Branching Brownian motion, mean curvature flow and the motion of hybrid zones

Sarah Penington

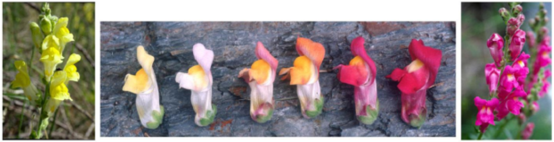
Joint work with Alison Etheridge and Nic Freeman

Mathematical Institute
University of Oxford

Hybrid zones

Suppose two species live close to each other and interbreed, but the offspring have lower evolutionary fitness.
Hybrids are found in a narrow interface between the two populations.
How does the interface evolve? (on a suitable space- and time-scale)

Hybrid zones



Spatial Λ-Fleming-Viot process (SLFV) with types a, A

$w_t(x) :=$ proportion of type a at spatial position x at time t

Poisson point process Π on $\mathbb{R} \times \mathbb{R}^2 \times \mathbb{R}_+ \times (0,1]$. At each $(t,x,r,u) \in \Pi$,

1. Choose a parental location z uniformly at random in $\mathcal{B}_r(x)$.
2. Choose a parental type α according to $w_{t-}(z)$, i.e. $\alpha = a$ with probability $w_{t-}(z)$.
3. Replace a fraction u of the population in $\mathcal{B}_r(x)$ with type α:

$$w_t(y) = (1-u)w_{t-}(y) + u\mathbb{1}_{\{\alpha=a\}}, \quad \forall y \in \mathcal{B}_r(x).$$

We call u the impact of the event.

Relative fitnesses

AA individuals have relative fitness 1
Aa individuals have relative fitness $1 - s$
aa individuals have relative fitness 1

Let w be proportion of type a.
Proportions of aa, Aa and AA individuals are w^2, $2w(1-w)$ and $(1-w)^2$.

$$\begin{aligned}\mathbb{P}(\text{new gamete is type } a) &= \frac{w^2 + 2w(1-w)\cdot\frac{1}{2}(1-s)}{1-2sw(1-w)} \\ &= (1-s)w + s(3w^2 - 2w^3) + \mathcal{O}(s^2)\end{aligned}$$

$$\begin{aligned}\mathbb{P}(\text{majority of } 3 \text{ i.i.d. Bernoulli}(w) \text{ r.v.s are } 1) &= w^3 + 3w^2(1-w) \\ &= 3w^2 - 2w^3.\end{aligned}$$

SLFV with selection against heterozygosity (SLFVS)

Fix $u \in (0,1]$, $s > 0$, $\mathcal{R} > 0$. Let μ be a finite measure on $(0, \mathcal{R}]$ and let Π be a Poisson point process on $\mathbb{R} \times \mathbb{R}^2 \times (0, \mathcal{R}]$ with intensity measure

$$dt \otimes dx \otimes \mu(dr).$$

If $(t, x, r) \in \Pi$, with probability $1 - s$ the event is neutral:

1. Choose a parental location z uniformly at random within $\mathcal{B}_r(x)$, and a parental type, α, according to $w_{t-}(z)$.
2. For every $y \in \mathcal{B}_r(x)$, set $w_t(y) = (1-u)w_{t-}(y) + u\mathbb{1}_{\{\alpha = a\}}$.

With probability s the event is selective:

1. Choose three 'potential' parental locations z_1, z_2, z_3 uniformly at random in $\mathcal{B}_r(x)$, and then types $(\alpha_i)_{i=1,2,3}$, according to $(w_{t-}(z_i))_{i=1,2,3}$ independently. Let α denote the majority type of $(\alpha_i)_{i=1,2,3}$.
2. For every $y \in \mathcal{B}_r(x)$, set $w_t(y) = (1-u)w_{t-}(y) + u\mathbb{1}_{\{\alpha = a\}}$.

SLFVS dual

The dual process $(\mathcal{P}_t)_{t\geq 0}$ is a $\bigcup_{k\geq 1}(\mathbb{R}^2)^k$-valued Markov process with $\mathcal{P}_0 = z_0$ and for $t \geq 0$, $\mathcal{P}_t = (\xi_t^1, \ldots, \xi_t^{N_t})$. At each event $(t, x, r) \in \Pi$, with probability $1 - s$:

1. For each $\xi_{t-}^i \in \mathcal{B}_r(x)$, independently mark the corresponding lineage with probability u.
2. If at least one lineage is marked, all marked lineages disappear and are replaced by a single lineage, whose location is drawn uniformly at random from within $\mathcal{B}_r(x)$.

With probability s:

1. For each $\xi_{t-}^i \in \mathcal{B}_r(x)$, independently mark the corresponding lineage with probability u.
2. If at least one lineage is marked, all marked lineages disappear and are replaced by three lineages, whose locations are drawn independently and uniformly from within $\mathcal{B}_r(x)$.

In both cases, if no lineages are marked, then nothing happens.

Duality relation

After running dual for time t, the set of lineages at $x \in \mathbb{R}^2$ votes a with probability $w_0(x)$ and votes A otherwise. Votes at different locations are independent.
Trace votes back through the branching and coalescing structure, carrying the majority vote back at each branch point, to get a vote at the root - call this $\text{Vote}_{w_0}(\mathcal{P}_t)$.
Weak moment duality:

$$\mathbb{E}_{w_0}\left[\int_{\mathbb{R}^2} \psi(x) w_t(x) dx\right] = \int_{\mathbb{R}^2} \psi(x) \mathbb{P}_x[\text{Vote}_{w_0}(\mathcal{P}_t) = a] dx.$$

Rescaling limits of the SLFVS

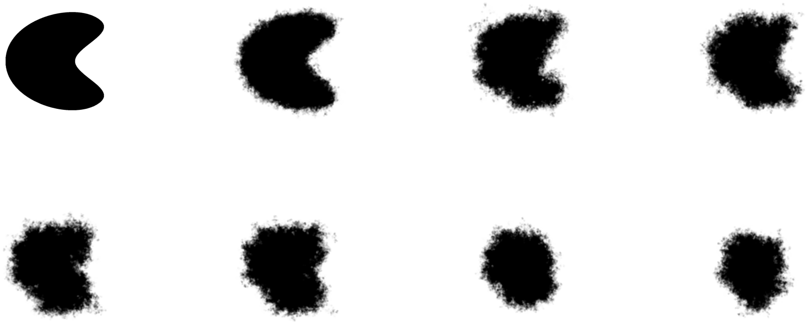
Let $(w_t^n)_{t\geq 0}$ denote the SLFVS with impact parameter $u_n = n^{-1+2\alpha}$, bounded radius distribution and selection parameter $s_n = \varepsilon^{-2}n^{-2\alpha}$, and initial condition $w_0^n(x) = w_0(n^{-\alpha}x)$.

Theorem (Etheridge, Véber, Yu 2014)

If $\alpha < 1/4$ then (after a constant time and space rescaling) a spatially averaged version of $(w_{nt}^n(n^\alpha x))_{t\geq 0}$ converges to the solution of

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

Simulations



Thanks to Jerome Kelleher

Curvature flow

Suppose for each t, $X_t : S^1 \to \mathbb{R}^2$ is a smooth embedding.
Let $N_t(\phi)$ denote the inwards normal vector to X_t at $X_t(\phi)$.
Let $\kappa_t(\phi)$ denote the curvature of X_t at $X_t(\phi)$.

Definition

X is a motion by curvature flow if

$$\frac{\partial X_t(\phi)}{\partial t} = \kappa_t(\phi) N_t(\phi)$$

for all t, ϕ.

$X_t(\cdot)$ shrinks to a point as $t \to T$ for some $T < \infty$.

Allen-Cahn equation

Suppose $g_0 : \mathbb{R}^2 \to [0,1]$ is such that $\Gamma = \{x \in \mathbb{R}^2 : g_0(x) = 1/2\}$ is a smooth embedding of S^1 with $g_0 < 1/2$ inside Γ and $g_0 > 1/2$ outside Γ.

Let $(\Gamma_t)_{t \le T}$ be the motion by curvature flow with $\Gamma_0 = \Gamma$ and let $d(x,t)$ denote the signed distance of x from Γ_t (negative inside Γ_t). Take $T^* < T$.

Theorem (Chen, 1990)

Suppose $g(t,x)$ is a solution to

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

with initial condition $g(0,x) = g_0(x)\ \forall x$. Then for $k \in \mathbb{N}$, $\exists\, a(k), c(k) < \infty$ s.t. for $a\varepsilon^2 |\log \varepsilon| \le t \le T^*$,

- *for x s.t. $d(x,t) \ge c\varepsilon |\log \varepsilon|$, $g(t,x) \ge 1 - \varepsilon^k$*
- *for x s.t. $d(x,t) \le -c\varepsilon |\log \varepsilon|$, $g(t,x) \le \varepsilon^k$.*

Rescaling limits of the SLFVS

Let $(w_t^n)_{t\geq 0}$ denote the SLFVS with impact parameter $u_n = n^{-1+2\alpha}$, bounded radius distribution and selection parameter $s_n = \varepsilon_n^{-2} n^{-2\alpha}$, and initial condition $w_0^n(x) = w_0(n^{-\alpha}x)$.

Suppose $\Gamma = \{x \in \mathbb{R}^2 : w_0(x) = 1/2\}$ is a smooth embedding of S^1 with $w_0 < 1/2$ inside Γ and $w_0 > 1/2$ outside Γ.

Let $(\Gamma_t)_{t\leq T}$ be the motion by curvature flow with $\Gamma_0 = \Gamma$ and let $d(x,t)$ denote the signed distance of x from Γ_t (negative inside Γ_t).

Theorem (Etheridge, Freeman, P. 2016)

If $\alpha < 1/4$ and $\varepsilon_n = o(1)$, $\varepsilon_n^{-2} = o(\log n)$ then (after a constant time and space rescaling) for $k \in \mathbb{N}$, $\exists\, b(k), c(k) < \infty$ s.t. for n sufficiently large, for $b\varepsilon_n^2 |\log \varepsilon_n| \leq t \leq T^*$,

- *for a.e. x s.t. $d(x,t) \geq c\varepsilon_n |\log \varepsilon_n|$, $\mathbb{E}_{w_0}[w_{nt}^n(n^\alpha x)] \geq 1 - \varepsilon_n^k$*
- *for a.e. x s.t. $d(x,t) \leq -c\varepsilon_n |\log \varepsilon_n|$, $\mathbb{E}_{w_0}[w_{nt}^n(n^\alpha x)] \leq \varepsilon_n^k$.*

Probabilistic proof of Allen-Cahn result

Let $g_0 : \mathbb{R}^2 \to [0,1]$.
Let $(W_t^i)_{i \in N_t}$ be the particles at time t in a 2-dimensional ternary BBM with branching rate ε^{-2}.
Majority voting procedure:

- each particle W_t^i has a vote which is independent Bernoulli$(g_0(W_t^i))$
- carry votes back through tree - carry majority vote back at each branch point.

Let Vote$_{g_0}(\mathbf{W}_t)$ denote vote at the root.

Proposition (Duality relation)

Suppose $g_0 \in C^2(\mathbb{R}^2)$. Then

$$g(t,x) = \mathbb{P}_x(\textit{Vote}_{g_0}(\mathbf{W}_t) = 1)$$

is a solution to $\frac{\partial g}{\partial t} = \frac{1}{2}\Delta g + \frac{1}{\varepsilon^2} g(1-g)(2g-1)$.

Probabilistic proof of Allen-Cahn result

Let $\text{Vote}(\mathbf{B}_t)$ denote result of a majority vote on 1D ternary BBM with branching rate ε^{-2} where particle B_t^i votes 1 iff $B_t^i \geq 0$.

Fact

$\mathbb{P}_x(\textit{Vote}(\mathbf{B}_t) = 1) = 1 - \mathbb{P}_{-x}(\textit{Vote}(\mathbf{B}_t) = 1).$

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Lemma

For $x \geq 0$, $\mathbb{P}_x(\textit{Vote}(\mathbf{B}_t) = 1) \geq \mathbb{P}_x(B_t \geq 0)$.

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Lemma

For $x \geq 0$, $\mathbb{P}_x(\mathit{Vote}(\mathbf{B}_t) = 1) \geq \mathbb{P}_x(B_t \geq 0)$.

Proposition

For $k \in \mathbb{N}$, $\exists\, a(k), c(k) < \infty$ *s.t. for* $a\varepsilon^2 |\log \varepsilon| \leq t \leq T^*$, $x \geq c\varepsilon|\log \varepsilon|$,

$$\mathbb{P}_x(\mathit{Vote}(\mathbf{B}_t) = 1) \geq 1 - \varepsilon^k.$$

Probabilistic proof of Allen-Cahn result

Suppose $\Gamma = \{x \in \mathbb{R}^2 : g_0(x) = 1/2\}$ is a smooth embedding of S^1 with $g_0 < 1/2$ inside Γ and $g_0 > 1/2$ outside Γ.
Let $(\Gamma_t)_{t \leq T}$ be the motion by curvature flow with $\Gamma_0 = \Gamma$ and let $d(x,t)$ denote the signed distance of x from Γ_t (negative inside Γ_t).

Theorem

For $k \in \mathbb{N}$, $\exists\, a(k), c(k) < \infty$ *s.t. for* $a\varepsilon^2|\log\varepsilon| \leq t \leq T^*$,

- *if* $d(x,t) \geq c\varepsilon|\log\varepsilon|$, $\mathbb{P}_x(\mathit{Vote}_{g_0}(\mathbf{W}_t) = 1) \geq 1 - \varepsilon^k$
- *if* $d(x,t) \leq -c\varepsilon|\log\varepsilon|$, $\mathbb{P}_x(\mathit{Vote}_{g_0}(\mathbf{W}_t) = 1) \leq \varepsilon^k$.