Pulsed perturbations in population dynamics
Ludovic Mailleret

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Pulsed perturbations in population dynamics

MOMI 2023

Ludovic Mailleret

M2P2, UMR ISA, INRAE, CNRS, Université Côte d'Azur
Macbes (ex Biocore), Inria d'Université Côte d’Azur

with: S. Nundloll, N. Bajeux, B. Ghosh, F. Aubree,
V. Calcagno, F. Hamelin, V. Lemesle & F. Grognard
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
Institut Sophia Agrobiotech
UMR INRAE, CNRS, Université Côte d’Azur

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Methods
• comparative and functional genomics
• population and community ecology
• mathematical and computer modelling
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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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 $\mu$

Continuous introductions$^1$

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

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

Pulsed introductions$^2$

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


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 $T \to 0$
Framework for studying pulsed introductions

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Augmentation biological control
Augmentation biological control

Fight pests through regular introductions of natural enemies

- parastitoids or predators
- supplied by biofabrics

General predator-prey model
\[
\begin{align*}
\dot{x} &= f(x) - g(.y, \text{pest/prey}) \\
\dot{y} &= h(.y) - m(.y, \text{BCA/predator})
\end{align*}
\]

Natural enemy introductions
\[
y(kT^n) = y(kT) + \mu T, \quad \forall n \in \mathbb{N}
\]

How different introduction strategies affect pest control?
Augmentation biological control

Fight pests through regular introductions of natural enemies

- parasitoids or predators
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Natural enemy introductions

\[
\{ y(kT^+) = y(kT) + \mu T, \forall n \in \mathbb{N} \}
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How different introduction strategies affect pest control?
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 $\bar{x}$

$$\Pi (T, x_0, t_0) = \int_{t_0}^{t_f} (\tau - t_0) d\tau, \quad x(t_f) \triangleq \bar{x}$$
Augmentation biological control
Null model: no density dependance in BCA population

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\]
Augmentation biological control
Null model: no density dependence in BCA population

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

\[
\begin{align*}
\dot{x} &= f(x) - g(x, y)y \\
\dot{y} &= h(x, y)y - m(.)y
\end{align*}
\]

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

\[
g(.) \uparrow \quad \theta \in (0, 1]: \text{ - DD index}
\]
Augmentation biological control (2)

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Negative density dependance in BCA population

Pest control is achieved iff

\[ f'(0) < \frac{g'(0)}{\theta} \quad \text{and} \quad \mu > \frac{1 - \theta}{\theta T} \left( 1 - e^{-m \frac{\theta f'(0)}{g'(0)} T} \right) \left( 1 - e^{-mT} \right) \]

\[ \left( e^{-m \frac{\theta f'(0)}{g'(0)} T} - e^{-mT} \right) \]

\(^a\text{Nundloll et al. 2010}\)

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
Augmentation biological control (2)

Negative density dependance in BCA population

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\[ f'(0) < \frac{g'(0)}{\theta} \quad \text{and} \quad \mu > \frac{1 - \theta}{\theta T} \left( 1 - e^{-m \frac{\theta f'(0)}{g'(0)} T} \right) \left( 1 - e^{-m T} \right) \]

\[ \frac{e^{-m \frac{\theta f'(0)}{g'(0)} T}}{\left( e^{-m \frac{\theta f'(0)}{g'(0)} T} - e^{-m T} \right)} \]

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Augmentation biological control (3)

Positive density dependance in BCA population

Per capita predation/natality increases with BCA population size

\[
\begin{align*}
\dot{x} &= f(x) - g(x)q_f(y)y \\
\dot{y} &= h(g(x)q_f(y))q_r(y)y - m(.)y
\end{align*}
\]

Component Allee effects:

\[q_f(\cdot), q_r(\cdot)\] increasing
Augmentation biological control (3)

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\]

Component Allee effects:

\( q_f(.) \), \( q_r(.) \) increasing
Augmentation biological control (3)

Positive density dependance in BCA population

- 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

DNA helix
Pulsed migration from mainland to island

: AA genotype, fitness (1+s)
: aa genotype, fitness 1

1 Aubree et al. 2023
Pulsed migration from mainland to island

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Pulsed migration from mainland to island

: AA genotype, fitness (1+s)
: aa genotype, fitness 1
: aA genotype, fitness (1+hs)

stochastic framework (genet. drift + selection)

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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In a nutshell:

• sufficiently deleterious alleles favored by migr. pulsedness
• neutral and beneficial alleles disfavored
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\(^1\)

\[
\left\{ \begin{array}{l}
\dot{x} = f(x) - Ex.
\end{array} \right.
\]

1: Schaefer (1954)

Pulsed removals (first attempt)\(^2\)

\[
\left\{ \begin{array}{l}
\dot{x} = f(x), \\
\quad x(kT^+) = x(kT) - \tilde{E}x.
\end{array} \right.
\]

2: from Lu et al. (2003)

• Mean taking effort in the continuous model

\[
\langle E_c \rangle = \frac{\dot{x}E}{x} = \frac{Ex}{x} = E
\]
Framework for studying pulsed removals (1)

Compare different patterns of removals for a given taking effort $E$

Continuous removals\(^1\)

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\langle E_c \rangle = \frac{\dot{x}E}{x} = \frac{Ex}{x} = E
\]
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:

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

⇒ more frequent removals shall be smaller...

A well-posed pulsed taking model reads:

\[
\begin{align*}
\dot{x} &= f(x), \\
\ x(kT+1) &= e^{-ET} x(kT).
\end{align*}
\]
Framework for studying pulsed removals (3)

Desired property: mean taking effort constant to allow comparisons

Solve:

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

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Framework for studying pulsed removals (3)

Desired property: mean taking effort constant to allow comparisons

Solve:

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

\Rightarrow more frequent removals shall be smaller...

A well-posed pulsed taking model reads:

\[ \begin{cases} \dot{x} = f(x), \\ x(kT+) = e^{-ET} x(kT). \end{cases} \]
Pulsed harvests
Pulsed harvesting

Assuming logistic growth, we get the ‘pulsed Schaefer model’

\[
\begin{align*}
\dot{x} &= rx \left(1 - \frac{x}{K}\right), \\
x(kT^+) &= e^{-ET} x(kT).
\end{align*}
\]

Properties:

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

(i.e. similar to continuous model)
Pulsed harvesting

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

(i.e. similar to continuous model)
Pulsed harvesting (2)

Compute the mean yield over a time period $T$:

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

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
- more frequent (less intense) harvests are better
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Properties:

- temporal pattern of pulsed harvests matters
- more frequent (less intense) harvests are better
Pulsed vaccination
Pulsed vaccination (1)

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

Continuous vaccination at rate $\Psi$ in the susceptible population:

\[
\begin{align*}
\dot{S} &= b - \mu S - \beta SI - \Psi S \\
\dot{I} &= \beta SI - \mu I - \alpha I
\end{align*}
\]

In such a model:

\[R_{eff} = \frac{\beta S^*_c}{\alpha + \mu} = \frac{\beta}{(\alpha + \mu)(\psi + \mu)}\]

Vaccination prevents disease spread when

\[\psi > \frac{b\beta}{\alpha + \mu} - \mu\]

\(^2\)model adapted from Onyango & Müller, 2014
Pulsed vaccination (1)

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Continuous vaccination at rate $\Psi$ in the susceptible population

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R_{\text{eff}} = \frac{\beta S^*_c}{\alpha + \mu} = \frac{\beta}{(\alpha + \mu)} \frac{b}{(\Psi + \mu)}
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Vaccination prevents disease spread when

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

---

\(^2\)model adapted from Onyango & Müller, 2014
Pulsed vaccination (2)

A comparable pulsed vaccination model reads\(^3\)

\[
\begin{align*}
\dot{S} &= b - \mu S - \beta SI \\
\dot{I} &= \beta SI - \mu I - \alpha I \\
S(kT) &= e^{-\Psi T} S(kT)
\end{align*}
\]

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

\[
R_{eff} = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau
\]

\(^3\)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 \( \Psi \) is difficult, and ultimately uninformative.

Yet, numerics show vaccination may fail for large
Pulsed vaccination prevents disease spread when:

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

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$\frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau$
Pulsed vaccination (3)

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Unfortunately, isolating \( \Psi \) is difficult, and ultimately uninformative.

Yet, numerics show vaccination may fail for large \( T \)

\[
\frac{1}{T} \int_0^T S^*(\tau, \Psi) d\tau
\]

Vaccination succeeds for \( \Psi = 0.5 \), \( \Psi = 1 \), and \( \Psi = 10 \) as shown in the graph.
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:
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:

\[
\begin{align*}
\dot{x} &= rx \left( \frac{x}{K_a} - 1 \right) \left( 1 - \frac{x}{K} \right), \\
x(kT^+) &= e^{-mT} x(kT).
\end{align*}
\]
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: \(^4\)
- 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 harmful, pulsed even more than continuous
- immigration beneficial, pulsed even more than continuous

How do pulsed migration, migration period and Allee effects interact at the metapopulation scale?
Pulsed migration and the Allee effect (2)

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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)

Keitt et al. (2001): populations ‘pinned’ at intermediate migration
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
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 pinned
Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period $T$

**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 $T$

**pulsed** migration

**continuous** migration

emerging patterns for larger periods $T$: pop-up effect
Pulsed migration and the Allee effect (4)

The effects of pulsed migration, and migration period $T$

**pulsed** migration

**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 occurrence 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

- Ballooning dispersal
- Climate
- Behavior
- Human activities

Ballooning dispersal (© Barnett)

Carlton et al., 2017, Science
Rafting transportation of individuals after tsunamis

Ballast waters (© W. Carter)

Date intercepted
Richness
Some disagree on the pulsed vaccination framework

Comparing vaccinations on the basis of $\Psi$ is unfair

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

$$\psi \int_0^T S^*_c \, d\tau = \frac{\psi bT}{(\psi + \mu)}$$

Pulsed vaccinations should verify:

$$S(kT^+) = S(kT) - \frac{\psi bT}{(\psi + \mu)}$$

With

$$R_0 = \frac{\beta}{(\alpha + \mu)} \frac{1}{T} \int_0^T S^*(\tau, \Psi) \, d\tau$$
Some disagree on the pulsed vaccination framework. Comparing vaccinations on the basis of $\Psi$ 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)