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

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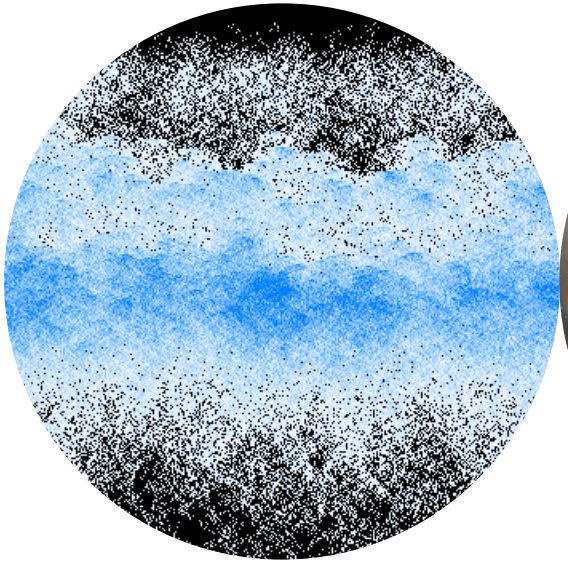

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introduction

- 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

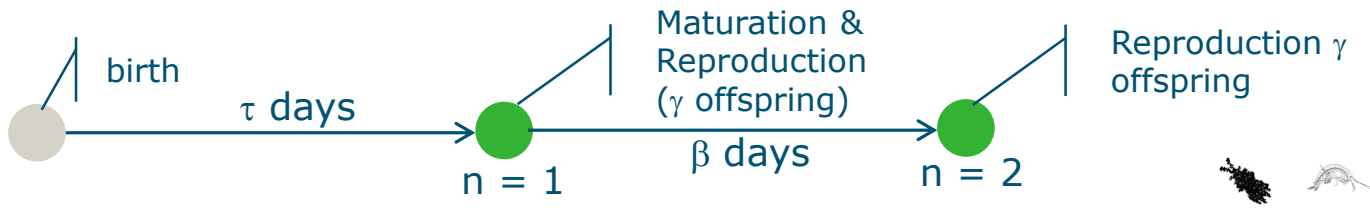
- Single-species IBM & simple ODE analogue
- Adding competition to both
- Exploring spatial versions

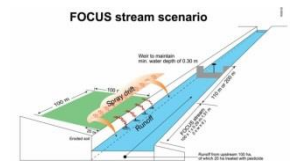
→ The stability characteristics of the system

→ 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 μ_b

6) Simple density regulation μ_{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-α form!

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*Baveco et al. (2014), ET&C

Single-species: IBM & Logistic growth model

From IBM to Logistic equation coefficients

μ_{DD} → α

	μ_b	τ	γ	β	n
Dimension	d^{-1}	d	ind	d	
Asellus	0.001	70	20	-	1
Gammarus	0.01	130	16	20	5
Chironomus	0.0007	22	87	-	1
mayfly	0.006	101	38	-	1

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

Euler-Lotka equation

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

r	λ (=e^r)
d^{-1}	d^{-1}
0.0418	1.0427
0.0173	1.0175
0.1960	1.2165
0.0300	1.0305

population growth rates

Stress induced mortality μ_{tox} → $r_{stress} = r - \mu_{tox}$

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Logistic growth: stress & recovery

analytic solution and equilibrium density:

$$N_t = \frac{N_0}{\left(1-\frac{N_0\alpha}{r}\right)e^{-rt}+\frac{N_0\alpha}{r}} \qquad N^* = r/\alpha$$

$$\frac{dN}{dt} = r * N - \alpha * N^2$$

Chronic stress → lower N^*

Recovery from single pulse:

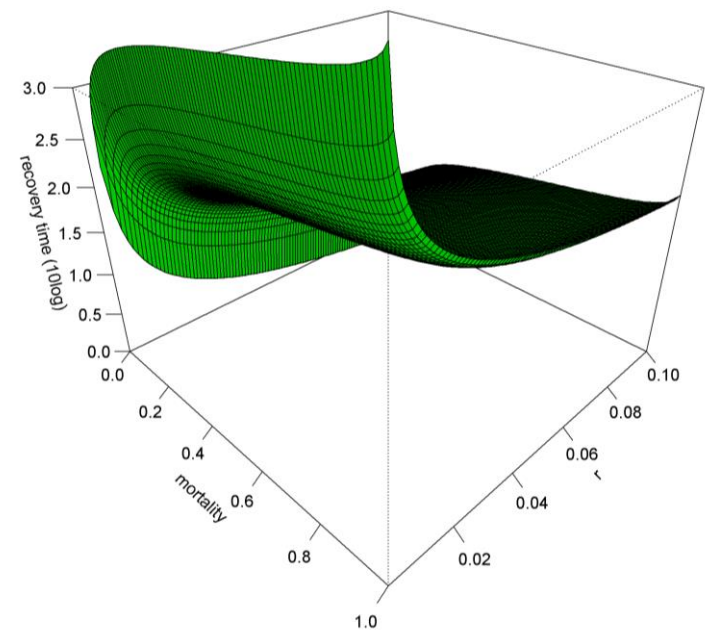
time to recovery after a stress survived by fraction x (when population was in equilibrium state):

$$T = \frac{1}{r} ln \frac{c(1-x)}{x(1-c)}$$

c is the fraction of control population size that should be reached for recovery (e.g. 0.95)

No impact of density-dependence rate α on recovery!

(but only with 'global' density-dependence!)



Recovery time (^{10}logT) depending on growth rate *r* and impact (induced mortality) of the stress event

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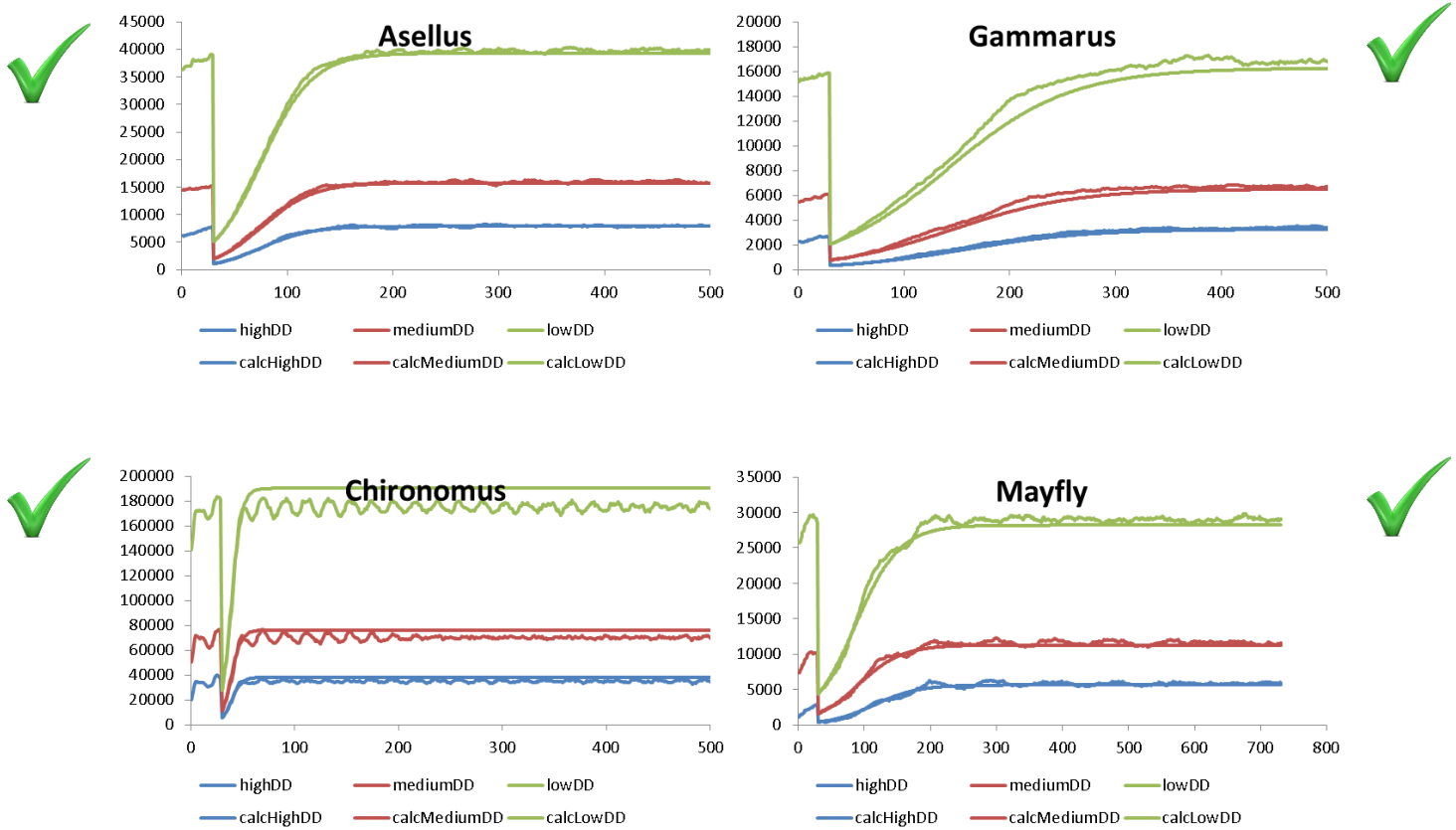
Single-species IBM & Logistic growth model

Recovery dynamics IBM = Logistic



Baveco et al. (2014), ET&C, SI_C

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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: $\alpha_{12} * N_2$ $\qquad$ $\alpha_{11} * \alpha_{12} * N_2$

Species 2, added mortality risk from species 1: $\alpha_{21} * N_1$ $\qquad$ $\alpha_{22} * \alpha_{21} * N_1$

Logistic equation → The Lotka-Volterra competition model!

Another well-studied system!

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

(the r-α counterpart of the r-K model analysed in:
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.)

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Lotka-Volterra (LV) competition model

The graphical analyses, found in every ecology text book

Bifurcation analysis: transitions between alternative stable states

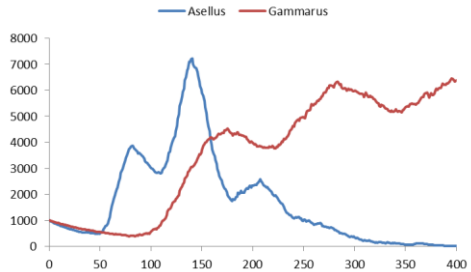
check whether LV model really predicts the stability characteristics of the IBM

α_{AG}	α_{GA}	outcome	
0.1	0.1	*Asellus* AND *Gammarus*	COEXISTENCE
0.1	0.5	*Asellus*	COMPETITIVE EXCLUSION
5	0.1	*Gammarus*	COMPETITIVE EXCLUSION
3	1	*Gammarus* OR *Asellus*	BI-STABILITY

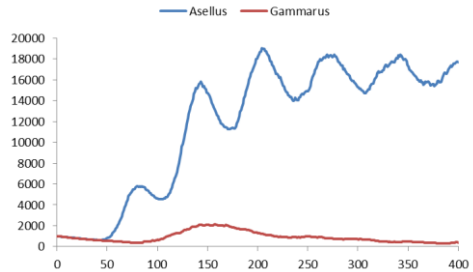
IBM competition

COMPETITIVE EXCLUSION

✓ *Gammarus* wins

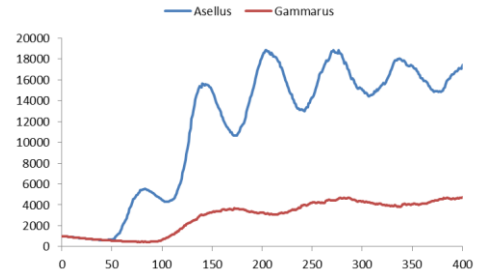


✓ *Asellus* wins

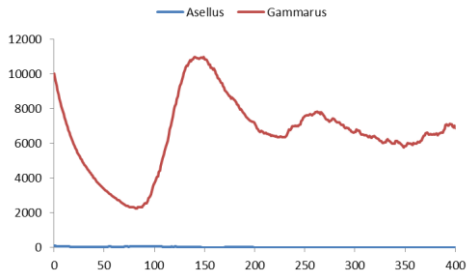


COEXISTENCE

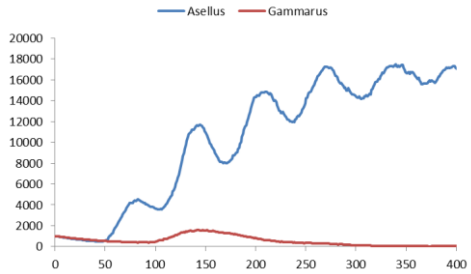
✓ *Asellus* & *Gammarus*



✓ BI-STABIILITY



Gammarus wins (initial *G* = 100 x initial *A*)



Asellus wins (initial *A* = initial *G*)

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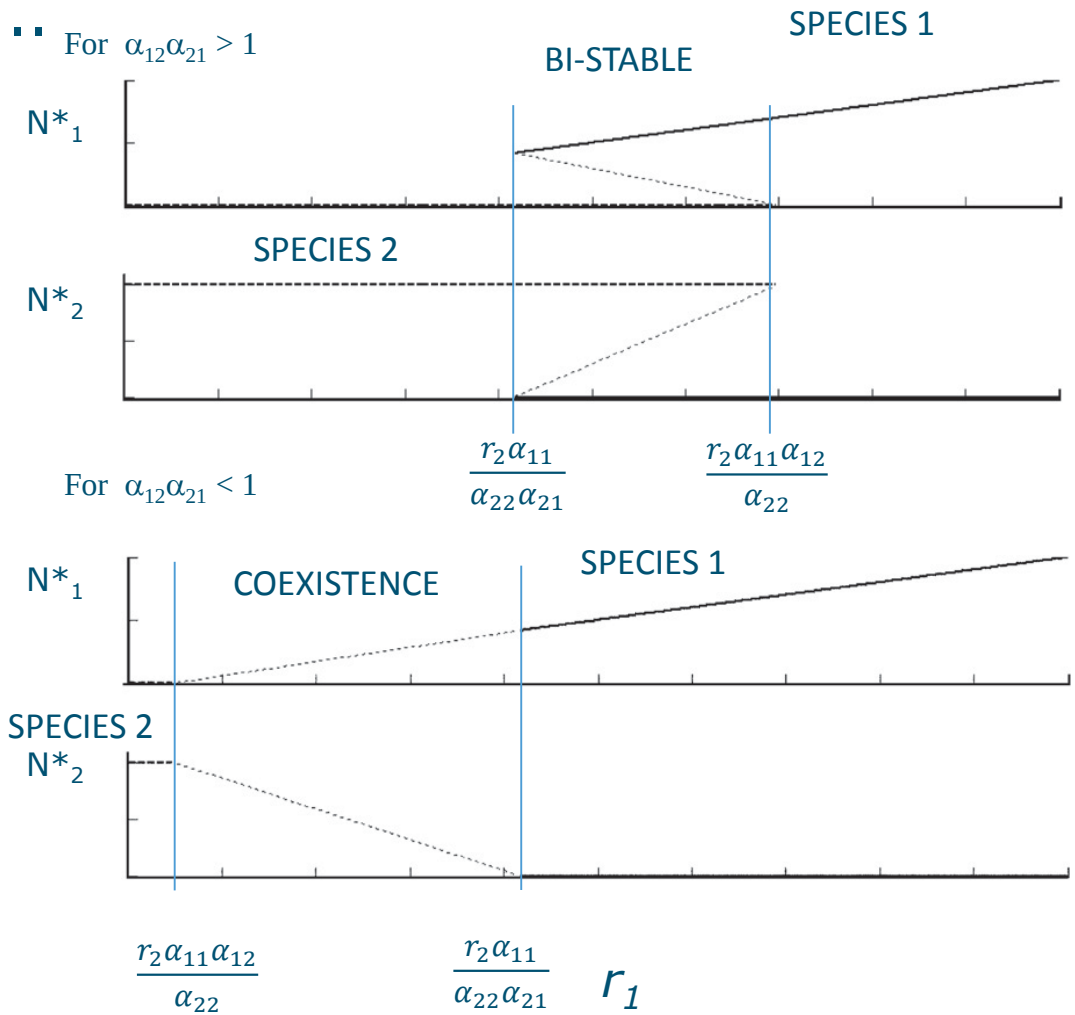
LV - stress impact on stability properties

Bifurcation diagram for 'control parameter' *r* predicts what will happen...

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

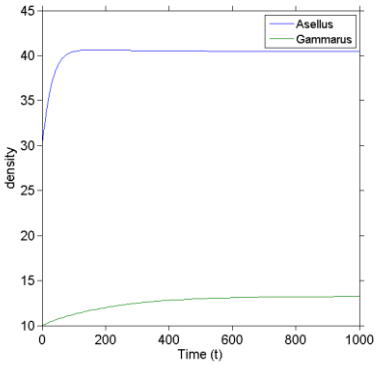


Adapted from: Chisholm, R. A. and E. Filotas (2009)

Example dynamics with pulsed stress

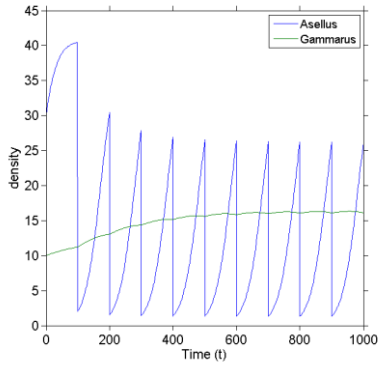
No exposure

COEXISTENCE



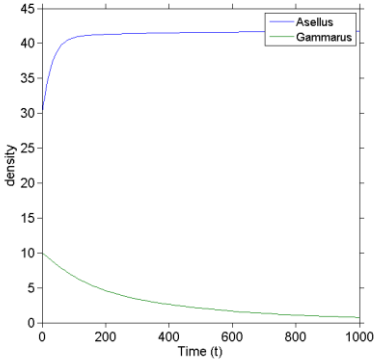
Pulsed exposure of Asellus

COEXISTENCE

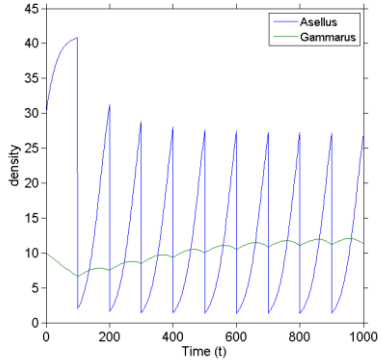


Pulsed exposure of *Asellus* leads to higher density of *Gammarus,* same stability regime

EXCLUSION



COEXISTENCE



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

Impact repeated pulses = impact average exposure

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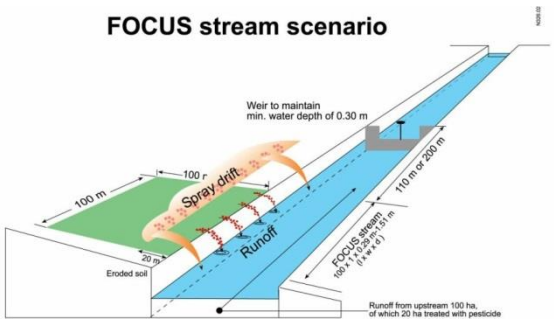
Becoming spatial

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.
E.g., van Nes, E. H. and M. Scheffer (2007). "Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift." American Naturalist 169(6): 738-747.

- 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

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Exploring: IBM & bi-stability & no mobility

500m ditch as 500 patches of 1 m^2(x = 1..500); 800 days simulation

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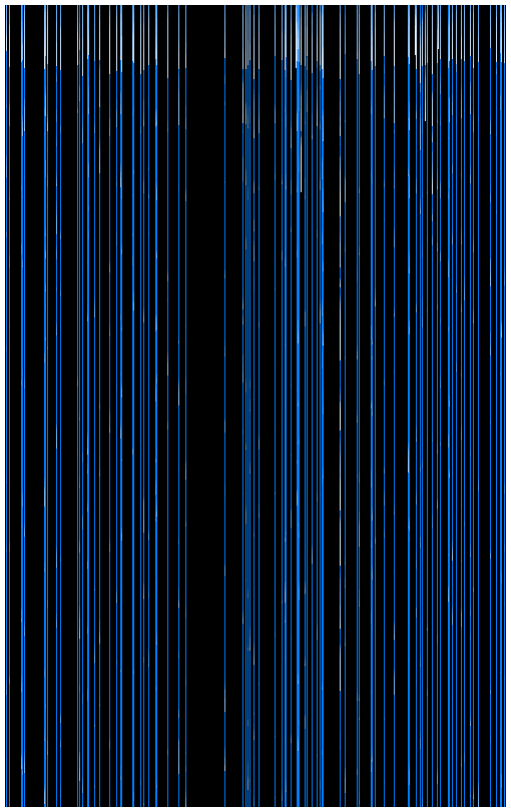
0 P(movement) = 0 500

0

↓ t

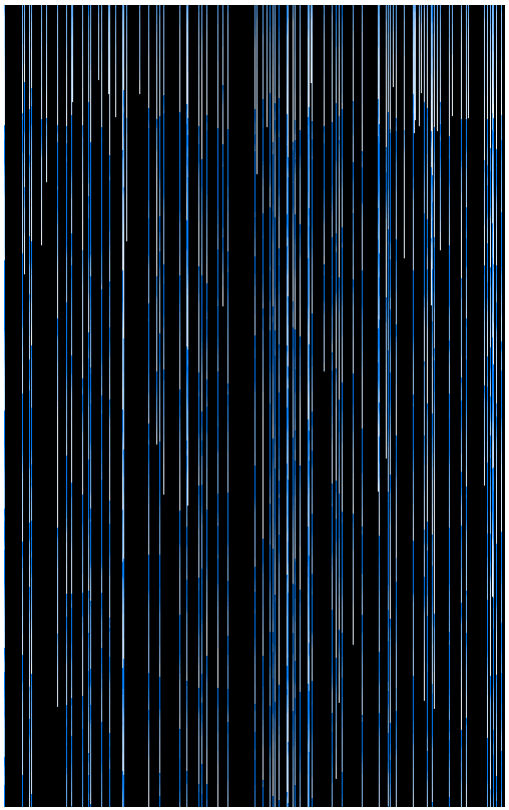
800



X →

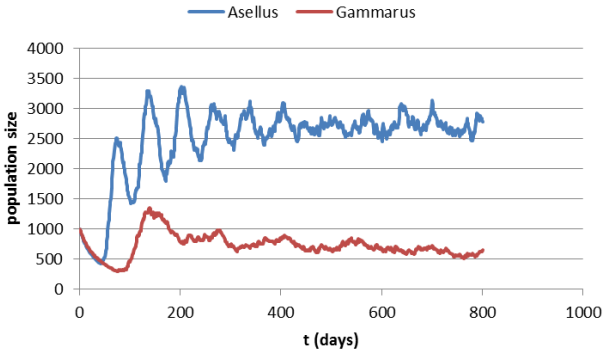
GAMMARUS

0 P(movement) = 0 500

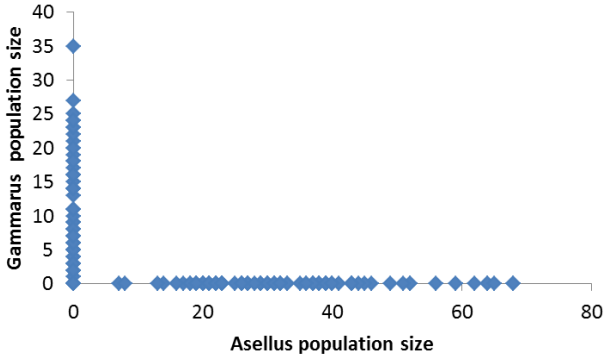


X →

Whole ditch population size



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



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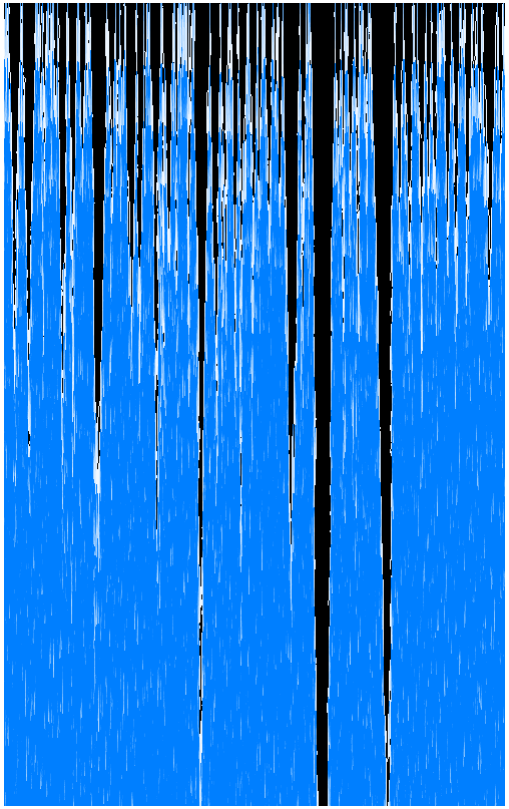
IBM & bi-stability & limited mobility

ASELLUS

P = 0.01



GAMMARUS

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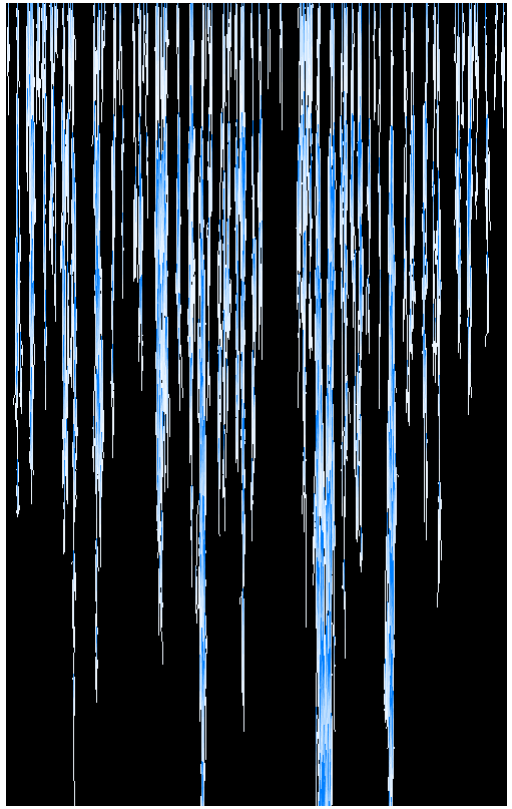
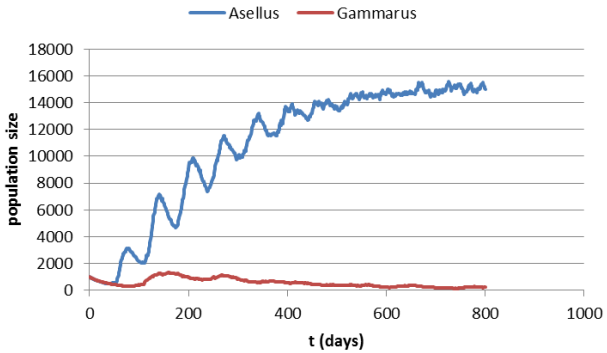


↓ t

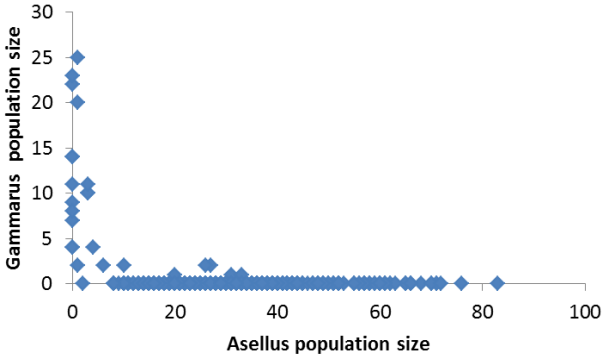
X →

X →

Whole ditch population size



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



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IBM & bi-stability & limited mobility & stress

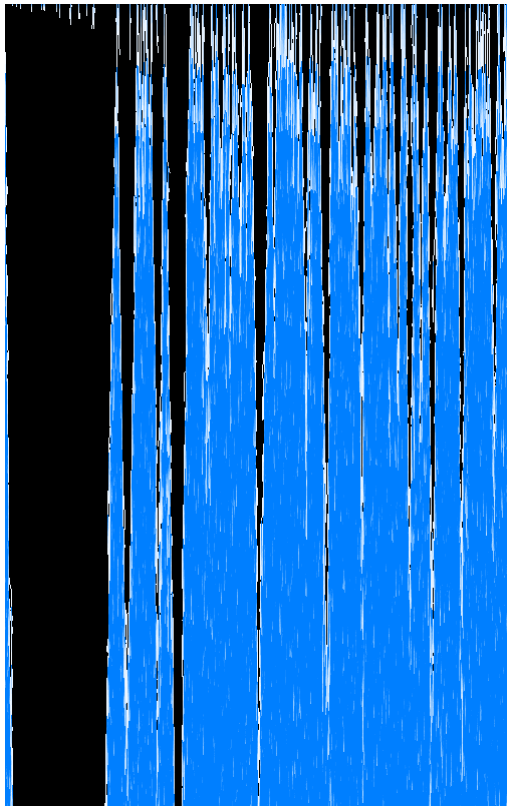
- Adding chemical stress, acting on *Asellus*
- Pulse once every 30 days
- Spatial gradient in intensity:

$$\mu_{tox} = \exp(-0.03 * x)$$

IBM & bi-stability & limited mobility & stress

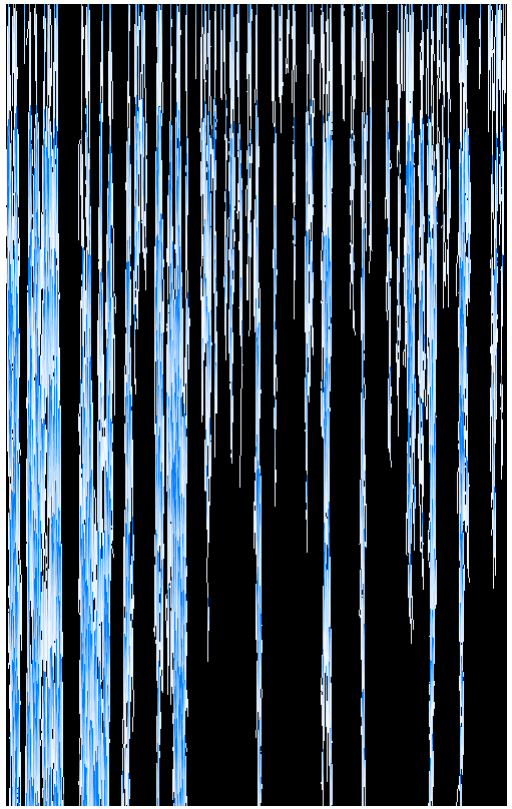
ASELLUS

P = 0.01



GAMMARUS

P = 0.01

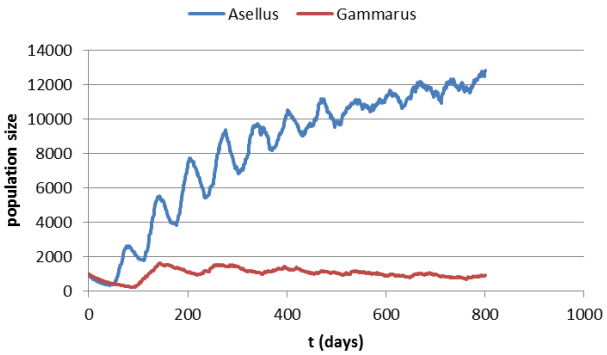


↓ t

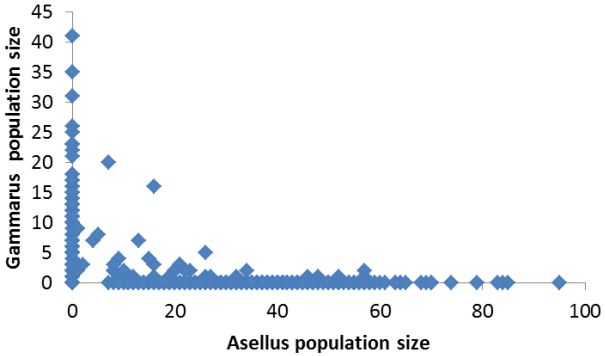
X →

X →

Whole ditch population size



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



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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:

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LRI The Long-range Research initiative

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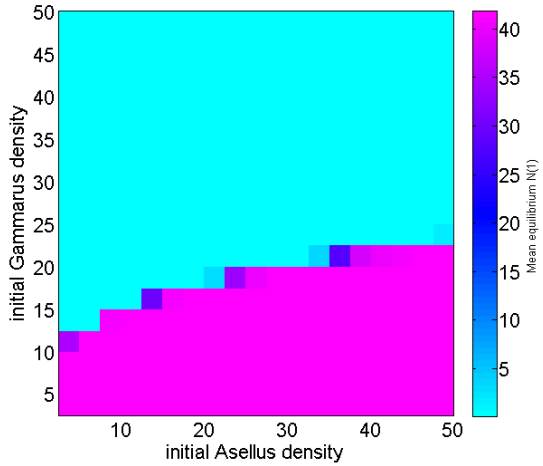
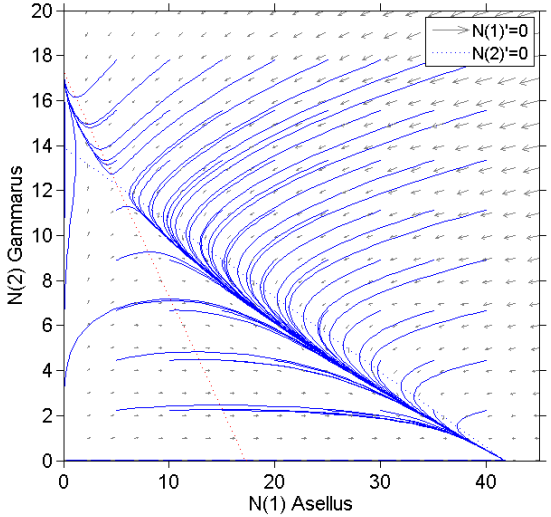
LV - Bi-stability





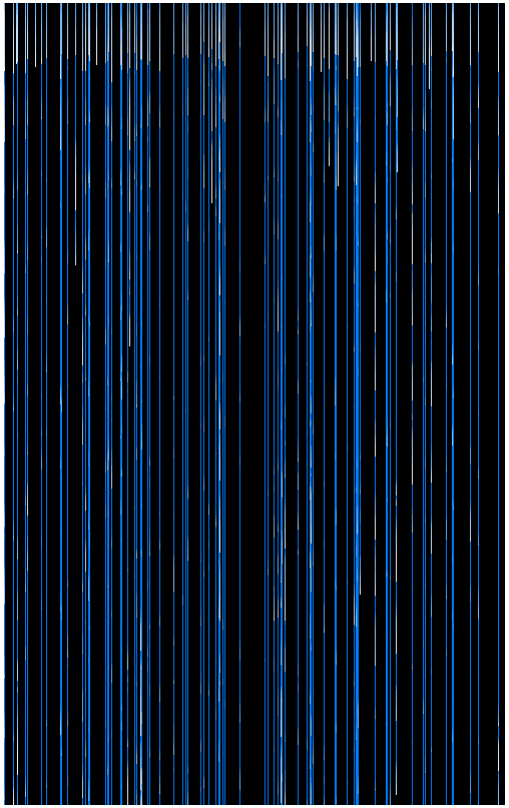
Basin of attraction for the two alternative stable states (purple: *Asellus* present at density N*=41.8, light-blue: *Gammarus* present at density N*=17.3).

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

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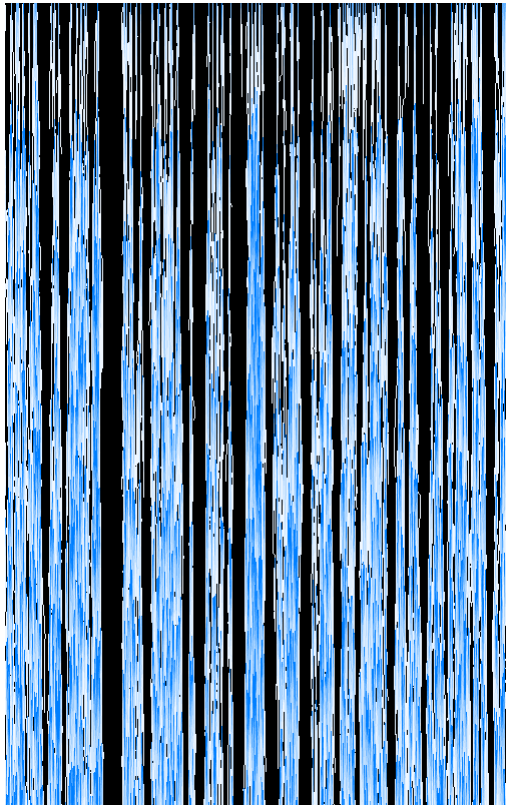
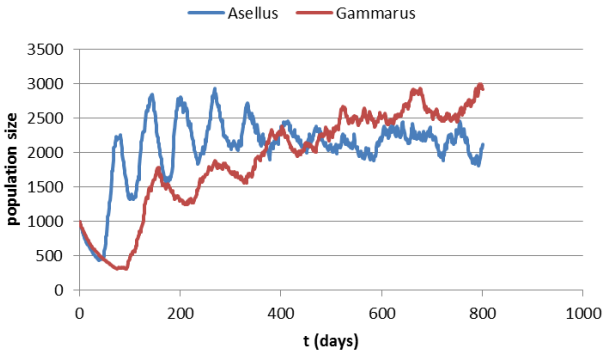


↓ t

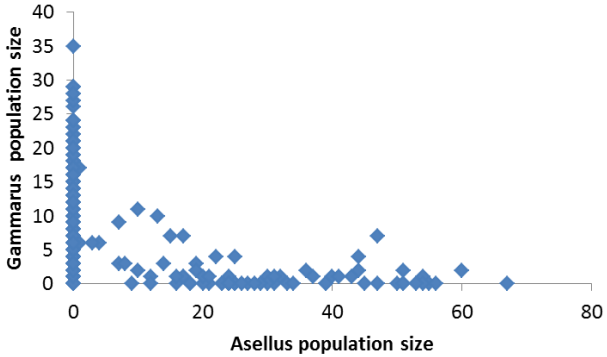
X →

X →

Whole ditch population size



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



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ASELLUS

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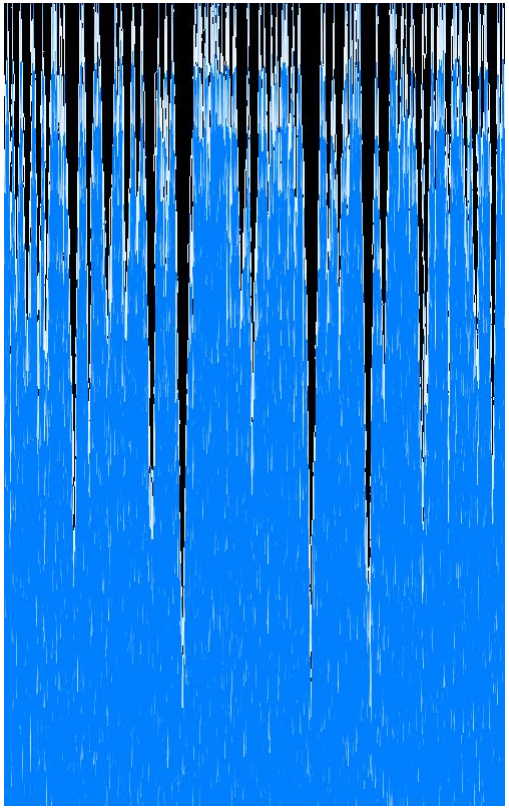

GAMMARUS

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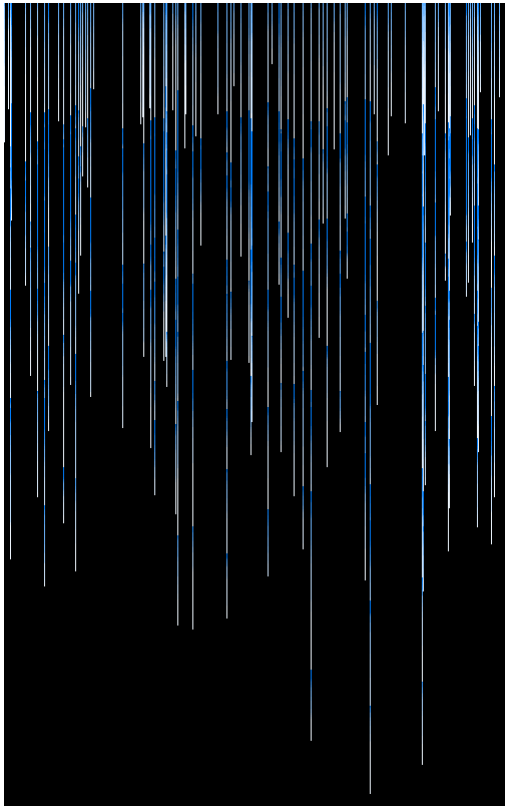
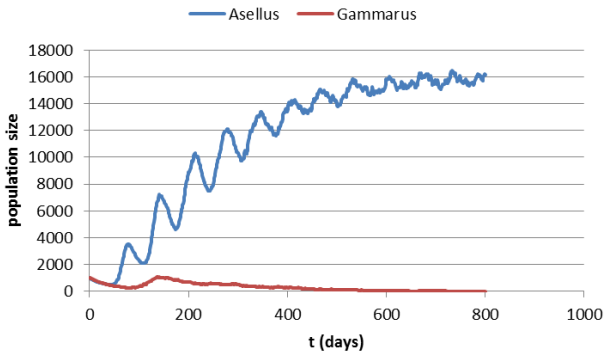


↓ t

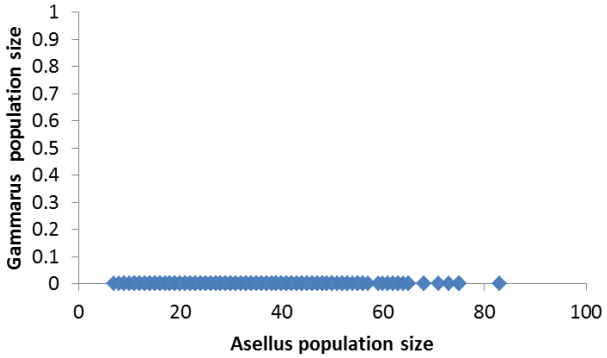
X →

X →

Whole ditch population size



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



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IBM & bi-stability & limited mobility & stress

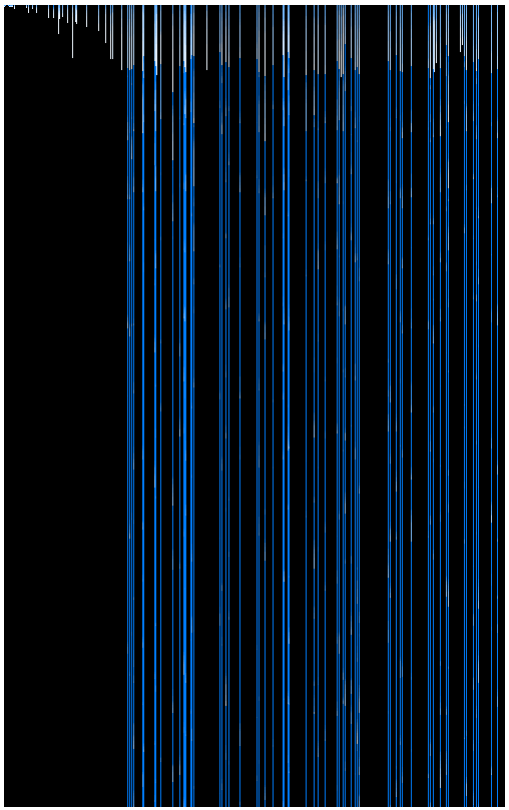
ASELLUS

0 P(movement) = 0 500

0

↓ t

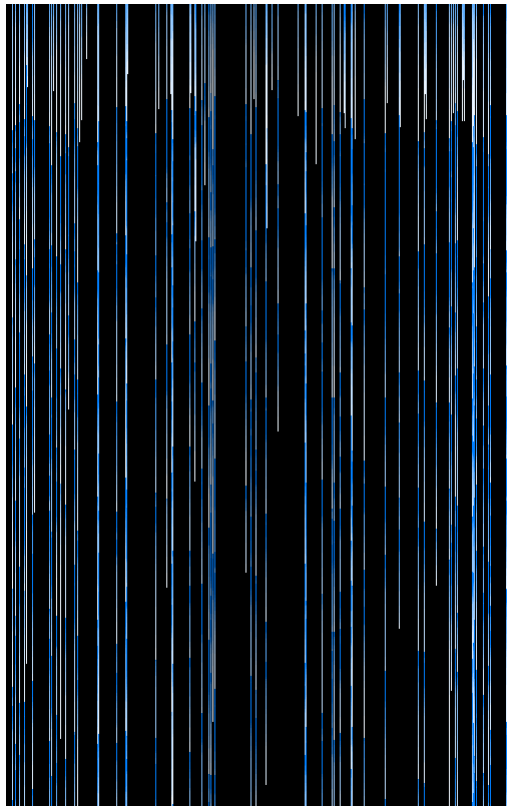
800



X →

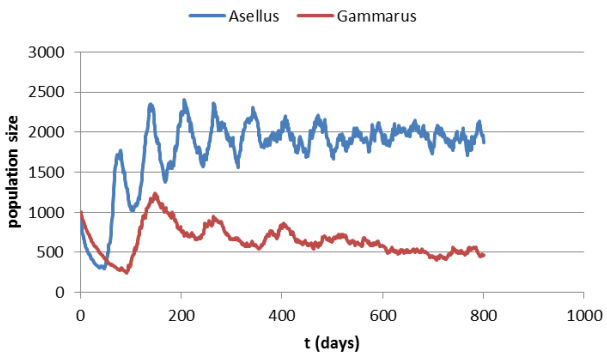
GAMMARUS

0 P(movement) = 0 500

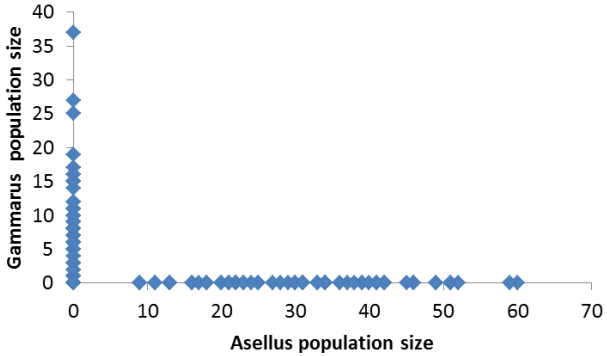


X →

Whole ditch population size



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

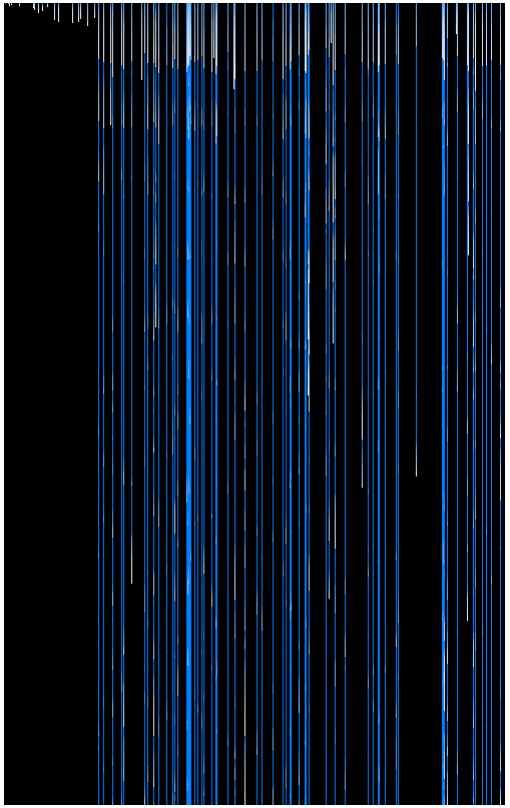


ALTERRA WAGENINGEN UR

IBM & bi-stability & limited mobility & stress

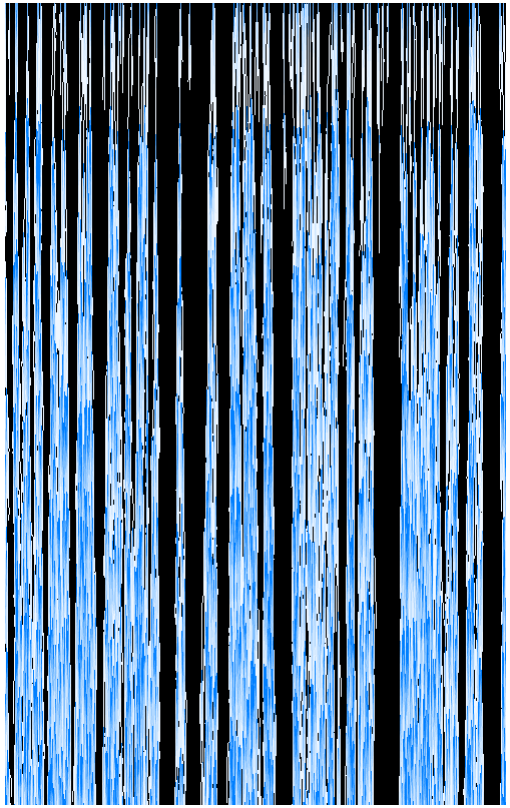
ASELLUS

P = 0



GAMMARUS

P = 0.01

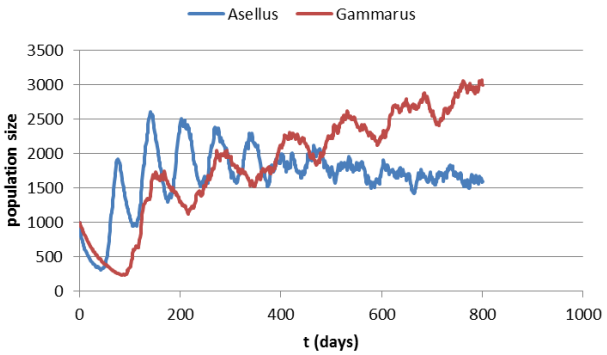


↓ t

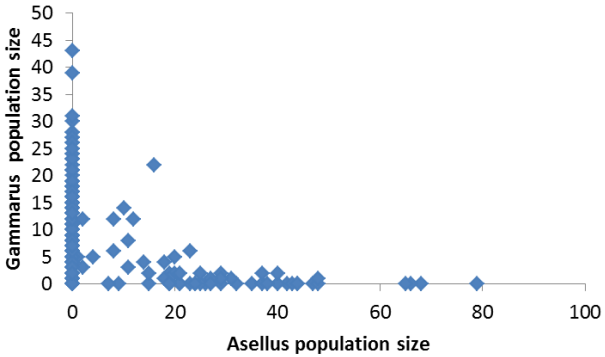
X →

X →

Whole ditch population size



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



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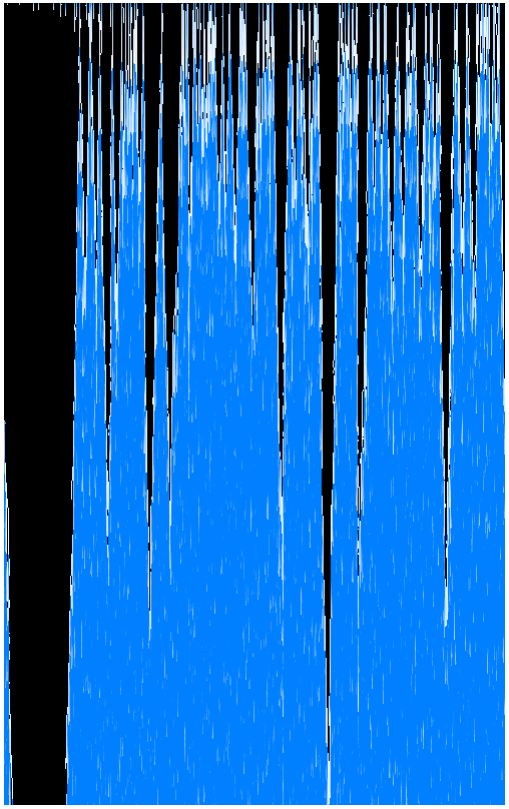
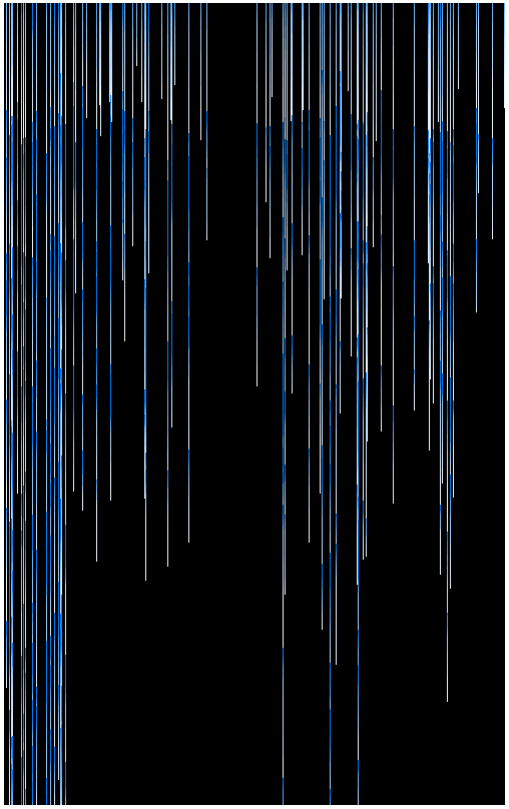
ASELLUS

P = 0.01



GAMMARUS

P = 0

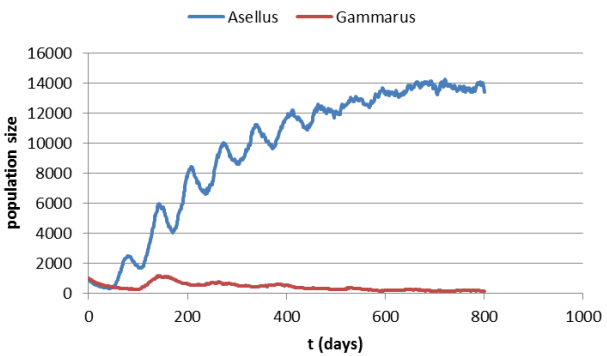


↓ t

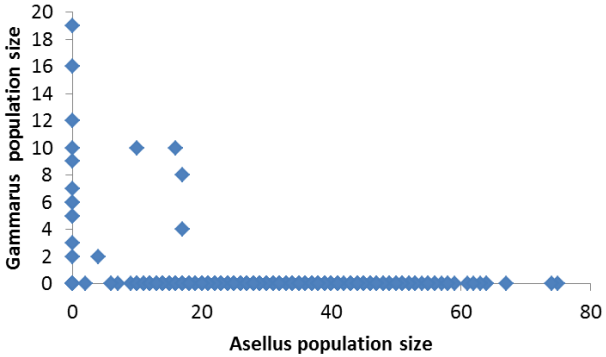
X →

X →

Whole ditch population size



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



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