Some implications of neutral evolution for ecology

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Work with

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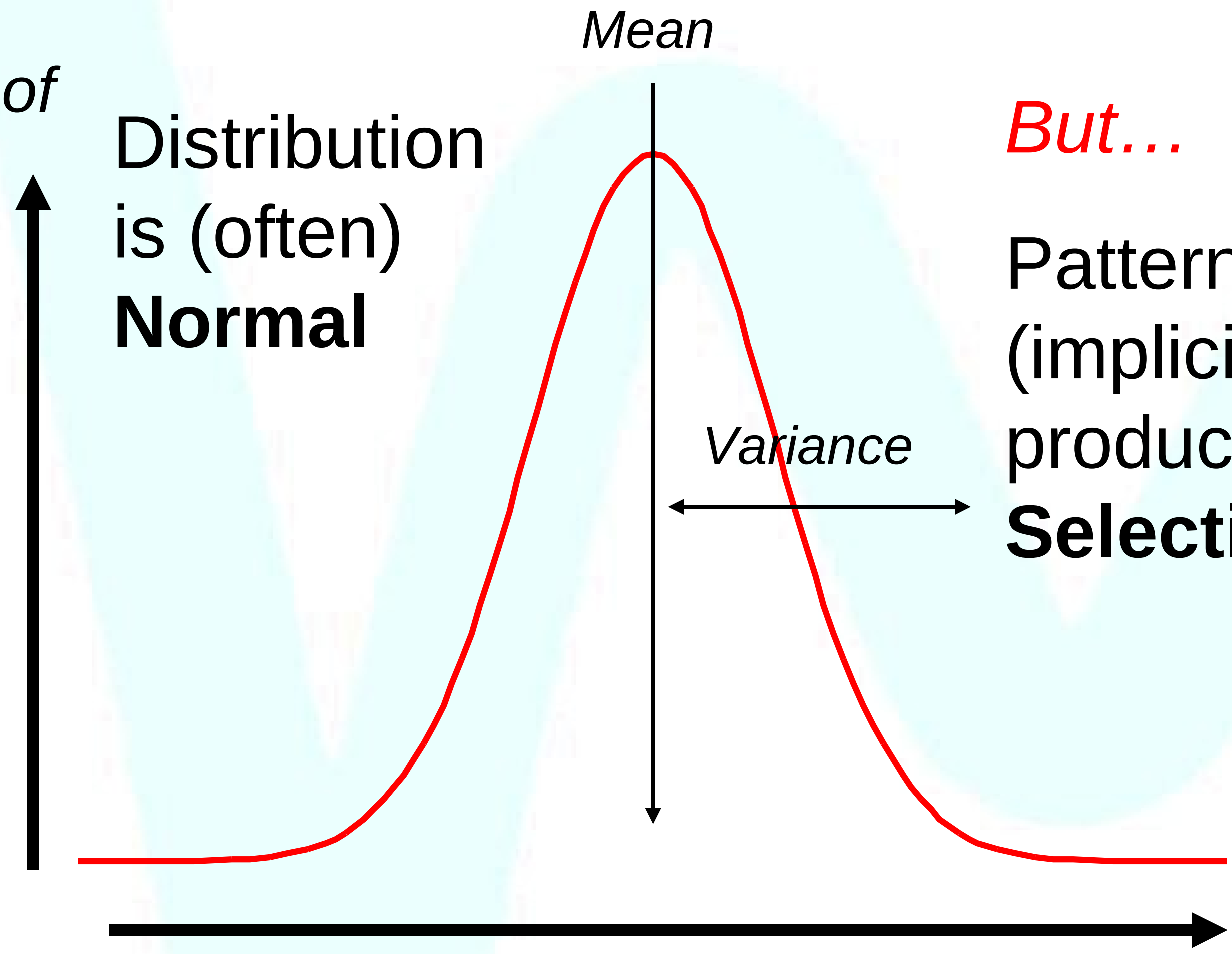
Characterising a Species

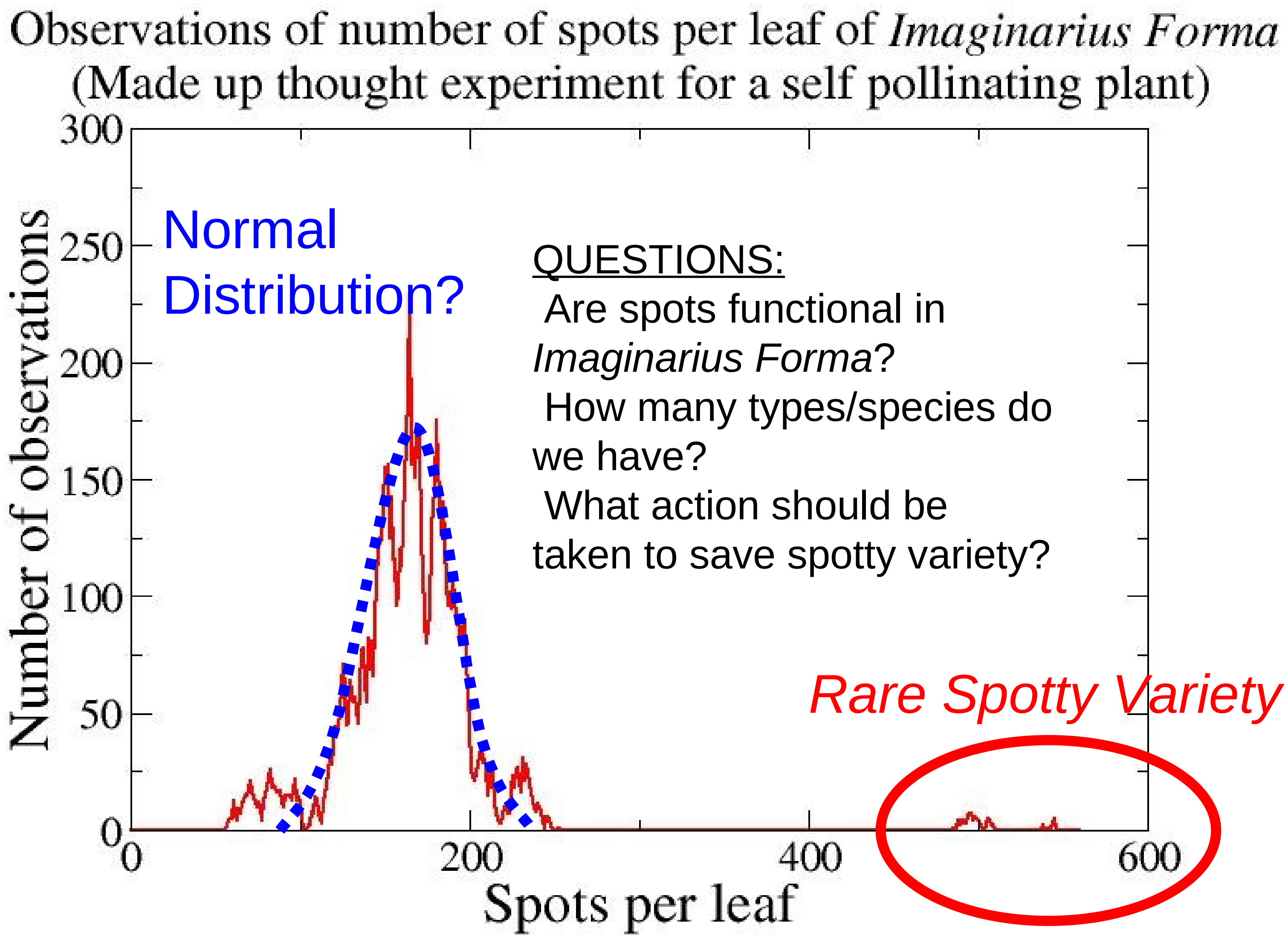
Distribution is (often) **Normal**



But…

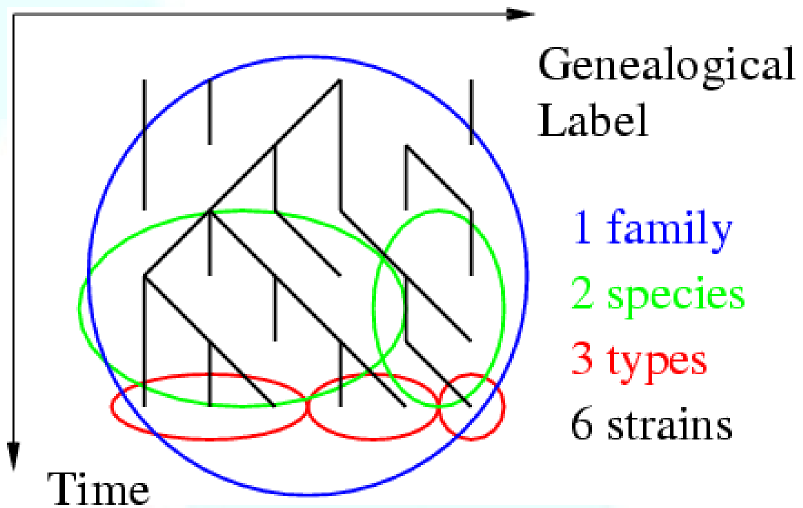
Pattern is (implicitly) produced by **Selection.**

Test Problem



Defining Diversity

- Ecological Sense: “number” of different species or types
- Requires definition of species:
  - *Biological Species concept?*
  - *Phenotypically distinct?*
  - *Genotypic species concept?*



- “Species” don't exist, but individuals form clusters
- Evolution definition of diversity: number of different clusters on a chosen threshold

The Neutral Model

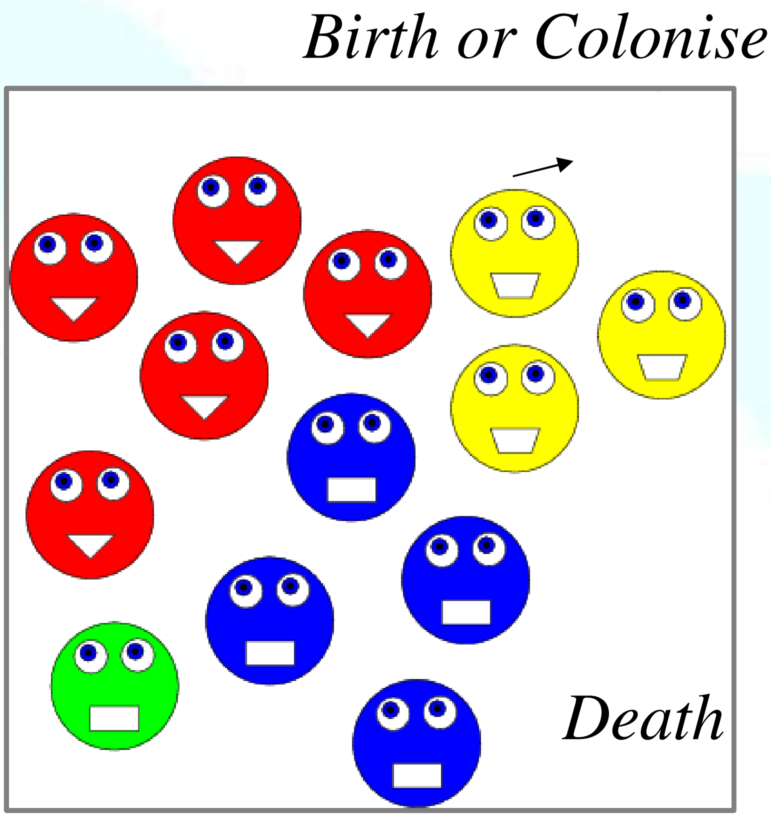
- Assume that all individuals are 'equal'
    - Valid for Phenotypes that do not have function
    - Genotypes, considering the part of the genome that does not code for protein synthesis (12% of Human DNA is variable! *Redon et al. Nature. doi:10.1038/nature05329*)
  - Each individual has the same probability to die (p_k), or give birth (p_b), in a time step
    - For simplicity, assume the total population (N) has reached equilibrium ($p_k = p_b$)
- Mutations (and/or colonisation) can occur, reproduction is asexual

The ecological model

- Consider N individuals each labeled by species:

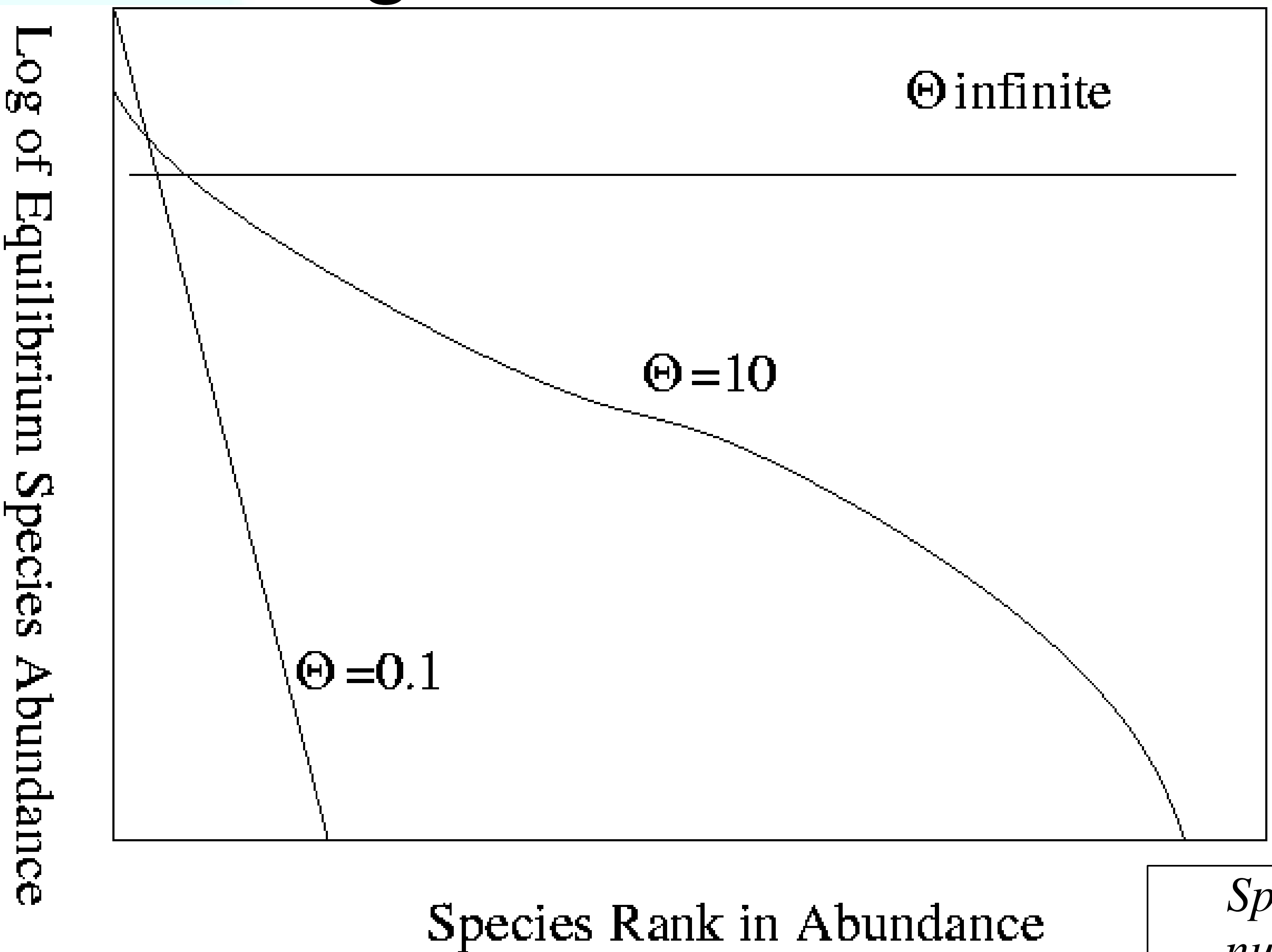
TIMESTEP:

- Pick an individual (from N) and mark it to die.
- Pick an individual (from N) and copy it, *or* with probability p_m, colonise with a new species.
- Kill the marked individual.



Same as a mutation!

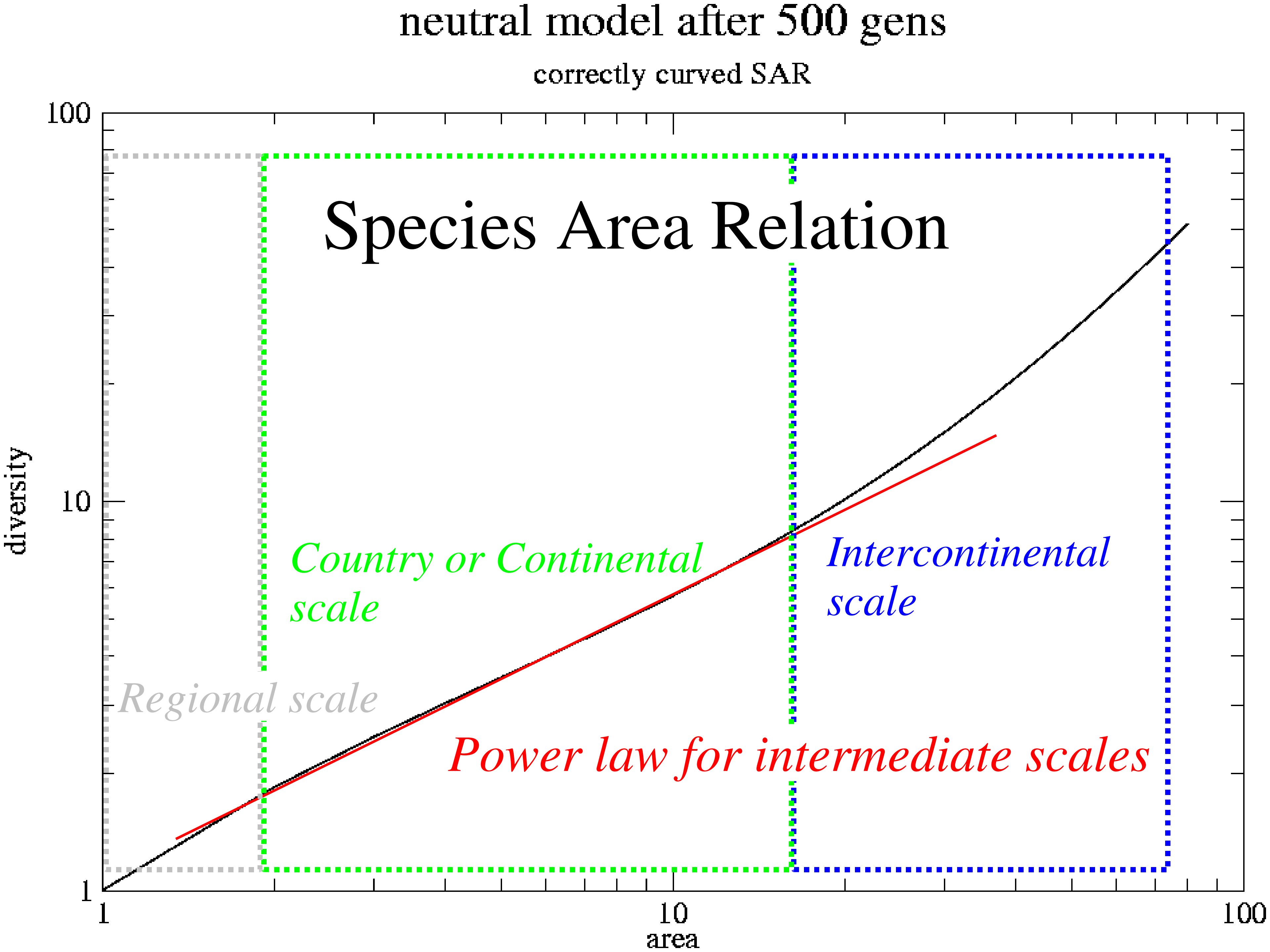
Ecological Model Results



Number of individuals

Species number ordered by size

Θ = (population size)(probability of a new species)



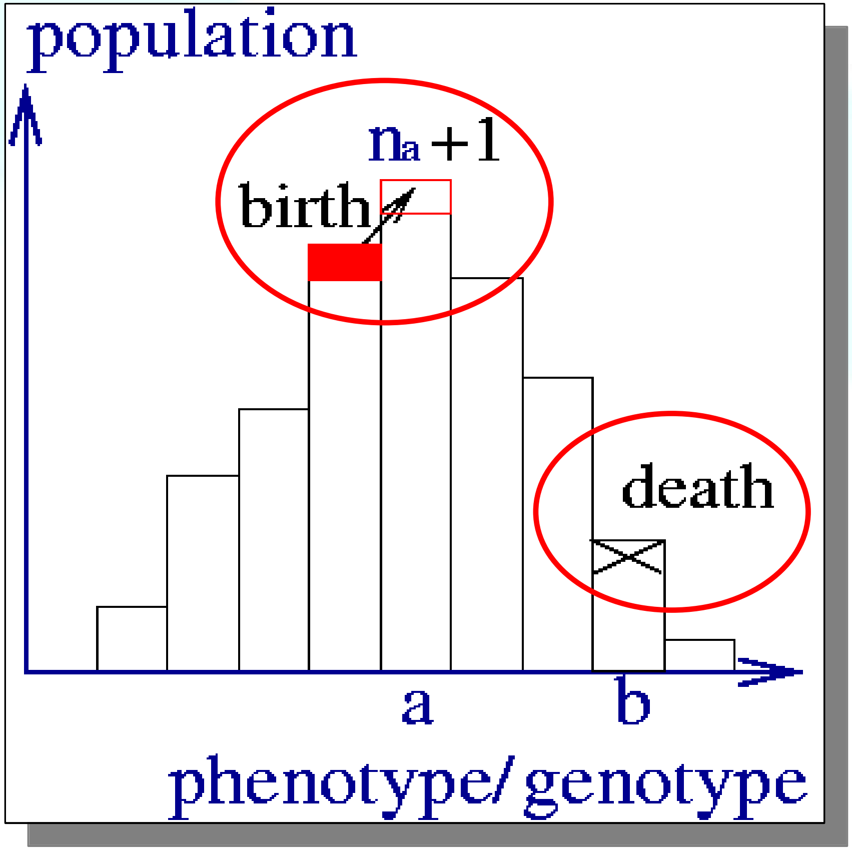
neutral model after 500 gens
correctly curved SAR
Species Area Relation
Country or Continental scale
Intercontinental scale
Regional scale
Power law for intermediate scales
diversity
area
100
10
1
1
10
100

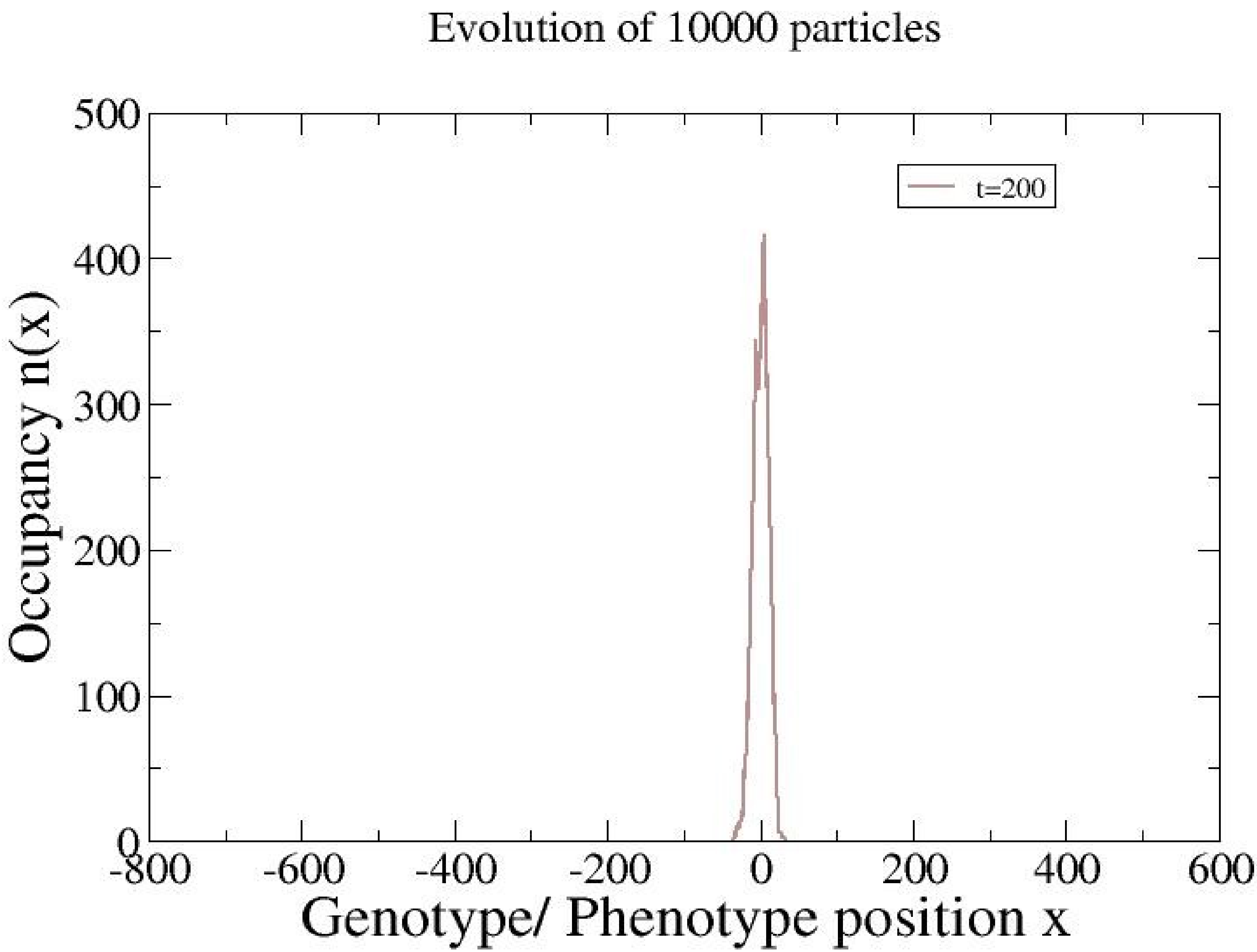
An evolution model

- Consider N individuals each labeled by phenotype position:

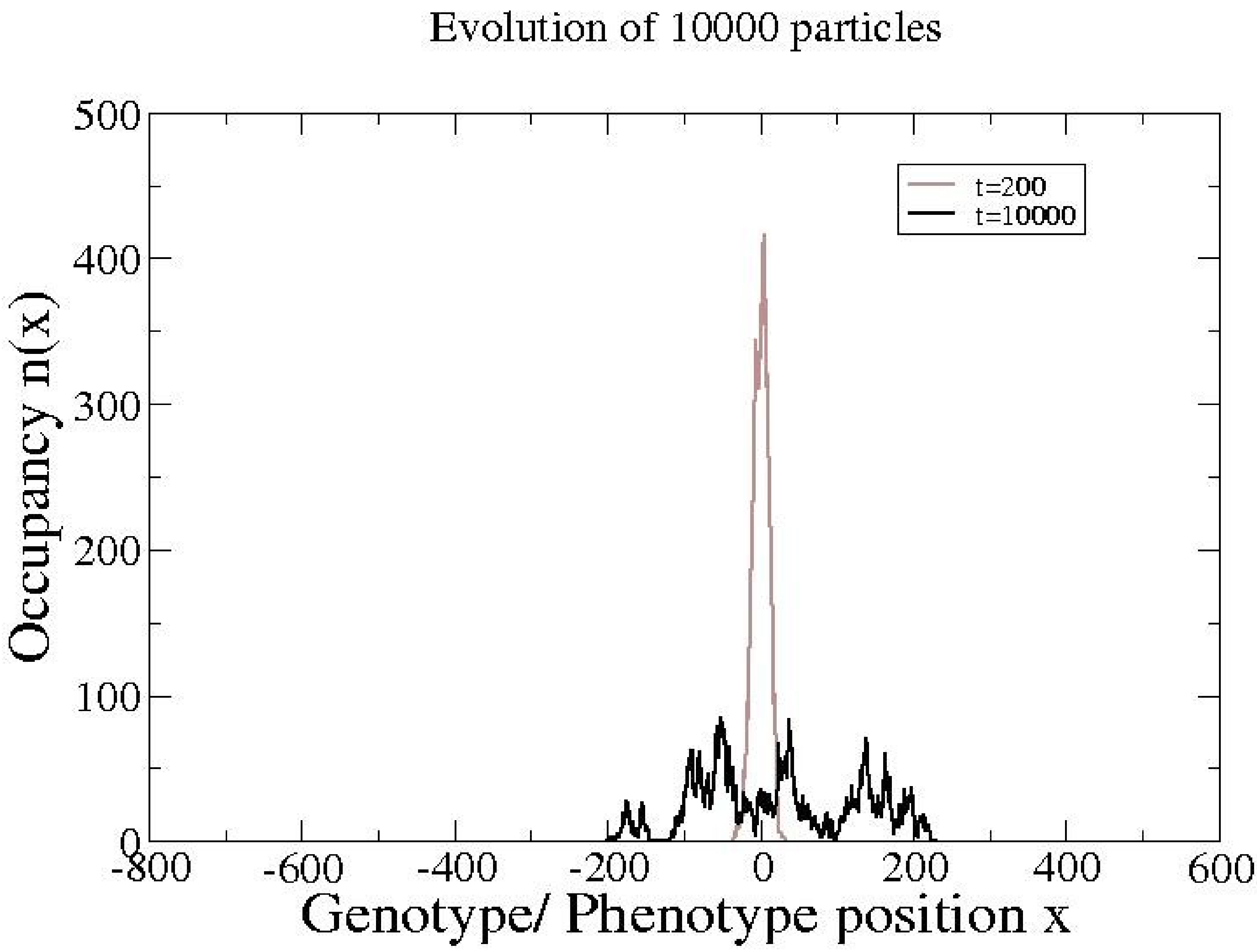
TIMESTEP:

- Pick an individual (from N) and mark it to die.
- Pick an individual (from N) and copy it. With probability p_m Mutate to a similar type.
- Kill the marked individual.





Evolution of 10000 particles
t=200
Occupancy n(x)
500
400
300
200
100
0
-800
-600
-400
-200
0
200
400
600
Genotype/ Phenotype position x



Evolution of 10000 particles
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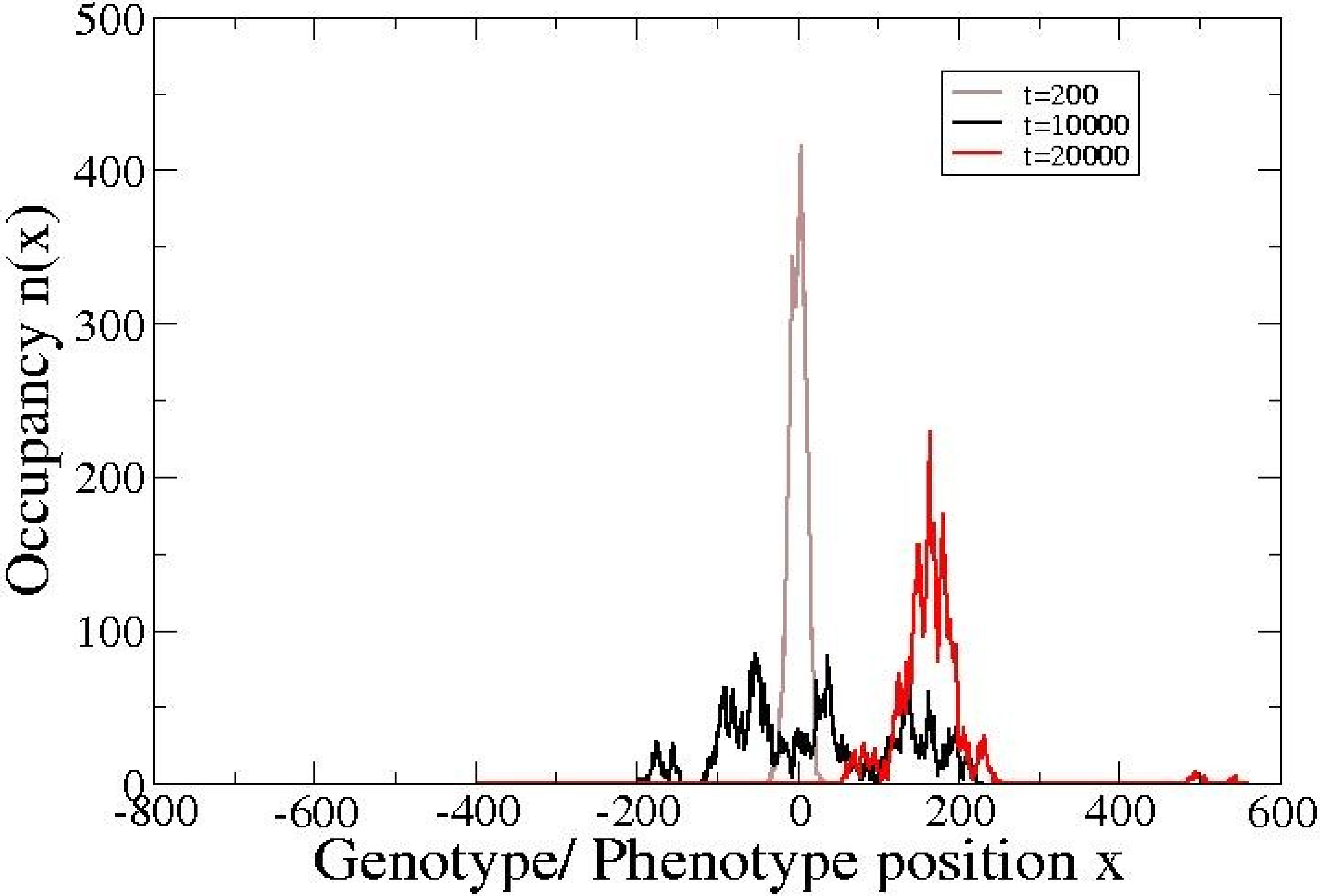
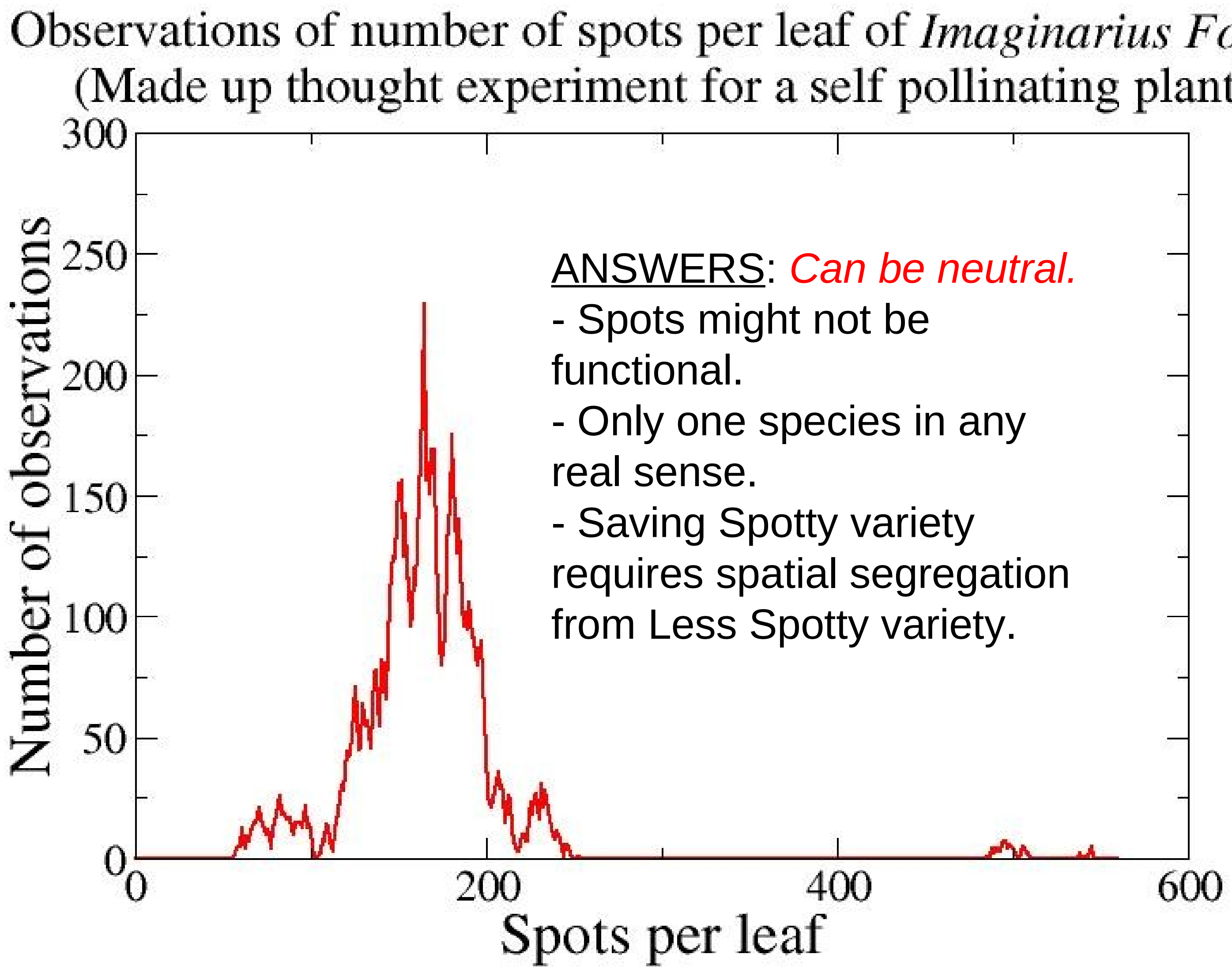
Evolution of 10000 particles

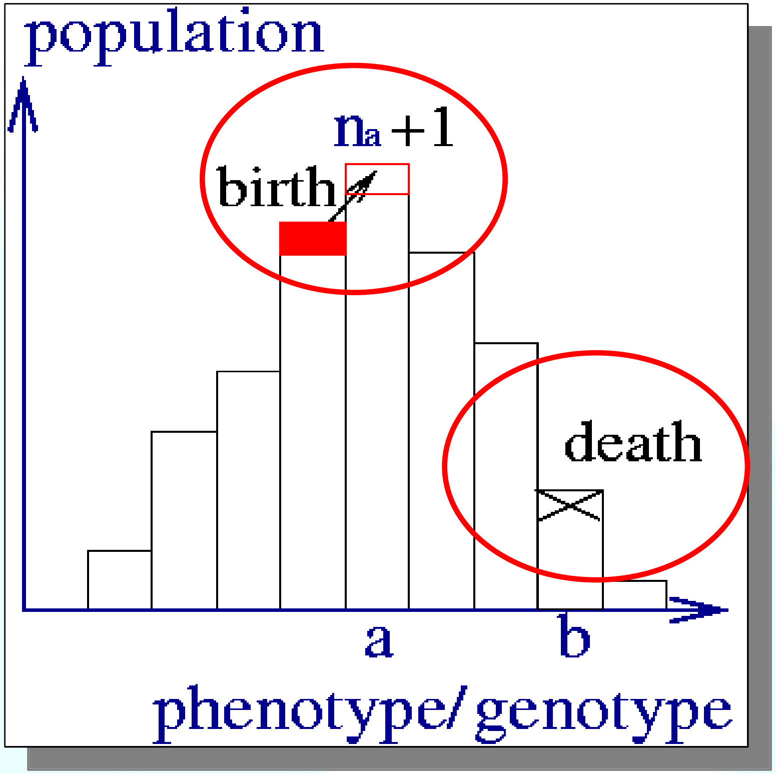


Test Problem



ANSWERS: *Can be neutral.*
- Spots might not be functional.
- Only one species in any real sense.
- Saving Spotty variety requires spatial segregation from Less Spotty variety.

Solution: first try (1)



$$p_b(a) = \frac{n_a}{N}(1 - p_m) + \frac{p_m}{2}\frac{n_{a+1} + n_{a-1}}{N}$$

$$p_k(a) = \frac{n_a}{N}$$

Solution: first try (2)

- Mean field argument:

$$\langle n_a(t+1) - n_a(t) \rangle = p_b(a) - p_k(a)$$

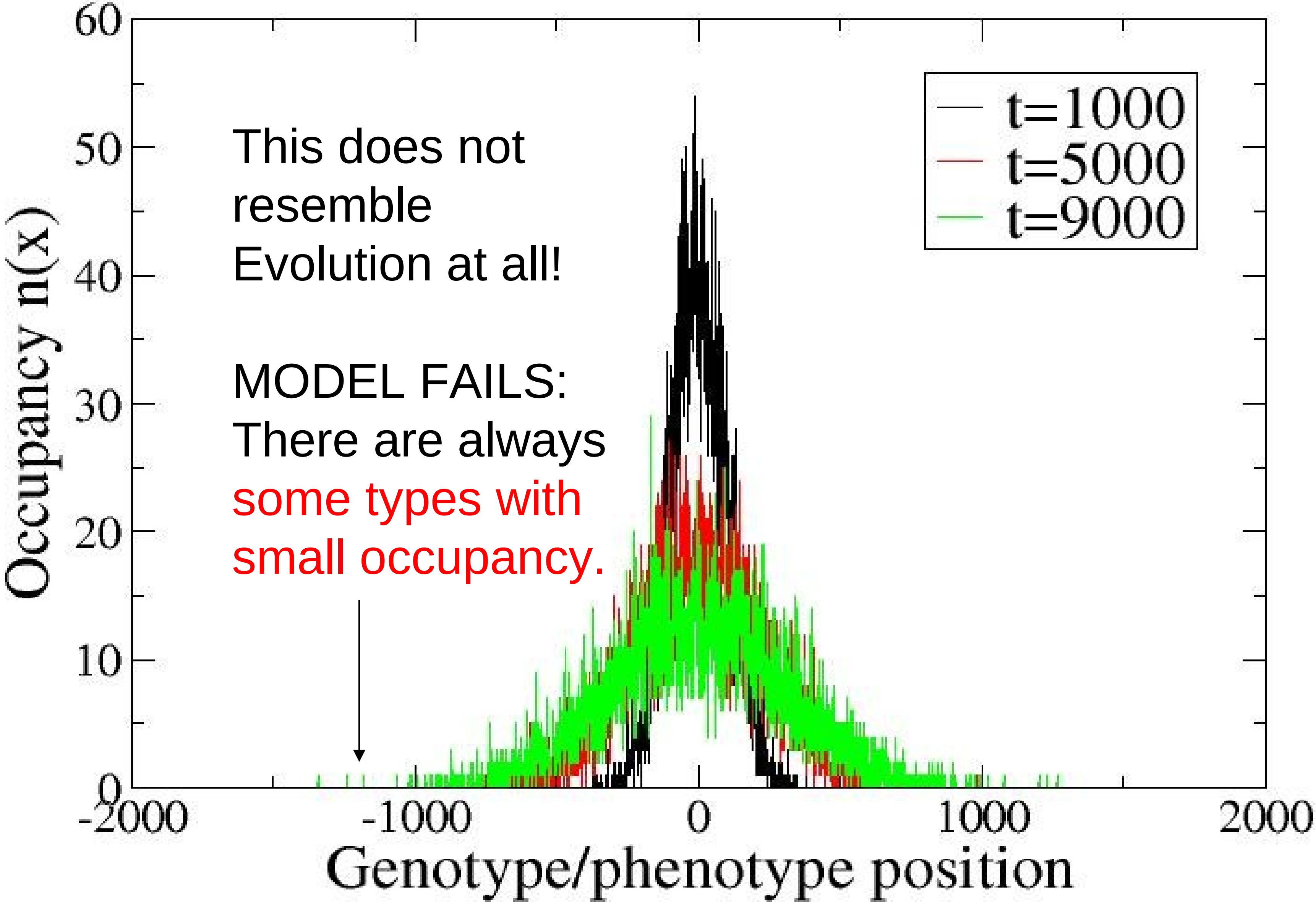
  - Expect this to be valid when N large?

- This becomes:

$$\langle n_a(t+1) - n_a(t) \rangle = \frac{p_m}{2N}\left[n_{a+1}(t) + n_{a-1}(t) - 2n_a(t) \right]$$

- This is just the diffusion of N particles!

Diffusion of 10000 particles



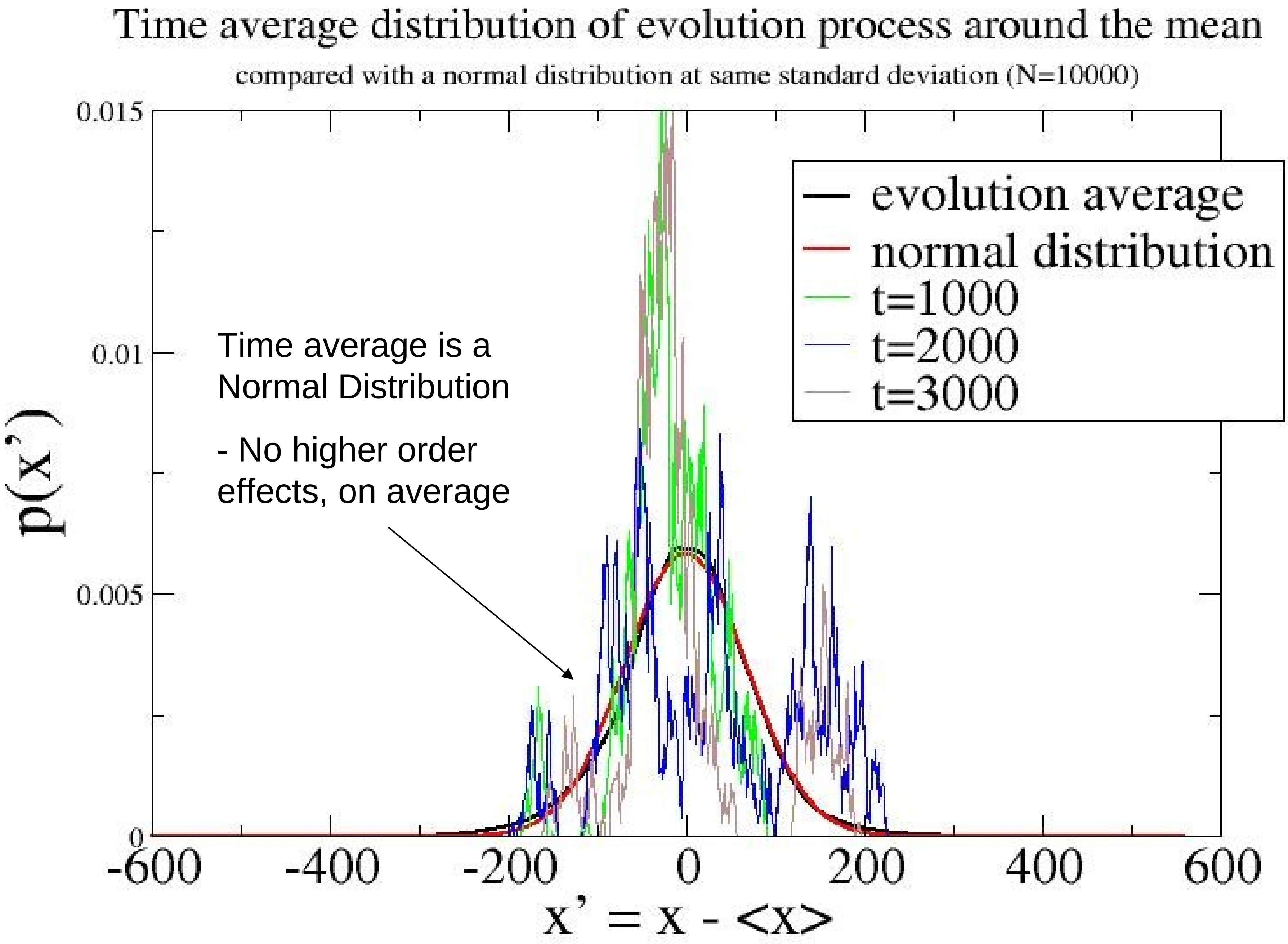
Solution

- Simplify the model – consider only first two moments of the distribution
- Peak is a Gaussian distribution of area *1* with dynamic mean μ and width w.

- Select death location x
- Select birth location y, mutated by 1 with probability P_m
- Remove $1/N$ from death location and place at birth location
- Update μ and w

Solution method

- Write down equations for the change in the mean and the variance of the peak position μ and the width w
- Take continuous limit to obtain Stochastic Differential Equations
- Solve!
- This works because the distribution is normal only when *averaged over time*, measured *relative* to the *current mean position*


Time average distribution of evolution process around the mean
compared with a normal distribution at same standard deviation (N=10000)
Time average is a Normal Distribution
- No higher order effects, on average
evolution average
normal distribution
t=1000
t=2000
t=3000
p(x')
x' = x - <x>
0.015
0.01
0.005
0
-600
-400
-200
0
200
400
600

Solving for the width

Mutation distance

Generation time

$$d(w^2) = \left(p^* - \frac{2w^2}{N} \right) dT + \frac{2w^2}{\sqrt{N}} dW$$

dW is Random, mean 0

Change in variance (in a timestep) = Deterministic part + Noise part

Solution at steady state:

$$p(w)dw = \frac{(Np_m)^2}{2w^5} e^{\frac{Np_m}{2w^2}} dw$$

Power-law decay at large w

Neutral Clustering results

- Mean width: $\langle w \rangle = \sqrt{\dfrac{N p_m \pi}{8}}$

Fluctuations in w also ~ $N^{0.5}$

- Position: $\langle x \rangle_{\text{RMS}} = \sqrt{T(p_m + w^2)}$ $\sqrt{\dfrac{p_m T}{2}}$

With time in generations... $\langle x \rangle_{RMS}$ is independent of N !

- Compare with diffusion:

$$\langle x \rangle_{\text{RMS}} = \sqrt{\frac{p_m T}{N}} \qquad \langle w \rangle_{\text{RMS}} = \sqrt{\frac{p_m T}{N}}$$

- Diffusion “does nothing” in infinite populations... evolution does “more”!

Neutral evolution results

- Selection produces a stable peak, neutrality produces an *unstable* peak.
- Characteristic peak width, but large fluctuations *(multiple clusters).*
- Peak centre diffuses *independently* of population size!
- Provides null model for expected phenotype distributions, *non-trivial* distributions are probable.

Reference

Lawson and Jensen:
"Neutral Evolution as Diffusion in phenotype space: reproduction with mutation but without selection"
*Physics Review Letters, March 07 (**98**, 098102)*
www.arxiv.org/abs/q-bio/0609009

Thank you for your attention!

Diversity in models

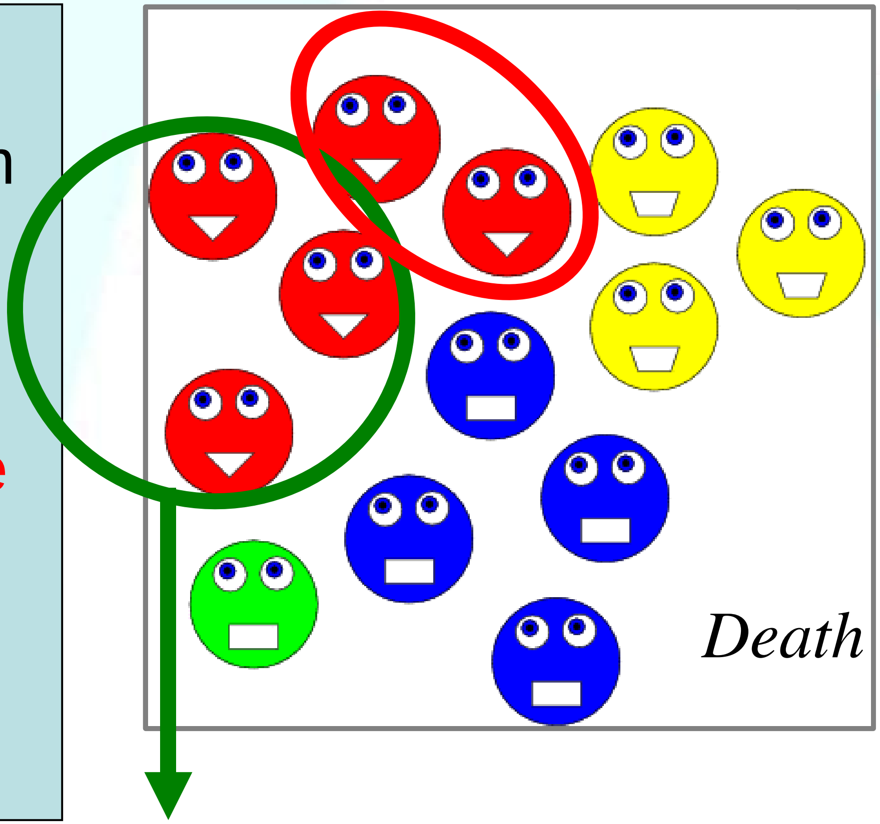
- We expect a “species”:
  - To be “different enough” from other species.
  - To be constant in time. An individual of a species today is comparable with an individual of that species in the past.
- A model discussing species diversity must accurately represent:
  - Species Abundance Distribution
  - Species Lifetime Distribution
  - Species Area Relation
  - etc....

Updated ecological model

- Consider N individuals each labeled by species:

TIMESTEP:

- Pick an individual (from N) and mark it to die.
- Pick an individual (from N) and with probability p_a a proportion speciate allopatrically.
- Kill the marked individual.



Mutate proportion of population allopatrically

How long do species survive?

Cutoff time determined by probability of mutation