Stochastic foundations of movement ecology I: *Biological invasions are non-Markovian reaction-transport processes*

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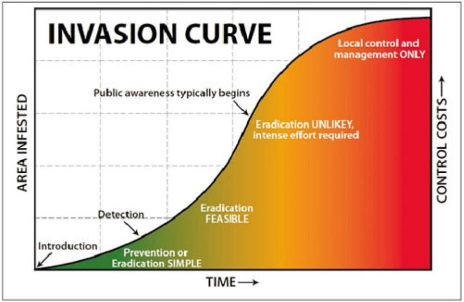
3. It affects Biodiversity and has important economical consequences



Well-known invasions

1. **Plants:** An estimated 18.6 km^2 of public natural areas are lost to invasive exotic plant species every day.

Cheatgrass Invasion

Native Shadscale/Bunchgrass

Invasive Cheatgrass

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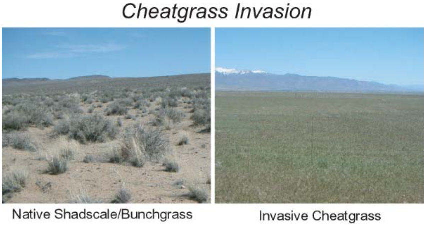

Or in our own garden

Well-known invasions

1. Grey Squirrel invasion in Britain in 1900

THE RED HAS LOST – SO ACCEPT THE GREY

STEPHEN HARRIS believes that the vast sums spent on saving the red squirrel and eradicating its nemesis, the grey, are a waste of money. Here, he offers a rational solution to a thorny issue.

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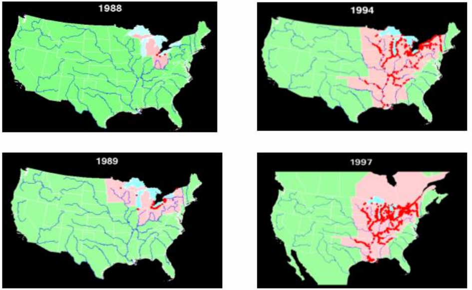
2. Zebra mussel invasion in USA



The physics behind BI

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- It takes place during the pauses
- Obey the classical kinetics laws

Old model

The Oldest model: Fisher's model

Assumptions:

- Animals move by diffusion. There are no pauses, i.e., it is a Markovian process
- Reproduction obeys a logistic growth

The model obeys the Reaction-diffusion equation:

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + r\rho(1-\rho)$$

where $\rho(x,t)$ is the number density of individuals.

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We can sum up both rates because they are Markovian (independent) processes

Generalizations of the Fisher's model

Reaction-Dispersal

Assumptions:

- Animals jump according to a dispersal kernel $\Phi(x)$. Pause's duration are exponentially distributed, i.e., it is a Markovian process
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The model obeys the Reaction-dispersal equation:

$$\frac{\partial \rho}{\partial t} = \lambda \left[\int_{-\infty}^{\infty} \rho(x-z,t)\Phi(z)dz - \rho(x,t) \right] + r\rho(1-\rho)$$

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Long-distance dispersal

Dispersal kernels in biological invasions:

$$\begin{aligned}
\Phi(z) &= \frac{1}{2\alpha} e^{-|z|/\alpha} \ \textbf{(Laplace)} \\
\Phi(z) &\sim |z|^{-2n-2},\ 0 < n < \frac{1}{2} \ \textbf{(Power law)} \\
\Phi(z) &\sim e^{-(z/z_0)^c},\ c < 1 \ \textbf{(Stretched exponential)} \\
\Phi(z) &\sim \frac{e^{-\ln^2(z/z_0)/\alpha}}{z} \ \textbf{(Log-normal)}
\end{aligned}$$

Generalizations of the Fisher's model

Diffusion with memory

Assumptions:

- Animals move by diffusion but there is memory, inertia or correlation between jumps. It is a non-Markovian process
- Reproduction obeys a logistic growth

The diffusion equation with memory, inertia or correlation between jumps obeys the Telegrapher's equation:

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}$$

How can it be obtained?

- By combining continuity equation $\frac{\partial\rho}{\partial t}+\frac{\partial J}{\partial x}=0$ and the Cattaneo equation for J, $\tau\frac{\partial J}{\partial t}+J=-D\frac{\partial\rho}{\partial x}$

Diffusion with memory

- Following the derivation by Goldstein and Kac based on the balance equations for particle moving to the right and to the left and introducing a persistence probability.
- From Continuous-Time Random Walk formalism by considering a waiting-time PDF of the form $\varphi(t) = te^{-t/\tau}/\tau^2$ and the diffusion limit for the dispersal kernel.

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More details in:

V. Méndez, S. Fedotov and W. Horsthemke, *Reaction-Transport Systems: Mesoscopic Foundations, Fronts, and Spatial Instabilities* (Springer-Verlag, Berlin, 2010)

How to include reactions?

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Some authors simply add the reaction rate term to the rhs of the Telegrapher's equation:

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Comment

They "**forget**" that diffusion with memory is no longer a Markovian processes. There is no macroscopic of mesoscopic derivation. It exhibits a undesirable property: It does not reduce to the kinetic equation in the homogeneous case: When $\rho(x,t) = \rho(t)$ it follows

$$\tau \frac{d^2 \rho}{dt^2} + \frac{d\rho}{dt} = r\rho(1-\rho)$$

How to include reactions?

Recently, some authors (N. Isern and J. Fort, Phys. Rev. E **80**, 057103 (2009)) proposed the finite-time difference equation

$$\rho(x,t+T)-\rho(x,t) = [\rho(x,t+T)-\rho(x,t)]_m+[\rho(x,t+T)-\rho(x,t)]_g$$

where m means migration and g growth.

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where m means migration and g growth.

Comment

The premise that the growth and dispersal processes remain uncoupled during a finite time interval and contribute simply additively to the total change of the density holds **only** if the dispersal process is Markovian

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However, the authors do the following:

$$
\begin{aligned}
[\rho(x,t+T)-\rho(x,t)]_m &= \int_{-\infty}^{\infty}\rho(x-z,t)\Phi(z)dz-\rho(x,t) \\
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and Taylor-expanding up to $O(T^2)$

$$[\rho(x,t+T)-\rho(x,t)]_g = T\left(\frac{\partial\rho}{\partial t}\right)_g+\frac{T^2}{2!}\left(\frac{\partial^2\rho}{\partial t^2}\right)_g$$

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Identifying $\left(\frac{\partial\rho}{\partial t}\right)_g = r\rho(1-\rho)$ and Taylor-expanding the LHS up to $O(T^2)$

$$\rho(x,t+T)-\rho(x,t) = T\frac{\partial\rho}{\partial t} + \frac{T^2}{2!}\frac{\partial^2\rho}{\partial t^2}$$

How to include reactions?

they obtain

$$\tau \frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho) + \tau F'(\rho) F(\rho)$$

where $F(\rho) = r\rho(1-\rho)$, $D = \sigma^2/2T$ and $\tau = T/2$.

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This equation has some undesirable behaviors:

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For additional undesirable properties of this equation see: V. Méndez, D. Campos and W. Horsthemke, Phys. Rev. E **90**, 042114 (2014)

How to include reactions?

CTRW

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CTRW

Generalized Master Equation for the mean field density $\rho(x,t)$

$$\frac{\partial \rho}{\partial t} = \int_0^t K(t-t') \left[\int_{-\infty}^{\infty} \rho(x-x', t-t') \Phi(x') dx' - \rho(x,t') \right] dt'$$

where $K(t)$ is the **memory kernel** defined in the Laplace space as $K(s) = \frac{s\varphi(s)}{1-\varphi(s)}$ and $\varphi(t)$ is the **waiting-time** PDF

- Markovian CTRW: $\varphi(t)$ is an exponential distribution
- non-Markovian CTRW: $\varphi(t)$ is NOT an exponential distribution

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Can we add a non-linear reaction kinetic to the RHS of the non-Markovian ME?
In general, the answer is NO!!

Consider a reaction kinetics $\frac{d\rho}{dt} = F(\rho)$ where $F(\rho)$ is a positive non-linear function of ρ

Define

$$F(\rho) = r(\rho)\rho$$

with

$$r(\rho) = r_+(\rho) - r_-(\rho)$$

where $r_\pm(\rho)$ are the **per-capita growth and death rates**.

Reaction-CTRW

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Invasion velocity

For most populations $F(\rho)$ is logistic, i.e, $F(\rho) = r\rho(1-\rho)$ with r the **intrinsic growth rate** and $r_+(\rho) = r$, $r_-(\rho) = r\rho$.

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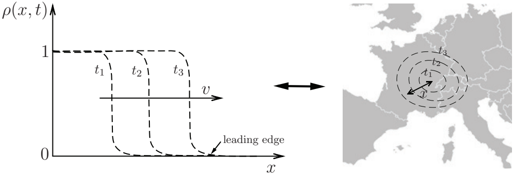
- We assume the existence of a travelling wave from an initial condition with compact support connecting the un-invaded state ($\rho = 0$) to the invaded state ($\rho = 1$)
- Since the invasion wave propagates into the unstable state we can determine the invasion velocity by analyzing the motion of the tail of $\rho(x,t)$.



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- For Model A

  $$\frac{H-r}{\hat{K}(H-r)} = \tilde{\Phi}(p) - 1$$

  For Model B

  $$\frac{H-r}{\hat{K}(H)} = \tilde{\Phi}(p) - 1$$

  with $H = -\partial G/\partial t$ and $p = \partial G/\partial x$

  $$\hat{K}(H) = \int_0^{\infty} e^{-Ht} K(t) dt, \ \tilde{\Phi}(p) = \int_0^{\infty} e^{xp} \Phi(x) dx$$

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- The **waiting-time PDF** $\varphi(t)$ and the **intrinsic growth rate** r can be obtained from **Life statistics**

Invasion velocity

Life Statistics:

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Life Statistics:

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- Fertility function: $m(t)$ rate of offspring produced by a female at age t
- Maternity function: $l(t)m(t)$
- The intrinsic growth rate r is solution to the Euler's equation

$$\int_{a_0}^{a_f} e^{-rt} l(t)m(t)dt = 1$$

Invasion velocity

- The waiting-time PDF is the time between two successive generations

$$\varphi(t) = \frac{l(t)m(t)}{\int_{a_0}^{a_f} l(t)m(t)dt}$$

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- $\varphi(t)$ cannot be an exponential distribution. It is peaked. **The invasion process is non-Markovian**
- For invasion in 2D

$$\tilde{\Phi}(p)=2\pi\int_0^\infty r\Phi(r)I_0(rp)dr$$

Example: Muskrat Invasion

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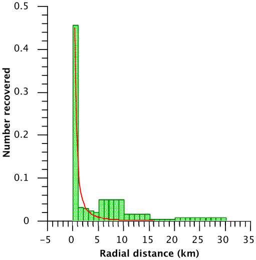
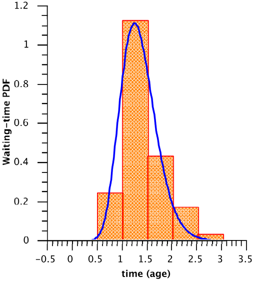
- The observed invasion velocity was **11 km/yr** between 1905 and 1930





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- Model A is adequate for species that take their brood with them during the first stages of their life
- From histograms of dispersal distances, fertility and survival as function of the age we can estimate r, $\varphi(t)$ and $\Phi(r)$. The invasion speed predicted by Model A is **8.74 km/yr**.

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- Some authors make use of non-physical models
- The CTRW provides a good framework. There are two possibilities
- The invasion velocity of Model A is adequate to model **BI**

Thank you!