity set by competition coefficients α_{AG} and α_{GA}

	μ_b	τ	γ	β	n	α_{ii}
	d^{-1}	d	ind	d		$m^2 ind^{-1} d^{-1}$
Asellus	0.001	70	20	-	1	0.001
Gammarus	0.01	130	16	20	5	0.001

Life-history coefficients

Simple model

Deterministic, mean-field (non-spatial), ordinary differential equation model (ODE) counterpart

$$\begin{cases} \frac{dN_1}{dt} = r_1 * N_1 - \alpha_{11} * N_1 * (N_1 + \alpha_{12} * N_2) \\ \frac{dN_2}{dt} = r_2 * N_2 - \alpha_{22} * N_2 * (N_2 + \alpha_{21} * N_1) \end{cases}$$

$$1 = \sum_{x=1}^{w} \left(m_x \cdot l_x \cdot \lambda^{-x} \right)$$

Euler-Lotka equation

r (=ln λ)	λ (=e^r)
d^{-1}	d^{-1}
0.0418	1.0427
0.0173	1.0175

Population growth rate

Results

Strong interaction: $\alpha_{12}\alpha_{21} > 1$

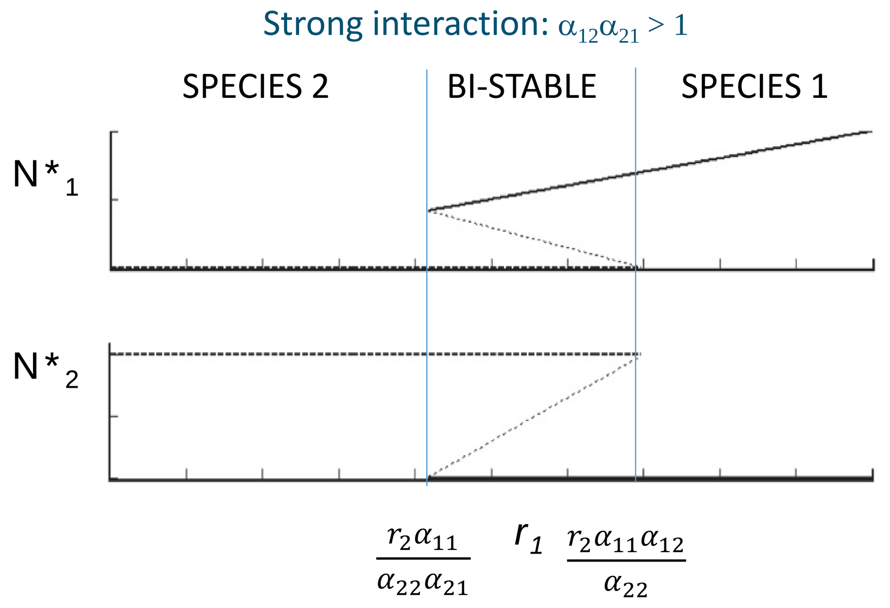


Figure 1. Bifurcation diagram: outcome of competition depends on r_1 (stress-dependent). Analytically derived from ODE model [2].

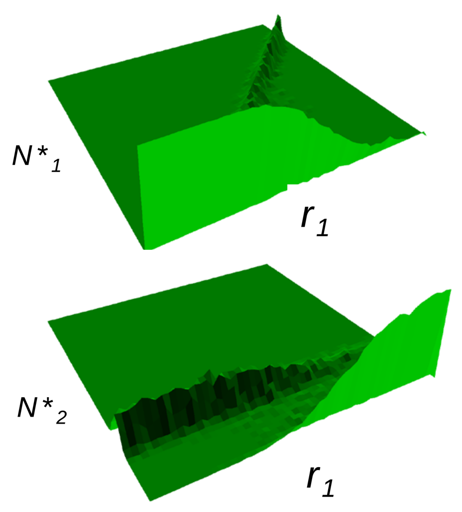


Figure 2. Bifurcation diagram constructed from IBM simulations (z-axis: frequency of runs with this *N* as equilibrium density)

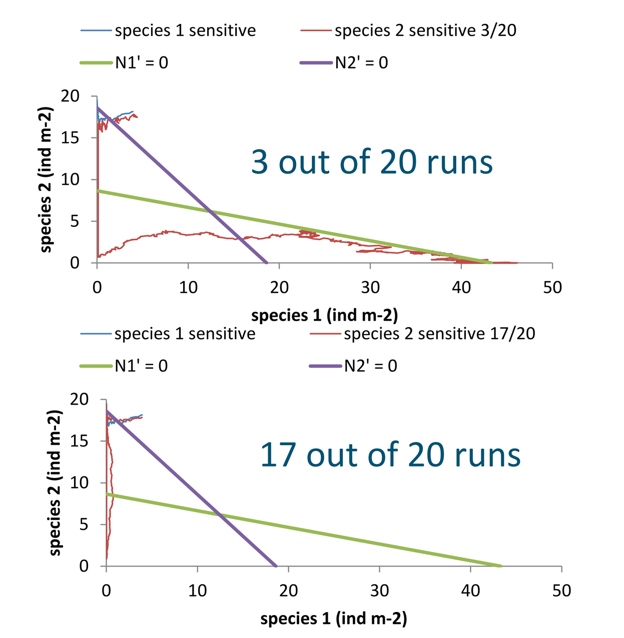


Figure 3. Phase-plane plots with trajectories of 20 IBM simulations and null-isoclines of ODE

Well-mixed system

- For strong interaction ($\alpha_{12}\alpha_{21} > 1$) the system may have alternative stable states (bi-stability) (Fig. 1)
- (chronic) stress may move the system into another stability region (Fig. 1)
- Deterministic ODE model predicts the impact of a stress event quite well, even when in the bi-stability region
- Stochastic IBM has for the same setting a probabilistic outcome: some runs ending up in one equilibrium state, others in the alternate state (Fig. 3). This is caused by random variation in the state of the population and the impact of stress (mortality)

Spatially-extended system

- Mobility of the species is low, relative to the spatial dimensions
- In systems with ASS, the transition to alternate state may take the form of a traveling front of one state taking over [3]
- In systems in a transient state (with a traveling front), stress may reverse the direction of a traveling front
- Another cause of 'unpredictability' in stochastic IBMs: even in homogeneous systems the distribution pattern in terms of local dominance, at the onset of the stress, may vary between runs and determine whether the system ends up in one or the alternate state

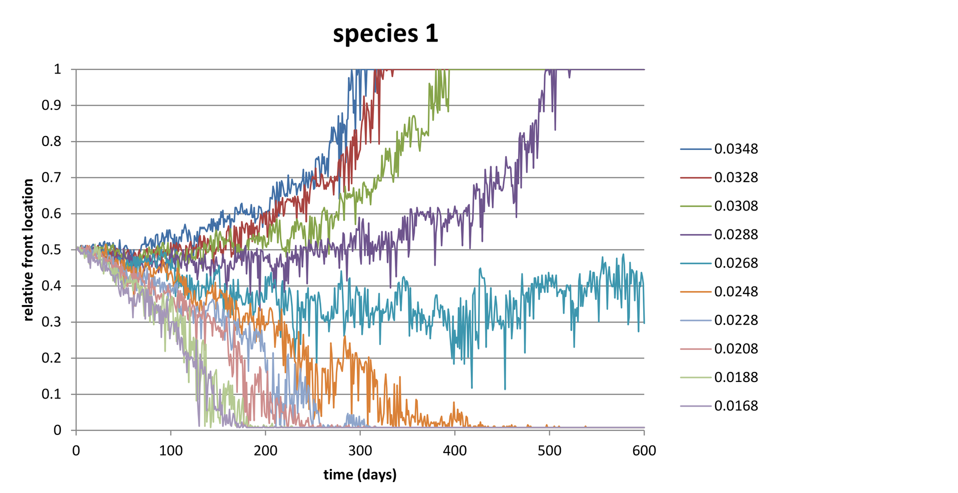


Figure 4. The reduction in r_1 that is required to reverse the direction of a traveling front in a bi-stable system (the Maxwell Point [3]) is determined here from IBM simulations. Ditch 256 m length. Initial spatial state: left part "only species 1", right part "only species 2". Without stress a traveling front of species 1 overtakes the whole system. With r_1 reduced to approximately <0.027, the front is reversed.

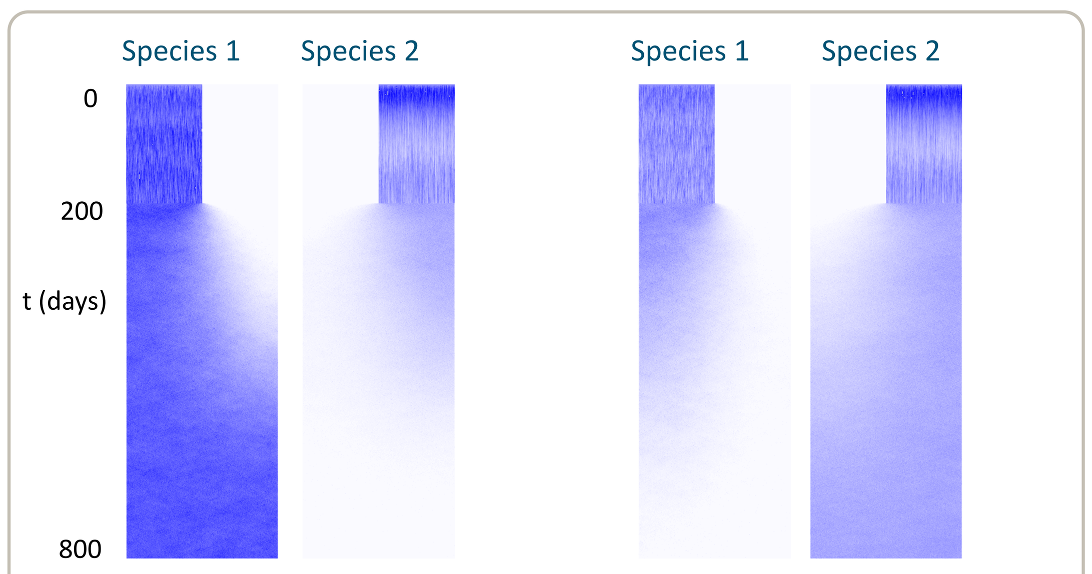


Figure 5. Space-time plots with the density of species 1 and 2 for r_1 = 0.0328 and 0.0208 (see figure 4). X-axis: distance (1-256 m); y-axis: time (days) with t = 0 at the top. Before day 200 no movement was allowed. Left: species 1 takes over; right: species 2 takes over.

Implications Risk Assessment

Small for systems that do not have ASS. It should be taken into account that stress may very easily change the outcome of competition. But this can be predicted quite well from competition models. Impacts on both species have to be considered, even if the stress affects only one.

Large for systems with ASS. Random variation in population state, impact of the stressor and spatial distribution (even in homogeneous systems), that inevitably arises in stochastic models and experimental systems, make that under seemingly the same conditions the system may develop to more than one of the equilibrium states. Methods dealing with this possibility as yet need to be developed.

References

[1] Baveco, J. M., S. Norman, I. Roessink, N. Galic and P. J. V. d. Brink (2014). Comparing population recovery after insecticide exposure for four aquatic invertebrate species using models of different complexity. Environmental Toxicology and Chemistry **33**(7): 1517-1528.

[2] Chisholm, R. A. and E. Filotas (2009). Critical slowing down as an indicator of transitions in two-species models. Journal of Theoretical Biology **257**(1): 142-149.

[3] van de Leemput, I. A., E. H. van Nes and M. Scheffer (2015). Resilience of Alternative States in Spatially Extended Ecosystems. PLoS ONE **10**(2): e0116859.

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