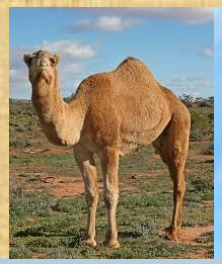
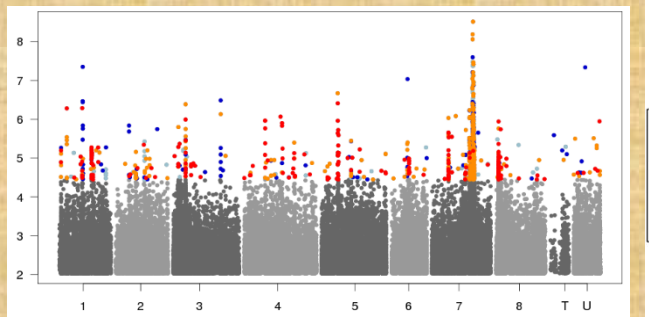
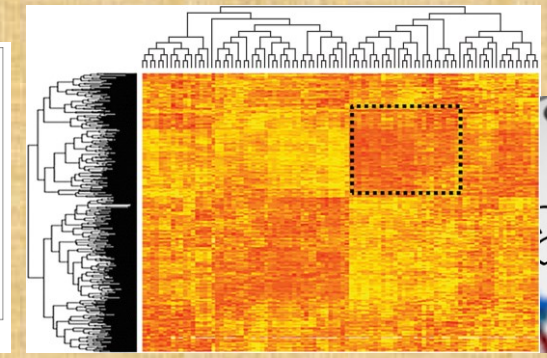



Genomics of speciation and adaptation: Introduction

18.02.2020, Clément Lafon Placette






Speciation: a question as old as human kind

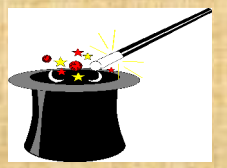
How do discrete forms of life arise and stay distinct?

Kaluli people of Papua New Guinea

People covered the earth but there was nothing else: no plants, no animals... The people became cold and hungry. Then one man directed one group to become trees and they did. He directed another to become fish, another banana and so forth. The few people left became the ancestors of present-day human beings.

Spontaneous generation (Aristotle)

Life arise from non-living matter in an appropriate form



Species: reality or view of the human mind?

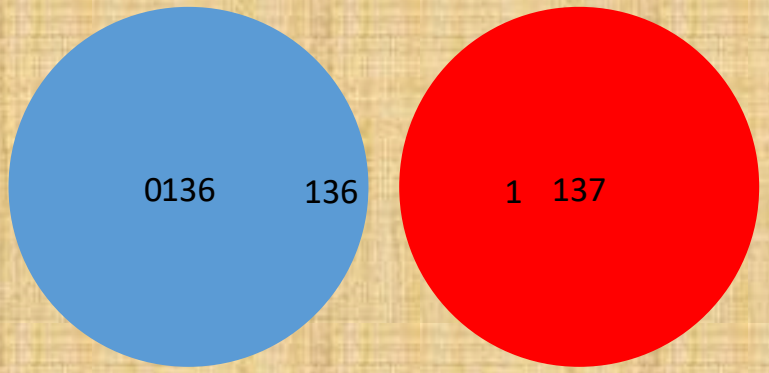
A way for the human brain to classify continuous variation?

Or are species real discrete entities?

Arfak Mountains, New Guinea

Concordance between independent approaches to determine species?

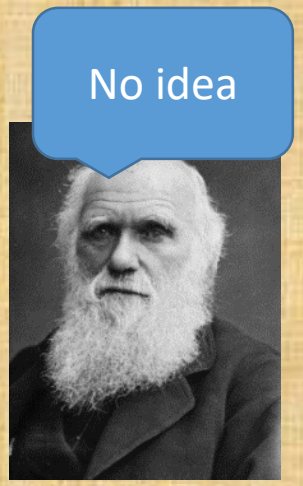
Vernacular names of birds given by Arfak tribesmen



Linnaean bird species in Arfak mountains

Mayr, 1963

Species: reality or view of the human mind?



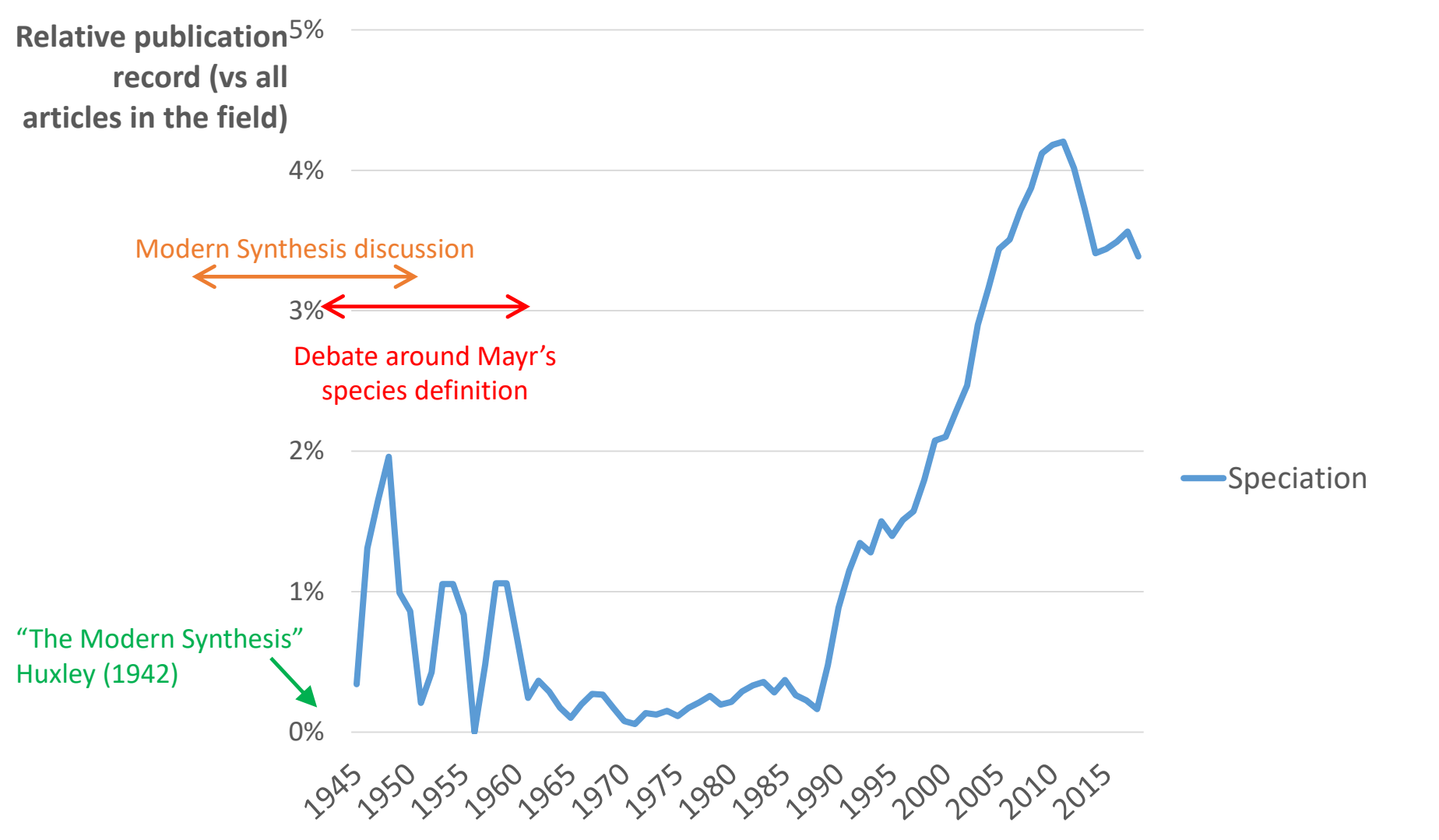
Darwin did not resolve this question, or was at least ambiguous

"I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety"

Diversification = speciation, mostly as a result of local adaptation (and sexual selection)

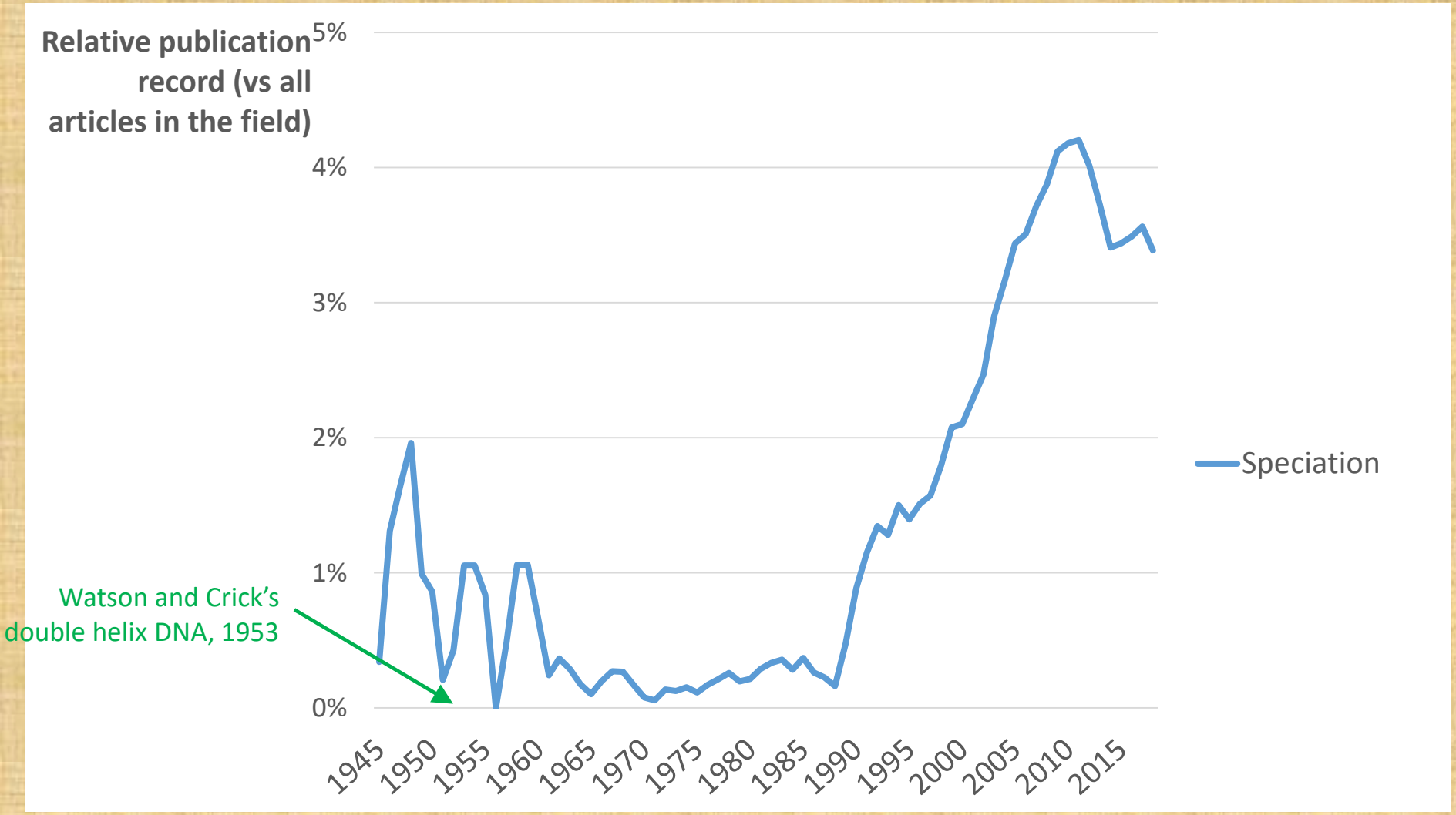
Interest for speciation goes like fashion: by waves

Data: WoS

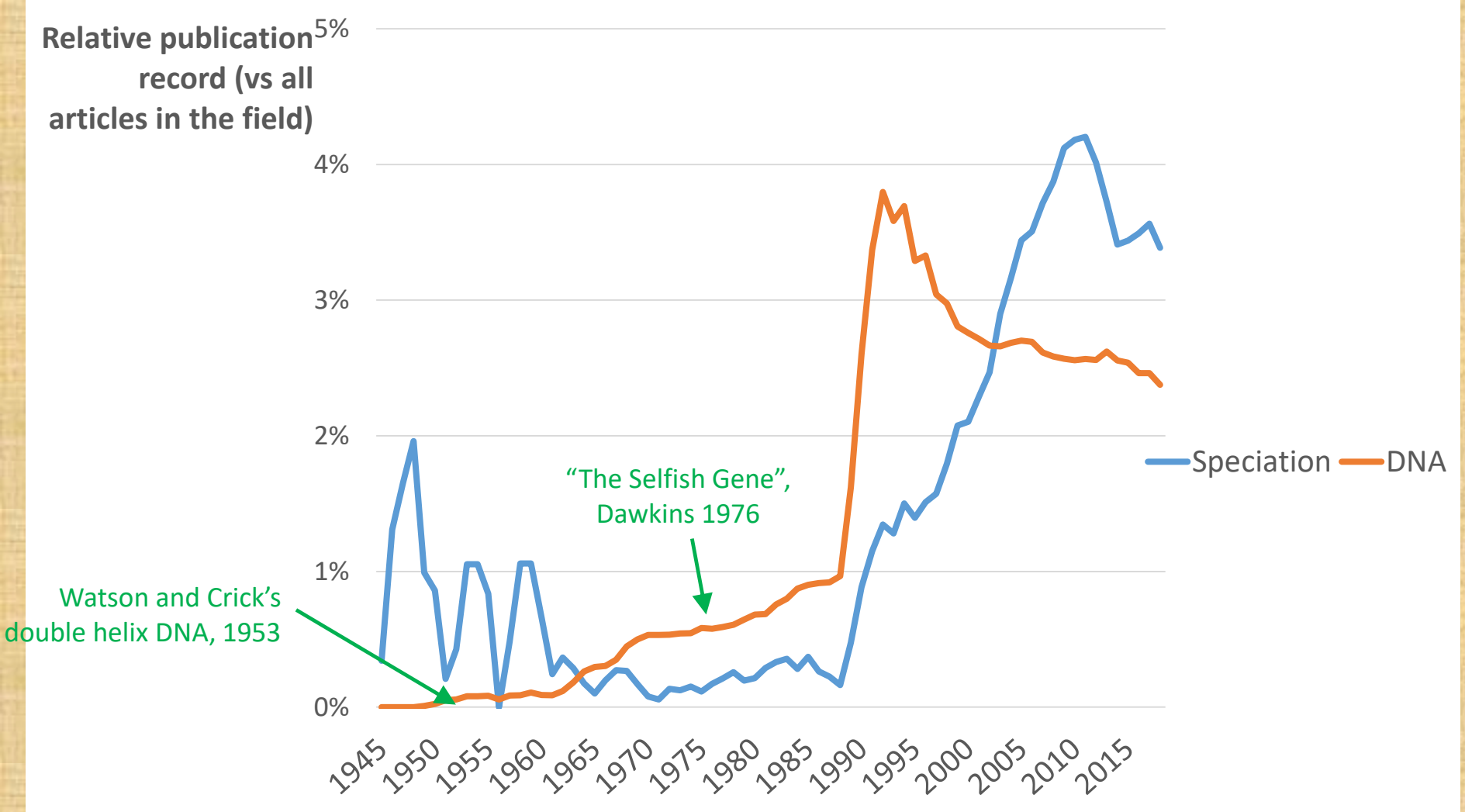


Speciation got neglected for nearly 30 years

Data: WoS



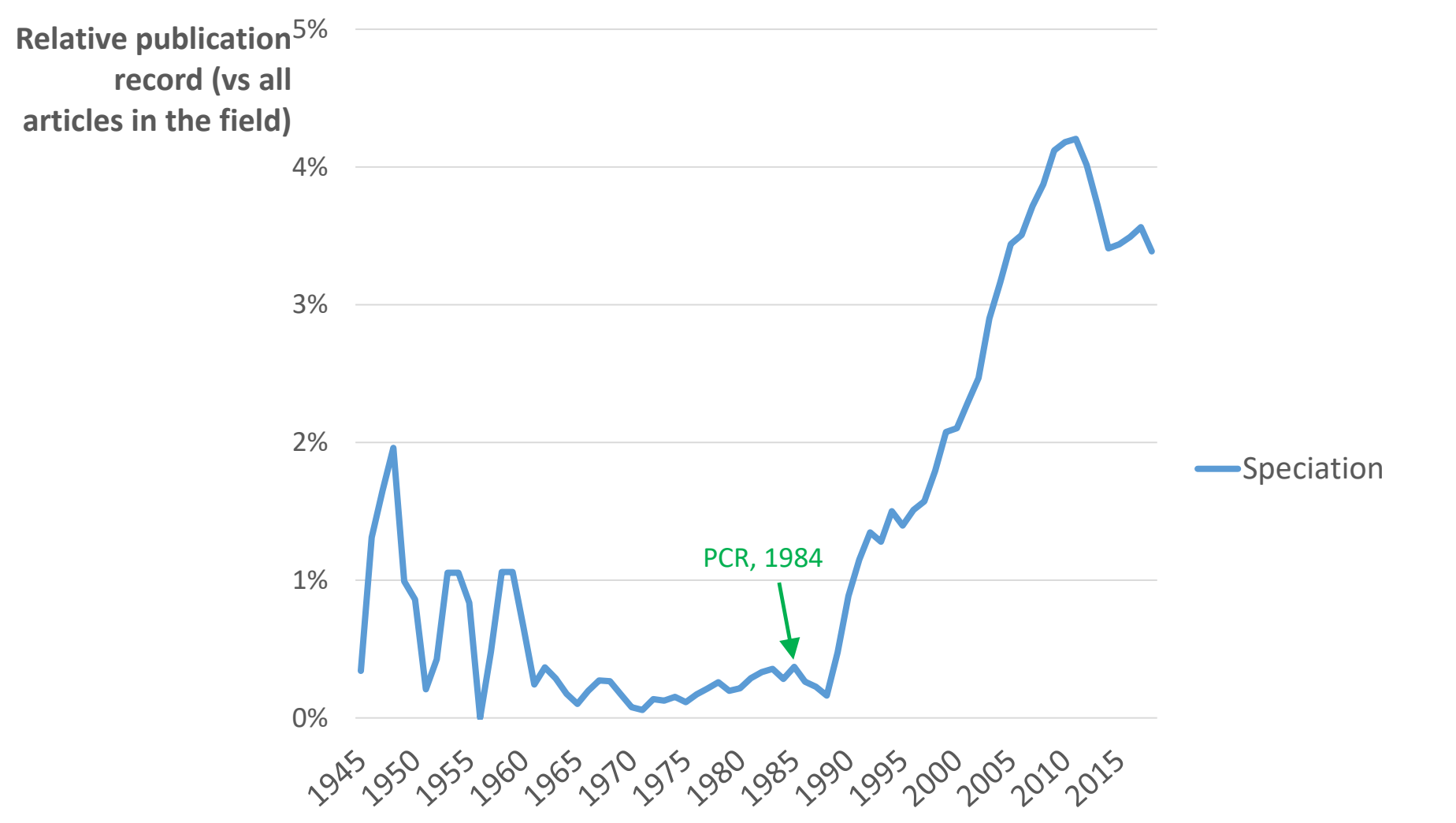
For nearly 30 years, evolutionary biologists focused on DNA and the source of *variation*, just like the modern synthesis



Data: WoS

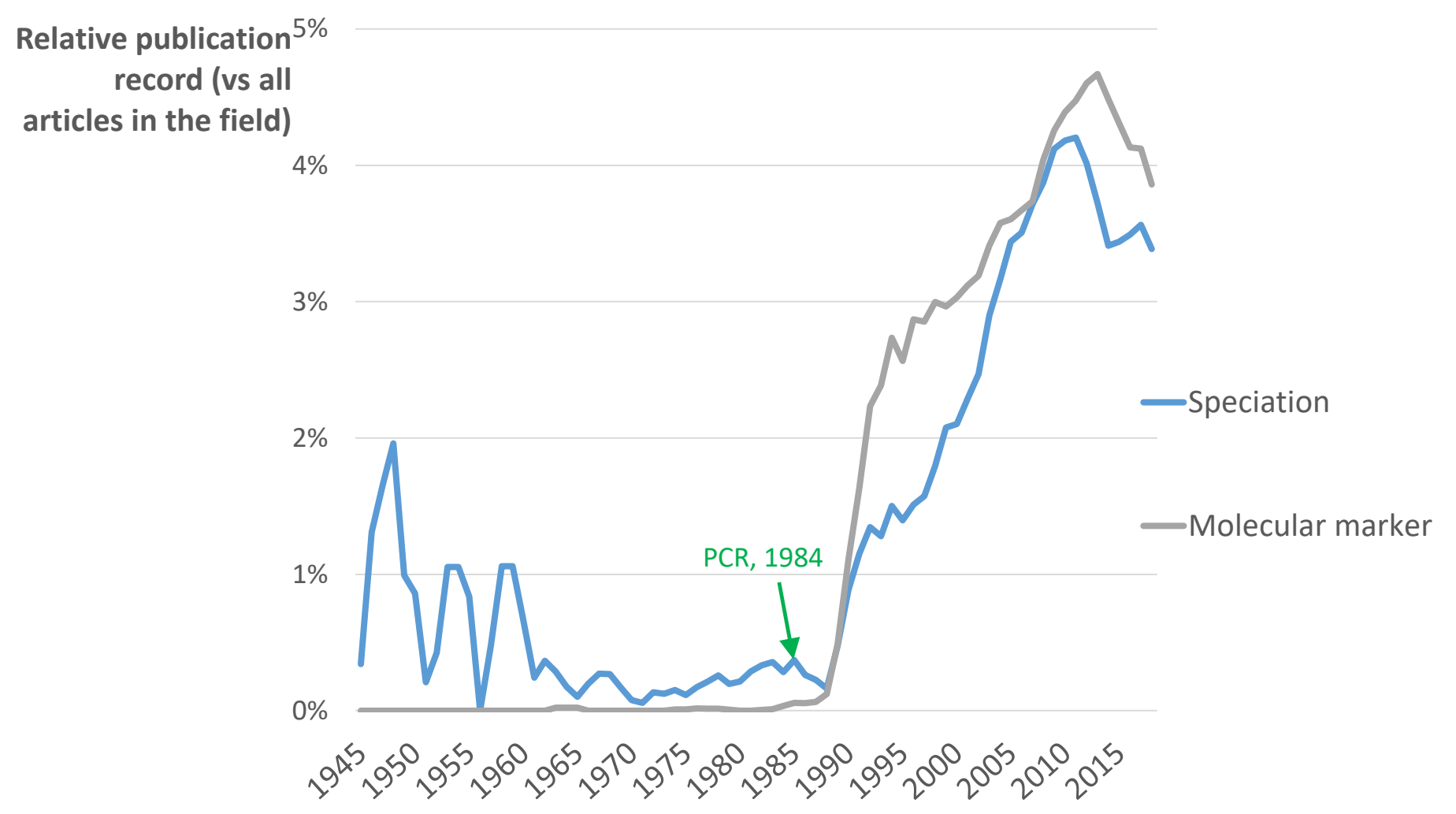
A savior came to rescue speciation research…

Data: WoS



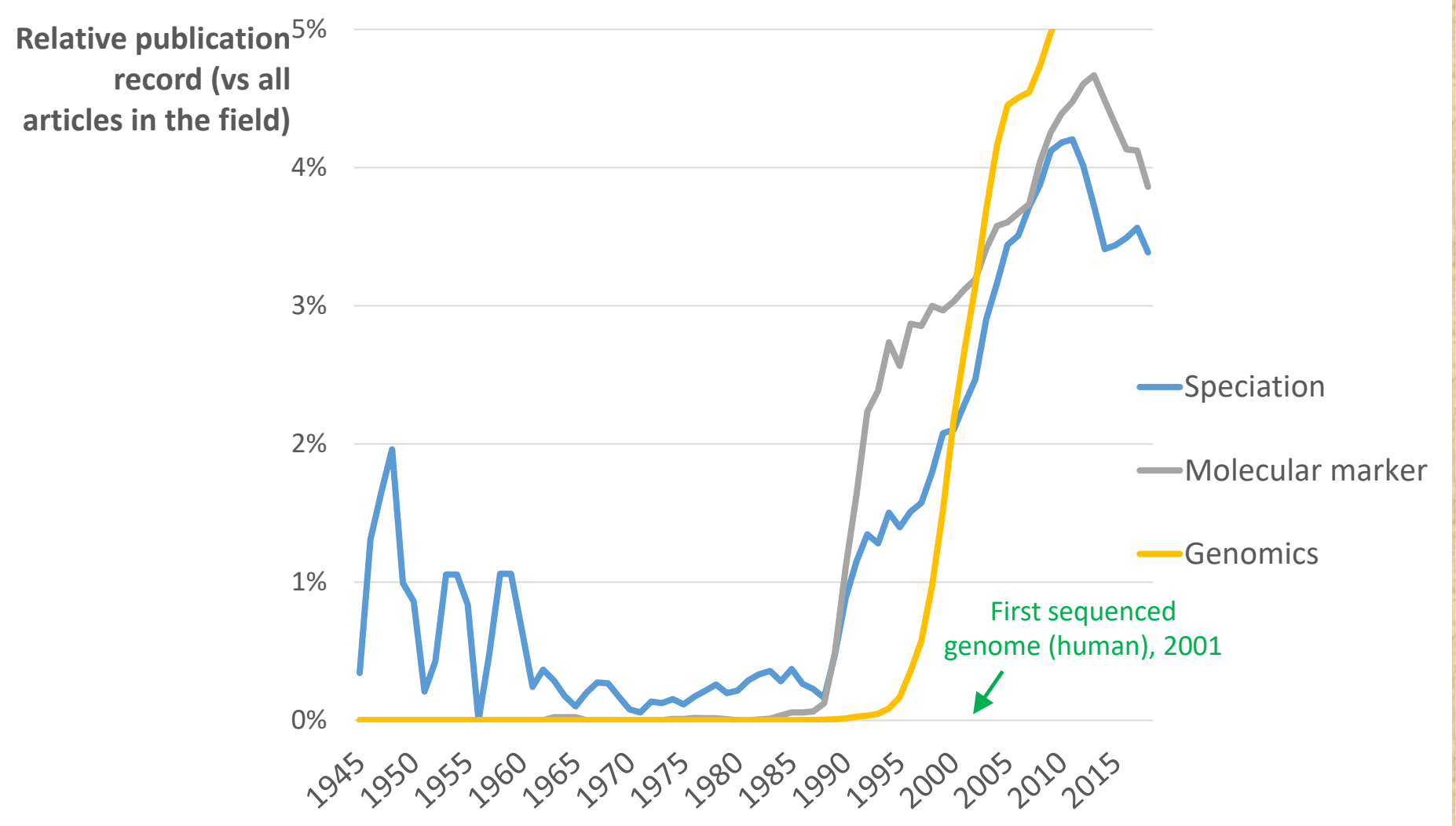
PCR allowed the development of molecular markers

Data: WoS



And now, NGS?

Data: WoS

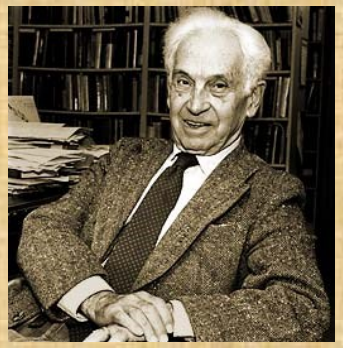


What is a species anyway?
Go to menti.com, code 18 83 08

A/ Species are groups of interbreeding natural populations that are reproductively isolated from other such groups

B/ A species is a lineage which occupies an adaptive zone minimally different from that of any other in its range and which evolves separately from all lineages outside its range

C/ A species is the smallest exclusive monophyletic group of common ancestry



Let's just pick our definition

In this course: **"Species are characterized by substantial but not necessarily complete reproductive isolation"** Coyne & Orr 2004

From the 'Biological Species Concept' (Mayr, 1942→1995): "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups"

In other words, focus on *how species emerge*, the processes,
= **how/why/when hybridization barriers arise**,
which maintain genetic distinctiveness

We will consider ecological differentiation as a reproductive barrier

Plan of the lecture

- Types of hybridization barriers
  - Prezygotic barriers
  - Postzygotic barriers
- Emergence of hybridization barriers: genetic drift *vs* selection
- Allopatric, parapatric, sympatric speciation, secondary contact
- Genomics: some new with the old?
- What is driving speciation?
- Organization of the course

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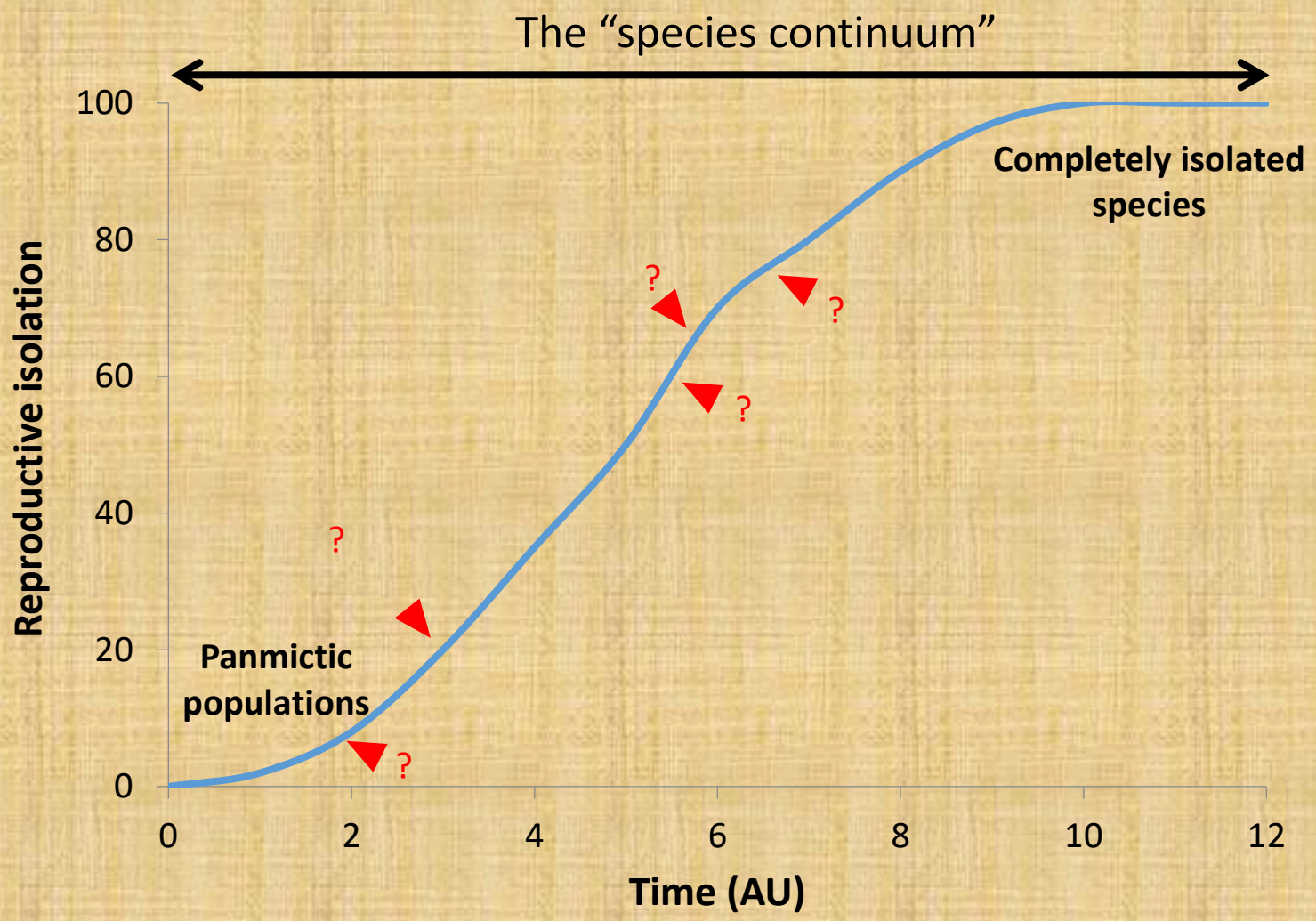
Reproductive isolation, a sum of different hybridization barriers



Plan of the lecture

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  Prezygotic barriers

  Postzygotic barriers

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Pre-zygotic barriers

Ecological differentiation

Animals: behavioral differentiation

P. axillaris

P. integrifolia

Single Gene–Mediated Shift in Pollinator Attraction in *Petunia*

Maria Elena Hoballah, Thomas Gübitz, Jeroen Stuurman, Larissa Broger, Mario Barone, Therese Mandel, Alexandre Dell'Olivo, Maeva Arnold, Cris Kuhlemeier

Published March 2007. DOI: https://doi.org/10.1105/tpc.106.048694

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Some examples

López-Fernández and Bolnick, 2007

Lepomis cyanellus

Intraspecific embryo

Hybrid embryo

L. megalotis

Liger is huuuuge, but sterile

Solanum chilense Hybrid *S. peruvianum*

Florez-Rueda et al., 2016

Bateson-Dobzhansky-Müller incompatibility, a simple model to explain PoZHB

A+B = negative epistasis
→impaired hybrid

Bomblies and Weigel, 2007

The “snowball effect” model

Two lineages start to evolve separately.

Every <time unit>, *m* mutations appear in each of two lineages

At time *t*, the total number of mutation pairs between lineages is:

Go to menti.com, code 28 36 53

Orr, 1995

The “snowball effect” model

Two lineages start to evolve separately.

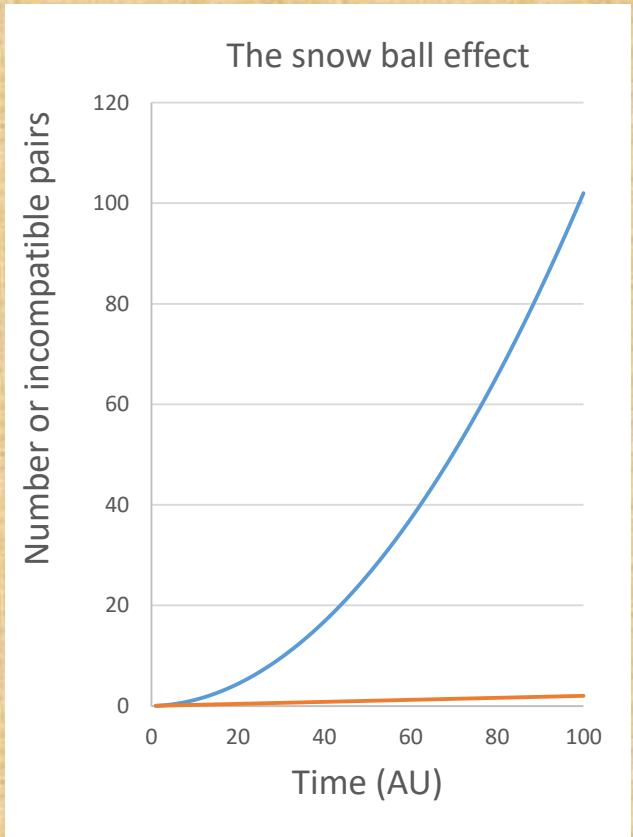
Every <time unit>, *m* mutations appear in each of two lineages

At time *t*, the number of new nucleotide pairs between lineages

- is not just $\sum_{t_0}^{t} m$, the total number of mutations
- but $(\sum_{t_0}^{t} m)^2$, the total number of combinations

Among all the possible new pairs,
there is a probability *p* that some causes hybrid incompatibility

With *m* = 1, p = 1%

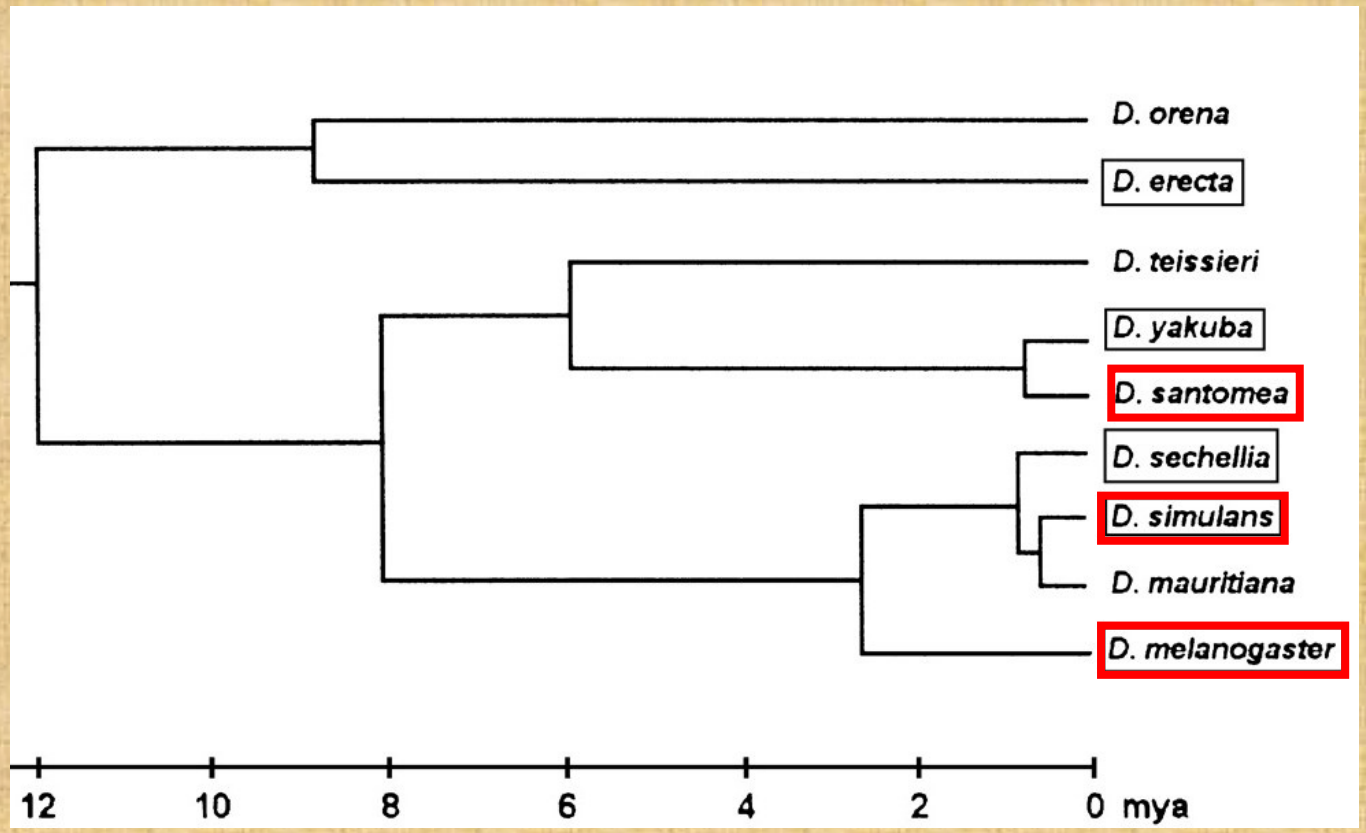


Postzygotic hybridization barriers
(BDM incompatibilities)
are predicted to arise much faster than in a linear fashion

Problem is: barely demonstrated experimentally
“the missing snowball”

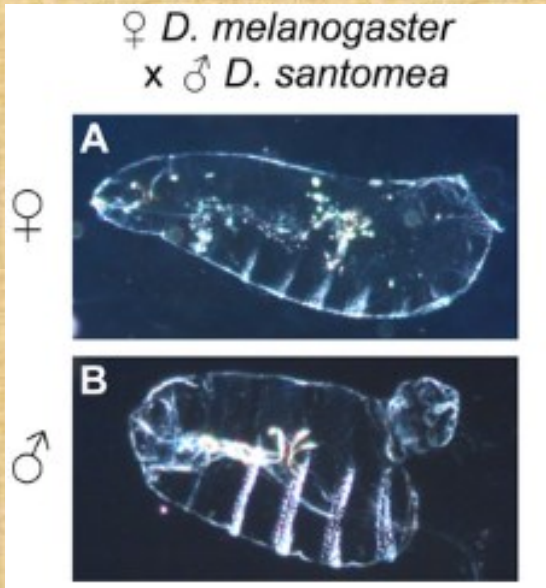
Orr, 1995

Such a case in Drosophila?



Matute et al., 2010

Such a case in Drosophila?

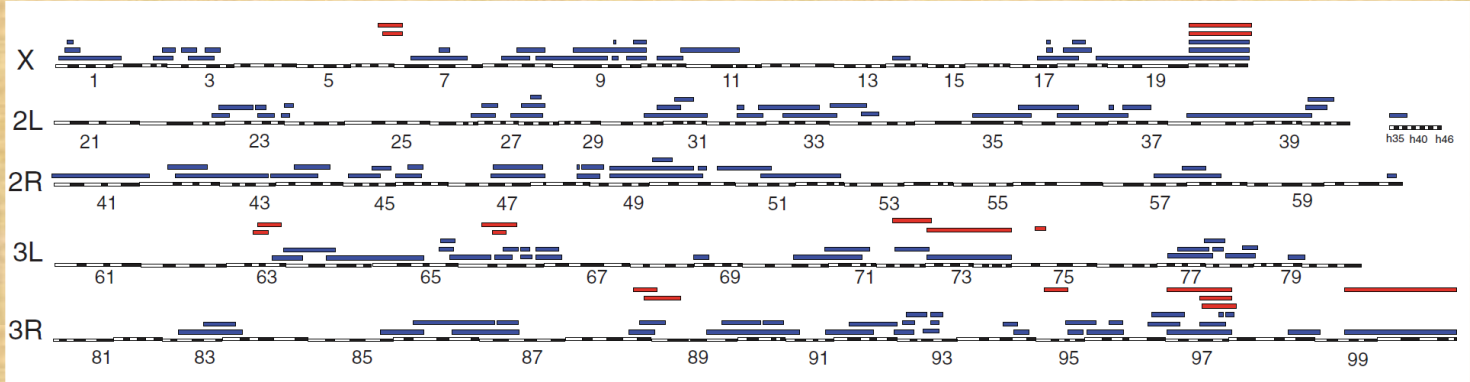


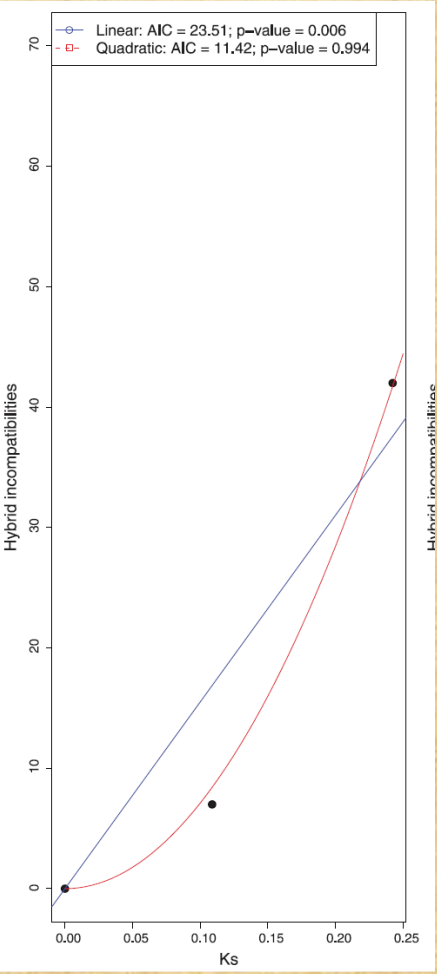
Crossing between the 3 species: identification of all hybrid incompatibilities

Mapping the genetic combinations causing them

Counting the number of combinations

Relation to genetic distance: bingo





Matute et al., 2010

The “snowball effect” model

Two lineages start to evolve separately.

Every <time unit>, *m* mutations appear in each of two lineages

Does not take into account population genetics processes

At time *t*, the number of new nucleotide pairs between lineages

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- but $(\sum_{t_0}^{t} m)^2$-1, but the total number of combinations

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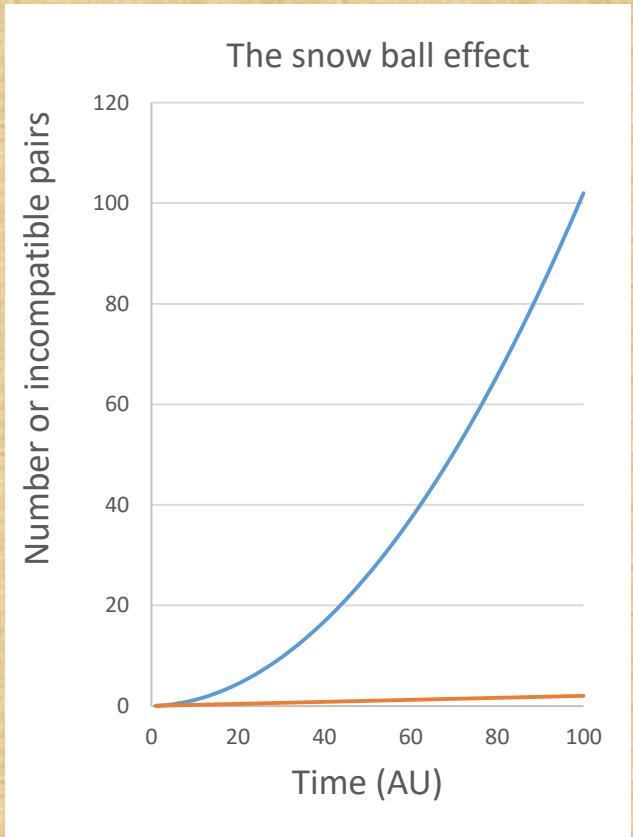

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Genetic drift vs selection

Genetic drift: either by neutral evolution, or “founder effect”

Natural selection: either as byproduct or selection on hybridization barriers directly (reinforcement)

Hot debate up to the 90s, now relatively resolved. Mostly selection

Hyb. barriers as byproducts of selection

An obvious case: sexual selection

Selection acts on hybridization barriers directly: Reinforcement

If hybrids are maladapted, this is costly fitness-wise

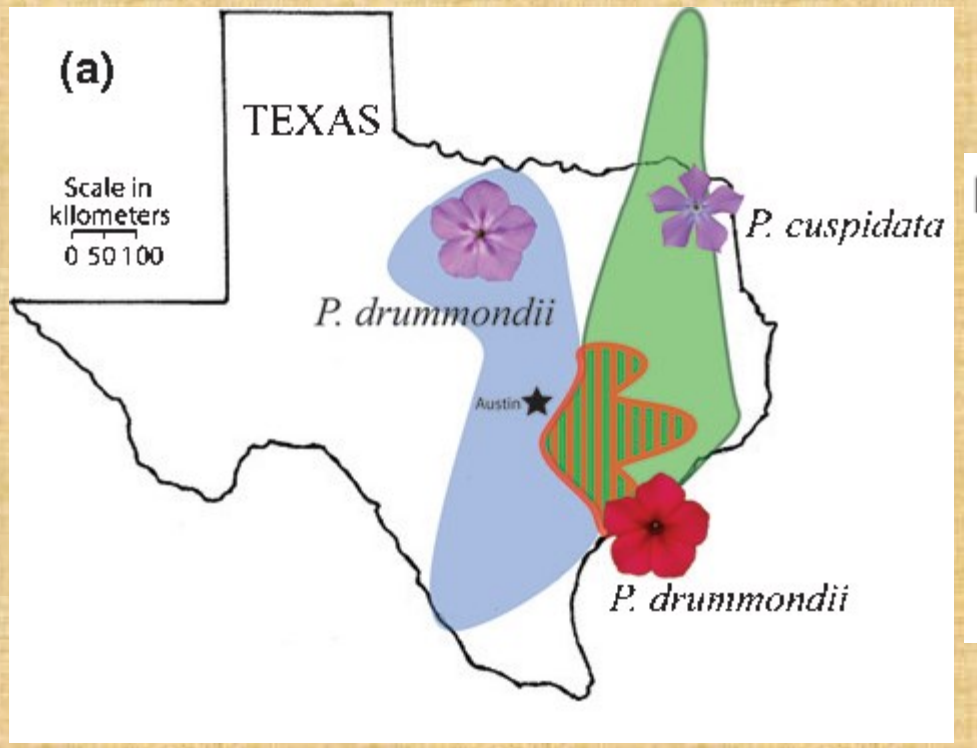
Positive selection to prevent hybridization

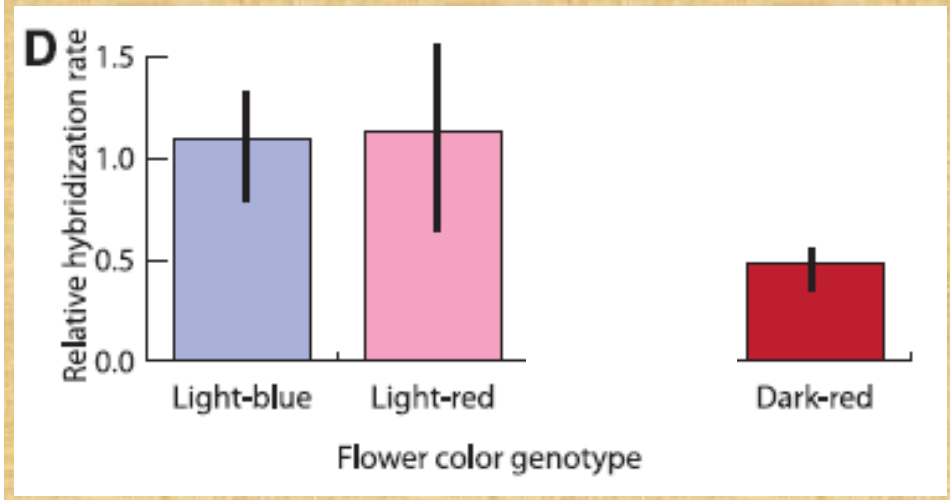
Expectations:

In allopatry, low level of prezygotic barriers

But in sympatry (second contact zone), high level

A possible case in *Phlox*





Hopkins, 2013; Hopkins and Rausher, 2012

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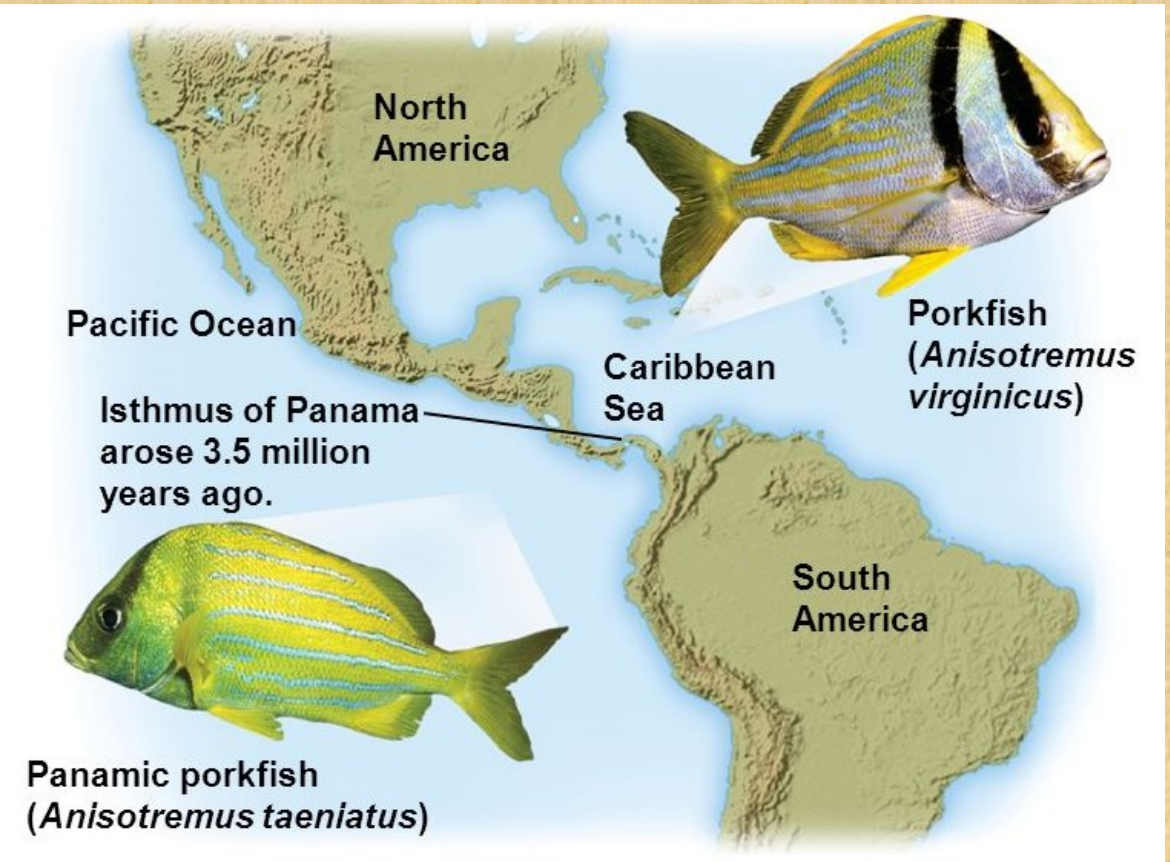
Allopatric speciation



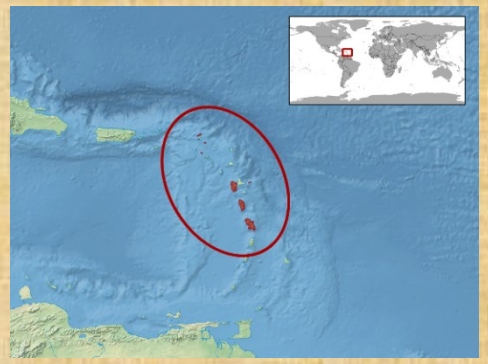
Geographic separation = no gene flow

→ They evolve separately

→ Possibility for new hybridization barriers to arise, either as a byproduct of differential selection, or neutral evolution.

Allopatric species do not always reach complete reproductive isolation

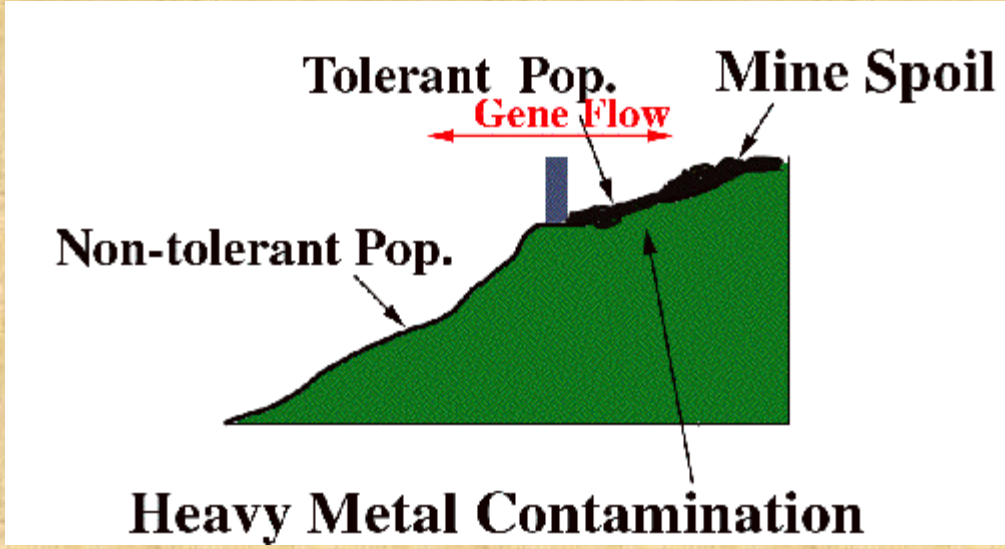
Lesser Antillean iguana
Iguana delicatissima



Introduction = extensive hybridization

Green iguana
Iguana iguana

Parapatric speciation



http://www.as.wvu.edu/~kgarbutt/EvolutionPage/Speciation.htm

Gene flow is not limited by geographical barriers

But hybrids will be maladapted
→ selection against hybrids (*extrinsic* hyb. barrier)
→ Reduction in gene flow

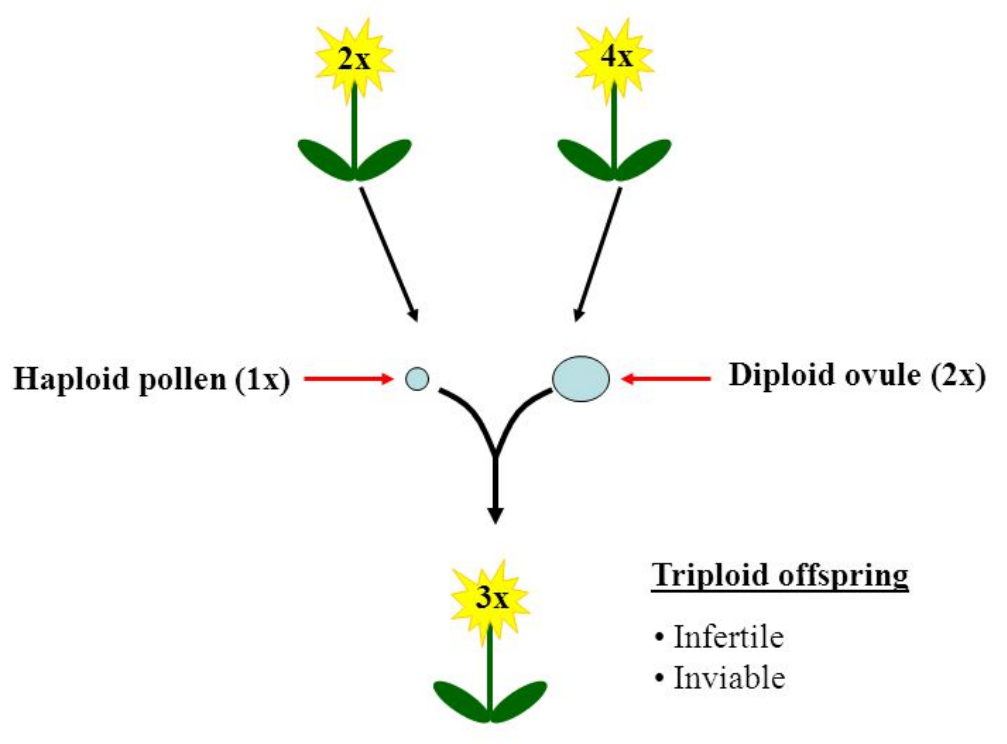
Sympatric speciation

Intuitively much harder to conceive:

- constant gene flow and recombination must counteract selection

- ecological coexistence

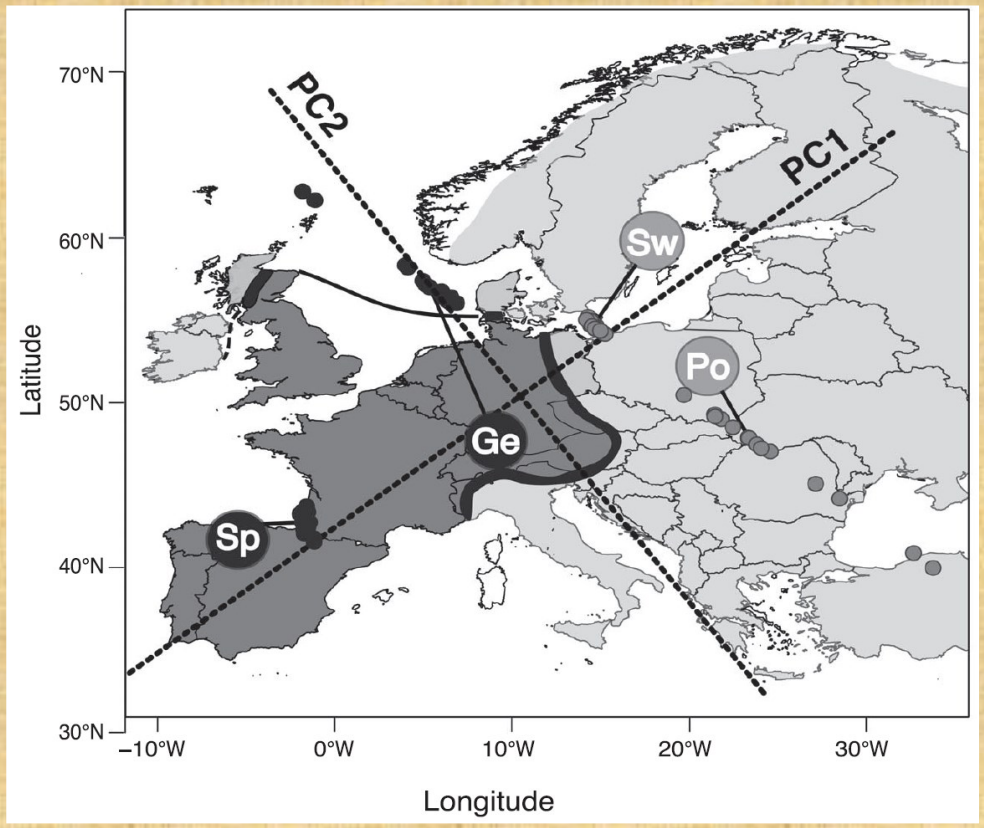
Polyploid speciation



Allo/sympatric speciation, how to know?

Corvus cornix

Corvus corone



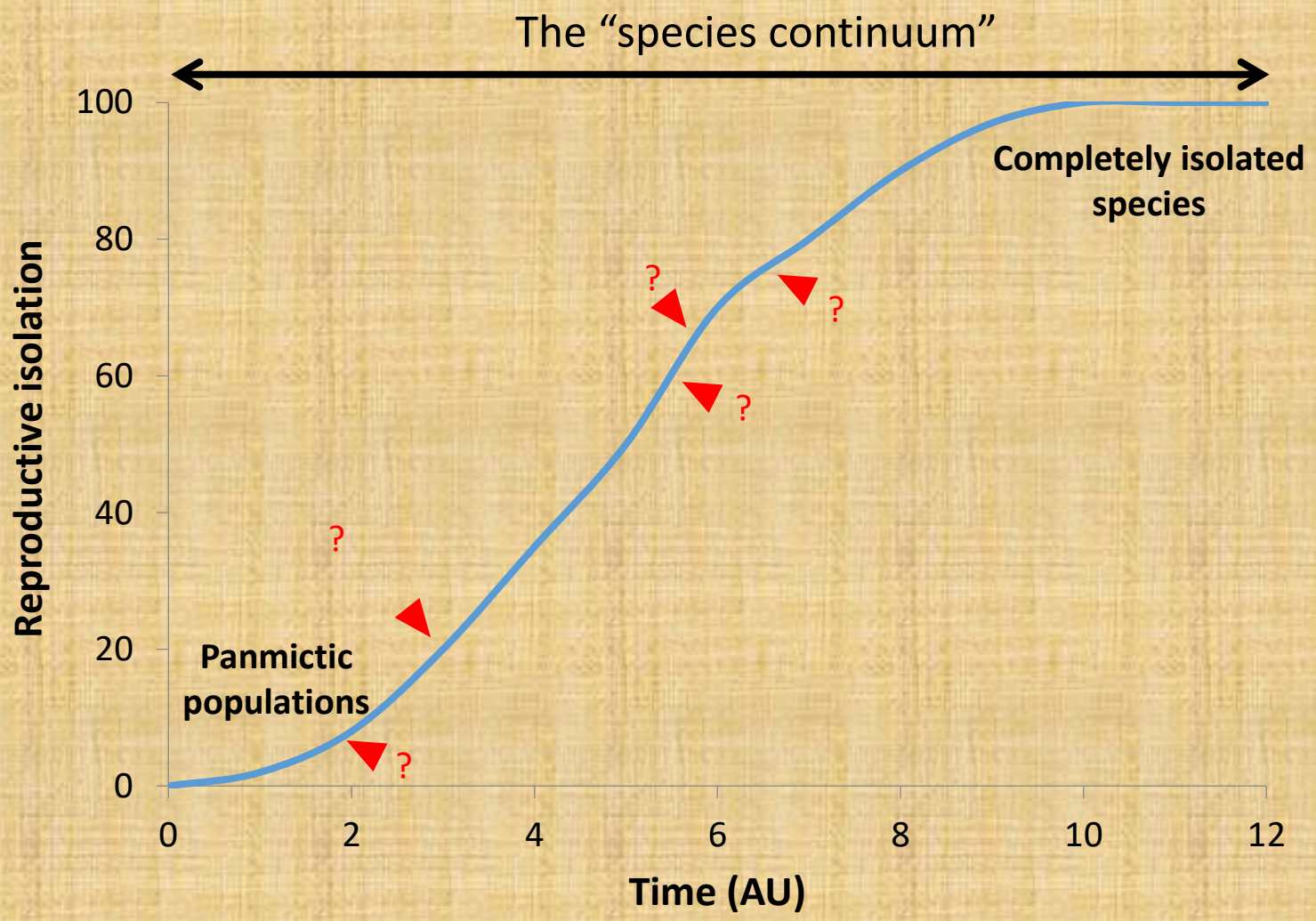
Allopatric is often considered as null hypothesis

Are species sister taxa? Are they mostly located in sympatry or allopatry?

Genetic diversity should inform on life history: is the contact zone the oldest, or is it a newly colonized region?

What matters as evidence of speciation is REALIZED gene flow in the wild

Assessing experimentally the whole reproductive isolation is nearly impossible



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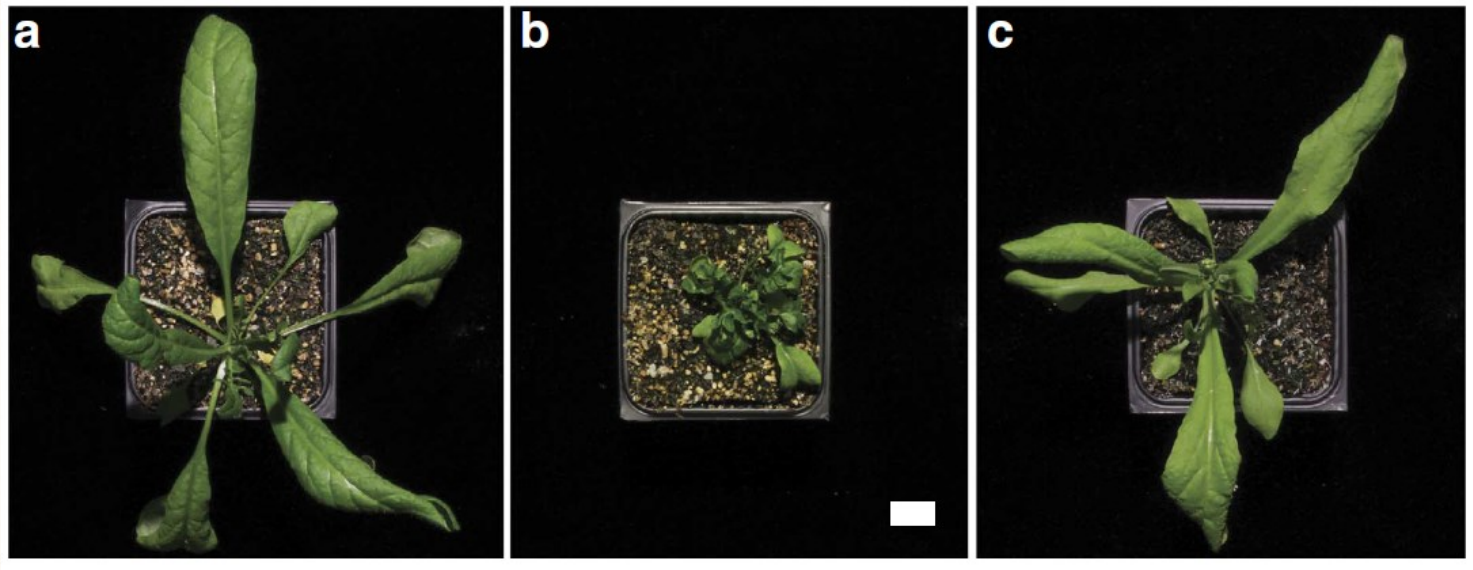
Adaptation and speciation genomics: some new with the old?

Focus on *how species emerge*, the processes

Speciation genomics: some new with the old?

The genomic loci responsible for a hybridization barrier can be mapped (QTL…) = **speciation genes**!

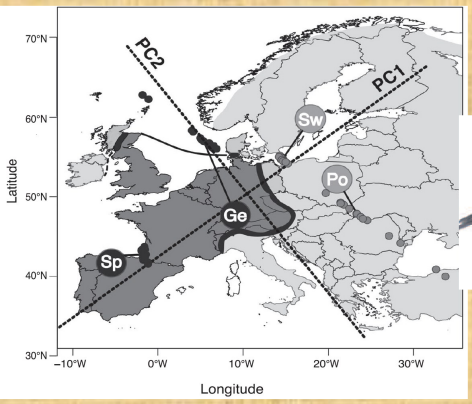
Capsella rubella F2 hybrid *C. grandiflora*

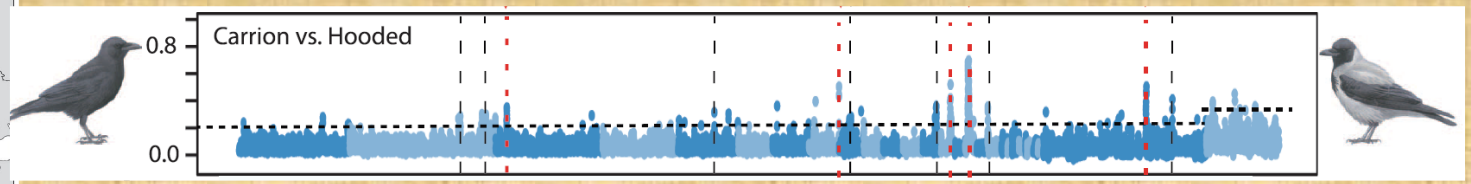


You will find the *speciation genes* responsible during one of the practicals

Speciation genomics: some new with the old?

Measure of gene flow **across the genome**





What is the extent of gene flow? (where are they in the “species continuum”?)

Are there genomic regions reluctant to gene flow?
(= responsible for any hybridization barriers?)

Dating of the gene flow?
Ancient introgression in some parts of the genome vs recent ones?

You will test some of these questions in practicals

Poelstra, 2014

Alpine *A. arenosa*

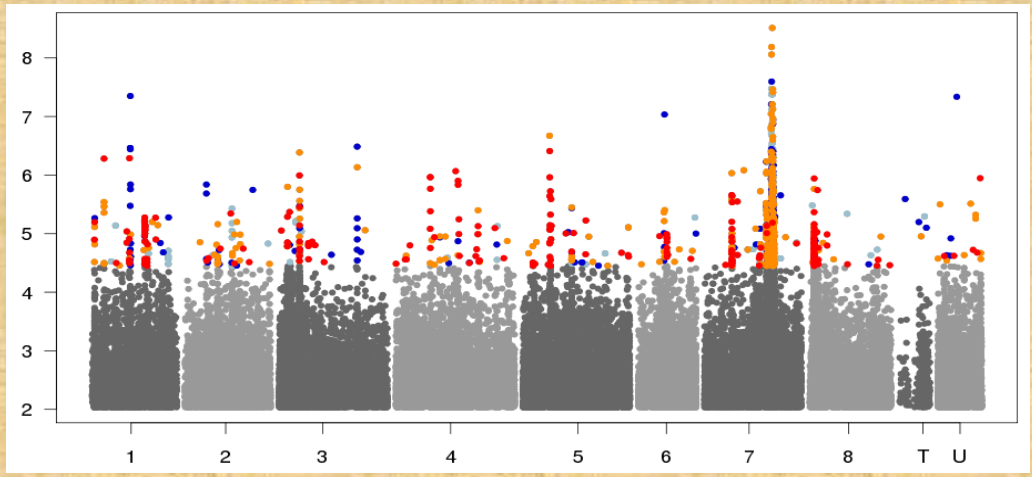
Adaptomics: some new with the old?

Foothill *A. arenosa*

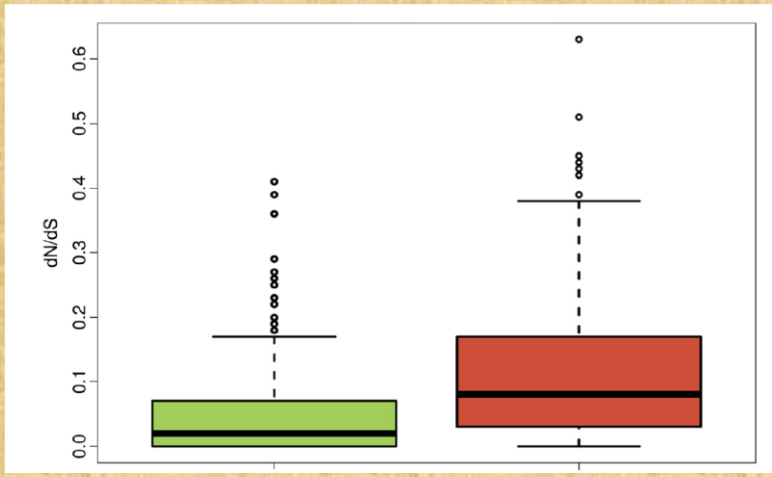
Allele frequencies **genome-wide**

Are there some alleles preferentially found in adapted populations? Identification of mutations selected under constraint

Genetic differentiation between two populations



Infer the type/strength of selection



Combined with speciomics: are *speciation genes* under selection? = evolutionary forces driving hybridization barriers

You will test some of these questions in practicals

We are thinking “selfish gene”

Richard Dawkins

Adaptomics/speciomics:
We are looking for specific alleles that have been selected in a given population

Not for an individual

Unit of selection: gene (Dawkins), not individual (Darwin)

For Dawkins: Individuals are too temporary and too variable to be this unit.

We are “survival machines”, merely “boxes” for genes.

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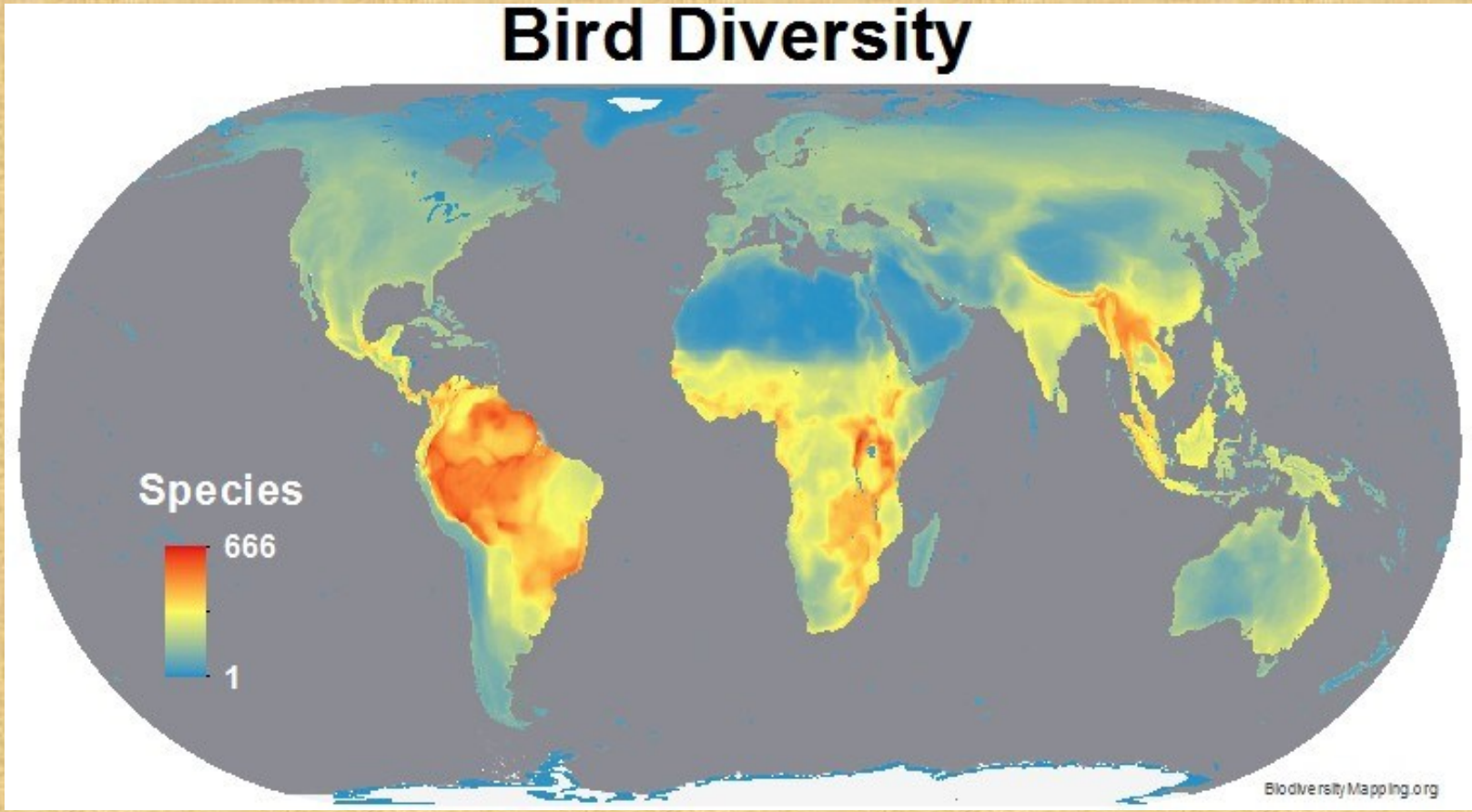
Out of the gene-oriented view on speciation



What promotes speciation and extinction (diversification)?

Environment? Traits?

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Radka Reifová (Dpt of Zoology)

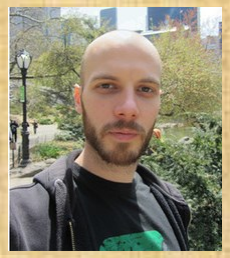
Postzygotic barriers
Secondary contact zones
Speciomics methodologies

Me (Dpt of Botany)

Sexual selection
Concepts in population genomics
Hybrid speciation

Roswitha Schmickl (Dpt of Botany)

Reticulate evolution and reconstructing phylogeny



Antonin Macháč (Center for Theoretical Studies)

Macroecology, species diversification

Filip Kolář (Dpt of Botany)

Ecological speciation

Nelida Padilla (Dpt of Botany)

Polyploid speciation

Petr Smykal (Palacky University in Olomouc)

Speciation by domestication

Ashish Kumar Pathak (Dpt of Botany)

Speciation QTL practical

Magdalena Bohutinská (Dpt of Botany)

Adaptomics practical

Veronika Konečná (Dpt of Botany)

Adaptomics practical

Manon Poignet (Dpt of Zoology)

Interspecies gene flow practical

Stephen Schlebush (Dpt of Zoology)

Interspecies gene flow practical

The lectures, practicals and exams

The lectures

Each one = a theoretical aspect of speciation
Every Tuesday 13.10-14.40

The practicals

Based on research cases
Question oriented
“Digested” bioinformatics
Grouped into 3 hours classes, not every week
On Wednesdays, 13.10-16.10

The exams

Theory: oral exams
Practicals: article-like report for each practical (3 practicals)