Adaptive evolution : a population approach

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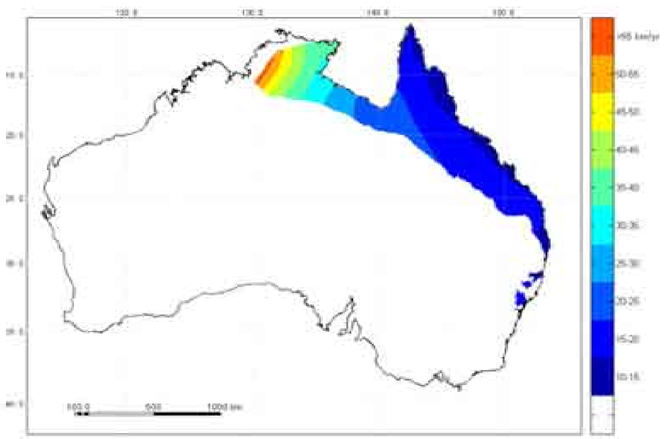

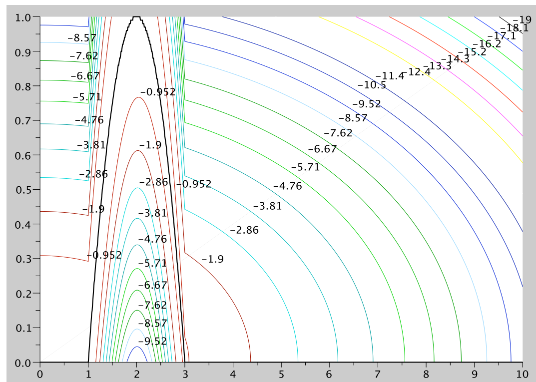

OUTLINE OF THE LECTURE

Interaction between a physiological trait and space

I. Space and physiological trait

II. Selection of dispersal (bounded domain)

III. Selection of dispersal (full space)

See also A. Arnold, L. Desvillettes, C. Prevost, talk of K.-Y. Lam

Setting the model

Adaptation to the evironment in a spatial ecology model

- $x \in \Omega$ space variable
- $\theta \in \Theta$ physiological trait

$$\partial_t n(x,\theta,t) \overbrace{= D\partial^2_{xx} n(x,\theta,t)}^{\text{dispersion/motility}} + \overbrace{\alpha\partial^2_{\theta\theta} n(x,\theta,t)}^{\text{mutations}} + \overbrace{n(x,\theta,t)\Big(K(x,\theta) - \rho(x,t)\Big)}^{\text{reproduction}}$$

$$\rho(x,t) = \int_0^\infty n(x,\theta,t)\, d\theta$$

This is still an advantage on reproductive rate.

Question : (Bouin, Mirrahimi) What is the speed of a traveling wave ?

Evolution of Dispersal

Question Selection without a proliferative advantage ?

The context of Hastings, Dockery, Lou, Kim :

- no advantage regarding the reproductive rate $K(x)$
- motility of individuals is subject to selection and mutations

Called : Spatial sorting

Evolution of Dispersal

We model it for $x \in \Omega,\ \theta > 0$ + Neuman

$$\partial_t n(x,\theta,t) \overbrace{= \theta \partial^2_{xx} n(x,\theta,t)}^{\text{dispersion/motility}} + \overbrace{n(x,\theta,t)\Big(K(x) - \rho(x,t)\Big)}^{\text{reproduction}} \overbrace{+ \varepsilon^2 \partial^2_{\theta\theta} n(x,\theta,t)}^{\text{mutations on motility}}$$

$$\rho(x,t) = \int_0^\infty n(x,\theta,t)\, d\theta$$

Remark : Parameters as θ are not given they are selected

Question : which dispersal rate θ is selected ?

Evolution of Dispersal

We can again ask the question of rare mutations

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + n_\varepsilon(x,\theta,t)\Big(K(x) - \rho_\varepsilon(x,t)\Big) + \varepsilon^2 \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n_\varepsilon(x,\theta,t)\, d\theta$$

Can we argue with the same argument as for proliferative advantage ?

Evolution of Dispersal

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$$\rho_\varepsilon(x,t) = \int_0^\infty n_\varepsilon(x,\theta,t)\, d\theta$$

For ε small, $n_\varepsilon(x,\theta,t) \geq 0$

$$\begin{cases} \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + n_\varepsilon(x,\theta,t)\Big(K(x) - \rho_\varepsilon(x,t)\Big) = 0 \\ +\text{Neuman boundary condition} \end{cases}$$

the first eigenvalue $H\Big(\theta, \langle \rho_\varepsilon(\cdot,t)\rangle\Big)$ vanishes. Therefore

$$n_\varepsilon(x,\theta,t) \approx N(x,t)\delta(\theta = \overline{\theta}(t)),$$

Evolution of Dispersal

We can again ask the question of rare mutations

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + n_\varepsilon(x,\theta,t)\Big(K(x) - \rho_\varepsilon(x,t)\Big) + \varepsilon^2 \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n_\varepsilon(x,\theta,t)\, d\theta$$

When a mutant has an advantage, it diffuses everywhere and invades the domain Ω

Therefore we expect (as before) that

$$n_\varepsilon(x,\theta,t) \approx N(x,t)\delta(\theta = \overline{\theta}(t)),$$

Evolution of Dispersal

The Gaussian approximation to $n_\varepsilon(x,\theta,t) \approx N(x,t)\delta(\theta = \overline{\theta}(t))$,

$$n_\varepsilon(x,\theta,t) \approx N_\varepsilon(x,t)e^{\frac{\varphi_\varepsilon(\theta,t)}{\varepsilon}},$$

a corrector as in homogenization.

The dominant terms in the expansion are

$$\partial_t\varphi(\theta,t) = |\nabla_\theta\varphi|^2 + \theta\partial^2_{xx}N_\varepsilon(x,\theta,t) + N_\varepsilon\Big(K(x) - \rho_\varepsilon(x,t)\Big) + O(\varepsilon)$$

Define the effective Hamiltonian $H(\theta,t)$ as the principal eigenvalue

$$\begin{cases} \theta\partial^2_{xx}N_\varepsilon(x,\theta,t) + N_\varepsilon\left(K(x) - \rho_\varepsilon(x,t)\right) = H\Big(\theta, \langle\rho_\varepsilon(\cdot,t)\rangle\Big)N_\varepsilon \quad x \in \Omega \\ +\text{Neuman boundary condition} \end{cases}$$

Evolution of Dispersal

We get

$$\partial_t \varphi(\theta, t) = |\nabla_\theta \varphi|^2 + \theta \partial^2_{xx} N_\varepsilon(x, \theta, t) + N_\varepsilon \Big(K(x) - \rho_\varepsilon(x, t) \Big) + O(\varepsilon)$$

$$\theta \partial^2_{xx} N_\varepsilon(x, \theta, t) + N_\varepsilon \left(K(x) - \rho_\varepsilon(x, t) \right) = H\Big(\theta, \langle \rho_\varepsilon(\cdot, t) \rangle\Big) N_\varepsilon \quad x \in \Omega$$

therefore the limit is

$$\begin{cases} \partial_t \varphi(t, \theta) = |\nabla_\theta \varphi|^2 + H\Big(\theta, \langle \bar{\rho}(\cdot, t) \rangle\Big) \\ \max_\theta \varphi(t, \theta) = 0 \quad = \varphi(t, \bar{\theta}(t)) \end{cases}$$

Evolution of Dispersal

We get

$$\partial_t \varphi(\theta,t) = |\nabla_\theta \varphi|^2 + \theta \partial^2_{xx} N_\varepsilon(x,\theta,t) + N_\varepsilon\Big(K(x) - \rho_\varepsilon(x,t)\Big) + O(\varepsilon)$$

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therefore the limit is

$$\begin{cases} \partial_t \varphi(t,\theta) = |\nabla_\theta \varphi|^2 + H\Big(\theta, \langle \bar\rho(\cdot,t)\rangle\Big) \\ \max_\theta \varphi(t,\theta) = 0 \qquad = \varphi(t, \bar\theta(t)) \end{cases}$$

To be compared to the 'usual constrained H.-J. equation

$$\begin{cases} \partial_t \varphi(t,\theta) = |\nabla_\theta \varphi|^2 + R\Big(\theta, \varrho(t)\Big) \\ \max_\theta \varphi(t,\theta) = 0 \qquad = \varphi(t, \bar\theta(t)) \end{cases}$$

Evolution of Dispersal

How do we handle this ? Along the dynamics

$$H\Big(\overline{\theta}(t), \langle \bar{\rho}(\cdot, t) \rangle\Big) = 0 \qquad \text{(pessimism principle)}$$

$$\rho_\varepsilon \approx N\varepsilon(x, \overline{\theta}(t), t) := \overline{N}(x, t)$$

we can identify the limit of $N_\varepsilon(x, \theta, t)$ as the solution to

$$\begin{cases} -\overline{\theta}(t)\partial^2_{xx}\overline{N} = \overline{N}\left(K(x) - \overline{N}(x,t)\right), & x \in \Omega \\ +\text{Neuman boundary condition} \end{cases}$$

Evolution of Dispersal

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What useful information do we conclude from this analysis?

$$\frac{d}{dt}\overline{\theta}(t) = (-D^2\varphi)^{-1}.\nabla_\theta H\Big(\overline{\theta}(t), \langle\bar{\rho}(\cdot,t)\rangle\Big)$$

Which behaviour?

Evolution of Dispersal

Theorem When $K \neq Cst$,

$$\nabla_\theta H\Big(\overline{\theta}(t), \langle \overline{\rho}(\cdot, t)\rangle\Big) < 0.$$

Evolution of Dispersal

Proof We can normalize the eigenvalue problem in x as

$$\theta\partial^2_{xx}N_\varepsilon(x,\theta,t)+N_\varepsilon\left(K(x)-\rho_\varepsilon(x,t)\right)=H\Big(\theta,\langle\rho_\varepsilon(\cdot,t)\rangle\Big)N_\varepsilon,\qquad \int_x N_\varepsilon^2dx=Cst$$

Then

$$-\theta\int_x|\nabla N_\varepsilon(x,\theta,t)|^2dx+\int_x N_\varepsilon^2\left(K(x)-\rho_\varepsilon(x,t)\right)dx=H\Big(\theta,\langle\rho(\cdot,t)\rangle\Big)$$

$$-\int_x|\nabla N_\varepsilon|^2dx-2\theta\int_x\nabla N_{\varepsilon,\theta}\nabla N_\varepsilon+2\int_x N_\varepsilon N_{\varepsilon,\theta}\left(K-\rho_\varepsilon\right)dx=H_\theta\Big(\theta,\langle\rho(\cdot,t)\rangle\Big)$$

But at $\bar\theta(t)$ one has

$$-\theta\int_x\nabla N_{\varepsilon,\theta}\nabla N_\varepsilon+\int_x N_\varepsilon N_{\varepsilon,\theta}\left(K-\rho_\varepsilon\right)dx=H\Big(\bar\theta,\langle\rho(\cdot,t)\rangle\Big)=0.$$

Therefore

$$-\int_x|\nabla N|^2dx=H_\theta\Big(\theta,\langle\rho(\cdot,t)\rangle\Big)<0.$$

Evolution of Dispersal

$$\frac{d}{dt}\overline{\theta}(t) = (-D^2\varphi)^{-1}.\nabla_\theta H\Big(\overline{\theta}(t), \langle\bar{\rho}(\cdot,t)\rangle\Big)$$

$$\nabla_\theta H\Big(\overline{\theta}(t), \langle\bar{\rho}(\cdot,t)\rangle\Big) < 0$$

Conclusion

- $\overline{\theta}(t)$ decreases. Do not move in a bounded domain !
- Already known, but here we give the dynamics

Intuition :

- A mutant with small dispersal diffuses less
- wins advantage by staying near the maximum of $K(x)$

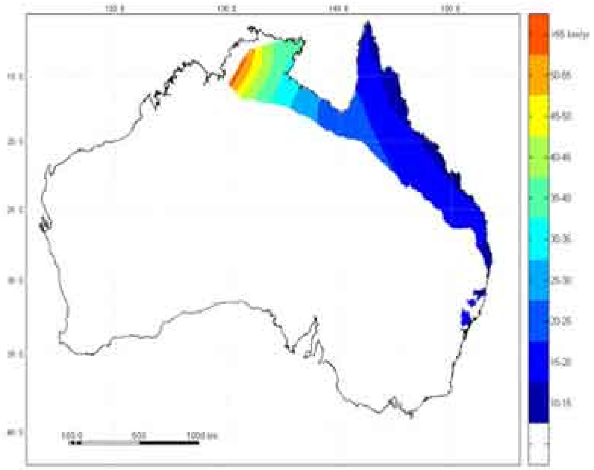
Accelerating waves

Conclusion Do not move in a bounded domain !

One can ask the same question for invasion fronts : $\Omega = \mathbb{R}^d$

Accelerating waves

Example of the cane toads invasion in Australia



Accelerating waves

In full space the solution is an invasion front à la Fisher/KPP for

$$\partial_t n(x,\theta,t) = \theta \partial^2_{xx} n(x,\theta,t) + rn(x,\theta,t)\left(1 - \rho(x,t)\right) + \alpha \partial^2_{\theta\theta} n(x,\theta,t)$$

$$\rho(x,t) = \int_0^\infty n(x,\theta,t)\, d\theta, \qquad\qquad n(x=+\infty,t) = 0$$

Many rescalling possible

They always show that large values of θ are selected at the front of the wave.

Accelerating waves (scale 1)

Scaling 1 : Front in x, $\theta \in (0, \Theta)$

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \varepsilon^2 \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + r n_\varepsilon(x,\theta,t)\,(1 - \rho_\varepsilon(x,t)) + \alpha \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n(x,\theta,t)\,d\theta, \qquad n_\varepsilon(x = +\infty, t) = 0$$

On the front, $n_\varepsilon \approx Q(\theta) e^{\lambda(x-ct)/\varepsilon}$

$$[\theta\lambda^2 + c\lambda + r]Q - \alpha \partial^2_{\theta\theta} Q = 0$$

In other words, the principal eigenvalue is $c\lambda$ which gives both

$$c = c^*(\lambda), \qquad Q(\theta, \lambda) = \text{eigenfunction}$$

Accelerating waves (scale 1)

It remains to compute λ by the standard approach through H.-J. equation (Barles, Evans, Souganidis)

$$n_{\varepsilon}(x, \theta, t) \approx e^{u(x,t)/\varepsilon} N_{\varepsilon}(x, \theta, t)$$

We find

$$\partial_t u_{\varepsilon} N_{\varepsilon}(x, \theta, t) + \theta |\partial_x u_{\varepsilon}|^2 N_{\varepsilon} = r(1 - \rho_{\varepsilon}) N + \alpha \partial^2_{\theta\theta} N_{\varepsilon}$$

Therefore in the front $N_{\varepsilon} \approx Q$ and

$$\max\left(u, \partial_t u - c^*(\partial_x u)\partial_x u\right) = 0$$

In other words

$$c^*(\partial_x u) = \text{effective Hamiltonian}$$

Accelerating waves (scale 1)

Conclusion We can compute the speed of the front thanks to this H.-J. equation

With $\theta \in (0, \Theta)$

$$c^*(\partial_x u) \geq 2r\sqrt{\frac{\Theta}{2}}$$

front is faster than the average

$$c^*(\partial_x u) \underset{\alpha \to 0}{\longrightarrow} 2r\sqrt{\Theta}$$

Accelerating waves (scale 2)

Scaling 2 : Front in x, small mutations

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \varepsilon^2 \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + r n_\varepsilon(x,\theta,t)\,(1-\rho_\varepsilon(x,t)) + \alpha \varepsilon^2 \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n(x,\theta,t)\,d\theta, \qquad n_\varepsilon(x=+\infty,t)=0$$

Rationale behind this rescaling

$$\theta \approx \sqrt{\alpha r} t, \qquad x_{front} \approx \sqrt{\theta}\, t \approx (\alpha r)^{1/4} t^{3/2}$$

(not the hyperbolic scaling)

$$(t,x,\theta) \to (t/\varepsilon,\ x/\varepsilon^{3/2},\ \theta/\varepsilon).$$

Accelerating waves (scale 2)

Scaling 2 : Front in x, small mutations

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \varepsilon^2 \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + r n_\varepsilon(x,\theta,t)\left(1-\rho_\varepsilon(x,t)\right) + \alpha \varepsilon^2 \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n(x,\theta,t)\, d\theta, \qquad\qquad n_\varepsilon(x=+\infty,t)=0$$

Use the Hopf-Cole/WKB change of variable $n_\varepsilon = e^{u_\varepsilon/\varepsilon}$

$$\begin{cases} \partial_t u = \theta|\partial_x u|^2 + \alpha|\partial_\theta u|^2 + r(1-\rho(x,t)) \\ \max_\theta u(x,\theta,t) \le 0 \qquad 0 = u\Big(x,\bar\theta(x,t),t\Big) \end{cases}$$

The constraint can be inactive (extinction)

$$\max_\theta u(x,\theta,t) < 0 \qquad \rho(x,t) = 0$$

Accelerating waves (scale 2)

Scaling 2 : Front in x, small mutations

$$\begin{cases} \partial_t u = \theta|\partial_x u|^2 + \alpha|\partial_\theta u|^2 + r(1-\rho(x,t)) \\ \max_\theta u(x,\theta,t) \leq 0 \qquad\quad 0 = u\Big(x, \bar\theta(x,t), t\Big) \end{cases}$$

What is the canonical equation ! New phenomena : The canonical is a PDE

$$\partial_t u = \theta|\partial_x u|^2 + \alpha|\partial_\theta u|^2 + r(1-\rho(x,t)) := R(x,\theta,t)$$

$$\partial_\theta u(x,\bar\theta(t),t) = 0.$$

$$\frac{\partial}{\partial t}\bar\theta(x,t) = -\frac{\partial_{\theta t} u}{\partial_{\theta\theta} u}, \qquad\qquad \frac{\partial}{\partial x}\bar\theta(x,t) = -\frac{\partial_{\theta x} u}{\partial_{\theta\theta} u}$$

Accelerating waves (scale 2)

Scaling 2 : Front in x, small mutations

$$R_\theta = |\partial_x u|^2 + 2\theta \partial_x u \partial_{x\theta} u + 2\alpha \partial_\theta u \partial_{\theta\theta} u$$

$$\frac{\partial}{\partial t}\bar{\theta}(x,t) = -\frac{\partial_{\theta t} u}{\partial_{\theta\theta} u}, \qquad \frac{\partial}{\partial x}\bar{\theta}(x,t) = -\frac{\partial_{\theta x} u}{\partial_{\theta\theta} u}$$

The canonical is a Burgers type equation

$$\frac{d}{dt}\bar{\theta}(x,t) = -\frac{|\partial_x u|^2 + 2\bar{\theta}(x,t)\partial_x u \partial_{x\theta} u}{\partial_{\theta\theta} u}$$

$$\frac{d}{dt}\bar{\theta}(x,t) - 2\partial_x u \, \bar{\theta}(x,t)\frac{\partial}{\partial x}\bar{\theta}(x,t) = \frac{|\partial_x u|^2}{-\partial_{\theta\theta} u} > 0$$

Numerically shocks are observed on the fittest traits.

Accelerating waves (scale ")

Scaling 3 : Traveling wave in x, small mutations

$$\varepsilon \partial_t n_\varepsilon(x,\theta,t) = \theta \partial^2_{xx} n_\varepsilon(x,\theta,t) + r n_\varepsilon(x,\theta,t)\,(1-\rho_\varepsilon(x,t)) + \alpha \varepsilon^2 \partial^2_{\theta\theta} n_\varepsilon(x,\theta,t)$$

$$\rho_\varepsilon(x,t) = \int_0^\infty n(x,\theta,t)\, d\theta, \qquad n_\varepsilon(x=+\infty,t)=0$$

?

Other examples Selection of competitive/colonize phenotype in tumor growth (Orlando, Gatenby, Brown).

Collaborators for this programm

Vincent Calvez 

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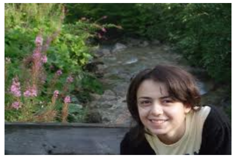
Sepideh Mirrahimi 

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