evolutionary dynamics on networks:

selection versus drift

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evolution

Two "forces" underlying evolutionary change:

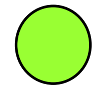
- selection – survival of the fittest and all that,
- drift or "neutral evolution" – traits tend to saturate in populations, even *without* selection.

What follows is a simple model aimed at exploring the interplay between these.

Evolutionary dynamics on graphs
Nature, Vol. 433, No. 7023. (2005), pp. 312-316.
Lieberman, Hauert and Nowak

the Moran process

n beans
in a bag:



choose a bean

choose another bean

the first over-writes
the second

& back in the bag

eventually all the beans
will be the same colour

the moran process with fitnesses

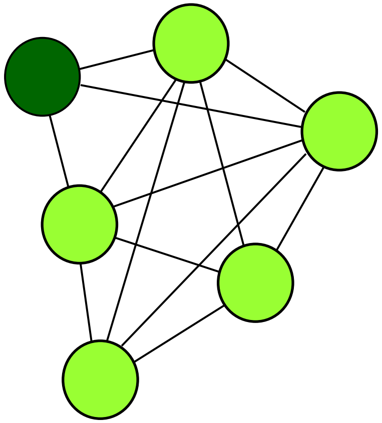
- beans may have different "fitnesses"
- we choose the first bean with probability proportional to its fitness
- the second bean is just random

fitter beans *tend* to end up occupying the bag

- suppose almost all beans have fitness = 1
- a single bean has fitness $r > 1$
- only two absorbing states: mutant dies out, or mutant saturates
- saturation probability:

$$\rho^* = \frac{1 - 1/r}{1 - 1/r^n}$$

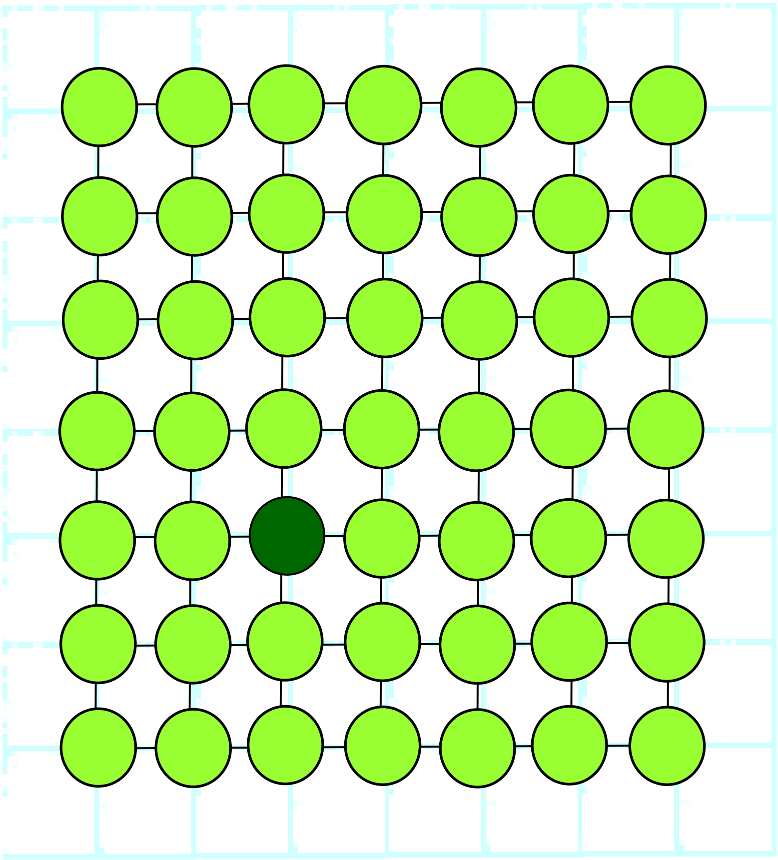
Moran process on a network



- 1^{st} site chosen $\propto$ fitness
- 2^{nd} site is a neighbour
- on a fully connected graph the saturation probability is still

$$\rho^* = \frac{1-1/r}{1-1/r^n}$$

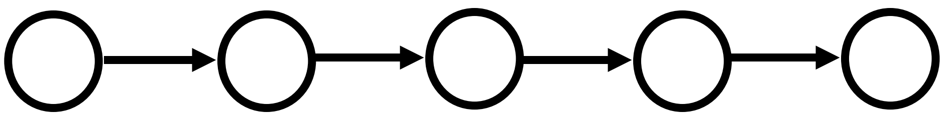
what about on a lattice?



- saturation probability is the *same* as for the fully-connected network:

$$\rho = \rho^*$$

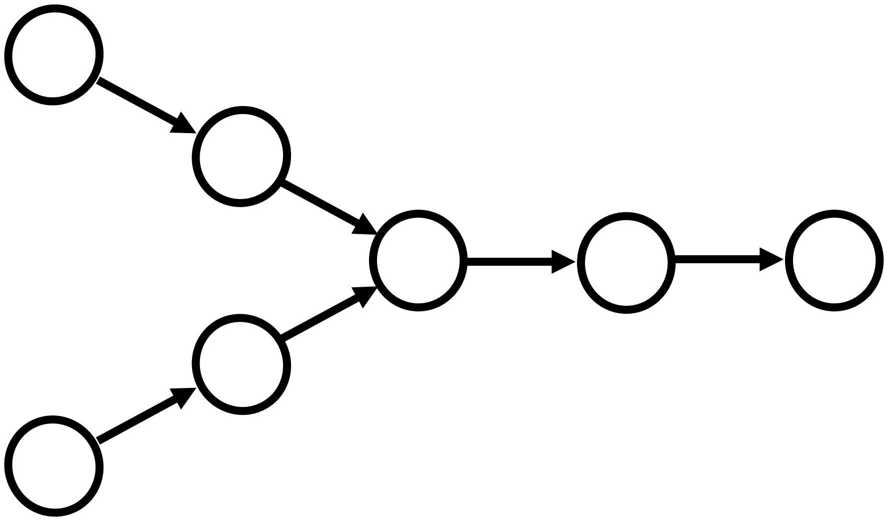
what about this then?



$$\rho = \frac{1}{n} < \rho^*$$

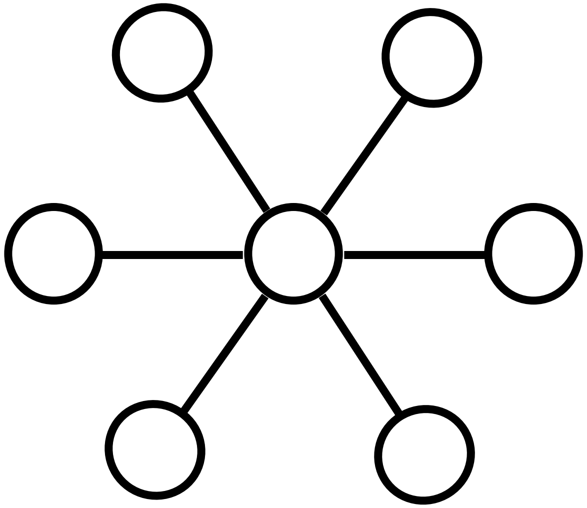
a "suppressor" of fitness:
it counts for nothing

and this?



$\rho = 0$

and this?

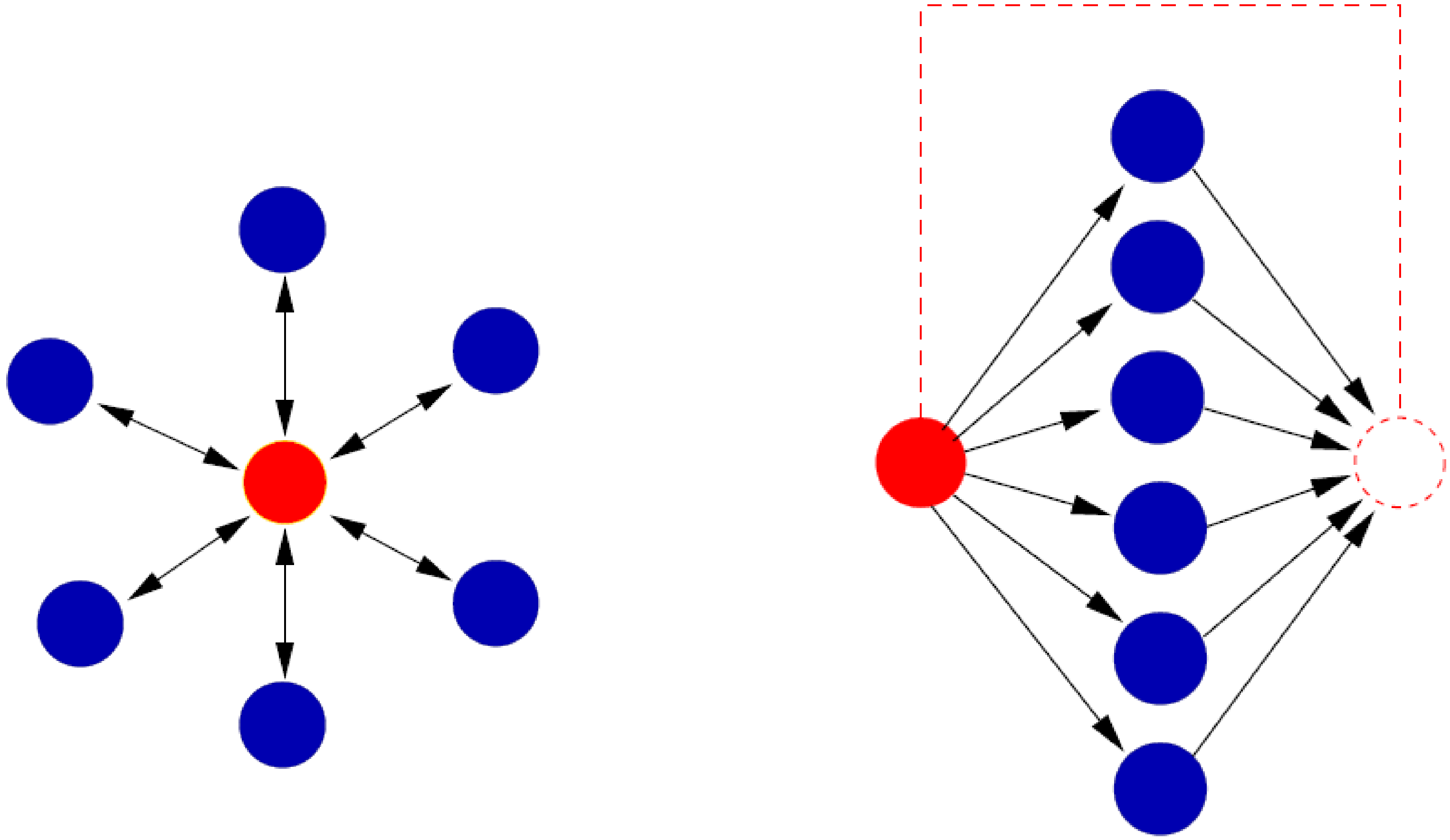


$$\rho = \frac{1 - 1/r^2}{1 - 1/r^{2n}} > \rho^*$$

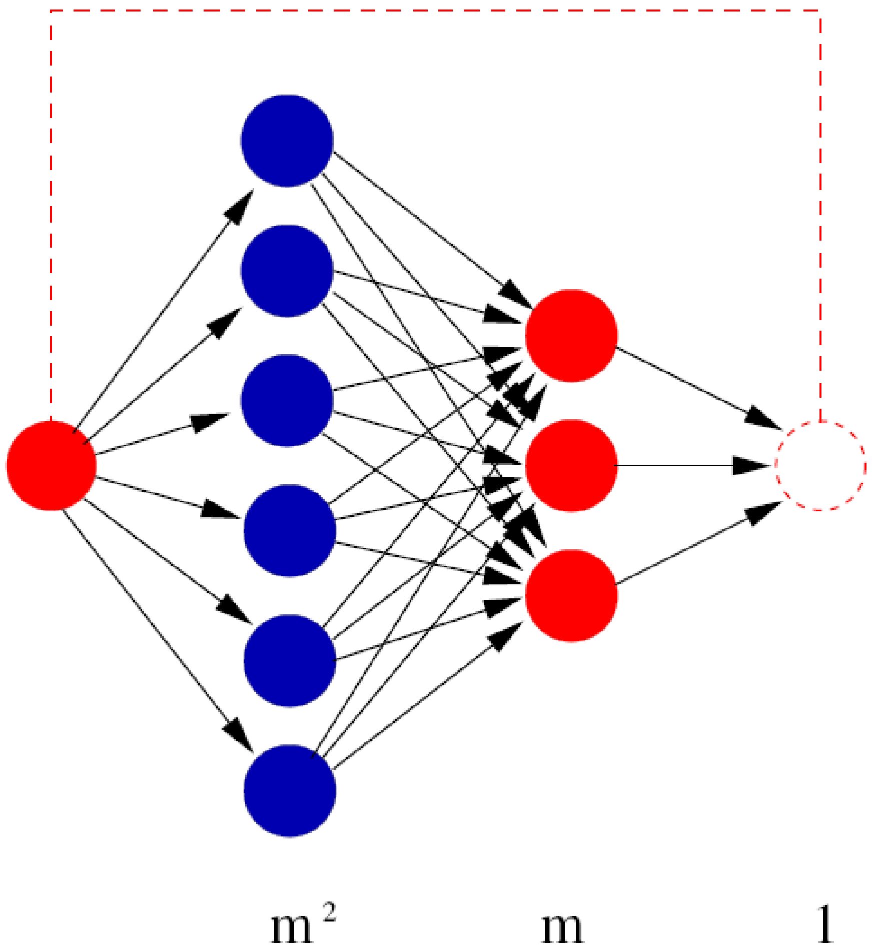
an "amplifier" of fitness:

a fitness of r does as well as a r^2 would in the fully connected case

another view of the star network



an arbitrary amplifier of fitness...



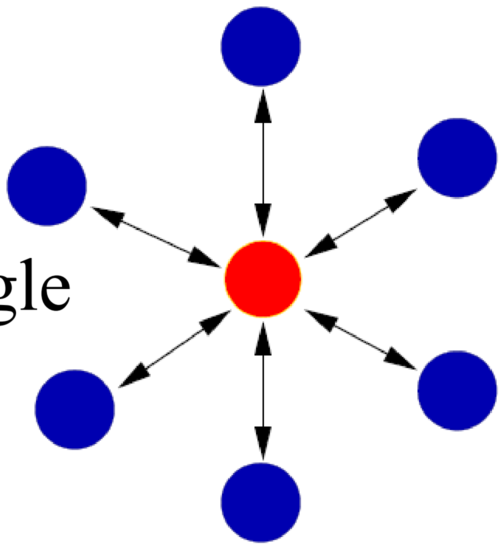
With enough fan-in, and lots of layers,

$$\rho \rightarrow 1$$

r does as well as ∞

Q1: what's going on?

- the hub is "hot": spokes are "cold"



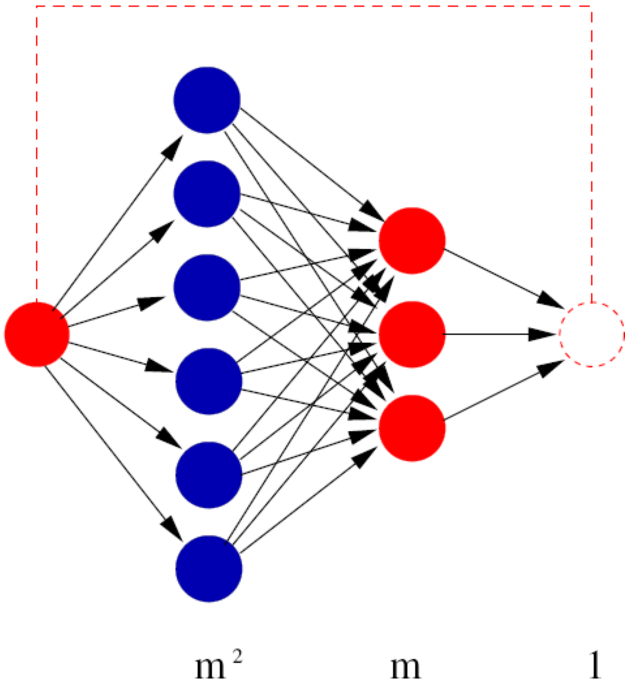
- the relevant measure is the chance a single spoke gets copied *to another spoke*

- to do this it needs to be
  - chosen to replicate (into hub)
  - immediately chosen again (as hub)

- a mutant gets a "boost" of r in both of these steps, hence r^2

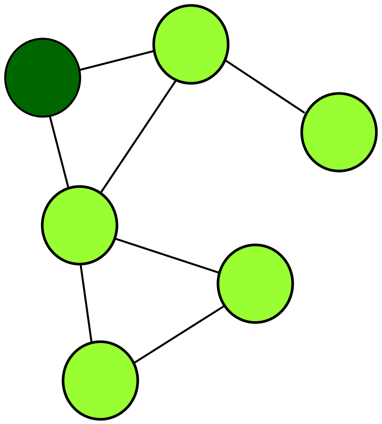
Q1: what's going on?

- the biggest layer is "cold"
- the relevant measure is the number of cold nodes
- a mutant gets a "boost" of r for each layer it has to get through
- L boosts in a row leads to r^L



Q2: does this generalise?

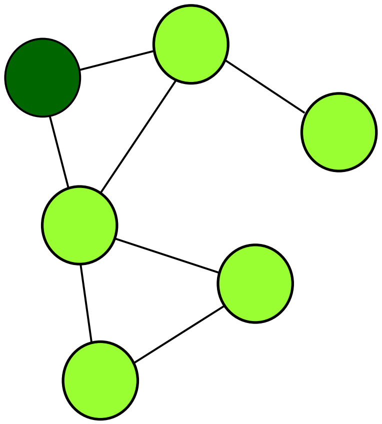
Moran process:



- **<u>fitness</u>** enters via the birth site
- deaths are
  - contingent on the birth site
  - **<u>neutral</u>**

“FB→ND”

a very similar process...

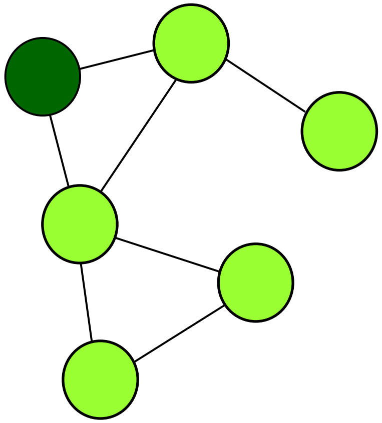


consider re-ordering things slightly:

- first choose a death site, neutrally
- then choose a birth site from among its neighbours, based on fitness

"ND→FB"

4 processes in the family

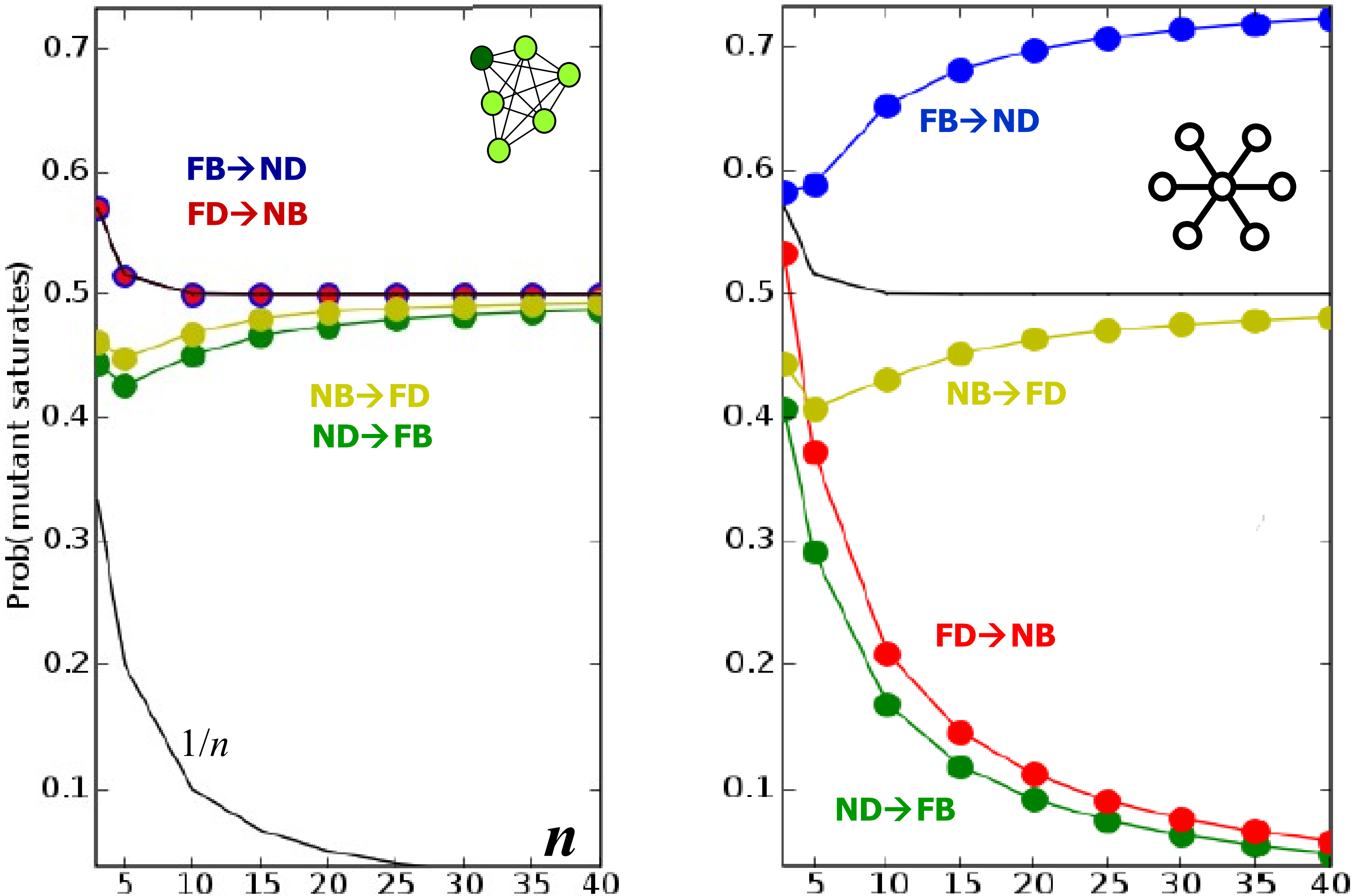


- FB→ND   (Moran)
- ND→FB
- NB→FD
- FD→NB

i.e. ***un***fitness determines the death site

Which do you think is more "realistic"?

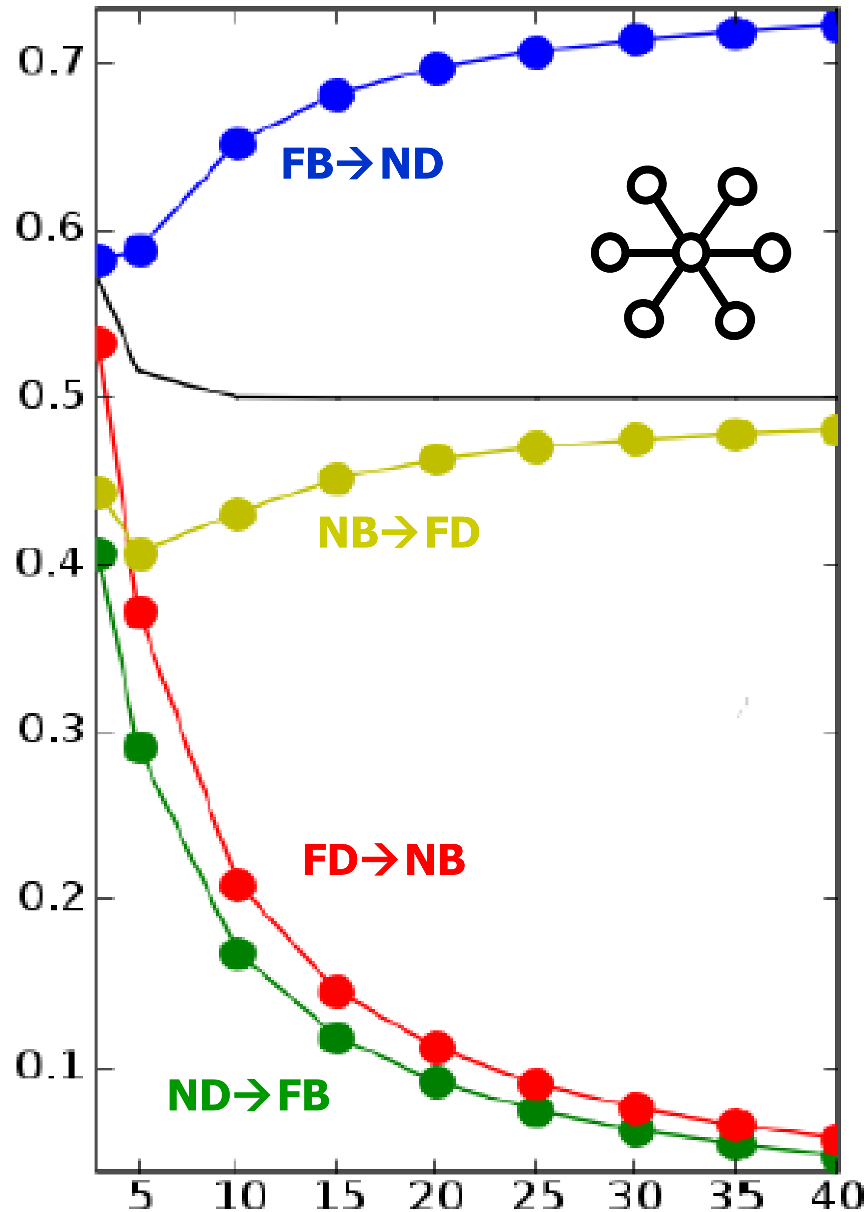
what happens (exact calculation)

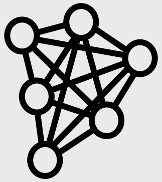
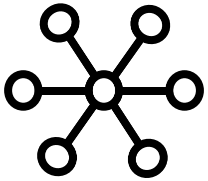
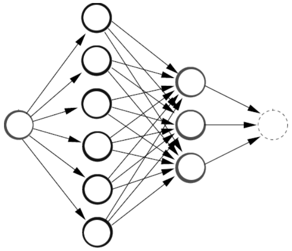


suppressors

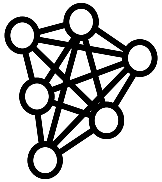
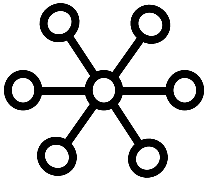
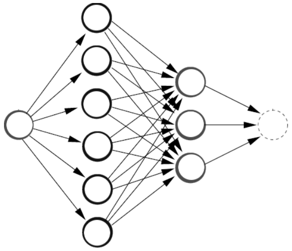
The star network is an amplifier *only* under the Moran process

Under the other alternatives it is a suppressor!



111 nodes:			
FB→ND	**.50**	**.74**	**.70**
NB→FD	**.50**	**.48**	**.72**
FD→NB	**.50**	**.02**	**.05**
ND→FB	**.50**	**.02**	**.04**

time to fixation

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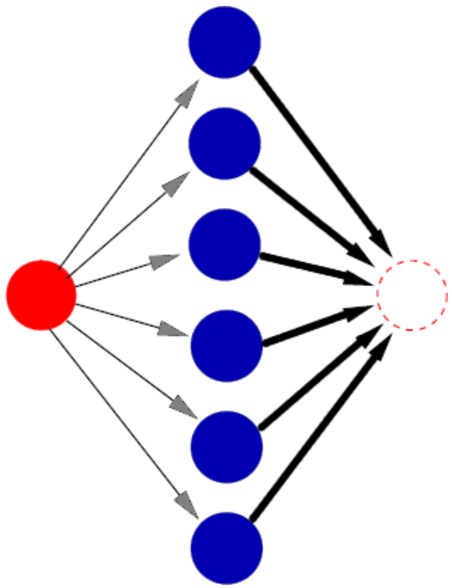
$\tau \approx 60000$

$\tau \approx 200$

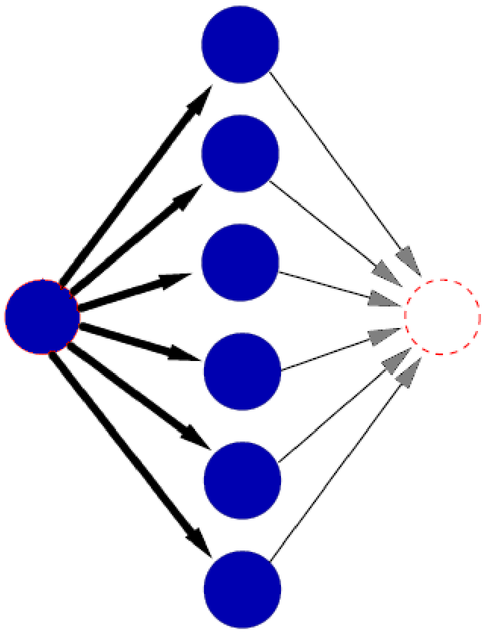
$\tau \approx 800$

why such suppression by death-first?

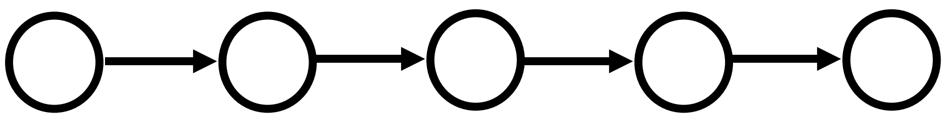
birth-first:
hub gets over-written



death-first:
hub over-writes



$$\rho \approx \frac{1}{n}$$

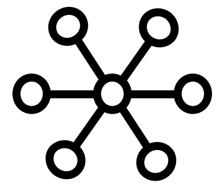


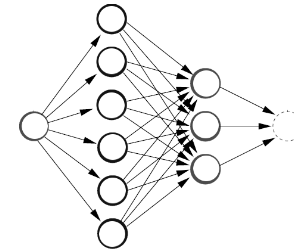
conclusions

I’ve looked at several evolutionary dynamics that allow both selection and random drift to play a role

None of them is “right”, but I suspect they all happen...

Whether births are contingent on deaths, or *vice versa*, is much more important than which of these is tied to “fitness”





only amplifies under Moran

amplifies under birth-first dynamics

strong suppressors under death-first dynamics