Individual-based simulation models of multi-species systems under the impact of chemicals: Complex dynamics can lead to changes in population recovery times and regime shifts

Hans Baveco[1], Andreas Focks[1], Frederik De Laender[2] & Paul van den Brink[1,4]

[1] Alterra, Wageningen University and Research centre, Wageningen, The Netherlands. Contact: Hans.Baveco@wur.nl

[2] Université de Namur ASBL, Rue de Bruxelles 61, 5000 Namur, Belgique

[3] Wageningen University, Wageningen UR, PO Box 47, 6700 AA Wageningen, The Netherlands

Introduction

Accounting for species interactions may increase the realism of prospective ERA. Lab and mesocosm studies have shown delayed recovery in the presence of a competitor. Species interactions may however also lead to emergent complex dynamics and alternative stable states (ASS). With ASS sudden shifts to alternative state may occur following disturbances – a characteristic that would be extremely relevant for ERA.

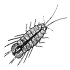
Models may play an important role in identifying the potential for ASS in multi-species systems, especially when IBMs are combined with simpler, analytically tractable models. In the following we start to formulate the wider consequences of dealing with competition systems in ERA. As a first step, we identify what might go wrong with our estimates of recovery and recovery times when these are based on a single-species view and single-species models, when the actual system contains competitive interactions. As a second step, we show how much of the behaviour of the system we remain unaware of when we address competition but a-priori limit ourselves in the analysis to the region in parameter space associated with stable coexistence.

Material & Methods

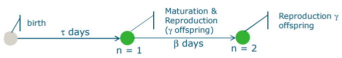
MODELS

Box 1

Individual-based Model (IBM)



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



Competition: 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

Box 2

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

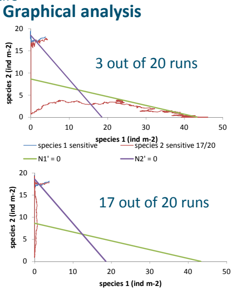
r (=ln λ)	λ (=e^r)
d^{-1}	d^{-1}
0.0418	1.0427
0.0173	1.0175

Population growth rate

ANALYSIS TOOLS

Box 3

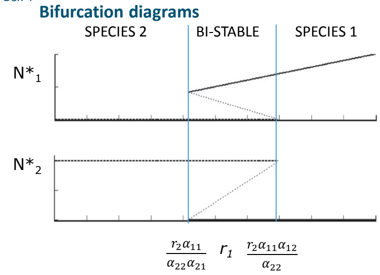
Graphical analysis



Phase-plane plots with trajectories of 20 IBM runs and null-isoclines of ODE for coefficients leading to bi-stability

Box 4

Bifurcation diagrams



Bifurcation diagram for strong interaction case ($\alpha_{12}\alpha_{21} > 1$). Outcome of competition depends on r_1 (stress-dependent). Diagram analytically derived from ODE model [2]. It can also be obtained from IBM simulations.

We use the IBM (Box 1) and the equation-based competition systems (Box 2), parameterized for two aquatic species, *Asellus* and *Gammarus* [1]. Graphical analysis (Box 3) and bifurcation diagrams (Box 4) are used for understanding the behaviour of the system and for identifying the regions in parameter space with different stability outcome. We assume *Asellus* to be the sensitive target species (with density N_1), and *Gammarus* the potential competitor (N_2). Simulations start with *Asellus* at its equilibrium density in isolation (r_1/a_{11} = 41.8 ind m^{-2}), immediately reduced by chemical stress to 5% (2.09 ind m^{-2}). Simulations are run for all combinations of *Gammarus* initial density (1 to 30 ind m^{-2}) and competitive strength a_{12} (0.1 to 4.9). To cover the whole spectrum of possible outcome, we need to distinguish between the case of *Asellus* being a strong and a weak competitor, a_{21} set to 0.5 and to 0.2 respectively. To assess the consequences of restricting the analysis to the competitive coexistence region in parameter space, we compare the obtained results for the full range (see above) with results under competitive coexistence only.

Results

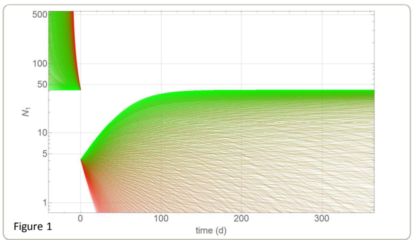


Figure 1

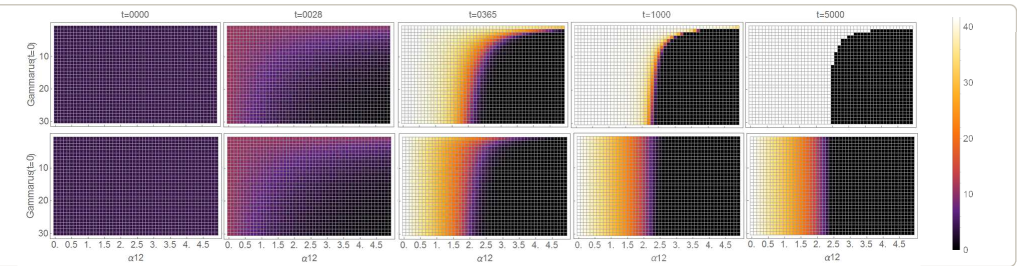


Figure 2

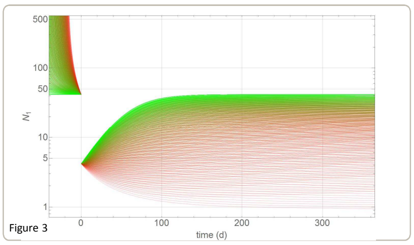


Figure 3

Figure 1. *Asellus* dynamcis for strong interactions and all combinations of initial density and competitive strength of *Gammarus*. Colours: low (green) to high (red) competitive strength. At t=0 the stress event occurs (95% mortality).

Figure 2. Grid plots with *Asellus* density over time (color legend at the right) after a 95% density reduction at t=0, for strong interactions (top row) and weak interactions (bottom row), varying initial densities (y-axis) and competitive strength (y-axis) of *Gammarus*.

Figure 3. As figure 1, but weak interactions and only the coefficients resulting in coexistence.

An observer of *Asellus* dynamics encounters a variety of behaviour, ranging from fast and slow recovery to quick extinction (Fig.1). Initial almost complete recovery might be followed by a decline to extinction. Such variety is related to the settings chosen for the competitor (Fig. 2) and easily explained from bifurcation diagrams (box 4). Many simulated cases might be considered unrealistic and could have been discarded a-priori when the system would have been monitored before the stress. Figure 1 indicates that this might be true for the deterministic system, but not for the stochastic IBM (not shown here). Alternative stable states can be an additional complicating factor as a stress event may cause a regime shift, implying that recovery may never take place. The results for analyses limited to the co-existence regime only (Fig. 3) show that an important part of the potential behaviour of the system, and thus many possible alternative outcomes for recovery times, will not be accounted for.

Implications Risk Assessment

When competition is relevant, it needs to be addressed in models aiming at quantifying recovery. Multi-species models need to address the whole parameter space and account for transient, non-equilibrium situations. Additional observations relevant to RA: 1) There is a need to better define reference states (initial conditions) of multi-species systems 2) Simple(r) models can prove useful, but more realistic, stochastic models (e.g., IBM) are indispensable for the reality check. Analysis methods developed for equation-based models can to some extent be adapted to deal with IBMs 3) Population recovery times as predicted from models without species interactions provide useful information, e.g. in form of minimum recovery times, but those will be realised under environmental conditions only in special cases 4) Model analyses of multi-species systems in combination with better characterisation of ecological parameters can be used to increase the understanding of chemical effects under real-world conditions.

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.

Acknowledgements – The ChimERA project is financed by the Long Range Initiative of CEFIC (www.cefic-lri.org) (project code: LRI-ECO19).