Evolutionary rescue, a mathematical analysis

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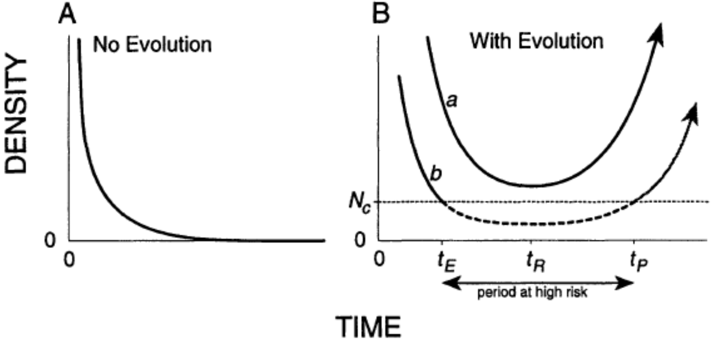
Contents

Definition (Evolutionary Rescue)

When a population, that would become extinct in the sole ecological context, persists thanks to evolutionary factors.

R. Gomulkiewicz & R. Holt "When does natural selection save a population from extinction" in Evolution ('95) : U-shaped curve.



Application areas :

- conservation of declining species.
- adaptation to climate change (moving optimum).
- emergence of resistance to antibiotics is an important example !

Theoretical and experimental results in evolutionary biology :

- R. Gomulkiewicz, R. Holt, G. Bell, A. Gonzalez, G. Martin, Y. Anciaux...
- Special issue on ER in Philos. Trans. R Soc. Lond. B Biol. Sci.
- A whole session on ER in "Evolution 2018".
- A reaction diffusion model by A. Kanarek and C. Webb ('10).

System proposed by Kanarek and Webb ('10)

$u = u(t, x)$ density of a species at time $t > 0$, position $x \in \mathbb{R}$.

$a = a(t, x)$ dynamical Allee threshold, considered as a mean trait evolution, at time $t > 0$ and position $x \in \mathbb{R}$.

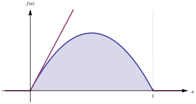
$$\begin{cases} \partial_t u = D \underbrace{\partial_{xx} u}_{dispersion} + r \underbrace{u\left(u - a^2\right)(1 - u)}_{bistable\ growth} & \textit{ECOLOGY} \\ \partial_t a = D \underbrace{\partial_{xx} a}_{dispersion} + D \underbrace{2(\partial_x a)(\partial_x(\ln u))}_{asymmetrical\ gene\ flow} \underbrace{-\varepsilon(1 - u)a}_{selection\ [1]} & \textit{EVOLUTION}. \end{cases}$$

1. whose strenght depends on the population density.

Contents

Fisher-KPP equation (logistic growth)

$$\partial_t u = \Delta u + ru(1-u).$$

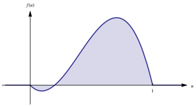


Theorem (Begins with Kolmogorov, Petrovsky, Piskunov (1937))

There is Hair Trigger Effect : any small amount of initial population drives the solution u towards 1 at large times, uniformly locally in space, i.e. invasion always occurs.

Equation with Allee effect (bistable growth)

$$\partial_t u = \Delta u + ru(u-\theta)(1-u), \quad 0 < \theta < \frac{1}{2}.$$



Theorem

Extinction for "small" initial population

vs.

Propagation for "large " initial population.

Threshold phenomena

- Aronson & Weinberger ('75), Fife & Mc Leod ('77) : threshold.
- Zlatŏs ('06) : sharp threshold for plateau-shaped initial data.
- Du & Matano ('10) : sharp threshold for a monotone one-parameter family of compactly supported initial data, $N = 1$.
- Poláčik ('11) : $N \geq 1$ (and more general nonlinearities).
- Muratov & Zhong ('13) : sharph threshold for $L^2 \cap L^\infty$ initial data, energy-based methods.

Contents

Missing results...

Consider, for some parameter $L > 0$,

$$\begin{cases} \partial_t u = \Delta u + f(u) \\ u(0,x) = u_0^L(x). \end{cases}$$

In many situations, it is known that the sharp threshold property holds : there is $L^\star > 0$ such that

- $L < L^\star \Longrightarrow$ extinction
- $L > L^\star \Longrightarrow$ propagation

but quantitative estimates of $L^\star$ were missing...

Some very new results

- For ignition or bistable nonlinearities (with threshold θ), we consider the initial data

$$u(0,x) = (\theta + \varepsilon)\mathbf{1}_{B_L}(x),$$

and obtain (rather) sharp estimates of $L_\varepsilon^\star$ as $\varepsilon \to 0$.

Quantitative estimates

$$\begin{cases} \partial_t u = \Delta u + ru(u-\theta)(1-u) \\ u(0,x) = (\theta+\varepsilon)\mathbf{1}_{B_L}(x). \end{cases}$$

Theorem (A., Ducrot and Faye ('19))

The sharp threshold $L_\varepsilon^\star$ satisfies

$$\frac{1}{\sqrt{r\theta(1-\theta)}} \leq \liminf_{\varepsilon\to 0} \frac{L_\varepsilon^\star}{\ln\frac{1}{\varepsilon}} \leq \limsup_{\varepsilon\to 0} \frac{L_\varepsilon^\star}{\ln\frac{1}{\varepsilon}} \leq \frac{2}{\sqrt{r\theta(1-\theta)}}.$$

Roughly speaking

$$L_\varepsilon^\star \approx \ln\frac{1}{\varepsilon}, \qquad \textit{as } \varepsilon \to 0.$$

Contents

Dynamical Allee parameter, $\theta \leftarrow \theta(t)$

$$\partial_t u = \partial_{xx} u + u(u - \theta(t))(1 - u).$$

- Poláčik ('11) : sharp threshold when

$$0 < \theta_{min} \leq \theta(t) \leq \theta_{max} < \frac{1}{2}.$$

- How about vanishing Allee parameter ($\theta(t) \to 0$ as $t \to +\infty$) ?...

NB : Trélat, Zhu, Zuazua ('18) : $\theta(t)$ as a control parameter...

Hair Trigger Effect for decreasing Allee parameter

Theorem (A. and Ducrot ('18))

Assume $\theta : [0,+\infty) \mapsto (0,1)$ *is continuous, decreasing and satisfies*

$$\Theta := \int_0^{+\infty} \theta(s)\, ds < +\infty.$$

Then

$$\partial_t u = \partial_{xx} u + u(u - \theta(t))(1-u),$$

enjoys the so-called Hair Trigger Effect.

A preliminary observation

Let $R > 0$ and $\theta_0 \in (0,1)$ be given. Consider the Dirichlet problem

$$\begin{cases} \dfrac{\partial v}{\partial t} = \dfrac{\partial^2 v}{\partial x^2} + f(\theta_0, v), & t > 0,\ x \in (-R, R), \\ v(t, \pm R) = 0, & t > 0, \end{cases}$$

supplemented with an initial data $v_0 \in H_0^1(-R, R)$. We consider the energy functional defined by

$$\mathcal{E}_{R,\theta_0}(\varphi) = \frac{1}{2}\int_{-R}^{R} |\partial_x \varphi(x)|^2\, dx + \int_{-R}^{R} -F(\theta_0, \varphi(x))\, dx.$$

- If $\mathcal{E}_{R,\theta_0}(v_0) < 0$ then the corresponding solution v does not go to extinction as $t \to +\infty$.

Energy estimates

Observe that $\partial_t u \geq \partial_{xx} u - \theta(t) u$ so that

$$u(t,x) \geq e^{-\int_0^t \theta(s)ds} w(t,x) \geq e^{-\Theta} w(t,x),$$

where

$$w(t,x) := (G(t,\cdot) * u_0)(x) \quad \text{solves the Heat equation.}$$

Lemma

There is $T \gg 1$ such that

$$v_0 := e^{-\Theta} \chi\left(\frac{\cdot}{\sqrt{T}}\right) w(T,\cdot) \in H_0^1(-\sqrt{T}, \sqrt{T})$$

satisfies $\mathcal{E}_{\sqrt{T},\theta(T)}(v_0) < 0$. Here χ is a smooth cut-off function supported in $(-1,1)$.

End of the proof

- Since θ is decreasing it follows from the comparison principle that, after time T, u is a supersolution of the equation where $f(\theta(t), u) \leftarrow f(\theta(T), u)$.

- From the preliminary observation ($R \leftarrow \sqrt{T}$, $\theta_0 \leftarrow \theta(T)$), u does not go to extinction.

- Last, prove that u does converge to 1 as $t \to +\infty$, that is the HTE. To do so we use parabolic regularity and that

$$\partial_t u_\infty = \partial_{xx} u_\infty + u_\infty^{1+p}(1 - u_\infty)$$

does enjoy the HTE [2] when $p \leq p_F = 2$.

2. Aronson and Weinberger ('78), using the so-called Fujita ('66) blow-up phenomena.

Contents

System proposed by Kanarek and Webb ('10)

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$$\begin{cases} \partial_t u = D \underbrace{\partial_{xx} u}_{dispersion} + r \underbrace{u\left(u - a^2\right)(1-u)}_{bistable\ growth} & ECOLOGY \\ \partial_t a = \quad ....\text{coming soon}.... & EVOLUTION \end{cases}$$

supplemented with $u_0(x)$ (say small and localized) and $0 < a_0 < 1$.

The evolution equation (without selection) [3]

$$
\begin{aligned}
a(t+dt,x) &= \frac{\frac{1}{2}u(t,x-dx)a(t,x-dx)+\frac{1}{2}u(t,x+dx)a(t,x+dx)}{\frac{1}{2}u(t,x-dx)+\frac{1}{2}u(t,x+dx)}\\
&\approx \frac{ua+\frac{1}{2}(dx)^2ua_{xx}+\frac{1}{2}(dx)^2u_xa_x+\frac{1}{2}(dx)^2u_{xx}a}{u+\frac{1}{2}(dx)^2u_{xx}}\\
&\approx \left(a+\frac{1}{2}(dx)^2a_{xx}+\frac{1}{2}(dx)^2\frac{u_x}{u}a_x+\frac{1}{2}(dx)^2\frac{u_{xx}}{u}a\right)\\
&\quad \times\left(1-\frac{1}{2}(dx)^2\frac{u_{xx}}{u}\right)\\
&\approx a+\frac{1}{2}(dx)^2a_{xx}+\frac{1}{2}(dx)^2\frac{u_x}{u}a_x
\end{aligned}
$$

3. Nagylaki ('75), Pease et al ('89), Kirkpatrick and Barton ('97) etc

If $\frac{1}{2}(dx)^2 \approx Ddt$ we get

$$\partial_t a = D\partial_{xx} a + D(\partial_x a)\,(\partial_x(\ln u)).$$

The first term gives the changes that occur through a simple mixing effect, while the second term arises because individuals migrating to a particular locality are more likely to come from contiguous areas with relatively high population density, causing the mean phenotype to become more like that of the most dense neighboring populations.

System proposed by Kanarek and Webb ('10)

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$$\begin{cases} \partial_t u = D \underbrace{\partial_{xx} u}_{dispersion} + r \underbrace{u\left(u - a^2\right)(1-u)}_{bistable\ growth} & ECOLOGY \\ \partial_t a = D \underbrace{\partial_{xx} a}_{dispersion} + D \underbrace{2(\partial_x a)(\partial_x(\ln u))}_{asymmetrical\ gene\ flow} \underbrace{-\varepsilon(1-u)a}_{selection^{4}} & EVOLUTION \end{cases}$$

supplemented with $u_0(x)$ (say small and localized) and $0 < a_0 < 1$.

4. whose strenght depends on the population density.

The genetic variance parameter ε

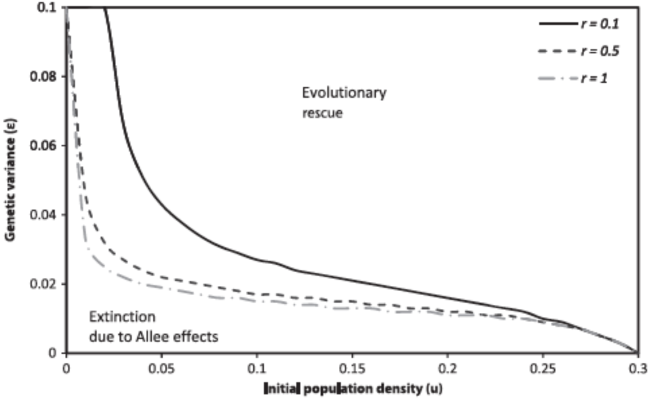
If $\varepsilon = 0$, then $a(t,x) \equiv a_0$ is no longer a dynamical parameter and the model reduces to the single bistable equation

$$\partial_t u = D\partial_{xx} u + ru(u - a_0^2)(1-u),$$

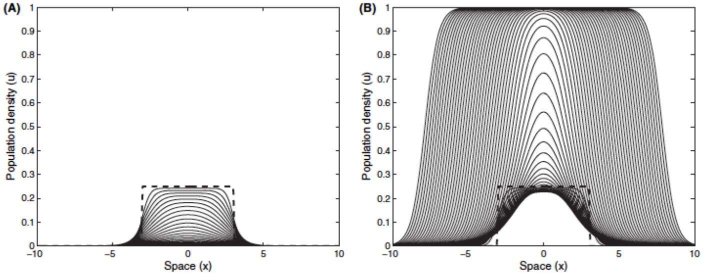
for which small species go extinct.

If $\varepsilon > 0$, numerical simulations by Kanarek and Webb suggest that small species may be saved from extinction...

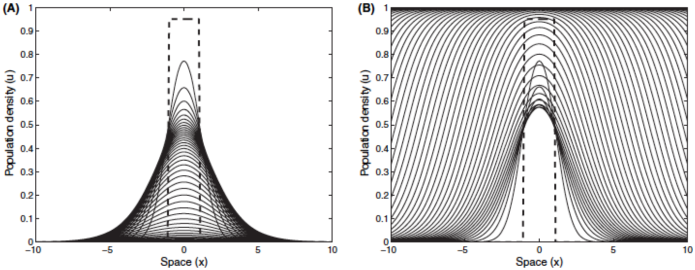
From Kanarek and Webb (without space) :



From Kanarek and Webb :



From Kanarek and Webb :



Existence of a solution

Proposition (A. and Ducrot ('18))

Let $(u_0, a_0) \in C(\mathbb{R}; [0,1]) \times (0,1)$ be a given initial data. Then the Cauchy problem admits, at least, a (classical) solution.

- The difficulty is to handle the term $\partial_x(\ln u)$, especially for small times when u_0 vanishes at some places.
- $a_0 \leftarrow a_0(x)$ is not considered here.
- Uniqueness is not known.

Evolutionary rescue result

Theorem (A. and Ducrot ('18))

Any small initial population, that would become extinct in the sole ecological context ($\varepsilon = 0$), will persist and spread thanks to evolutionary factors ($\varepsilon > 0$).

In other words, the Hair Trigger Effect holds true for the above system as soon as $\varepsilon > 0$.

Proof

- By contradiction assume that there is $T>0$ such that $u(t,x)\leq 1-\alpha<1$ for all $t\geq T$, $x\in\mathbb{R}$. Hence the EVOLUTION equation yields

$$\partial_t a \leq D\partial_{xx} a + D2(\partial_x a)(\partial_x(\ln u)) - \varepsilon\alpha a$$

so that

$$(a(t,x))^2 \leq \theta(t) := (a_0 e^{-\varepsilon\alpha(t-T)})^2,$$

and, by a comparison argument, the ECOLOGY equation falls into the regime of "one equation with a moving Allee effect" for which the HTE holds. This contradiction yields

$$\limsup_{t\to+\infty}\sup_{x\in\mathbb{R}} u(t,x)=1 \quad \text{(weak persistence property)}.$$

- Last, we prove that u does converge to 1.

Thanks for your attention.

Some very new results

- For degenerate monostable nonlinearities, we consider the initial data

$$u(0,x) = \varepsilon \mathbf{1}_{B_L}(x),$$

and obtain (not so) sharp estimates of $L_\varepsilon^\star$ as $\varepsilon \to 0$.

The degenerate monostable situation

For $p > p_F := \frac{2}{N}$:

$$\begin{cases} \partial_t u = \Delta u + r u^{1+p}(1-u) \\ u(0,x) = \varepsilon \mathbf{1}_{B_L}(x). \end{cases}$$

Theorem (A., Ducrot and Faye ('19))

The sharp threshold $L_\varepsilon^\star$ satisfies

$$\frac{1}{\varepsilon^{p/2}} \lesssim L_\varepsilon^\star \lesssim \frac{(\ln \frac{1}{\varepsilon})^{1/2}}{\varepsilon^{p/2}}, \qquad \text{as } \varepsilon \to 0.$$