



Ashok Maitra Memorial Lectures, March 2022

SOME MATHEMATICAL MODELS
OF EVOLUTION. MODELLING HYBRID ZONES:
Travelling waves in the Allen-Cahn equation
(and how to stop them)

Alison Etheridge
University of Oxford

Special thanks to Nick Barton, IST Austria

Recap of what we did last time

- ▶ Wright-Fisher/Moran models and diffusion limit

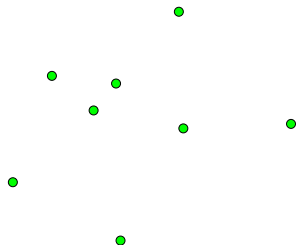
$$dp = -sp(1-p)dt + \sqrt{p(1-p)}dW;$$

- ▶ Kingman Coalescent/ Ancestral Selection Graph;
- ▶ Adding space: Kimura stepping stone model/ Wright-Malécot model;
- ▶ The pain in the torus;

... and we were beginning to discuss a model that addresses the pain in the torus.

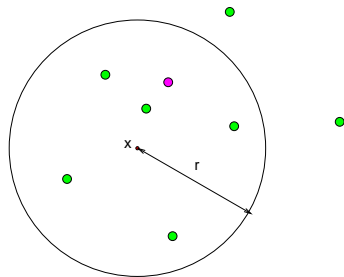
An individual based model

- ▶ Start with Poisson intensity λdx . **Events** rate $dt \otimes dx \otimes \xi(dr, du)$. Throw down ball $B(x, r)$.



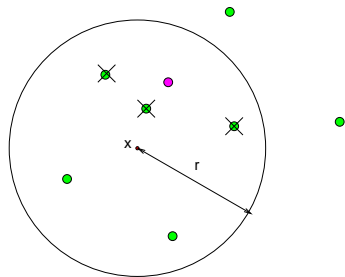
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- ▶ Choose **parent** from $B(x, r)$,



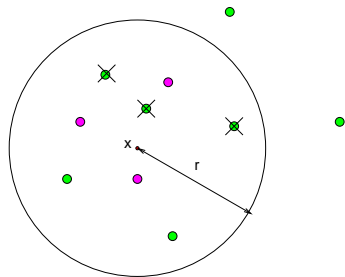
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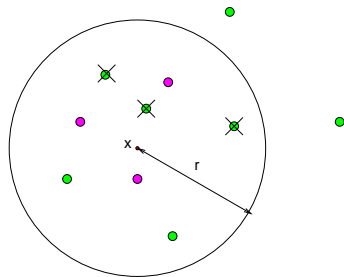
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Offspring inherit type of parent

$\lambda \rightarrow \infty$ limit (no space)

Start from $\text{Pois}(\lambda)$

If first reproduction event has 'impact' u

- ▶ $\text{Pois}((1 - u)\lambda)$ 'survivors';
- ▶ $\text{Pois}(u\lambda)$ offspring.

As $\lambda \rightarrow \infty$ proportion u of individuals die and are replaced by offspring of the type of the parent.

The Λ -Fleming-Viot process

State $\{\rho(t, \cdot) \in \mathcal{M}_1(K), t \geq 0\}$.

K space of genetic types.

- ▶ Poisson Point Process Π intensity $dt \otimes F(du)$
- ▶ if $(t, u) \in \Pi$, individual sampled at random from population at time $t-$ (i.e. choose $k \sim \rho(t-)$)
- ▶ proportion u of population replaced by offspring of chosen individual

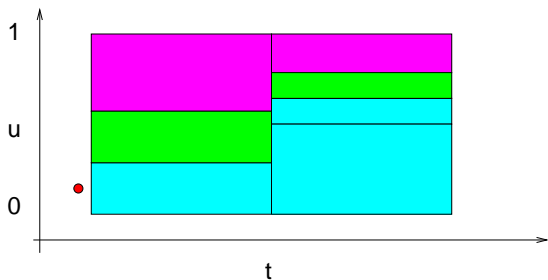
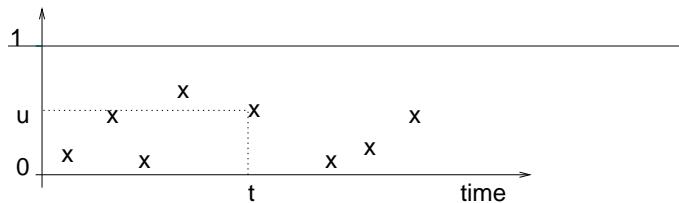
$$\rho(t, \cdot) = (1 - u)\rho(t-, \cdot) + u\delta_k.$$

$F(du) = \frac{\Lambda(du)}{u^2}$, Λ finite measure on $[0, 1]$.

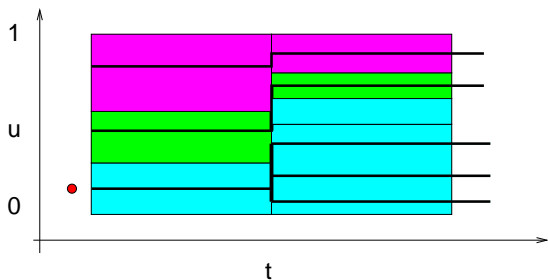
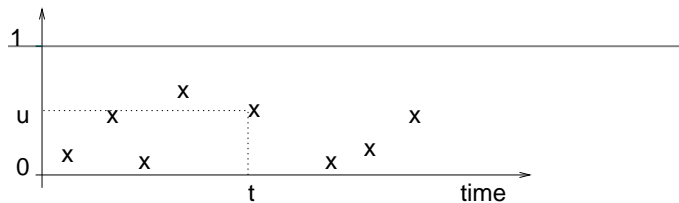
Donnelly & Kurtz (1999)

(‘Generalised Fleming-Viot process’, Bertoin & Le Gall 2003)

The Λ -Fleming-Viot process



The Λ -Fleming-Viot process



Λ -coalescents

Donnelly & Kurtz (1999), Pitman (1999), Sagitov (1999)

If there are currently n ancestral lineages, each transition involving j of them merging happens at rate

$$\beta_{n,j} = \int_0^1 u^j (1-u)^{n-j} \frac{\Lambda(du)}{u^2}$$

- ▶ Λ a finite measure on $[0, 1]$
- ▶ Kingman's coalescent, $\Lambda = \delta_0$

The spatial Λ -Fleming-Viot process

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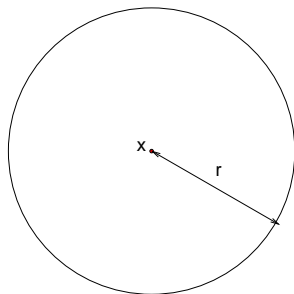
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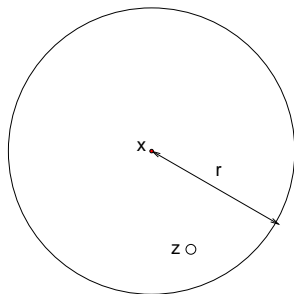


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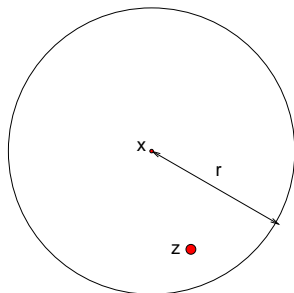


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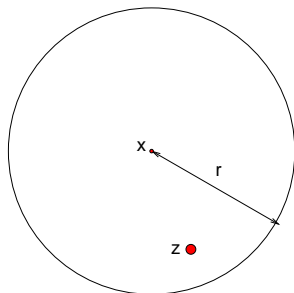
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For all $y \in B_r(x)$,

$$\rho(t, y, \cdot) = (1 - u)\rho(t-, y, \cdot) + u\delta_k.$$

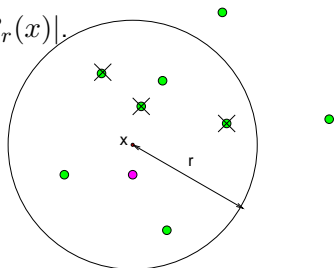


Backwards in time

- ▶ A *single* ancestral lineage evolves in series of jumps with intensity

$$dt \otimes \int_{(|x|/2, \infty)} \int_{[0,1]} \frac{L_r(x)}{\pi r^2} u \xi(dr, du) dx$$

on $\mathbb{R}_+ \times \mathbb{R}^2$ where $L_r(x) = |B_r(0) \cap B_r(x)|$.



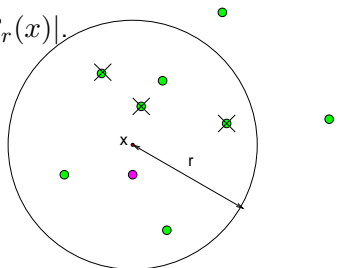
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- ▶ Lineages can coalesce when hit by same 'event'.



Introducing selection to the SLFV

$K = \{a, A\}$, $w(t, x) = \rho(t, x, a)$ proportion of type a

- ▶ (i) Two types, a, A . Weight type a by $(1 - s)$. If a reproduction event affects a region $B(x, r)$ in which current proportion of a -alleles is \bar{w} , then probability offspring are type a is

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- ▶ (ii) Neutral events rate $\propto (1 - s)$, selective events rate $\propto s$. At **selective** reproduction events, sample **two** potential parents. If types aa , then an a reproduces, otherwise an A does.

(Spatial) Ancestral selection graph

Evolution of ancestry due to neutral events as before:

- ▶ lineages evolve in a series of jumps;
- ▶ they can coalesce when covered by same event.

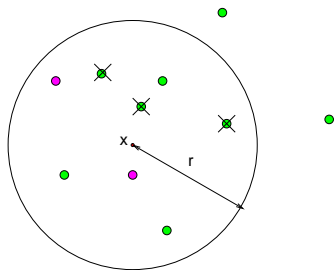
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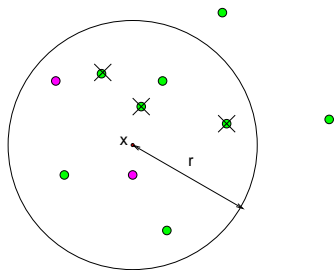
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A sampled individual is type a iff all lineages in the corresponding ASG are type a at any previous time.

When can we detect selection?

Neutral mutation rate, μ , sets timescale

- ▶ Mutation rates are low;
- ▶ Scaling limits are 'robust'.

Natural question:

When, and over what spatial scales can we expect to observe a signature of natural selection?

Scaling limits: Small 'neighbourhood size':

Fix $u \in (0, 1)$.

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Heuristics:

- ▶ At a 'branching' event in ASG, two lineages born at separation $\mathcal{O}(1/\sqrt{n})$.
- ▶ Probability they separate to $\mathcal{O}(1)$ before coalescing is
 - ▶ $d = 1$: $\mathcal{O}(1/\sqrt{n})$,
 - ▶ $d = 2$: $\mathcal{O}(1/\log n)$,
 - ▶ $d \geq 3$: $\mathcal{O}(1)$.
- ▶ Selection will only be visible if expect to see at least one pair 'separate' by time 1.

Scaling limits: Small 'neighbourhood size':

Fix $u \in (0, 1)$.

Set $n = 1/\mu$ and rescale: $w(nt, \sqrt{n}x)$.

Ability to detect selection depends on dimension:

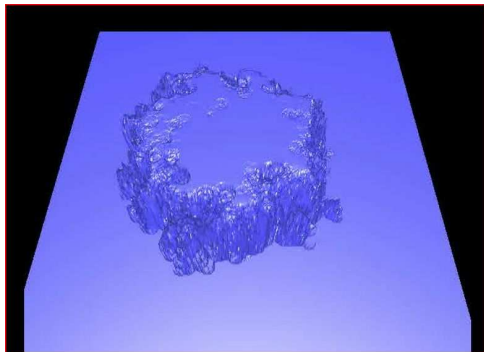
- ▶ $d = 1$, selection only visible if $s = \mathcal{O}(1/\sqrt{n}) = \mathcal{O}(\sqrt{\mu})$,
limiting ASG embedded in Brownian net;
- ▶ $d = 2$, selection only visible if
 $s = \mathcal{O}(\log n/n) = \mathcal{O}(\mu|\log(\mu)|)$,
limiting ASG 'Branching BM';
- ▶ $d \geq 3$, selection only visible if $s = \mathcal{O}(1/n) = \mathcal{O}(\mu)$,
limiting ASG Branching BM.

Technical challenges because $ns_n \rightarrow \infty$.

E., Freeman, Penington, Straulino (2017)

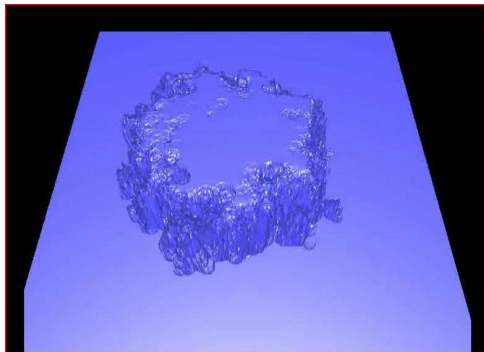
Spread of a favoured allele

Two types, a , A , relative fitnesses $1 : 1 + s$. If a reproduction event affects a region $B(x, r)$ in which current proportion of a -alleles is w , then probability offspring are type a is $\frac{w}{1+s(1-w)}$.



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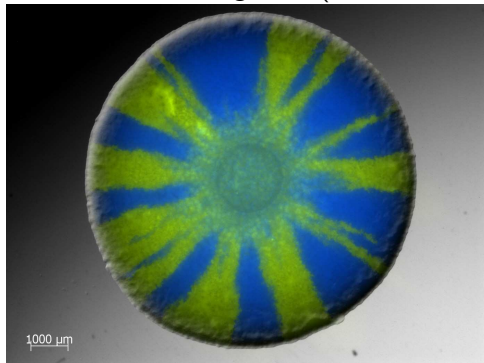
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Alternative interpretation: strong selection \sim range expansion

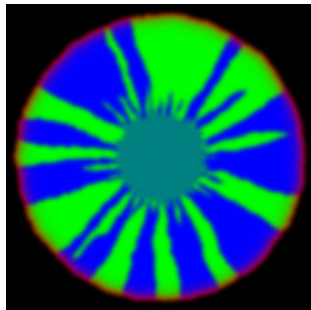
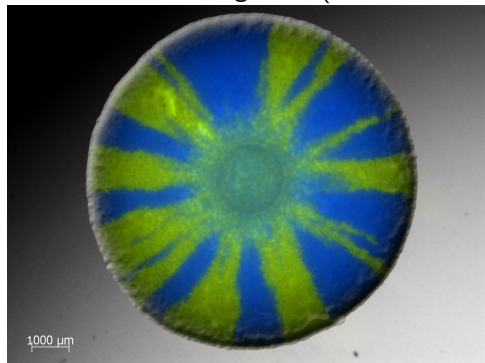
Range expansion

Pseudomonas aeruginosa (Kevin Foster)

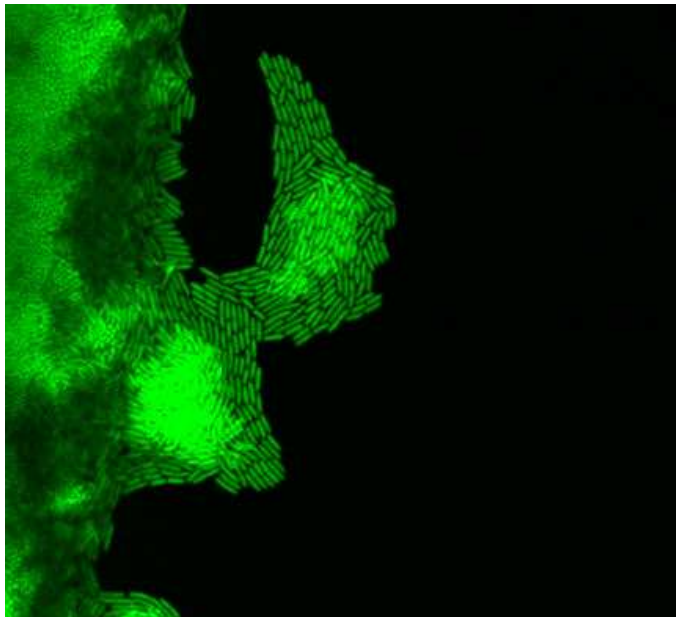


Range expansion

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What's really happening?



Hybrid Zones

A hybrid zone is a narrow geographic region where two genetically distinct populations are found close together and hybridise to produce offspring of mixed ancestry.

They are maintained by a balance between selection and dispersal.



With thanks to Nick Barton and his group

A mathematical model

Individuals carry two copies of a gene that occurs as a or A .

Hardy-Weinberg proportions: \bar{w} = proportion of a -alleles,

$$\frac{aa}{\bar{w}^2} \quad \left| \quad \frac{aA}{2\bar{w}(1-\bar{w})} \quad \right| \quad \frac{AA}{(1-\bar{w})^2}$$

Relative fitnesses:

$$\frac{aa}{1} \quad \left| \quad \frac{aA}{1-s} \quad \right| \quad \frac{AA}{1}$$

Reproduction

- ▶ Each heterozygote (aA) produces $(1 - s)$ times as many germ cells (cells of same genotype) as a homozygote (aa or AA);
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$$\begin{aligned}\bar{w}^* &= \frac{\left(\bar{w}^2 + \bar{w}(1 - \bar{w})(1 - s)\right)}{\left(\bar{w}^2 + 2\bar{w}(1 - \bar{w})(1 - s) + (1 - \bar{w})^2\right)} \\ &= \frac{\bar{w}^2 + \bar{w}(1 - \bar{w})(1 - s)}{1 - 2s\bar{w}(1 - \bar{w})}\end{aligned}$$

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A deterministic approximation

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In an infinite population, if $s = \frac{\alpha}{M}$ (where M is large), measuring time in units of M generations,

$$\frac{\Delta\bar{w}}{\Delta t} = \alpha\bar{w}(1 - \bar{w})(2\bar{w} - 1) + \mathcal{O}(s^2).$$

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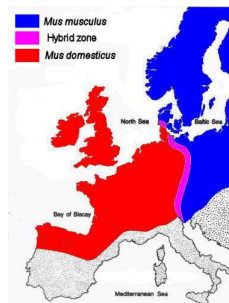
Add dispersal:

$$\frac{\partial w}{\partial t} = \frac{m}{2}\Delta w + \alpha w(1 - w)(2w - 1).$$

Hybrid zones and the Allen-Cahn equation

$$\frac{\partial w}{\partial t} = \frac{m}{2} \Delta w + \alpha w(1-w)(2w-1).$$

Other mechanisms can lead to hybrid zones; e.g. an abrupt change in the environment.



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Width of zone

$$\approx \sqrt{\frac{2m}{\alpha}}$$

Zooming out

Applying a diffusive rescaling $t \mapsto \frac{t}{\epsilon^2}$, $x \mapsto \frac{x}{\epsilon}$, the Allen-Cahn equation becomes

$$\frac{\partial w}{\partial t} = \frac{m}{2} \Delta w + \frac{\alpha}{\epsilon^2} w(1-w)(2w-1).$$

For convenience, set $m = 2$, $\alpha = 1$.

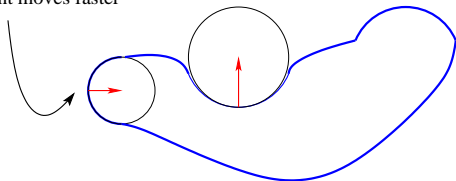
For sufficiently regular initial conditions, as $\epsilon \rightarrow 0$, the solution converges to the indicator function of a region whose boundary evolves according to *curvature flow*.

(Mean) Curvature flow

- ▶ $\Gamma_t : S^1 \rightarrow \mathbb{R}^2$ smooth embeddings;
- ▶ $\mathbf{n}_t(u)$ unit (inward) normal vector to Γ_t at u ;
- ▶ $\kappa = \kappa_t(u)$ curvature of Γ_t at u .

$$\frac{\partial \Gamma_t(u)}{\partial t} = \kappa_t(u) \mathbf{n}_t(u). \quad \text{Defined up to fixed time } T$$

This point moves faster



The Allen-Cahn equation and curvature flow

Let $d(x, t)$ be the signed distance from x to Γ_t . Choose w_0 such that $\Gamma_0 = \{x \in \mathbb{R}^2 : w_0(x) = \frac{1}{2}\}$, $w_0 < \frac{1}{2}$ inside Γ and $> \frac{1}{2}$ outside.

$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\varepsilon^2} w(1-w)(2w-1).$$

Theorem (Chen 1992)

Fix $T^* \in (0, T)$. Let $k \in \mathbb{N}$. There exists $\varepsilon(k) > 0$, and $a(k), c(k) \in (0, \infty)$ such that for all $\varepsilon \in (0, \varepsilon(k))$ and t satisfying $a\varepsilon^2 |\log \varepsilon| \leq t \leq T^*$,

1. for x such that $d(x, t) \geq c\varepsilon |\log \varepsilon|$, we have $w(t, x) \geq 1 - \varepsilon^k$;
2. for x such that $d(x, t) \leq -c\varepsilon |\log \varepsilon|$, we have $w(t, x) \leq \varepsilon^k$.

Finite populations; adding noise?

Hairer, Ryser & Weber (2012), $d = 2$ ($v = 2w - 1$)

$$dv = (\Delta v + v - v^3)dt + \sigma dW,$$

W a mollified space-time white noise.

- ▶ If the mollifier is removed, solutions converge weakly to zero;
- ▶ if intensity of W simultaneously converges to zero sufficiently quickly, recover the deterministic equation.

Will hybrid zones still evolve approximately according to curvature flow in the presence of random genetic drift?

finite population

... additive white noise is not a good model of genetic drift

Adding selection to the SLFV: majority voting

$$K = \{a, A\} \quad \{w(t, x), x \in \mathbb{R}^d, t \geq 0\} \text{ (proportion of type } a\text{)}$$

Two types of event:

- ▶ (i) Neutral events as above, rate $\propto (1 - s)$, (ii) selective events rate $\propto s$.
- ▶ At **selective** reproduction events, sample **three** 'potential' parents. If types aaa or aaA , then an a reproduces, otherwise an A does.

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$w \mapsto w + u(1 - w)$ with probability $w^3 + 3w(1 - w)^2$;
 $w \mapsto w - uw$ with probability $(1 - w)^3 + 3w(1 - w)^2$.

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$$\begin{aligned} \mathbb{E}[\Delta w] &= us \left\{ w^3(1 - w) + 3w^2(1 - w)^2 - w(1 - w)^3 - 3w^2(1 - w)^2 \right\} \\ &= us \cdot w(1 - w) \left(w^2 - (1 - w)^2 \right) = us \cdot w(1 - w)(2w - 1). \end{aligned}$$

A new proof in the deterministic case

Ternary branching Brownian motion



- ▶ Individual lifetime $\text{Exp}(1/\epsilon^2)$;
- ▶ During lifetime follows Brownian motion;
- ▶ Replaced by three offspring.

Majority voting in (Historical) BBM

Adaptation of idea of del Masi, Ferrari & Lebowitz (1986)

$\mathbf{W}(t)$ = historical ternary BBM.

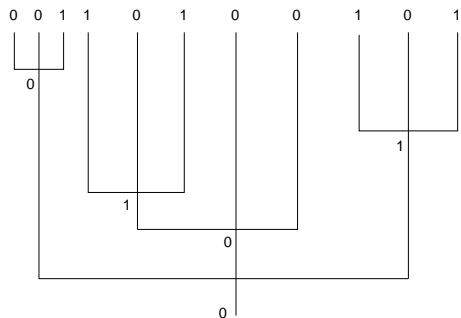
For a fixed function $w_0 : \mathbb{R}^2 \rightarrow [0, 1]$, define a voting procedure on $\mathbf{W}(t)$ as follows.

1. Each leaf, independently, votes 1 with probability $w_0(W_i(t))$ and otherwise votes 0.
2. At each branch point the vote of the parent particle is the majority vote of the votes of its three children.

This defines an iterative voting procedure, which runs inwards from the leaves of $\mathbf{W}(t)$ to the root.

Define $\mathbb{V}_{w_0}(\mathbf{W}(t))$ to be the vote associated to the root.

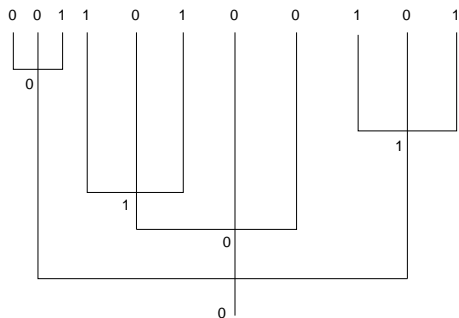
Majority voting and the Allen-Cahn equation



$\mathbf{W}(t)$ = historical BBM, branching rate $\frac{1}{\varepsilon^2}$; $w_0 : \mathbb{R}^2 \rightarrow [0, 1]$.

$$w(t, x) = \mathbb{P}_x^\varepsilon [\mathbb{V}_{w_0}(\mathbf{W}(t)) = 1]$$

Majority voting and the Allen-Cahn equation



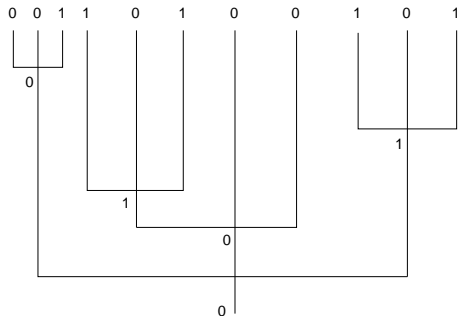
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Note that if probability of voting 1 is w , the probability that the majority of 3 independent votes is 1 is

$$w^3 + 3w^2(1 - w) = w(1 - w)(2w - 1) + w.$$

Majority voting and the Allen-Cahn equation



$\mathbf{W}(t)$ = historical BBM, branching rate $\frac{1}{\varepsilon^2}$; $w_0 : \mathbb{R}^2 \rightarrow [0, 1]$.

$$w(t, x) = \mathbb{P}_x^\varepsilon [\mathbb{V}_{w_0}(\mathbf{W}(t)) = 1]$$

solves

$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\varepsilon^2} w(1-w)(2w-1), \quad w(0, x) = w_0(x).$$

Probabilistic proof of Allen-Cahn result

Representation reduces result to

1. for x with $d(x, t) \geq c\varepsilon |\log \varepsilon|$, $\mathbb{P}_x^\varepsilon [\mathbb{V}_p(\mathbf{W}(t)) = 1] \geq 1 - \varepsilon^k$;
2. for x with $d(x, t) \leq -c\varepsilon |\log \varepsilon|$, $\mathbb{P}_x^\varepsilon [\mathbb{V}_p(\mathbf{W}(t)) = 1] \leq \varepsilon^k$.

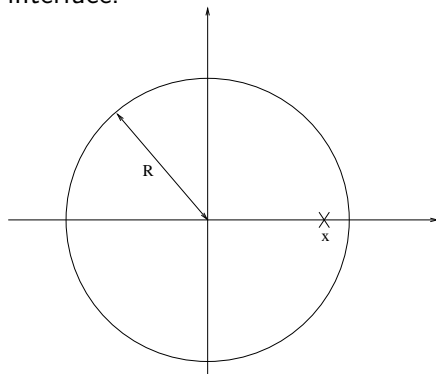
Proof in two steps:

- ▶ a one-dimensional analogue in the case $p(x) = \mathbf{1}_{\{x \geq 0\}}$,
(symmetry, monotonicity for this p and amplification of bias through majority voting)
- ▶ for two-dimensional BM W and one-dimensional BM B , couple so that $d(W_s, t - s)$ is well approximated by B_s when W_s is close to Γ_{t-s} . (uses regularity assumptions on initial condition)

Approach parallels approximation of solution by one-dimensional standing wave in Chen (1992).

Some heuristics

Majority voting increases bias. Suppose there is already a sharp interface.



For the point x ,

$$\mathbb{P}_x[W_{\delta t} \text{ outside ball}] = 1/2$$

$$\mathbb{P}_x[B_{\delta t} + \frac{1}{R}\delta t > R] = 1/2$$

$$x = R - \frac{1}{R}\delta t.$$

Generation of the interface results from lots of rounds of voting

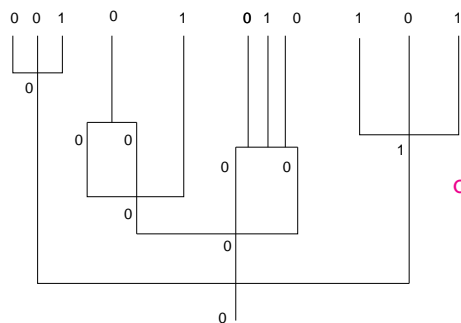
Proof for the 'stochastic' hybrid zones

Π is a Poisson point process on $\mathbb{R}_+ \times \mathbb{R}^2 \times (0, \infty)$ with intensity measure $dt \otimes dx \otimes \mu(dr)$. Dual process of branching and coalescing 'ancestral' lineages. **Tracing backwards in time:**

- ▶ Start with a single individual;
- ▶ at event $(t, x, r) \in \Pi$, independently mark each lineage in $\mathcal{B}_r(x)$ with probability u ;
- ▶ **if at least one lineage is marked,**
 1. if event is neutral, all marked lineages coalesce into a single lineage, whose location is drawn uniformly at random from within $\mathcal{B}_r(x)$.
 2. if event is selective, all marked individuals are replaced by *three* offspring individuals, whose locations are drawn independently and uniformly from within $\mathcal{B}_r(x)$.
- ▶ In both cases, if no individual is marked, then nothing happens.

Majority voting procedure defined as before.

Recasting the result



c.f. Ancestral selection graph

1. for x such that $d(x, \sigma^2 t) \geq d\varepsilon_n |\log \varepsilon_n|$, we have $\mathbb{P}_x [\mathbb{V}_p(\Xi^n(t)) = 1] \geq 1 - \varepsilon_n^k$.
2. for x such that $d(x, \sigma^2 t) \leq -d\varepsilon_n |\log \varepsilon_n|$, we have $\mathbb{P}_x [\mathbb{V}_p(\Xi^n(t)) = 1] \leq \varepsilon_n^k$.

E., Freeman, Penington (2017)

What if homozygotes not equally fit?

Relative fitnesses:

$$\begin{array}{c|c|c} aa & aA & AA \\ \hline 1 + \gamma s & 1 - s & 1 \end{array}$$

Equation becomes

$$\frac{\partial w}{\partial t} = \Delta w + sw(1-w)((2+\gamma)w-1).$$

Take $\gamma = \mathcal{O}(\varepsilon)$ and rescale:

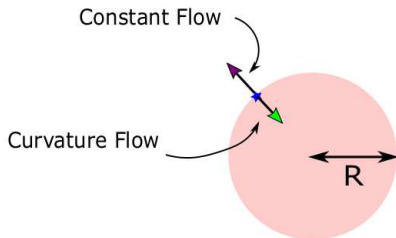
$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\varepsilon^2} w(1-w)(2w - (1 - \nu\varepsilon)).$$

Sensitivity to asymmetry (Mitch Gooding 2018)

$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\epsilon^2} w(1-w)(2w - (1 - \nu\epsilon)).$$

Limit a mixture of curvature flow and 'constant flow':

$$\frac{\partial \Gamma_t(u)}{\partial t} = (-\nu + \kappa_t(u)) \mathbf{n}_t(u). \quad \text{Defined up to fixed time } T$$



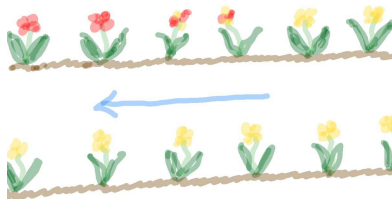
Invasions

$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\varepsilon^2} w(1-w)(2w - (1 - \nu\varepsilon)).$$

In $d = 1$, travelling wave solution

$$w(x, t) = \left(1 + \exp\left(-\frac{x + \nu t}{\varepsilon}\right) \right)^{-1}$$

wave speed $-\nu$, connects 0 at $-\infty$ to 1 at ∞



Blocking (E., Gooding, Letter (2022+))

Consider a domain $\Omega \subseteq \mathbb{R}^2$ (and containing the x -axis, say)

When do we have invasion?

$$\frac{\partial w}{\partial t} = \Delta w + \frac{1}{\epsilon^2} w(1-w)(2w - (1 - \nu\epsilon)), \quad w(0, x) = \mathbf{1}_{x_1 \geq 0}.$$

Theorem (Berestycki et al., 2016) (paraphrased)

Depending on the geometry of the domain:

1. complete invasion;
2. partial propagation;
3. total blocking.

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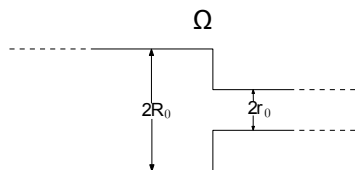
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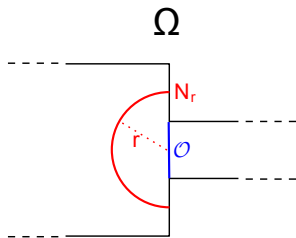
Depending on the geometry of the domain:

1. complete invasion;
2. partial propagation;
3. total blocking.



A precise statement

$$\begin{cases} \frac{\partial w}{\partial t} = \Delta w + \frac{1}{\varepsilon^2} w(1-w)(2w - (1 - \nu\varepsilon)); \\ \frac{\partial w}{\partial n} = 0, & w(x, 0) = 1_{x_1 \geq 0}; \end{cases}$$



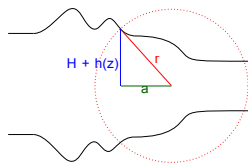
Theorem

Suppose $r_0 < r < \frac{d-1}{\nu} \wedge R_0$. Let $k \in \mathbb{N}$. Then $\exists \hat{\varepsilon}(k) > 0$ and $a(k), M(k) > 0$ such that $\forall \varepsilon \in (0, \hat{\varepsilon}), t \in (a(k)\varepsilon^2 |\log(\varepsilon)|, \infty)$,

$$x \in \{x = (x_1, \dots, x_d) : x_1 < -r - M(k)\varepsilon |\log(\varepsilon)|\} \implies w(x, t) \leq \varepsilon^k.$$

Other domains

$$\Omega = \left\{ (x_1, x'), x_1 \in \mathbb{R}, x' \in \mathbb{R}^{d-1}, \|x'\| \leq H + h(-x_1) \right\}$$



Theorem

Suppose that,

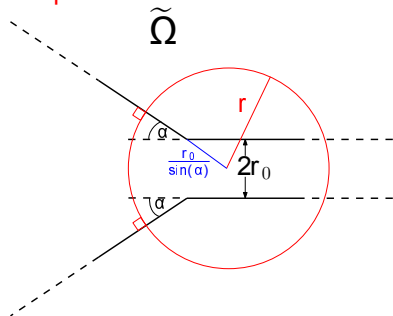
$$\inf_{z>0} \left\{ H + h(z) - \left(\frac{d-1}{\nu} \right) \frac{h'(z)}{\sqrt{1+h'(z)^2}} \right\} < 0.$$

Fix $k \in \mathbb{N}$. There exist $x_0 < 0$, $\hat{\epsilon}(k) > 0$ and $M(k) > 0$ such that for all $\epsilon \in (0, \hat{\epsilon})$, and $t \geq 0$,

$$\text{if } x_1 \leq x_0 - M(k)\epsilon |\log(\epsilon)| \text{ then } u^\epsilon(x, t) \leq \epsilon^k.$$

Key argument

Key is coupling around a portion of a spherical shell



If $r_0\nu < (d - 1) \sin \alpha$ wave blocked for small ε .

Effect of noise

- ▶ If genetic drift is weak (population density high), the spread of the favoured type is blocked;
- ▶ If genetic drift is strong (population density low), the favoured population spreads across the whole domain.

Proof uses duality; c.f. earlier slides on genic selection.