On hybrid zones and the effect of barriers

Ian Patrick Letter Restuccia

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UNIVERSITY OF OXFORD
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Gobierno de Chile

Thanks goes to

Work under the supervision of

Alison Etheridge

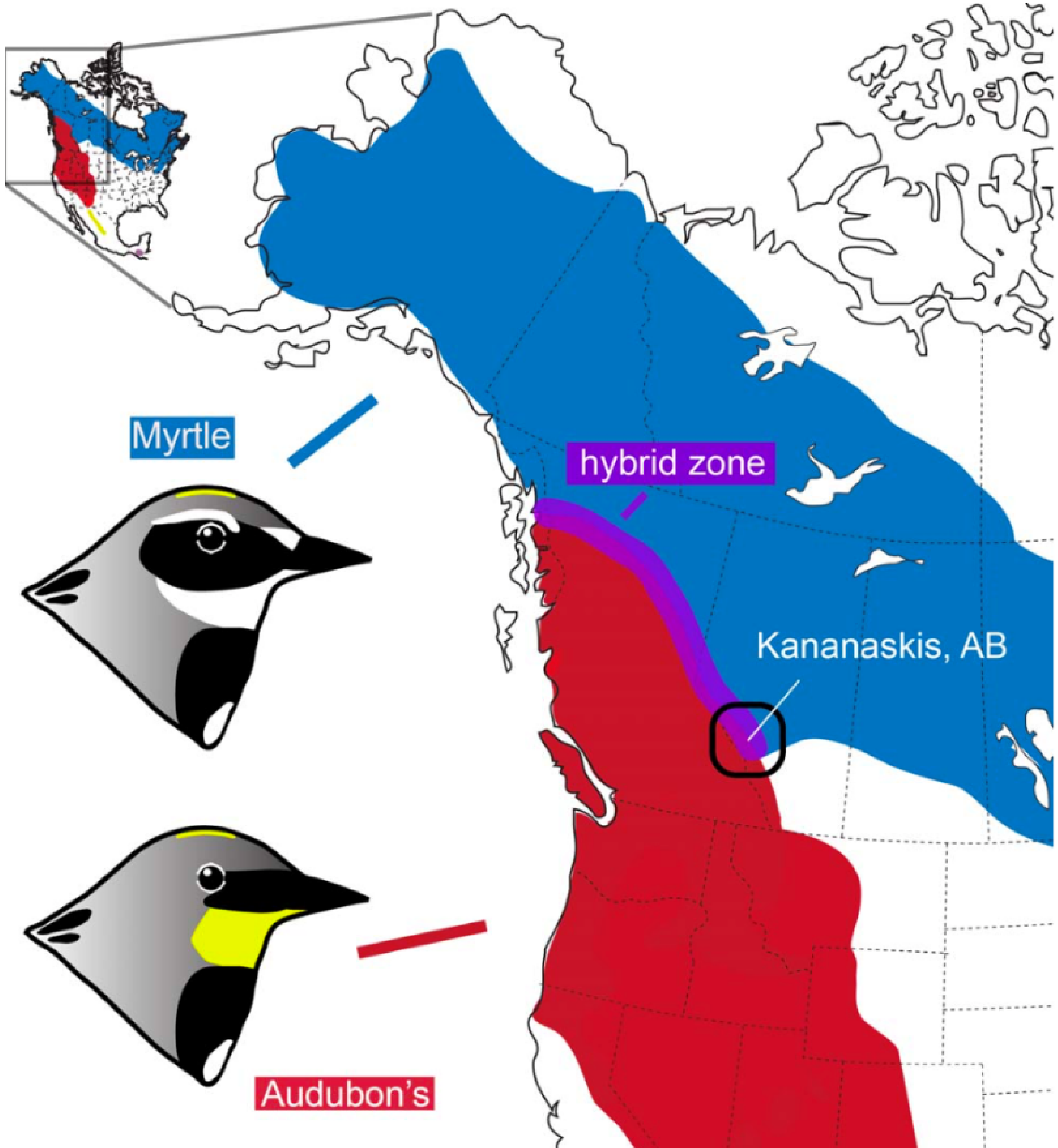
For many meaningful discussions

Kim Becker

Disclaimer

For pedagogical reasons technical details will be handwaved.

What are hybrid zones?



Hybrid zone: narrow geographic region where two genetically distinct populations are found and hybridise to produce mixed offsprings.

Example:
Warblers in the United States [1]

What are hybrid zones?

Antirrhinum (Flowers) in Europe [2]. Sparrows in the Italic Peninsula [3]

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Seen in mice, salmons and many other species [4].

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Why are there hybrid zones? Two hypothesis:

1.- A change in environment across space (stationary).

2.- Selection against hybrid individuals (dynamic).

How can we understand the evolution of hybrid zones under hypothesis 2?

Selection against hybrids: model

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Let $u(x,t)$ be the proportion of A alleles at position x and time t.

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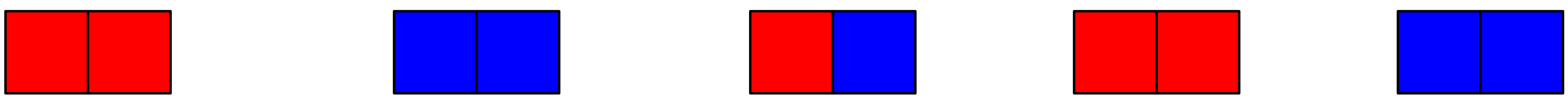

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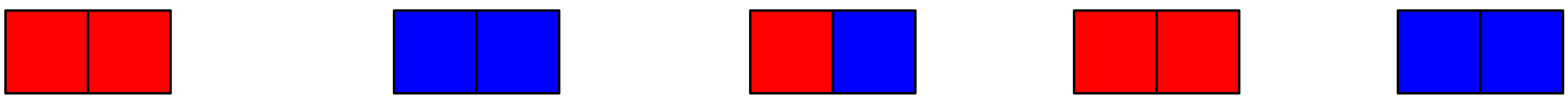

For reproduction: a sample of N individuals of type AB produces K gametes,
BB produces $K(1+s)$ and AA produces $K(1+s+\delta)$.

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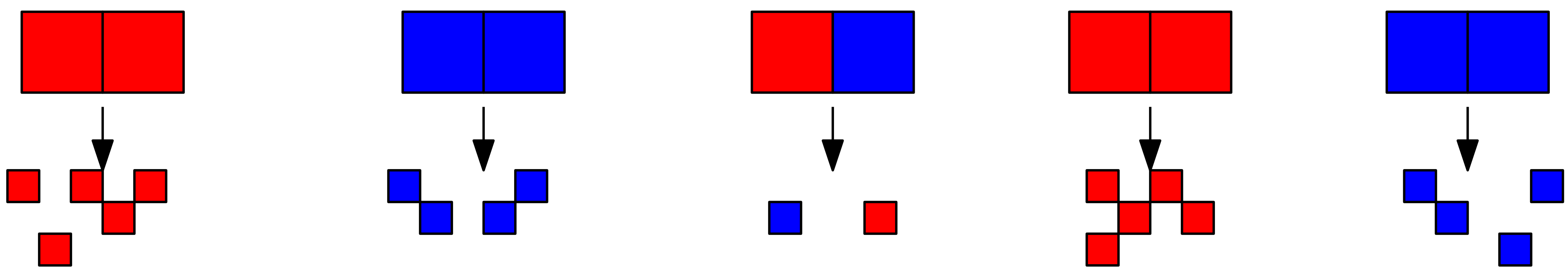

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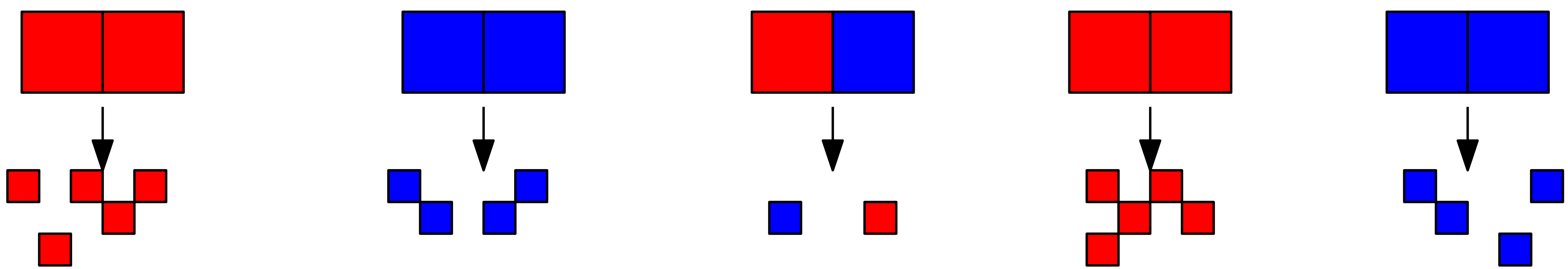

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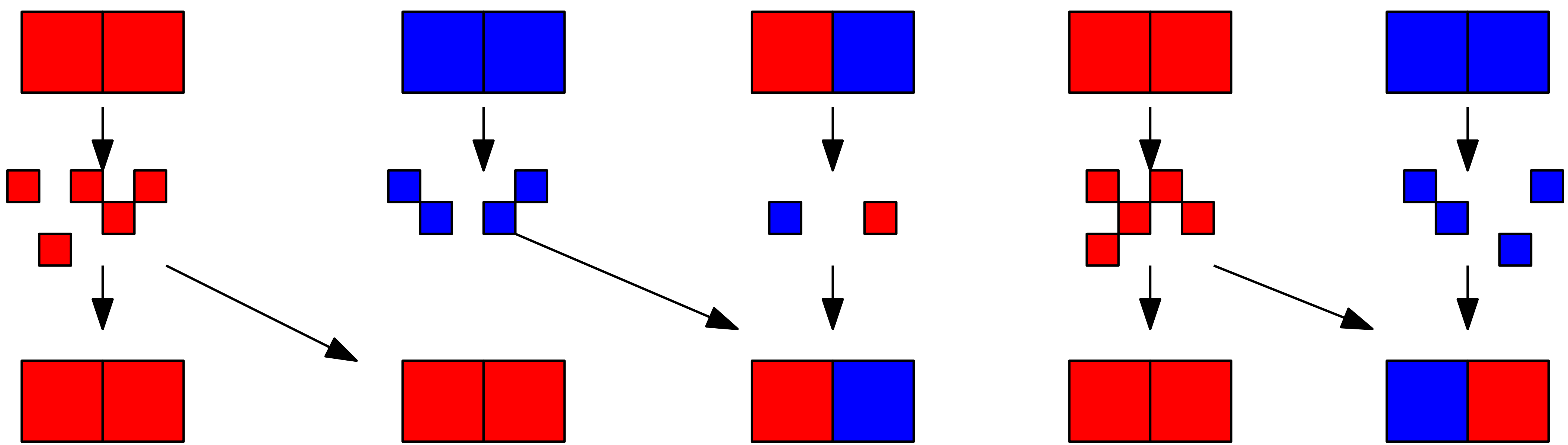

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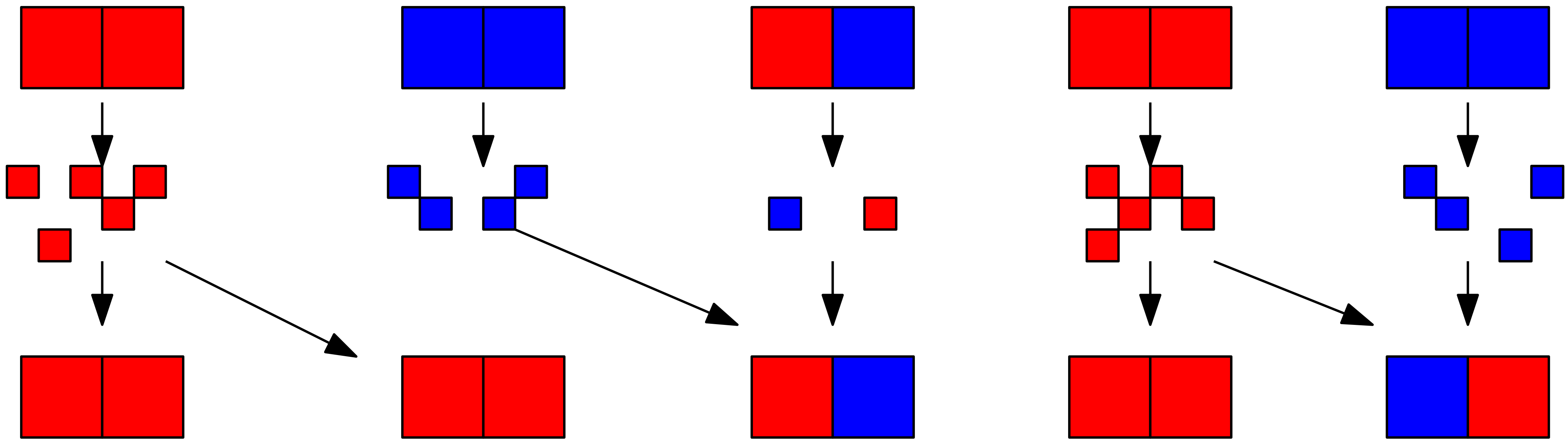

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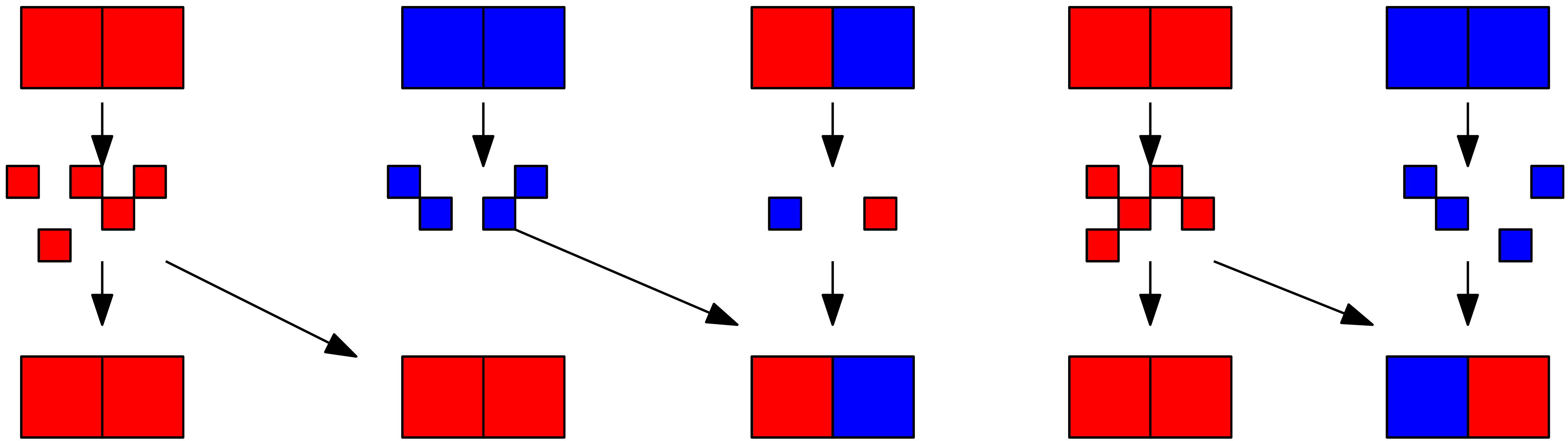

The local change of the allele A per reproductive event is

$$\mathbb{P}(\text{sampling allele } A \text{ at } x) - u(x,t) \sim Mu(x,t)(1-u(x,t))(2u(x,t)-(1-\gamma))$$

for some $M(s,\delta,K) > 0$ and $1 > \gamma(\delta) > 0$.

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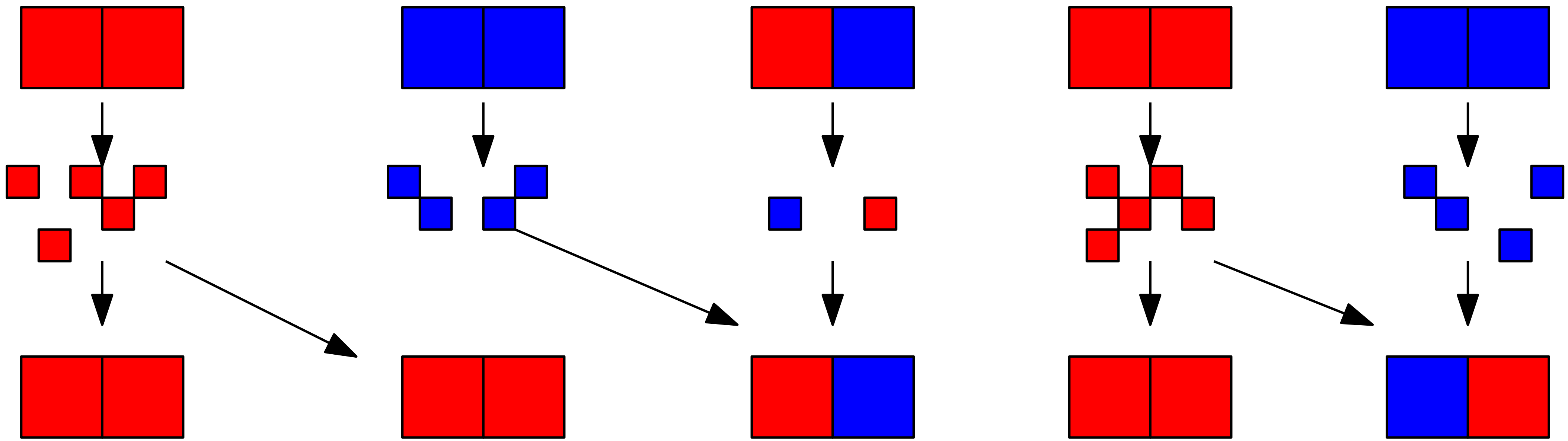

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for some $M(s,\delta,K) > 0$ and $1 > \gamma(\delta) > 0$.
Normalising $M = 1$, supposing finite variance movement of individuals and **ignoring genetic drift**:

$$\begin{aligned}\partial_t u &= \text{change by movement} + \text{change by reproduction},\\ &= \Delta u + u(1-u)(2u-(1-\gamma)).\end{aligned}$$

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Assuming **space homogeneity** we get:

$$(AC)\begin{cases}\partial_t u = \Delta u + u(1-u)(2u-(1-\gamma)) & t>0, x\in\mathbb{R}^d,\\ u(0,x)=u_0(x) & x\in\mathbb{R}^d.\end{cases}$$

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$$(AC_\epsilon)\begin{cases}\partial_t u = \Delta u + \frac{1}{\epsilon^2}u(1-u)(2u-(1-\epsilon\nu)) & t>0, x\in\mathbb{R}^d,\\ u(0,x)=u_0(x) & x\in\mathbb{R}^d.\end{cases}$$

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Video!

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Theorem 1 (Chen 1992 / Etheridge, Freeman, Penington + Gooding 2018)

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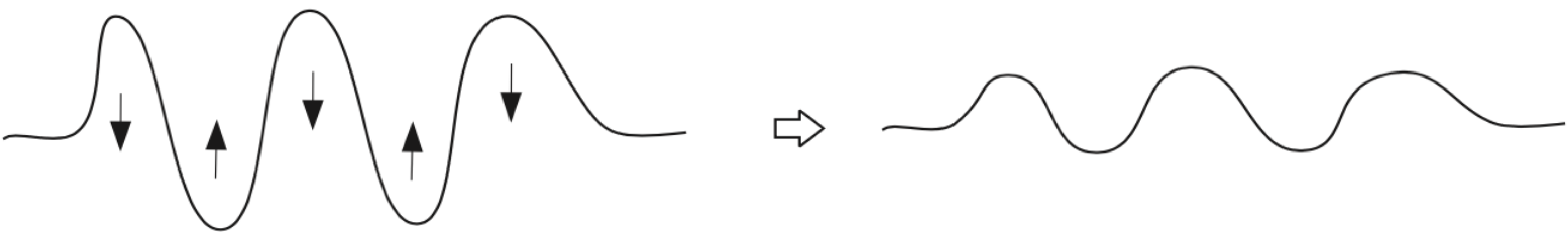

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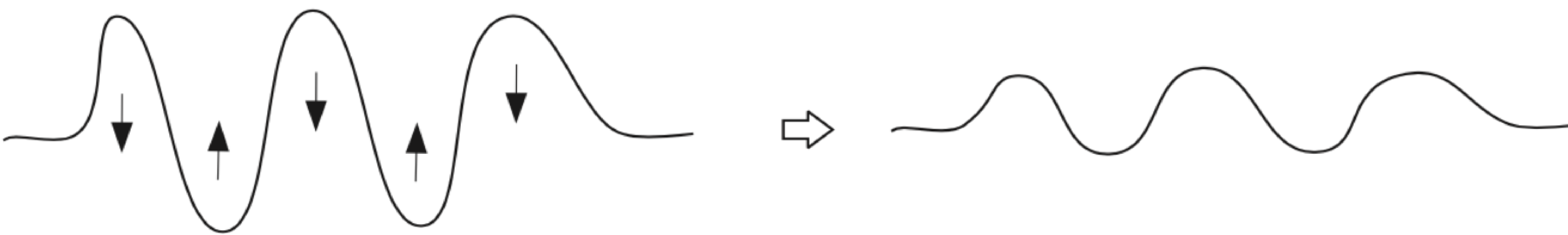

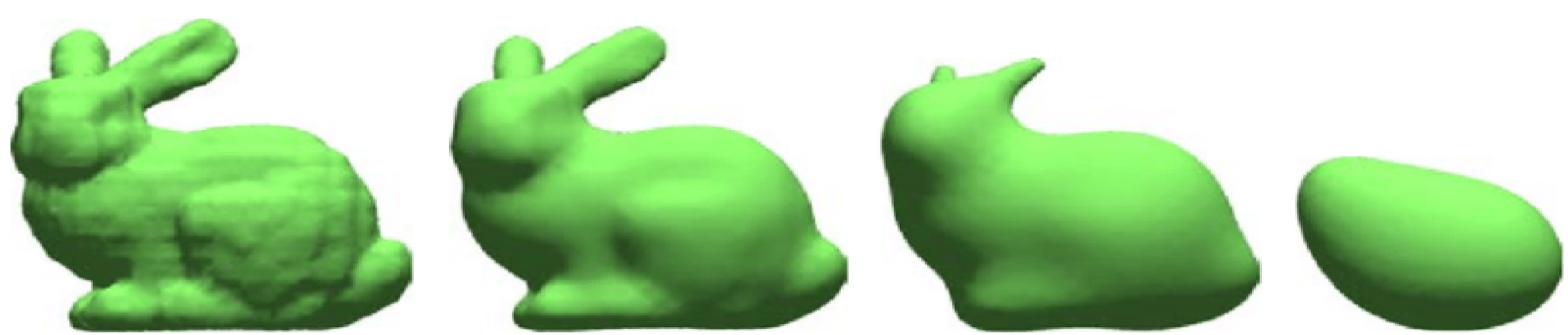

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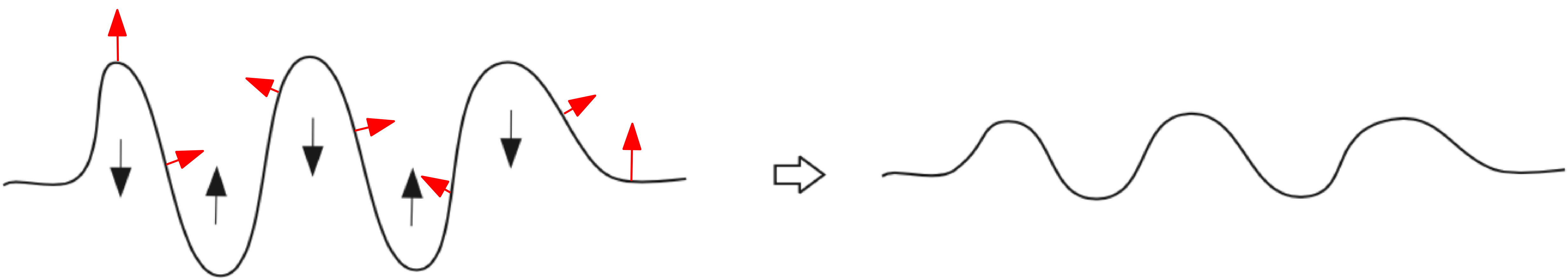
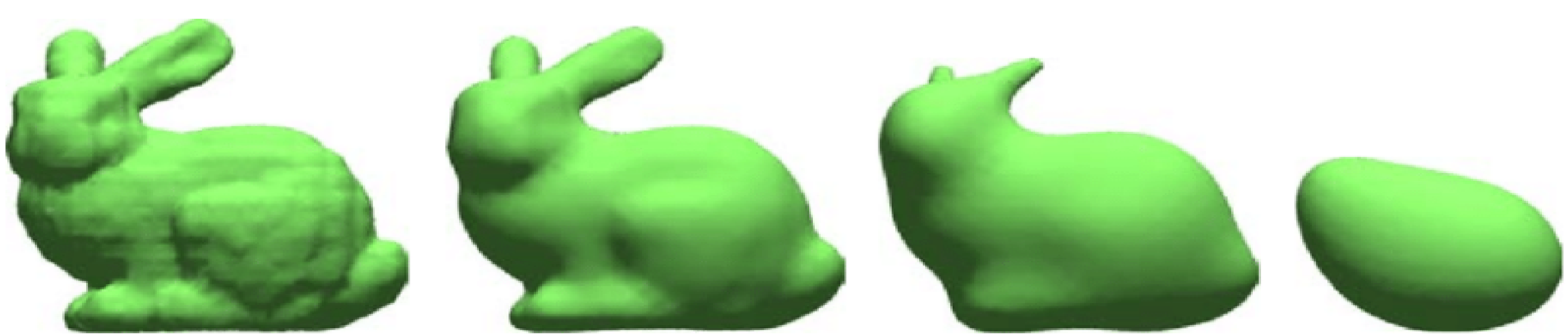
If $\nu \neq 0$, constant flow adds a velocity ν going *outside* the surface.





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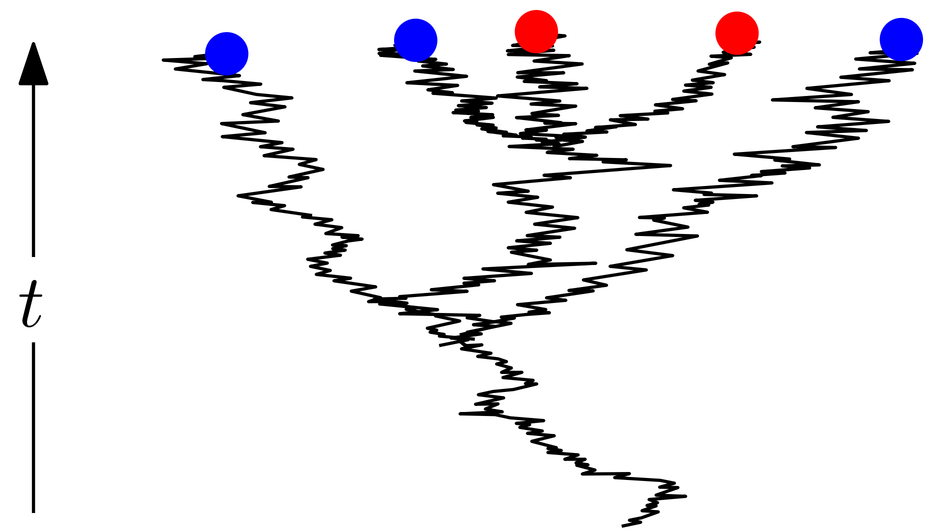

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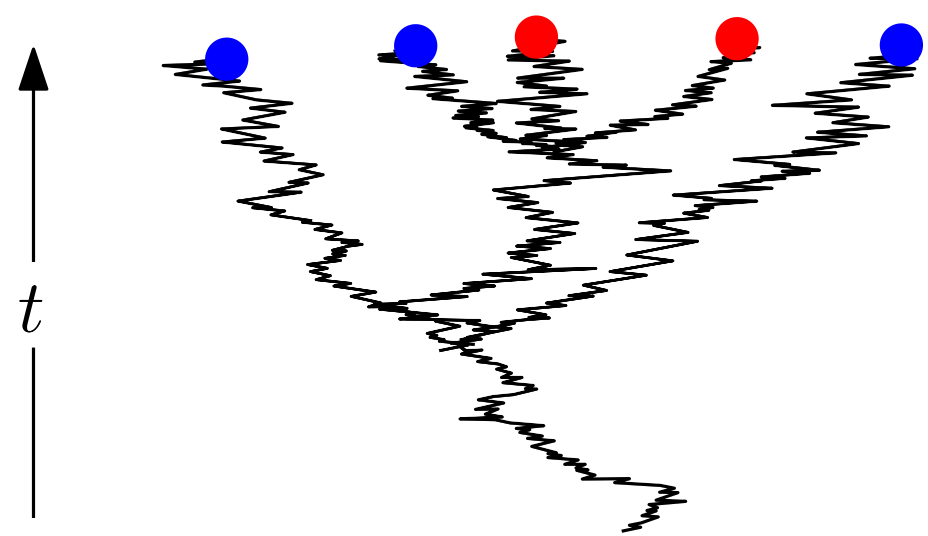

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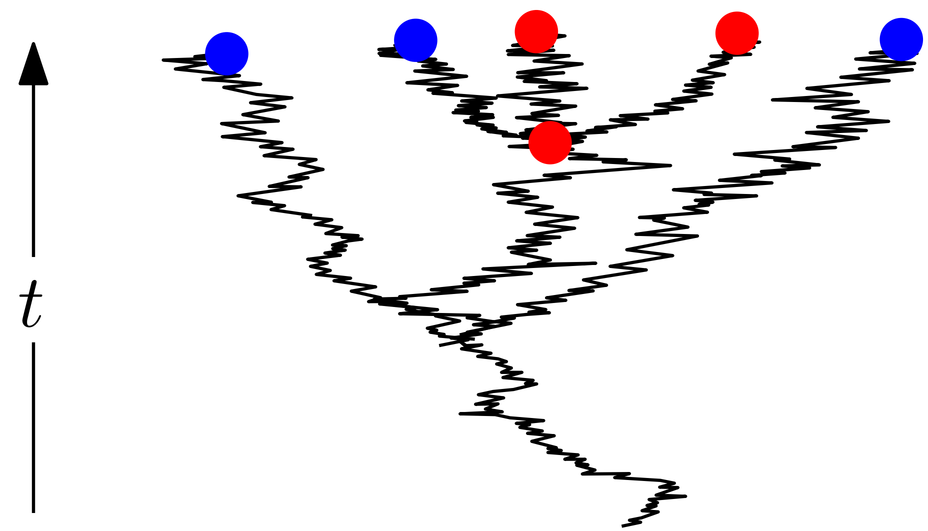

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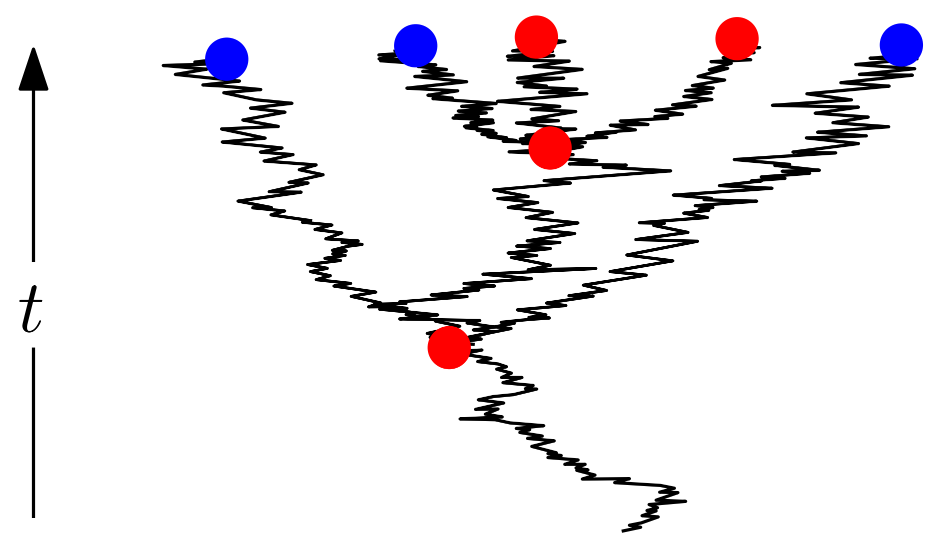

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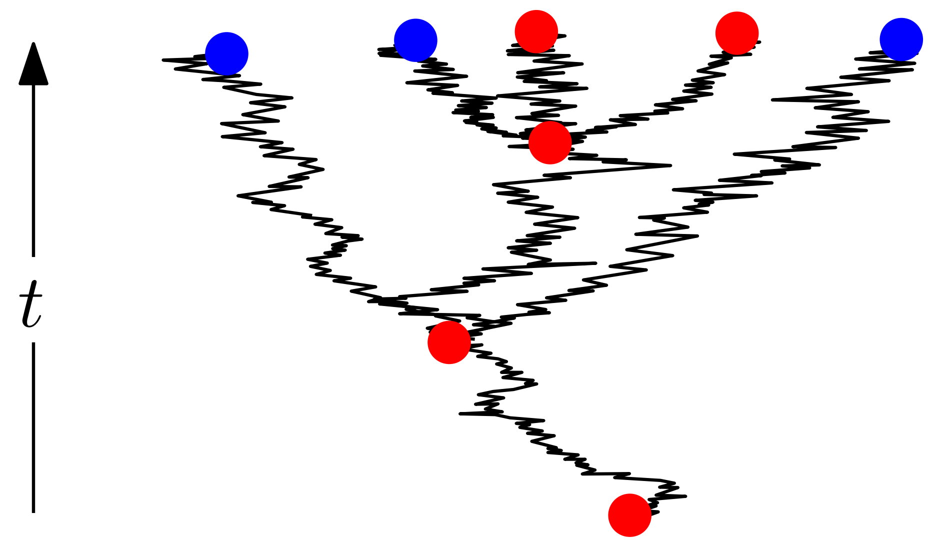

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Let $\mathbb{P}_x^\epsilon$ be the law where the BBM starts at x and $V = (1+\epsilon\nu)\epsilon^{-2}$.

Let $\mathbb{V}_{u_0}(\mathcal{W}(t))$ be the vote of the *root of the voting system*, with the vote of the leaves given by u_0.

Then $u(x,t) := \mathbb{P}_x^\epsilon[\mathbb{V}_{u_0}(\mathcal{W}(t)) = 1]$ solves (AC_ϵ) with $u(0,x) = u_0(x)$.

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$$u(x,t+h) \sim e^{-h(1+\epsilon\nu)\epsilon^{-2}}\mathbb{E}_x[u(W_h,t)] + (1-e^{-h(1+\epsilon\nu)\epsilon^{-2}})g(u(x,t)),$$

where $g(p)$ is probability that a branch point votes 1 if each offspring votes 1 with probability p.

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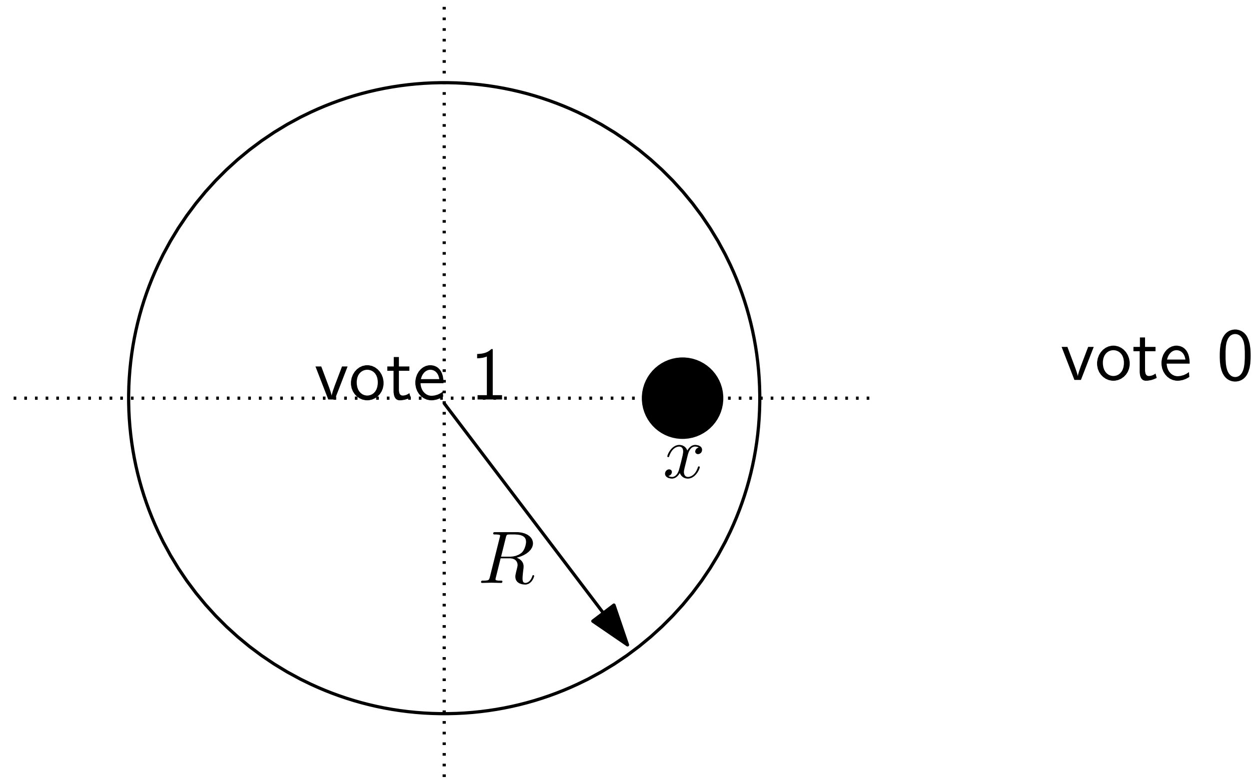

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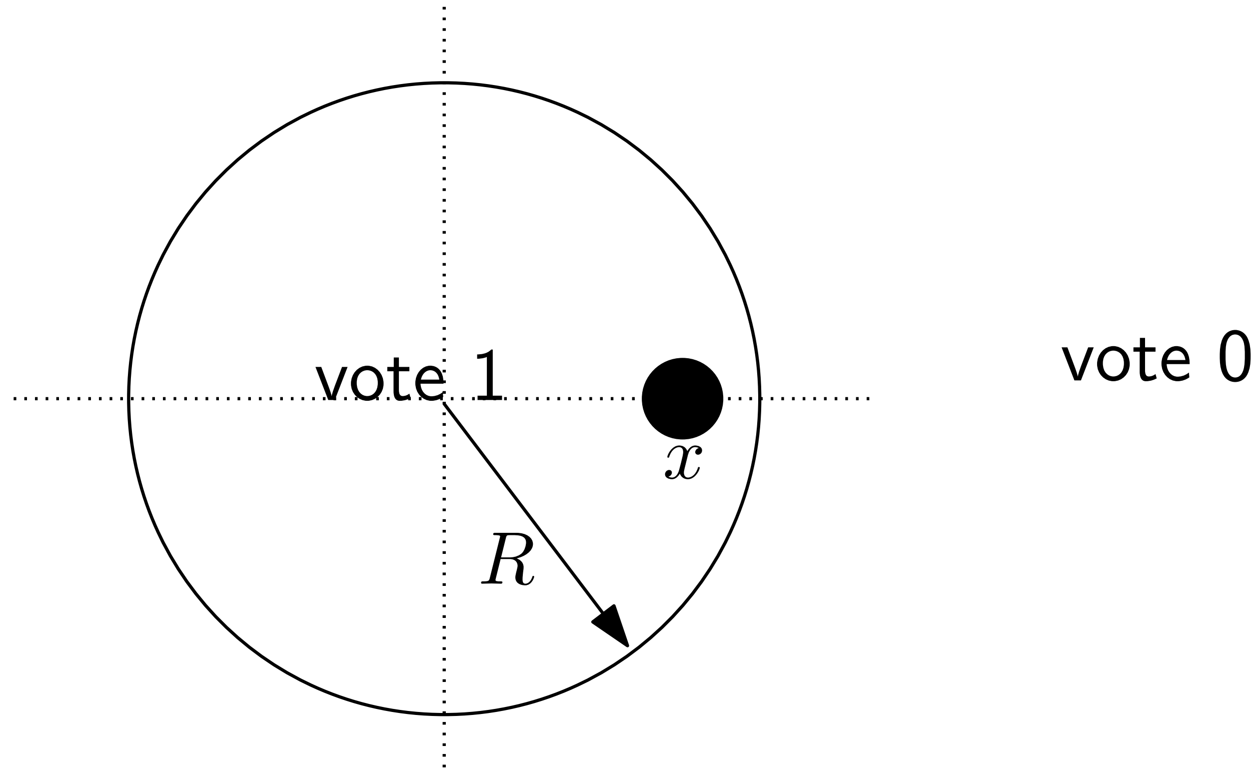

For small t: $\mathbb{P}_x(\mathbb{V}(\mathcal{W}(t)) = 1) \sim \mathbb{P}_{\|x\|}(\|W(t)\| < R)$

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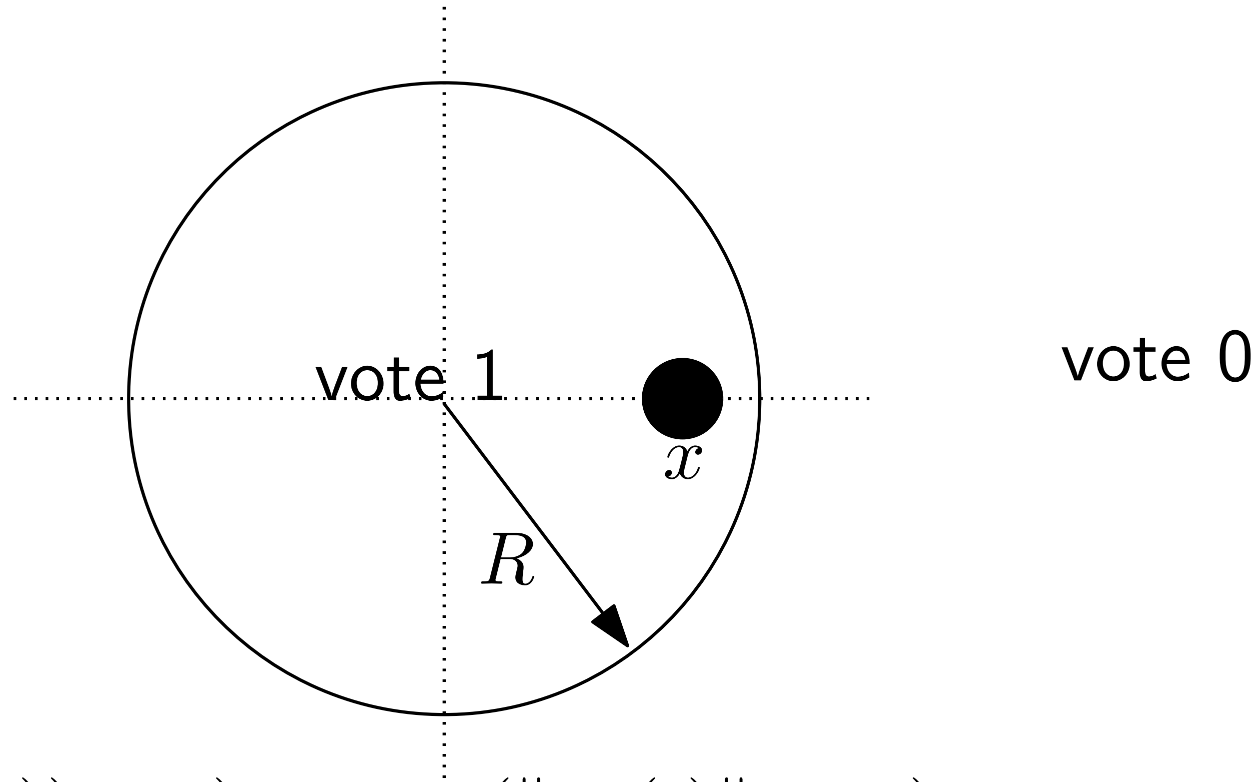

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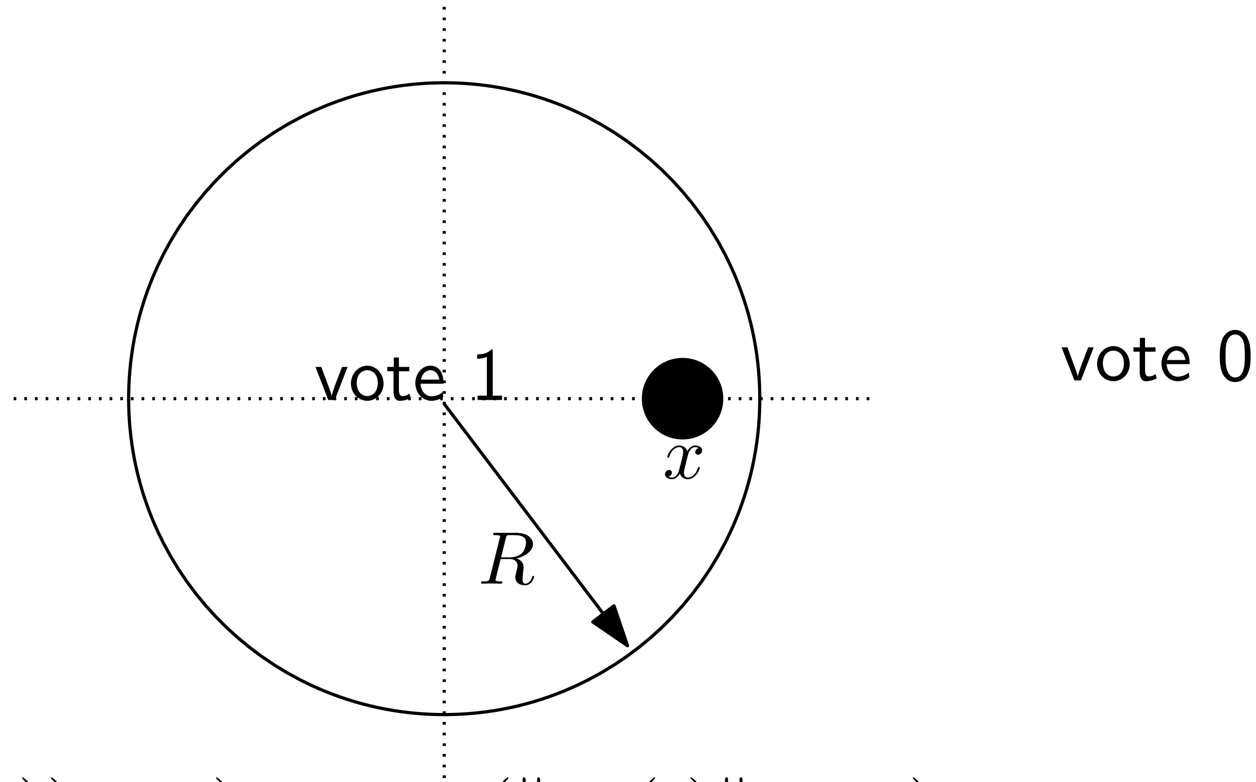

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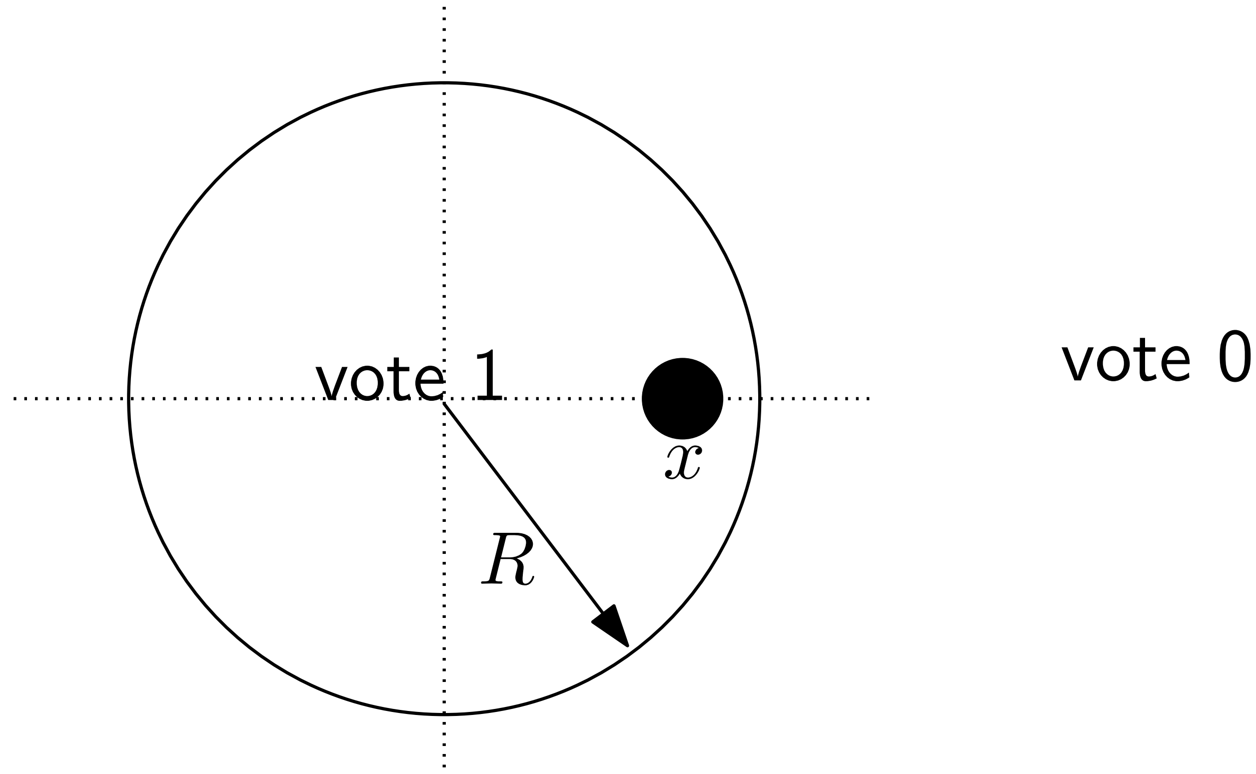

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$\Rightarrow$ the hybrid zone should move as curvature flow for small times.
For big times use Markov property + iterate carefully.

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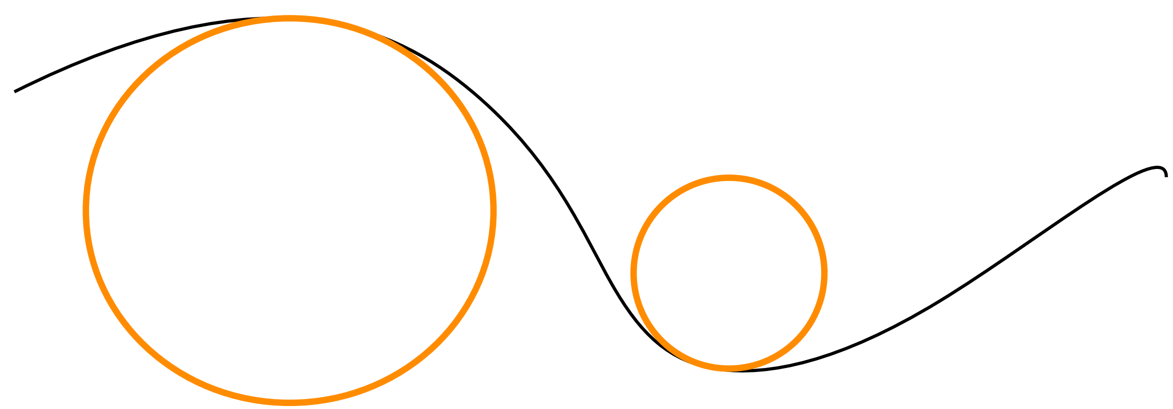
And $\partial\Gamma_0$ looks *locally* like a circle, we apply the first case.



What about barriers?

What if the space is not homogenous?

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Assuming barriers stop spreading of individuals:

$$(N-AC_\epsilon)\begin{cases}\partial_t u = \Delta u + \epsilon^{-2}u(1-u)(2u-(1-\nu\epsilon)) & t>0, x\in\Omega,\\ \partial_\nu u(t,x)=0 & x\in\partial\Omega,\\ u(0,x)=u_0(x) & x\in\Omega.\end{cases}$$

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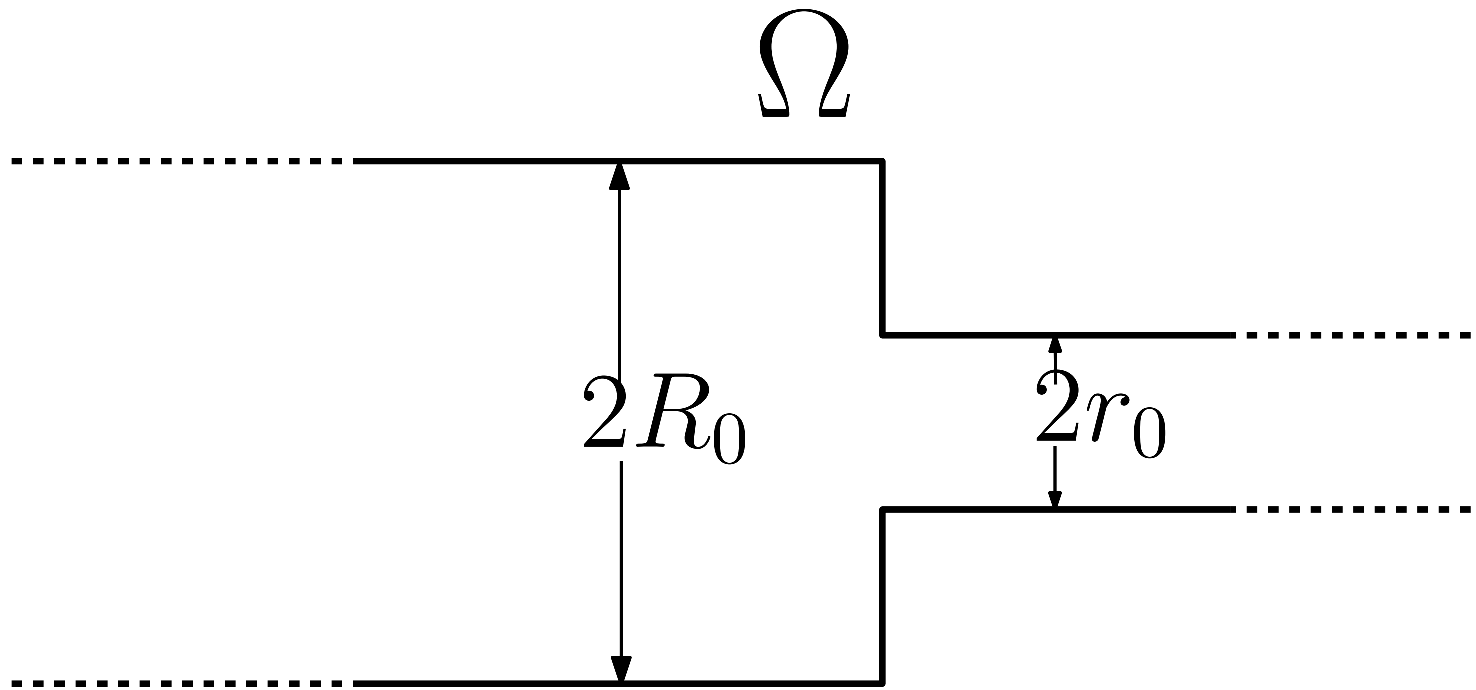
What can we say about the evolution of hybrid zones?

Mean curvature flow does not behave *well* with boundaries.

What about barriers? Prior results

Suppose that:



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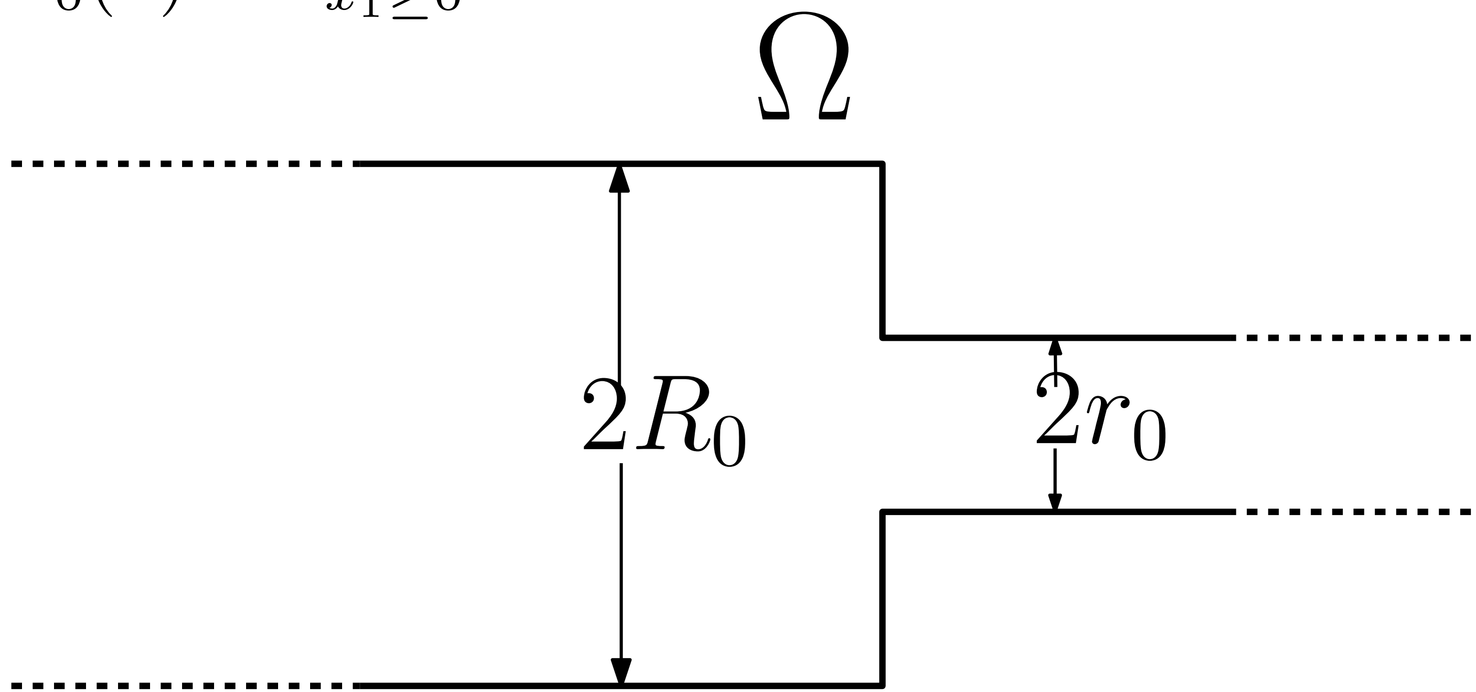

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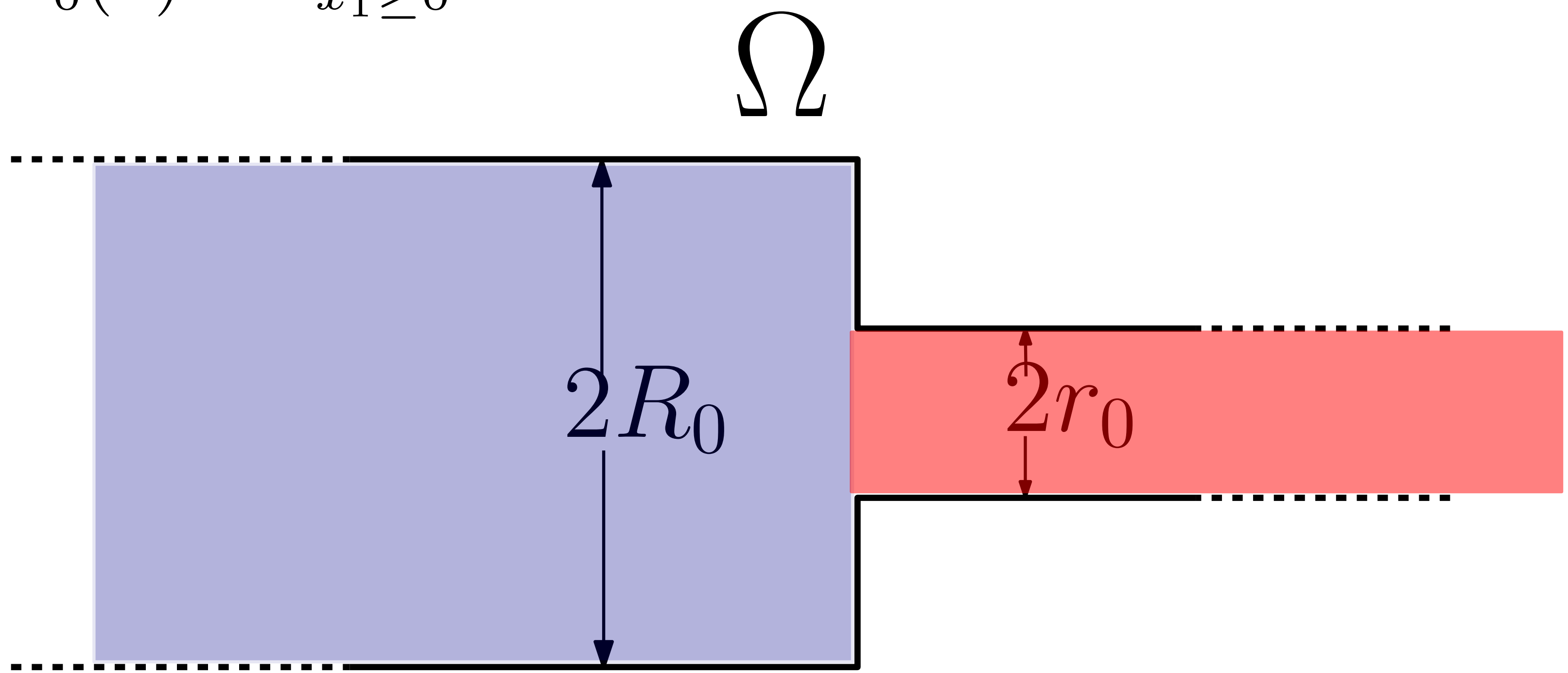

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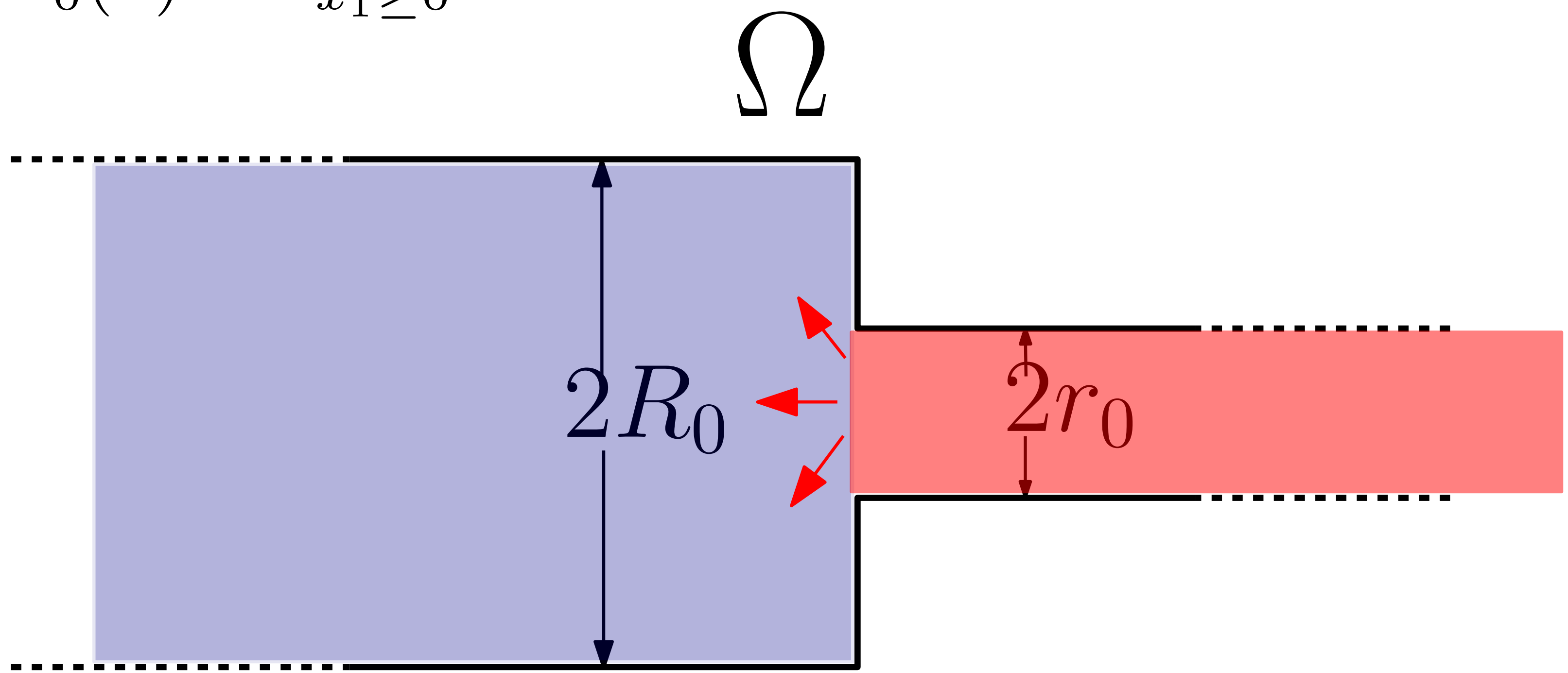

Red individuals have a selective advantage, want to invade.

Enviroment dipserses them, making self-mating harder.

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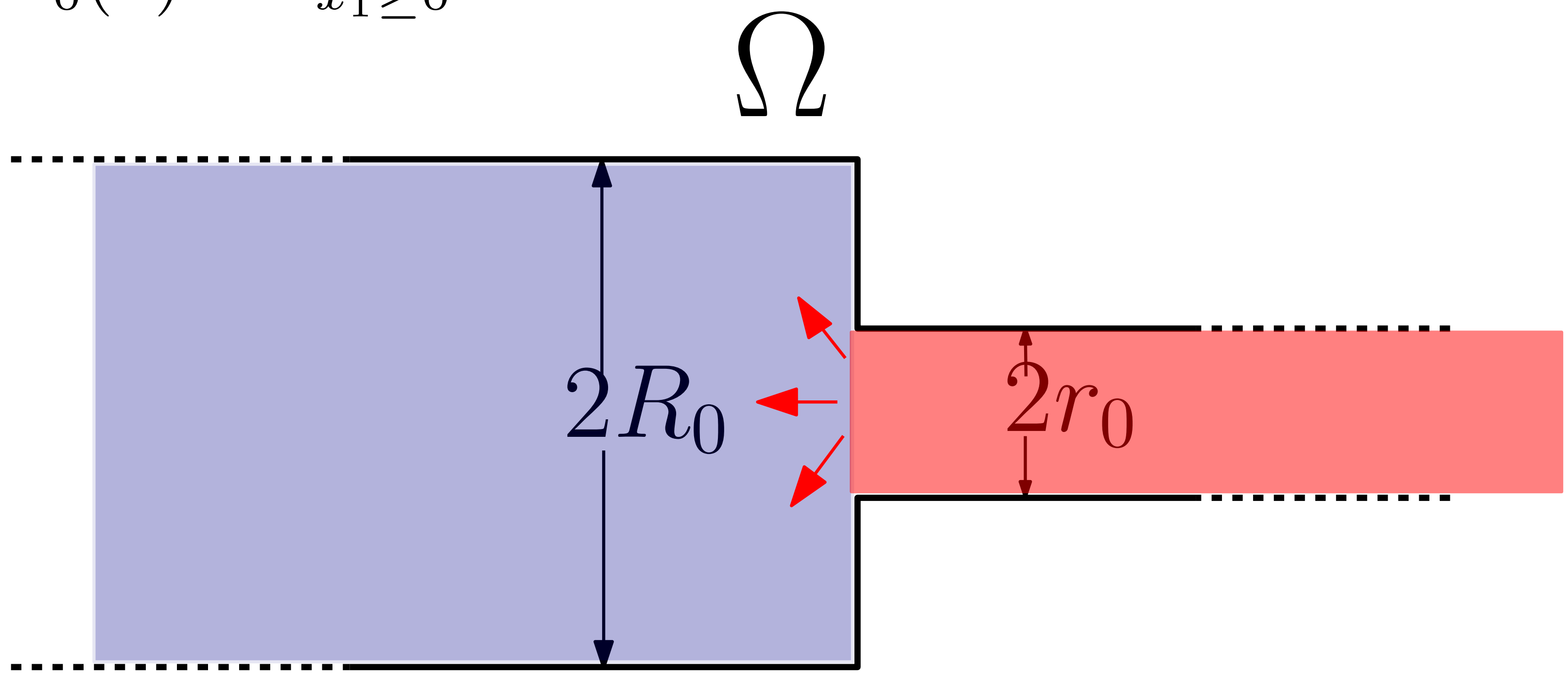

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Who wins? Dispersal or selection?

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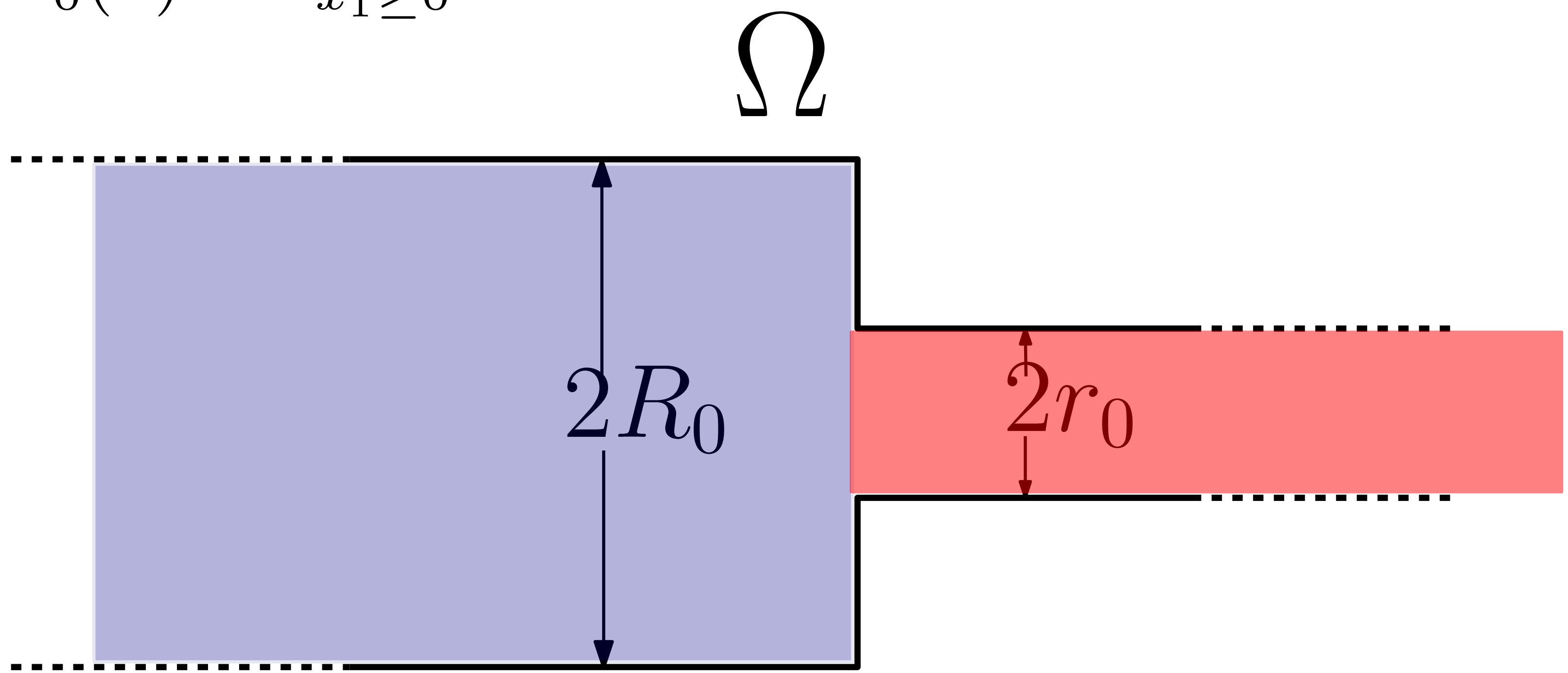

Theorem (Beresticky et al. 2017 *really short version*)

If r_0 is big enough in comparison to ν then *invasion* occurs.
If r_0 is small enough in comparison to ν then *blocking* occurs.

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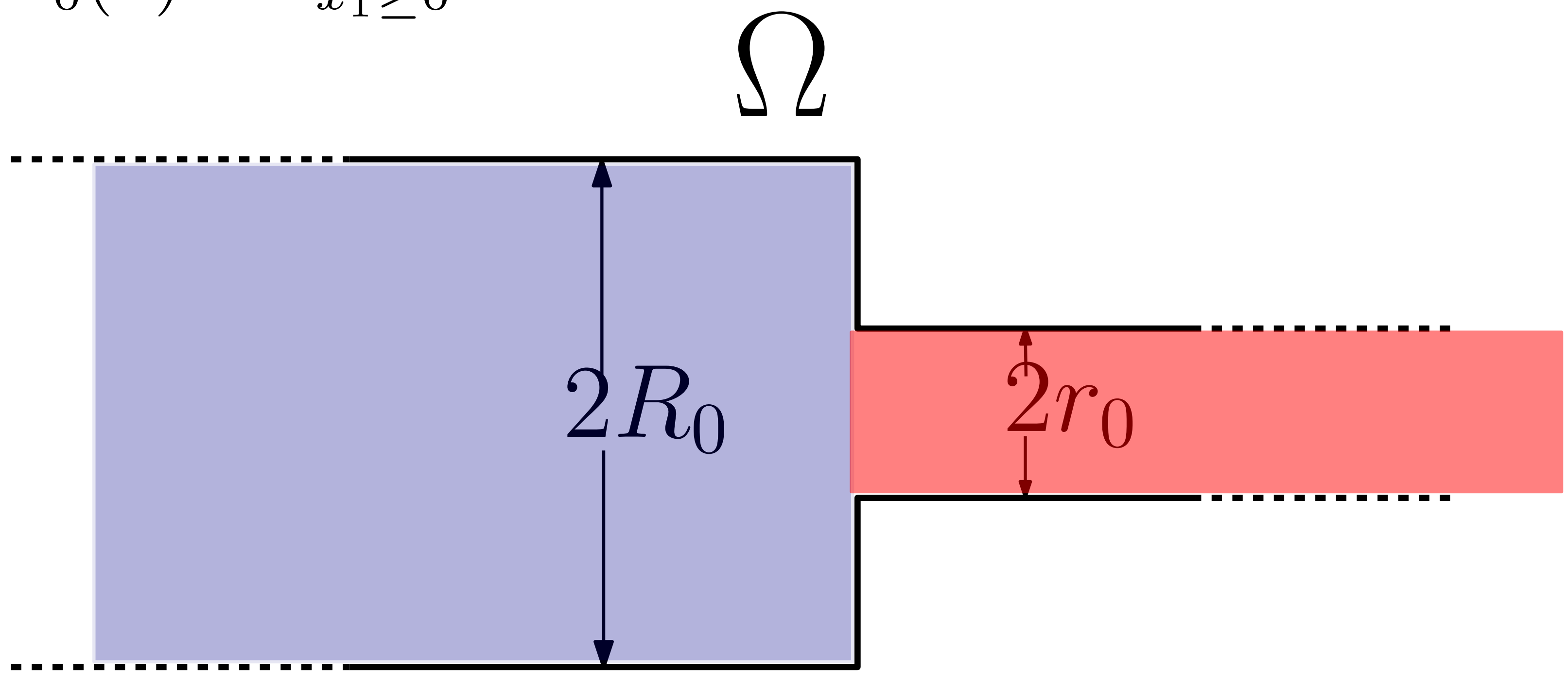

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Can we say more? Maybe using BBM and the voting system?

What about barriers? New results

Theorem 3 (Etheridge, L.)

Let $\mathcal{W}(t)$ be the historical paths of a Branching **reflected** B.M.

Let $\mathbb{V}_{u_0}(\mathcal{W}(t))$ be the vote defined in the same way as in Theorem 2.

Then $u(x,t) := \mathbb{P}_x^{\epsilon}[\mathbb{V}_{u_0}(\mathcal{W}(t)) = 1]$ solves $(N - AC_{\epsilon})$.

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Theorem 5 (Etheridge, L.)

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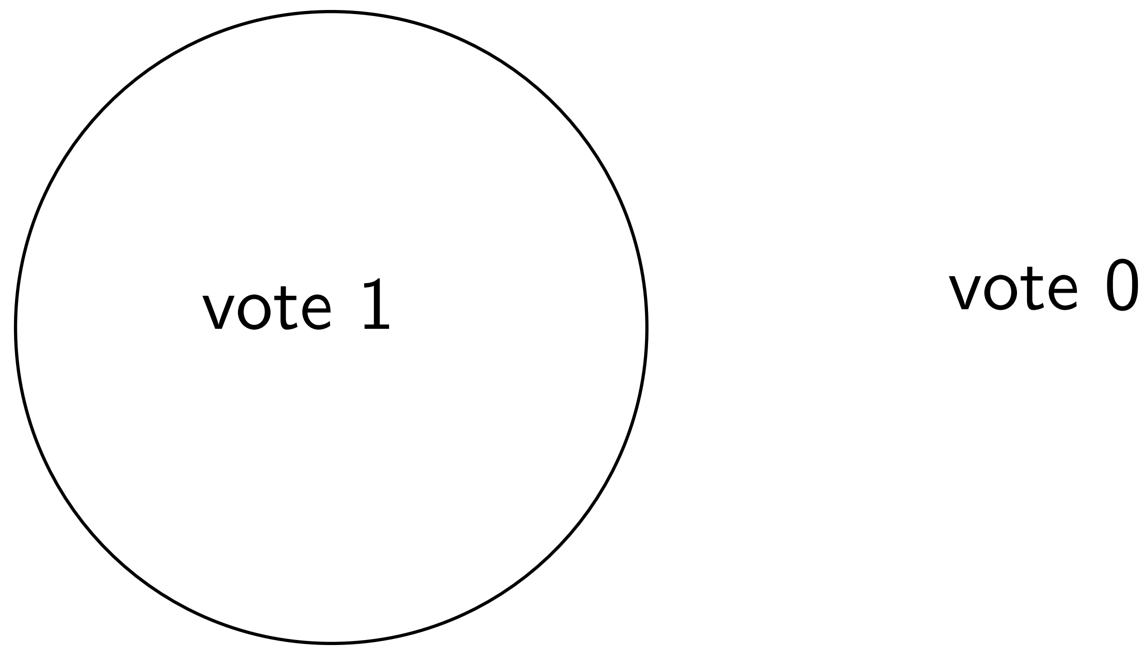
First (ironically) ignore the barriers and think $u_0(x) = 1_{B_R}$



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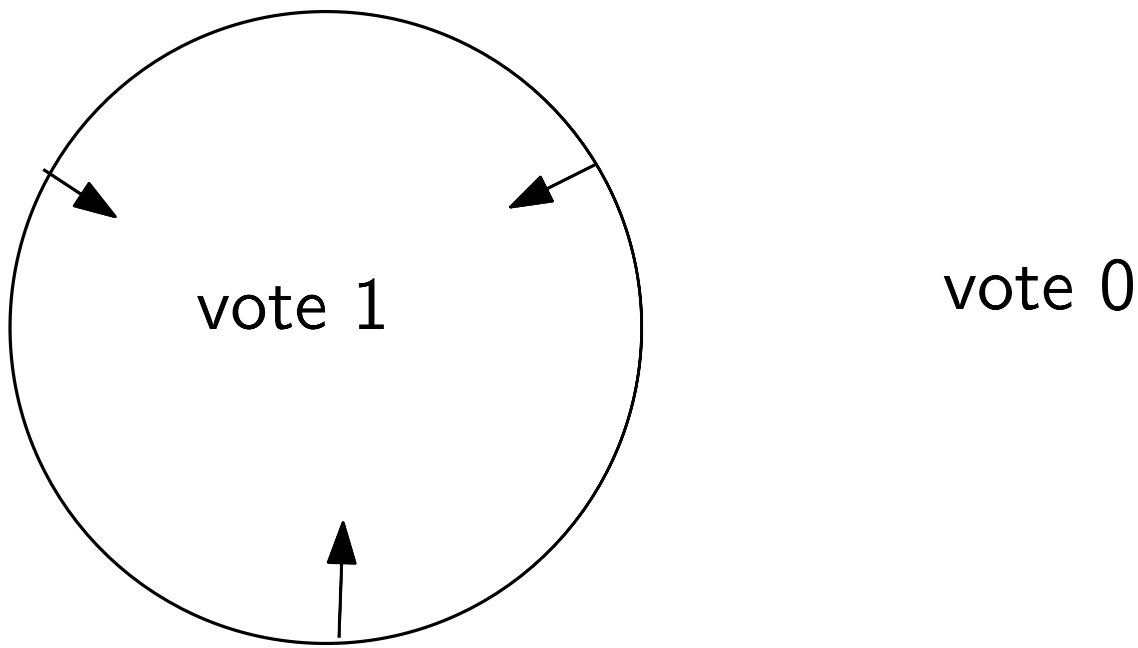

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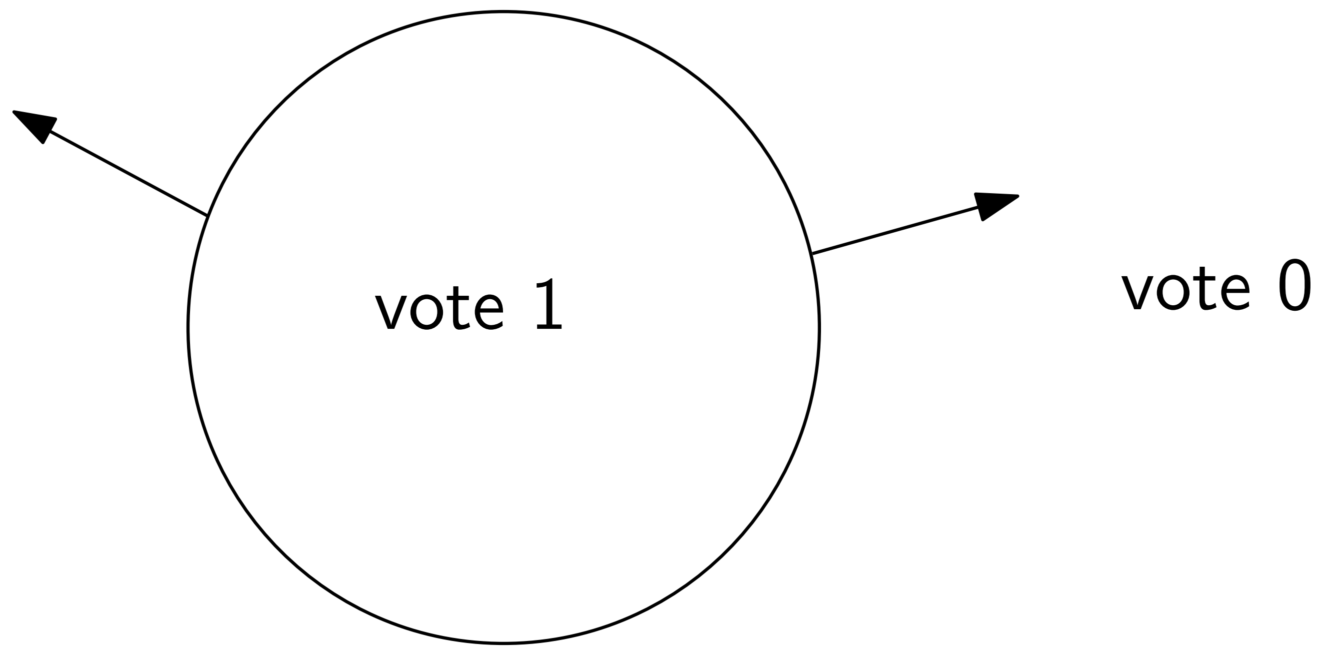

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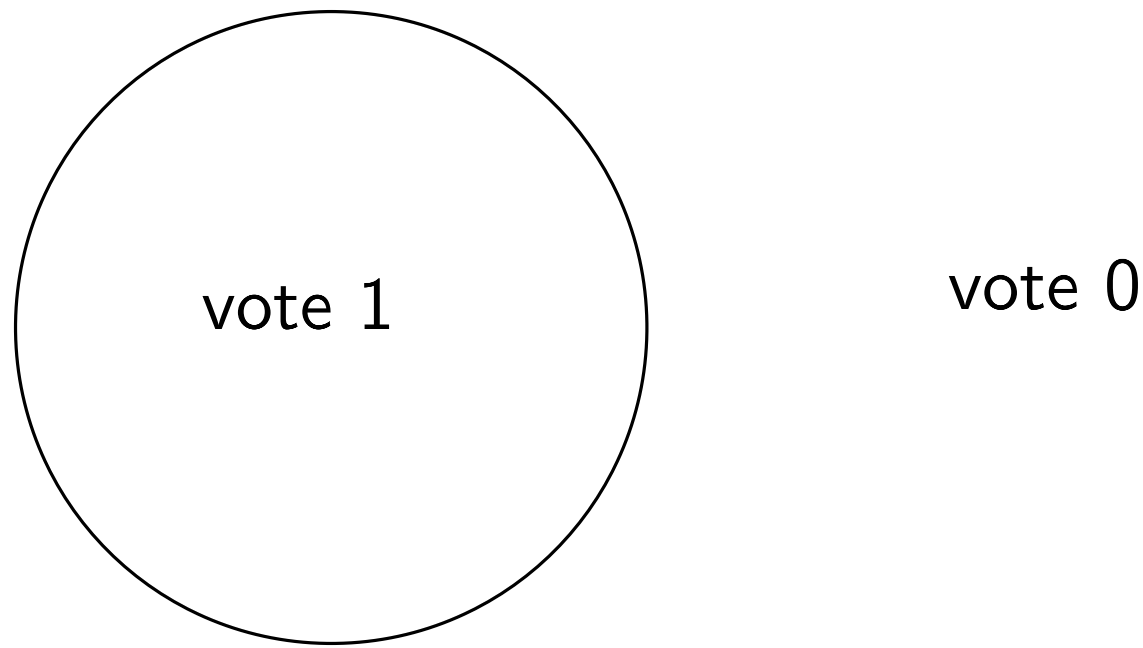

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Equilibrium if $R = (d-1)/\nu$. External push if $R > (d-1)/\nu$.

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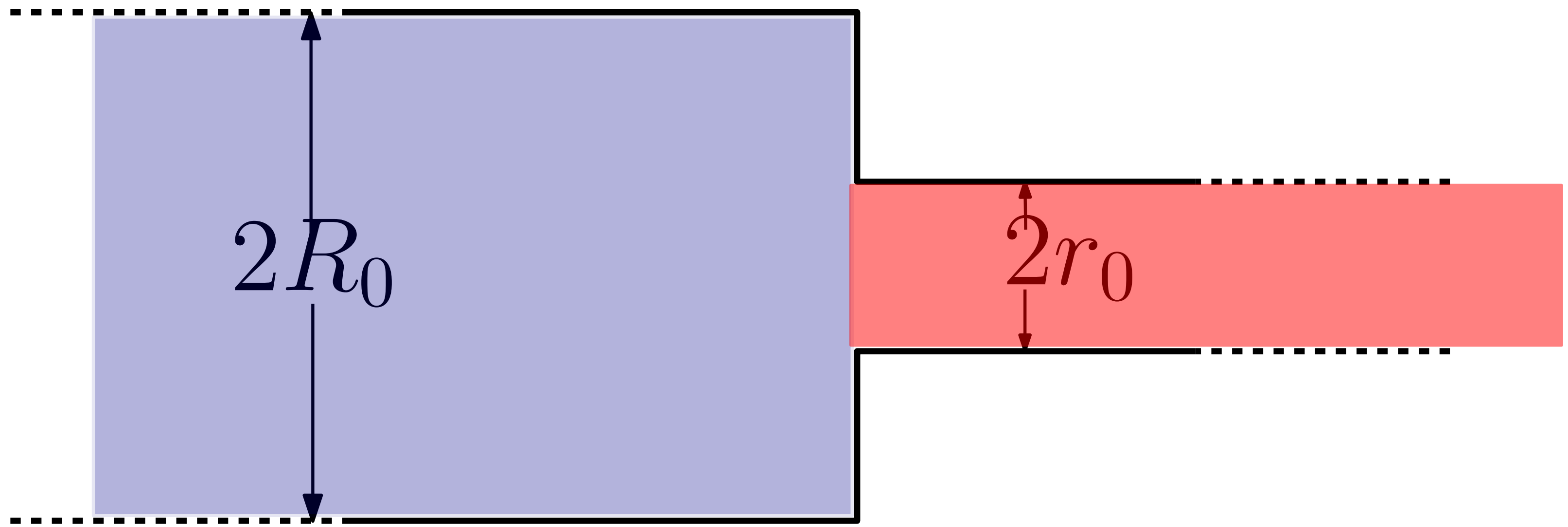
Now we think about the barrier $\quad u_0(x) = 1_{x\geq 0}$



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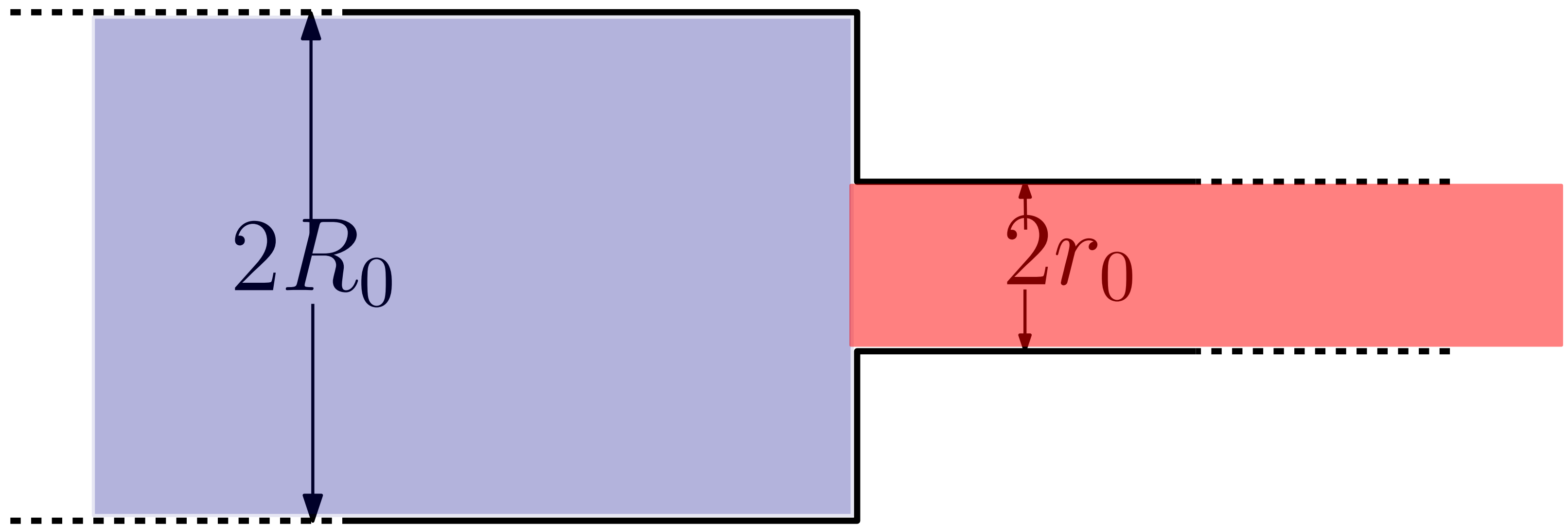

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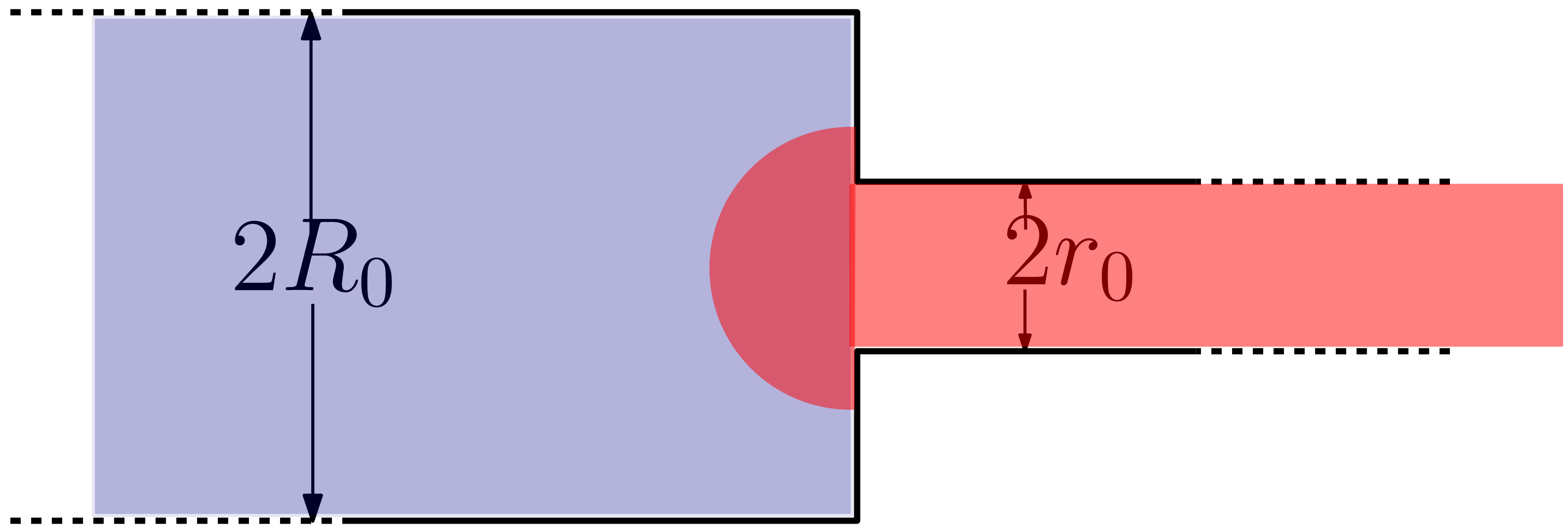

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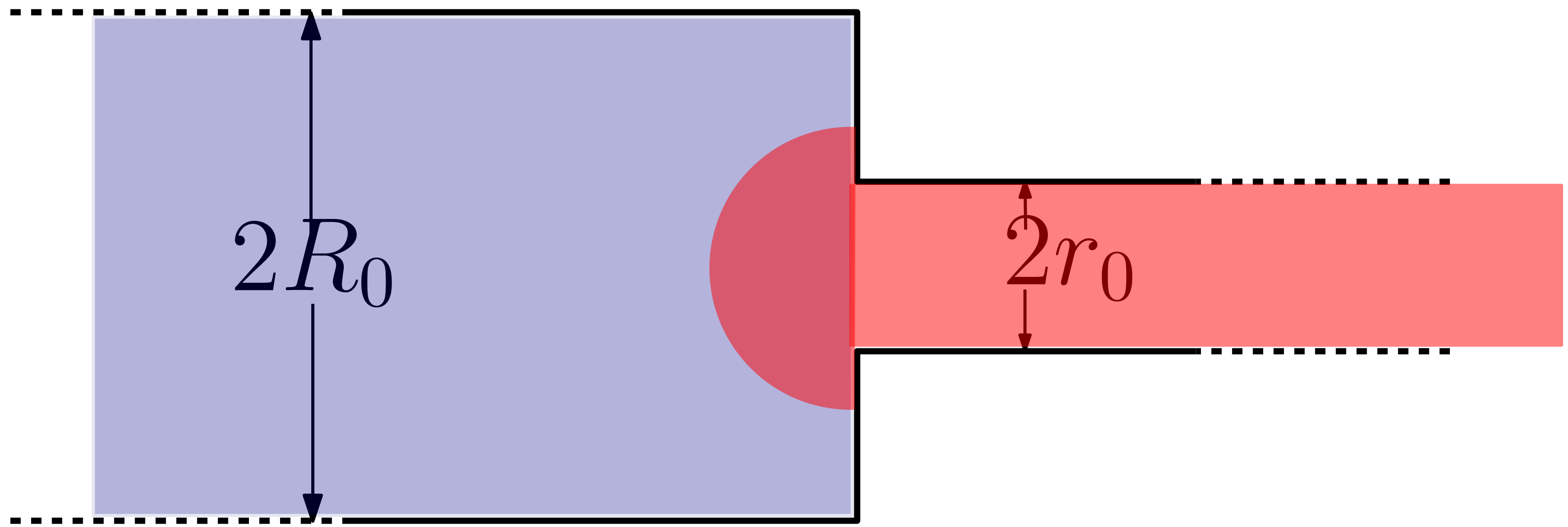

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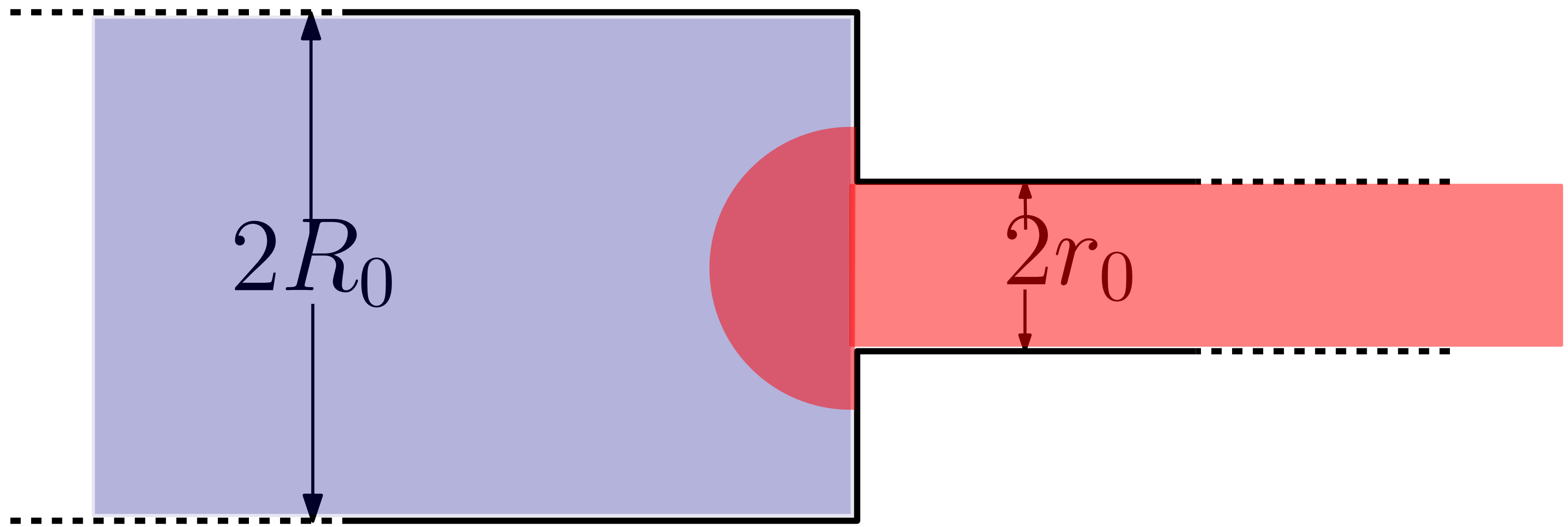

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$$r_0 < r \leq (d-1)/\nu \Rightarrow \text{Blocking}$$

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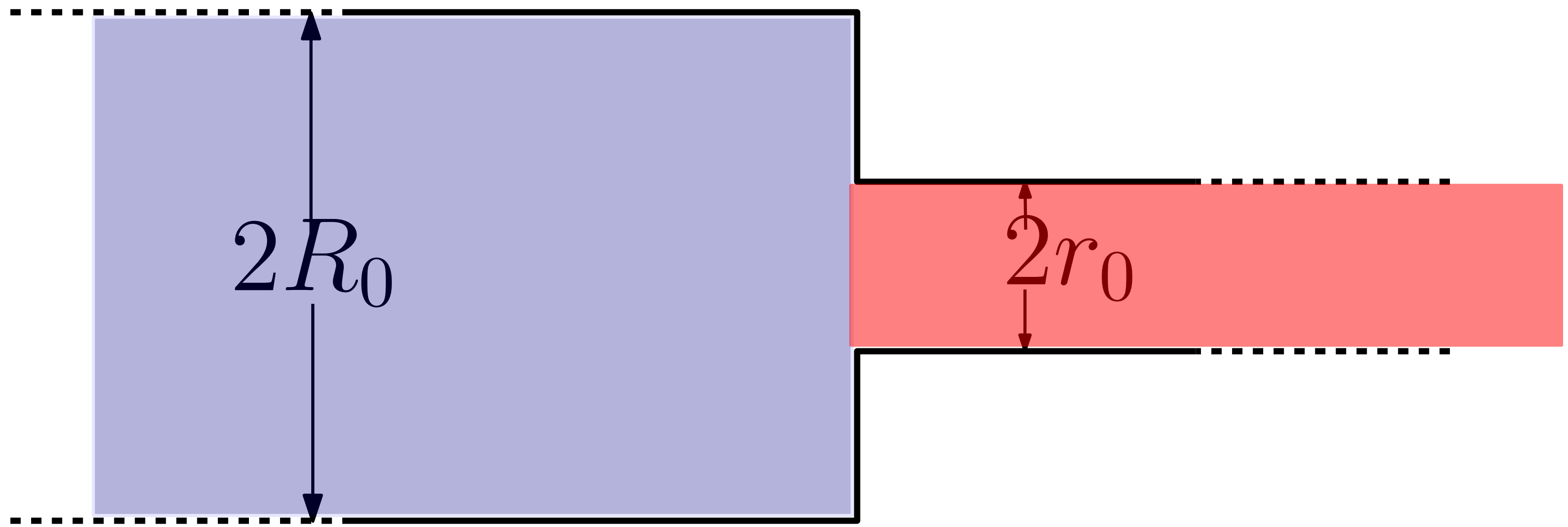

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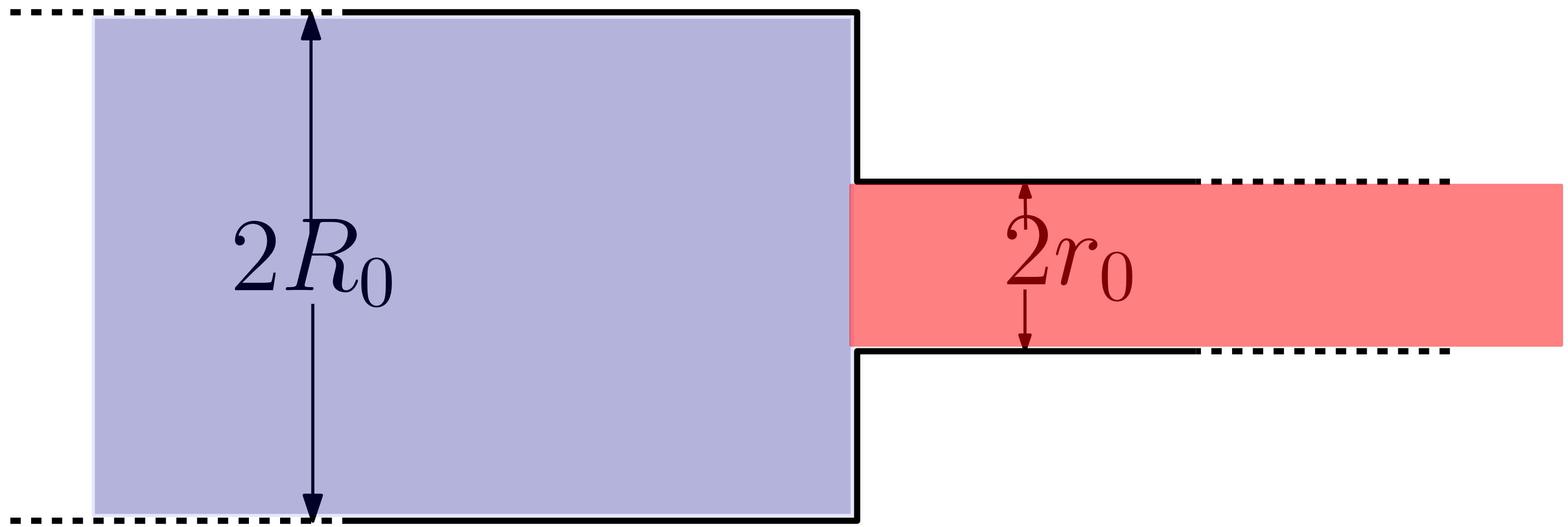

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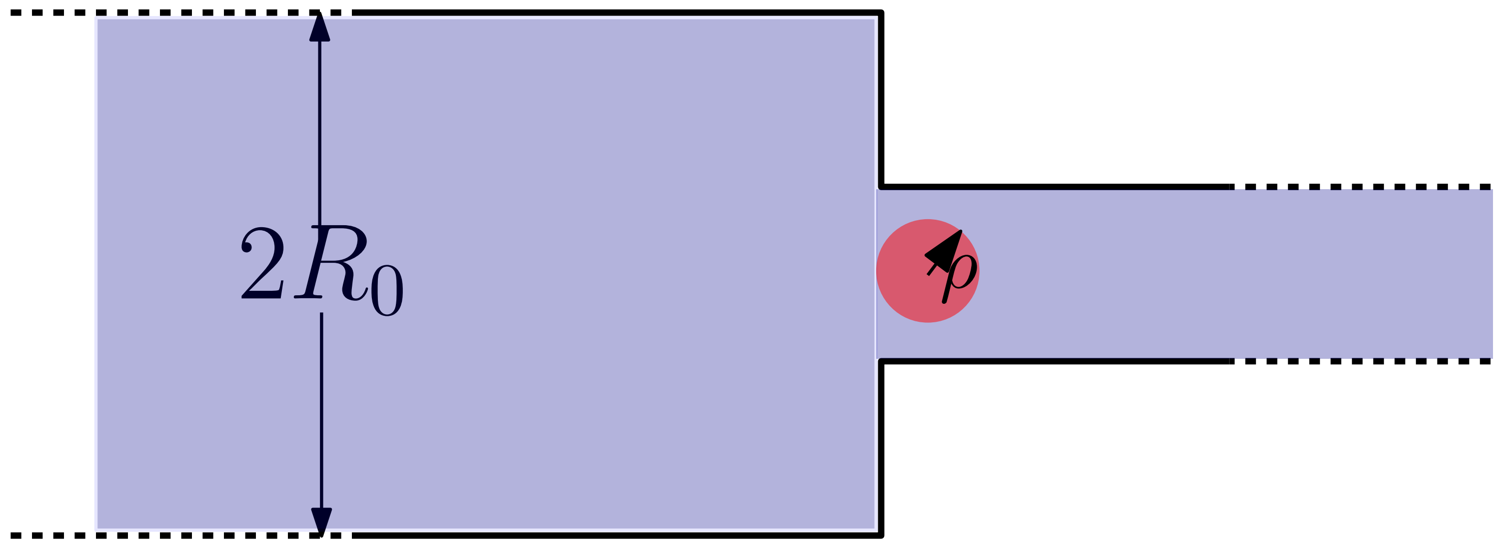

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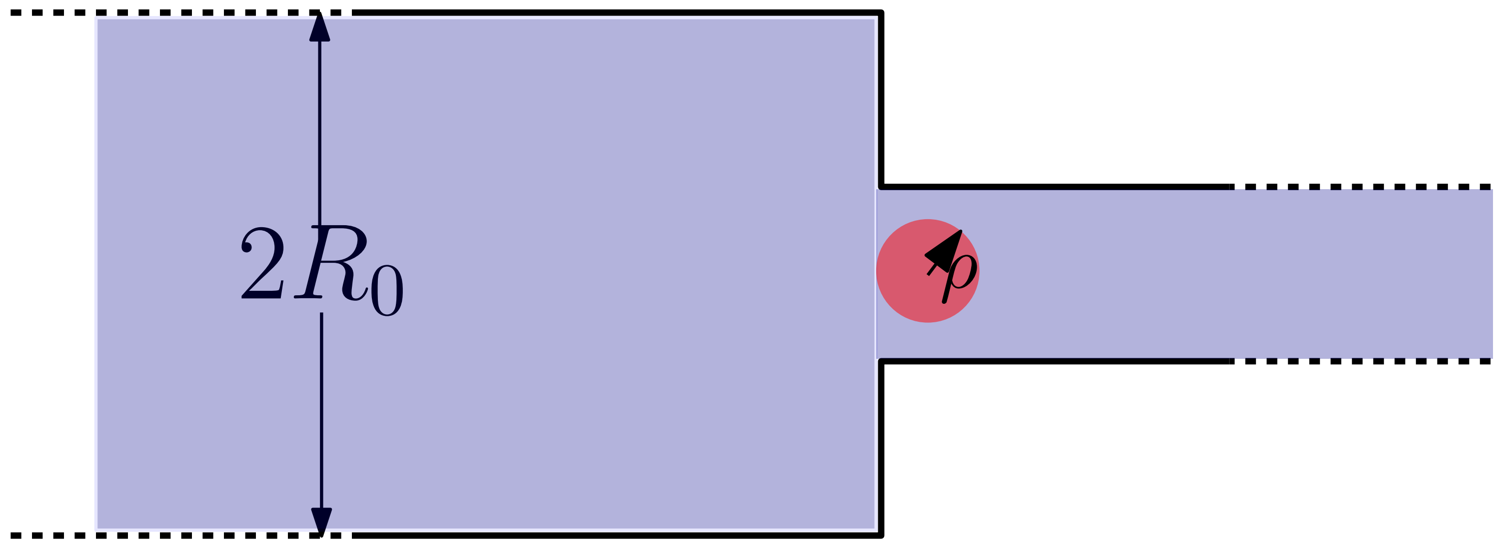

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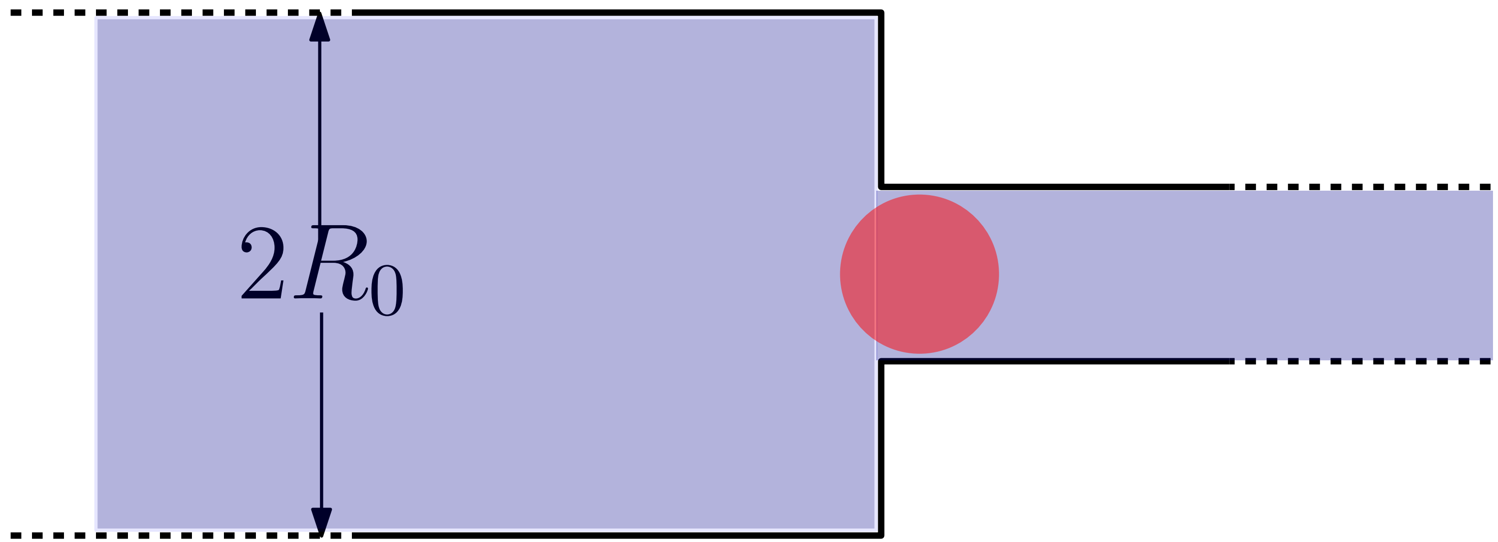

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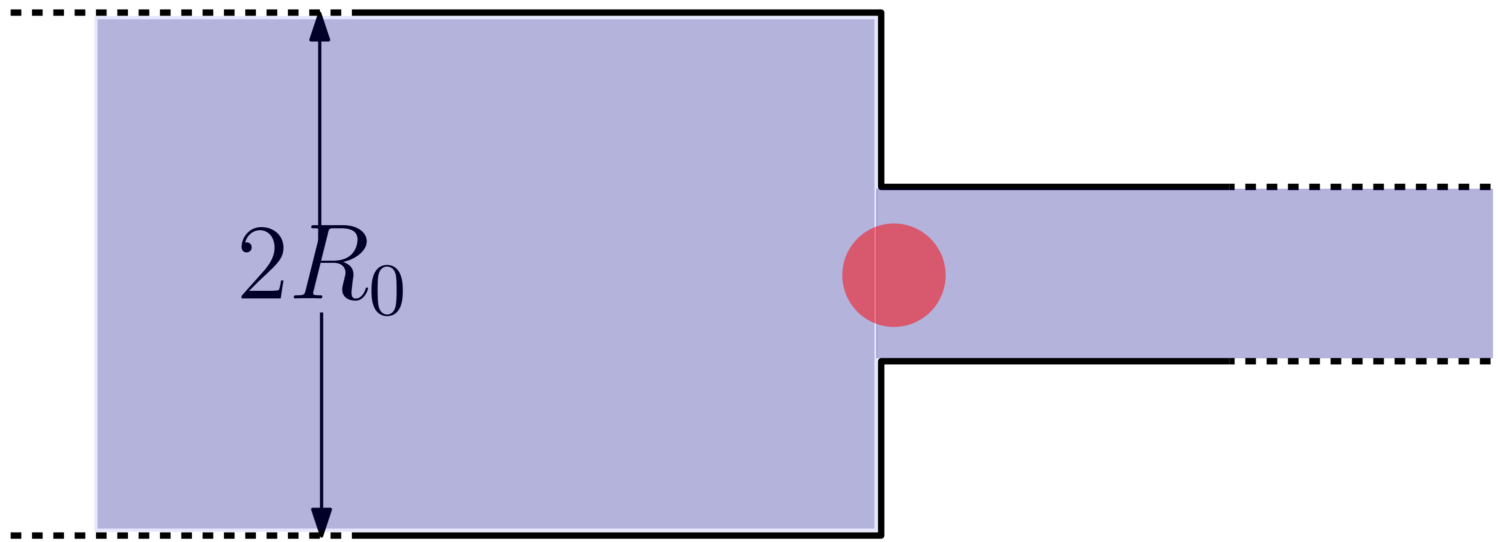

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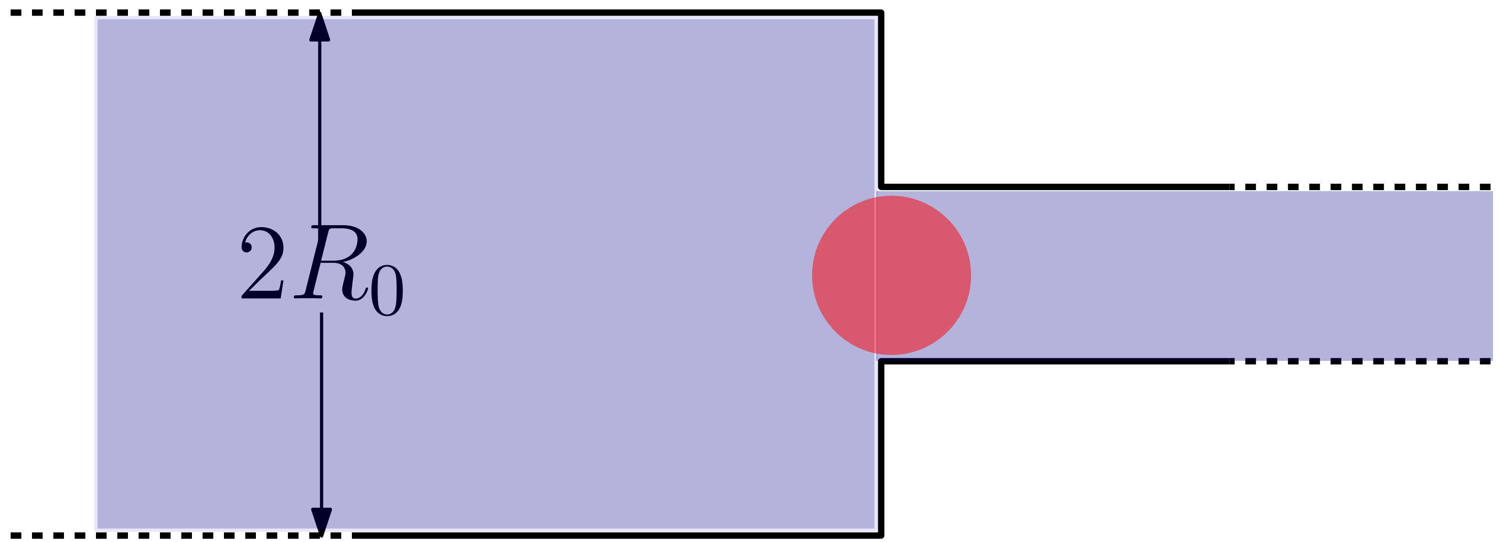

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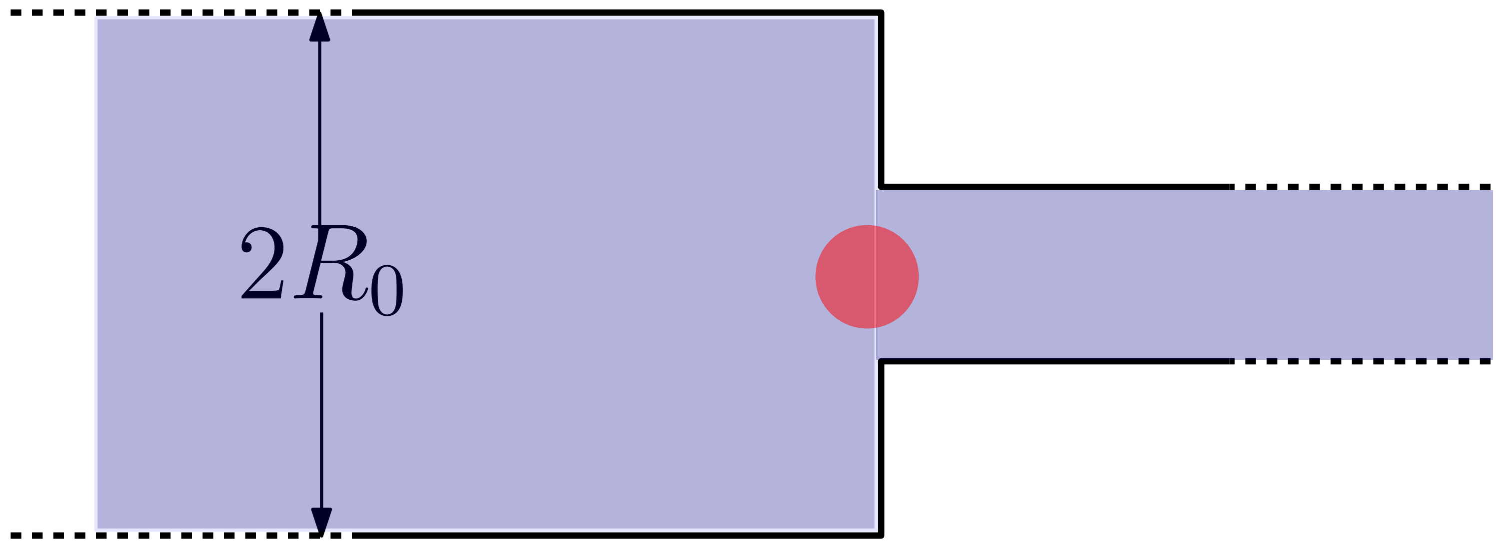

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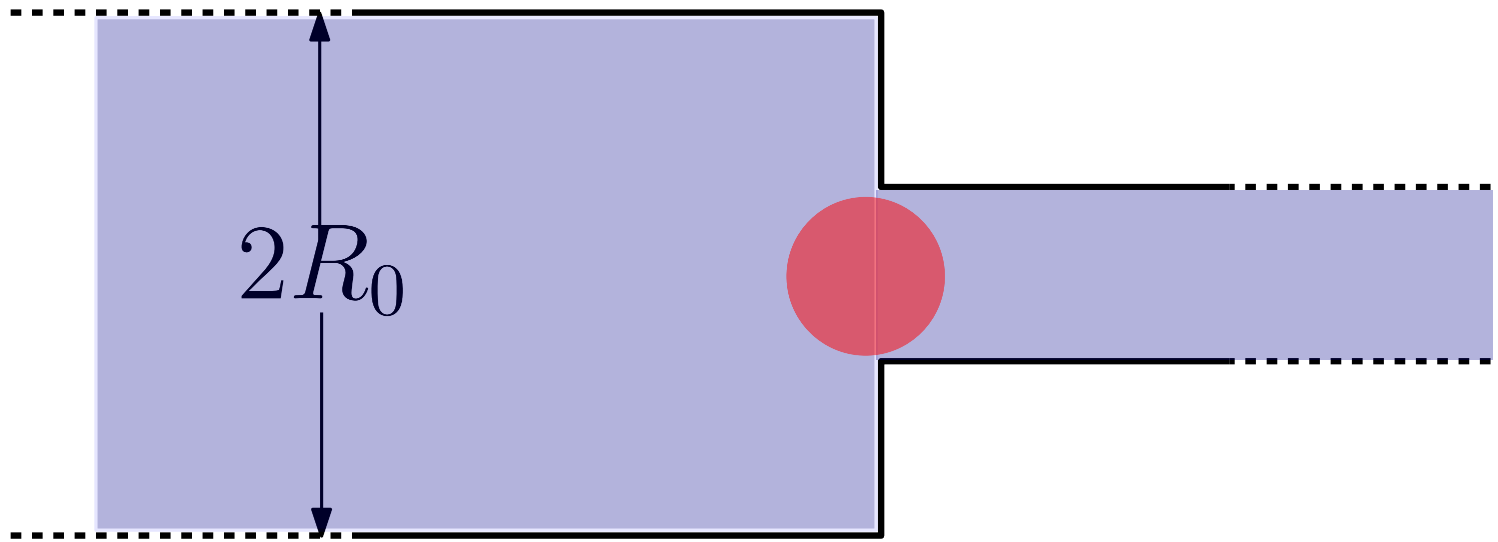

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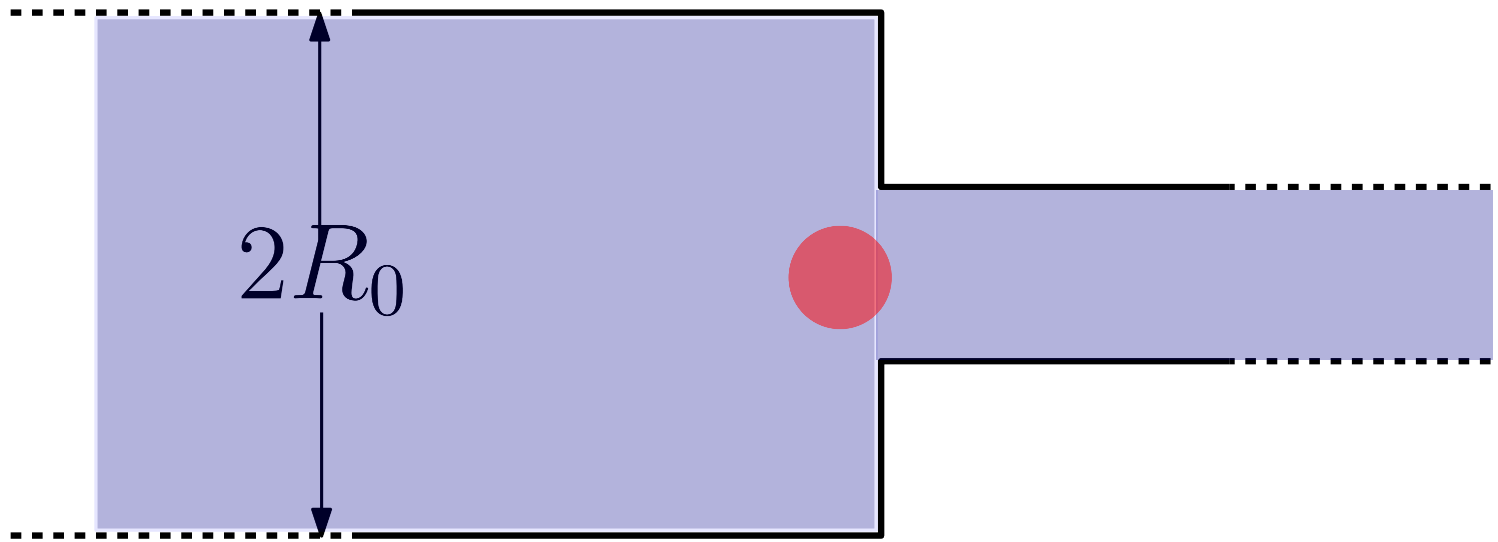

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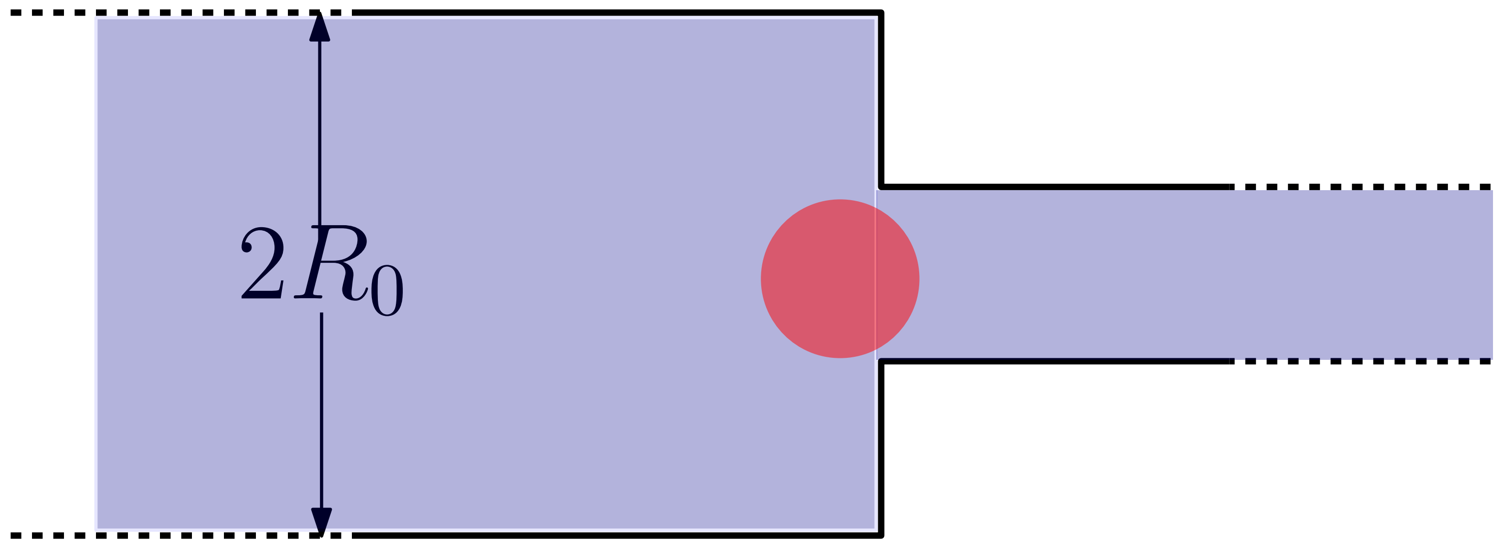

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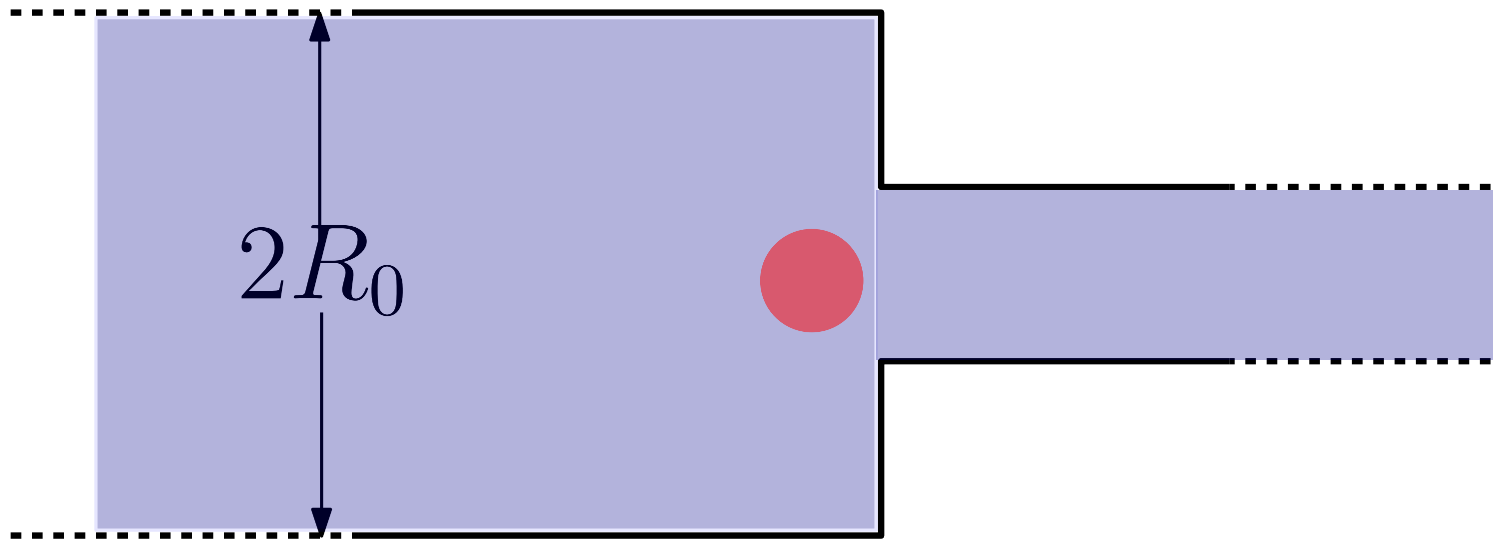

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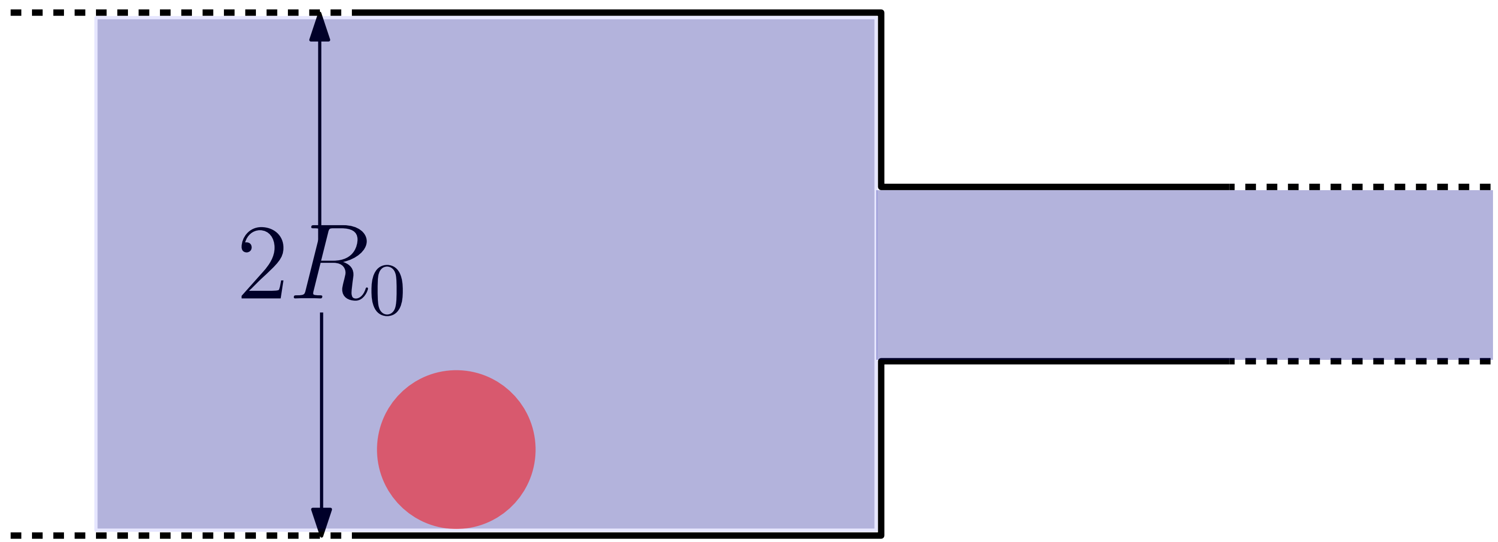

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We eventually can reach any point in Ω.
Any point of $(AC-\epsilon)$, for big time, is bounded below by ~ 1.

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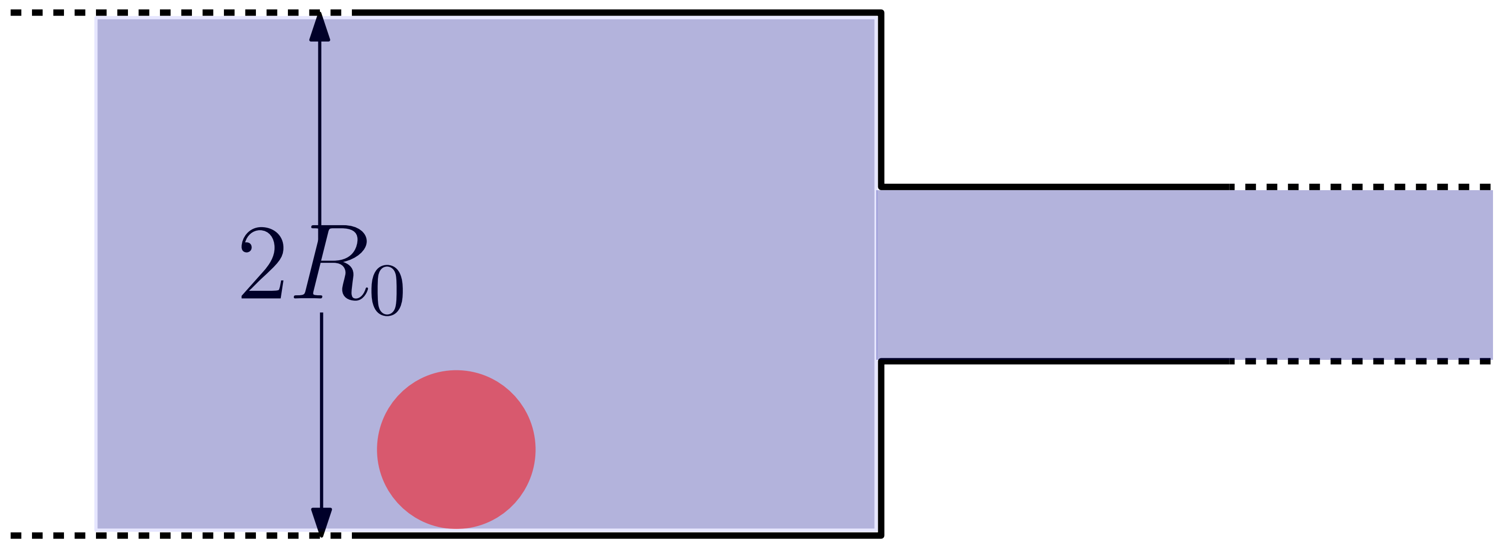

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$r_0 > \rho > (d-1)/\nu \Rightarrow$ invasion.

What about barriers? New results

Same idea works for many domains!

For blocking *cover openings* with *small balls perpendicular to the boundary*.

What about barriers? New results

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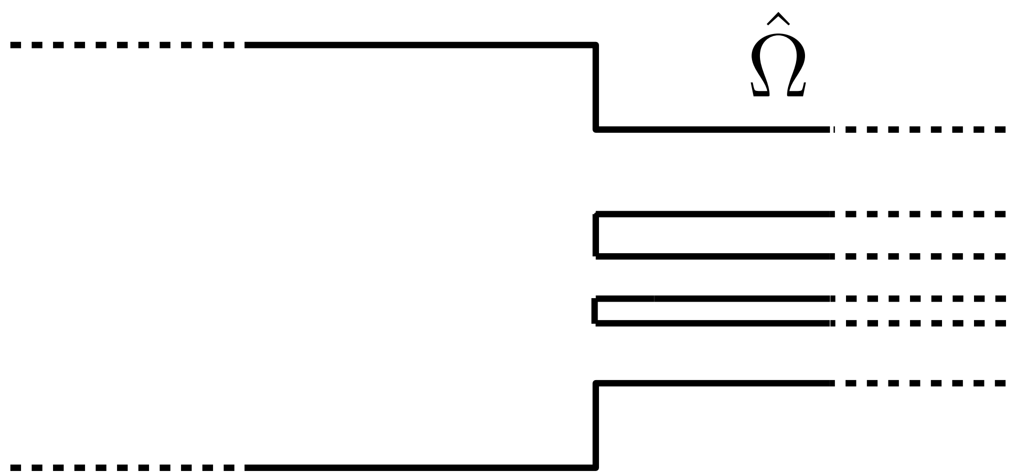

Openings smaller than $\frac{2(d-1)}{\nu}$.

What about barriers? New results

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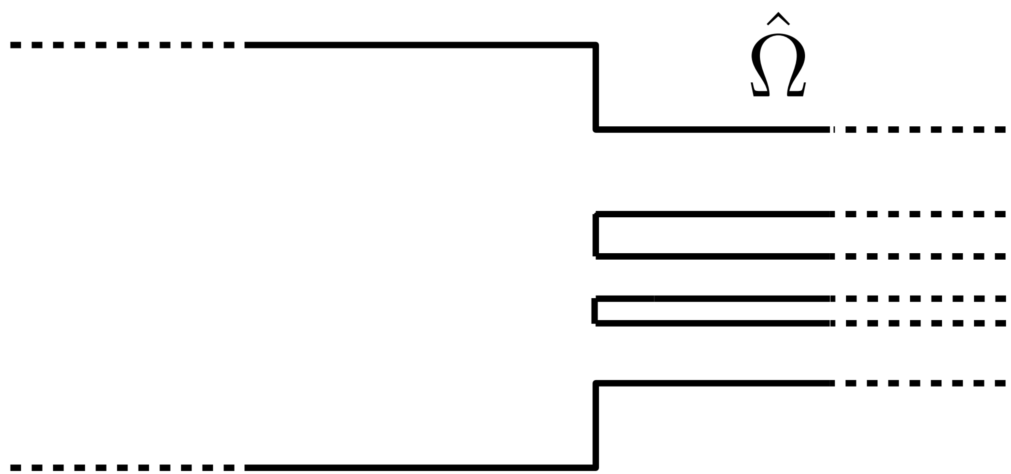

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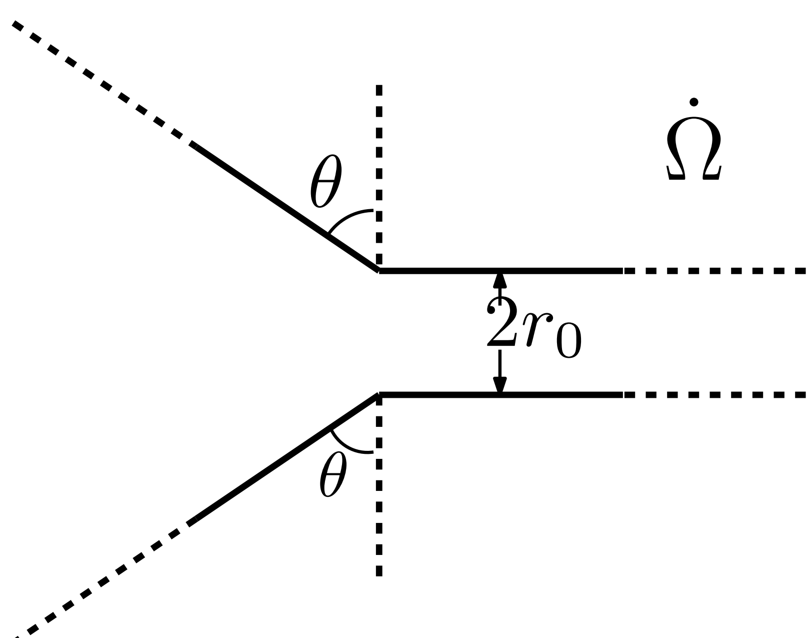

$r_0 \leq \cos(\theta)\frac{d-1}{\nu}$ (for perpendicularity).

What about stochasticity in the population?

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Basically, we add coalescence to the B.M.M. of Theorem $1/3$.

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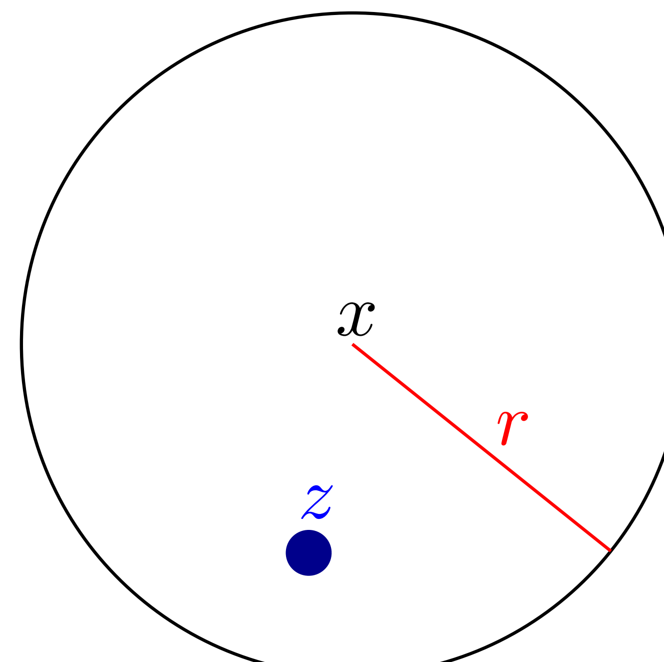
$$w(t,y) = (1-u)w(t^-,y) + uK.$$



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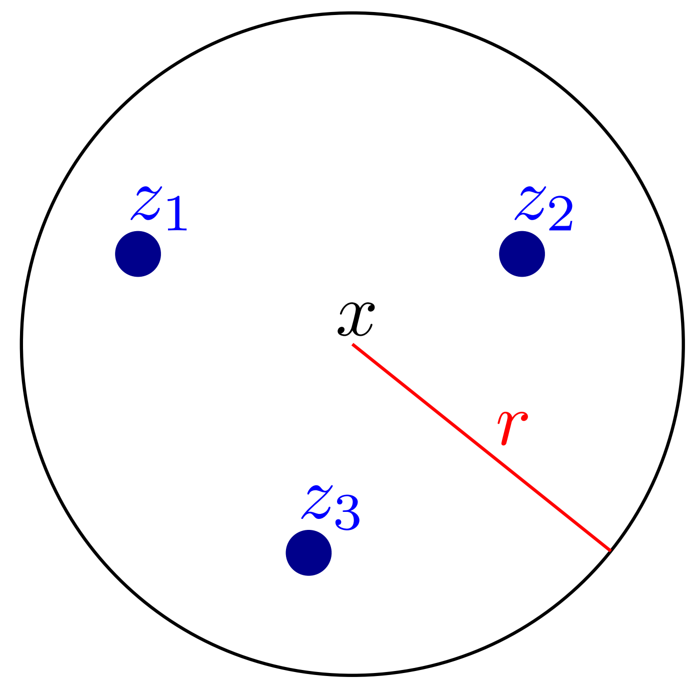

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type of individual at x at time $t \sim \mathbb{V}_{w(0,x)}(\mathcal{W}(t))$,

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Remark: one can define the SΛFVS with reflection in the boundary of poligonal domains by the method of images.

What about stochasticity in the population? The SΛFVS

Scale $x \to n^{\beta} x$ and $t \to nt$ for $0 < \beta < \frac{1}{4}$. And, for some $\epsilon_n \to 0$ fast enough,

$$u_n = \frac{u}{n^{1-2\beta}}, \qquad s_n = \frac{1+\epsilon_n \nu}{\epsilon_n^2 n^{2\beta}}, \qquad \gamma_n = \nu \epsilon_n.$$

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$\Rightarrow w^n(x,t) \sim u(x,t)$ with u the solution of $(N - AC_\epsilon)$.

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Theorem 4 (Etheridge, L.)(Scaling for small noise regime)

Let $\Omega = (\mathbb{R}_- \times B_{d-1}(x, R_0)) \cup (\mathbb{R}_+ \times B_{d-1}(x, r_0))$, for $r_0 < R_0$.

If $r_0 < \frac{d-1}{\nu}$, for big enough n, $\mathbb{E}_{1_{x \geq 0}}(w^n(t,x))$ is blocked.

If $r_0 > \frac{d-1}{\nu}$, for big enough n, $\mathbb{E}_{1_{x \geq 0}}(w^n(t,x))$ presents invasion.

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So $(\xi_t^n) \sim W(t)$

$\Rightarrow w^n(x,t) \sim$ solution to the heat equation.

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Remark: No blocking in this case! (The heat equation converges to a constant).

The *branching rate* of potential ancestor, $s_n n^{2\beta}$, could go to infinity.

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So we see BBM but with less particles. Harder to get blocking.

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Conjecture (Etheridge, L.)(Scaling for mild noise regime)

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Extra references

[1] David PL Toews, Irby J Lovette, Darren E Irwin, and Alan Brelsford.
Similar hybrid composition among different age and sex classes in themyrtle–audubon's warbler hybrid zone.

[2] Nick Barton and his group.

[3] Cassandra N. Trier,Jo S. Hermansen,Glenn-Peter Sætre,Richard I. Bailey.
Evidence for Mito-Nuclear and Sex-Linked Reproductive Barriers between the Hybrid Italian Sparrow and Its Parent Species.

[4] N H Barton and G M Hewitt.
Adaptation, speciation and hybrid zones.

(Pictures of MCF) Curve by Grayson (1987),
Bunny by C.Stocker (found in Voigt 2007).

On hybrid zones and the effect of barriers

Ian Patrick Letter Restuccia

15.11.2021 · Oxford probability seminar

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DEPARTMENT OF STATISTICS

Agencia Nacional de Investigación y Desarrollo

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