The implications of neutral evolution for neutral ecology

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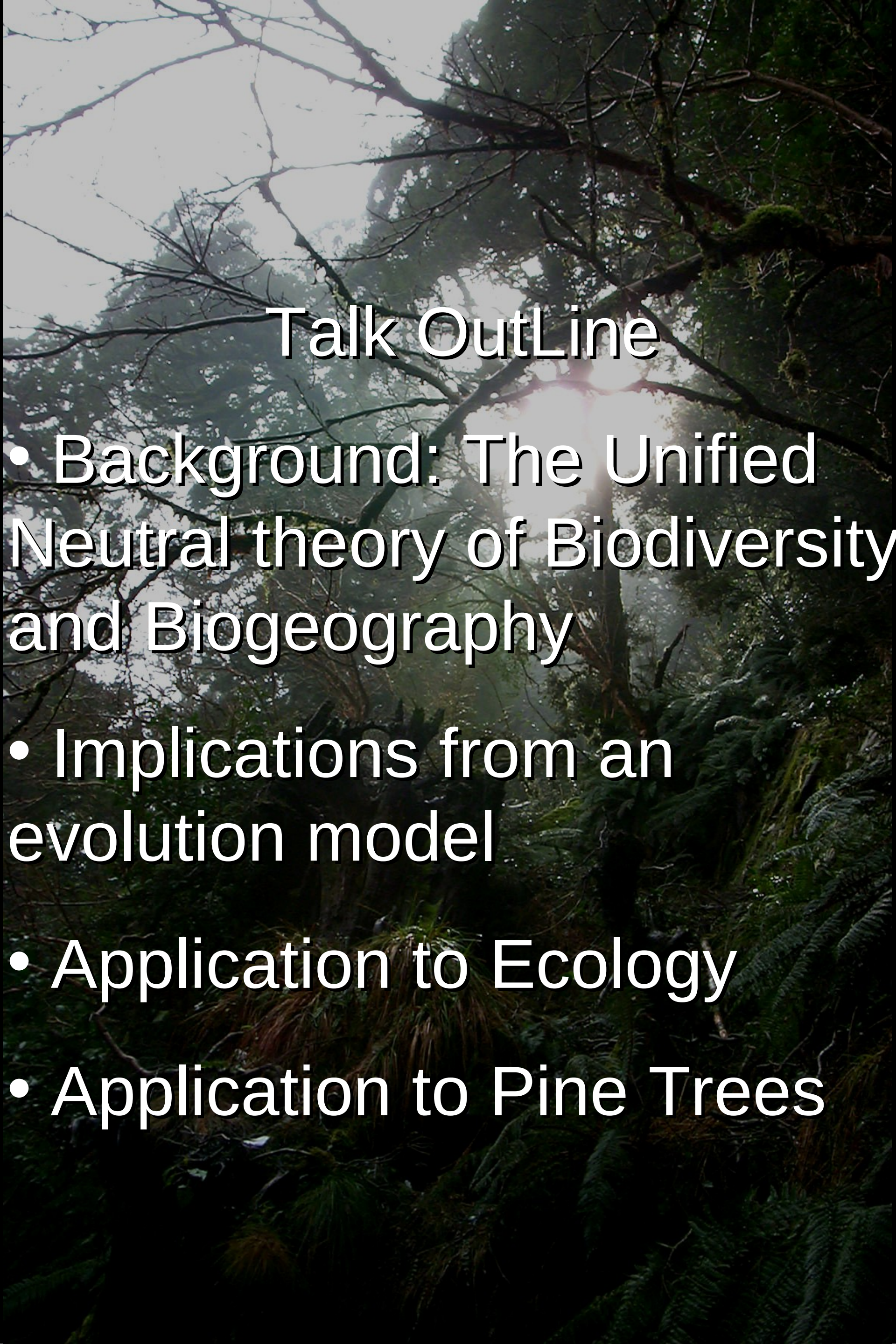
How is Diversity maintained?



Talk OutLine

- Background: The Unified Neutral theory of Biodiversity and Biogeography
- Implications from an evolution model
- Application to Ecology
- Application to Pine Trees

What is ecological neutrality?

All *individuals* are *equivalent.*

(with respect to their chances of having offspring in the next generation)

Probability of occurrence: “When Pigs Fly”

Why consider neutrality at all?

- Neutrality: theory of chance events.
- High observed diversities needed explaining, but no *general* theory.
- Evolution and ecology are inherently linked.
- Need a “null model” – minimum model that explains diversity.

The Neutral Model

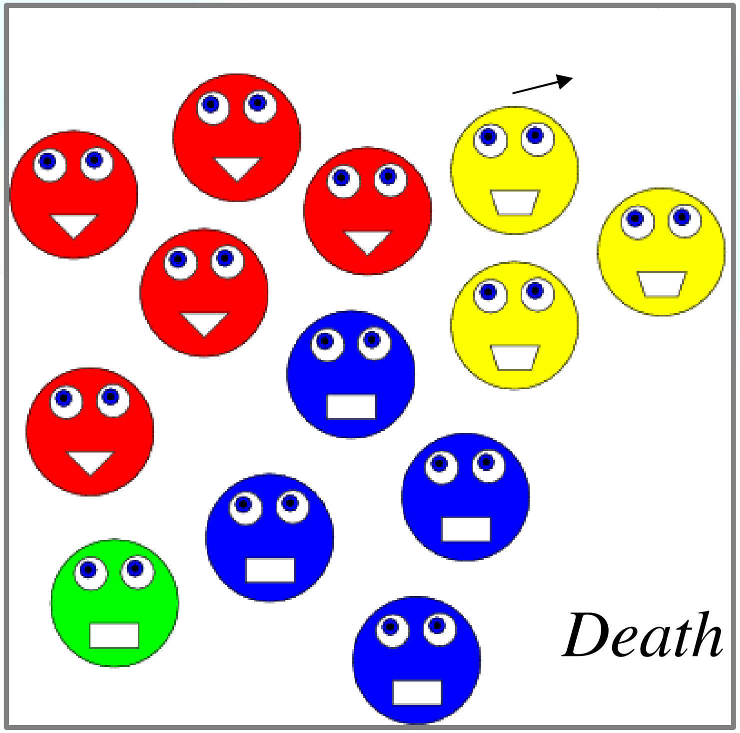
- Assume all individuals are 'equal'
    - Valid for Phenotypes without function
    - Genotype regions not coding for protein synthesis (12% of Human DNA is variable! *Redon et al. Nature. doi:10.1038/nature05329*)
  - Each individual has the same probability to die (p_k), or give birth (p_b), in a time step
    - For simplicity, assume the total population (N) has reached equilibrium ($p_k = p_b$)
- Mutations (and/or colonisation) can occur, reproduction is (a)sexual

The neutral 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.

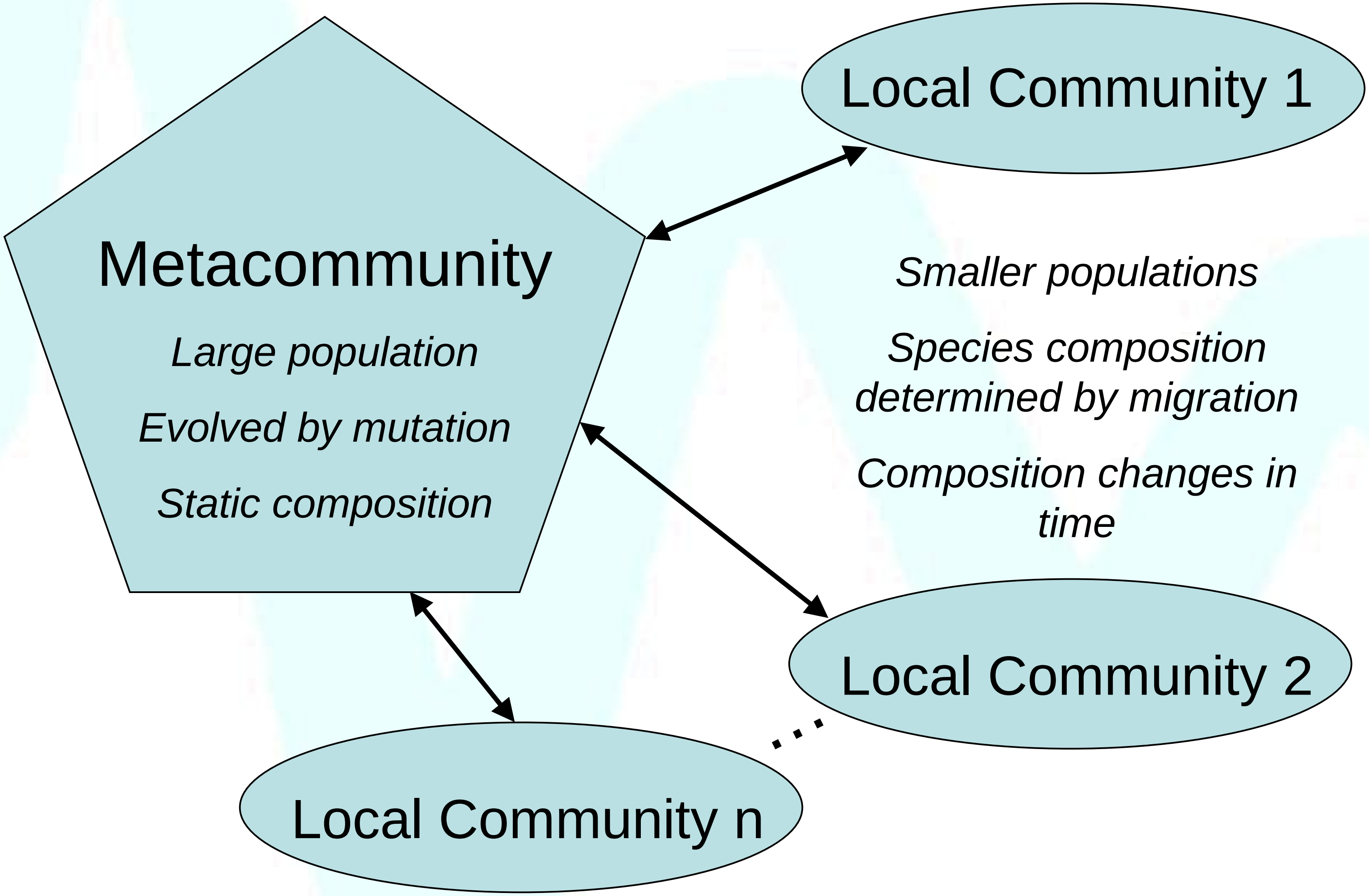


Same as a mutation…

Making the model work

- Common species are common at many sites - communities don’t exist in isolation
- Exchange individuals with a *metacommunity* of size $J_m >> N$
- Metacommunity composition changes much more slowly that local community

Full ecological model



Metacommunity

Large population

Evolved by mutation

Static composition

Local Community 1

Smaller populations

Species composition determined by migration

Composition changes in time

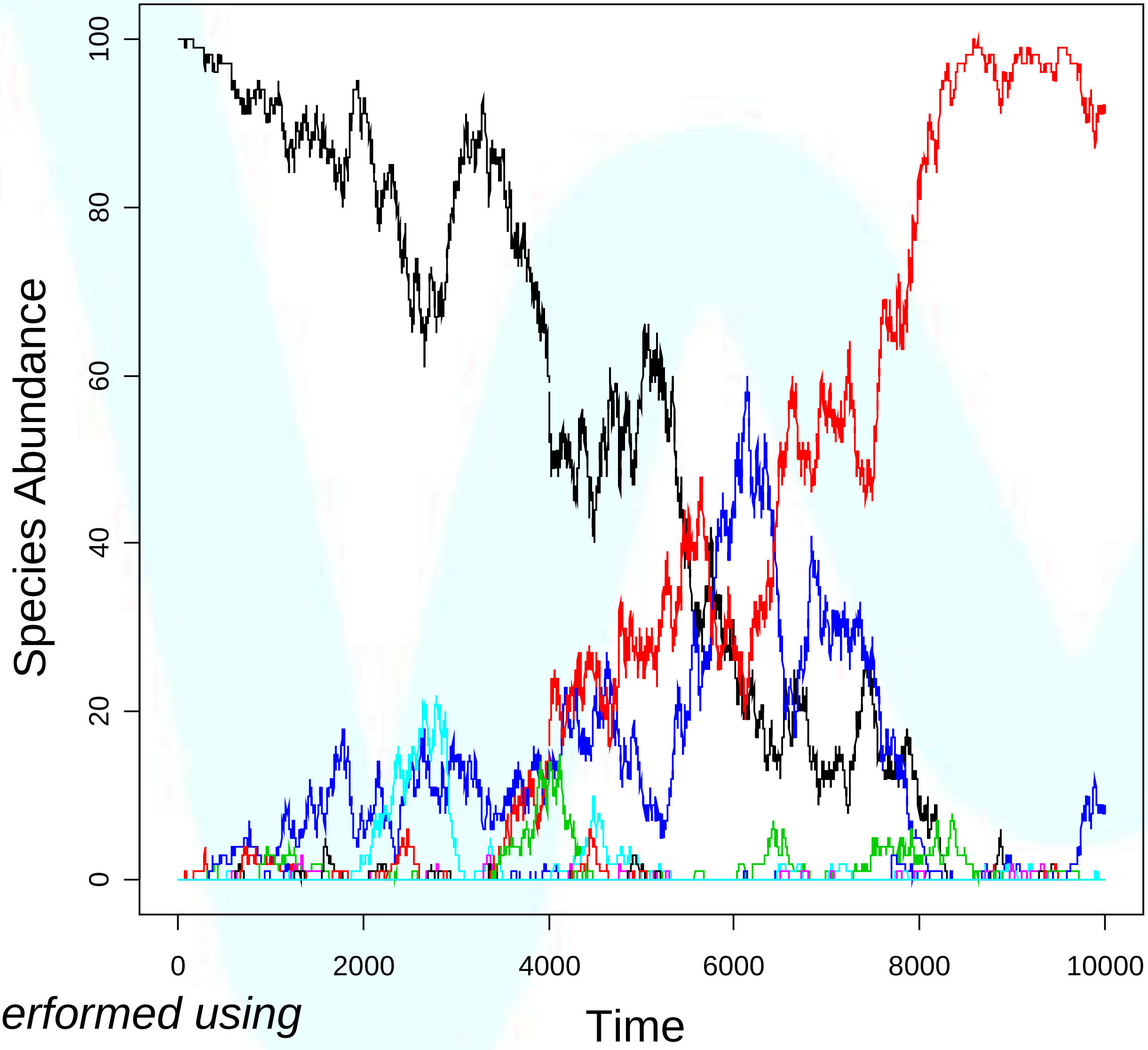
Local Community 2

Local Community n

Assumptions?

- Fixed population size
- All individuals are equivalent
- Individual life history is irrelevant
- There is a speciation “event”

Results of the model



$J_m = 100$

$P_m = 0.01$

Simulation performed using package UNTB in R

Initial results

- Explains Species Abundance Distributions
- But *Species Lifetimes* for abundant species in metacommunity is impossibly long!

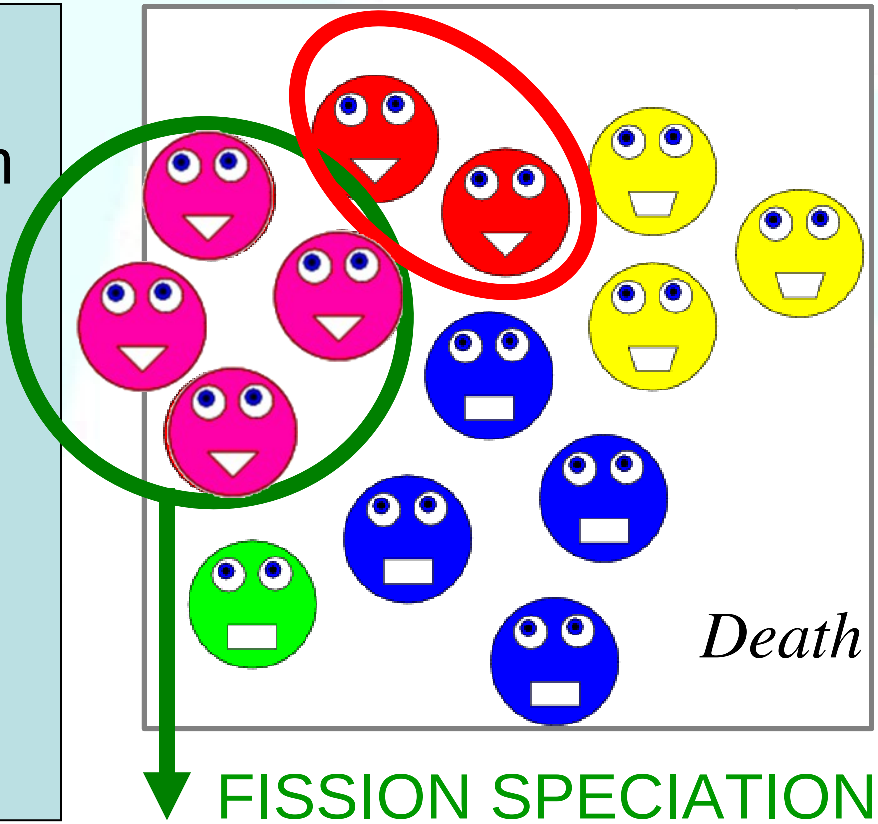
(longer than the *history of earth* for a common species to be replaced worldwide)

‘Fixed’ ecological model

- Consider N individuals each labeled by species:

TIMESTEP:

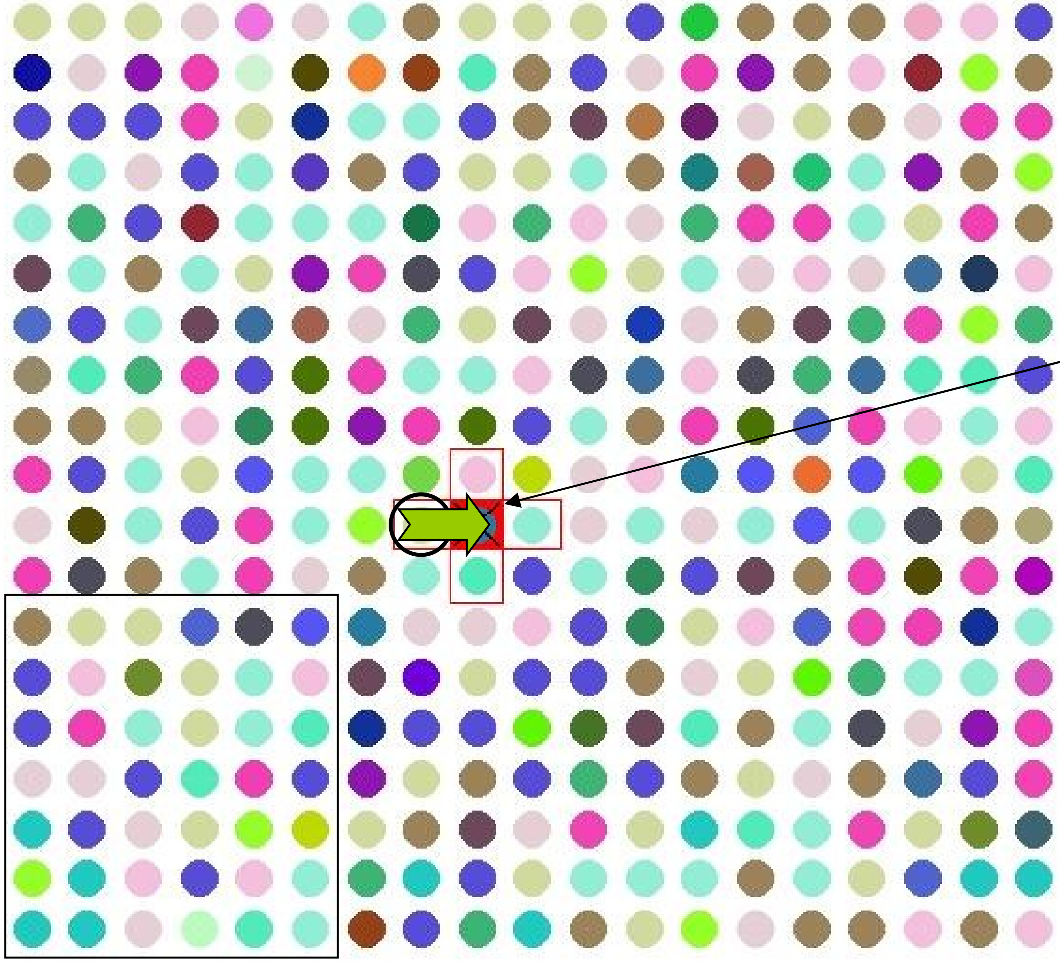
- Pick an individual (from N) and mark it to die.
- Pick an individual (from N) and copy. Prob. p_a a proportion speciate allopatrically.
- Kill the marked individual.



FISSION SPECIATION

Mutate proportion of population allopatrically

Spatial Version



Random Death

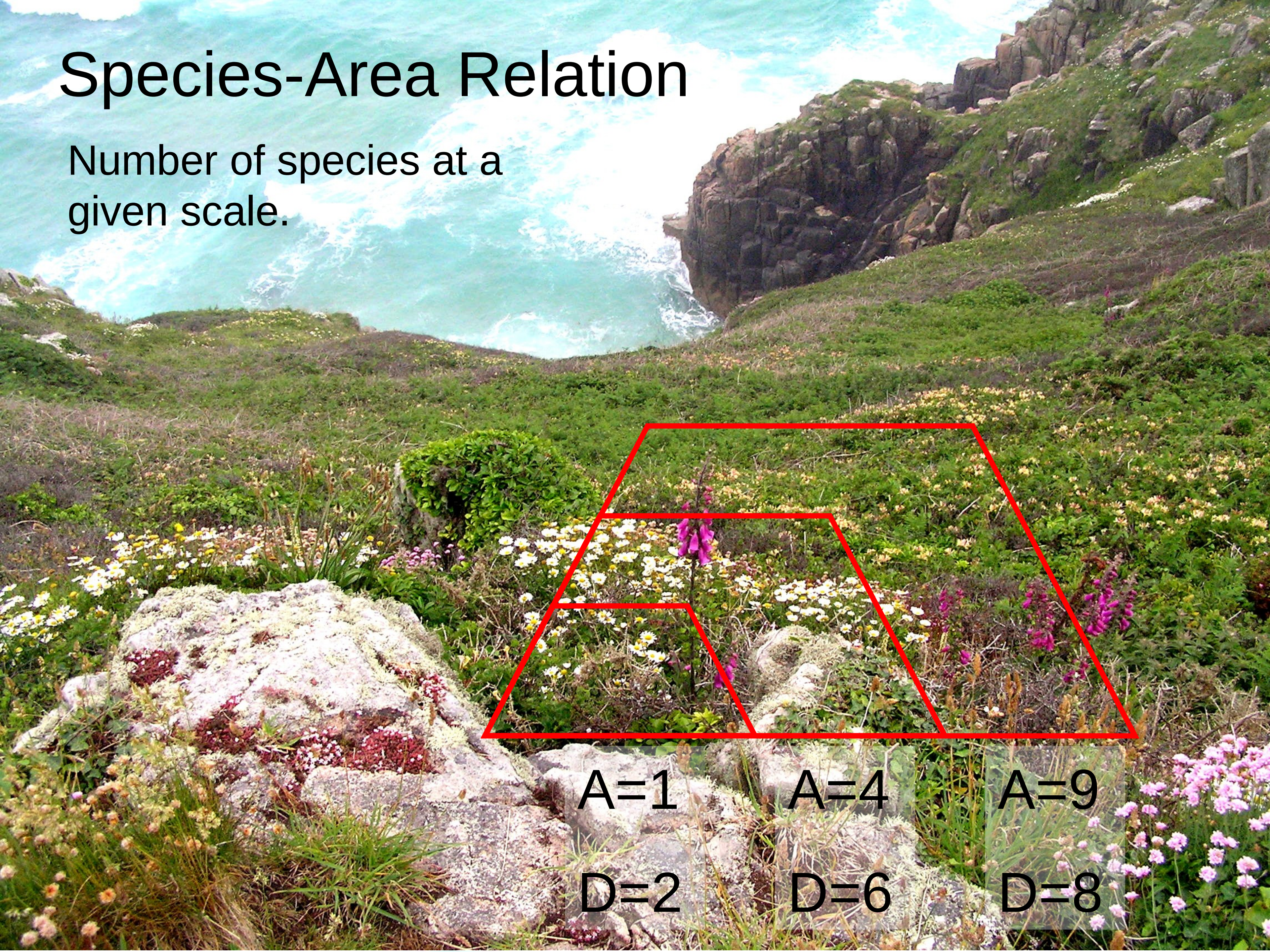
Local Reproduction

Local Community

- No need for metacommunity – space takes care of it!

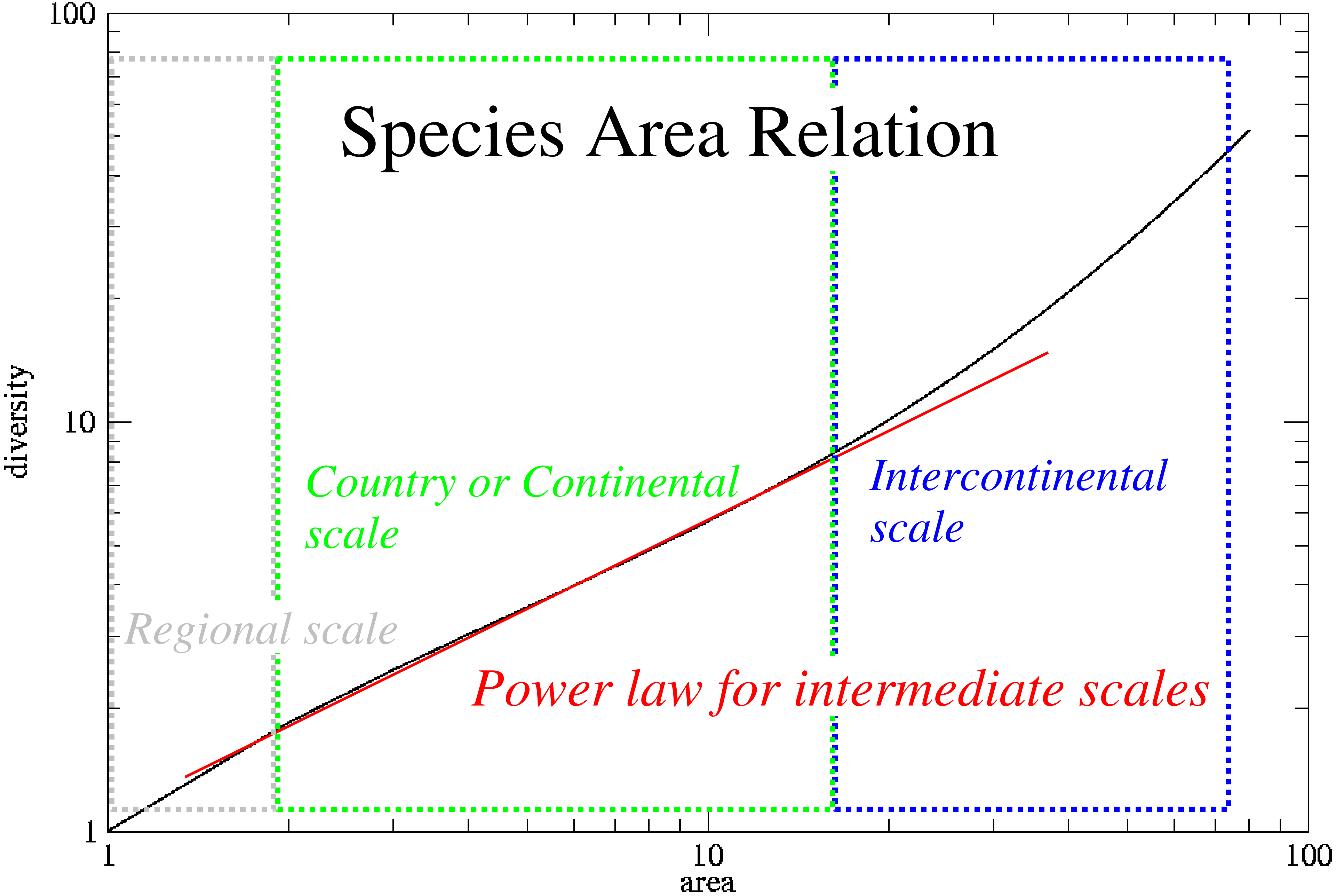
Species-Area Relation

Number of species at a given scale.



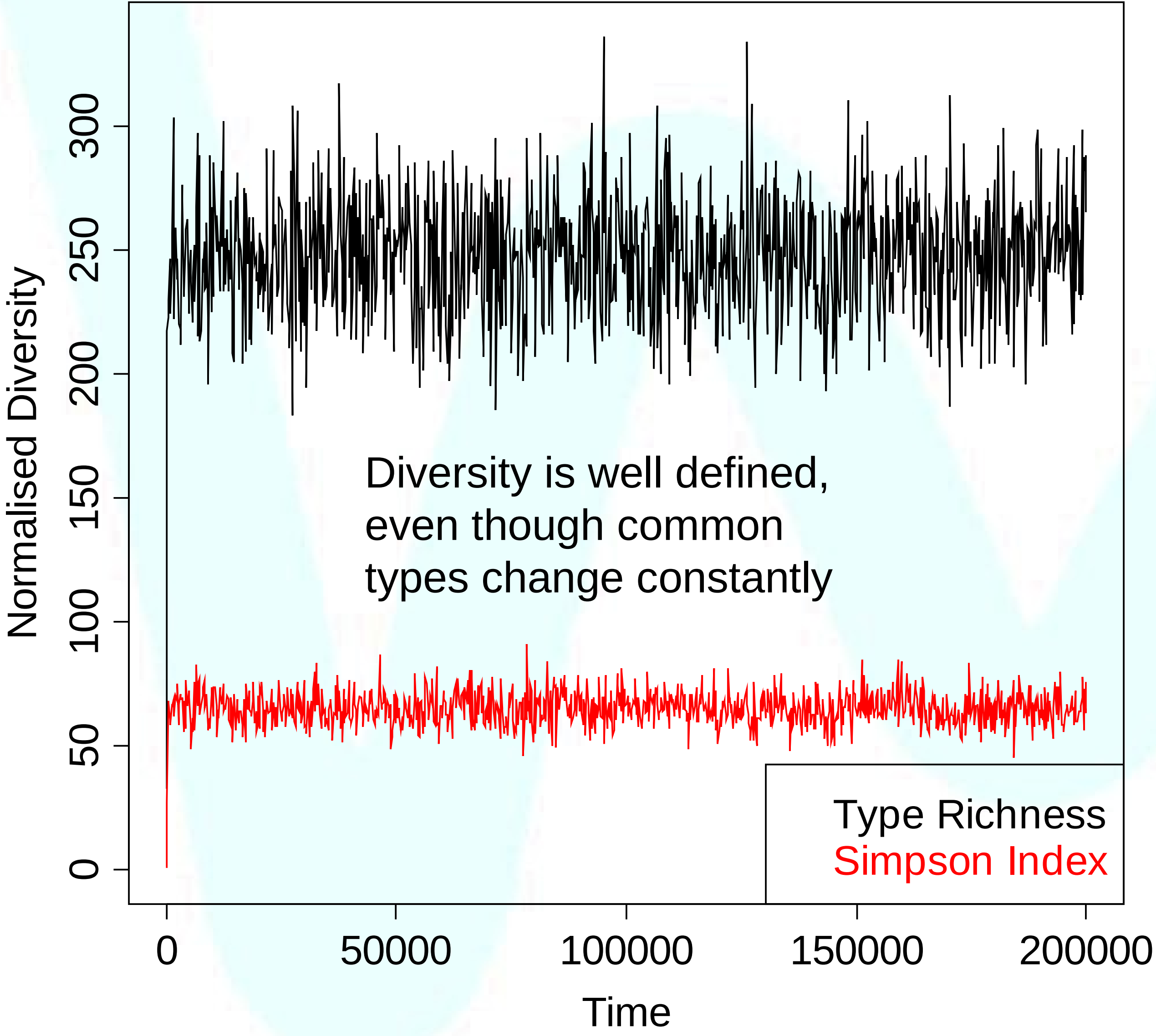
neutral model after 500 gens

correctly curved SAR



Diversity Time Series

(10000 individuals)



Results of extensions

- Explains the power law species area relation – and deviations from it
- Space is a satisfying explanation of metacommunity
- Although specific species change constantly, diversity is well defined
- Fission solves species lifetimes problem *(but what is it?)*

Success and failure

See: J Chave, Ecol. Lett. 2004

- Not good for birds (they move too much)
- Fits “non-persistent” fish species – but not dominant species
- Good fits to rainforests in Camaroon, Ecuador, Panama, Peru – poor on Barro Colorado Island
- Hard to distinguish from distributions of very specialised species in patchy terrain.

Success and failure

See: J Chave, Ecol. Lett. 2004

- Equivalence of individuals questionable (only 26% of species in one Rainforest).
- But per-capita averages of species often show equivalence.

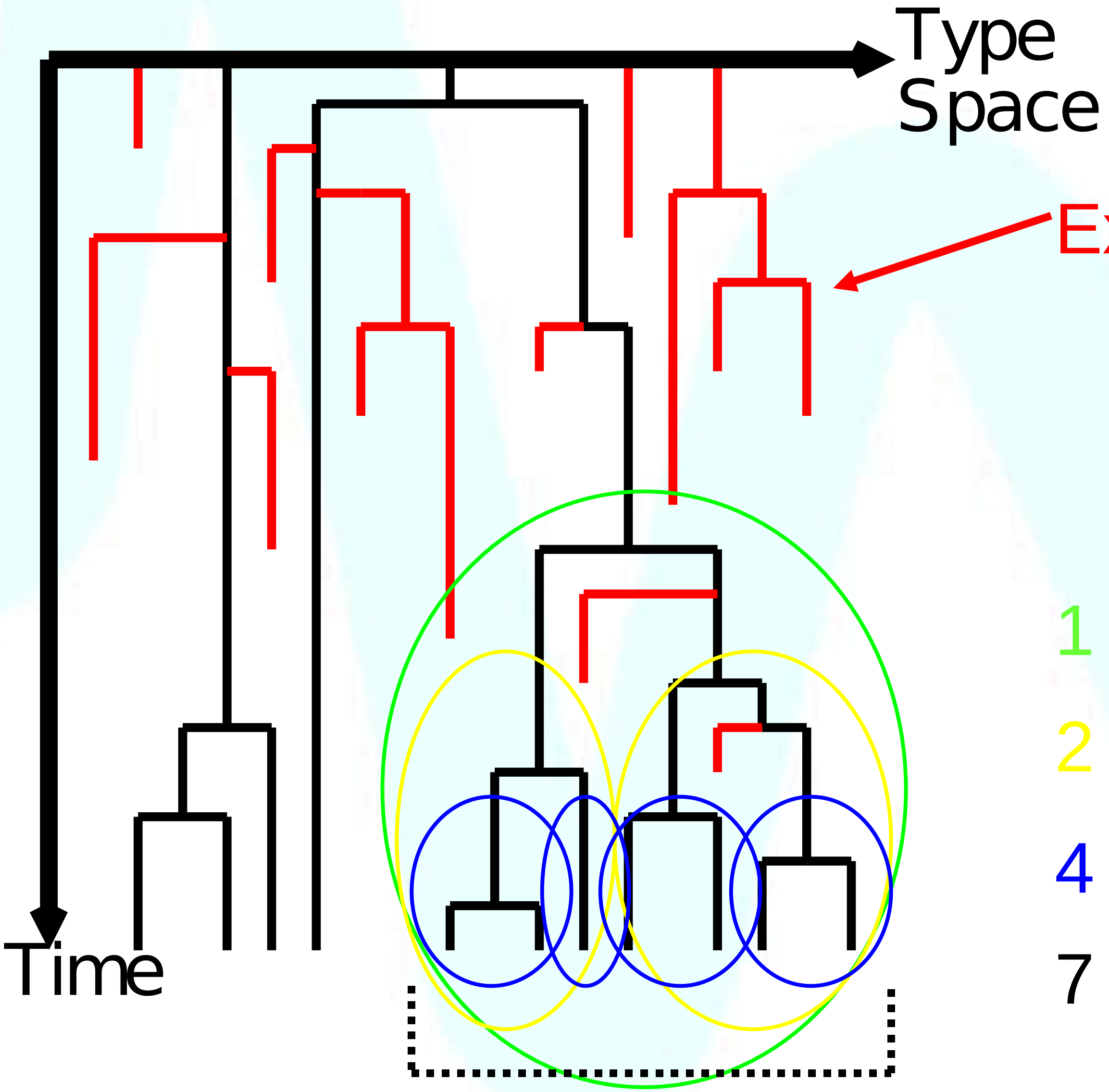
IN SHORT:

It works more often than you'd expect, but not always

Part 2: Observations.

- 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.
- But how different is “different enough”?
- How constant is constant?
- These concepts aren’t in the model!

The Lineage



Extinct Lineages

1 ‘family’

2 ‘species’

4 ‘types’

7 ‘lineages’

?

Diversity measures

- Measured diversity depends on diversity measure:
  - Species Richness:

    The "Number" of different types

$$D_{Raw} = \sum_{i} 1$$

Sum over species i

  - Simpson Diversity:

    Diversity measure accounting for different rarities

$$D_S = \frac{1}{\sum_{i} p_i^{\ 2}}$$

Proportion of species i from total population N

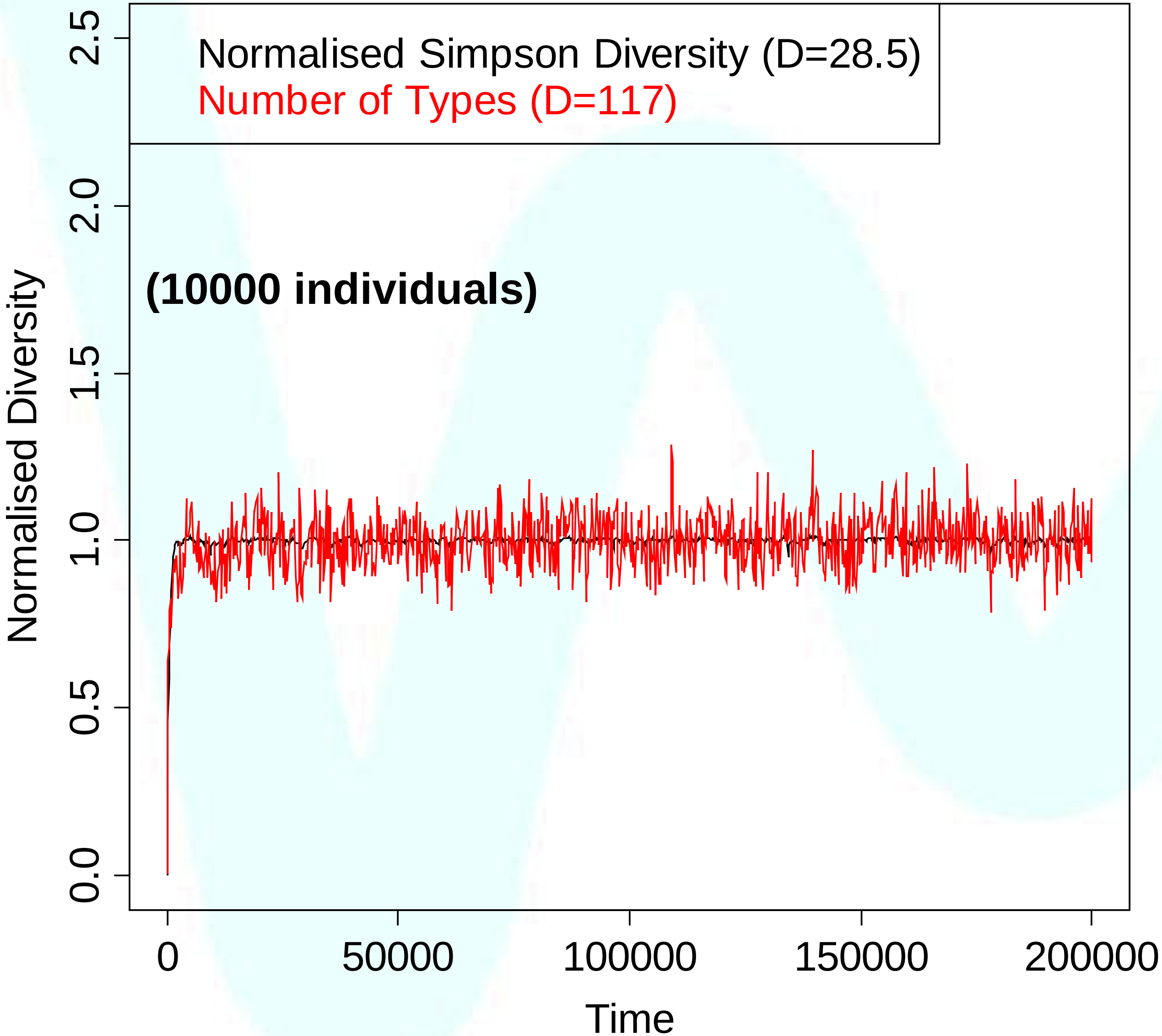
  - Rao Index:

    Diversity measure accounting for difference between types

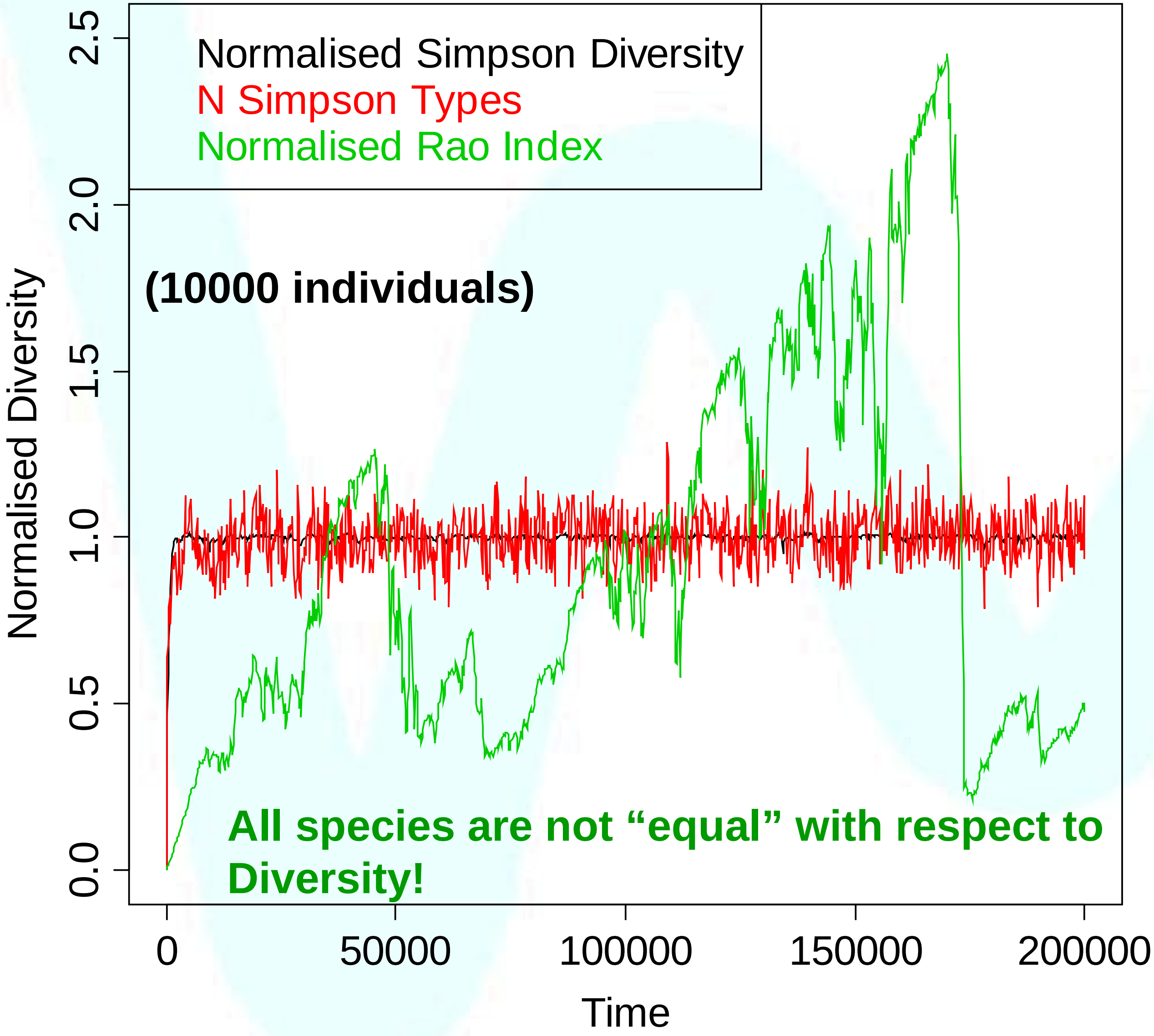
$$D_{Rau} = \sum_{i,j} d_{ij} \, p_i \, p_j$$

"Difference" between types

Diversity Time Series



Diversity Time Series

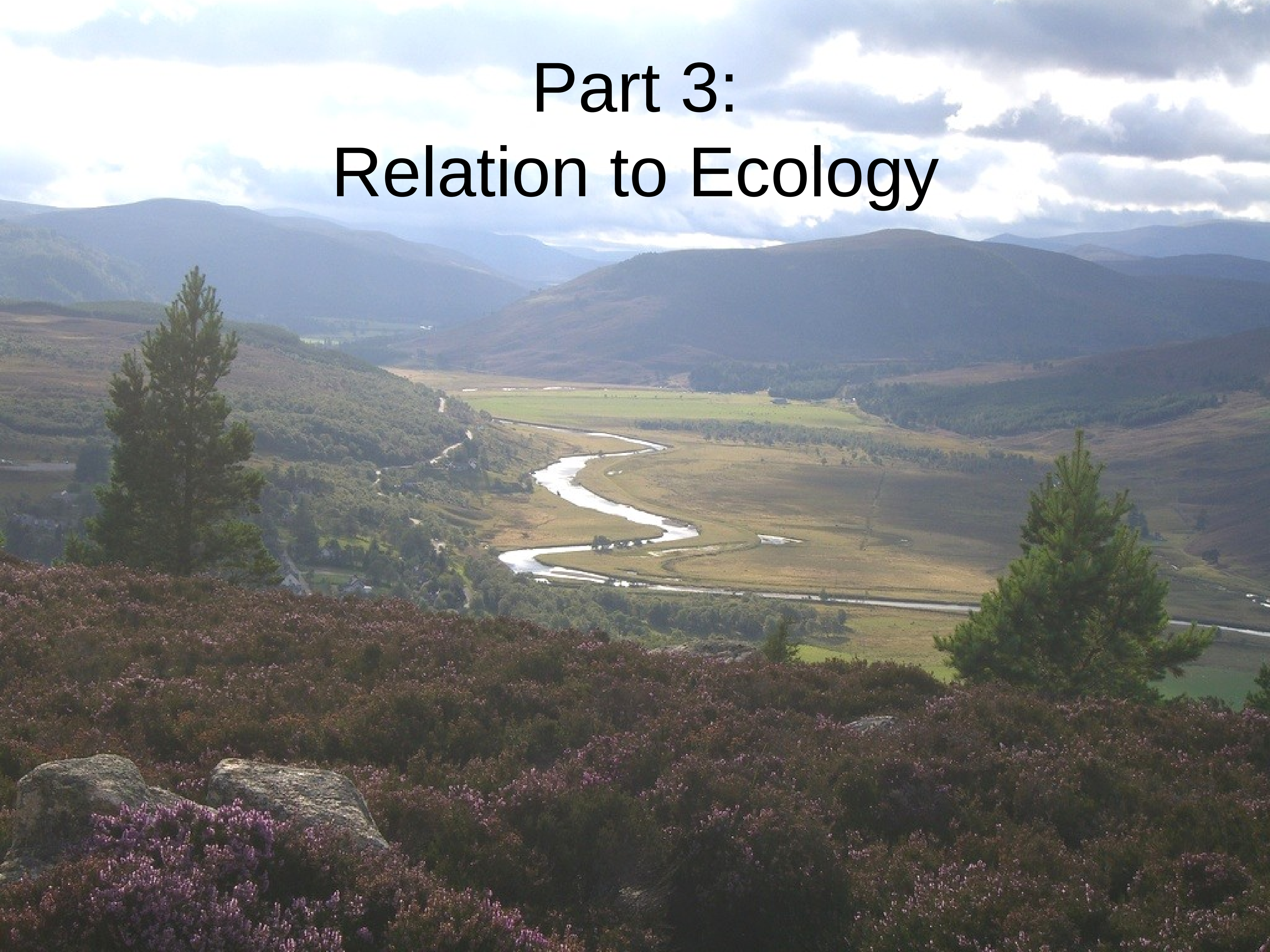


All species are not "equal" with respect to Diversity!

Assumptions?

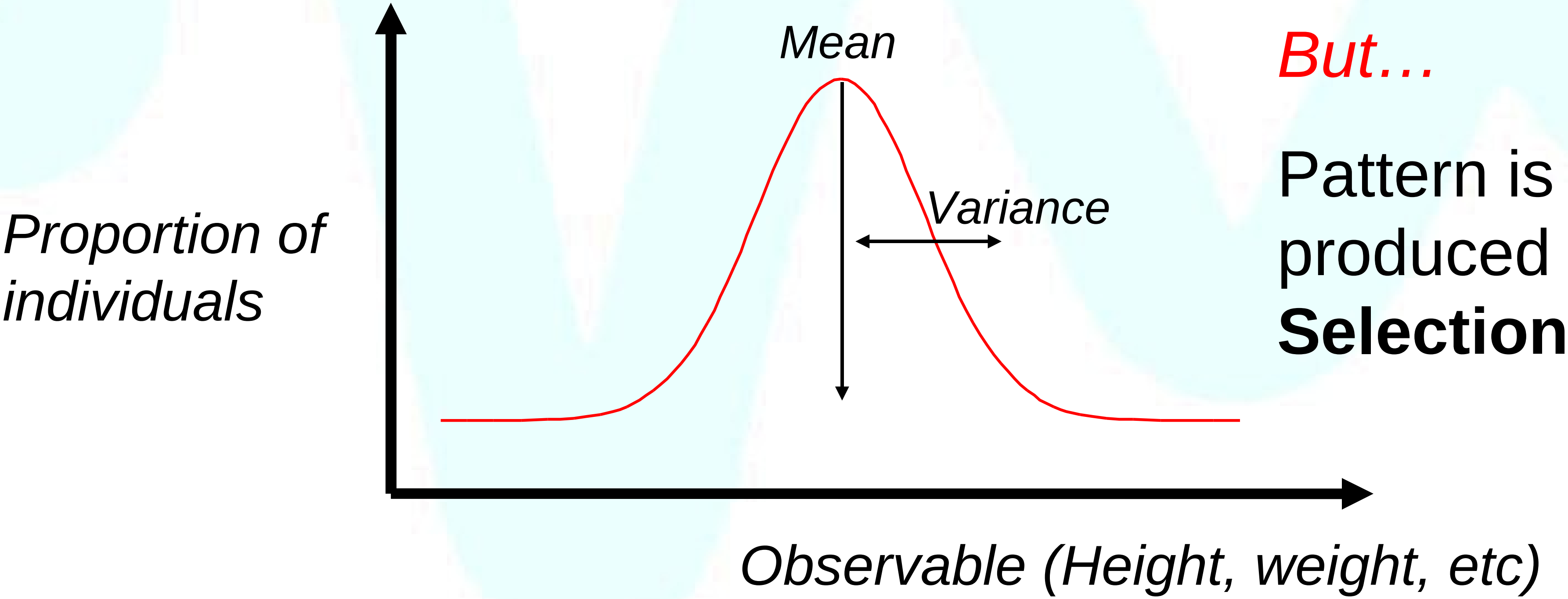
- Fixed population size
- All individuals are equivalent
- Individual life history is irrelevant
- There is a speciation “event”

Part 3:
Relation to Ecology



Phenotype Distribution

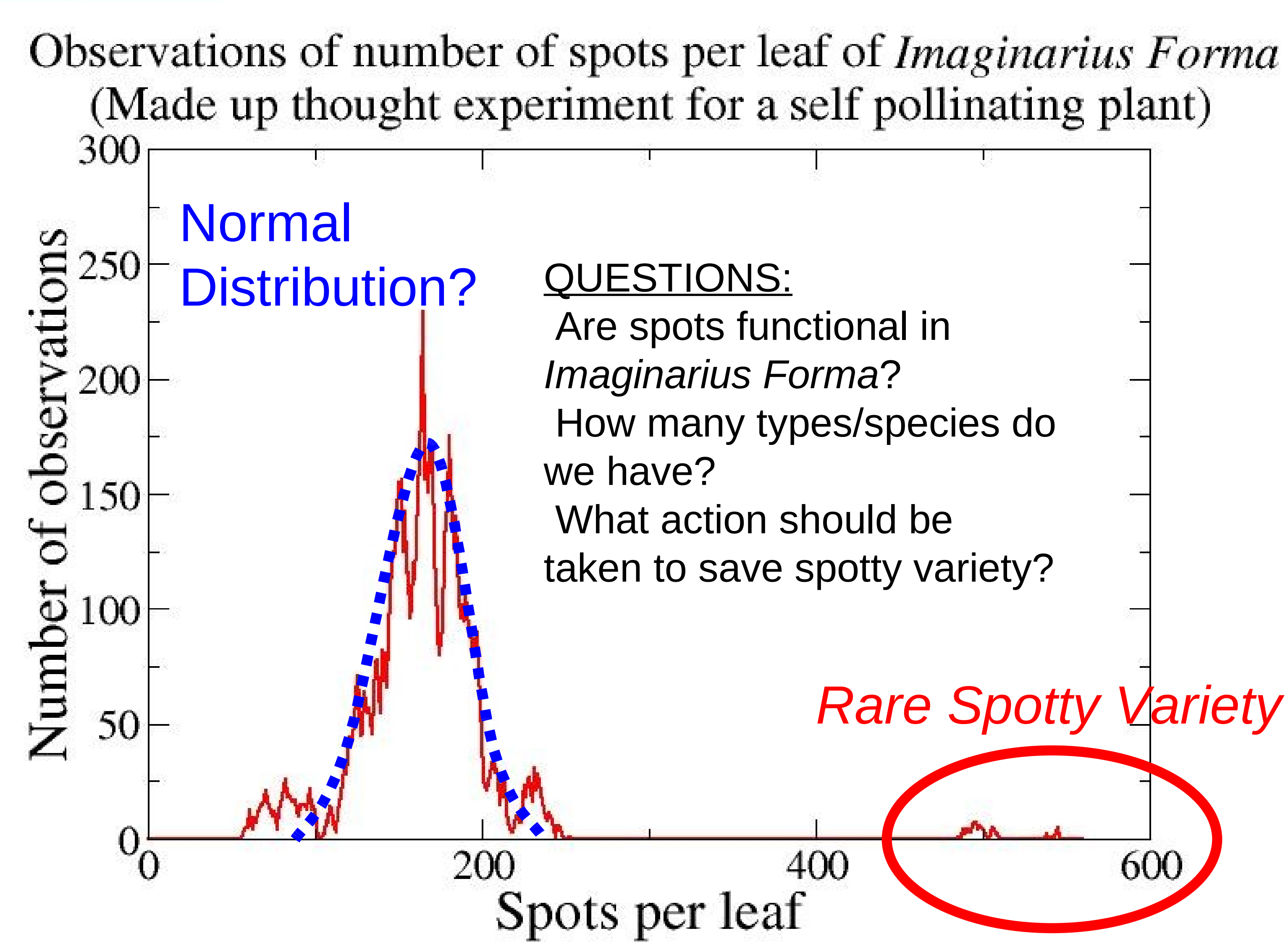
- Consider 1 dimensional case: mutations can be either to the left or to the right.
- Expected pattern is a Normal Distribution:



But…

Pattern is produced by **Selection.**

Test Problem



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

Normal Distribution?

<u>QUESTIONS:</u>

Are spots functional in *Imaginarius Forma*?

How many types/species do we have?

What action should be taken to save spotty variety?

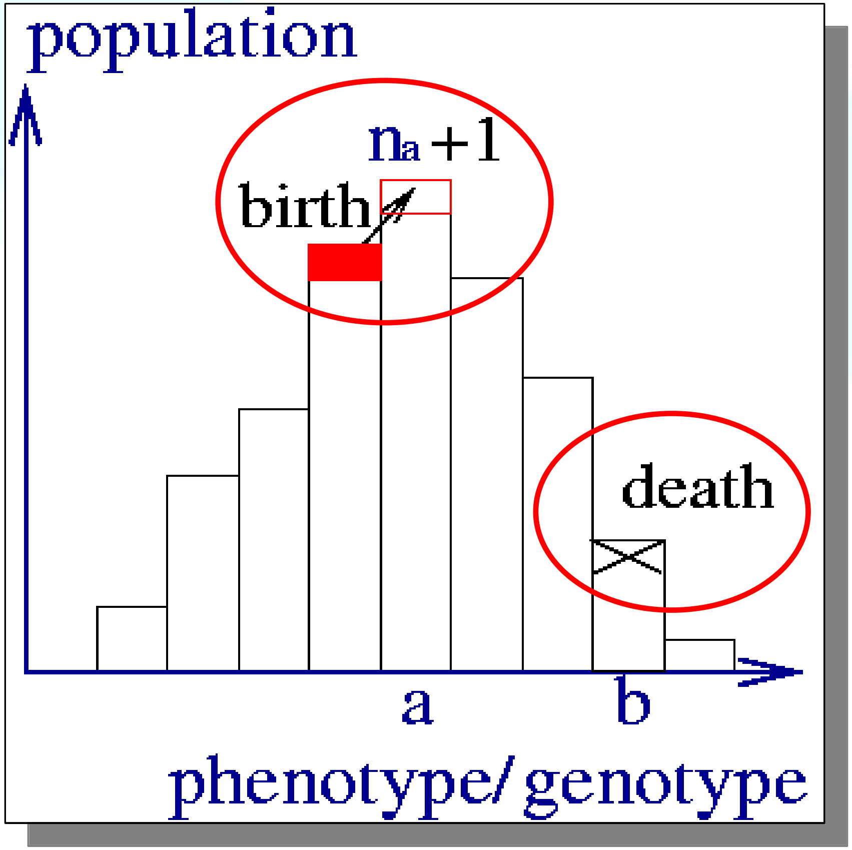
Rare Spotty Variety

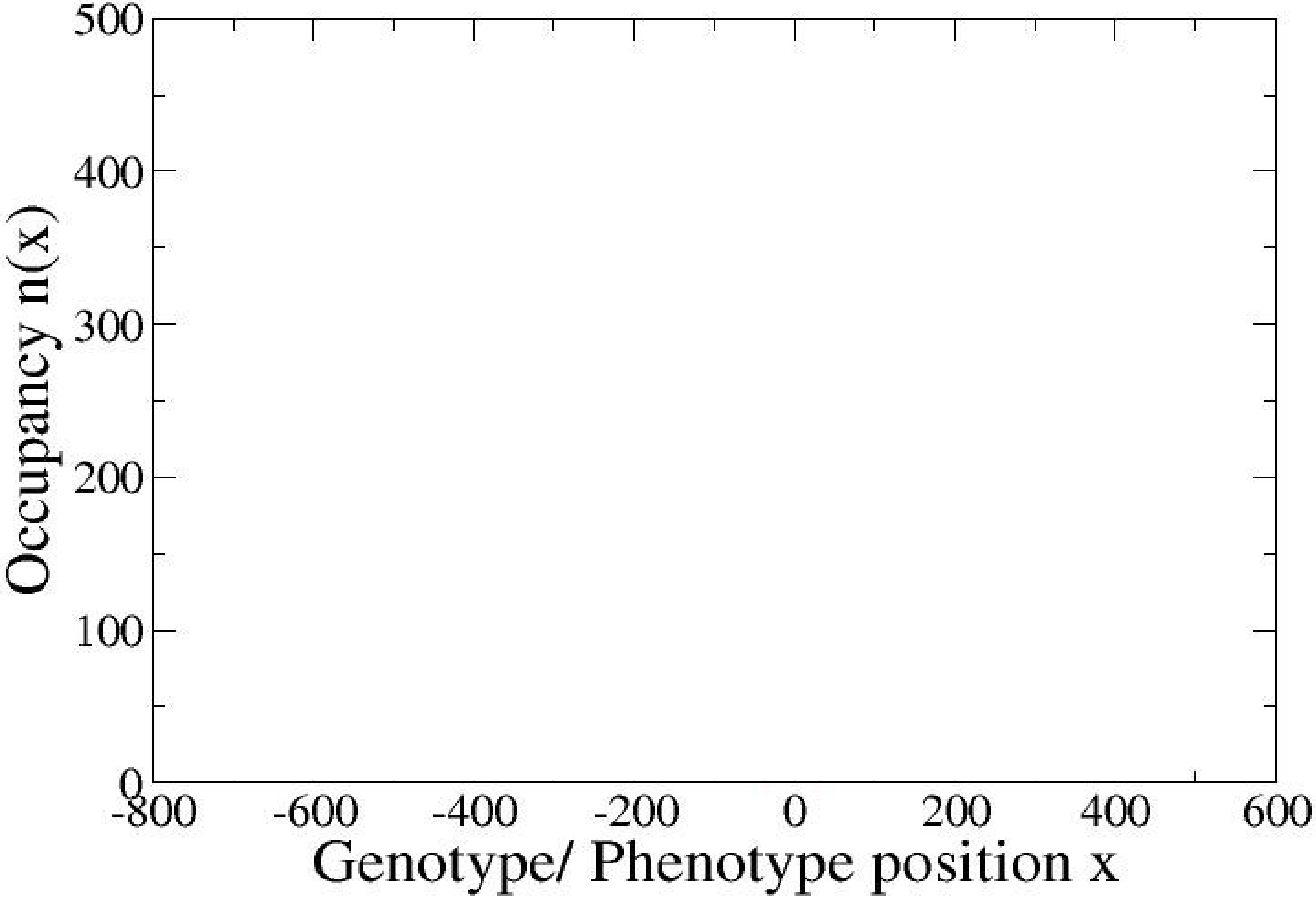
An evolution model

- Consider N individuals each labeled by phenotype position:

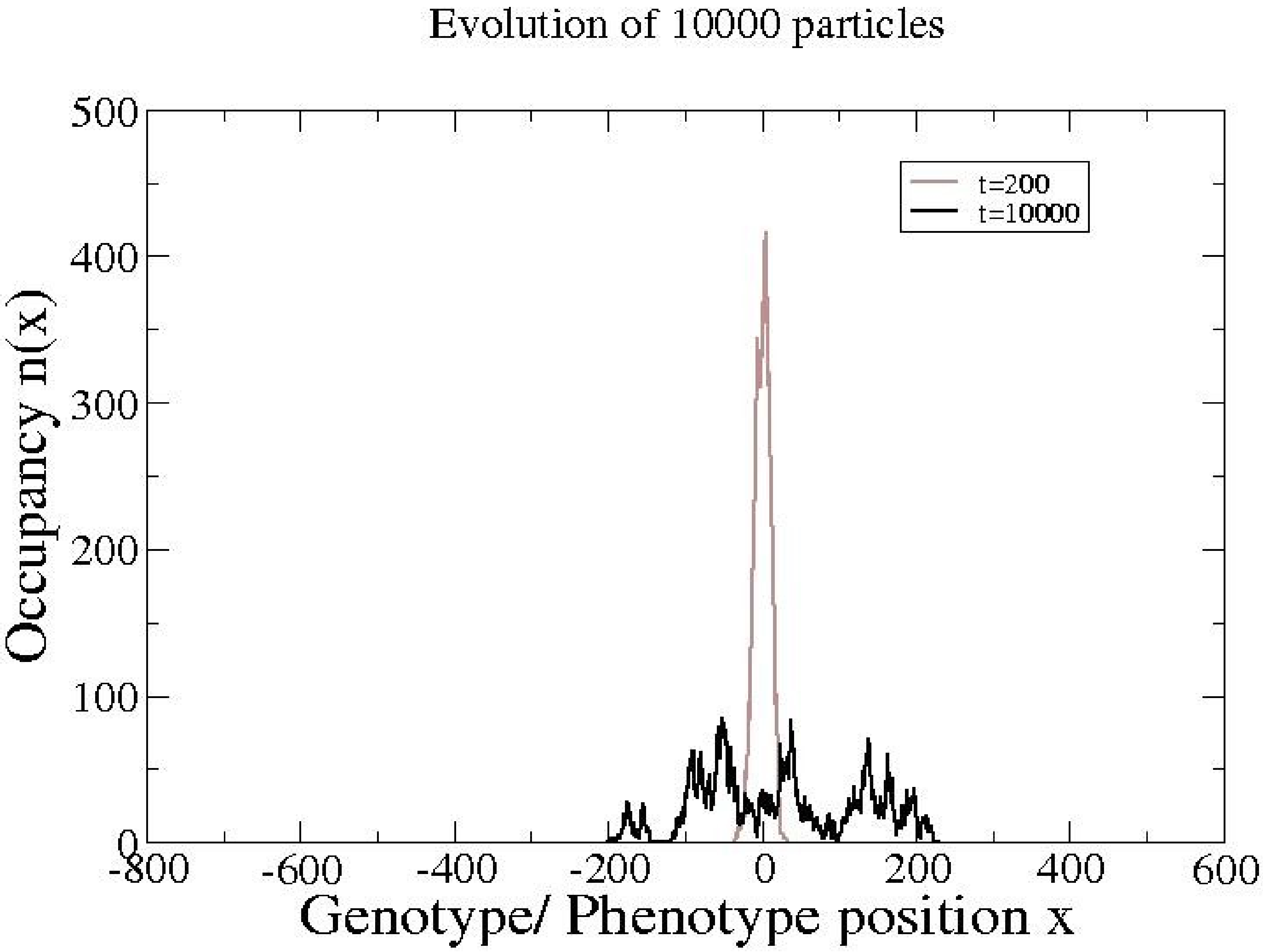
TIMESTEP:

- 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.



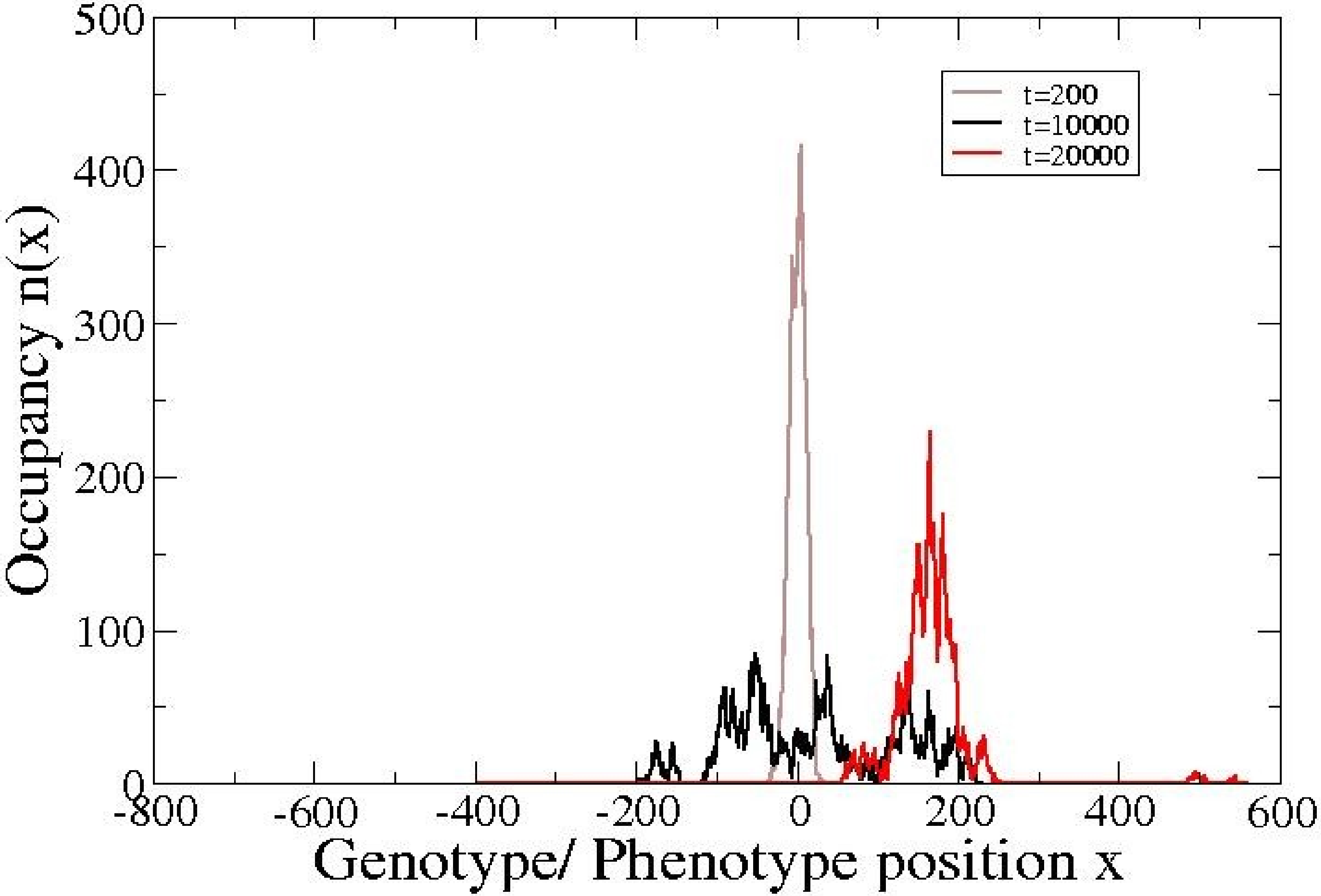


Evolution of 10000 particles

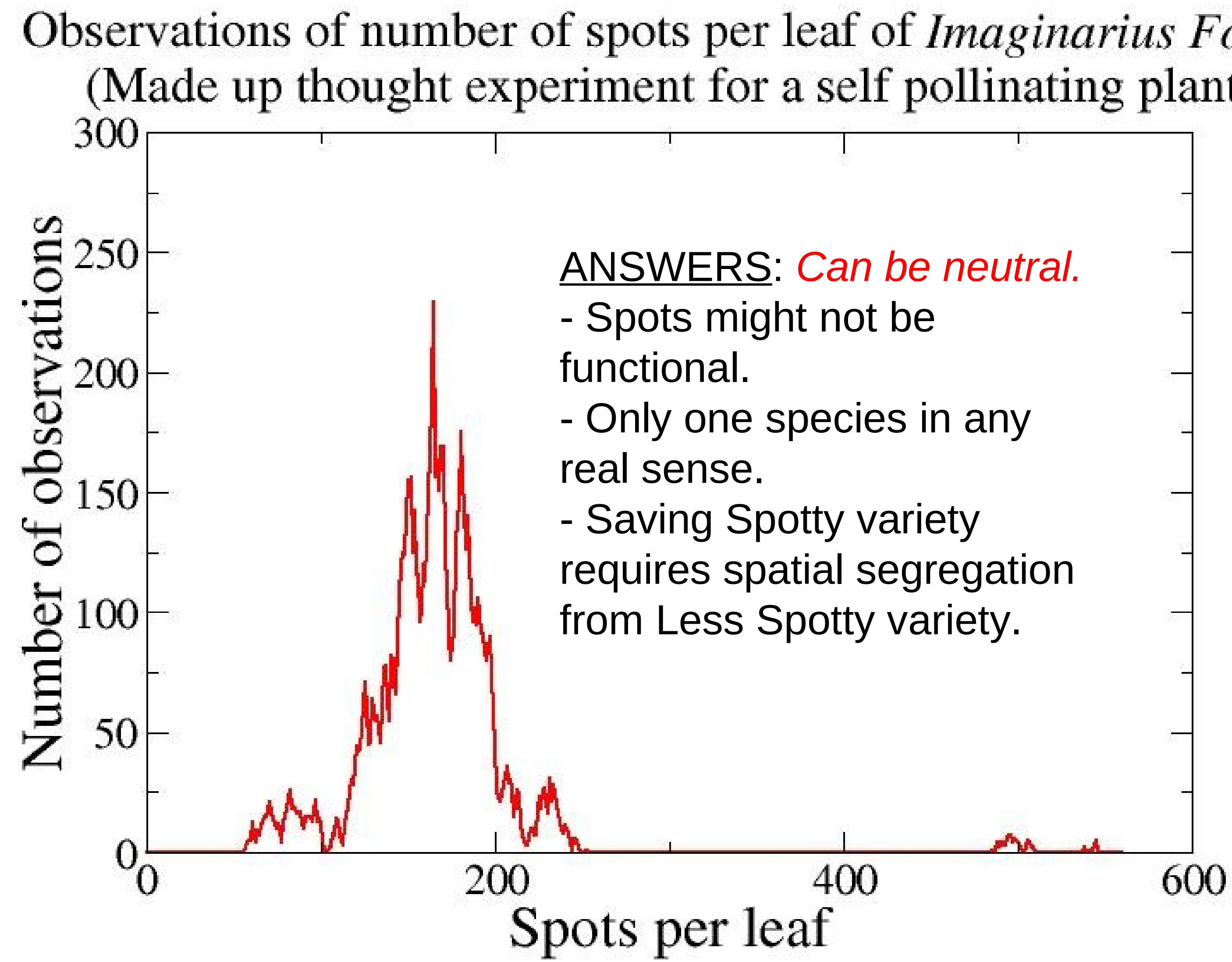


Evolution of 10000 particles

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

- 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…

Neutral Phenotype Results

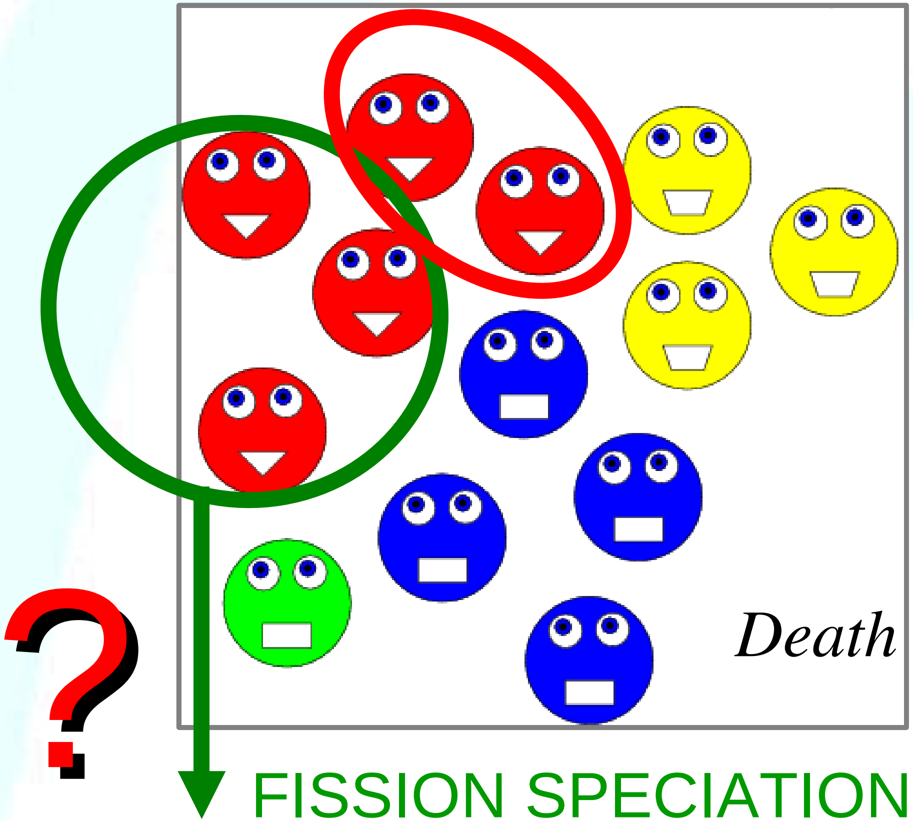
- Width of peak is proportional to fluctuations in the width of the peak.
  - *Corresponds to multiple clusters*
- Peak position drifts with constant speed when population size changes.
  - *Evolution speed is the same in small and large populations!*
- Obtain an analytic solution to act as a null hypothesis.
- Clearly, differences between types matter!

Fission Speciation

- Consider N individuals each labeled by species:

Fission ASSUMES a *neutral drift process*.

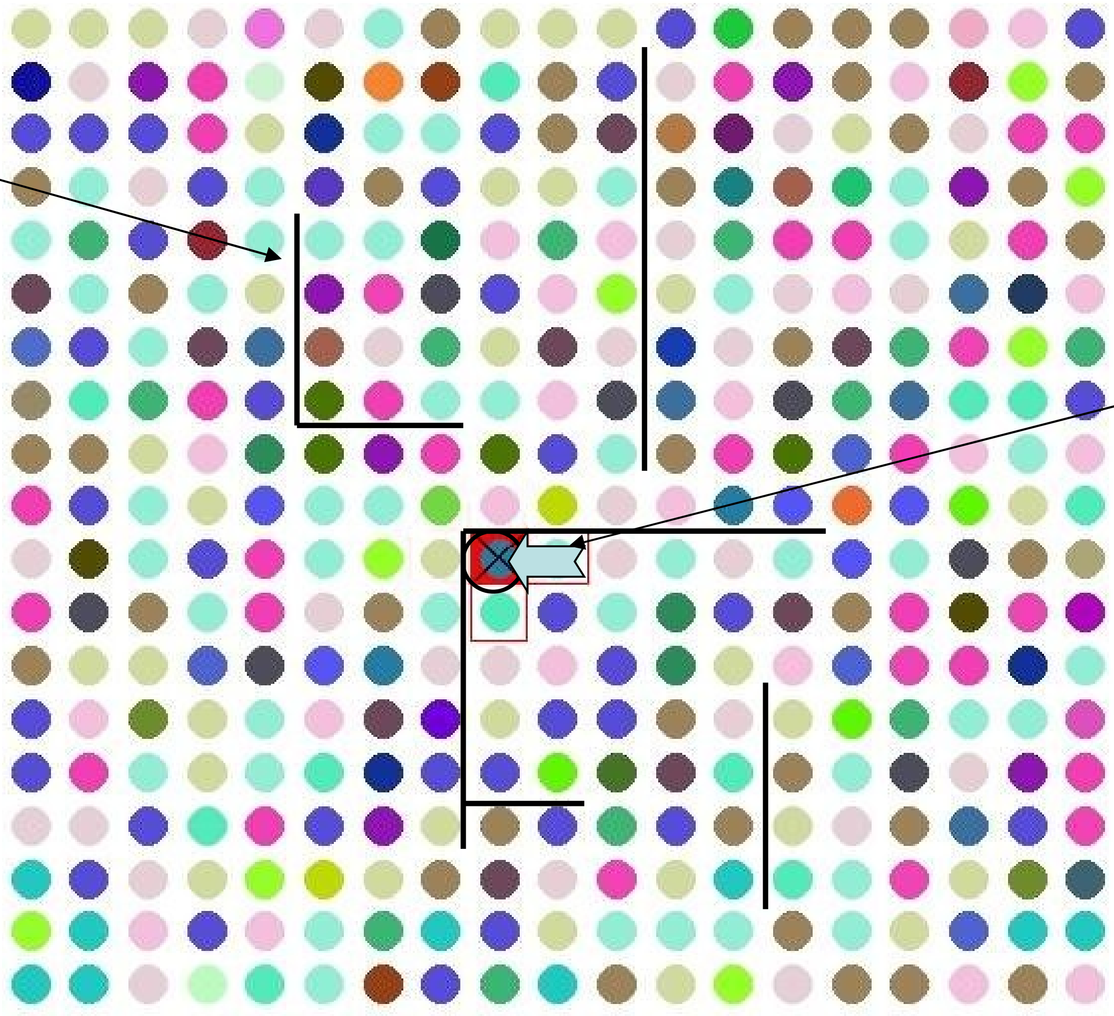
But differences can't change without a death!



FISSION SPECIATION

Mutate proportion of population allopatrically

Fix fission speciation?



Barriers

(move in time)

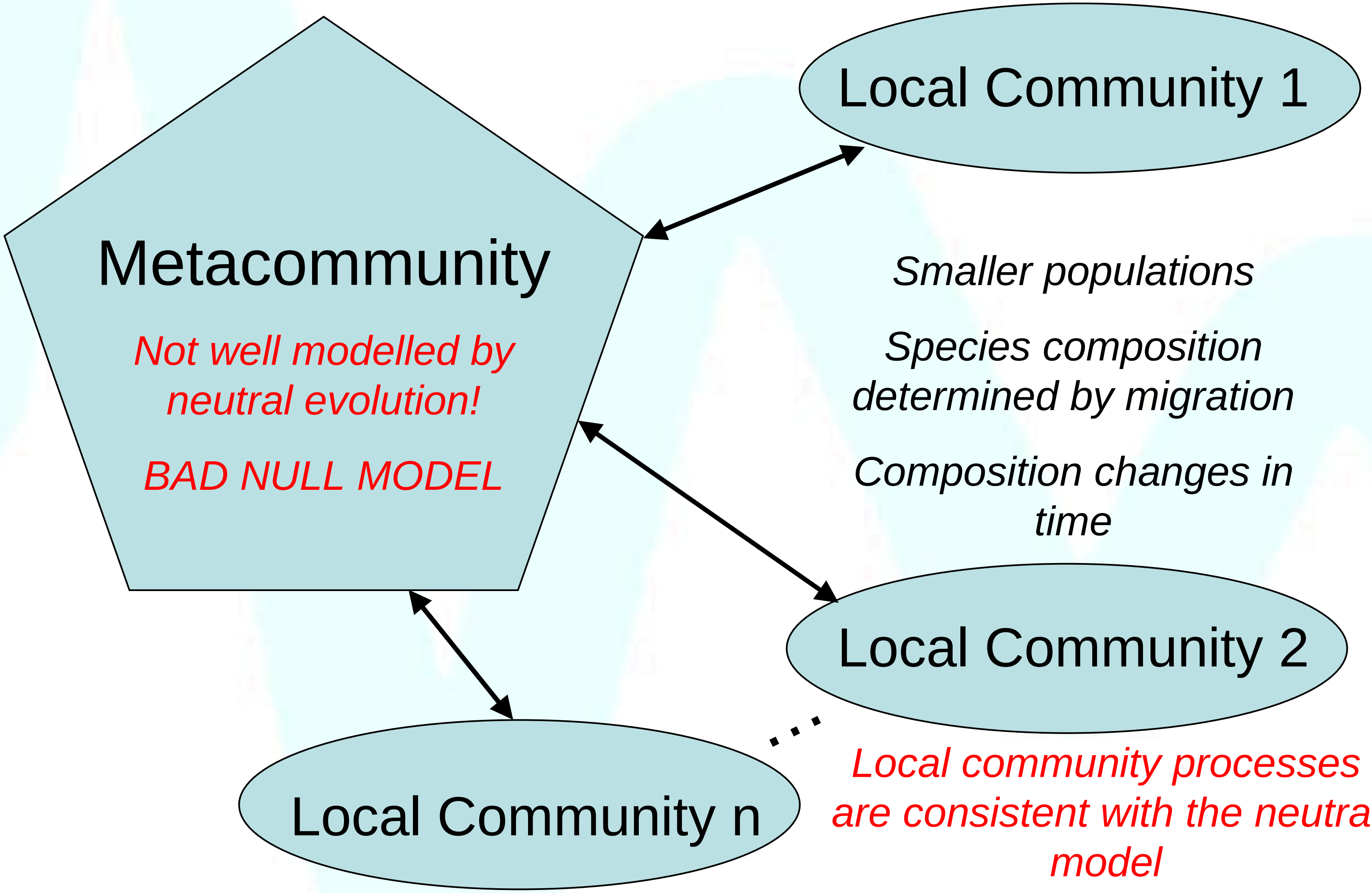
Random Death

Local Reproduction

Implications?

- There is no “natural” species definition – though arbitrary cut-offs still work.
- (Following holds in sexual case, where there is a natural species definition)
- No “speciation event” – but a “speciation process”.
- Fission speciation makes little sense in this context – and the fix is complex.
- So: neutral ecological model is not “parsimonious” for the metacommunity.

Full ecological model



Metacommunity

Not well modelled by neutral evolution!

BAD NULL MODEL

Local Community 1

Local Community 2

Local Community n

…

Smaller populations

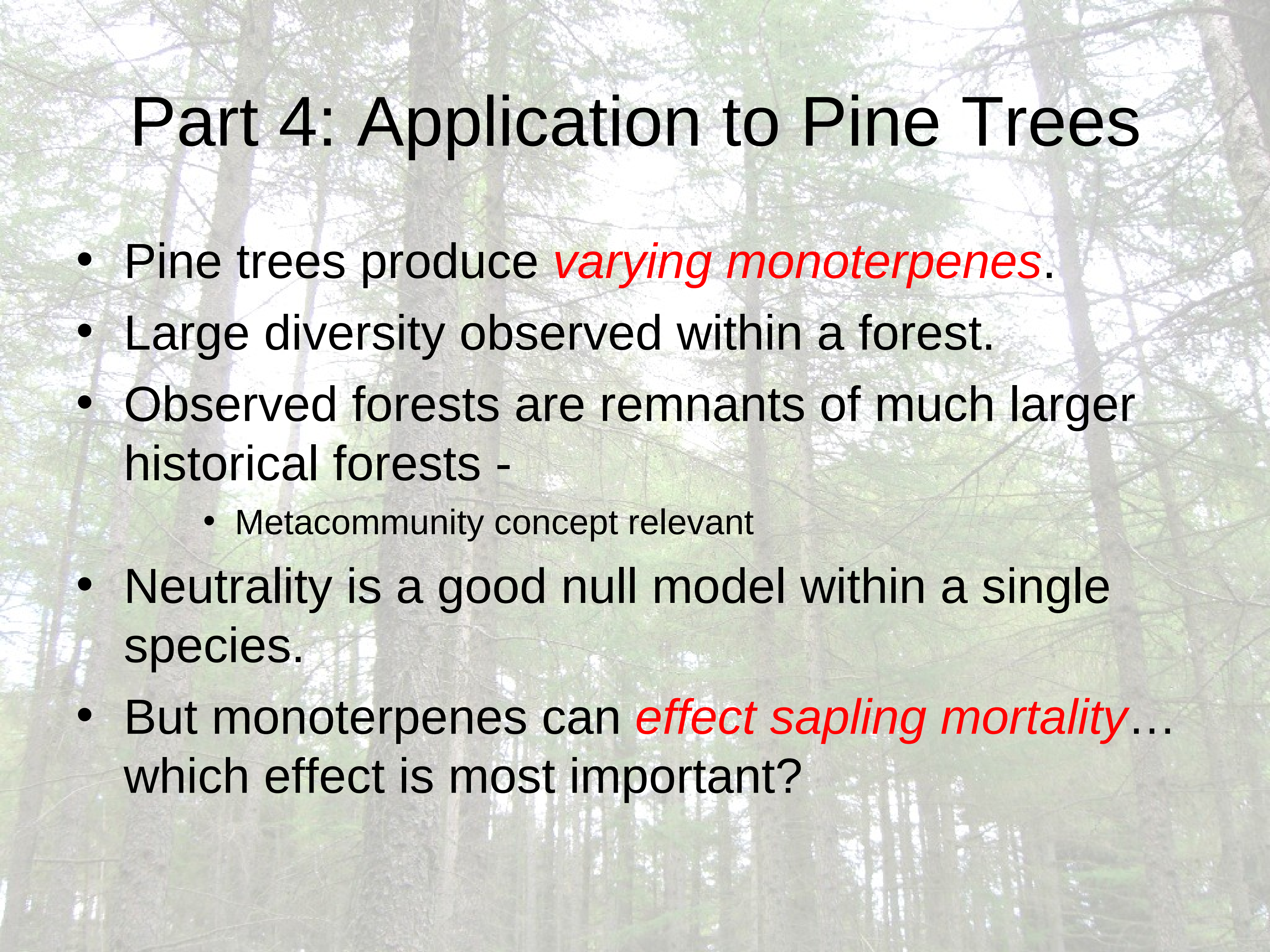
Species composition determined by migration

Composition changes in time

Local community processes are consistent with the neutral model

GOOD NULL MODEL

Part 4: Application to Pine Trees



- Pine trees produce *varying monoterpenes*.
- Large diversity observed within a forest.
- Observed forests are remnants of much larger historical forests -
    - Metacommunity concept relevant
- Neutrality is a good null model within a single species.
- But monoterpenes can *effect sapling mortality*… which effect is most important?

(not) A neutral model

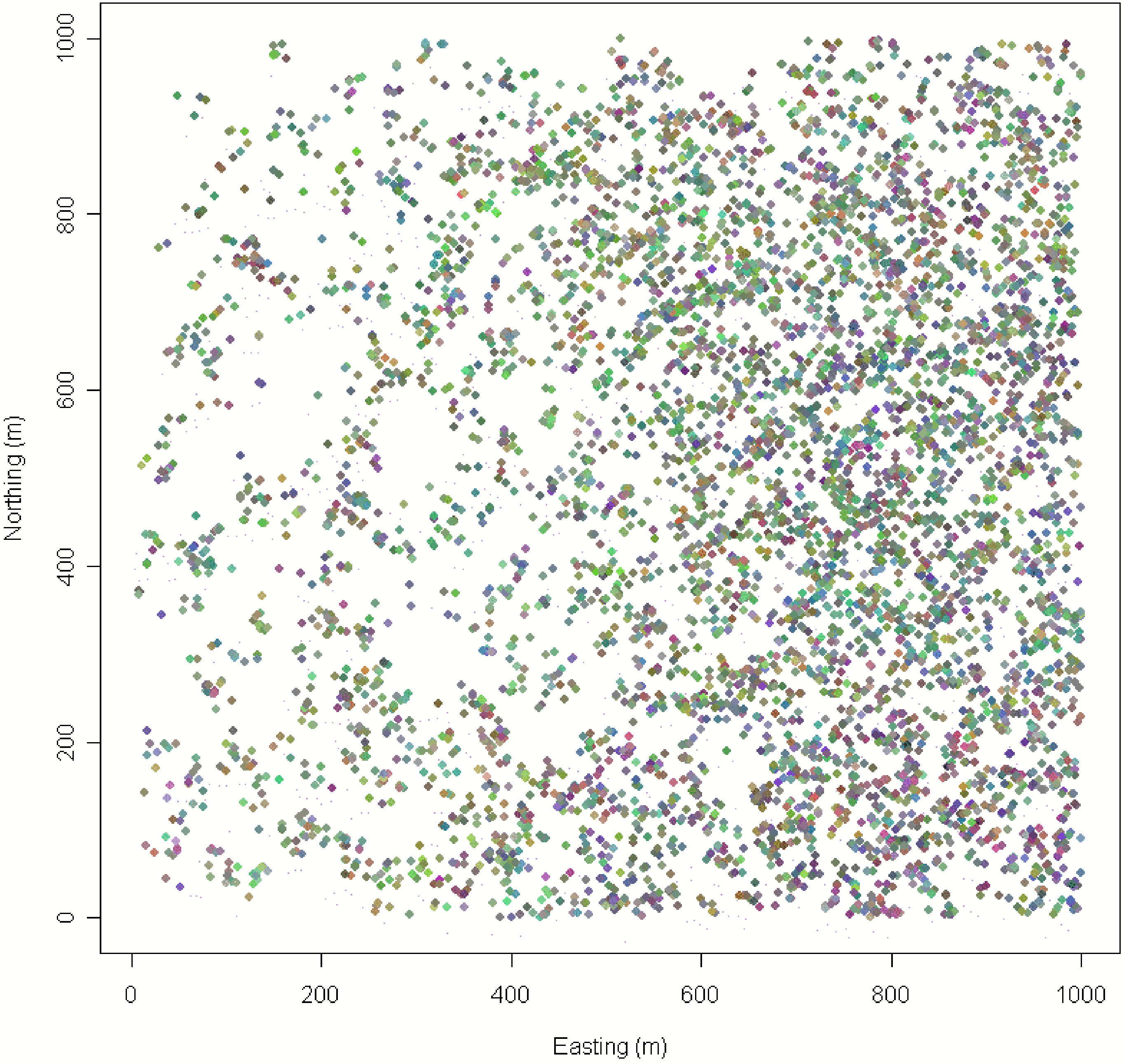
Work with Colin Beale and Jack Lennon

- Trees grow at a given location -
- And compete for resources.
- Therefore future success is driven by intensity of competition.
- Neutral model with respect to genotype, but not individuals.
- Resolves the problem of non-observation of individual level equivalence.

Model details

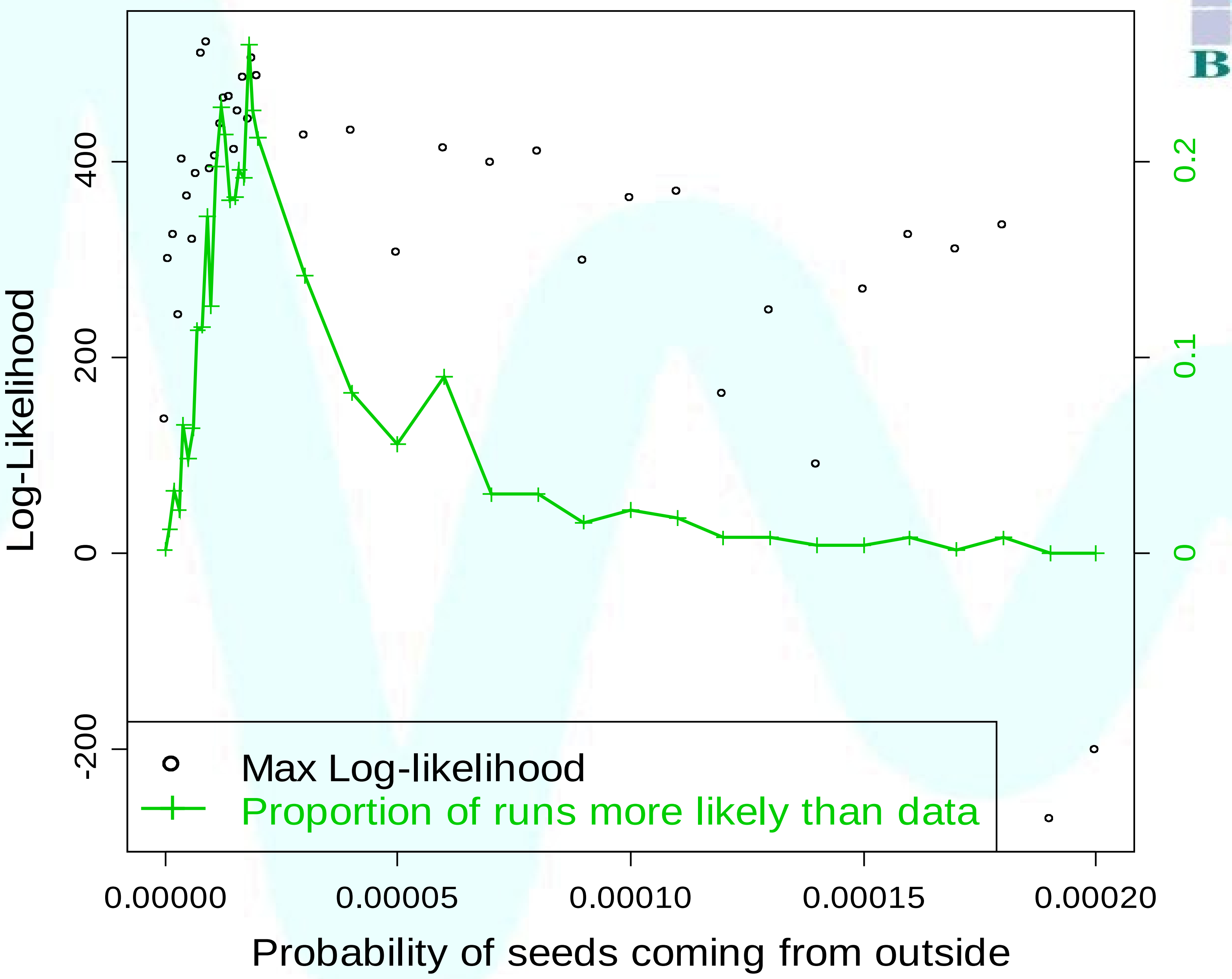
- Trees grow and *compete for space*
- Trees produce seeds, which *disperse*
- Seeds are *pollinated* by other trees, whilst still on the mother tree
- Diversity of local forest is maintained by occasional *external pollen*
- Monoterpene production is heritable

Equilibrium Genetic Distribution of a simulated forest.



Colour represents terpene concentrations

similar colour -
similar terpenes -
recent ancestry

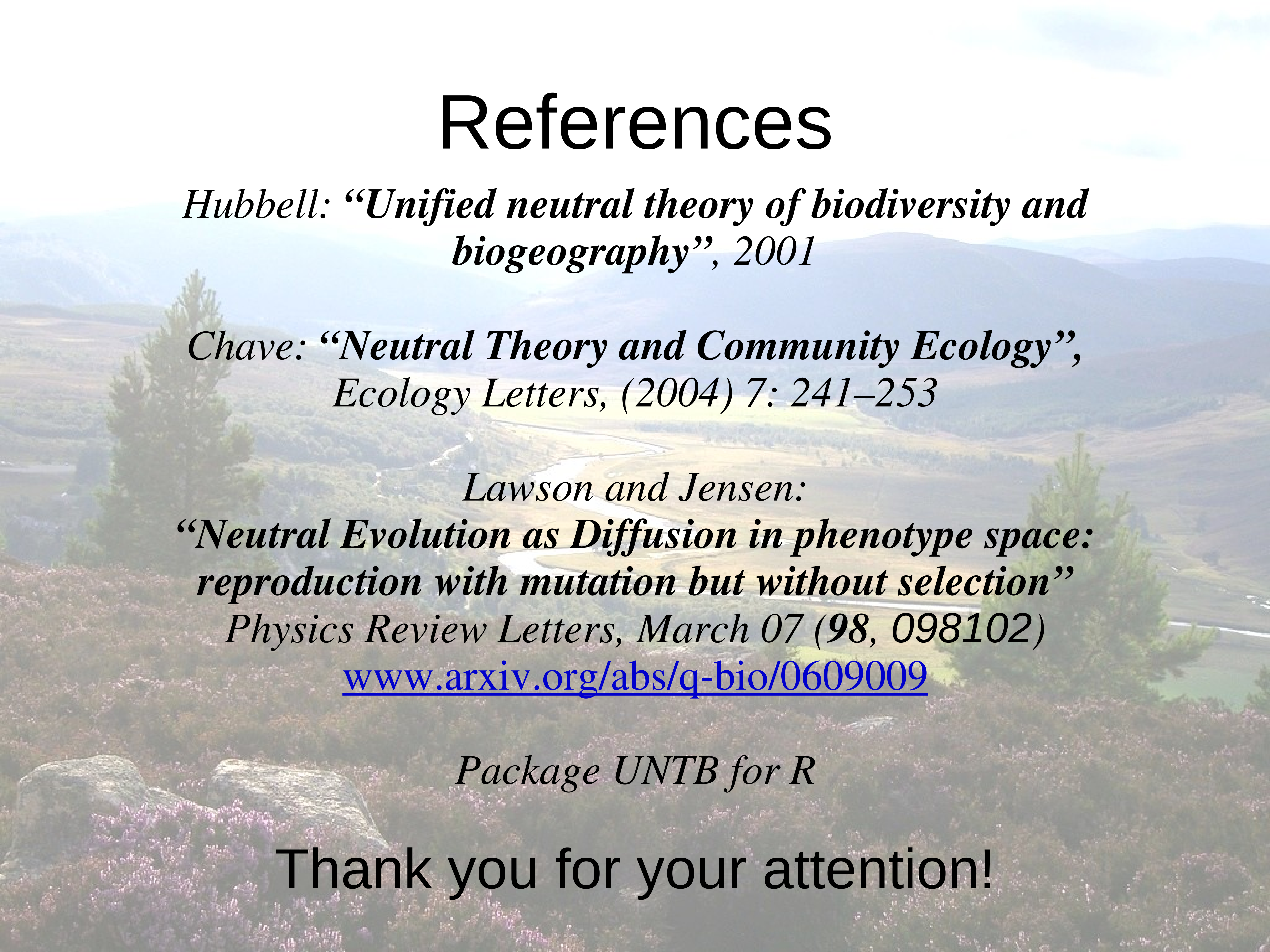

Log-Likelihood
400
200
0
-200
0.2
0.1
0
Max Log-likelihood
Proportion of runs more likely than data
0.00000
0.00005
0.00010
0.00015
0.00020
Probability of seeds coming from outside

Conclusions

- Neutrality is a useful concept for null models
- Ecological models can be informed by evolution
    - Speciation “event” - examined more closely
- Null models are useful to inform which processes are interesting

Beyond Neutrality

- Compare with other models
  - Deterministic Differential Equation Models
  - Stochastic models with selection
  - Network models, etc.
- Neutrality is not for life – its just for Christmas!
  - Solves some problems but is *just a null model*!



References

Hubbell: ***"Unified neutral theory of biodiversity and biogeography"****, 2001*

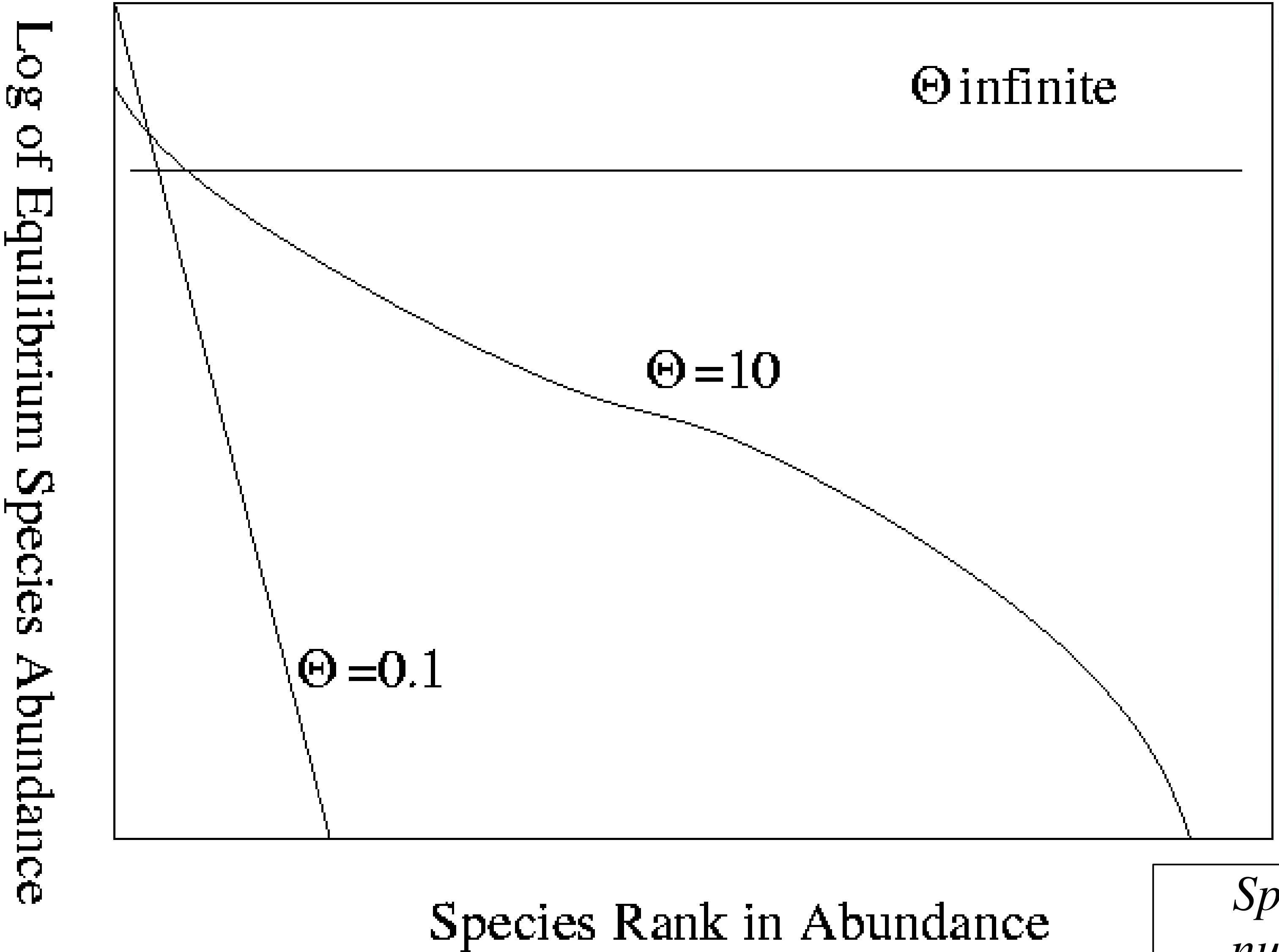
Chave: ***"Neutral Theory and Community Ecology",***
Ecology Letters, (2004) 7: 241–253

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

Package UNTB for R

Thank you for your attention!

Ecological Model Results



Number of individuals

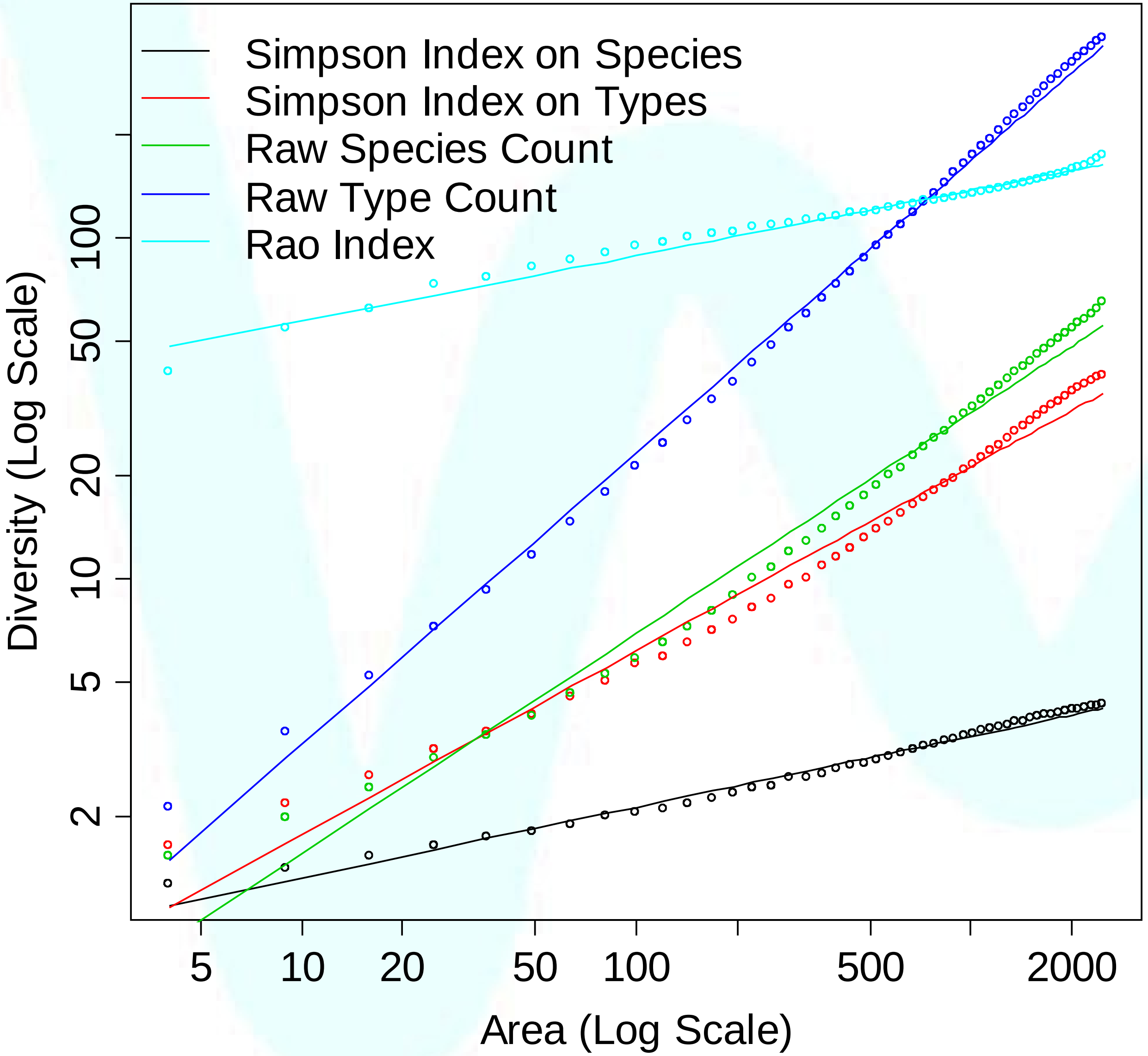
Species number ordered by size

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

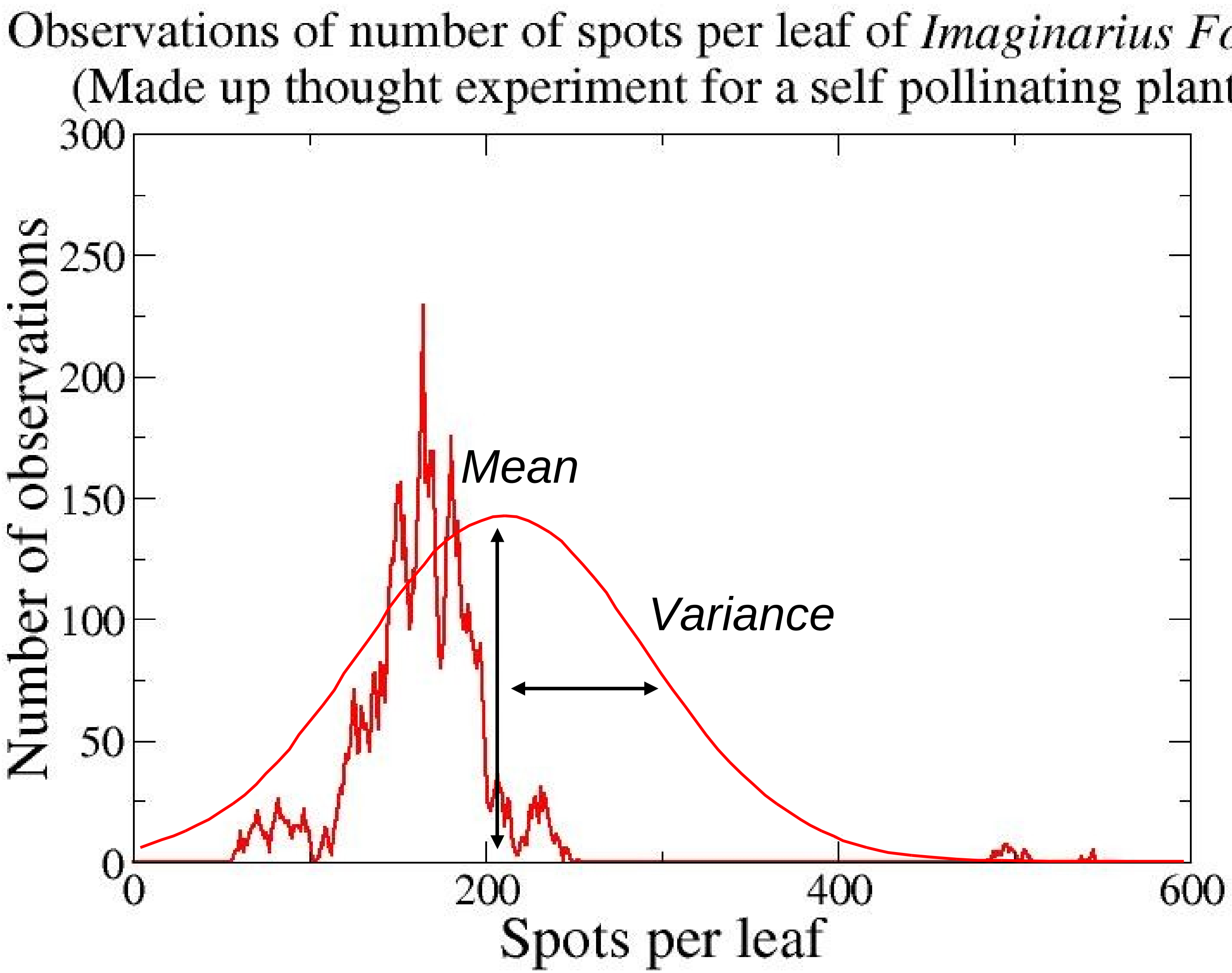
So what is diversity?

- Ecological Sense: “number” of different species or types
- Requires definition of species:
    - Biological Species concept?
    - Phenotypically distinct?
    - Genotypic species concept?
- Definition of genotypic species is arbitrary:
    - Cut-off in time to “last common ancestor”
- Need a *difference based* measure.

Species Area Relation



Test Problem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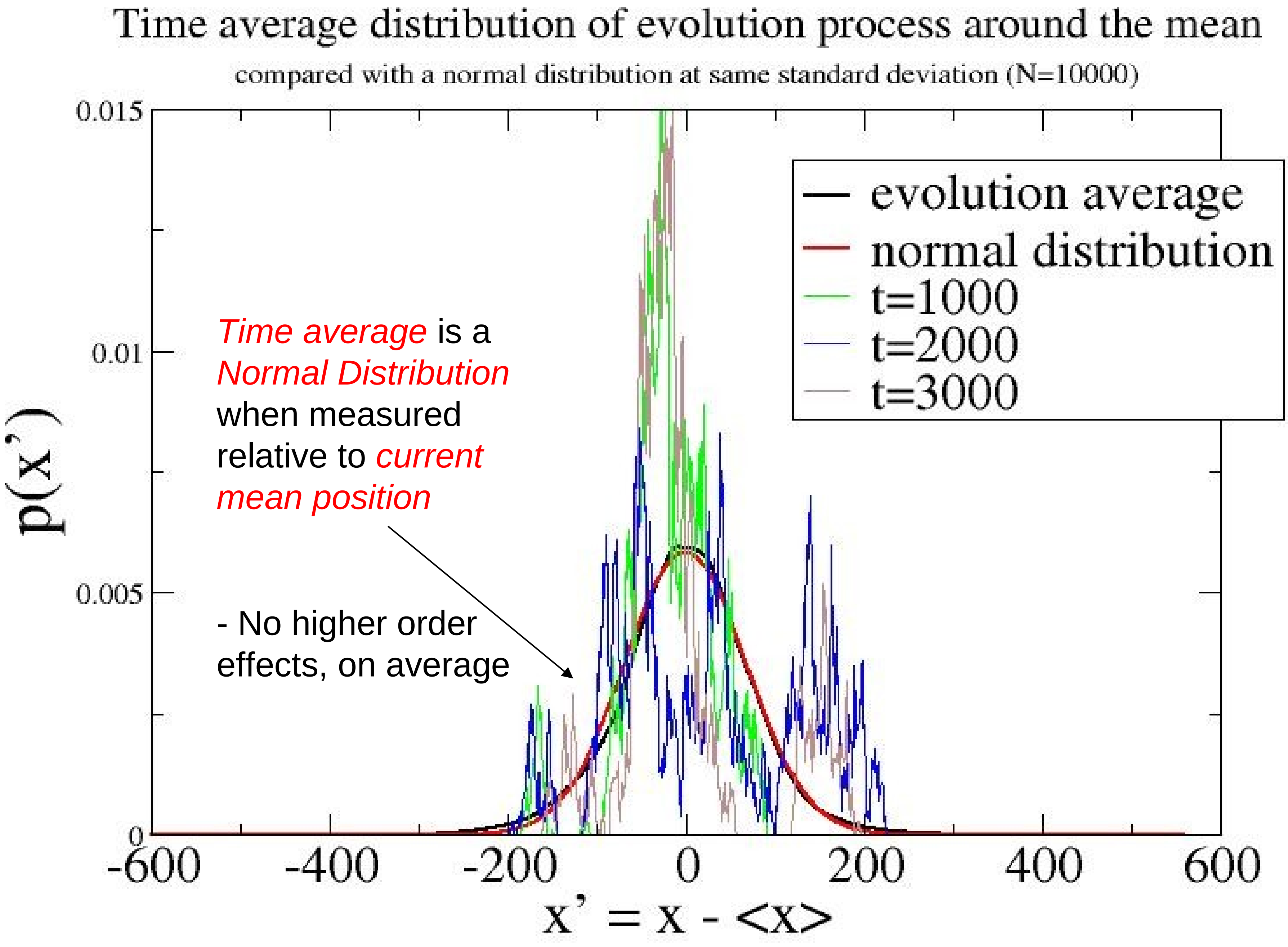


Time average is a *Normal Distribution* when measured relative to *current mean position*

- No higher order effects, on average

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

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

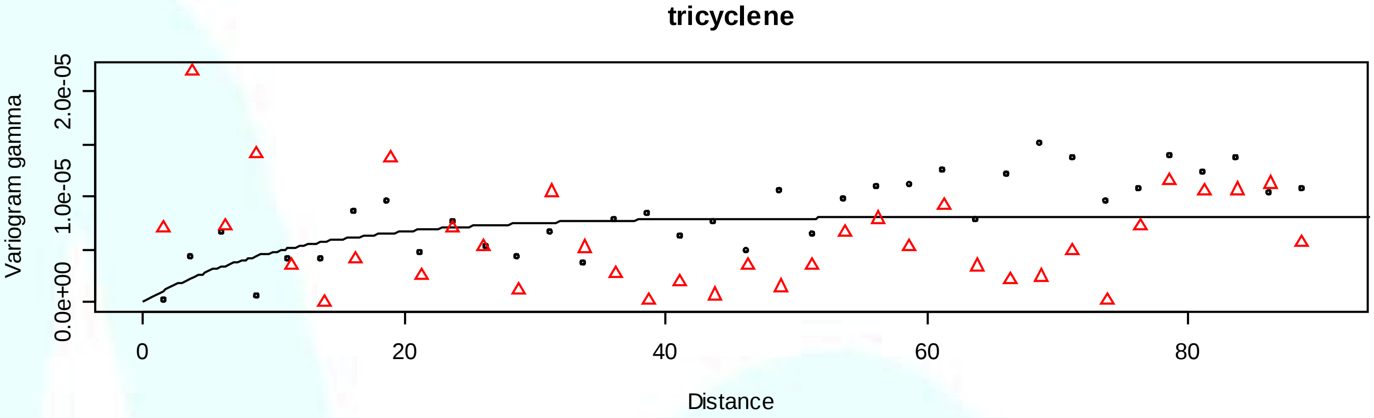
- Position: $\langle x \rangle_{\mathrm{RMS}} = \sqrt{T(p_m + w^2)}$ $\sqrt{\frac{p_m T}{2}}$

With time in generations... $<x>_{RMS}$ is independent of N !

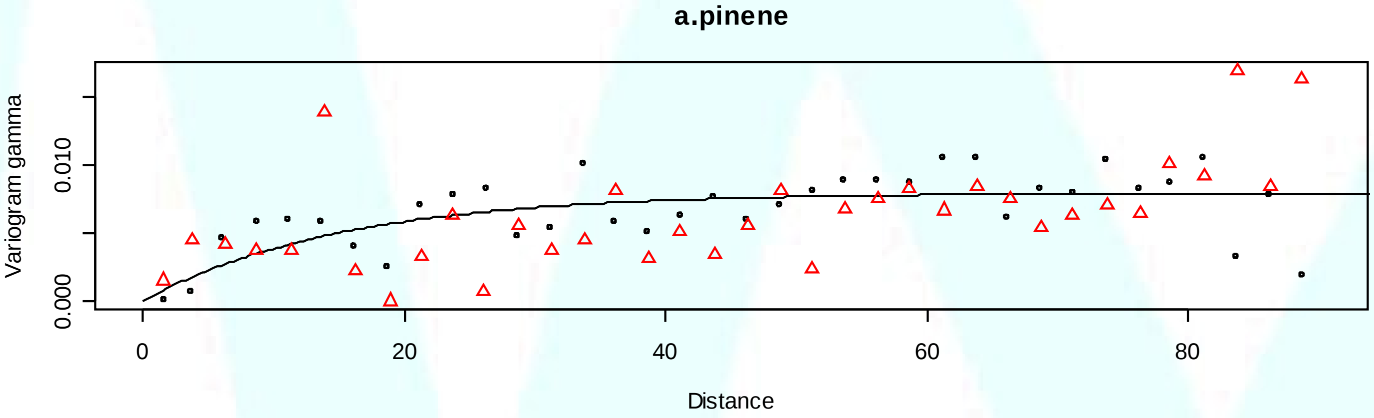
- Compare with diffusion:

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

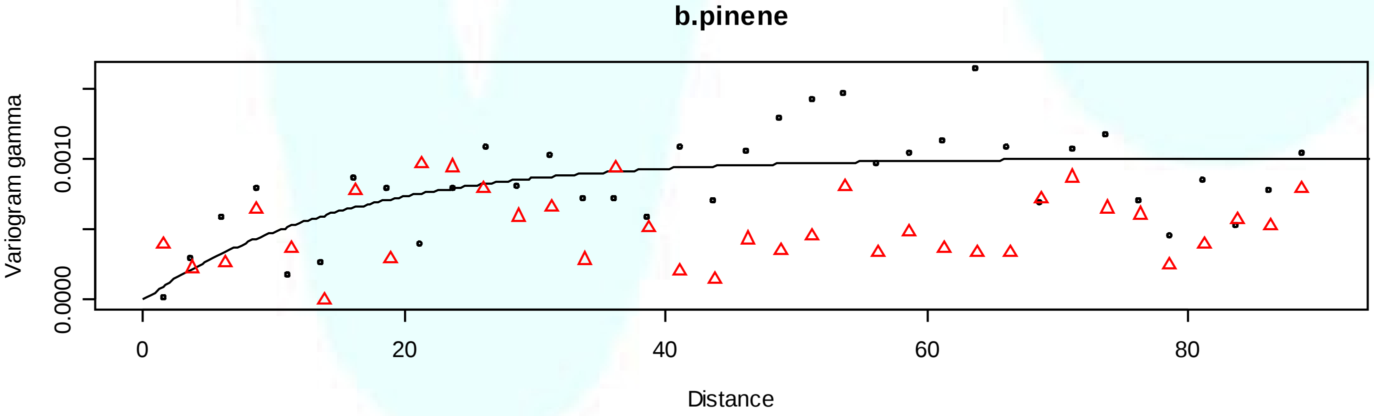
- Diffusion “does nothing” in infinite populations... evolution does “more”!



tricyclene



a.pinene



b.pinene

[Algebra]