EVOLUTION OF SPECIES' CLIMATIC NICHES: LINKING BIOGEOGRAPHY AND MACROEVOLUTION

Florian BOUCHER, SEMOVI, March 13th 2013

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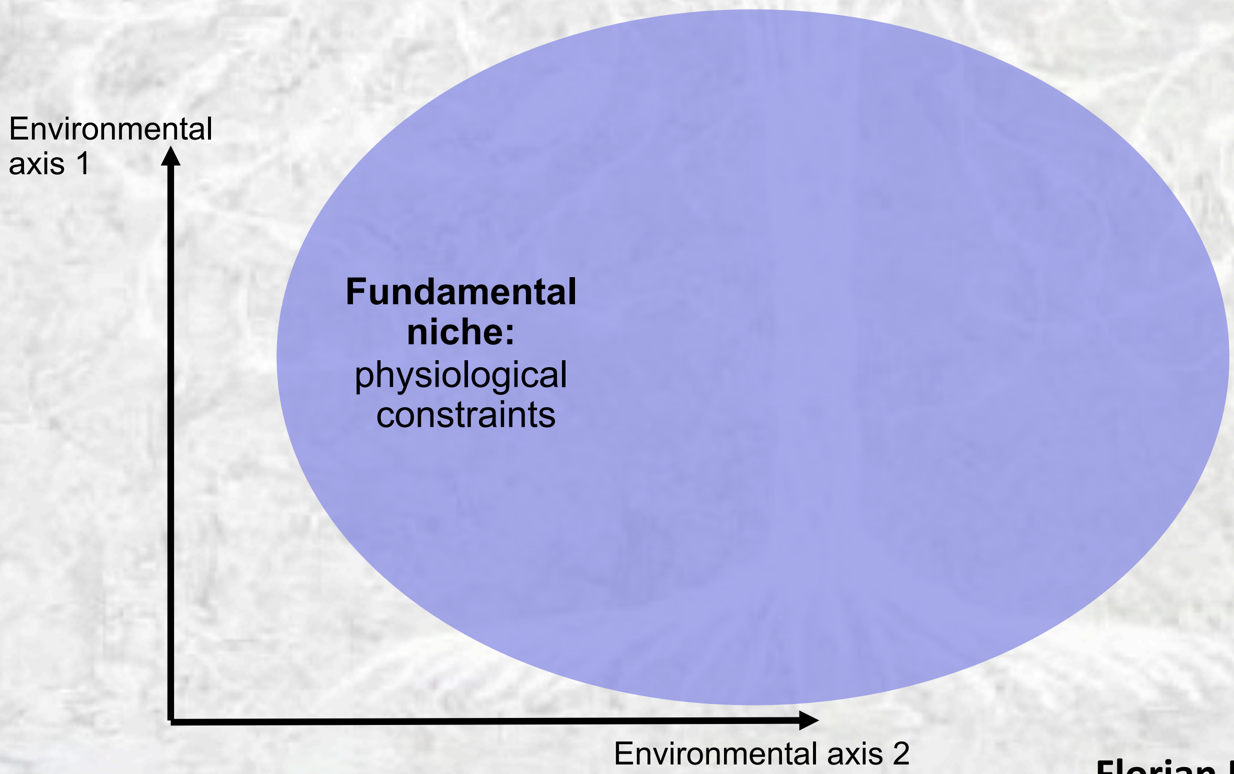

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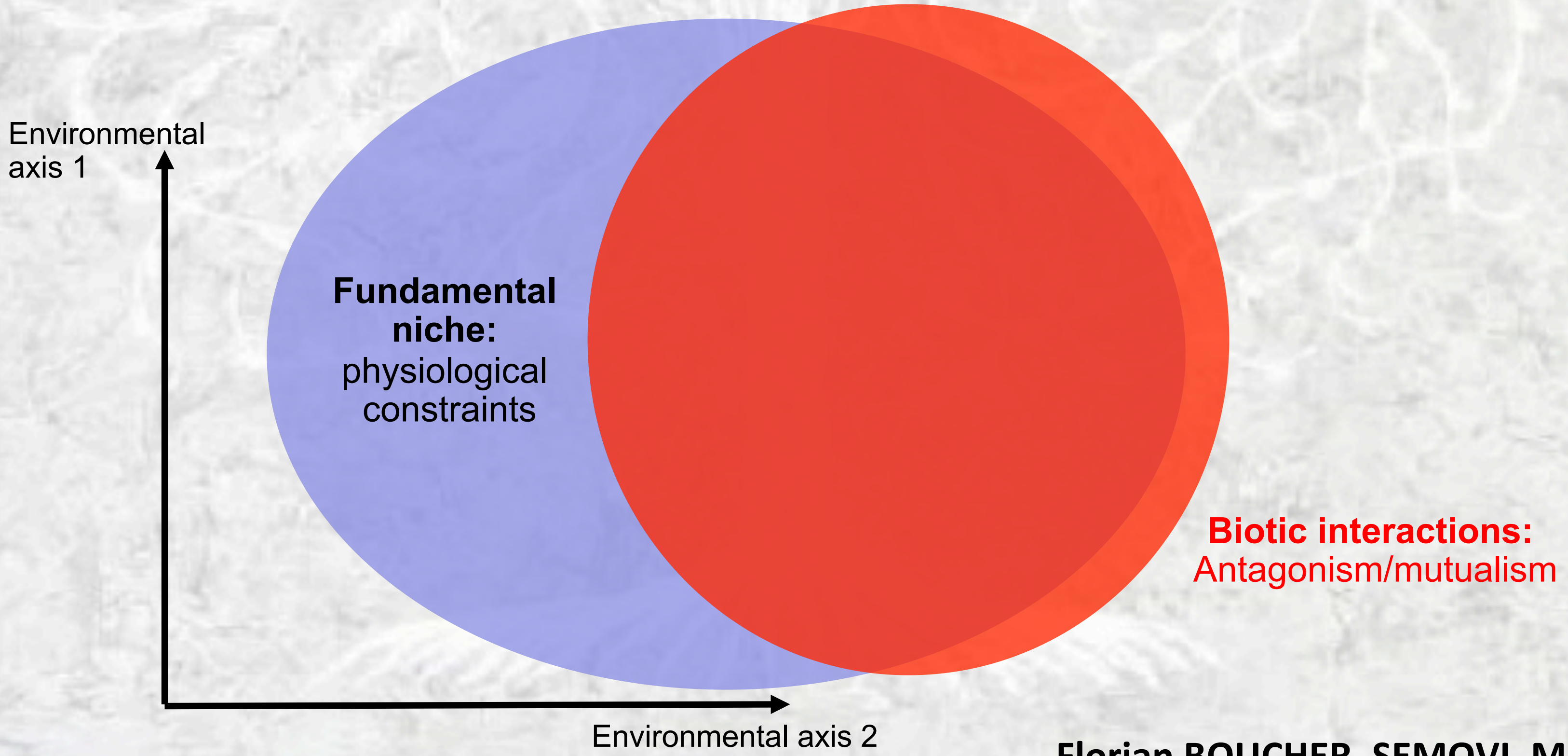

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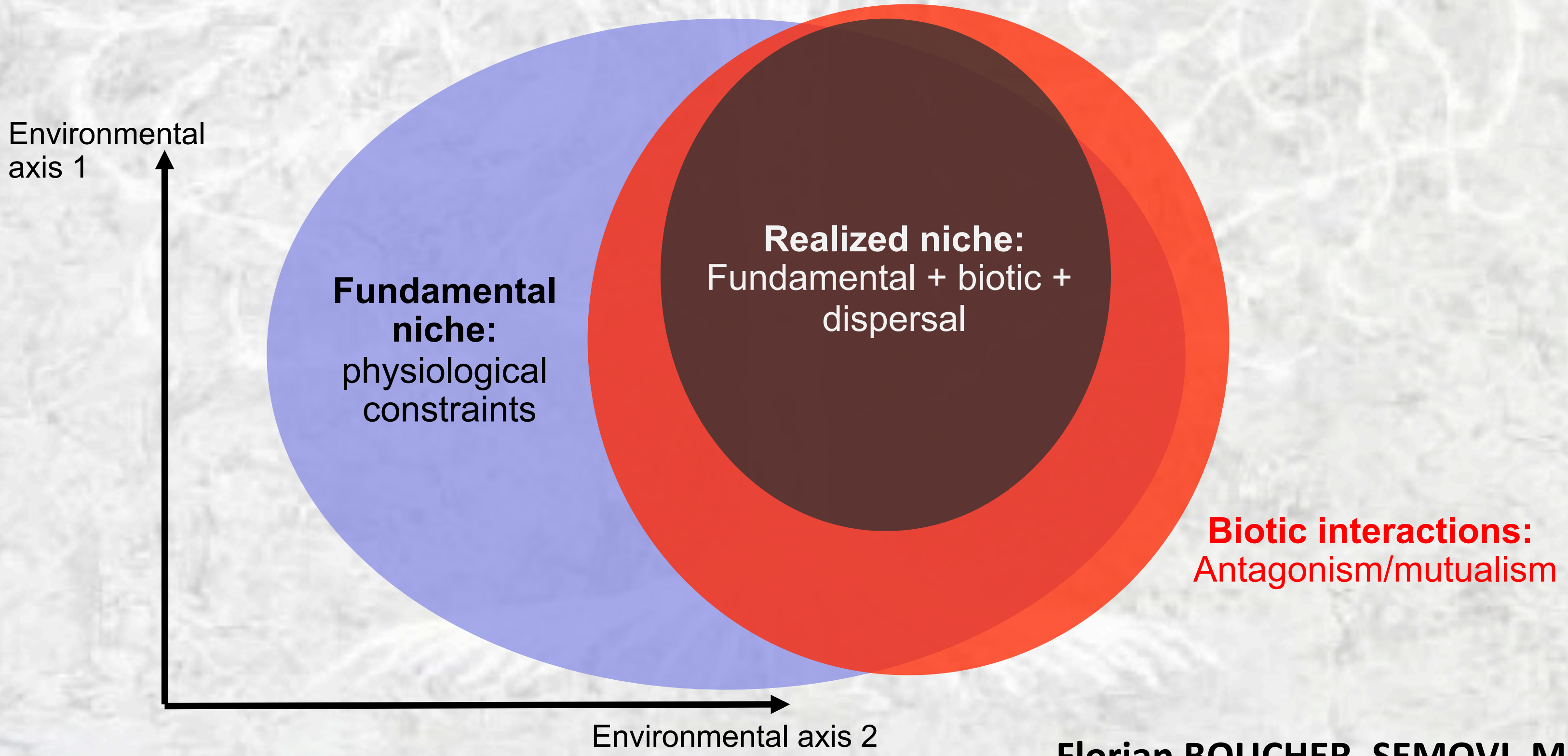


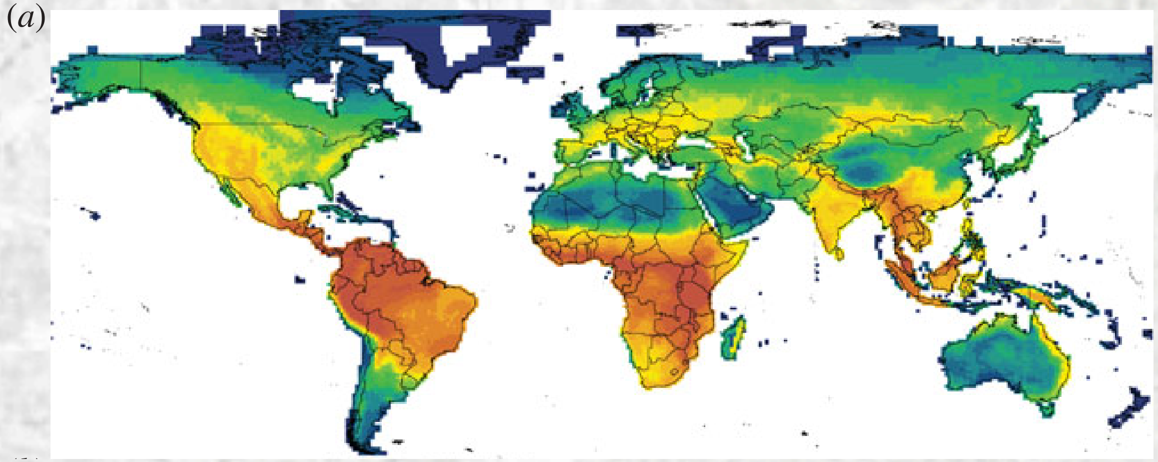
WHY DO WE CARE ABOUT NICHE EVOLUTION?

- **Fundamental question + consequences** on various questions:

- past biogeographic patterns

- diversity gradients

- speciation …



Latitudinal gradient in diversity in mammals, Buckley *et al.* 2010

MODELING NICHE EVOLUTION OVER GEOLOGICAL TIMESCALES

Use of the macroevolutionary toolbox for continuous traits:

- Niche represented as the **mean position** of a species over one (or several) environmental gradient(s) → huge simplification

- Species don't interact

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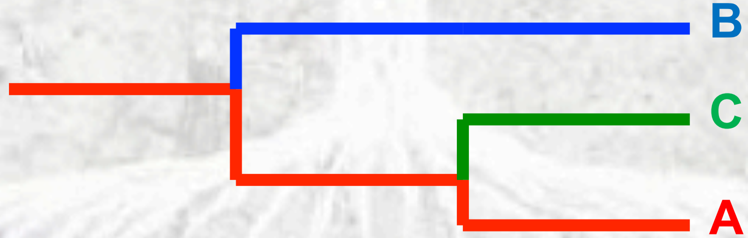
- Species don't interact
- **Phylogeny** gives us divergence times between species:



THE NEUTRAL MODEL: BROWNIAN MOTION

- **Analogue of drift** for geological timescales:

$dX(t) = \sigma.dt.dW$, where $dW \sim N(0,1)$ (Wiener process)

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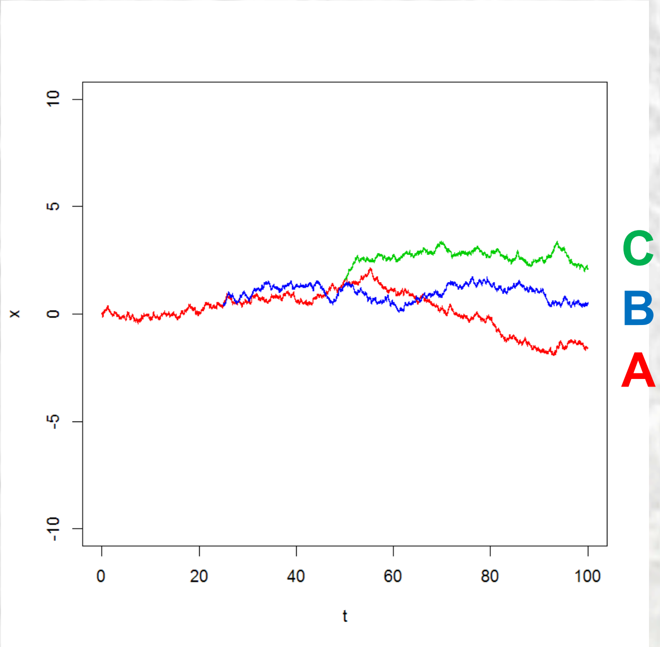

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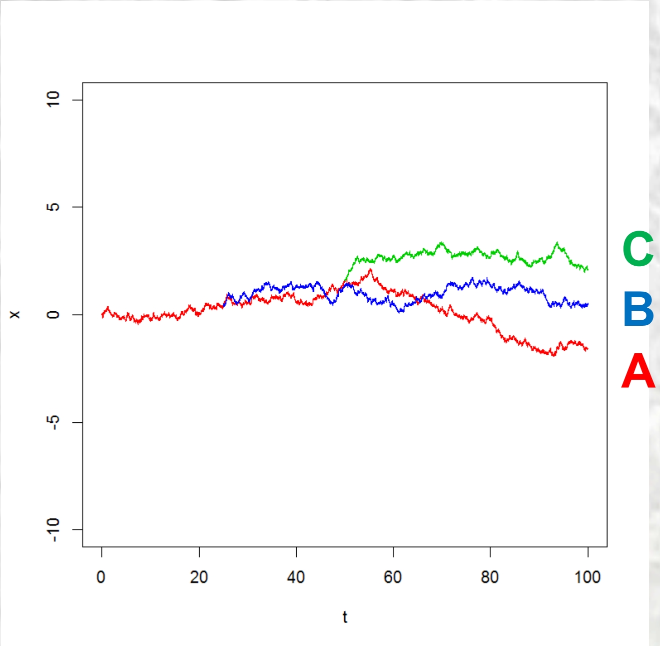

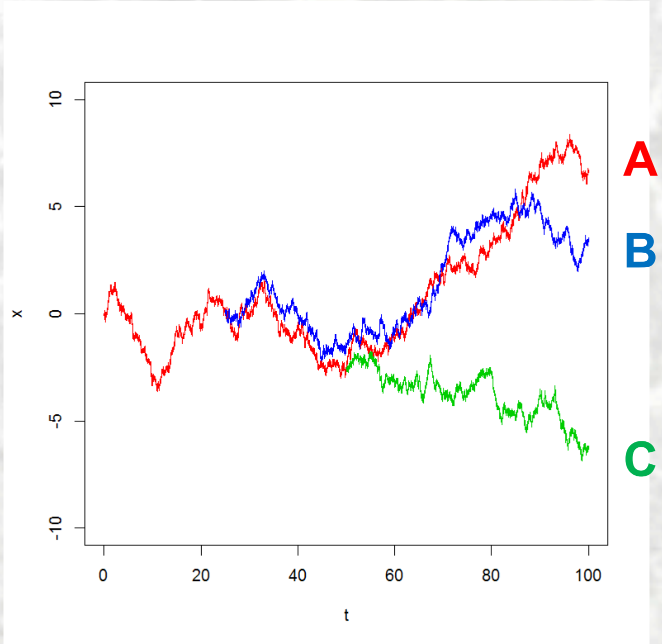

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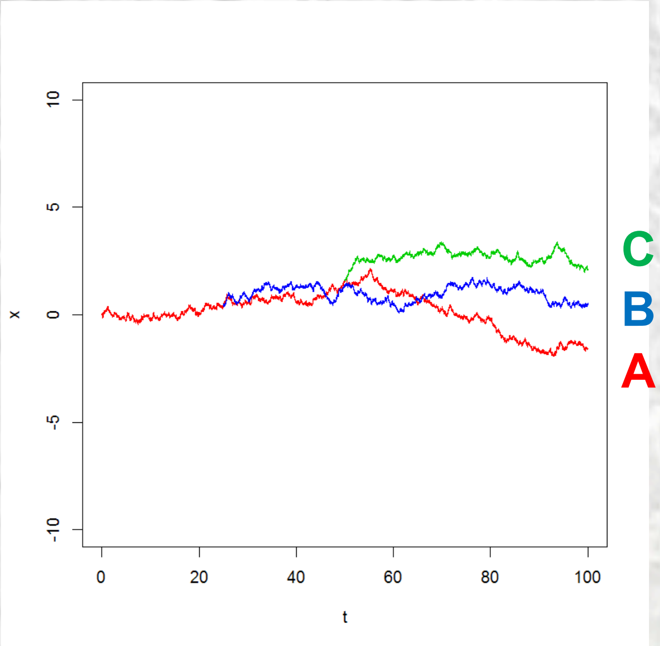
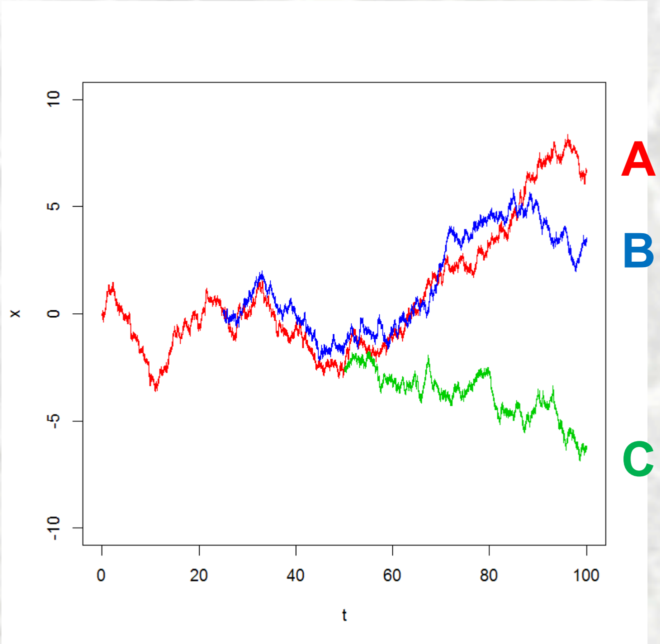


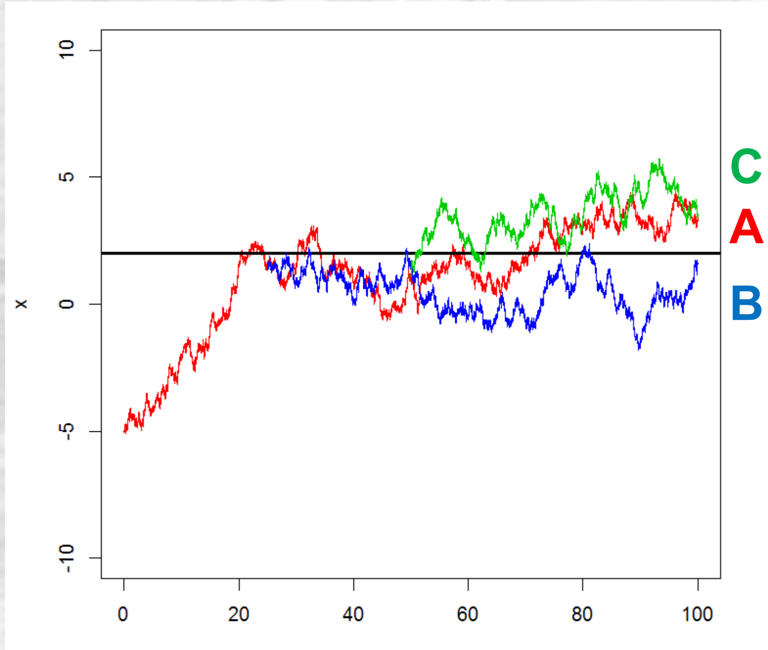


→ trait distance increases linearly with time since divergence (on average)

→ **Fundamental** model in macroevolution, used everywhere!

Two main deviations from Brownian Motion

- **Constraints** on niche evolution



- Modeled using an Ornstein-Uhlenbeck process:

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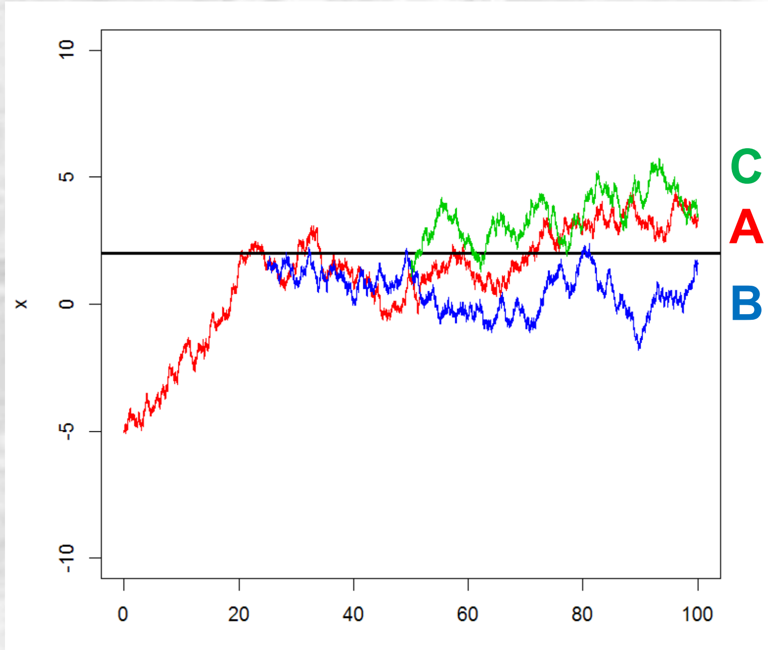

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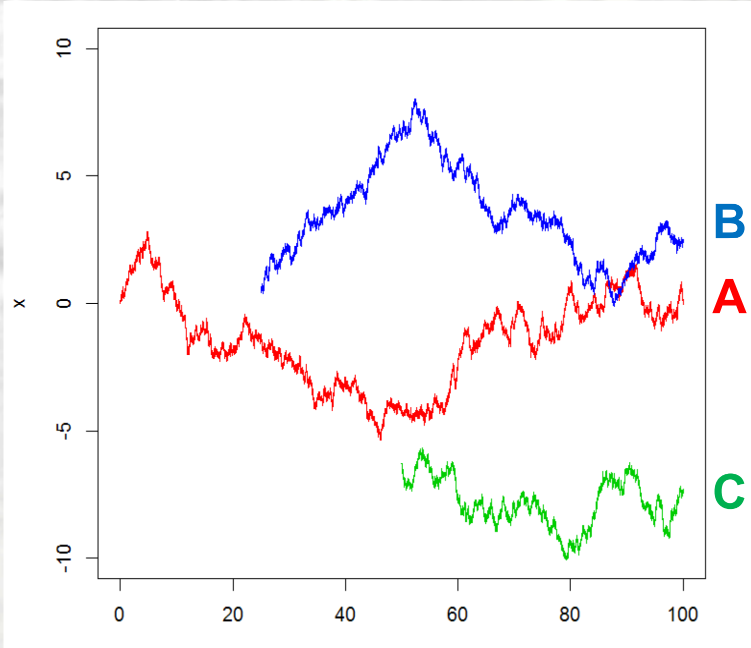

- Discrete shifts happen at speciation (Gould & Eldredge, 1979; Bokma 2008)

A CENTRAL CONCEPT: PHYLOGENETIC NICHE CONSERVATISM

Defined as ***'the tendency for species to retain main aspects of their ecology over time'*** (Harvey & Pagel, 1991)

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IDEA AND PERSPECTIVE

Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species

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REVIEW AND SYNTHESIS

Niche conservatism as an emerging principle in ecology and conservation biology

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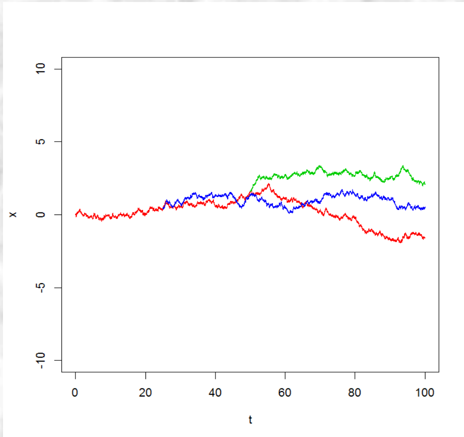
Niche conservatism as an emerging principle in ecology and conservation biology

Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes?

Michael D. Crisp[1] and Lyn G. Cook[2]

Consensus emerging on how to test for Phylogenetic Niche Conservatism (PNC): model comparison



Brownian Motion:

The neutral expectation,
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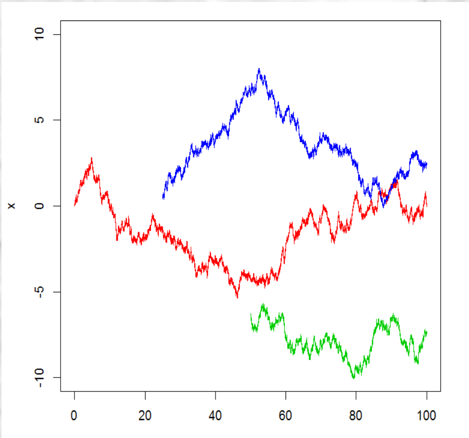

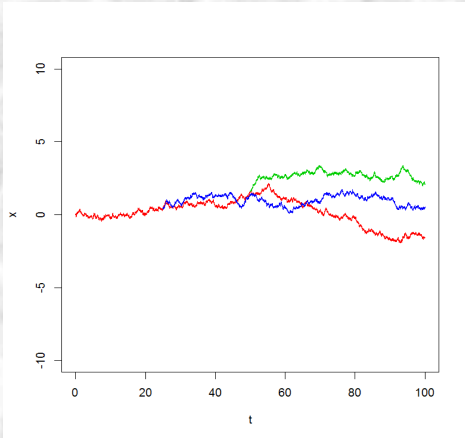

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Niche is labile or is even responsible for speciation (divergent selection)

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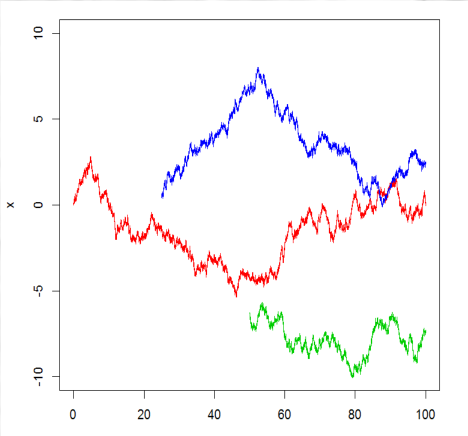
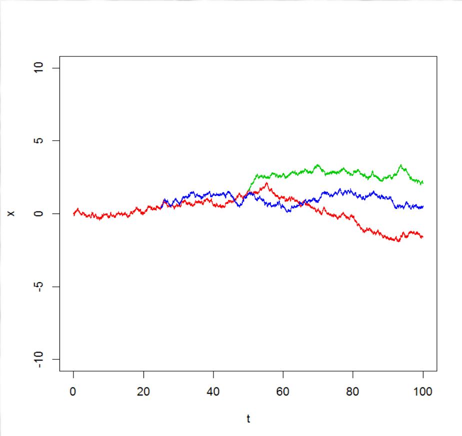
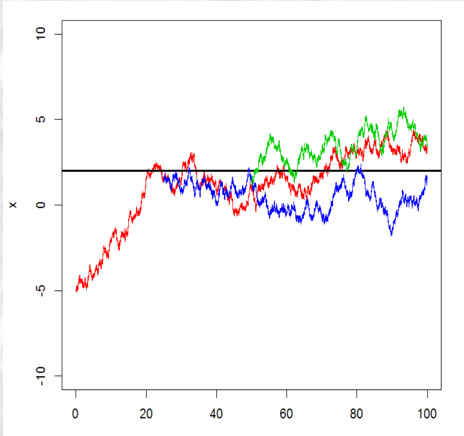

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OU:

Stabilizing selection on the niche → PNC!

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We usually work with realized niches → huge influence of geography

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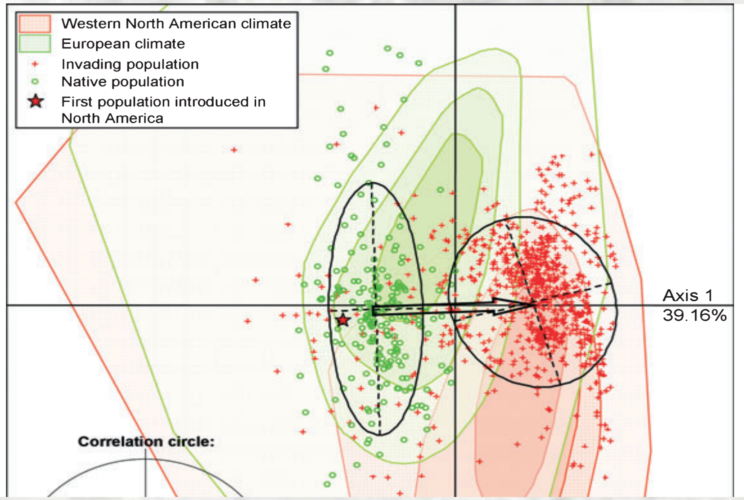

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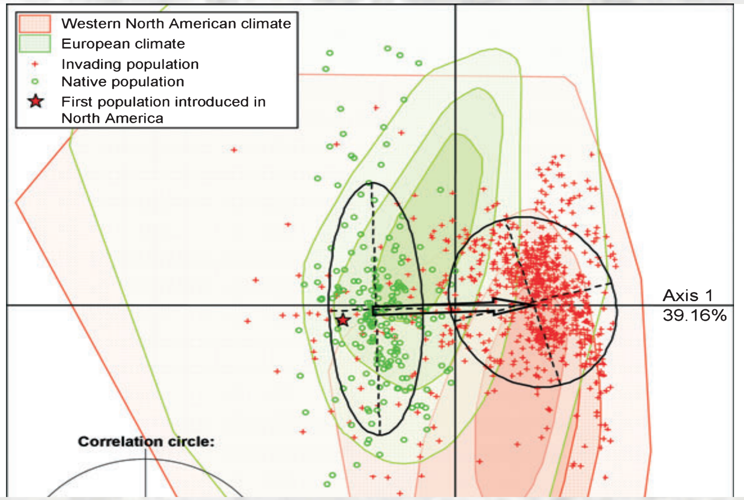

- **Space is bounded** → niche is bounded

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WHAT WOULD BE THE NEUTRAL EXPECTATION FROM A BIOGEOGRAPHIC POINT OF VIEW?

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RATIONALE: 1) simulate a with a **very simple model**, where we make the least assumptions possible and then 2) see what patterns it produces

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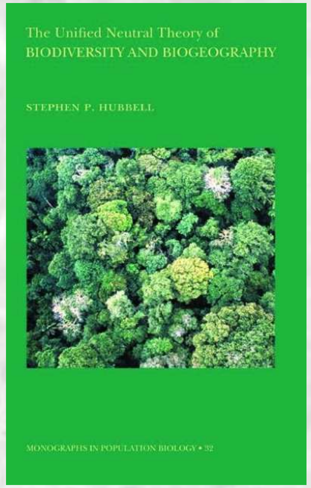
1) Simulate climatic niches evolving according to **Neutral Biodiversity Theory** (NBT, Hubbell 2001)

→ all individuals are functionally equivalent, whatever the species they belong to



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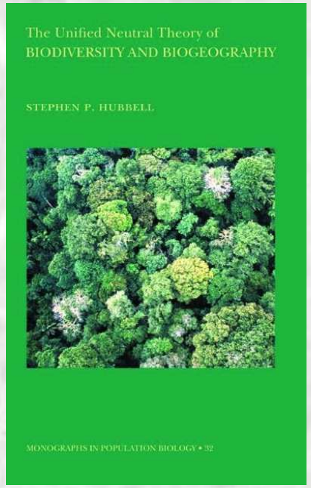

2) Compare the fit of different macroevolutionary models to the niches and trees produced: BM, Ornstein-Uhlenbeck, punctualism?

Simulation from the Neutral Biogeography Theory

- Landscape (continent) = rectangle with boundaries (51x21 pixels) ; maximum 20 individuals per community (pixel)
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Select an individual from the metacommunity

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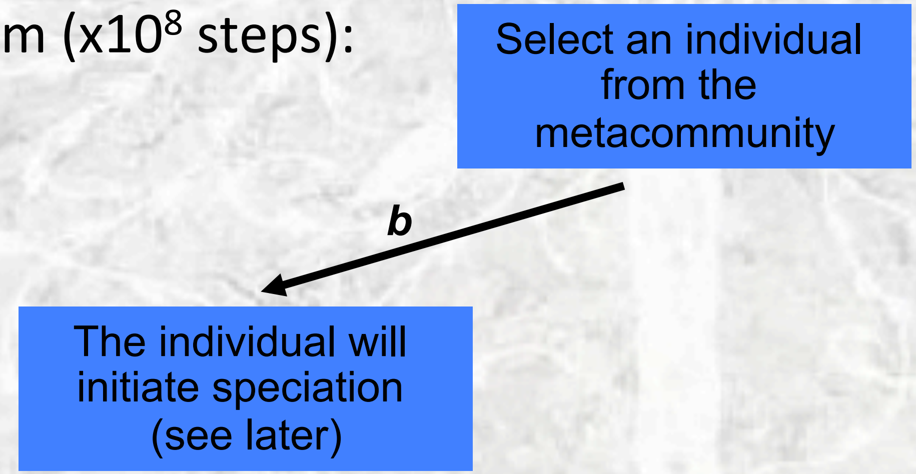

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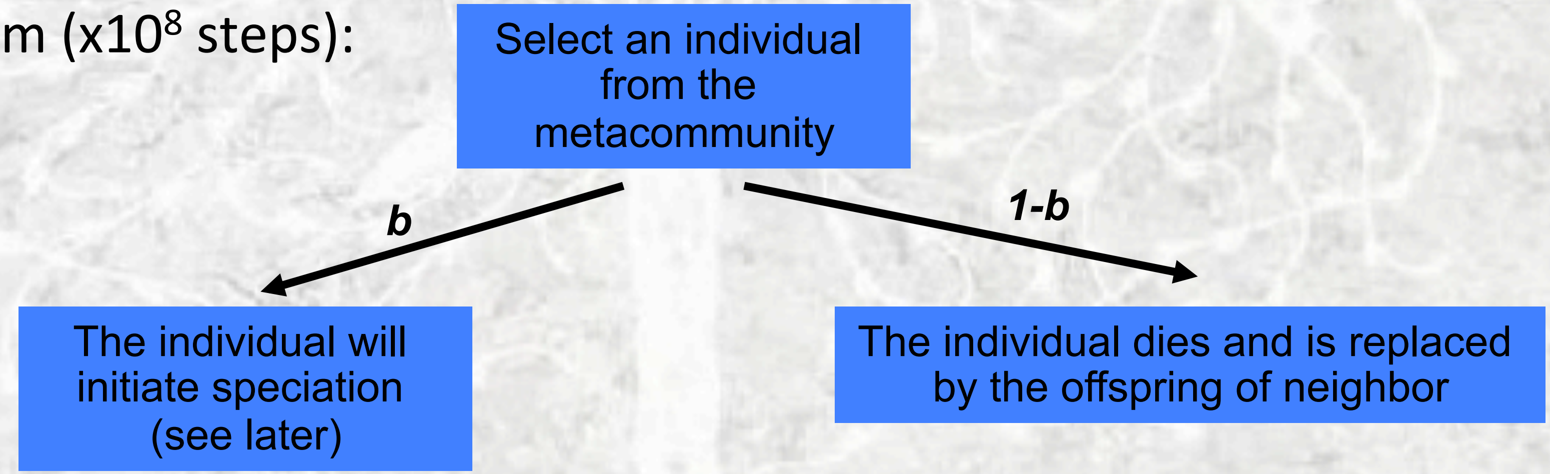

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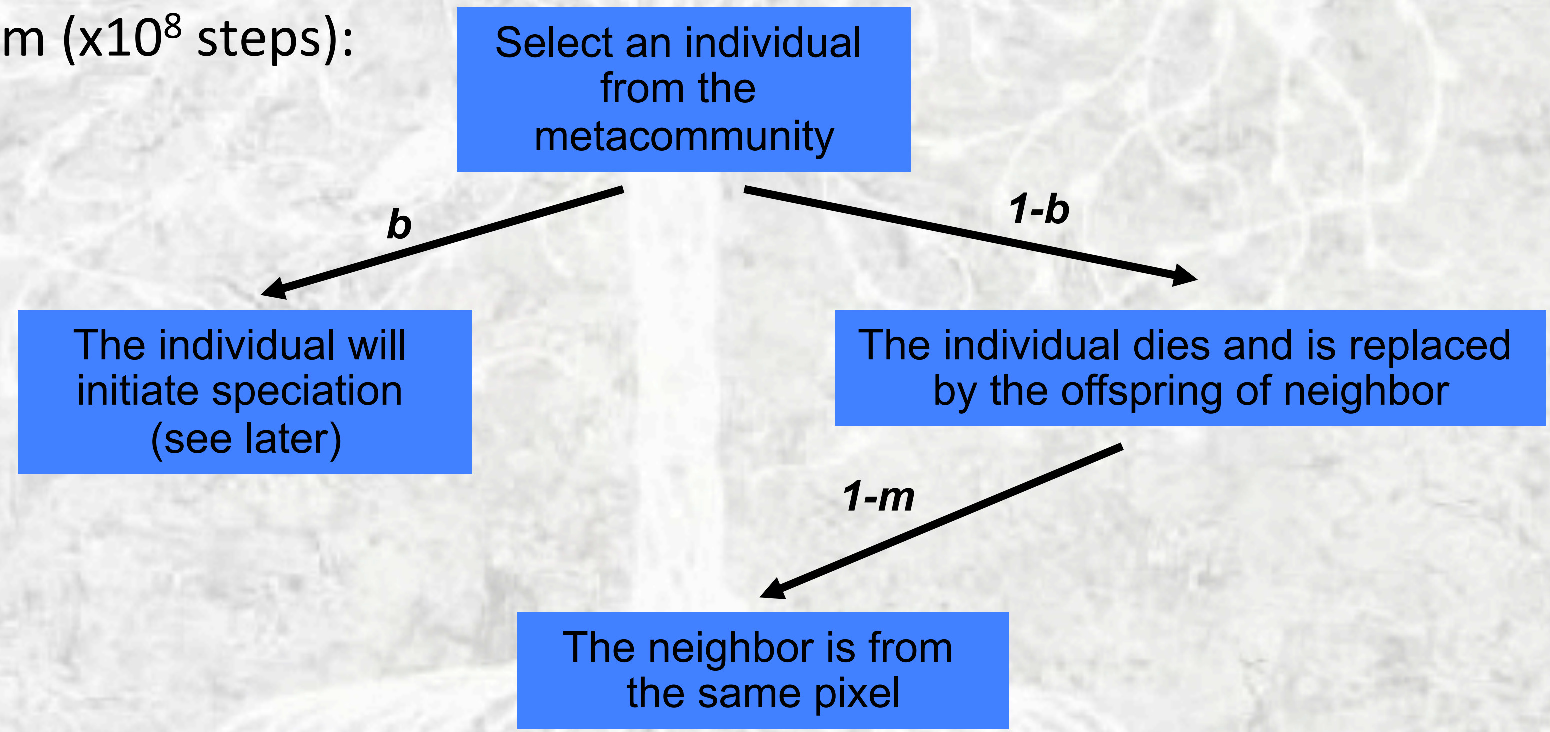

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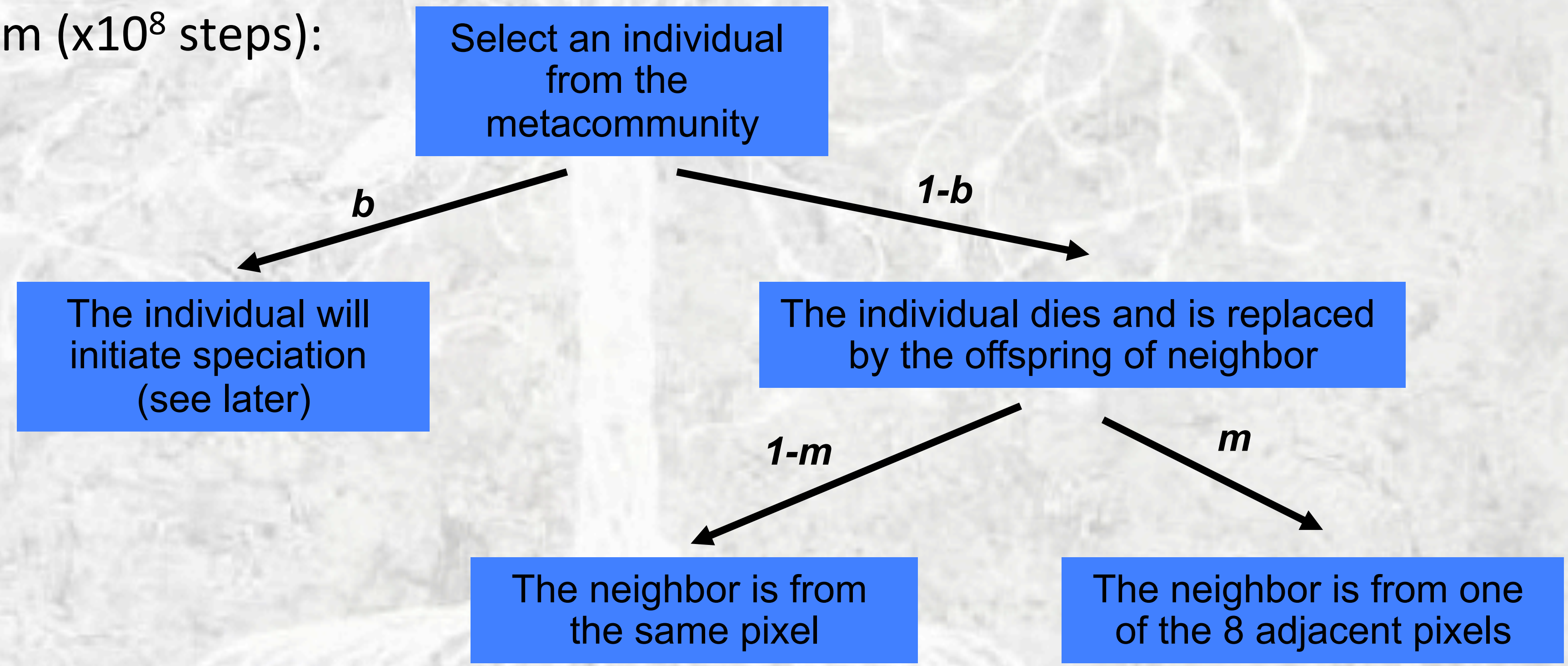
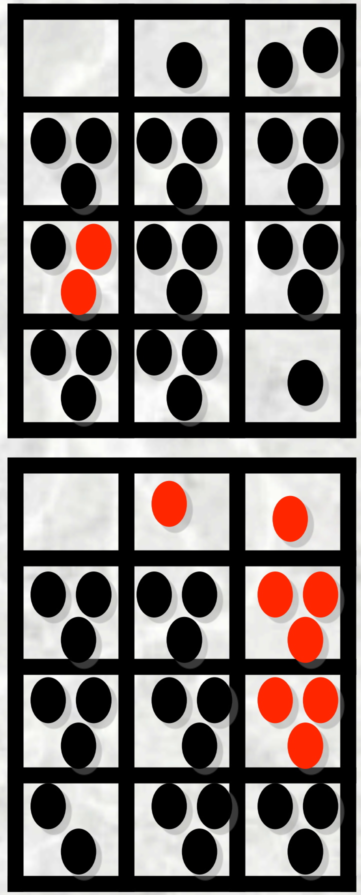


Simulation from the Neutral Biogeography Theory (2)

Two modes of speciation:

- **Random fission** (Hubbell 2001): a random fraction of conspecifics in the same pixel form the new species

- **Vicariance** (Pigot *et al.* 2010): a barrier cuts the species in two



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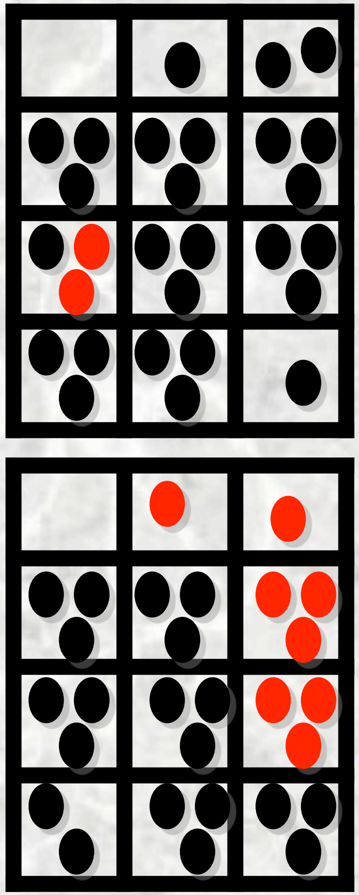

- **Vicariance** (Pigot *et al.* 2010): a barrier cuts the species in two

The environment does not influence the process

→ **all species have the same fundamental niche**, but we measure their realized niches (mean latitudinal position)

ANALYTICAL TREATMENT: ANAGENESIS

2 steps in the algorithm: death and reproduction (migration)

Equation for the evolution of the niche of one species, during anagenesis and before boundaries have been reached:

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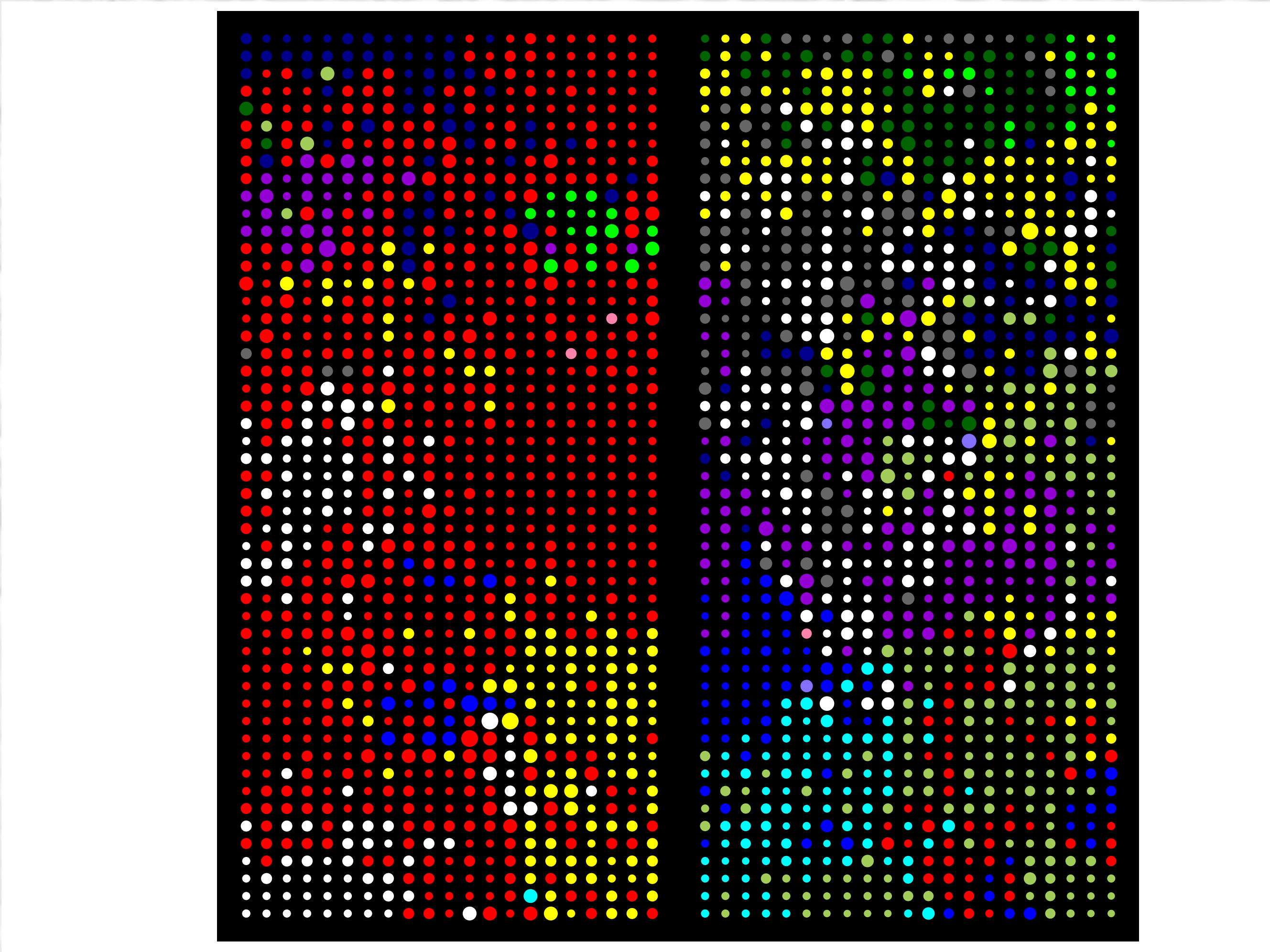
→ niche follows **random steps** with no prefered direction (1), with size depending on migration rate, niche breadth and population size (2-3)

ANALYSIS OF SIMULATION OUTCOMES

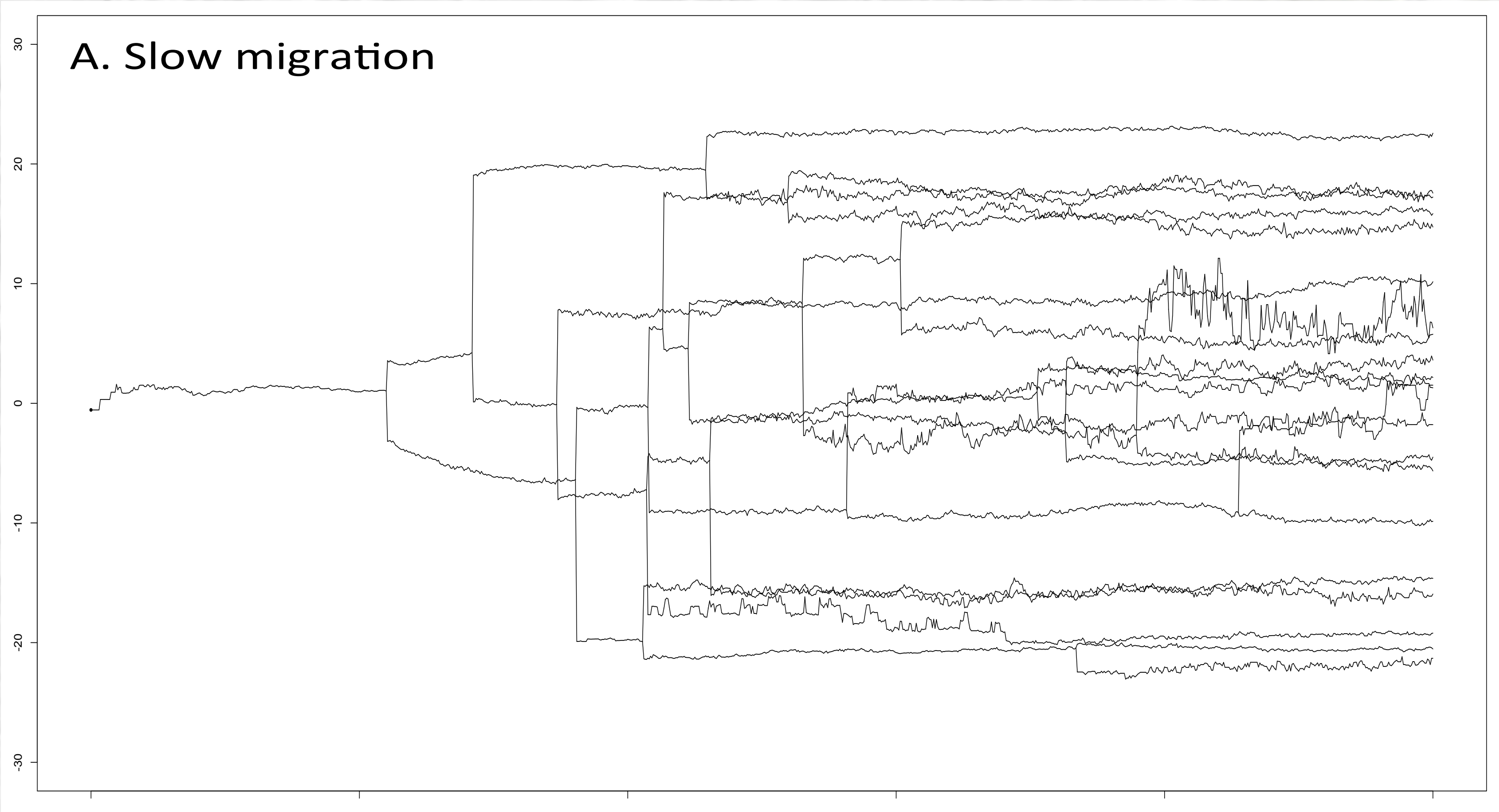
- 3600 simulations, parameters and mode of speciation vary:



Random Fission Vicariance

→ More very rare species and trees more imbalanced under Random Fission

NICHE EVOLUTION DURING SIMULATIONS



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→ **Niche shifts at speciation because of geographic splitting**

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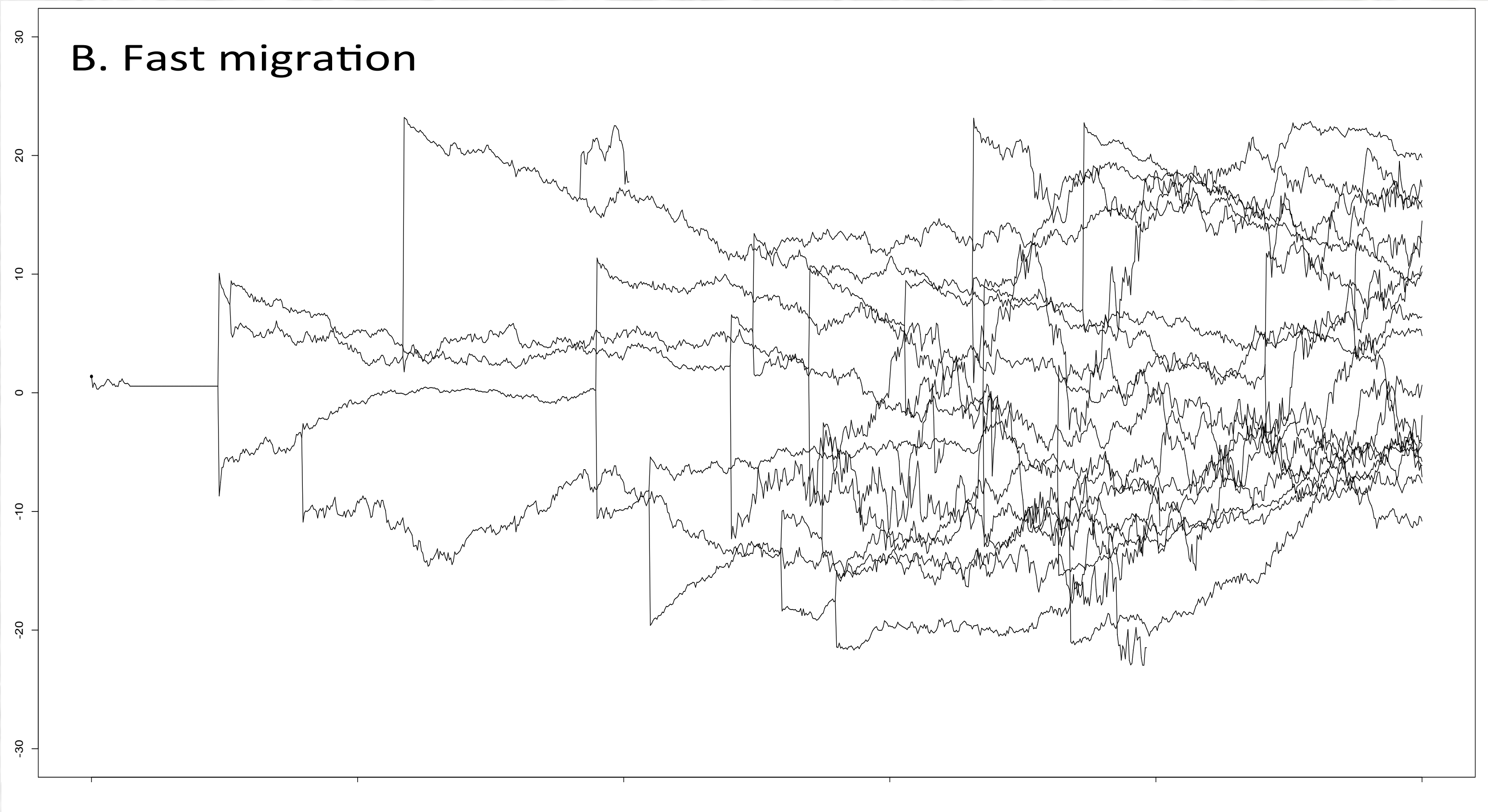

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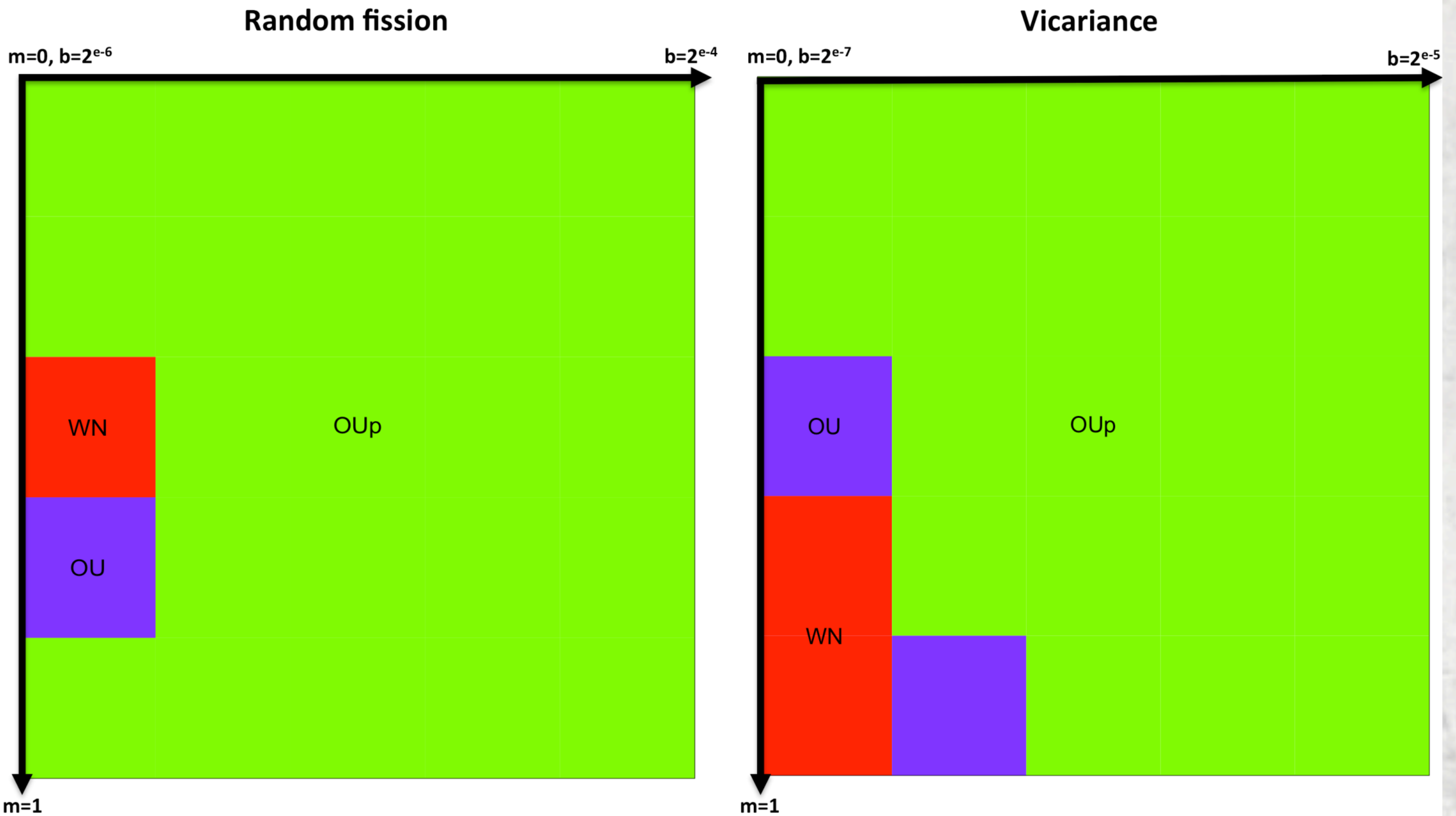
CAN CONSTRAINTS ON NICHE EVOLUTION ARISE SIMPLY THROUGH BOUNDED GEOGRAPHIC SPACE?

→ **Niches are attracted towards the middle of the landscape because of the boundaries**

COMPARISON TO MACROEVOLUTIONARY MODELS



→ OUp = {constraints + punctualism} always the best

→ Brownian Motion often gets the worse fit

OBJECTIVES

WHAT WOULD BE THE NEUTRAL EXPECTATION FROM A BIOGEOGRAPHIC POINT OF VIEW?

→ **If niches evolved primarily through biogeographic processes and no physiological constraint were present, we would expect to see both punctualism and constraints**

CASE STUDY: *DIPROTODONTIA* IN AUSTRALIA

Florian BOUCHER, SEMOVI, March 13th 2013

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Various models fitted to the evolution of their mean annual temperature (AIC comparison):

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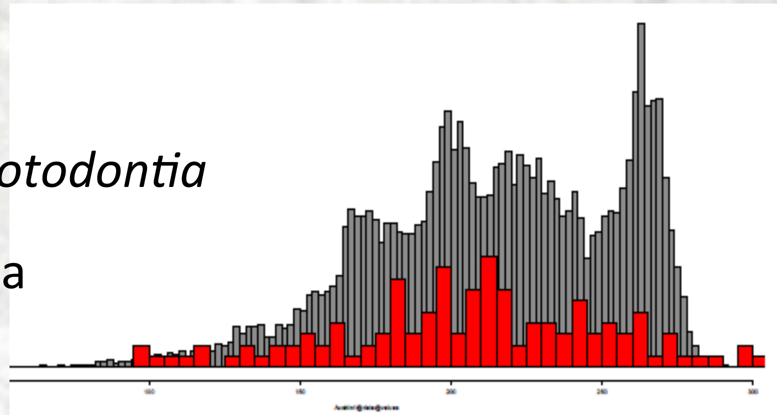
… or simply **neutral dynamics and dispersal limitation** in Australia + Tasmania + New Guinea?

→ Distribution of mean niches of *Diprotodontia* matches distribution of climate in Australia



CONCLUSION – TAKE HOME MESSAGES

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→ **The neutral expectation should be punctualism + constraints.**

LIMITATIONS OF THE STUDY

Processes are simplified:

- Migration in discrete steps
- Speciation is phenomenological

Climatic niches are more complex than a North-South gradient

Fundamental niches are not all equal of course…

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Fundamental niches are not all equal of course…

→ Conclusions are mainly **qualitative**

→ Neutral Theory must be seen as a **first order approximation of reality**, on which to base more realistic models

PERSPECTIVES FOR FUTURE STUDIES

Models with constraints may arise from various processes:

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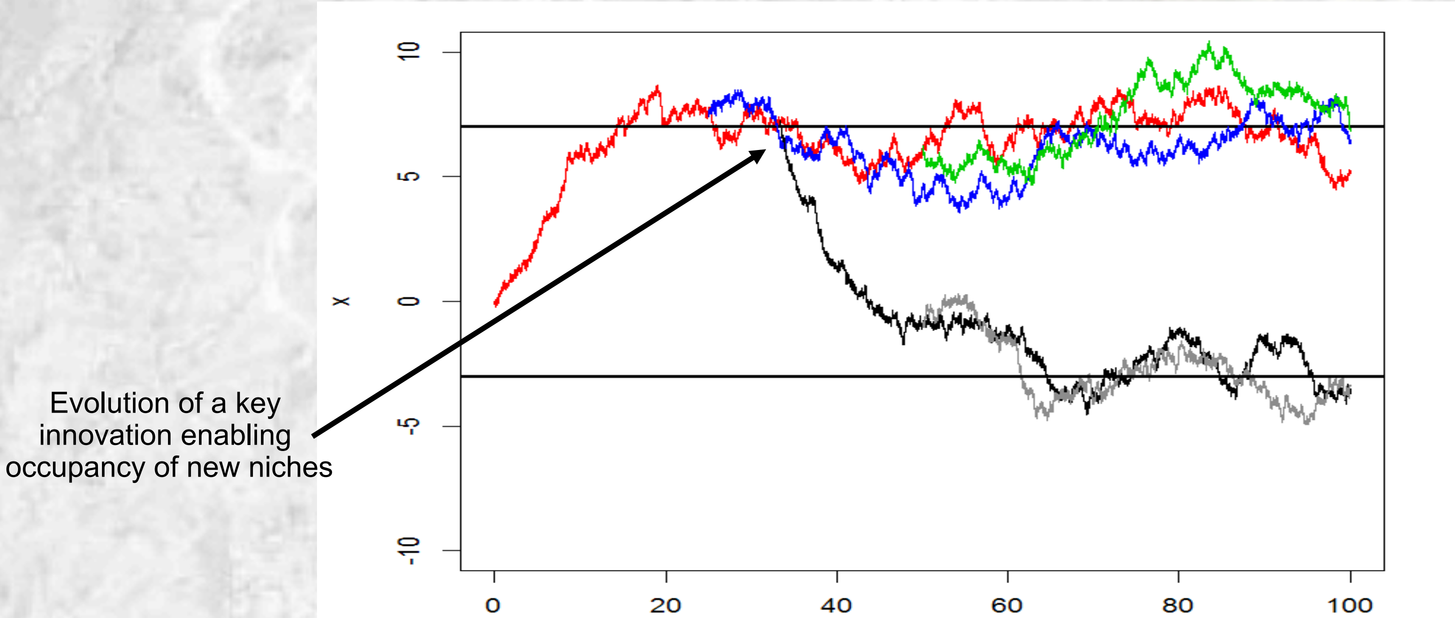
More elaborate models, where niches depend on traits/distribution should be used:



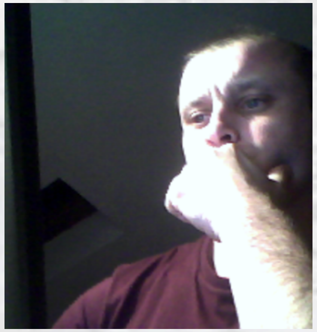
→ **tools are already developped** (e.g. Beaulieu *et al*. 2012), let's use them!

THANK YOU FOR YOUR ATTENTION

… and thanks to my collaborators:

Dr. Wilfried Thuiller, LECA, Univ. Grenoble

Dr. T. Jonathan Davies, McGill University, Montréal



Dr. Sébatien Lavergne, LECA, Univ. Grenoble