Impact of toxicant stress on the stability characteristics of 2-species competition models

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introduction

- Context: ChimERA* project
- Risk Assessment: Food-webs + species interactions (competition, predation) + spatially-explicit + coupled individual-based and diff. eq. models (IBMs and ODEs)
- Species interactions → complex dynamics!
- Well-studied (since the twenties!) mostly in simple models (ODE)
- To tap into this large body of knowledge & insights → relate our IBMs explicitly to simpler models (“paradigm systems”)
Contents

- Single-species IBM & simple ODE analogue
- Adding competition to both
- Exploring spatial versions

→ The stability characteristics of the system
→ Impact of stress
Single-species: IBM & Logistic growth model

A stochastic, spatially-explicit, IBM*

1) a relatively simple IBM
2) force constant environment
3) initial stable age/size-structure
4) 'remove' spatial structure
5) constant background mortality $\mu_b$
6) Simple density regulation $\mu_{DD}$

$$\mu = \mu_b + \mu_{DD} * N$$

$$\frac{dN}{dt} = (b - \mu_b - \mu_{DD} * N) * N = r * N - \mu_{DD} * N^2 = r * N - \alpha * N^2$$

the logistic growth model, in its original r-$\alpha$ form!

*Baveco et al. (2014), ET&C
Single-species: IBM & Logistic growth model

From IBM to Logistic equation coefficients

μb, background mortality; τ, age at reproduction; γ, clutch-size (female offspring); β, time between broods; n, number of broods

μbDD \rightarrow \alpha

Euler-Lotka equation

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

<table>
<thead>
<tr>
<th>Dimension</th>
<th>\mu_b</th>
<th>τ</th>
<th>γ</th>
<th>β</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asellus</td>
<td>0.001</td>
<td>70</td>
<td>20</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Gammarus</td>
<td>0.01</td>
<td>130</td>
<td>16</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Chironomus</td>
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<td>22</td>
<td>87</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>mayfly</td>
<td>0.006</td>
<td>101</td>
<td>38</td>
<td>-</td>
<td>1</td>
</tr>
</tbody>
</table>

μ_{tox}, stress induced mortality

r_{stress} = r - μ_{tox}

population growth rates
Logistic growth: stress & recovery

analytic solution and equilibrium density:

\[ N_t = \frac{N_0}{\left(1-\frac{N_0 \alpha}{r}\right)e^{-rt} + \frac{N_0 \alpha}{r}} \quad N^* = \frac{r}{\alpha} \]

Chronic stress \(\rightarrow\) lower \(N^*\)

Recovery from single pulse:

time to recovery after a stress survived by fraction \(x\) (when population was in equilibrium state):

\[ T = \frac{1}{r} \ln \frac{c(1-x)}{x(1-c)} \quad \text{c is the fraction of control population size that should be reached for recovery (e.g. 0.95)} \]

No impact of density-dependence rate \(\alpha\) on recovery!

(but only with ‘global’ density-dependence!)

Recovery time \((10\log T)\) depending on growth rate \(r\) and impact (induced mortality) of the stress event
Single-species IBM & Logistic growth model

Recovery dynamics IBM = Logistic

Baveco et al. (2014), ET&C, SI_C
Two-species competition models

Competition between *Asellus* and *Gammarus* added to IBM and Logistic equation, assuming competition increases mortality risk

IBM: including individuals of both species + interaction term

Species 1, added mortality risk from species 2: \( \alpha_{12} \times N_2 \) \( \alpha_{11} \times \alpha_{12} \times N_2 \)

Species 2, added mortality risk from species 1: \( \alpha_{21} \times N_1 \) \( \alpha_{22} \times \alpha_{21} \times N_1 \)

Logistic equation \( \Rightarrow \) The Lotka-Volterra competition model!

Another well-studied system!

\[
\begin{align*}
\frac{dN_1}{dt} &= r_1 \times N_1 - \alpha_{11} \times N_1 \times (N_1 + \alpha_{12} \times N_2) \\
\frac{dN_2}{dt} &= r_2 \times N_2 - \alpha_{22} \times N_2 \times (N_2 + \alpha_{21} \times N_1)
\end{align*}
\]

(the r-\(\alpha\) counterpart of the r-K model analysed in:
Lotka-Volterra (LV) competition model

The graphical analyses, found in every ecology text book

Bifurcation analysis: transitions between alternative stable states

check whether LV model really predicts the stability characteristics of the IBM

<table>
<thead>
<tr>
<th>$\alpha_{AG}$</th>
<th>$\alpha_{GA}$</th>
<th>outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.1</td>
<td><em>Asellus AND Gammarus</em></td>
</tr>
<tr>
<td>0.1</td>
<td>0.5</td>
<td><em>Asellus</em></td>
</tr>
<tr>
<td>5</td>
<td>0.1</td>
<td><em>Gammarus</em></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td><em>Gammarus OR Asellus</em></td>
</tr>
</tbody>
</table>
IBM competition

COMPETITIVE EXCLUSION

Gammarus wins

Asellus wins

COEXISTENCE

Asellus & Gammarus

BI-STABILITY

Gammarus wins (initial $G = 100 \times \text{initial } A$)

Asellus wins (initial $A = \text{initial } G$)
LV - stress impact on stability properties

Bifurcation diagram for ‘control parameter’ $r$ predicts what will happen...

...when chronic stress or repeating pulses lower the population growth rate $r$

For $\alpha_{12}\alpha_{21} > 1$

For $\alpha_{12}\alpha_{21} < 1$

Adapted from: Chisholm, R. A. and E. Filotas (2009)
Example dynamics with pulsed stress

**No exposure**

**COEXISTENCE**

Pulsed exposure of *Asellus* leads to higher density of *Gammarus*, same stability regime

**EXCLUSION**

Pulsed exposure of *Asellus* leads to coexistence with *Gammarus*, transition to another stability regime!

**Pulsed exposure of *Asellus***

Impact repeated pulses = impact average exposure
Becoming spatial

When the represented system in the IBM is e.g. that of a FOCUS scenario (ditch, stream or pond)

Spatial versions of the LV system in the bi-stable regime have been studied extensively.

Keywords:
- spatial heterogeneity – in our case e.g. gradient in exposure (→ gradient in r)
- mobility – with fast mixing the system behaves like the non-spatial system again, even with heterogeneity
Exploring: IBM & bi-stability & no mobility

500m ditch as 500 patches of 1 m² (x = 1..500); 800 days simulation

ASELLUS

GAMMARUS

0 500

P(movement) = 0  P(movement) = 0

0 500

Whole ditch population size

local [G] versus local [A] at t=800

Asellus  Gammarus

0 4000

500 3500

0 3000

500 2500

0 2000

500 1500

0 1000

500 500

0 0

800 0

800 0

800 0

800 0

Asellus population size

Gammarus population size

0 40

5 35

10 30

15 25

20 20

25 15

30 10

35 5

40 0

0 20 40 60 80 100

Asellus population size

0 40

5 35

10 30

15 25

20 20

25 15

30 10

35 5

40 0

0 20 40 60 80 100

Asellus population size
IBM & bi-stability & limited mobility

ASELLUS
P = 0.01

GAMMARUS
P = 0.01

Whole ditch population size

local [G] versus local [A] at t=800

Asellus population size
IBM & bi-stability & limited mobility & stress

- Adding chemical stress, acting on *Asellus*
- Pulse once every 30 days
- Spatial gradient in intensity:
  \[ \mu_{\text{tox}} = \exp(-0.03 \times x) \]
IBM & bi-stability & limited mobility & stress

ASELLUS

P = 0.01

GAMMARUS

P = 0.01

Whole ditch population size

local [G] versus local [A] at t=800
Conclusions

- A wealth of complex behaviour can be hidden in even a relatively simple IBM of interacting species
- To interpret the impact of chemical stress on such a system correctly, it is important to understand the stability regime
- It’s (nearly) impossible to infer from the time-series of both species’ abundance what is really going on
- Relating complex IBM to simpler models is a nice way (the only one?) to obtain this understanding
- NB for multi-species systems, a single-species based view of recovery is not appropriate
Thanks for your attention

**ChimERA**: an integrated modelling tool for ecological risk assessment – towards more ecologically realistic assessment of chemicals in the environment

Kindly funded by:
LV - Bi-stability

Basin of attraction for the two alternative stable states (purple: *Asellus* present at density $N^*=41.8$, light-blue: *Gammarus* present at density $N^*=17.3$).

Vector plot of the change in density, trajectories from a 10 x 10 grid of initial densities and the null-clines of the system.
IBM & bi-stability & limited mobility

ASELLUS
P = 0

GAMMARUS
P = 0.01

Whole ditch population size

local [G] versus local [A] at t=800
IBM & bi-stability & limited mobility

ASELLUS

P = 0.01

GAMMARUS

P = 0

Whole ditch population size

local [G] versus local [A] at t=800
IBM & bi-stability & limited mobility & stress

ASELLUS

0
P(movement) = 0
500
0

GAMMARUS

P(movement) = 0
500

Whole ditch population size

local [G] versus local [A] at t=800
IBM & bi-stability & limited mobility & stress

ASELLUS

\[ P = 0 \]

\[ \text{X} \rightarrow \]

GAMMARUS

\[ P = 0.01 \]

\[ \text{X} \rightarrow \]

Whole ditch population size

Local [G] versus local [A] at t=800

Asellus population size vs Gammarus population size
IBM & bi-stability & limited mobility & stress

ASELLUS

P = 0.01

GAMMARUS

P = 0

Whole ditch population size

local [G] versus local [A] at t=800