

Some implications of neutral evolution for ecology

Daniel Lawson

Bioinformatics and Statistics Scotland

Work with

Henrik Jeldtoft Jensen,
Imperial College London

Phenotype Distribution

Proportion of individuals

Distribution is (often) **Normal**

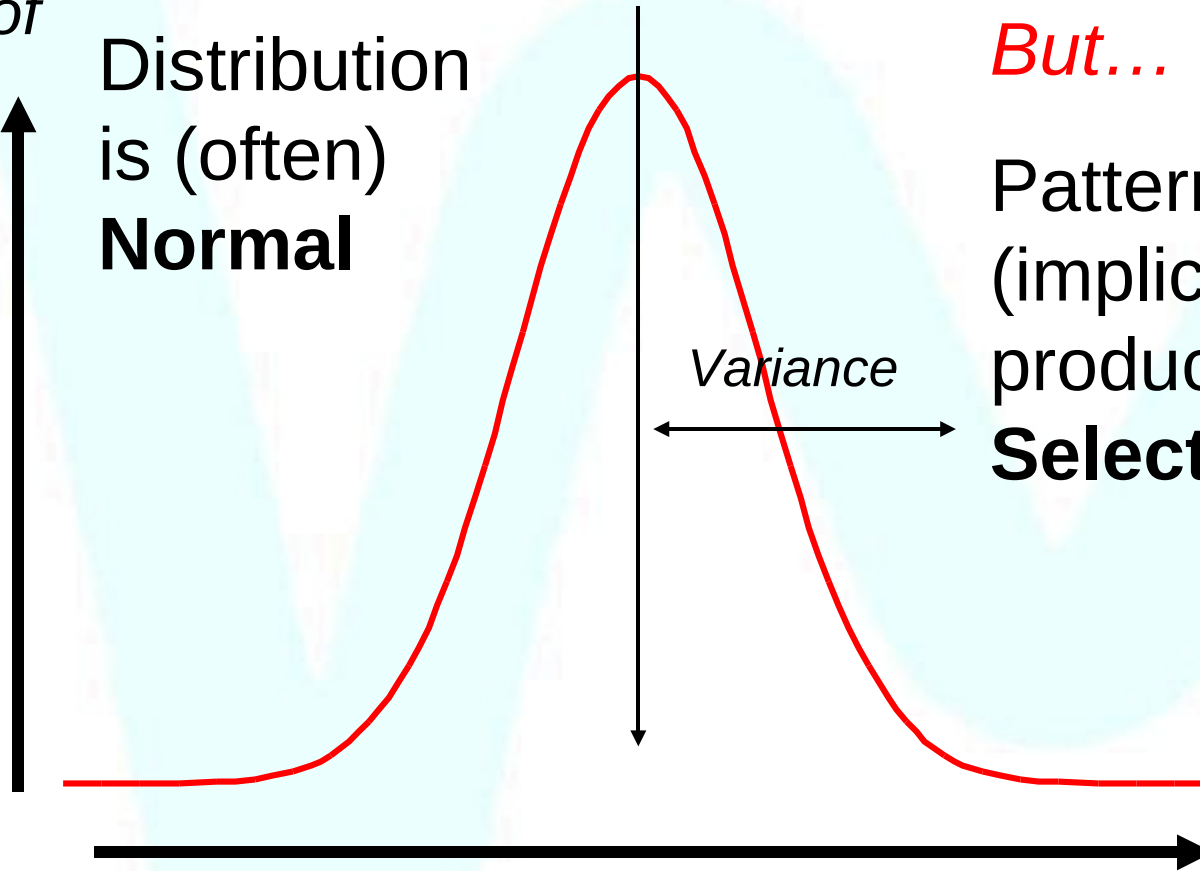
Mean

But...

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

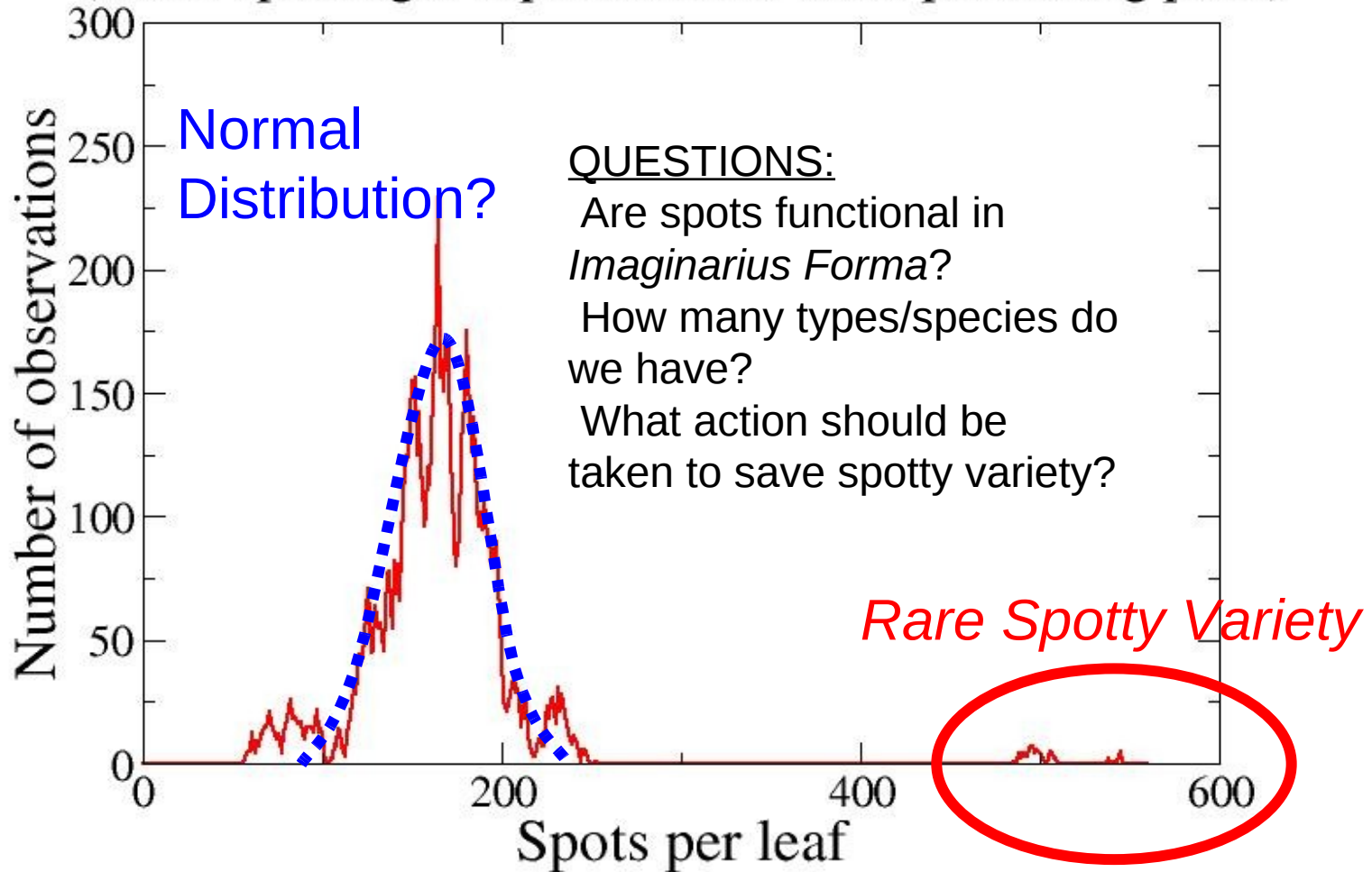
Variance

Observable (Height, weight, etc)



Test Problem

Observations of number of spots per leaf of *Imaginarium Forma*
(Made up thought experiment for a self pollinating plant)

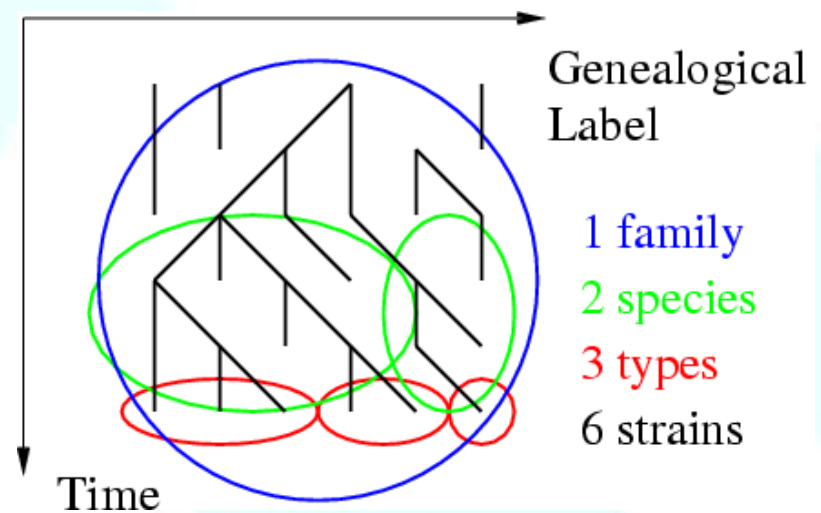


Defining Diversity

- 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

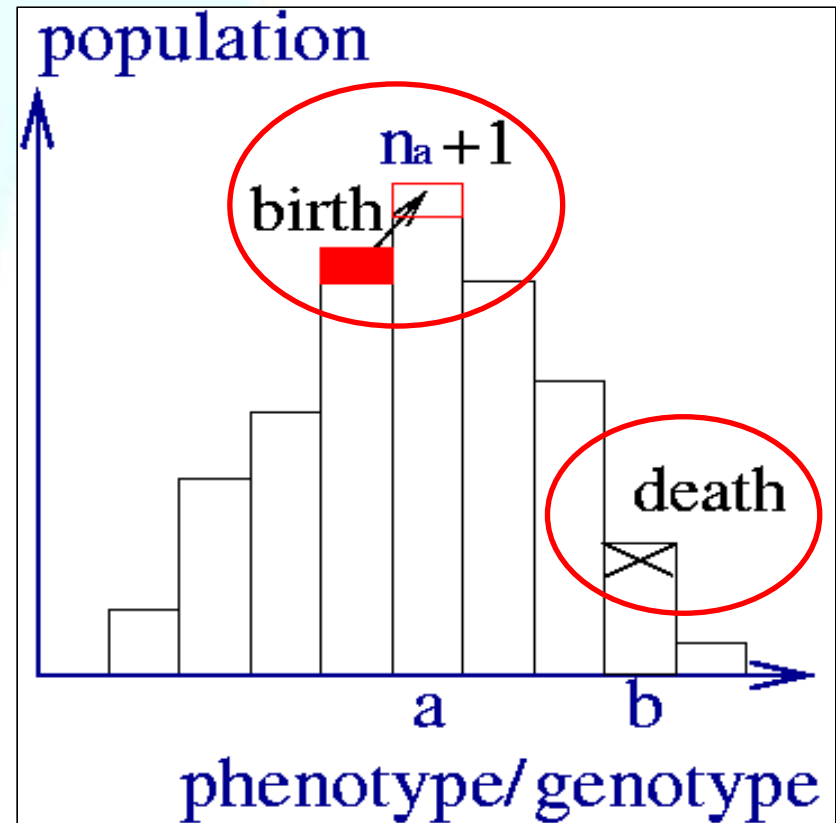
A neutral evolution model

- Consider N individuals each labeled by phenotype position:

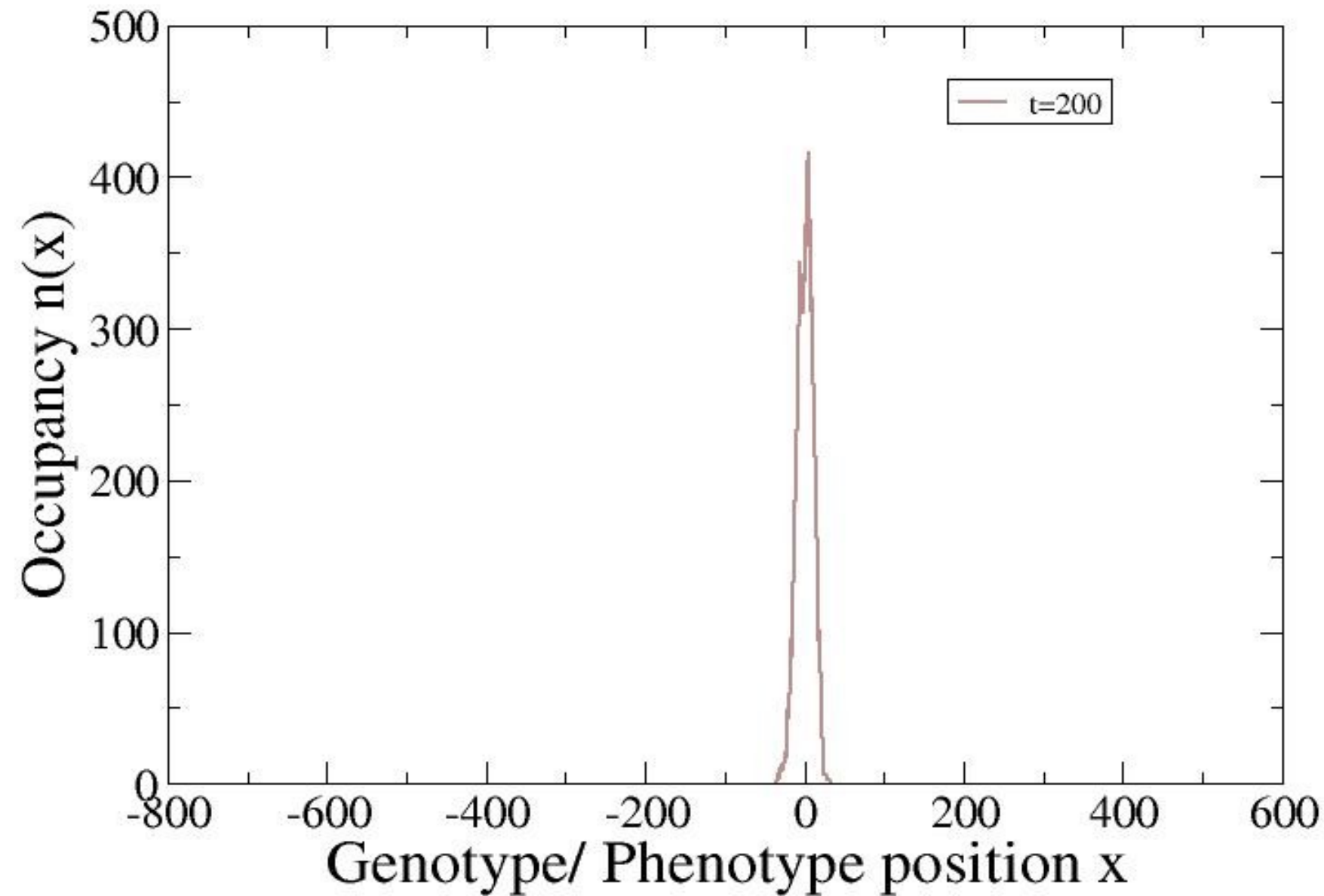
TIMESTEP:

- 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.

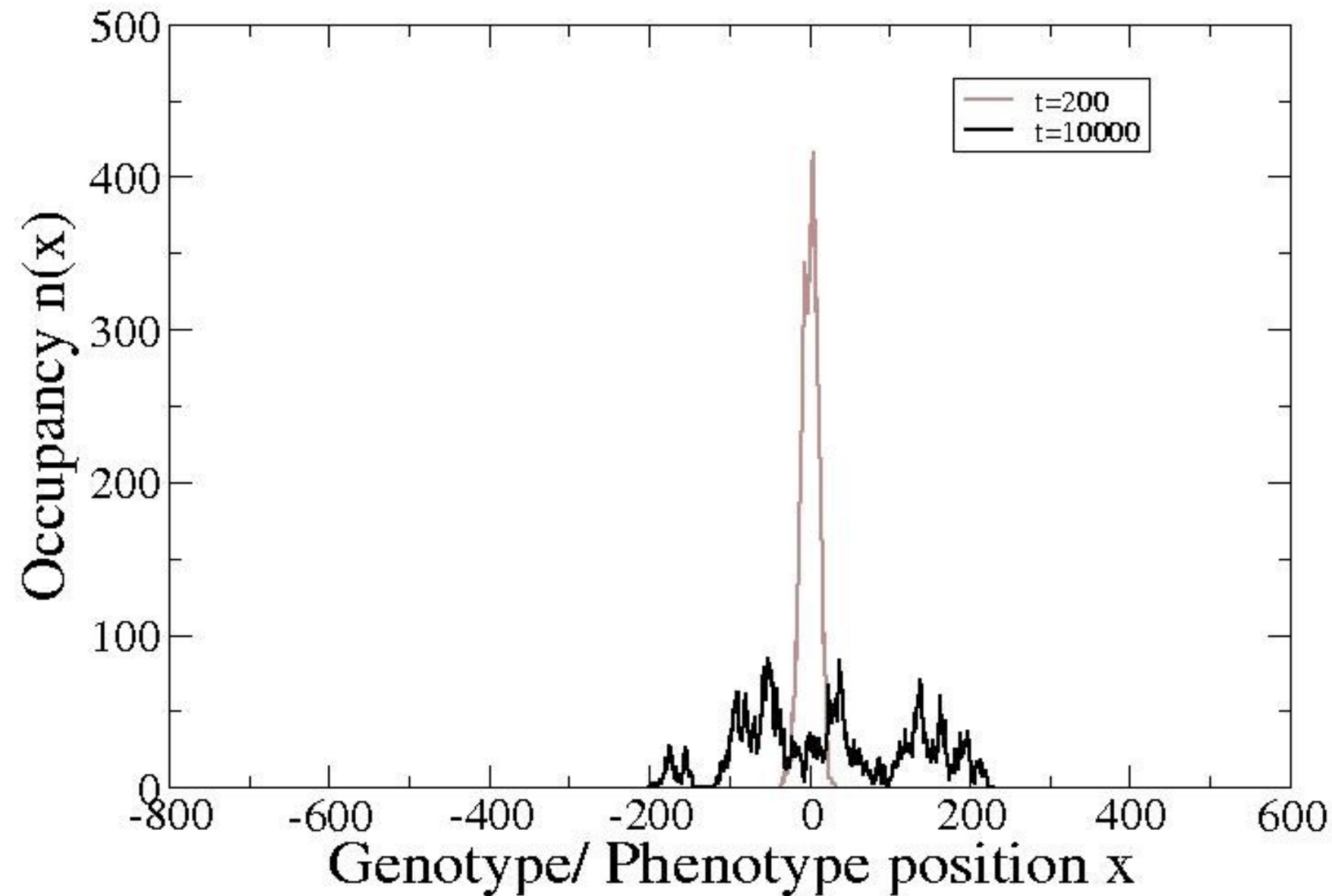
We follow a single neutrally evolving phenotype



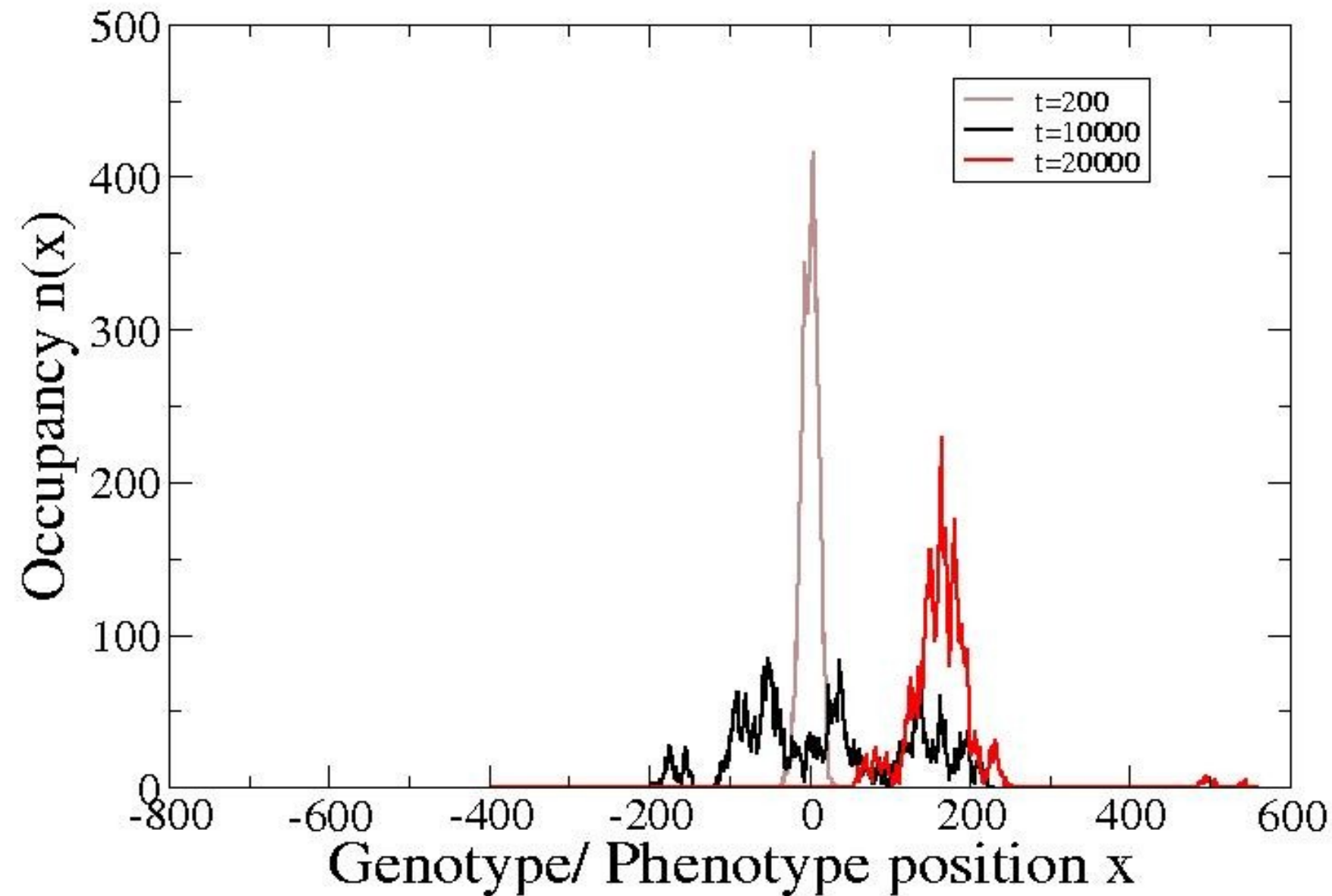
Evolution of 10000 particles



Evolution of 10000 particles

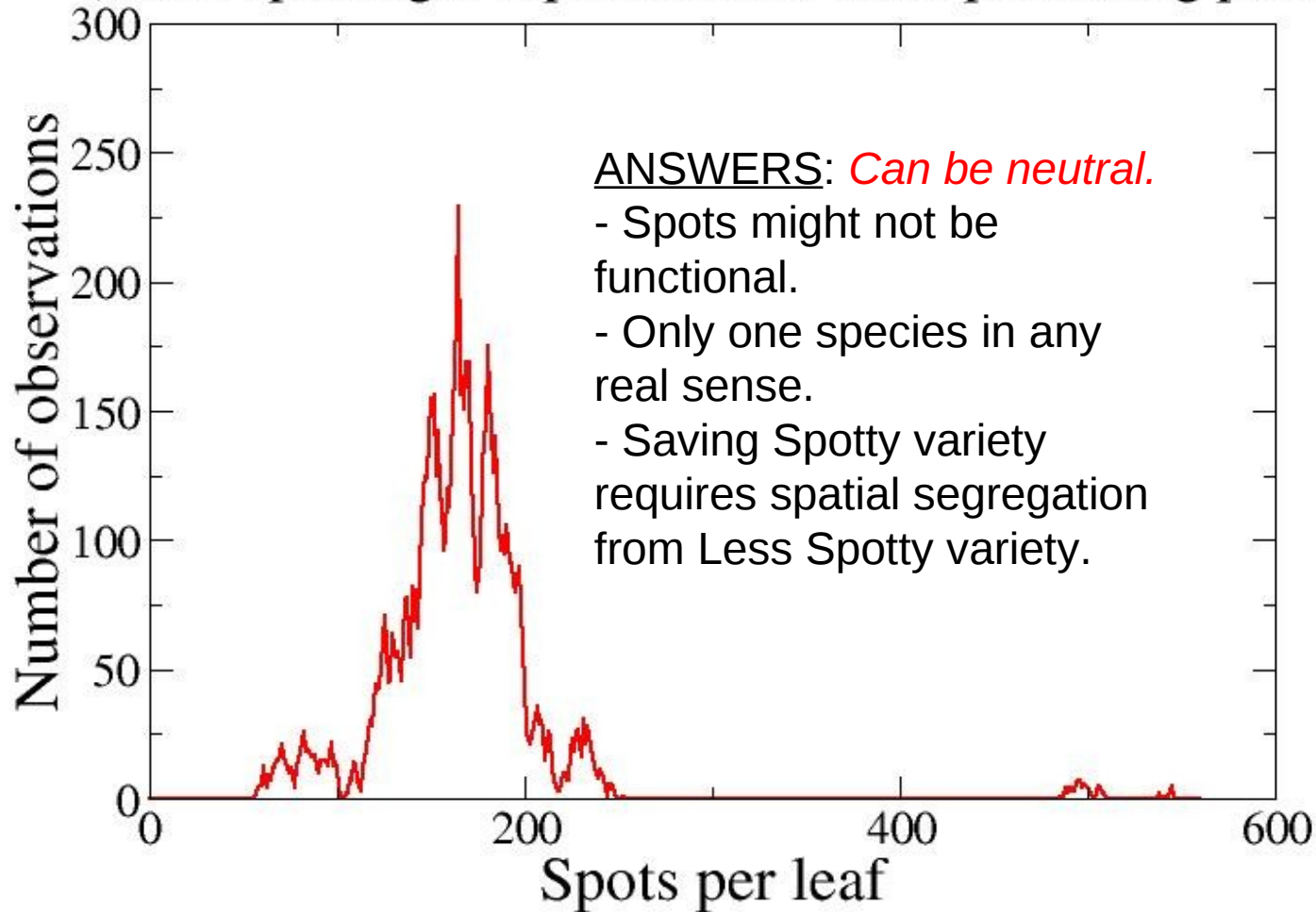


Evolution of 10000 particles



Test Problem

Observations of number of spots per leaf of *Imaginarium Forma*
(Made up thought experiment for a self pollinating plant)



Solution

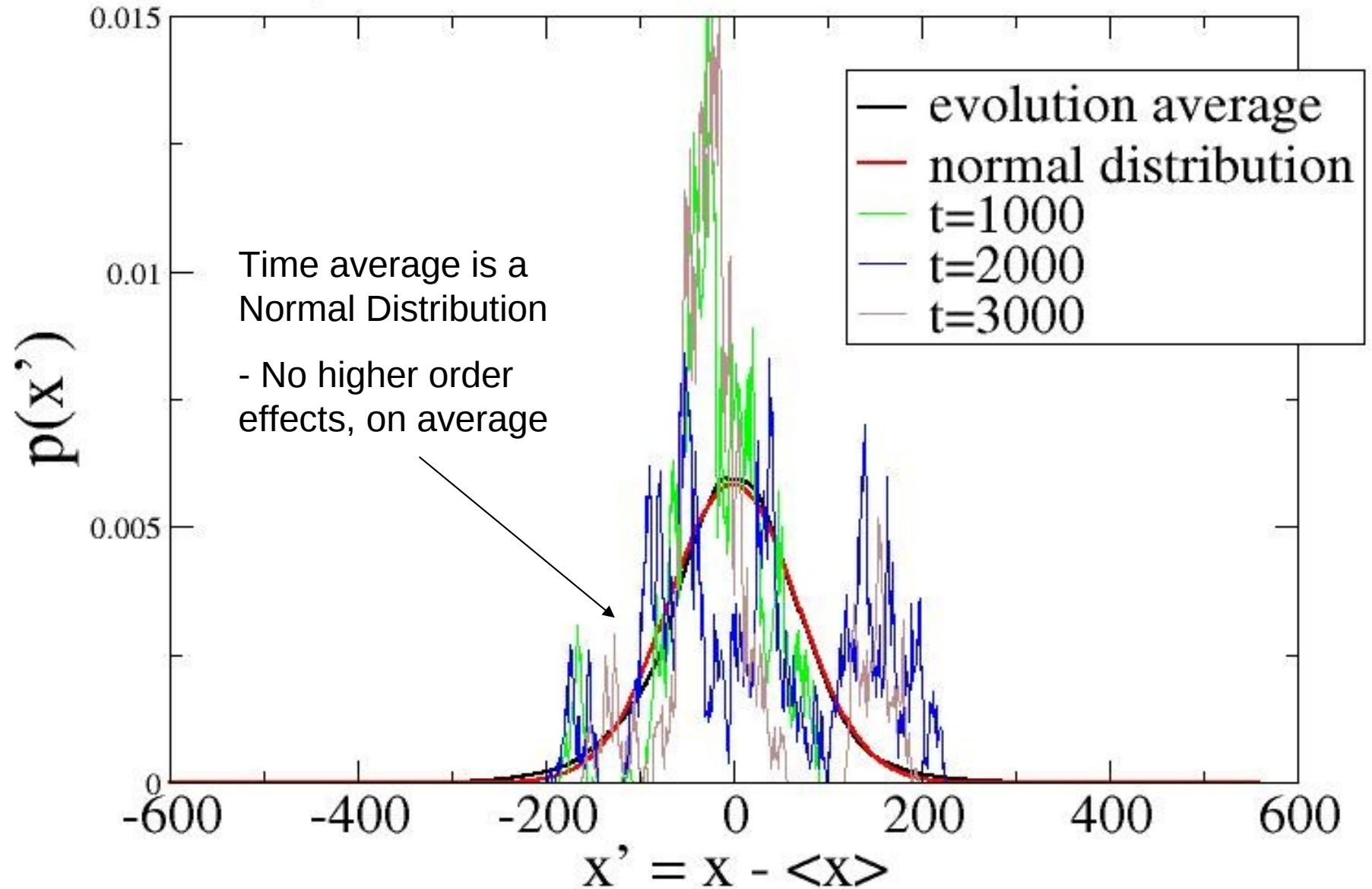
- Simplify the model – consider only first two moments of the distribution
- Peak is a Gaussian distribution of area 1 with dynamic mean μ and width w .

- 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 (N=10000)



Neutral Clustering results

- Mean width:

$$\langle w \rangle = \sqrt{\frac{N p_m \pi}{8}}$$

*Fluctuations in
w also $\sim N^{0.5}$*

- Position:

$$\langle x \rangle_{\text{RMS}} = \sqrt{T(p_m + w^2)} \quad \sqrt{\frac{p_m T}{2}}$$

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

Neutral evolution results

- Selection produces a stable peak, neutrality produces an *unstable* peak.
- Characteristic peak width, but large fluctuations (*multiple clusters*).
- Evolution speed *independent* of population size!
- (evolution) provides null model for expected (ecological) phenotype distributions: *non-trivial* distributions are probable.
- **Genotype** Distribution evolves similarly....
- As do **sexual** populations



Reference

Lawson and Jensen:

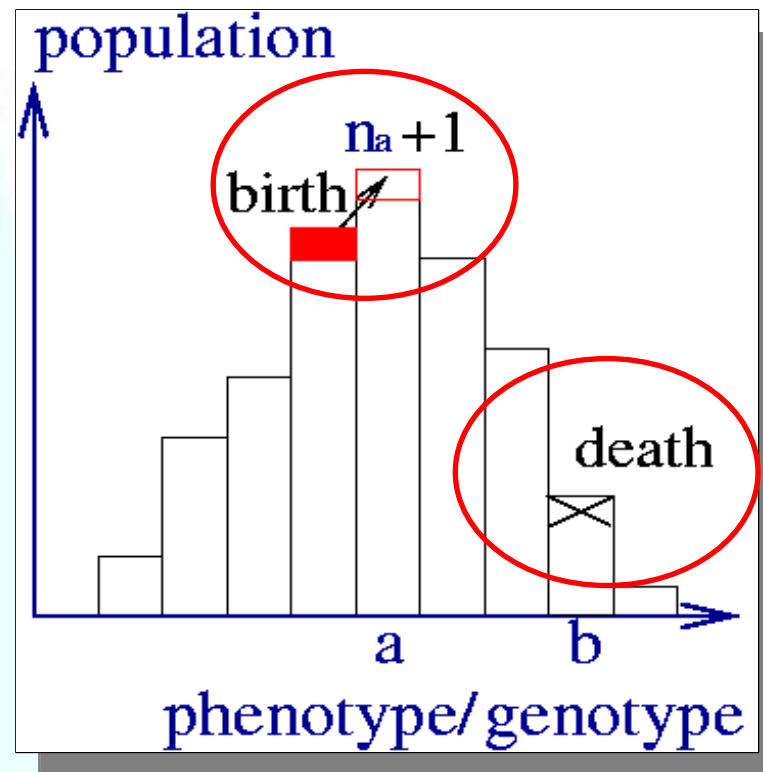
***“Neutral Evolution as Diffusion in phenotype space:
reproduction with mutation but without selection”***

Physics Review Letters, March 07 (98, 098102)

www.arxiv.org/abs/q-bio/0609009

Thank you for your attention!

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)

- Consider average behaviour:

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

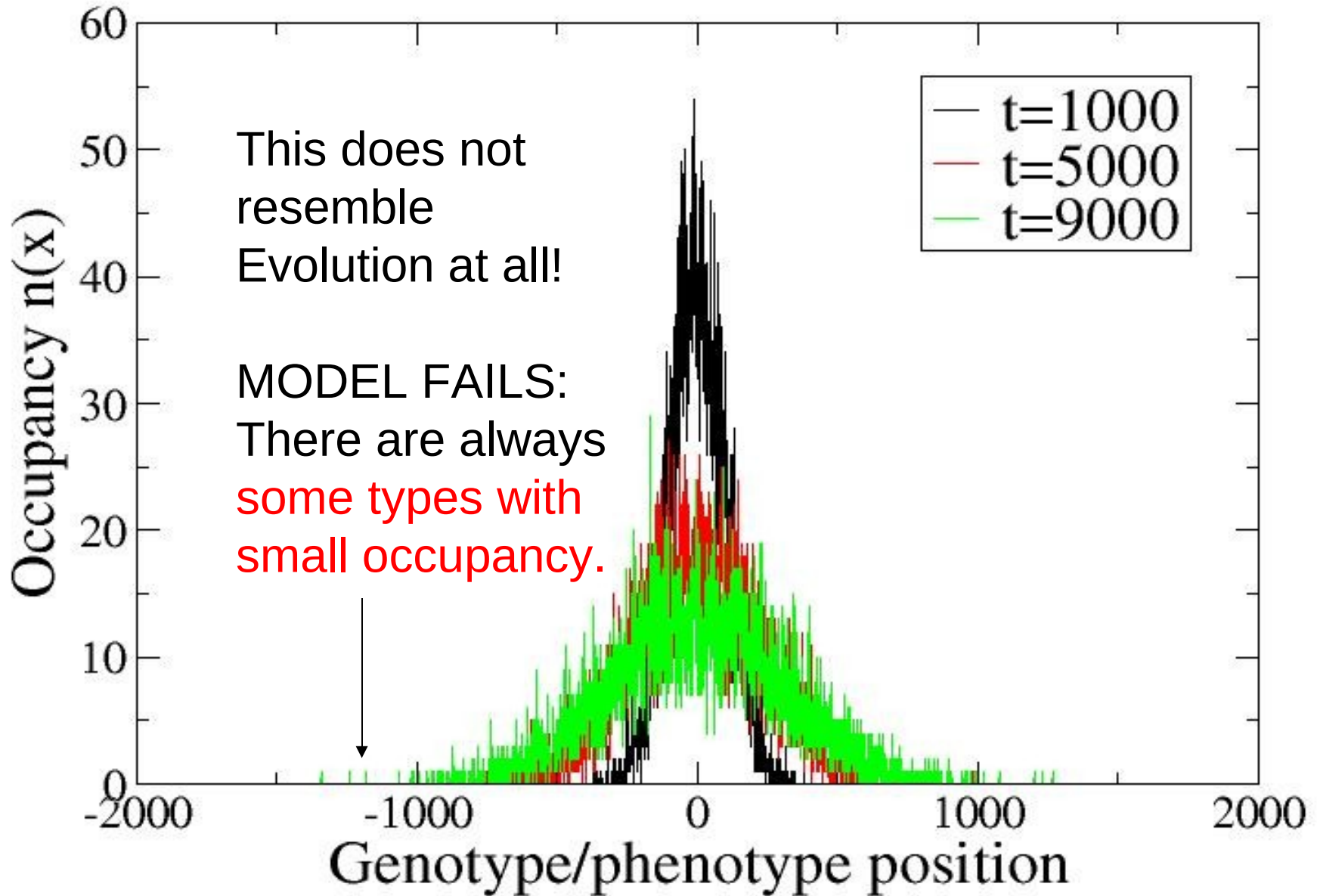
– Expect this to be valid when N large?

- This becomes:

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

- This is just the diffusion of N particles!

Diffusion of 10000 particles



Solving for the width

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

Mutation distance
Generation time

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