Pulsed perturbations in population dynamics

Ludovic Mailleret

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V. Calcagno, F. Hamelin, V. Lemesle & F. Grognard

Institut Sophia Agrobiotech

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200 pp. working on plant health issues

- interactions b. plants, pests/symbionts
- interactions b. pests and enemies
- population dynamics in time and space
- development of ecological pest management programs

Methods

- comparative and functional genomics
- population and community ecology
- mathematical and computer modelling

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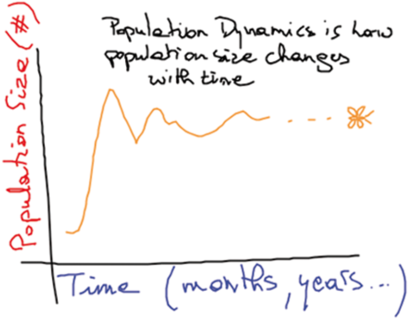
Population dynamics modelling

Understand how/why population sizes change with time and space

- predict plant pest and disease dynamics and evolution
- design control actions: external perturbations of population sizes



Main applications

- efficient and sustainable use of plant resistance
- optimization of biological control programs

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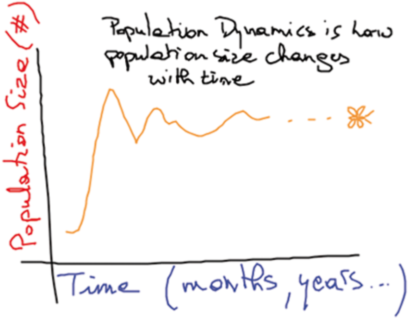
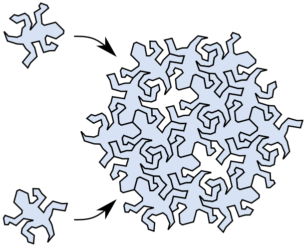


External perturbations of population size

Two main types of perturbations

- increase population size (introductions of individuals)
  - → immigration, reintroduction biology, biological control
- decrease population size (removal of a fraction of the population)
  - → emigration, harvesting, culling



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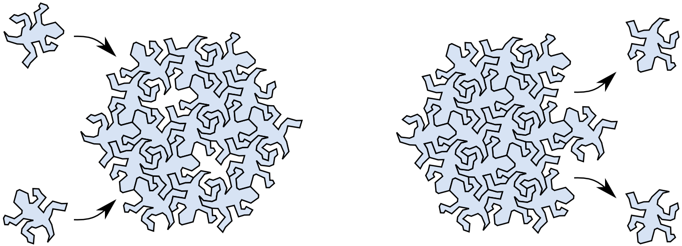
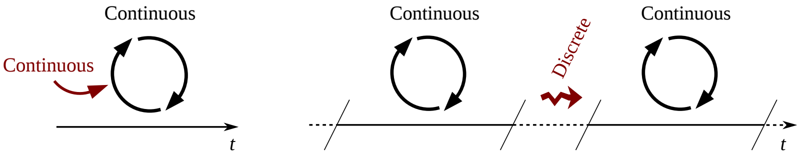


Continuous or pulsed perturbations

Both types of perturbation may occur:

- continuously over time
- as pulses at discrete time instants



- intensity of perturbations significantly influences population dynamics
- role of the temporal pattern of perturbations has been much less studied

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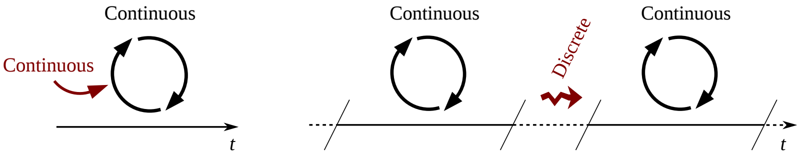

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Outline

Framework to study the influence of pulsed perturbations on population dynamics

- for a given perturbation effort
- role of temporal pattern (magnitude / frequency)

Investigate the two main perturbation types

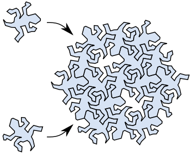
- pulsed introductions
- pulsed removals
- if time: pulsed introductions & removals

Pulsed introductions

with special emphasis on

augmentation biological control & adaptation under pulsed migration

Framework for studying pulsed introductions



Compare different patterns of introductions for a given introduction effort μ

Continuous introductions[1]

$$\left\{ \dot{x} = f(x) + \mu. \right.$$

1: Kermack, McKendrik (1932), Kostitzin (1937)

Pulsed introductions[2]

$$\begin{cases} \dot{x} = f(x), \\ x(kT^+) = x(kT) + \mu T. \end{cases}$$

2: Mailleret, Grognard (2006, 2009), Mailleret, Lemesle (2009)

Both models account for the same mean rate of introduction

- comparison of different introduction patterns through introduction period
- pulsed model reduces to continuous one as $T \to 0$

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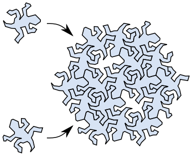

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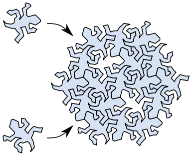

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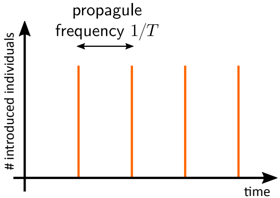
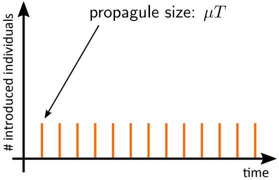
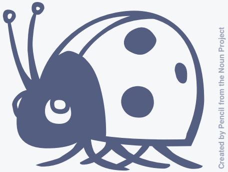




Augmentation biological control



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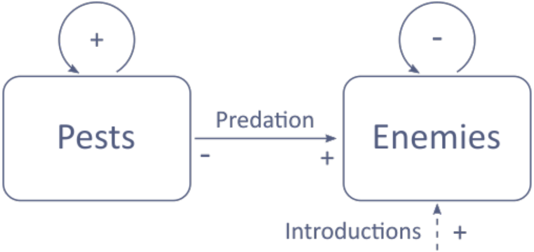

Fight pests through regular introductions of natural enemies

- parasitoids or predators
- supplied by biofabrics

- General predator-prey model

$$\begin{cases} \dot{x} = f(x) - g(.)y, & \text{pest / prey} \\ \dot{y} = h(.)y - m(.)y & \text{BCA / predator} \end{cases}$$

- Natural enemy introductions

$$\{ \; y(kT^+) = y(kT) + \mu T, \; \forall n \in \mathbb{N}$$

How different introduction strategies affect pest control ?

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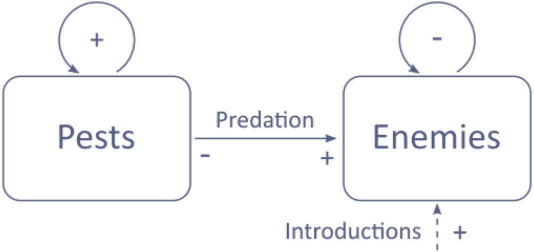

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Augmentation biological control

Null model : no density dependance in BCA population

Pest control is achieved provided[a] :

$$\mu > S = \sup_{x \geq 0} \frac{mf(x)}{g(x)}$$

[a] Mailleret, Grognard (2009)

- pest control always possible
- threshold intro. rate increases w. m et $f(.)$, decreases w. $g(.)$
- introduction strategy (T) does not impact stability

What about transient dynamics ?

- time for pest to fall below some damage threshold $\bar{x}$

$$\Pi(T, x_0, t_0) = \int_{t_0}^{t_f} (\tau - t_0) d\tau, \quad x(t_f) \triangleq \bar{x}$$

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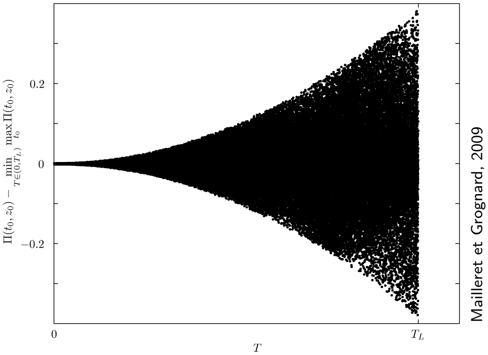
- $\mathbb{E}_{t_0 \in (0,T)}\left[\Pi(t_0, x_0)\right] = \min_T \left(\max_{t_0} \Pi(t_0, x_0)\right)$ (= **constant**)
- $\mathrm{Var}_{t_0 \in (0,T)}\left[\Pi(t_0, x_0)\right]$ increases with T

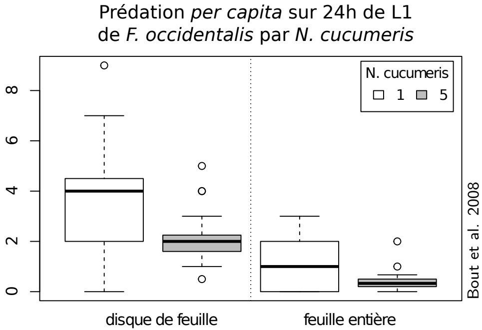
- mean transients not influenced by intro. strategy
- variance increases with larger/less frequent introductions

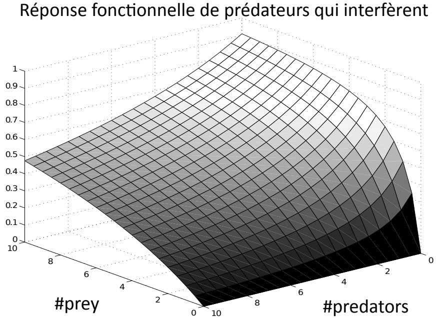


anomaly of $\Pi(t_0)$ w.r.t T, $t_0 \in (0, T)$

Augmentation biological control (2)

Negative density dependance in BCA population





Per capita predation decreases with BCA population size

$$\begin{cases} \dot{x} = f(x) - g(x,y)y \\ \dot{y} = h(x,y)y - m(.)y \end{cases}$$

$$g(x,y) = g\left(\frac{x}{\theta y + (1-\theta)}\right)$$

$g(.) \nearrow$; $\theta \in (0,1]$: $-$DD index

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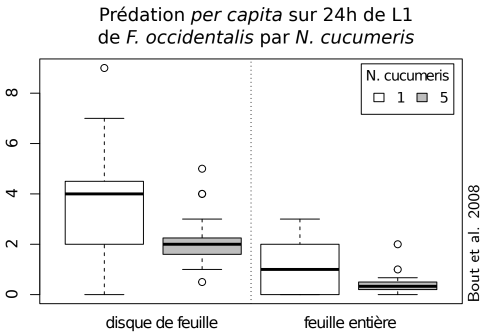

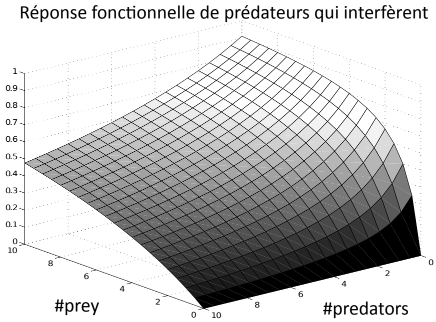

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Pest control is achieved iff[a]:

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[a] Nundloll et al. 2010

A biological and a strategy condition

- negative DD shall not be too strong
- threshold introduction rate increases with T ($\to +\infty$)
- too large T makes pest suppression impossible
- transients: the smaller the T, the faster pests are suppressed

When DD comes into play, introduction pattern has major impacts

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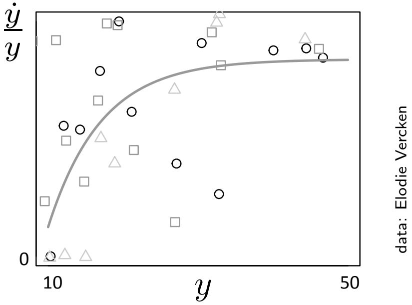
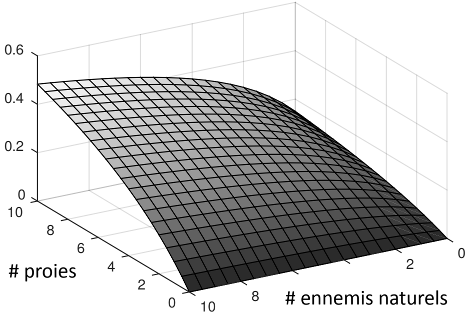
Augmentation biological control (3)

Positive density dependance in BCA population

Taux de croissance de trichogrammes



Réponse fonctionnelle avec DD positive



Per capita predation/natality increases with BCA population size

$$\begin{cases} \dot{x} = f(x) - g(x)q_f(y)y \\ \dot{y} = h(g(x)q_f(y))q_r(y)y - m(.)y \end{cases}$$

Component Allee effects :
$q_f(.), q_r(.)$ increasing

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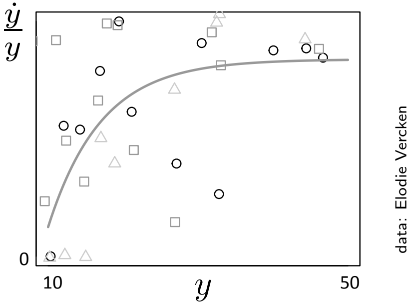

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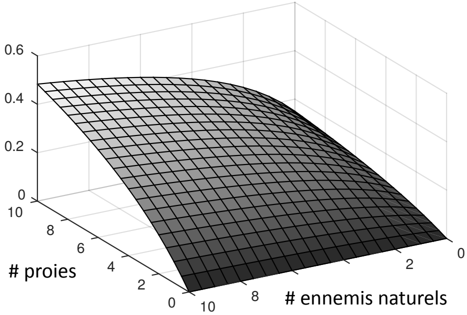

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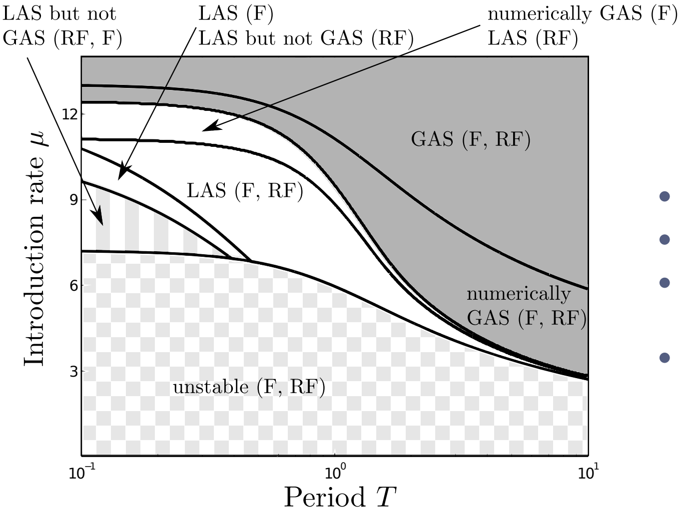
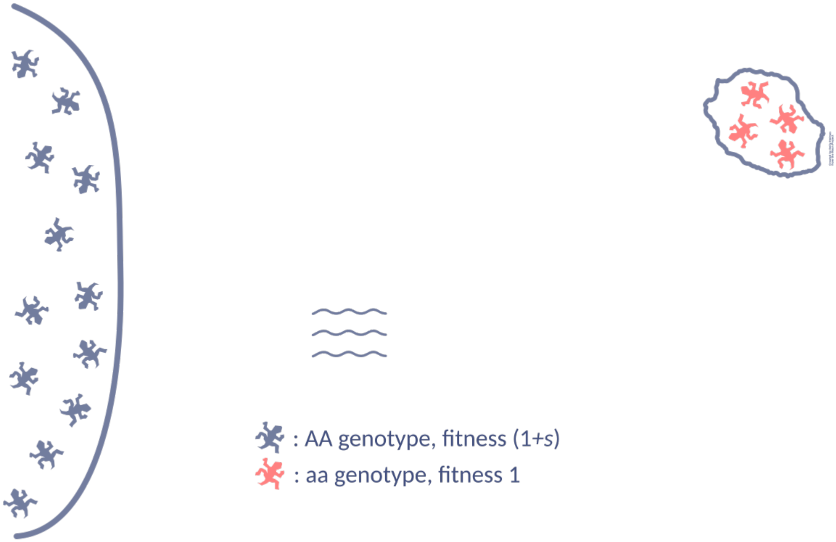


Bajeux et al. 2017

- reverted results compared to negative DD
- pest control facilitated by T large
- transients: the larger the T, the faster pest suppression
- what positive DD influences matters

Pulsed migration and adaptation

Pulsed migration from mainland to island[1]



[1] Aubree et al. 2023

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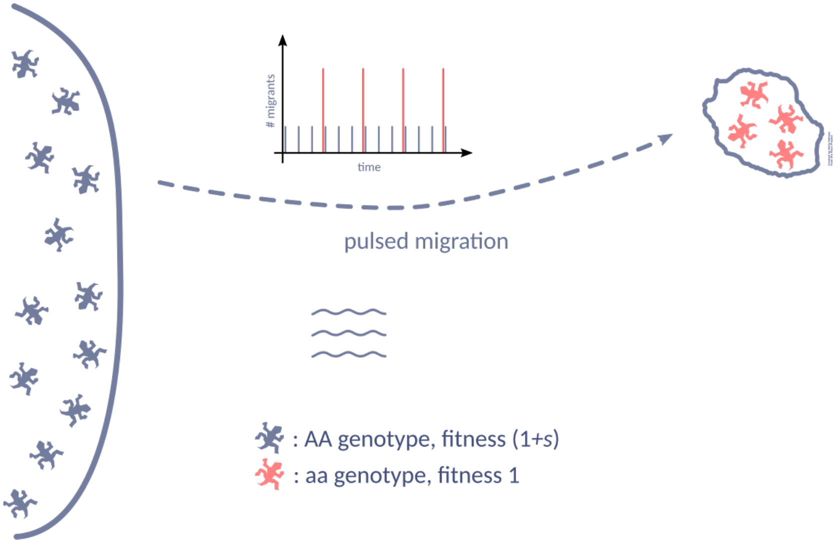

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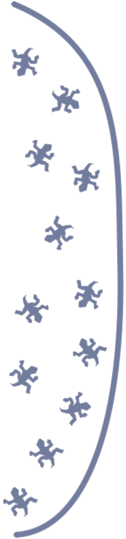

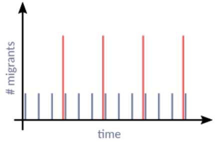

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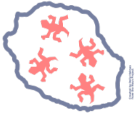

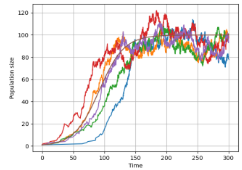

stochastic framework
(genet. drift + selection)

: AA genotype, fitness (1+s)

: aa genotype, fitness 1

: aA genotype, fitness (1+hs)

[1] Aubree et al. 2023

Pulsed migration from mainland to island (2)

In the long run AA genotype will overtake the island population

- is it faster (or not) with pulsed migration ?

AA fixation is (initially) faster with pulsed migration when:

$$s \; < \; \frac{-(K+1)^2}{2K^2(1+h(K-1))} \; < \; 0$$

In a nutshell:

- sufficiently deleterious alleles favored by migr. pulsedness
- neutral and beneficial alleles disfavored

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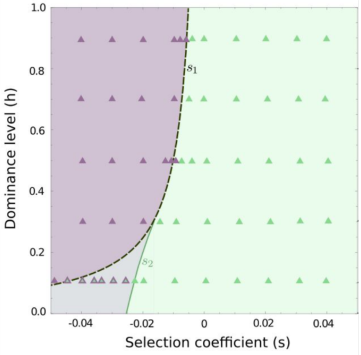
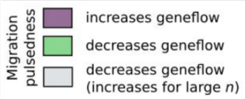
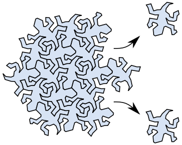




Pulsed removals

with special emphasis on harvesting and vaccination

Framework for studying pulsed removals (1)



Compare different patterns of removals for a given taking effort E

Continuous removals[1]

$$\left\{ \dot{x} = f(x) - Ex. \right.$$

1: Schaefer (1954)

Pulsed removals (first attempt)[2]

$$\begin{cases} \dot{x} = f(x), \\ x(kT^{+}) = x(kT) - \tilde{E}x. \end{cases}$$

2: from Lu *et al.* (2003)

- Mean taking effort in the continuous model

$$\langle E_c \rangle = \frac{\dot{x}_E}{x} = \frac{Ex}{x} = E$$

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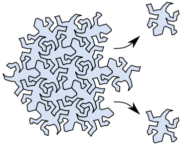

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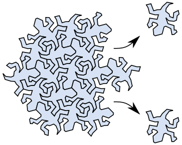


Compare different patterns of removals for a given taking effort E

- Mean taking effort in the pulsed model:

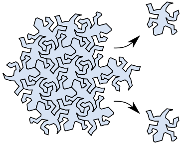
$$\langle E_p \rangle = \frac{1}{T}\int_{kT}^{(k+1)T} \frac{\dot{x}_E}{x}\,d\tau = \frac{1}{T}\int_{kT}^{kT^+} \frac{\dot{x}_E}{x}\,d\tau = \frac{1}{T}\int_{x(kT)}^{x(kT^+)} \frac{dx_E}{x},$$

so that:

$$\langle E_p \rangle = \frac{1}{T}\ln\left(\frac{1}{1-\tilde{E}}\right) \neq E$$

In Lu *et al.* (2003) framework, the mean taking effort varies with T

Framework for studying pulsed removals (3)



Desired property: mean taking effort constant to allow comparisons

Solve:

$$\langle E_p \rangle = E = \frac{1}{T} \ln\left(\frac{1}{1-\tilde{E}}\right) \Rightarrow \tilde{E} = 1 - e^{-ET}$$

$\Rightarrow$ more frequent removals shall be smaller...

A well-posed pulsed taking model reads:

$$\begin{cases} \dot{x} = f(x), \\ x(kT^+) = e^{-ET}\, x(kT). \end{cases}$$

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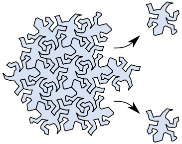

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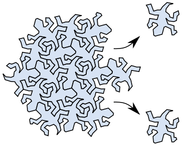

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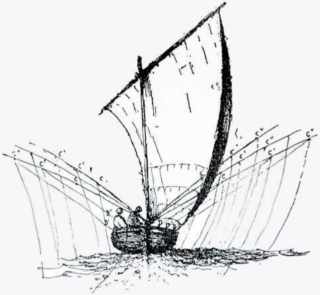
Pulsed harvests



Pulsed harvesting

Assuming logistic growth, we get the 'pulsed Schaefer model'

$$\begin{cases} \dot{x} = rx\left(1 - \dfrac{x}{K}\right), \\ x(kT^+) = e^{-ET}\, x(kT). \end{cases}$$

Properties:

- periodic solution $x_p^*(t)$, GAS if $E < r$
- $x^* = 0$ is GAS if $E > r$.

(*i.e.* similar to continuous model)

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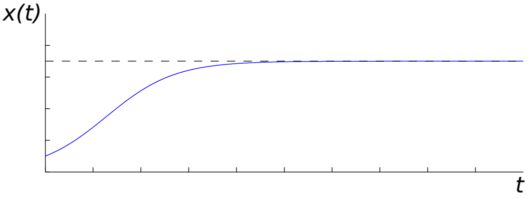

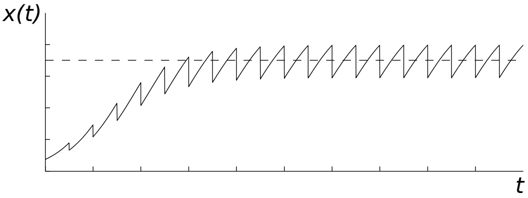

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Pulsed harvesting (2)

Compute the mean yield over a time period T:

$$Y_p(T) = \frac{\left(1 - e^{-ET}\right)\left(1 - e^{(E-r)T}\right)}{\left(1 - e^{-rT}\right)} \frac{K}{T}$$

This can be compared to continuous harvesting yield:

$$Y_c = KE\left(1 - \frac{E}{r}\right) = \lim_{T \to 0} Y_p(T)$$

Properties:

- temporal pattern of pulsed harvests matters
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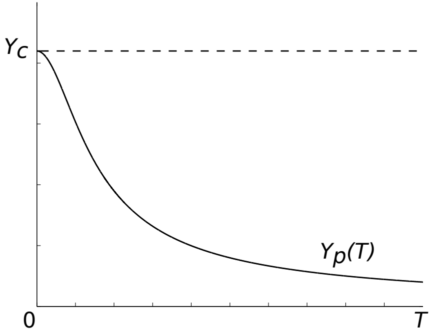
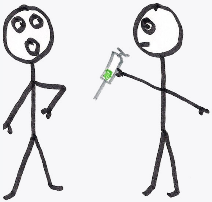
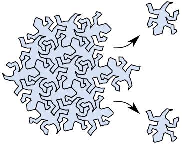


Pulsed vaccination



Pulsed vaccination (1)



Vaccination of individuals is also a form of removal of S individuals

Continuous vaccination at rate Ψ in the susceptible population[2]

$$\begin{cases} \dot{S} = b - \mu S - \beta SI - \Psi S \\ \dot{I} = \beta SI - \mu I - \alpha I \end{cases}$$

In such a model

$$\mathcal{R}_{eff} = \frac{\beta S_c^*}{\alpha + \mu} = \frac{\beta}{(\alpha + \mu)} \frac{b}{(\Psi + \mu)}$$

Vaccination prevents disease spread when

$$\Psi > \frac{b\beta}{\alpha + \mu} - \mu$$

[2]model adapted from Onyango & Müller, 2014

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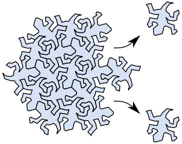

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Pulsed vaccination (2)

A comparable pulsed vaccination model reads[3]

$$\begin{cases} \dot{S} = b - \mu S - \beta SI \\ \dot{I} = \beta SI - \mu I - \alpha I \\ S(kT^+) = e^{-\Psi T} S(kT) \end{cases}$$

T-periodic infection free solution $S^*(t, \Psi)$, so that:

$$\mathcal{R}_{eff} = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau$$

[3] pulsed vaccination has originally been introduced by Agur *et al.*, 1993. Advocated as a more efficient vaccination strategy, a statement which is still debated today.

Pulsed vaccination (3)

Pulsed vaccination prevents disease spread when:

$$\frac{1}{T}\int_0^T S^*(\tau,\Psi)d\tau < \frac{(\alpha+\mu)}{\beta}$$

unfortunately, isolating Ψ is difficult, and ultimately uninformative

Yet, numerics show vaccination may fail for large

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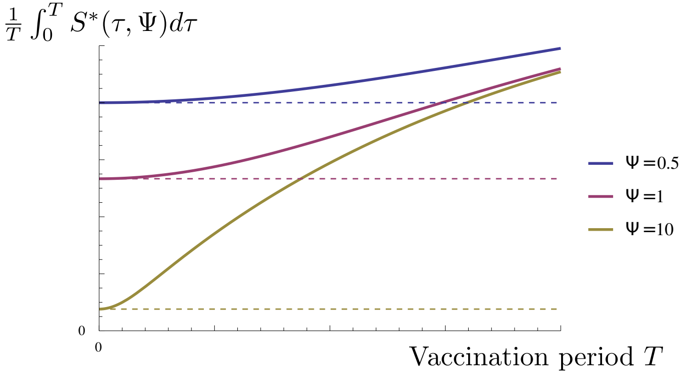

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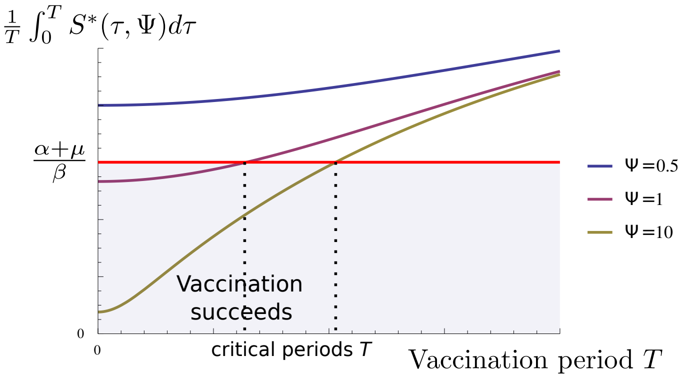
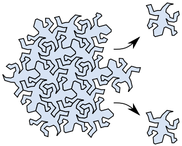


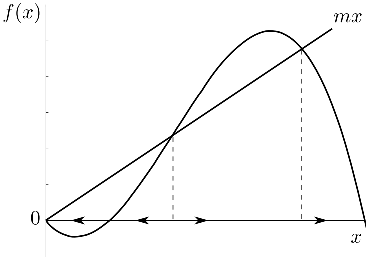
Mixing: pulsed migration

Pulsed migration and the Allee effect (1)



Emigration from a habitat is also a form of removal

- emigration is harmful to populations
- even more in species subjected to Allee effects



Pulsed emigration more harmful than continuous emigration:

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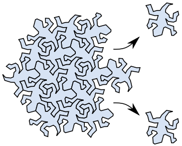

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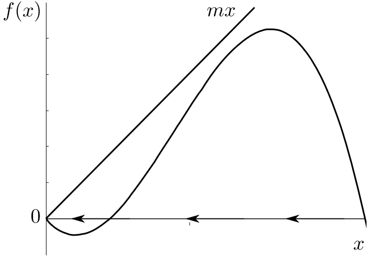

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$$

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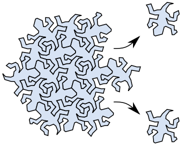

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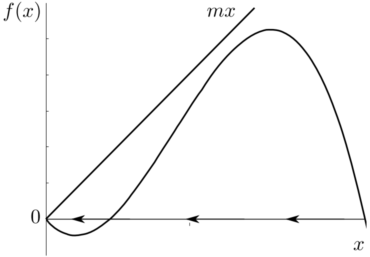


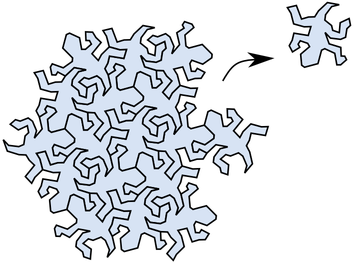
Pulsed emigration more harmful than continuous emigration:[4]

- for any $m > 0$, large T will always lead to pop. extinction

[4] Mailleret and Lemesle, 2009

Pulsed migration and the Allee effect (2)

In nature, migration is usually a bi-directional process



emigration & immigration

- emigration harmful, pulsed even more than continuous
- immigration beneficial, pulsed even more than continuous

How do pulsed migration, migration period and
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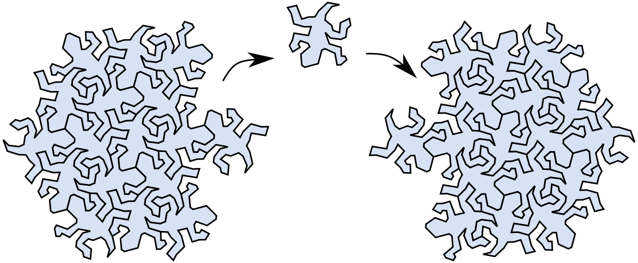

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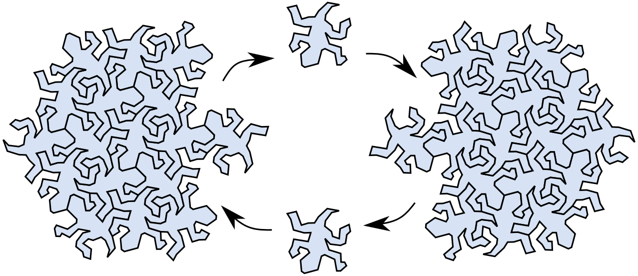

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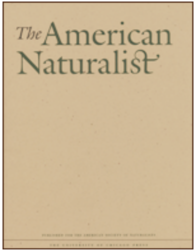
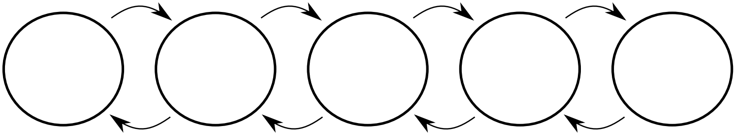
Pulsed migration and the Allee effect (3)

Keitt *et al.* (2001): populations 'pinned' at intermediate migration





Stepping stone, continuous migration

Pulsed migration and the Allee effect (3)

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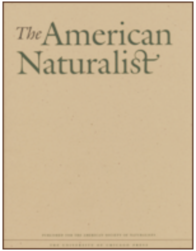

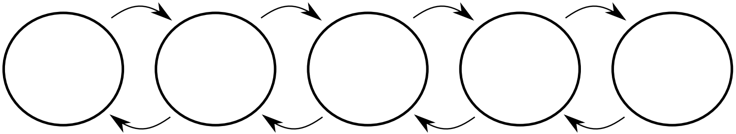

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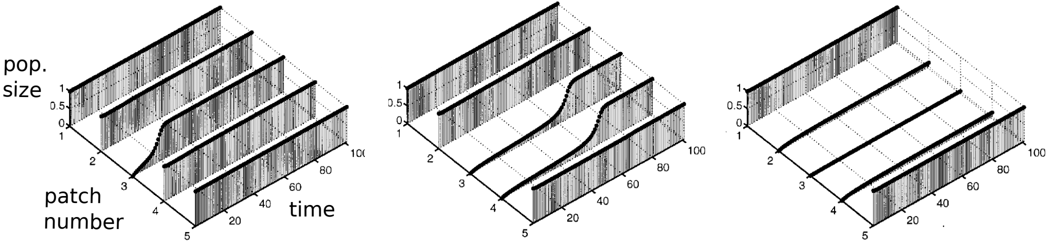
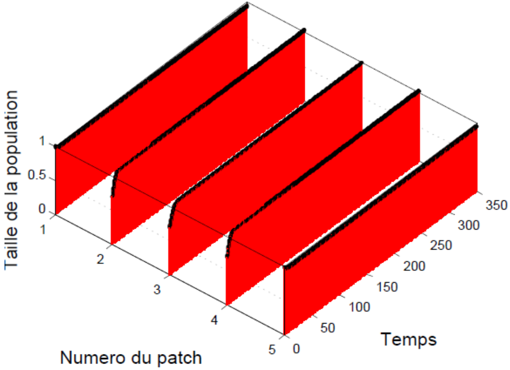
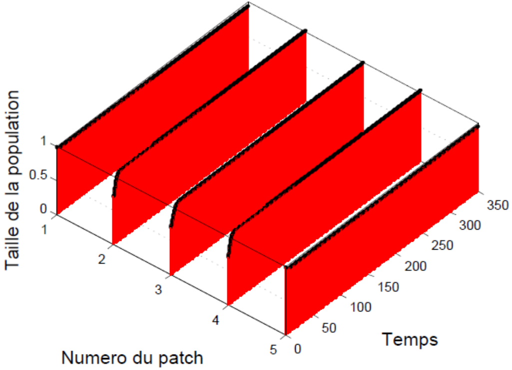


Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period T



pulsed migration



continuous migration

same effects as continuous migration: population stable

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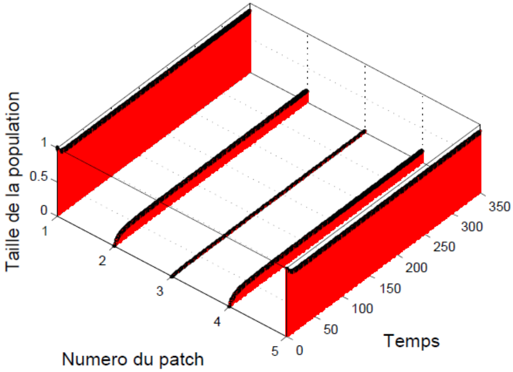

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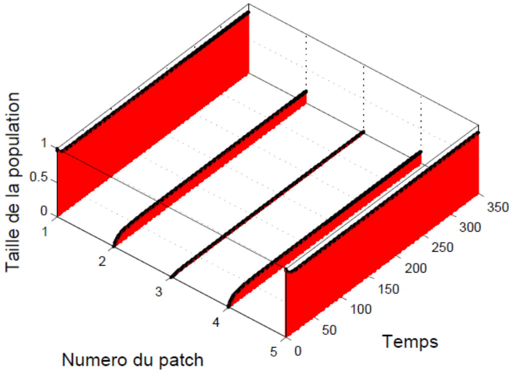

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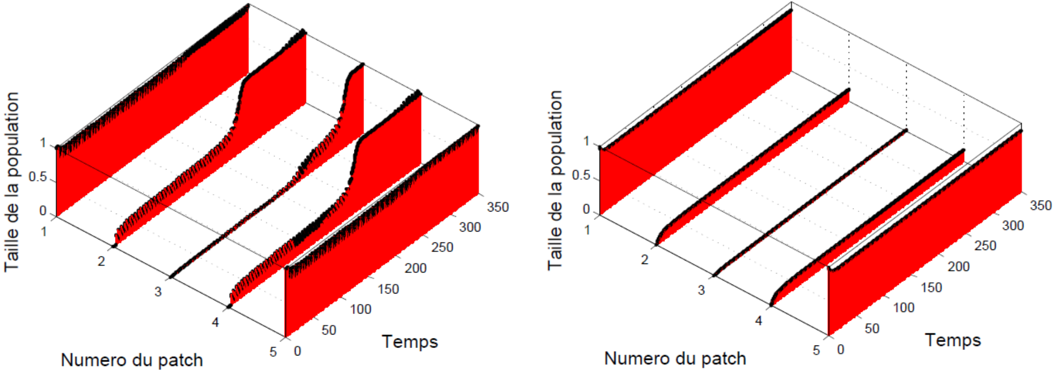
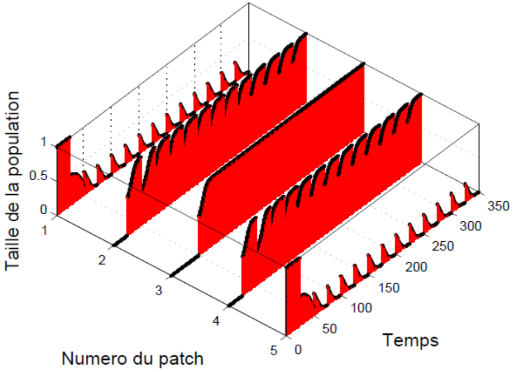


pulsed migration **continuous** migration

emerging patterns for larger periods T: invasion succeeds

Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period T



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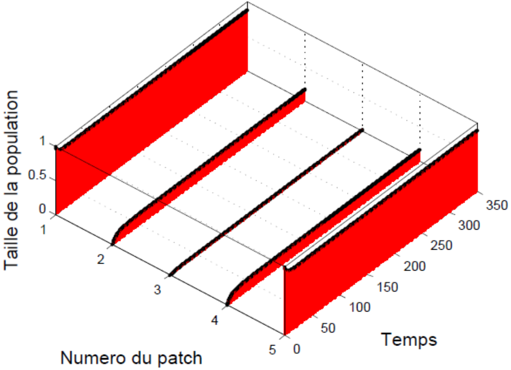

continuous migration

emerging patterns for larger periods T: pop-up effect

Pulsed migration and the Allee effect (4)

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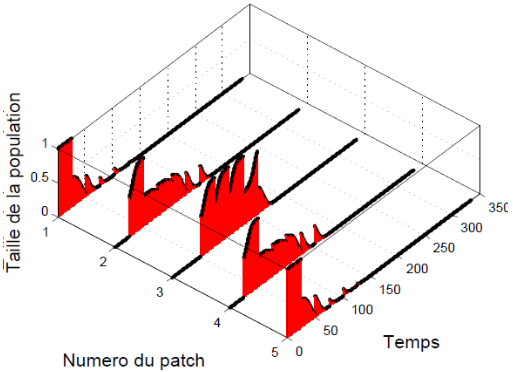

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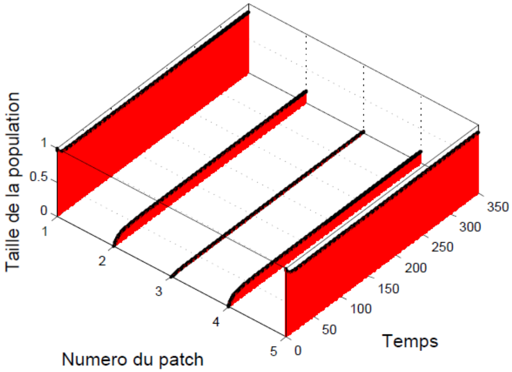
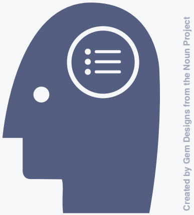


continuous migration

emerging patterns for larger periods T: global extinction

Conclusion



Take home messages

- Many populations are perturbed by pulsed introductions or/and removals, but this is rarely taken into account
- Temporal pattern of occurence of perturbations may have different impacts on population dynamics:
  - none (or almost none)
  - quantitative effects
  - qualitative effects, up to the emergence of new dynamical patterns
- General conclusions: not restricted to population dynamics *per se* (e.g. therapies against diseases)

Thank You !

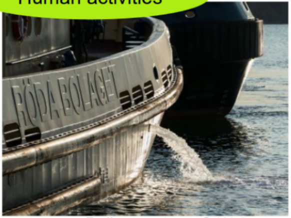
Do you have any questions?

Pulsed migration examples

Behavior

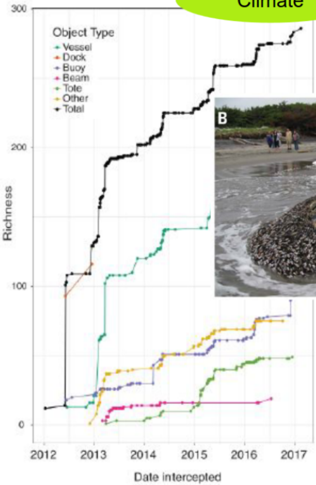
Ballooning dispersal
© Barnett

Human activities



Ballast waters © W.Carter

Climate



Carlton et al., 2017, *Science*

Rafting transportation of individuals after tsunamis

Pulsed vaccination revisited (1)

(F.Grognard incognito)

Some disagree on the pulsed vaccination framework

$\hookrightarrow$ Comparing vaccinations on the basis of Ψ is unfair

Only the **number of vaccines delivered** over T can be compared

$$\Psi \int_0^T S_c^* \, d\tau = \frac{\Psi b T}{(\Psi + \mu)}$$

Pulsed vaccinations should verify:

$$S(kT^+) = S(kT) - \frac{\Psi b T}{(\Psi + \mu)}$$

With

$$\mathcal{R}_0 = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau$$

Pulsed vaccination revisited (2)

Some disagree on the pulsed vaccination framework
$\hookrightarrow$ Comparing vaccinations on the basis of Ψ is unfair

Further computations show that

$$\frac{1}{T}\int_0^T S^*(\tau,\Psi)d\tau = \frac{b}{\Psi+\mu}$$

so that, vaccination prevents disease spread when

$$\Psi > \frac{b\beta}{\alpha+\mu} - \mu$$

condition independent on T, coincides with cont. vaccination.

Only nonlinear incidence rates[5], or density dependence, would discriminate between continuous and pulsed vaccination.

[5] *e.g.* Liu *et al.* (1986)