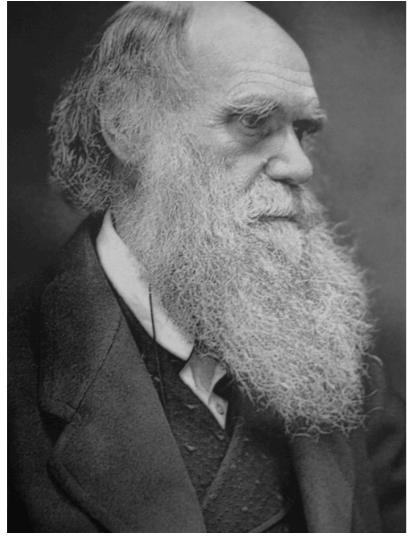


# Concepts, islands & continuums: a perspective on speciation genomics



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Centre for Ecological and Evolutionary Synthesis  
University of Oslo, Norway  
[@mark\\_ravinet.mark.ravinet@ibv.uio.no](mailto:@mark_ravinet.mark.ravinet@ibv.uio.no)

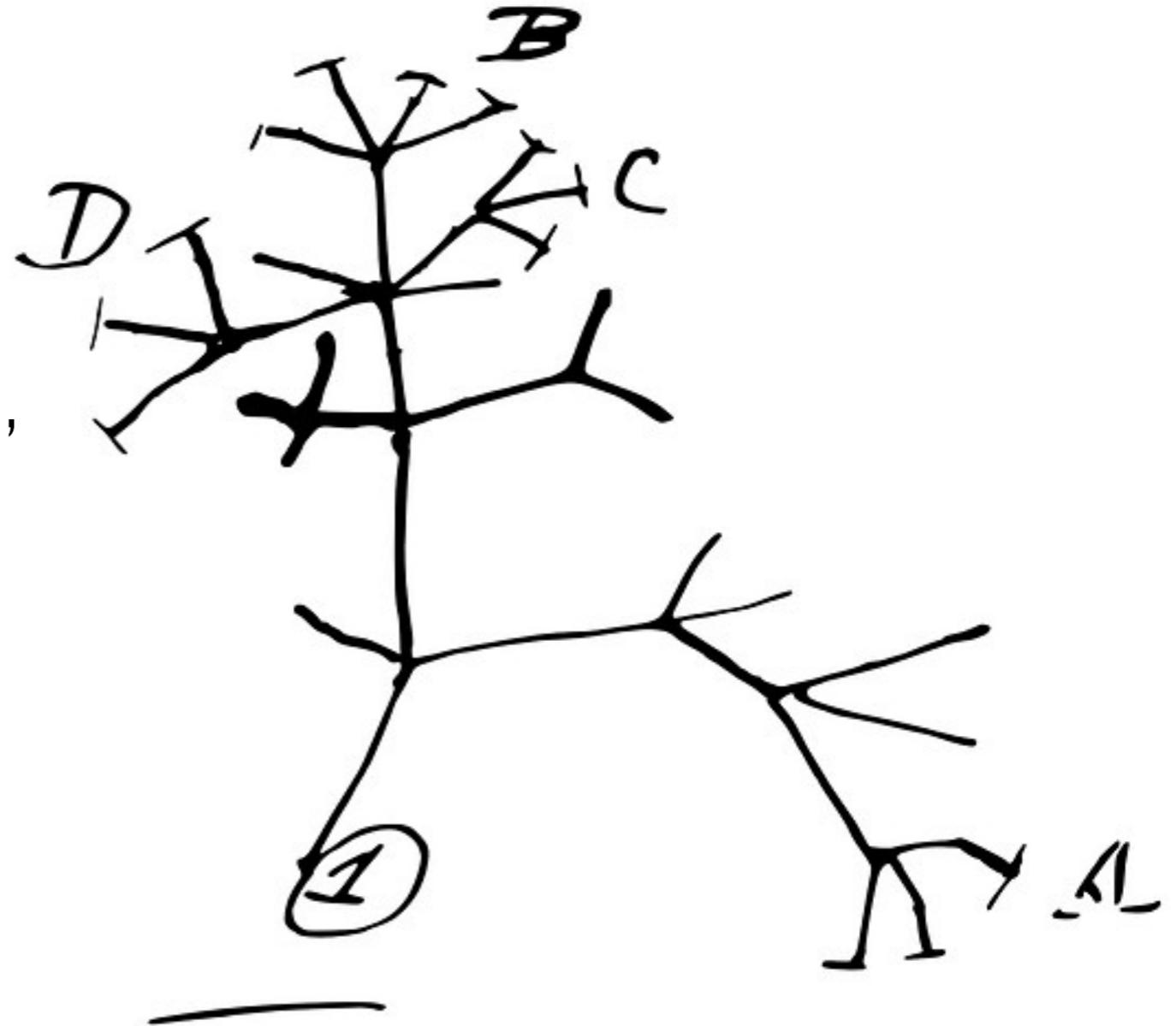
# Darwin and the origin



“...that mystery of mysteries...”

Charles Darwin (1859) *The Origin of Species*

I think



# Species concepts and the modern synthesis

“Species are groups of interbreeding natural populations... reproductively isolated from other such groups”

Ernst Mayr (1942) *Systematics and the Origin of Species*



“[The] existence of discrete groups... constitutes evidence that some mechanisms... [isolate] them”

Theodosius Dobzhansky (1937) *Genetics and the Origin of Species*

# Hybrid zones and gene flow

“Narrow regions in which genetically distinct organisms meet, mate and produce hybrids”

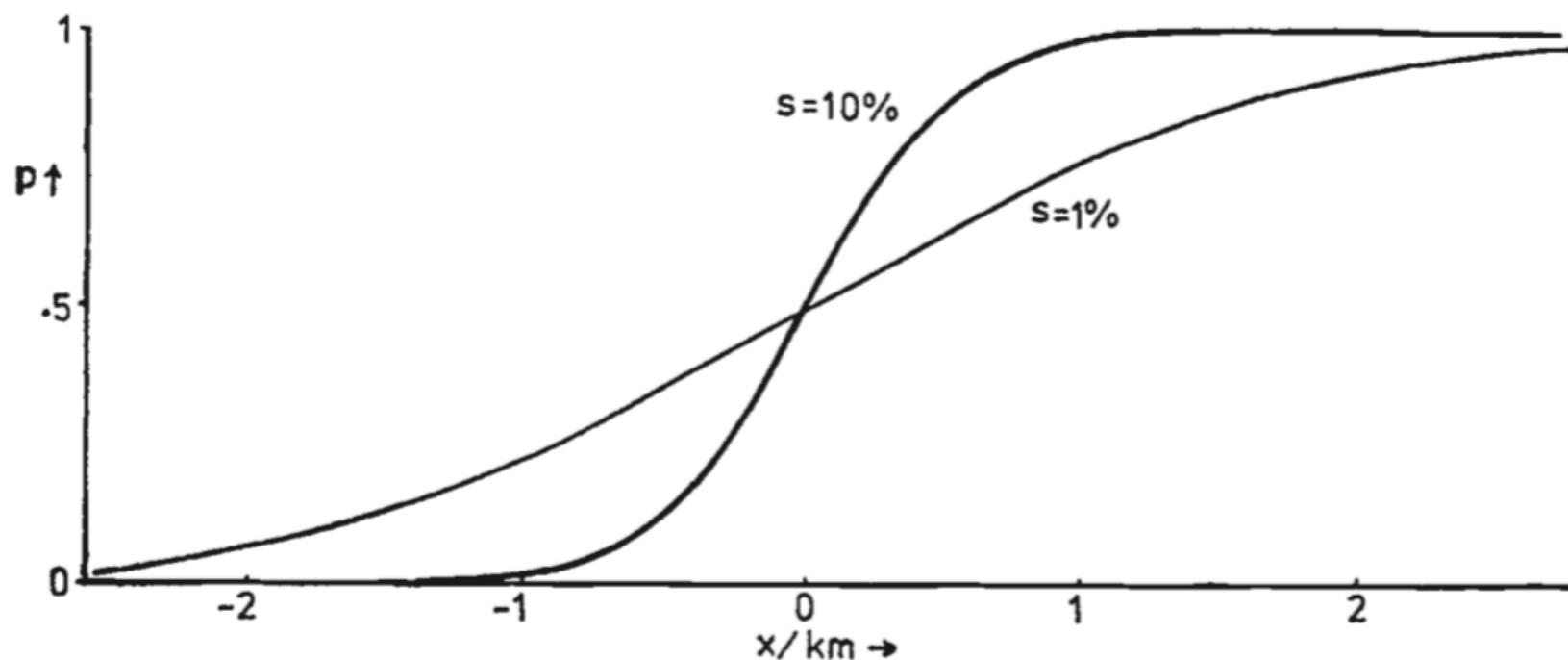


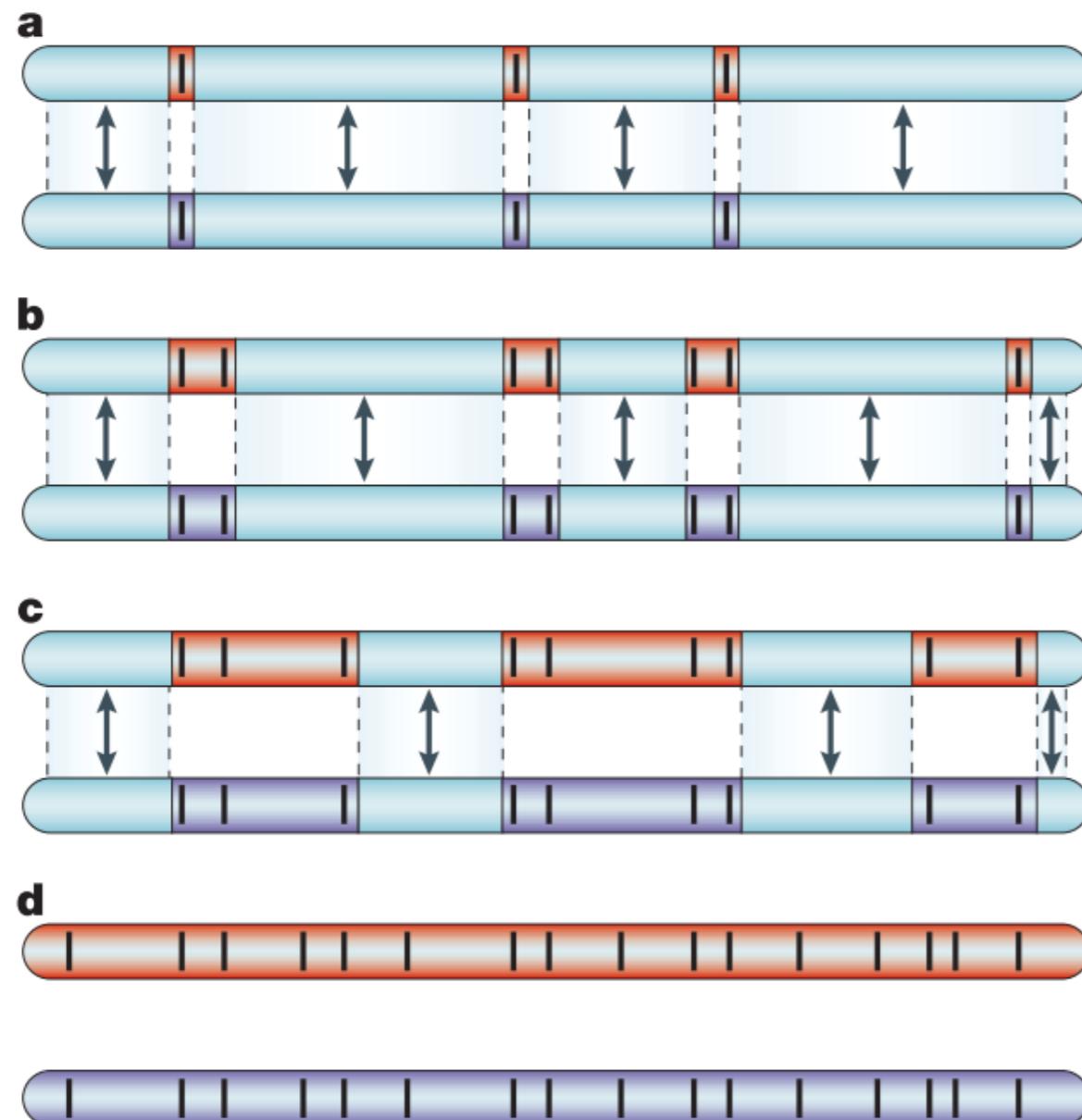
FIG. 1.—Hybrid zones produced by selection against heterozygotes;  
dispersal  $\sqrt{m} = 112 \text{ m.gen.}^{-\frac{1}{2}}$

Barton (1979) **Heredity**

“Maintained by a balance between dispersal and selection against hybrids”

Barton & Hewitt (1989) **Nature**

# The genic concept of speciation



Divergent loci resist gene flow

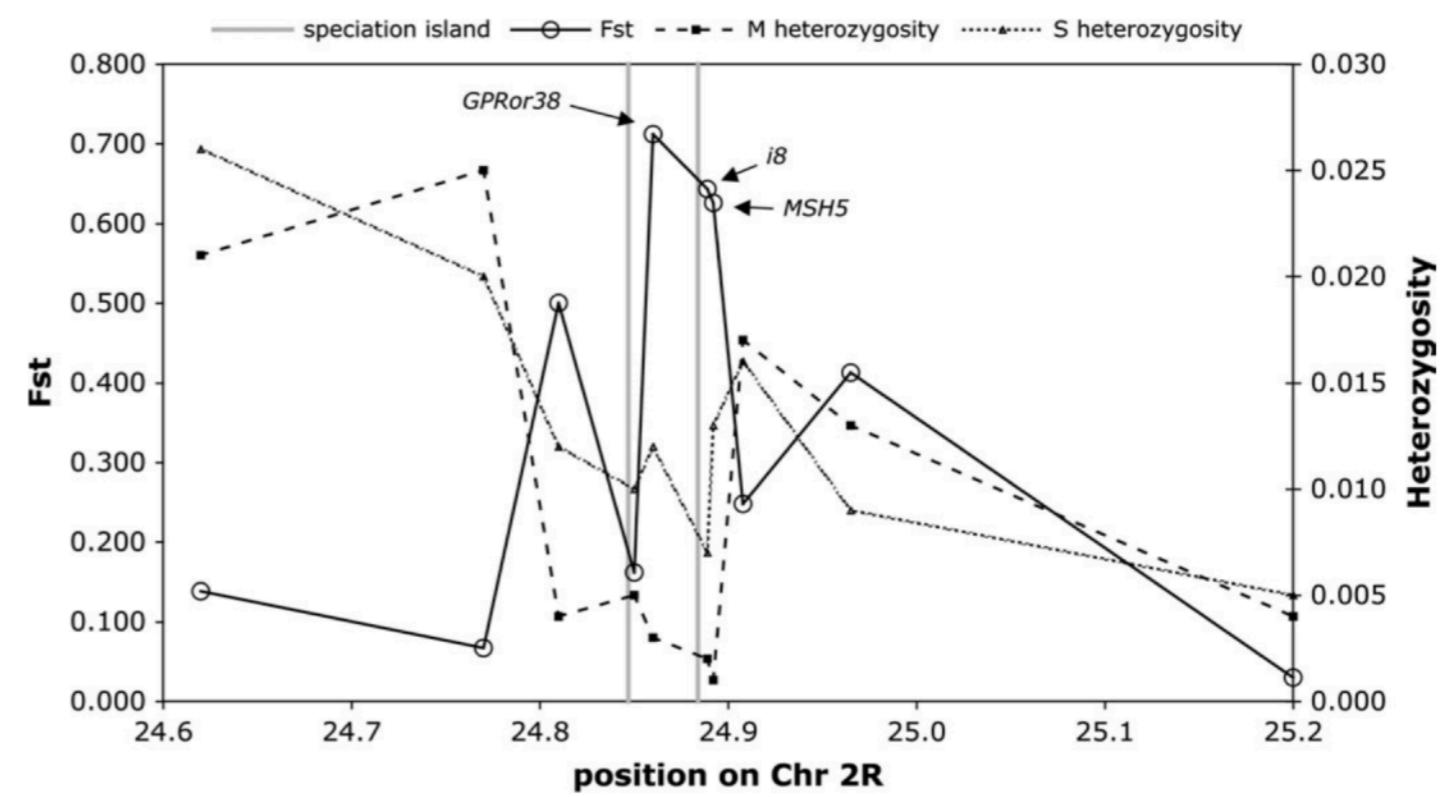
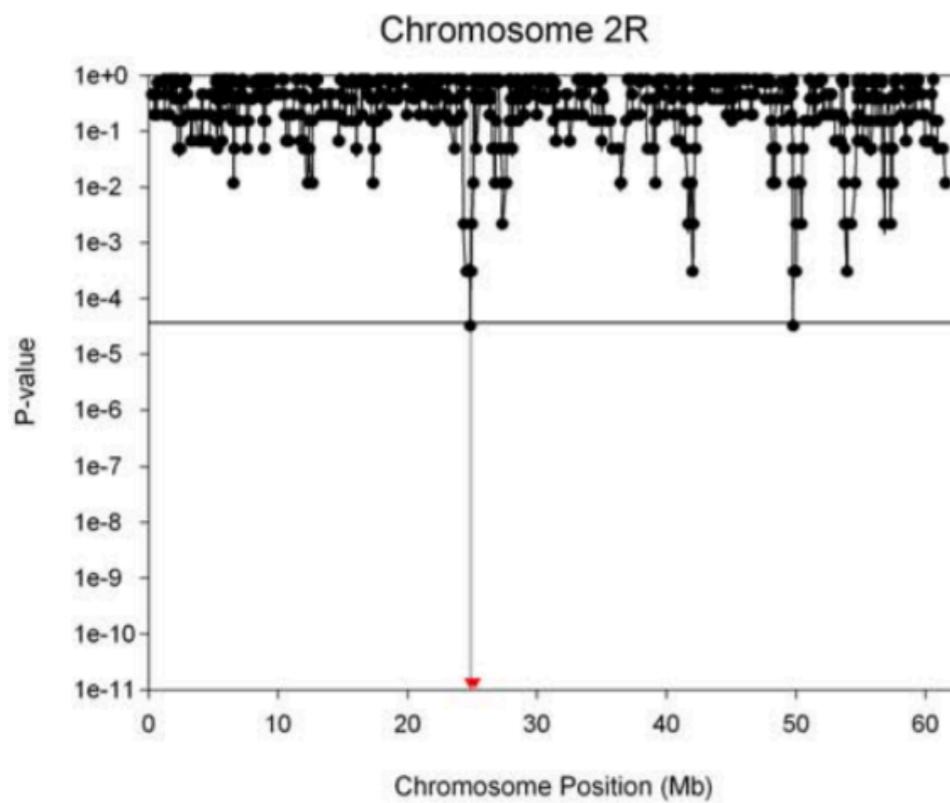
Gene flow continues but  
linkage builds and divergent  
regions grow

Complete reproductive  
isolation evolves

# The rise of speciation islands

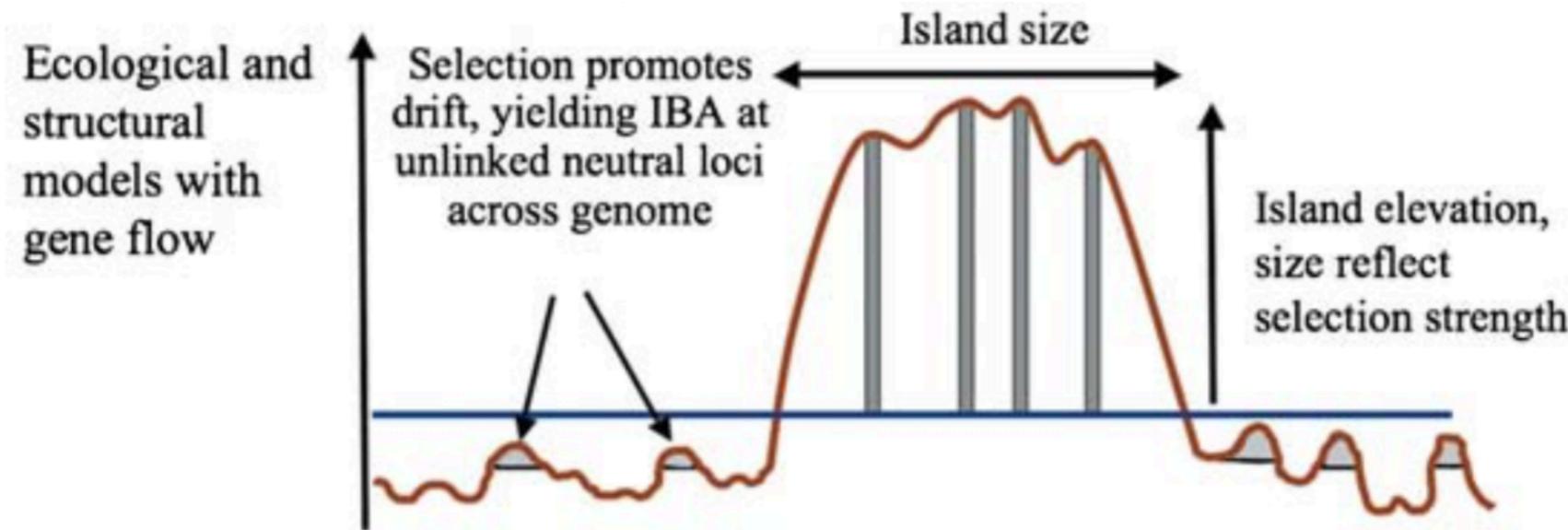


*Anopheles gambiae*  
M + S forms

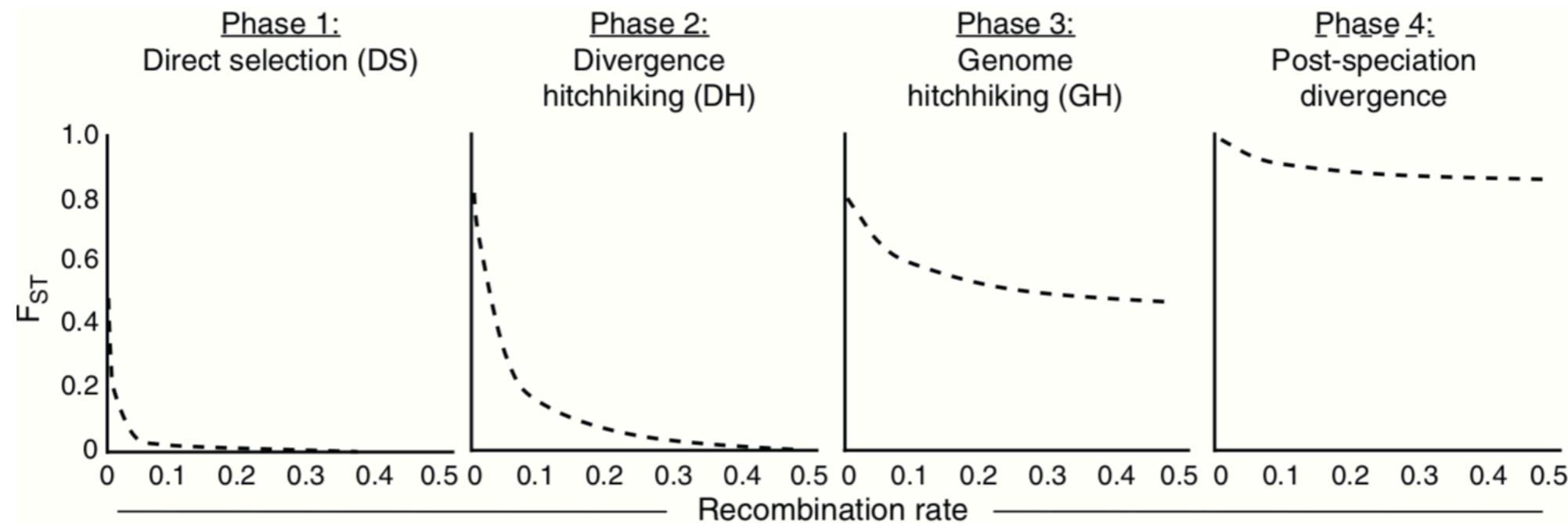


Turner et al (2005) **PLoS Biology**; Turner & Hahn (2007) **MBE**

# Speciation islands and processes



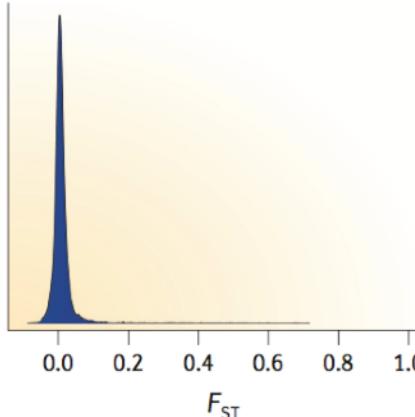
Nosil et al (2009) **Mol Ecol**



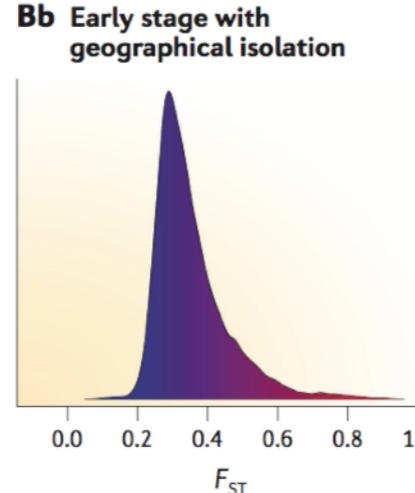
Feder et al (2012) **Trends in Genetics**

# Continuums and islands

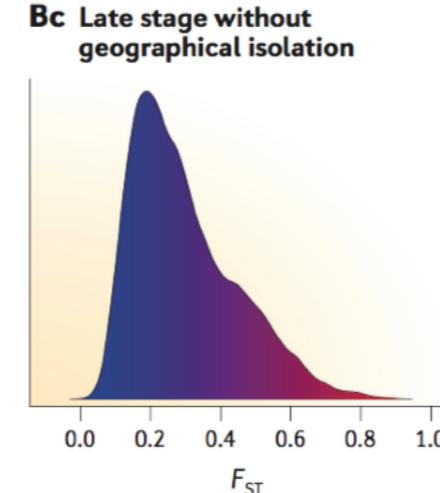
Ba Early stage without geographical isolation



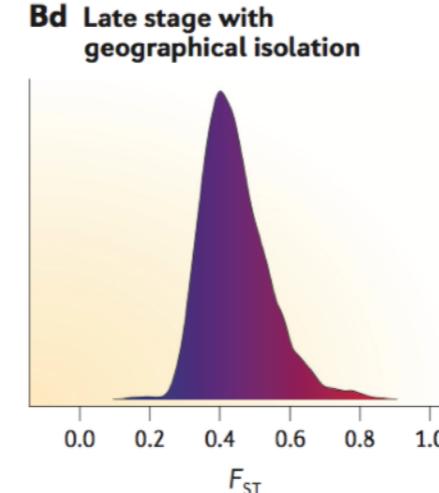
Bb Early stage with geographical isolation



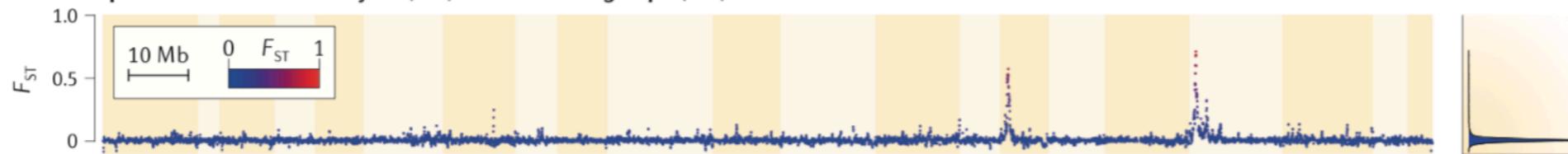
Bc Late stage without geographical isolation



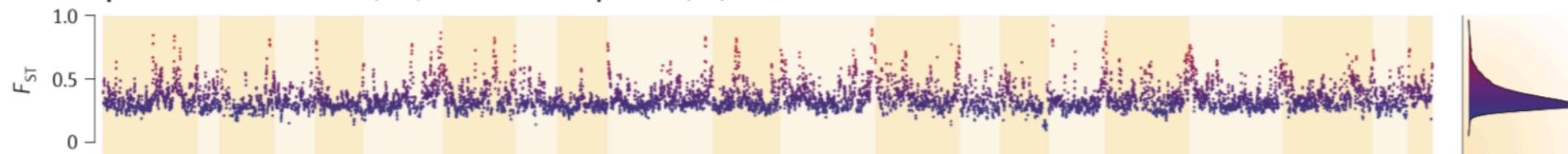
Bd Late stage with geographical isolation



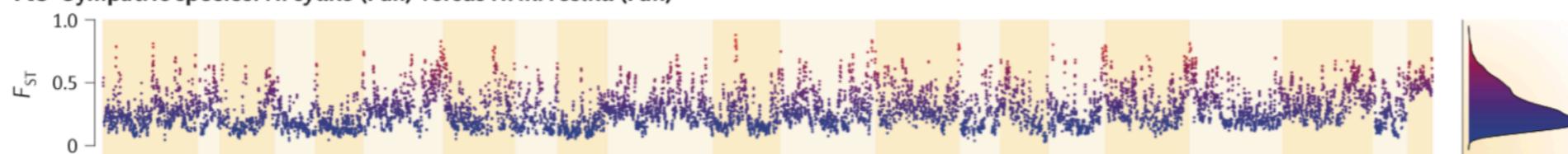
Aa Parapatric races: *H. m. amaryllis* (Per) versus *H. m. aglaope* (Per)



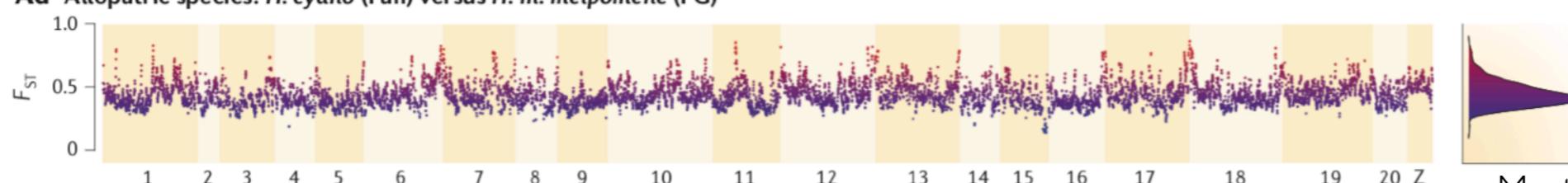
Ab Allopatric races: *H. m. rosina* (Pan) versus *H. m. melpomene* (FG)



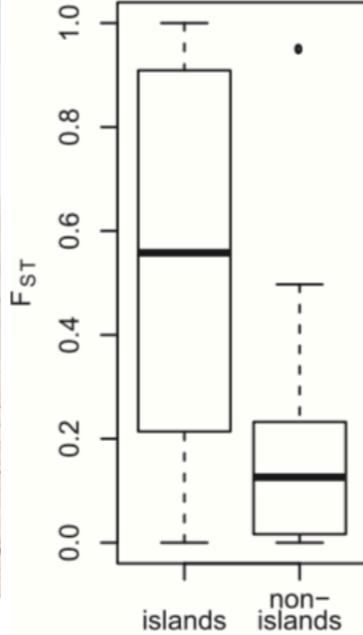
Ac Sympatric species: *H. cydno* (Pan) versus *H. m. rosina* (Pan)



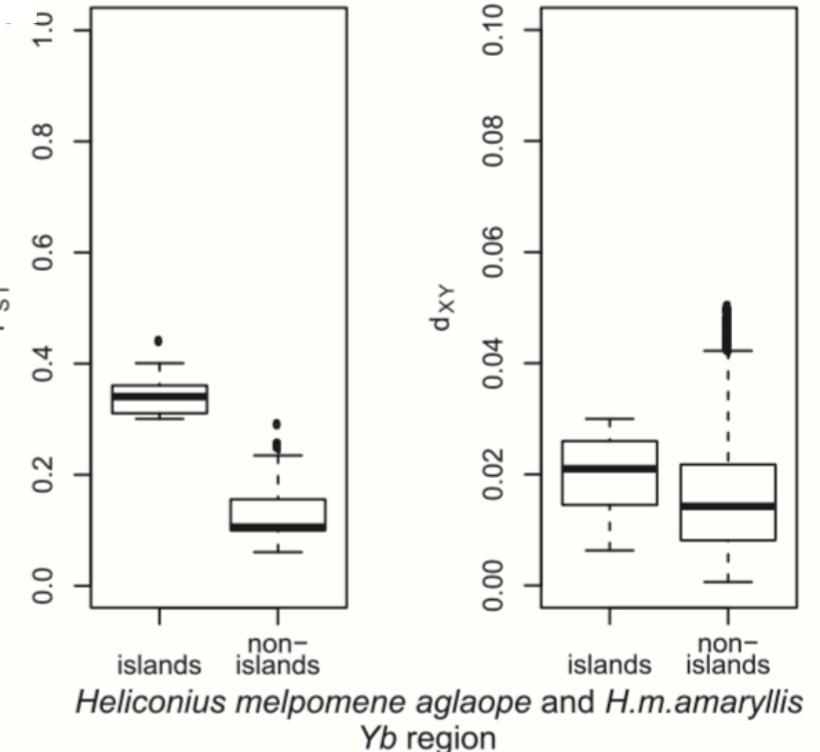
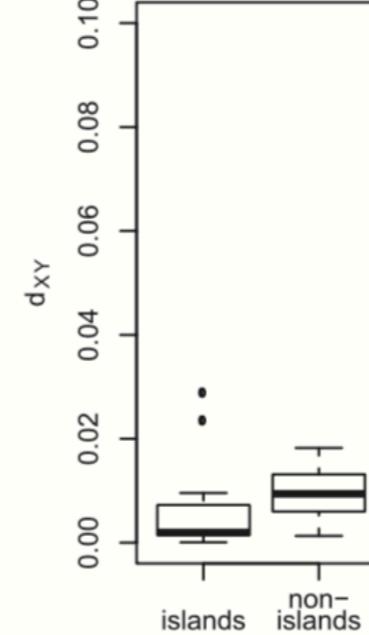
Ad Allopatric species: *H. cydno* (Pan) versus *H. m. melpomene* (FG)



# Mirages and alternative explanations



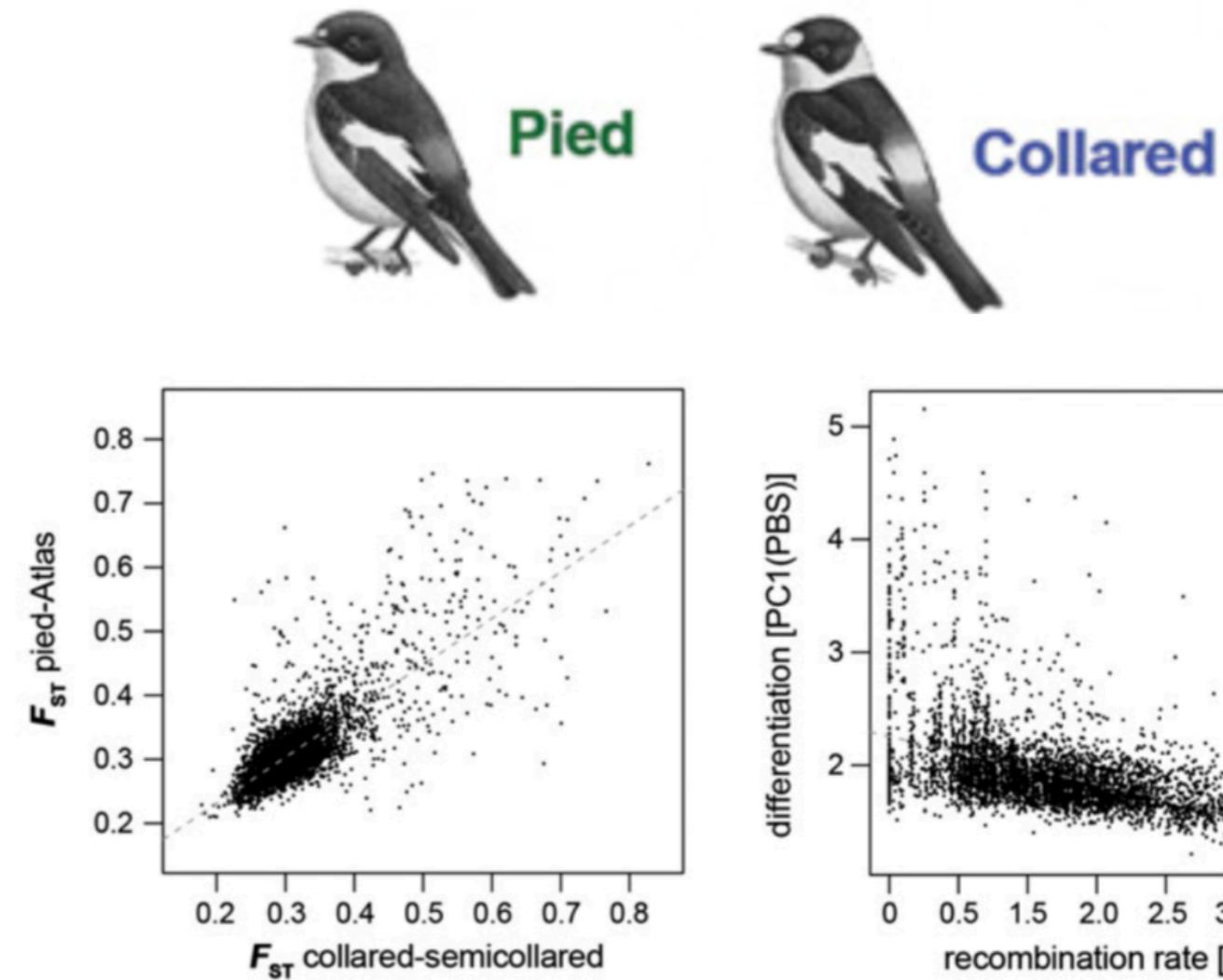
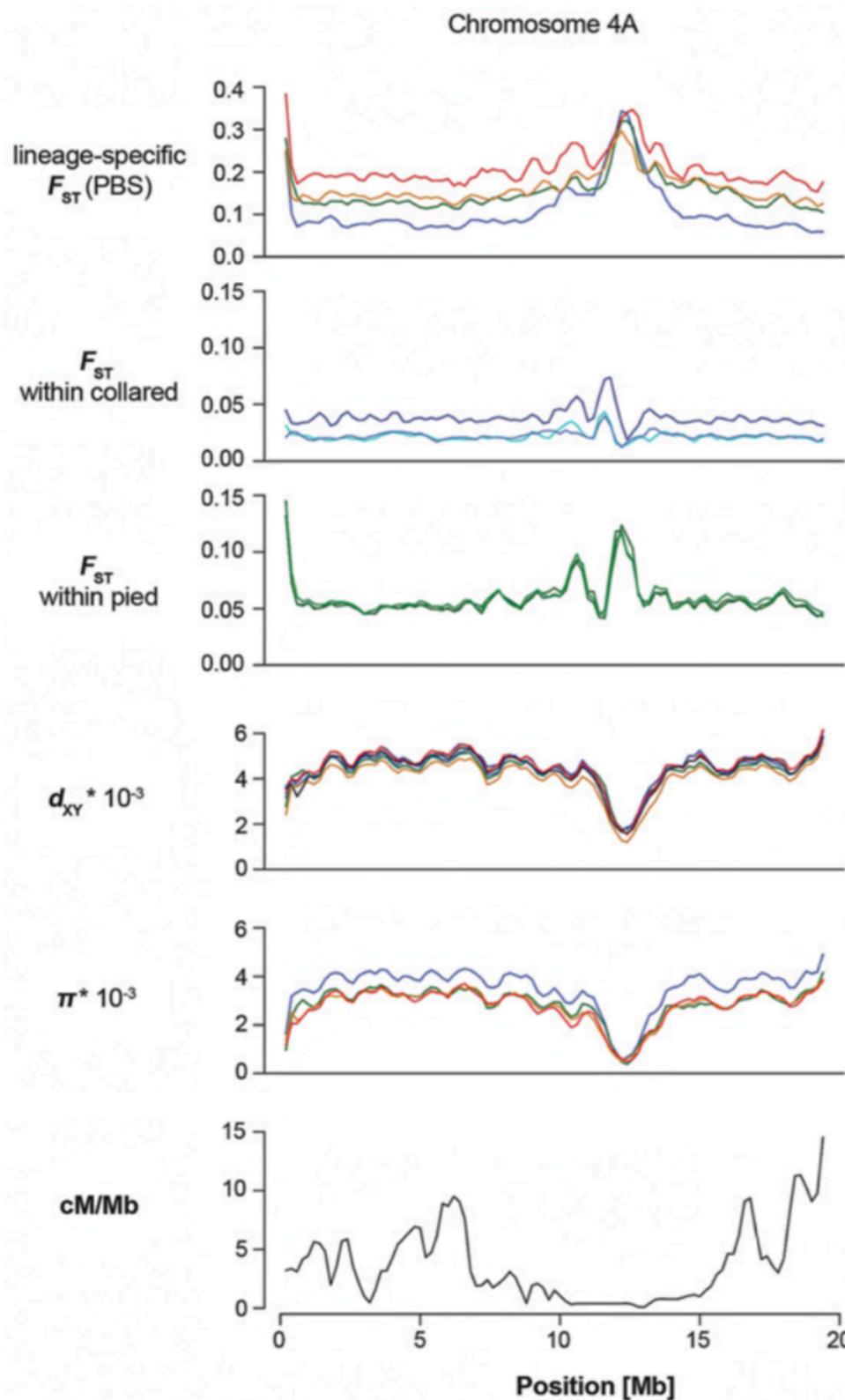
*Anopheles coluzzii* and *A. gambiae*



- Background selection
- Local adaptation after isolation
- Shared ancestral polymorphism

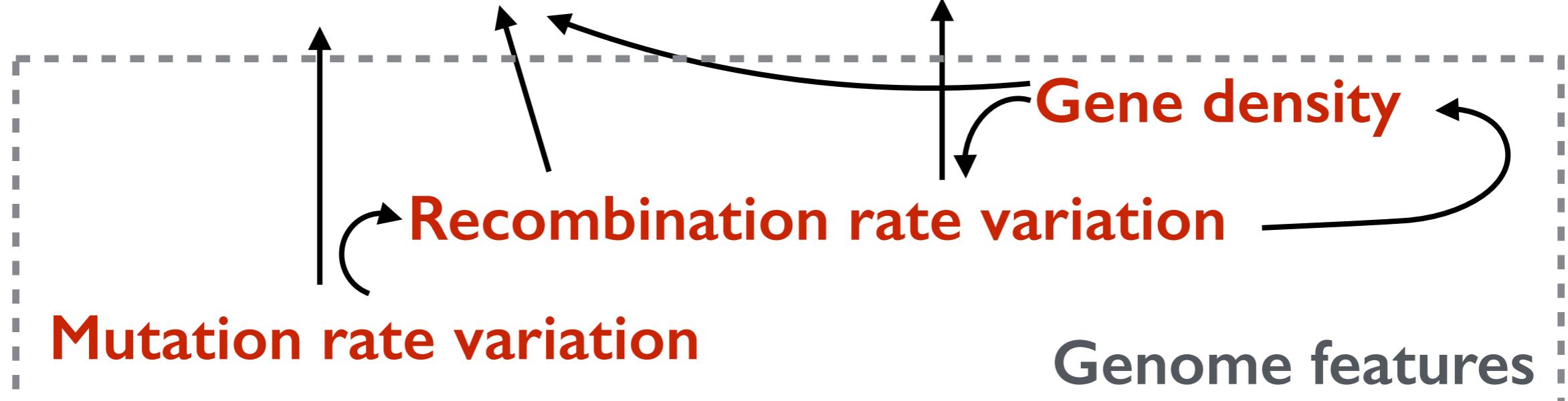
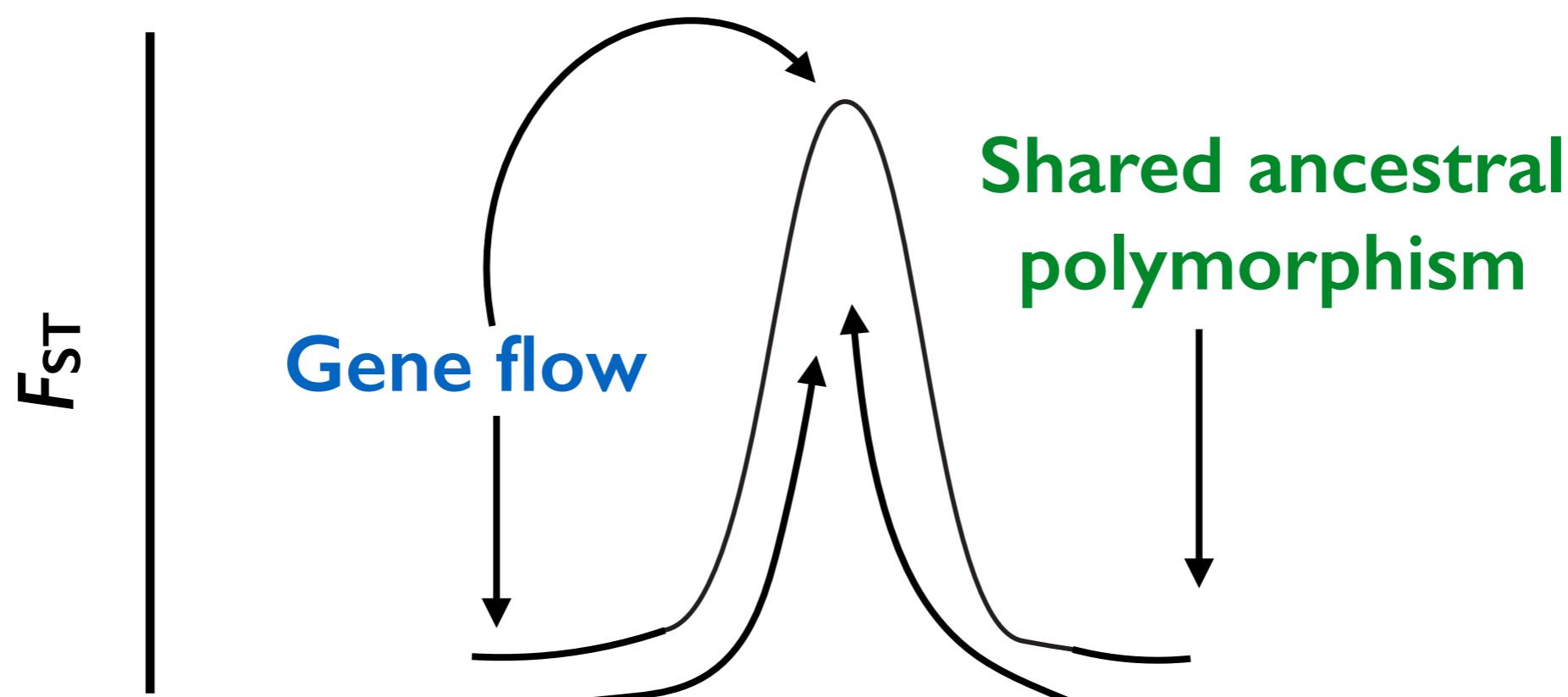
Noor & Bennett (2008) **Heredity**  
Cruickshank & Hahn (2014) **Mol Ecol**

# Linked selection and recombination

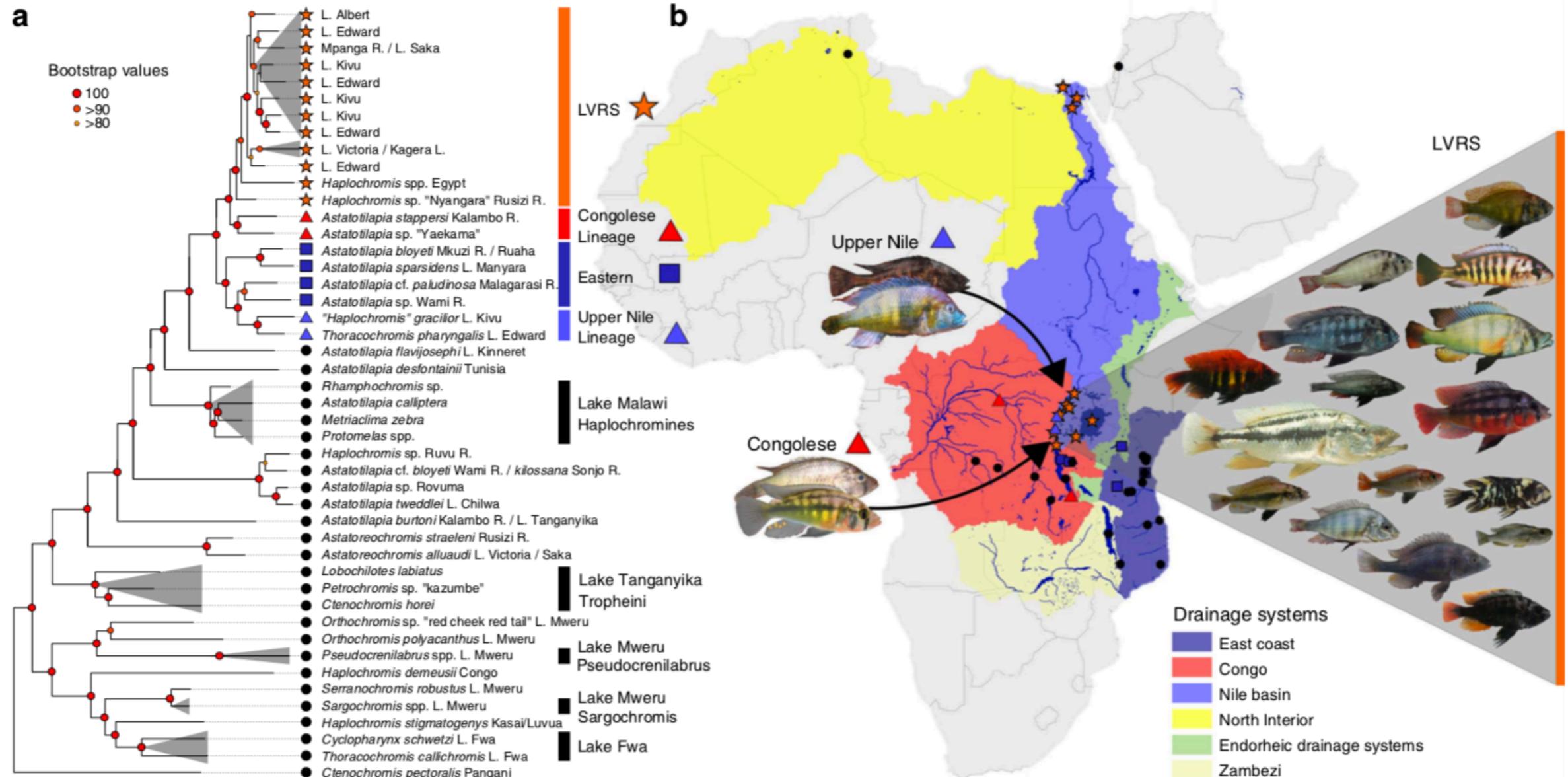


# Confounding factors

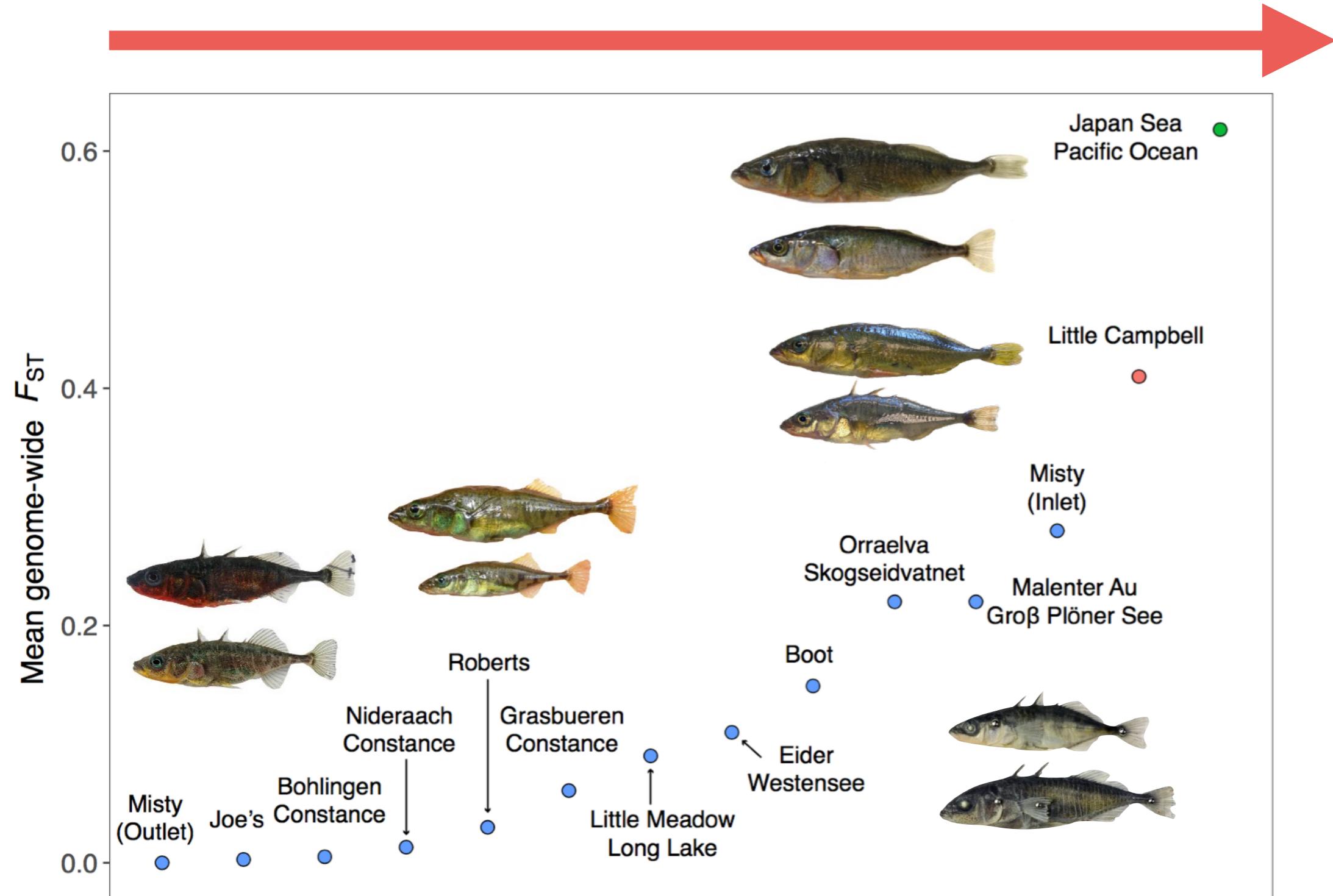
Demographic history



# The Lake Victoria cichlid radiation



# The stickleback speciation continuum



Roesti et al (2012) **Mol Ecol**

Roesti et al (2015) **Nat Comm**

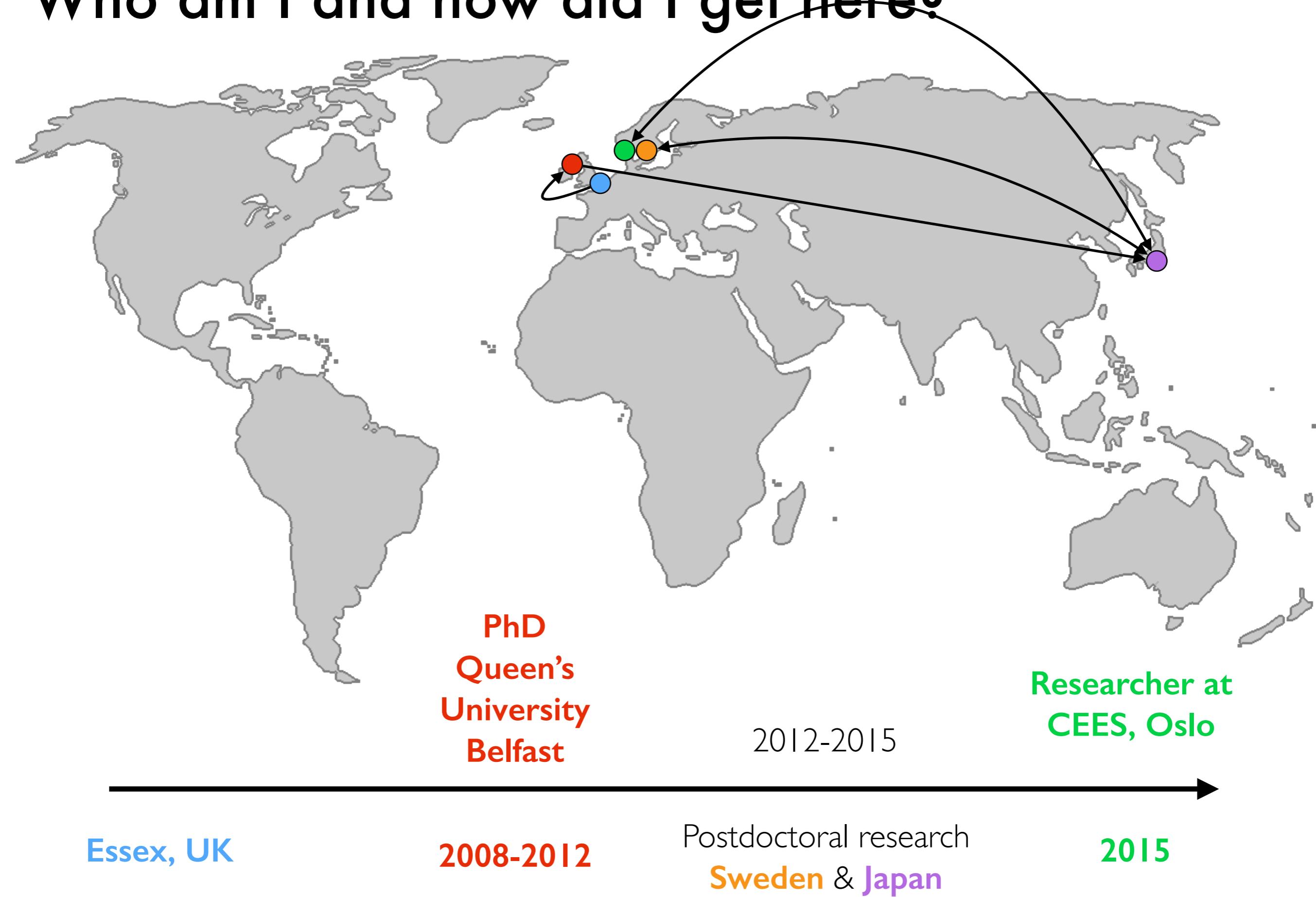
Ravinet et al (2018) **PloS Genetics**

Feulner et al (2015) **PloS Genetics**

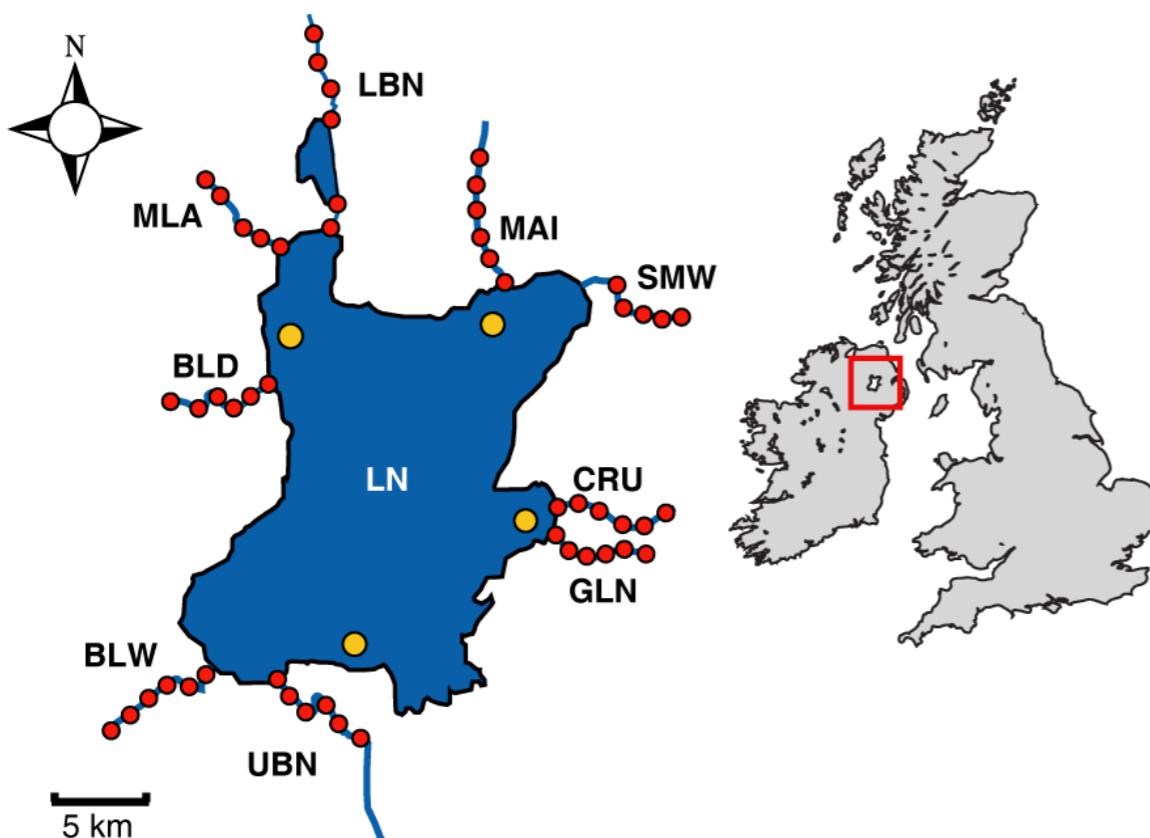
Kusukabe et al (2017) **Mol Ecol**

Marques et al (2016) **PloS Genetics**

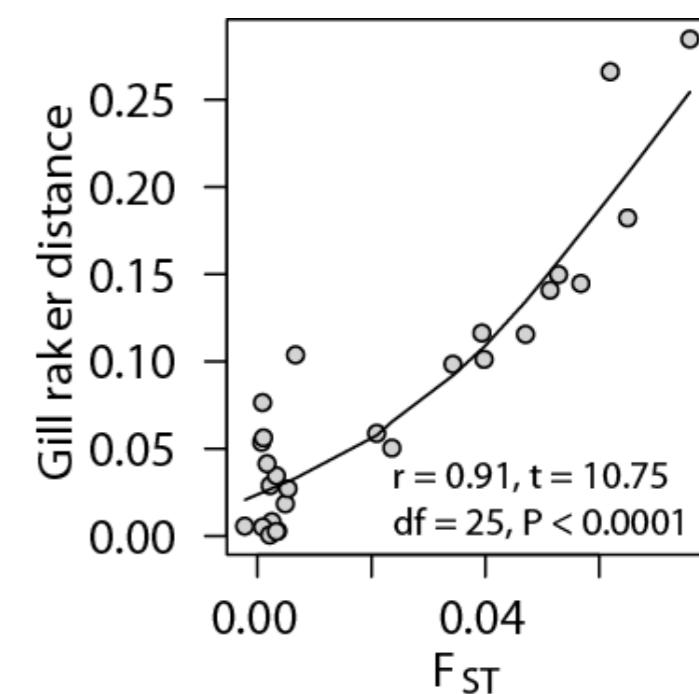
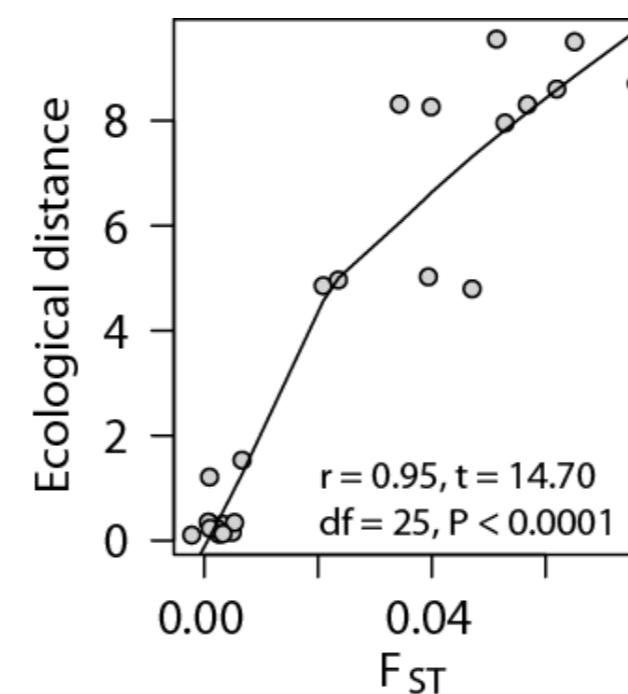
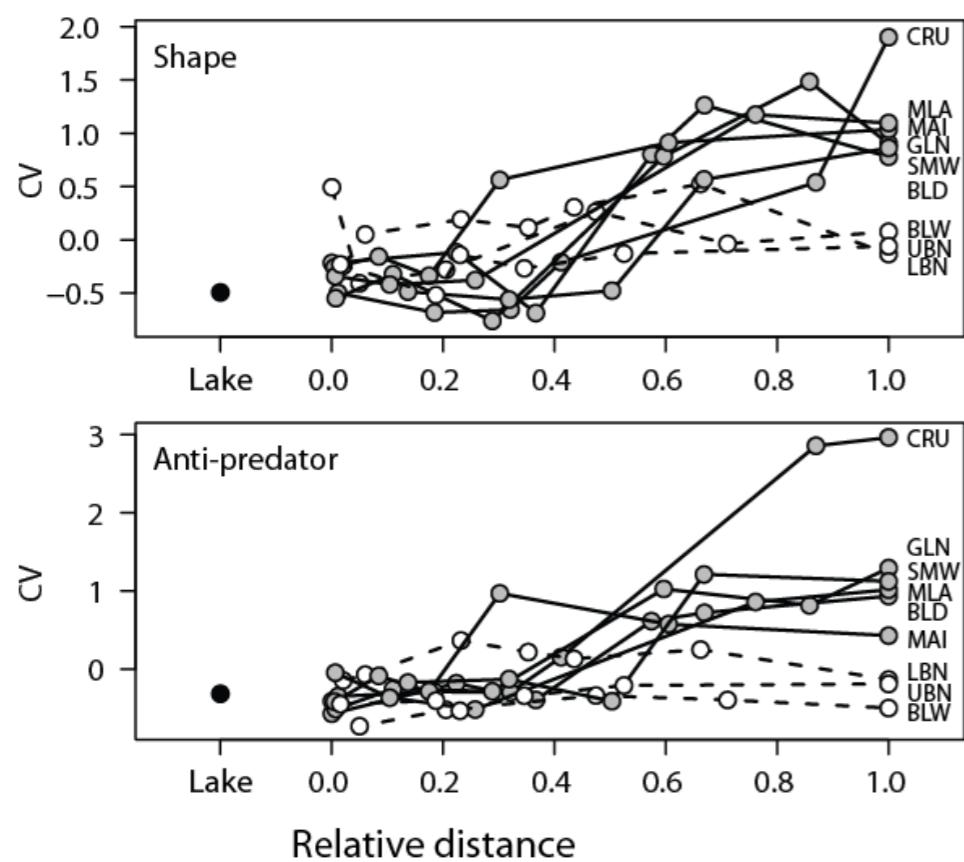
# Who am I and how did I get here?



# Parallel & non-parallel lake-stream stickleback evolution



*Gasterosteus aculeatus*



# Parallel & non-parallel divergence



Evolutionary Ecology Research, 2013, 15: 271–294

## On Irish stickleback: morphological diversification in a secondary contact zone

Mark Ravinet<sup>1,2</sup>, Paulo A. Prodöhl<sup>1</sup> and Chris Harrod<sup>1,3</sup>

<sup>1</sup>School of Biological Sciences, Queen's University Belfast, Belfast, UK, <sup>2</sup>Ecological Genetics Laboratory, National Institute of Genetics, Mishima, Japan and <sup>3</sup>Facultad de Recursos del Mar, Instituto de Investigaciones Oceanológicas, Universidad Antofagasta, Antofagasta, Chile

## MOLECULAR ECOLOGY

Molecular Ecology (2015)

doi: 10.1111/mec.13332

**SPECIAL ISSUE: DETECTING SELECTION IN NATURAL POPULATIONS: MAKING SENSE OF GENOME SCANS AND TOWARDS ALTERNATIVE SOLUTIONS**

### Shared and nonshared genomic divergence in parallel ecotypes of *Littorina saxatilis* at a local scale

MARK RAVINET,<sup>\*†</sup> ANJA WESTRAM,<sup>‡</sup> KERSTIN JOHANNESSON,<sup>\*</sup> ROGER BUTLIN,<sup>\*‡</sup>  
CARL ANDRÉ<sup>\*</sup> and MARINA PANOV<sup>A\*</sup>

<sup>\*</sup>Department of Marine Sciences—Tjärnö, University of Gothenburg, Hättesbäckvägen 8, 452 96 Strömstad, Sweden, <sup>†</sup>Ecological Genetics Laboratory, National Institute of Genetics, Yata 1111, Mishima 411-8540, Japan, <sup>‡</sup>Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK



nature  
ecology & evolution

ARTICLES

PUBLISHED: 22 MAY 2017 | VOLUME: 1 | ARTICLE NUMBER: 0158

## Contrasting effects of environment and genetics generate a continuum of parallel evolution

Yoel E. Stuart<sup>1\*</sup>, Thor Veen<sup>1†</sup>, Jesse N. Weber<sup>1†</sup>, Dieta Hanson<sup>2</sup>, Mark Ravinet<sup>3</sup>, Brian K. Lohman<sup>1</sup>, Cole J. Thompson<sup>1</sup>, Tania Tasneem<sup>4</sup>, Andrew Doggett<sup>4</sup>, Rebecca Izen<sup>1</sup>, Newaz Ahmed<sup>1</sup>, Rowan D. H. Barrett<sup>2</sup>, Andrew P. Hendry<sup>2</sup>, Catherine L. Peichel<sup>5†</sup> and Daniel I. Bolnick<sup>1</sup>

# Late stage speciation in sticklebacks



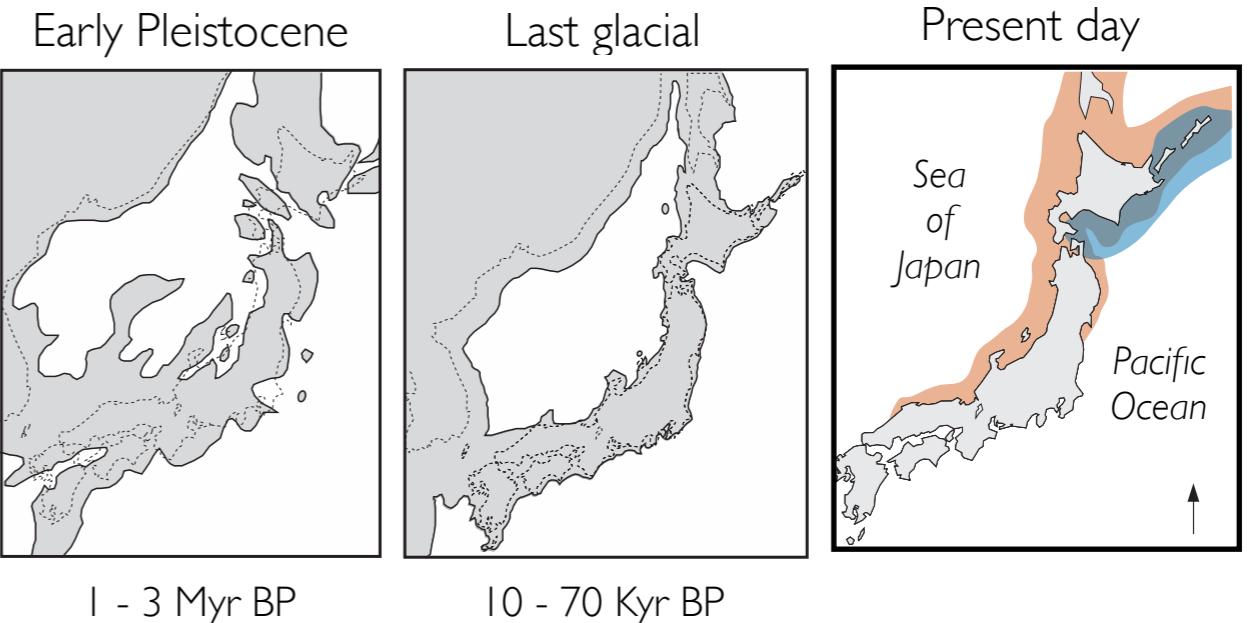
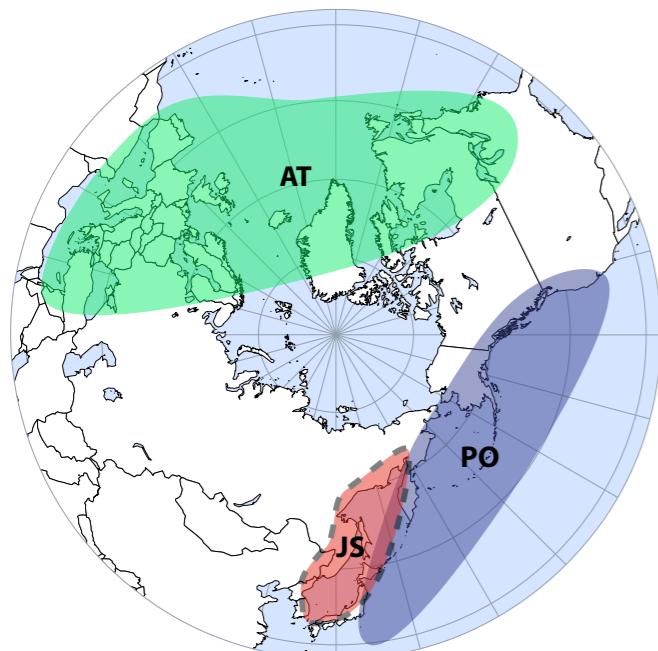
Three-spined stickleback

Pacific Ocean    Atlantic Ocean



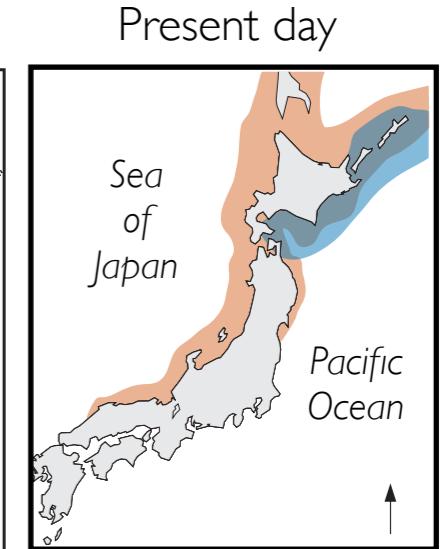
Japan Sea stickleback

Sea of Japan    Sea of Okhotsk

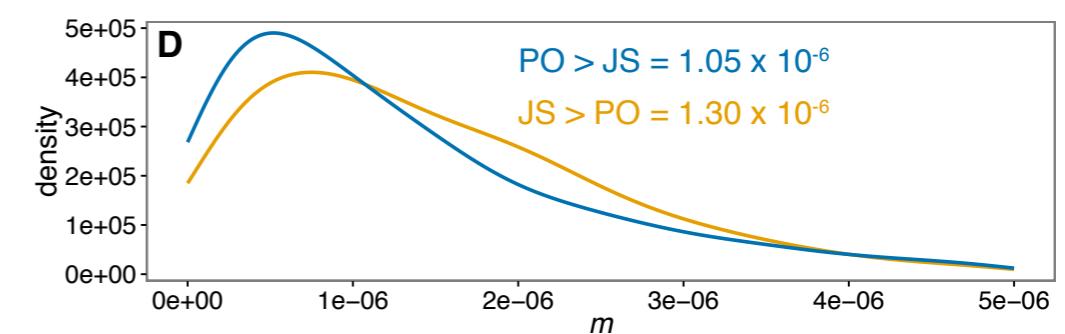
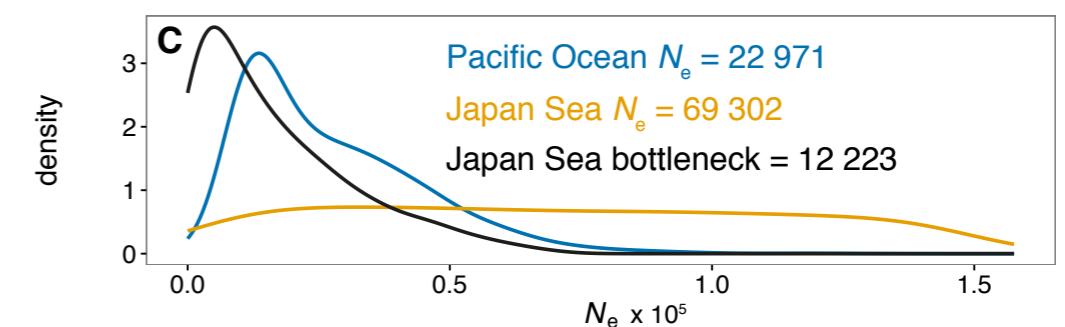
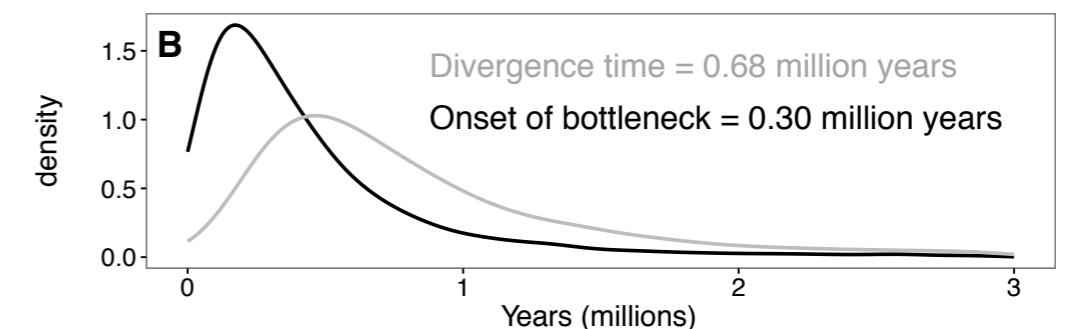
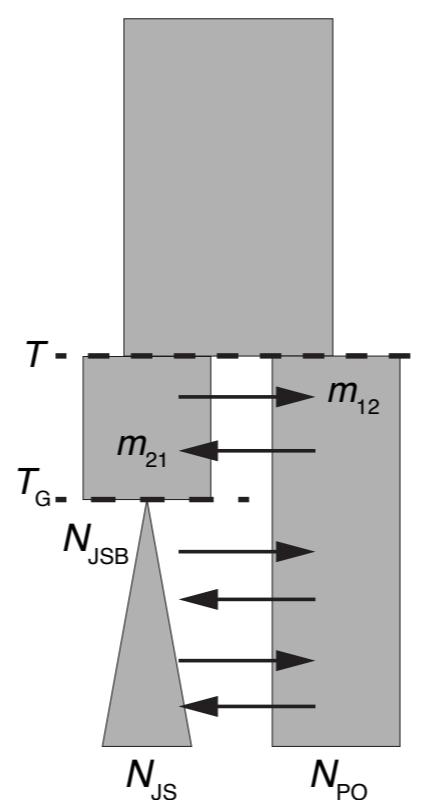


1 - 3 Myr BP

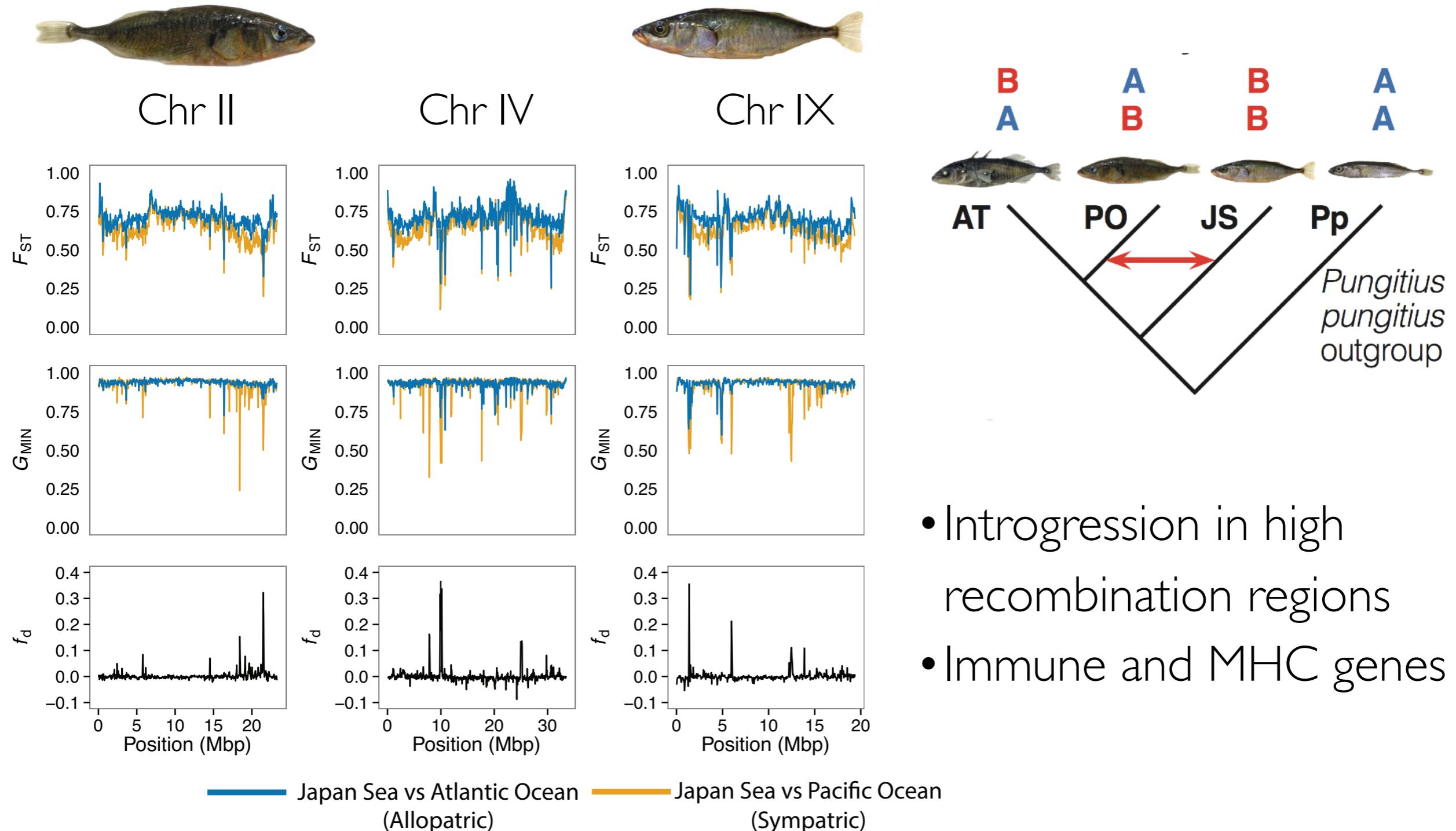
10 - 70 Kyr BP



**A** Constant migration + bottleneck



# Introgression localised in the genome



**House sparrow**  
*Passer domesticus*



## Hybrid speciation and the origin of the Italian sparrow

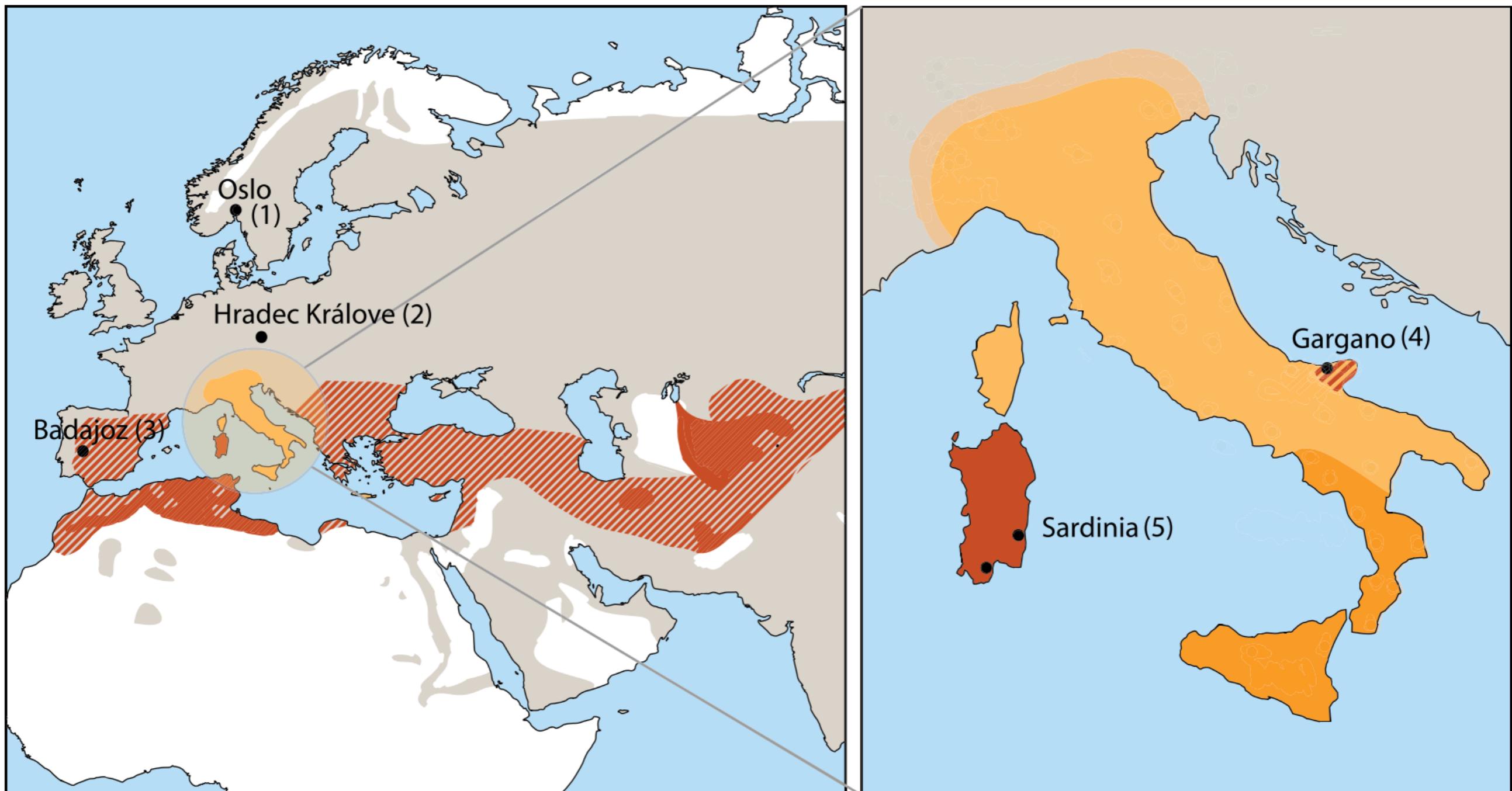


**Spanish sparrow**  
*Passer hispaniolensis*

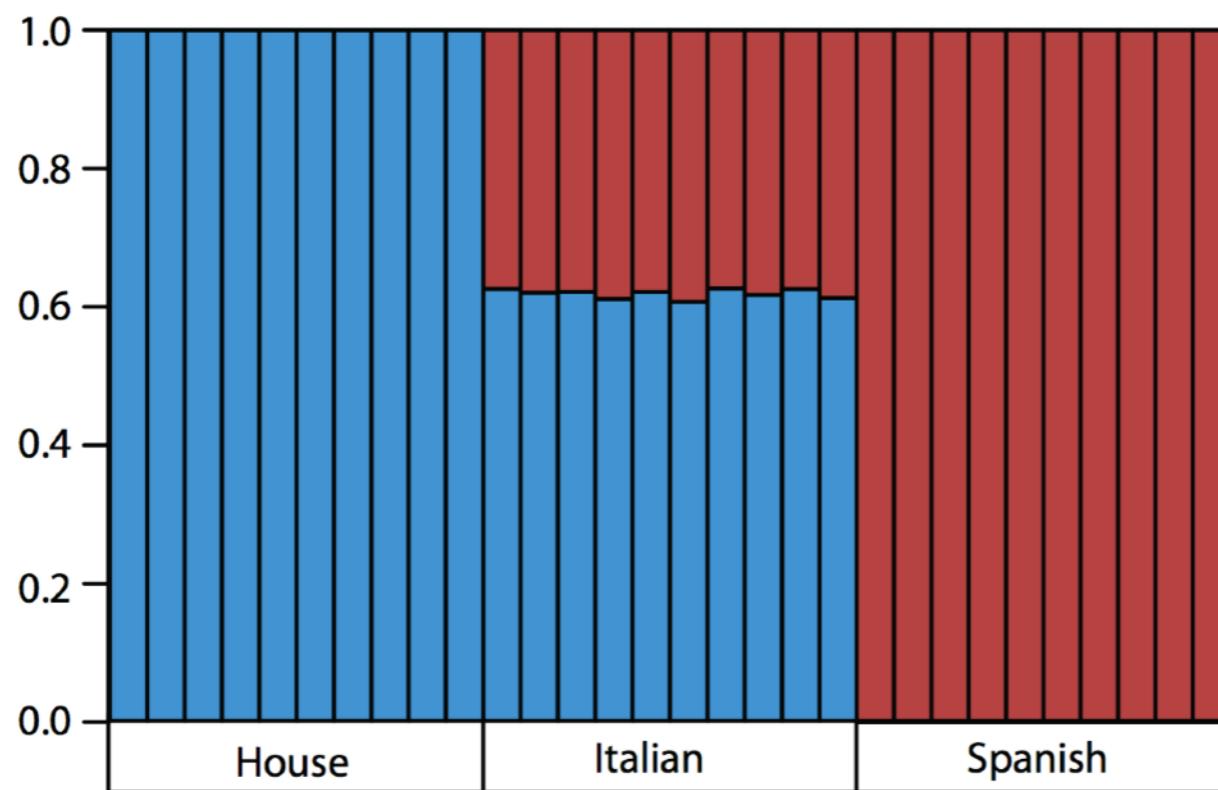
**Italian sparrow**  
*Passer italiae*



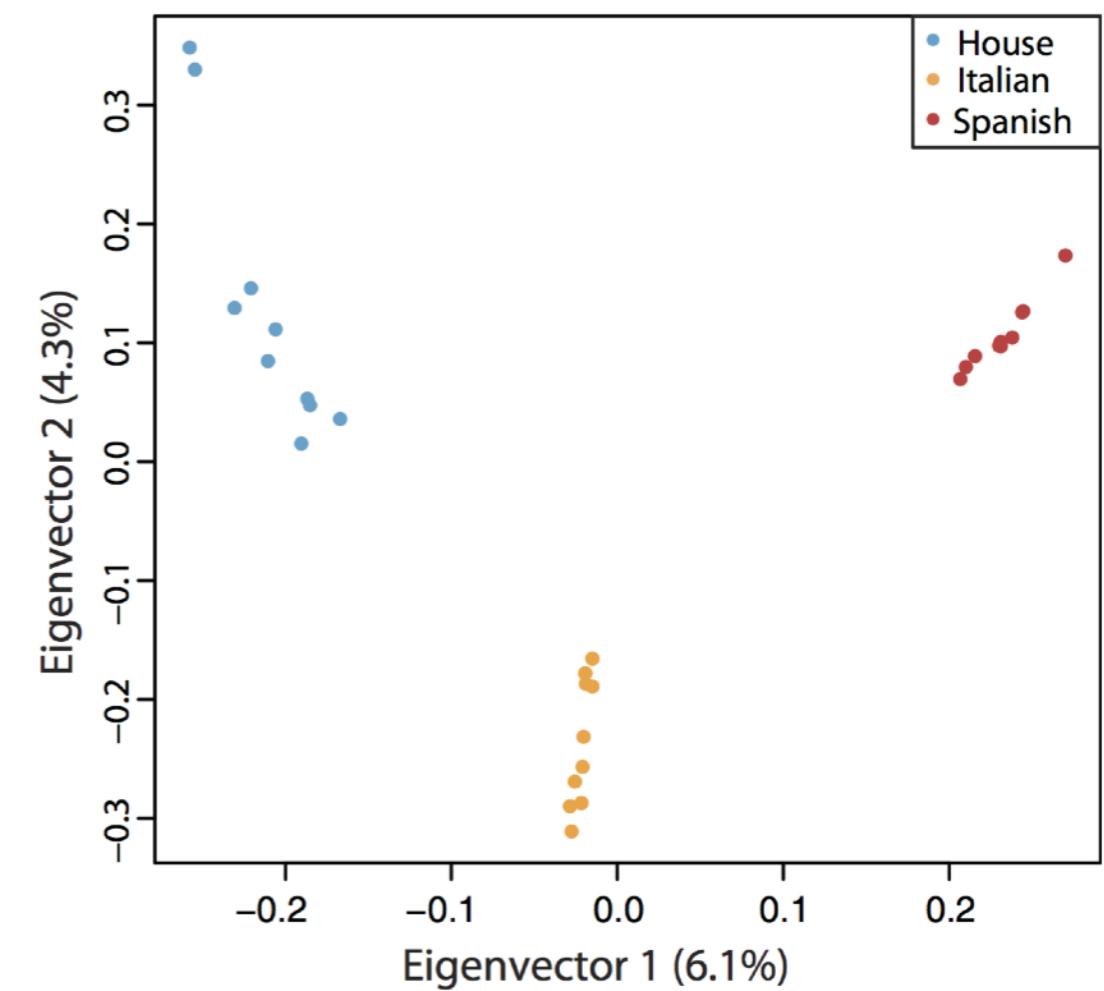
# Passer sparrow distribution in Europe



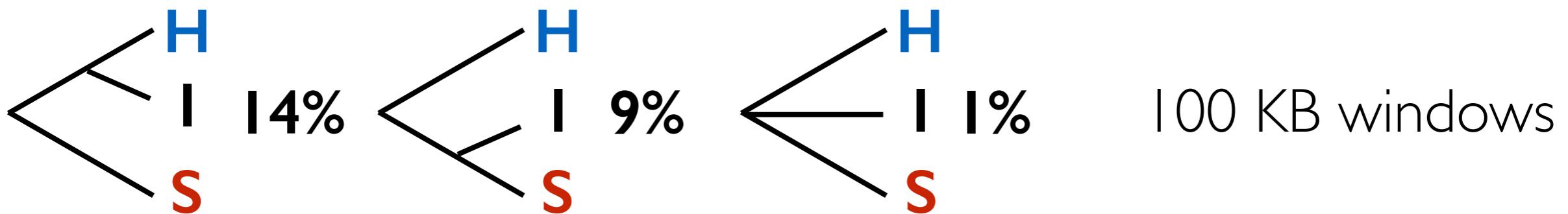
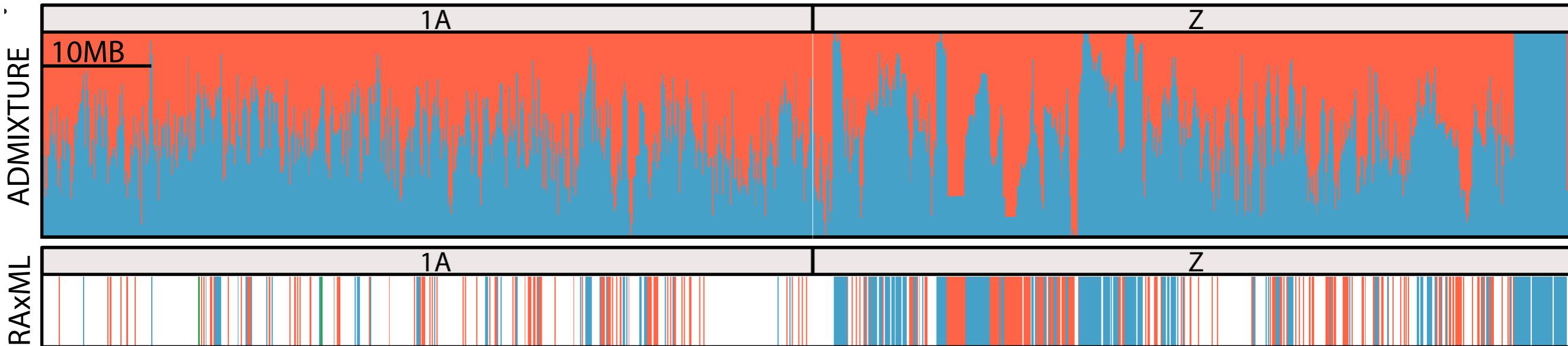
# Italian sparrows are a hybrid species



Analyses based on LD pruned, high quality  
270 K SNPs



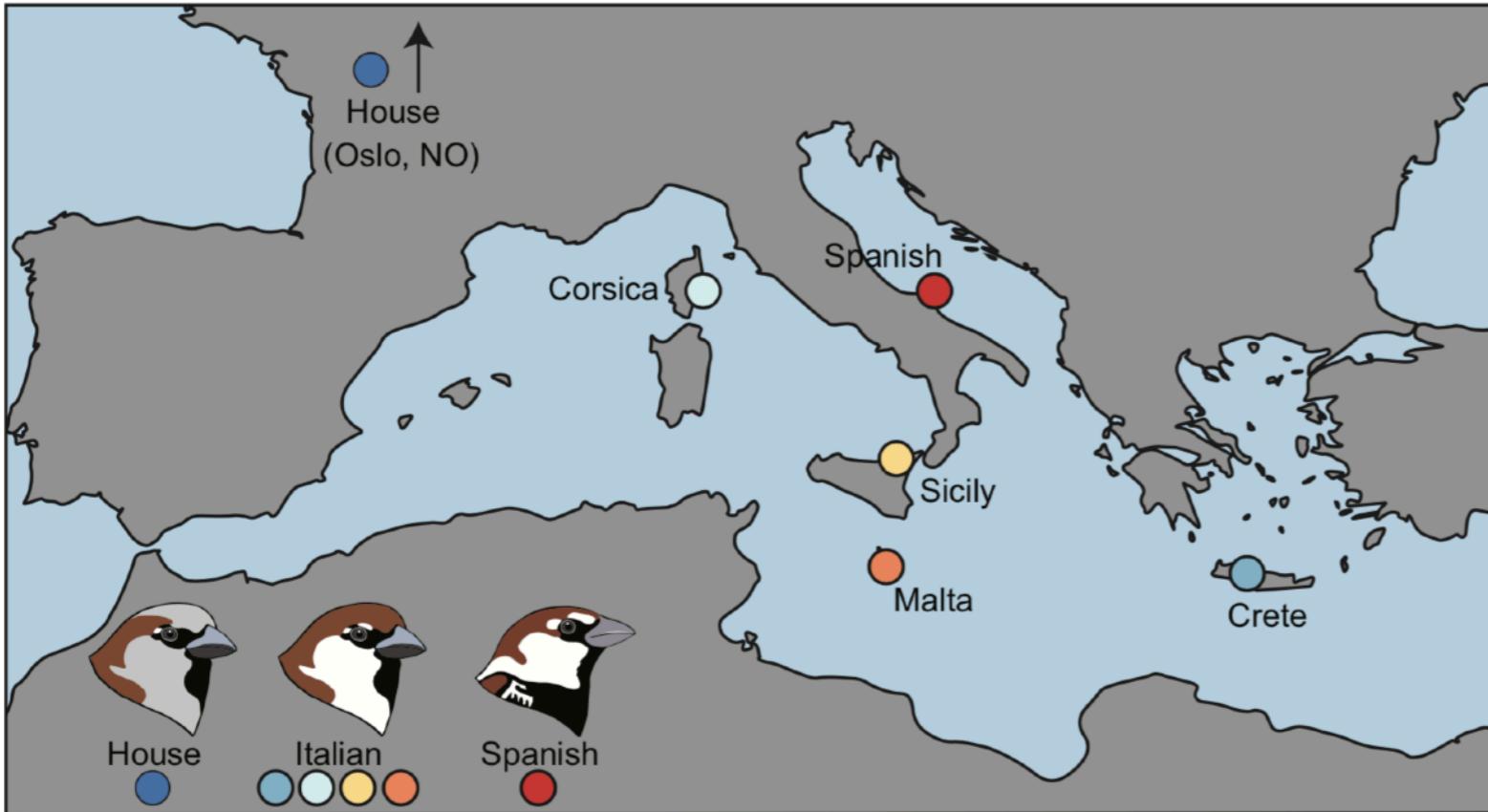
# Parental contributions vary across the genome



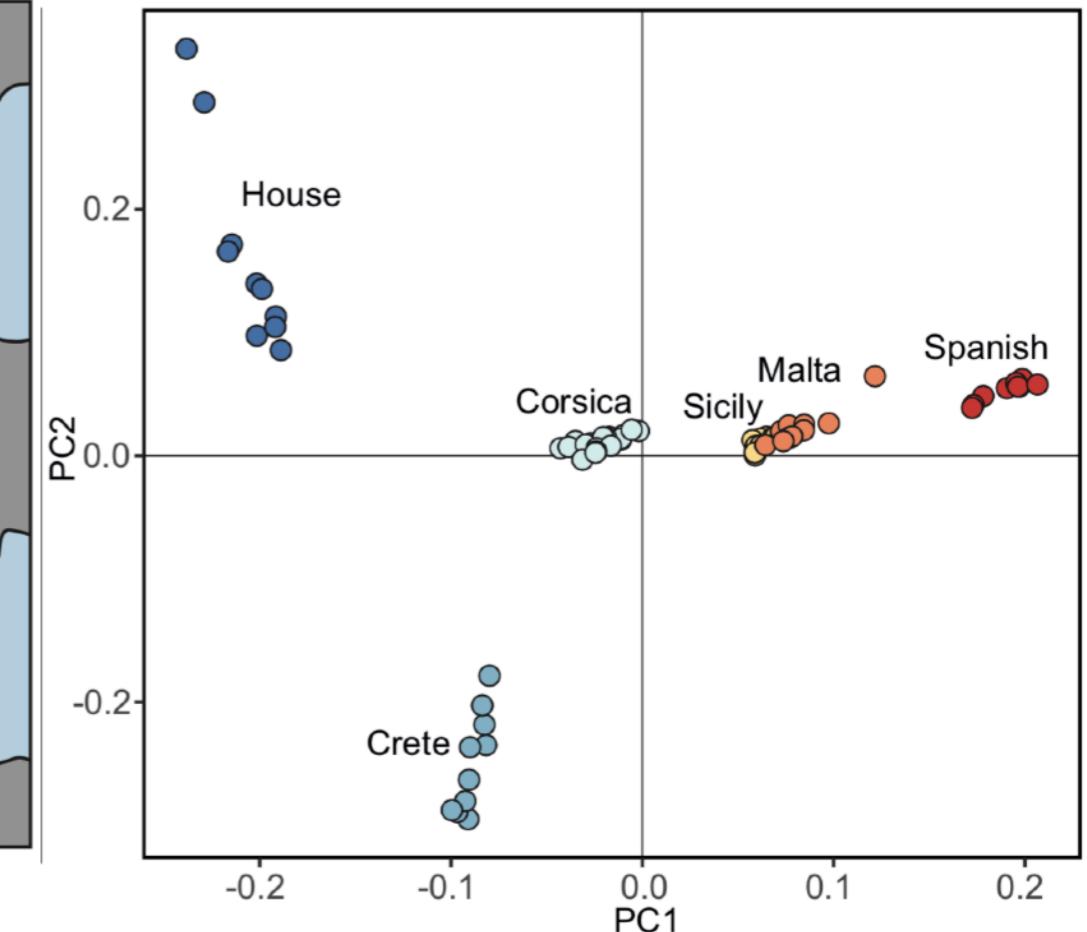
- Italian sparrow genome is a **mosaic**



# Parental contributions vary between island populations

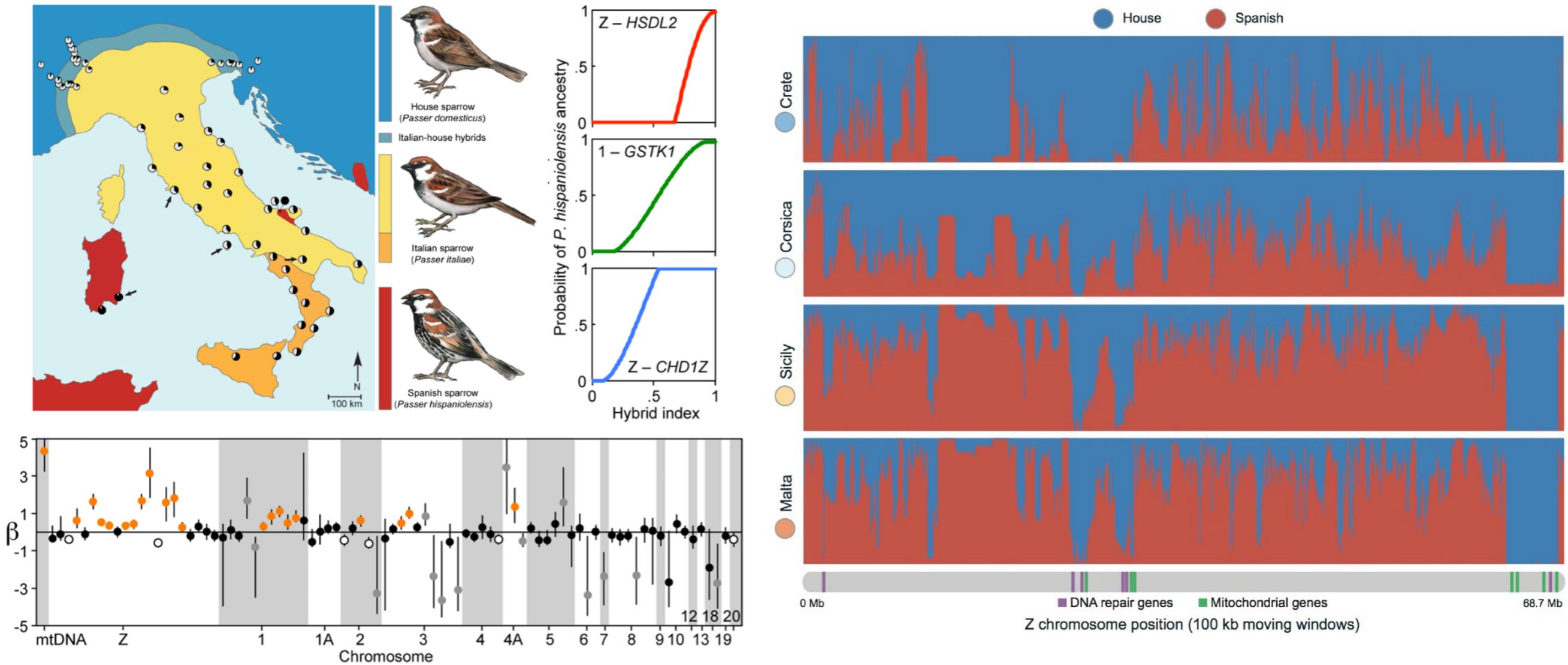


Spanish Malta Sicily Corsica Crete House



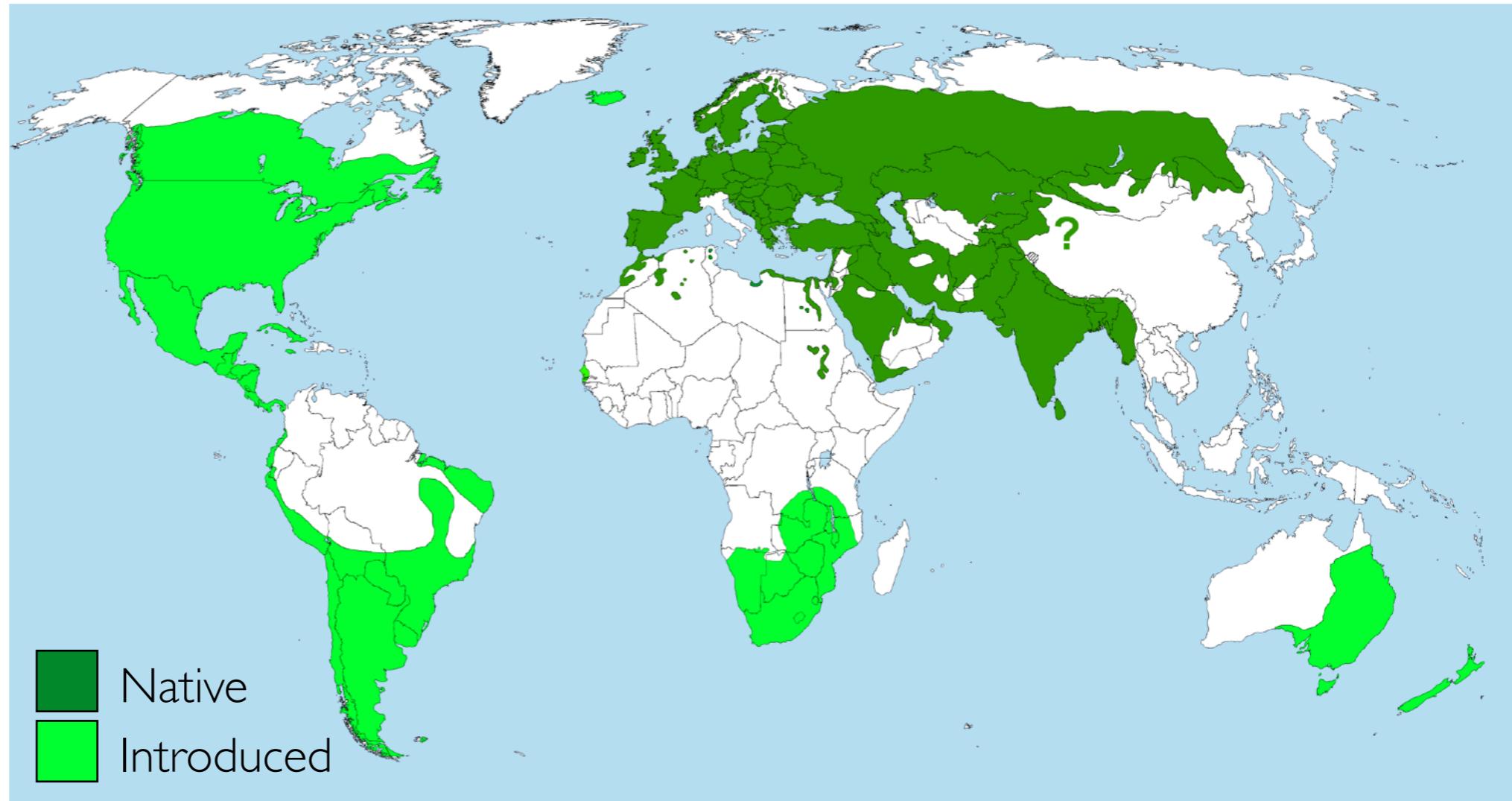
- Crete and Corsica are house-like
- Malta and Sicily are Spanish-like

# Reproductive isolation on sex chromosomes?



- More genes with steep clines on Z relative to autosome
- Overrepresentation of DNA damage and mitonuclear genes

# House sparrows - widespread and close to human society



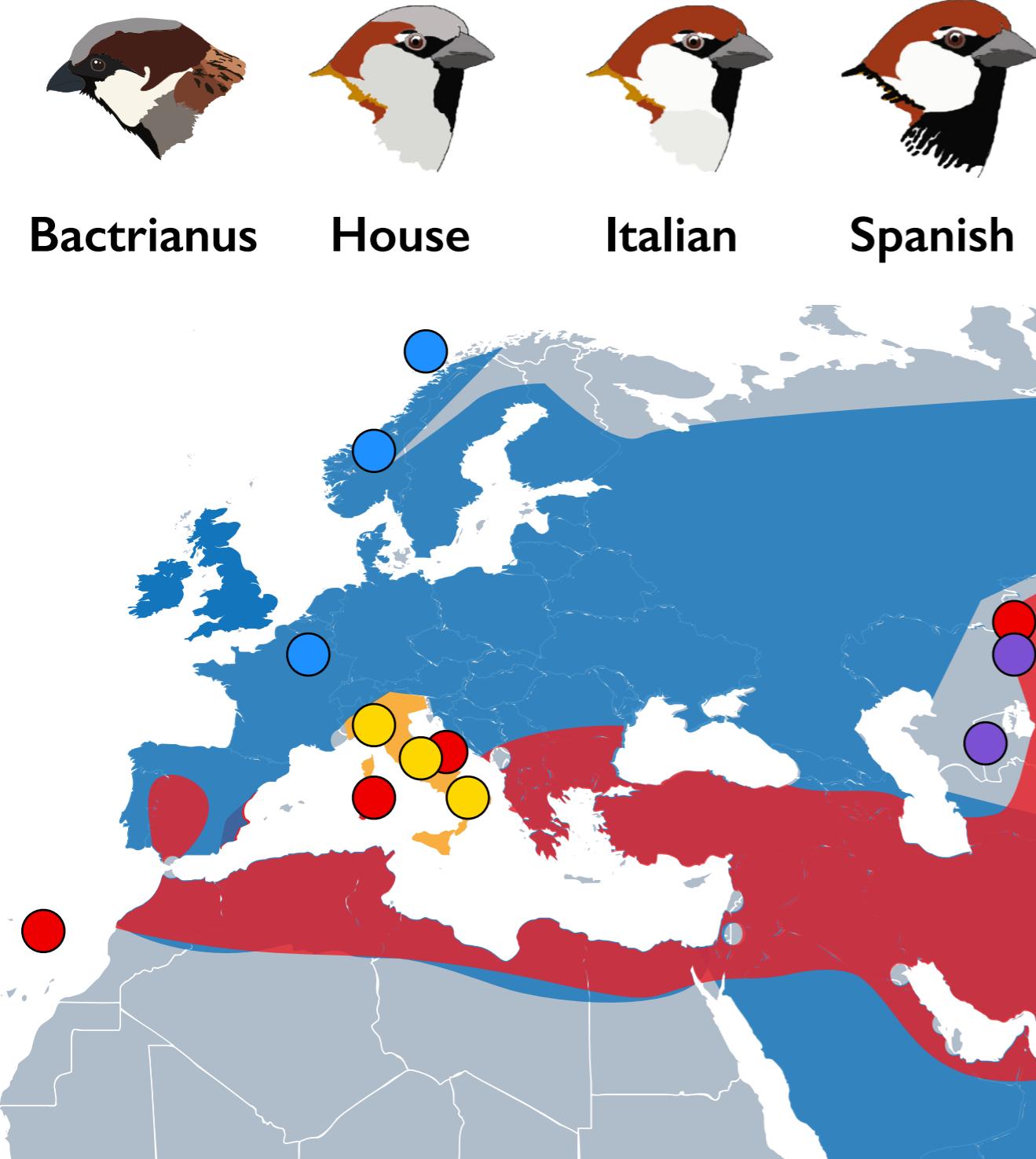
## How did the house sparrow evolve?

1. When & where did human-dependency arise?
2. What genes and phenotypes are involved?



*Passer domesticus*

# Eurasian sparrow population structure

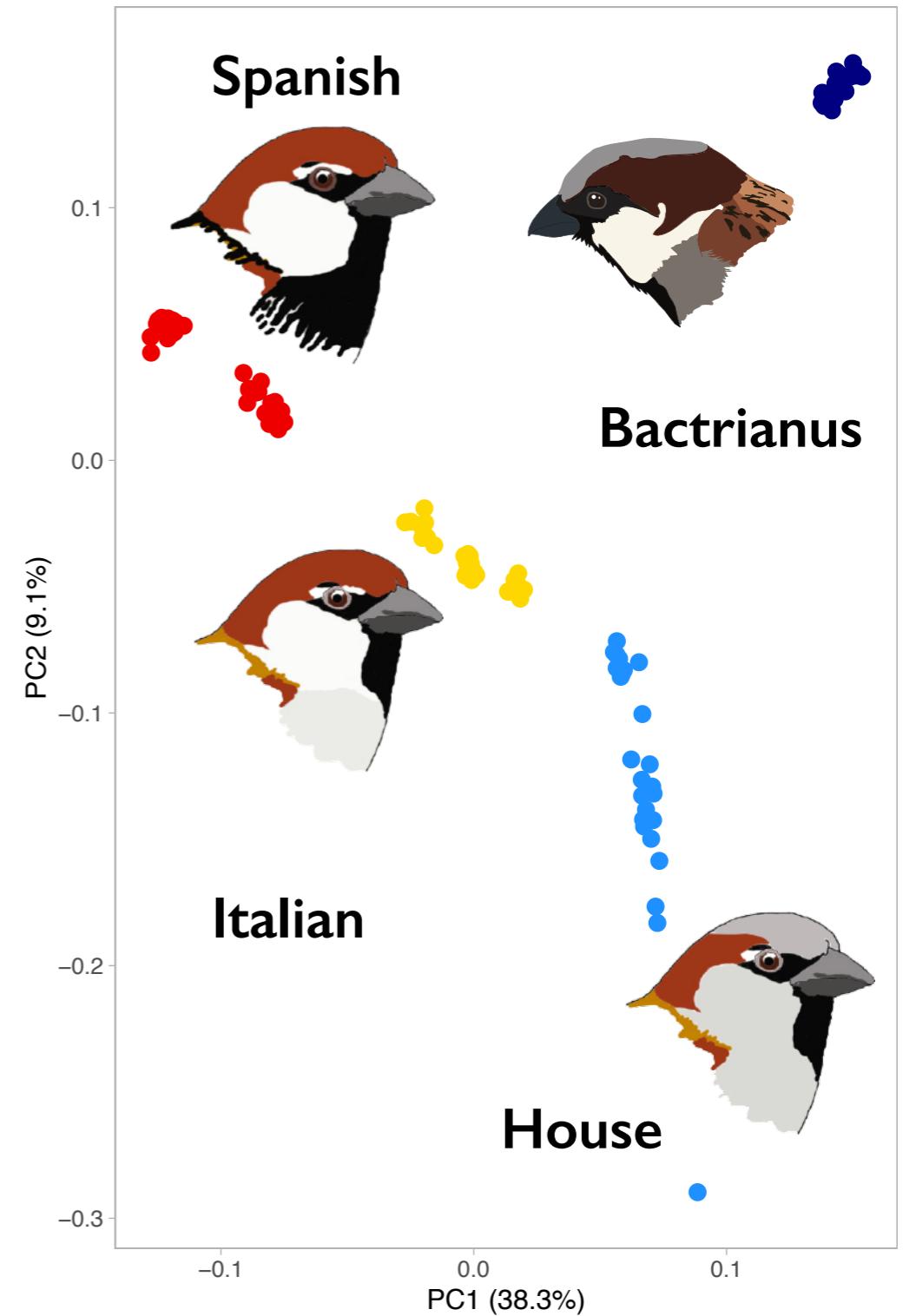


Bactrianus

House

Italian

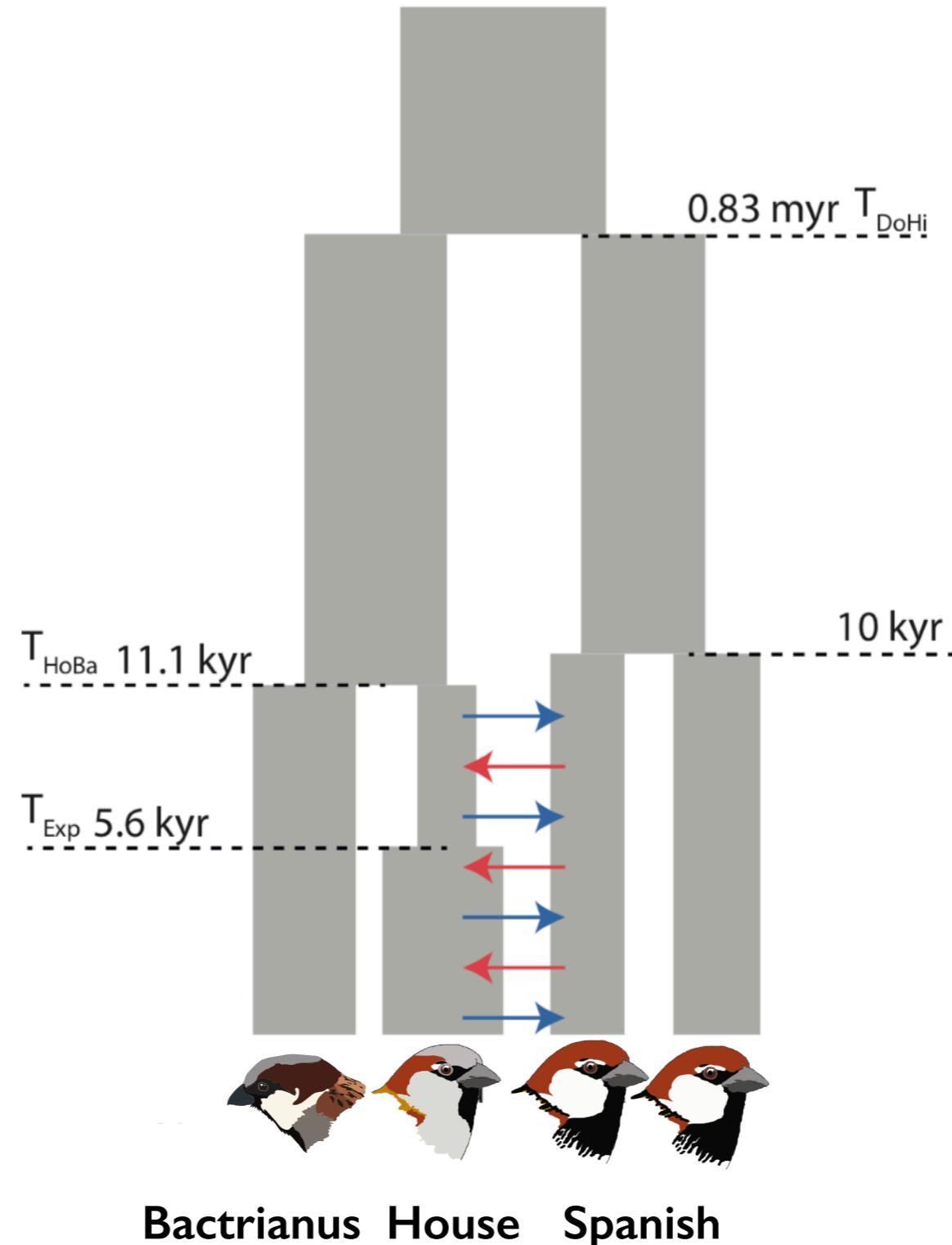
Spanish



Whole-genome resequencing,  $n = 120$ , 178,000 SNPs

Ravinet et al. (2018) **Proc B**

# Divergence occurred with migration

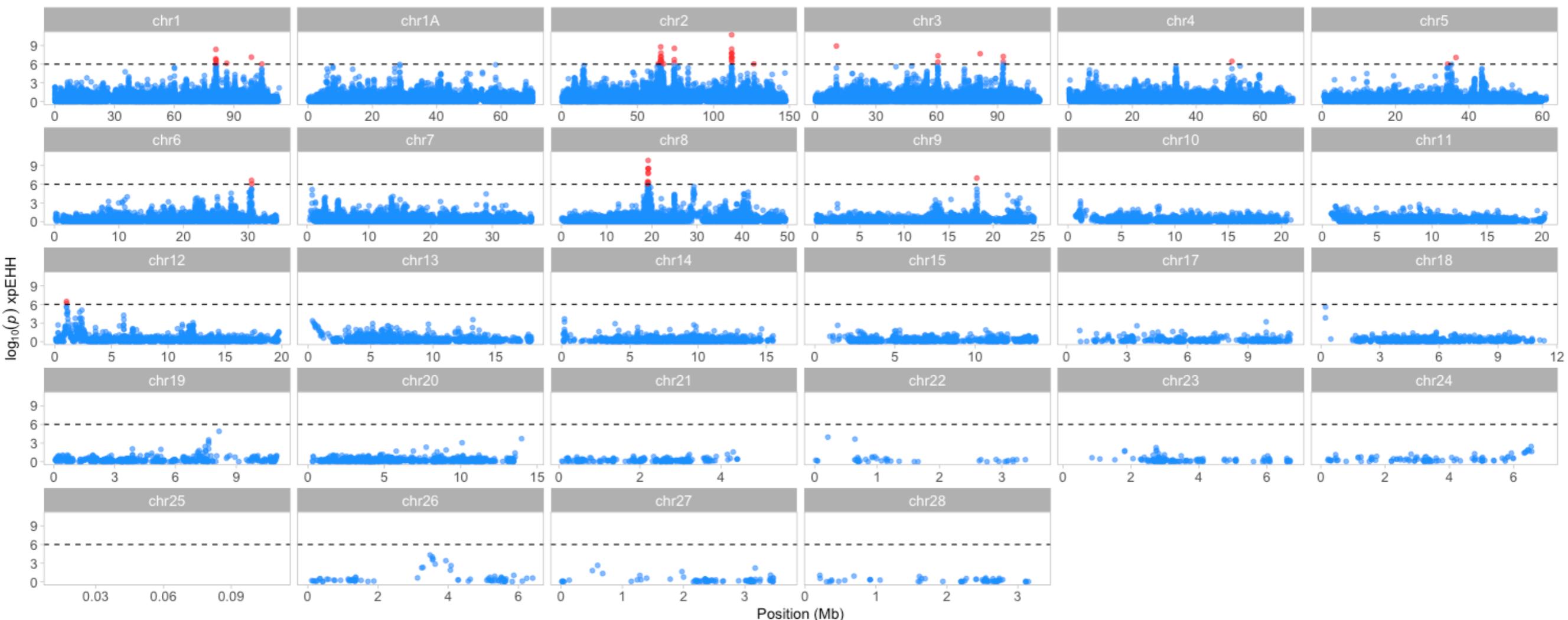


# Divergent selection between house and Bactrianus



vs.

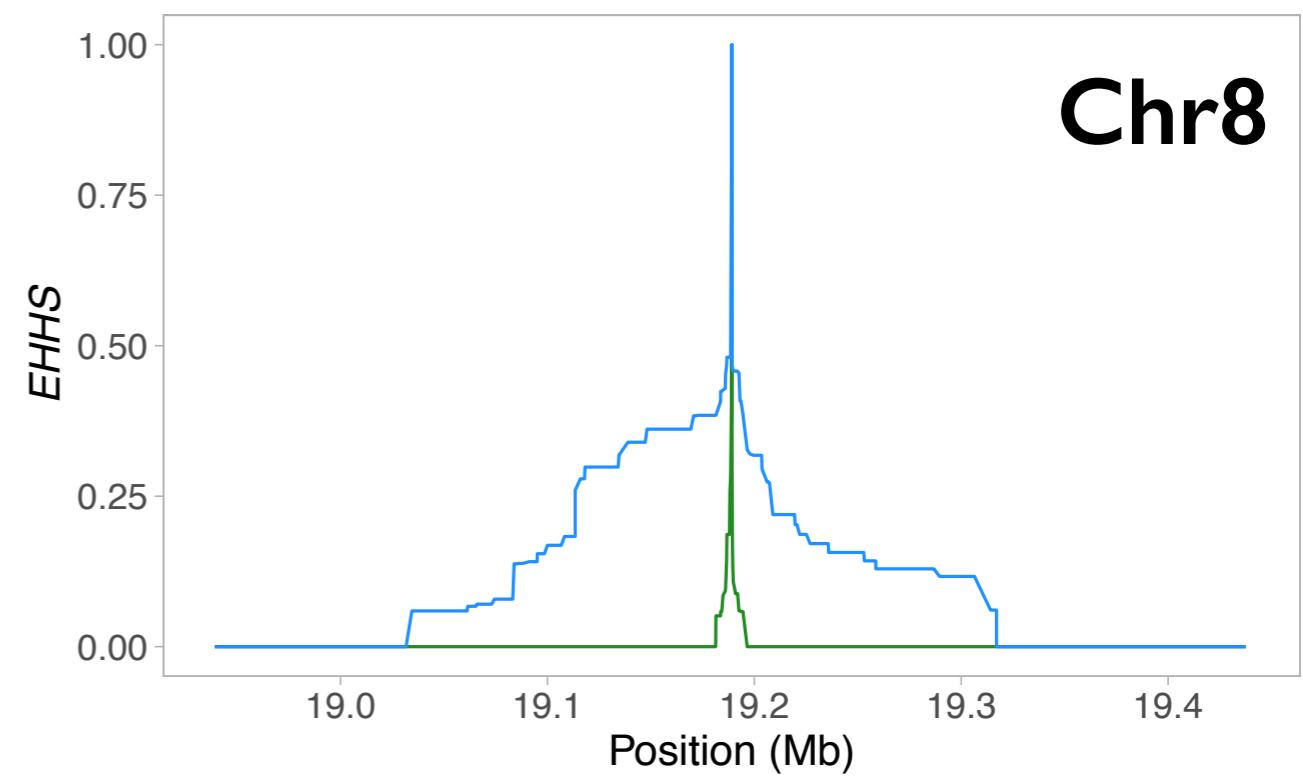
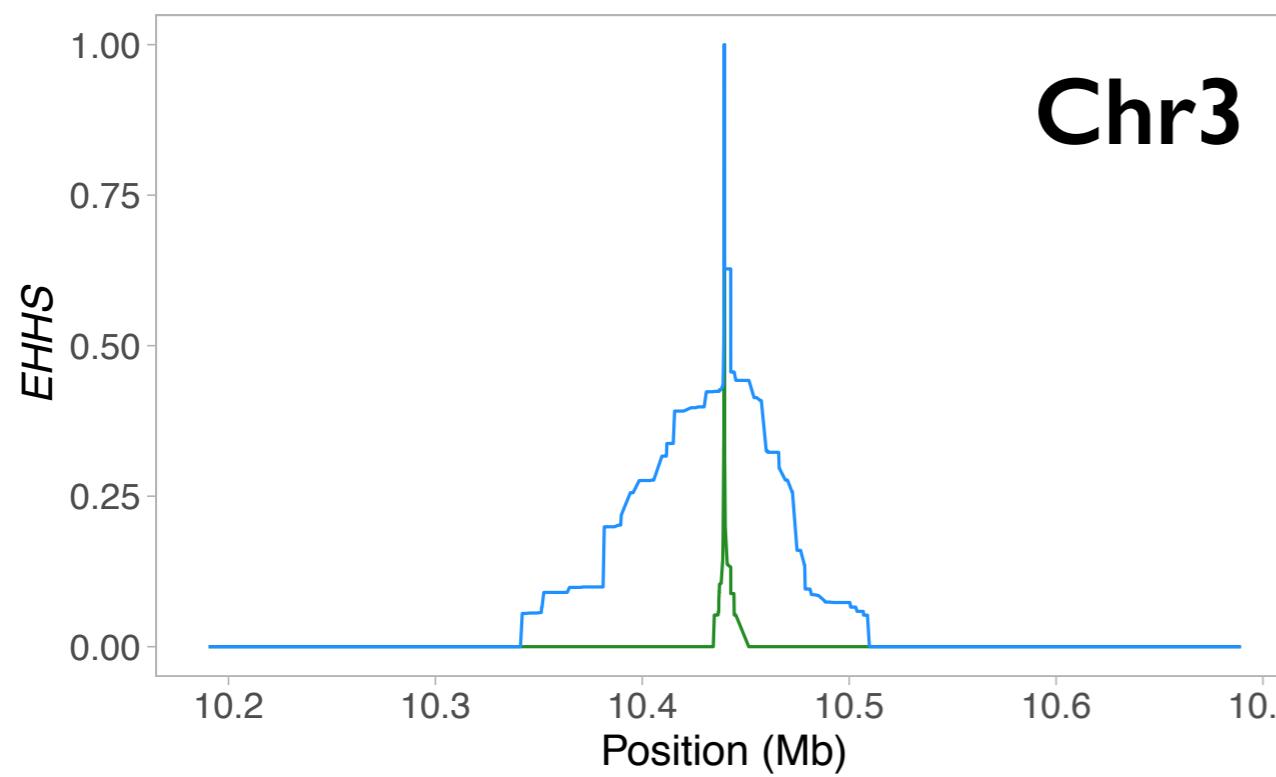
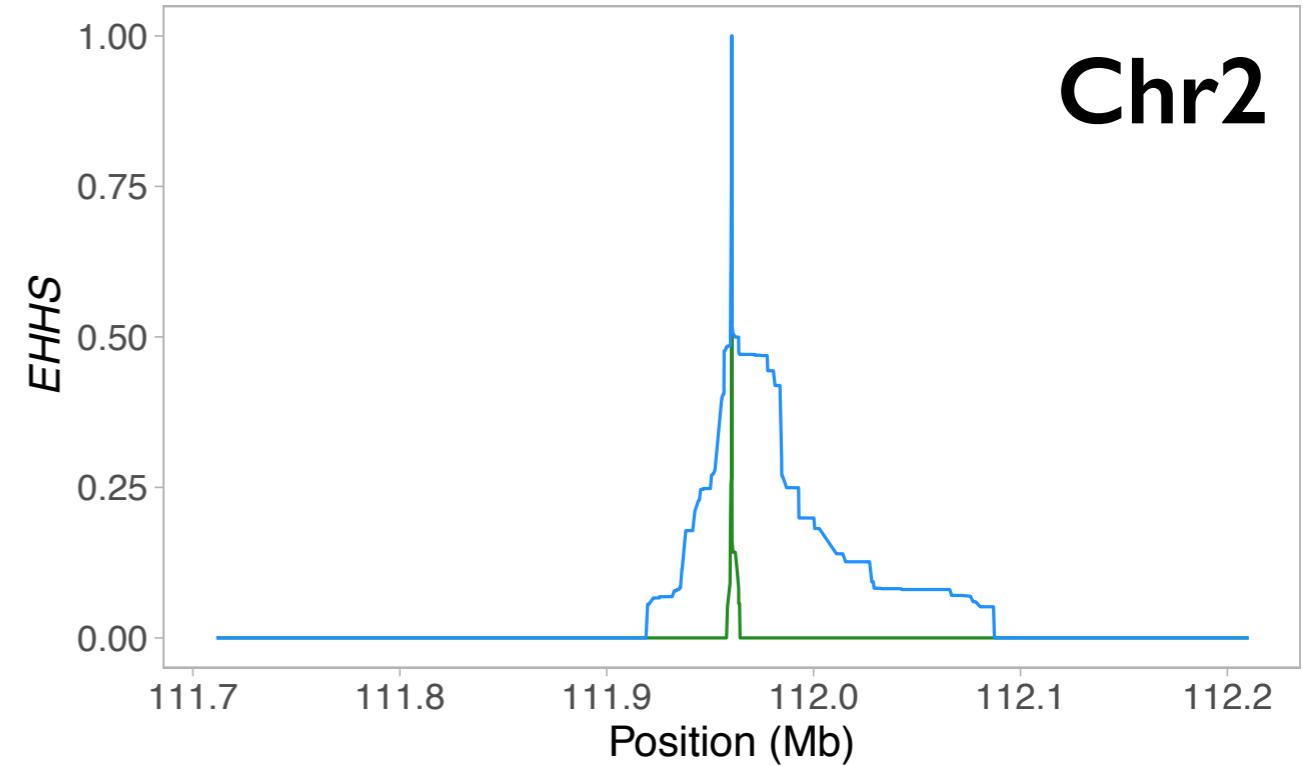
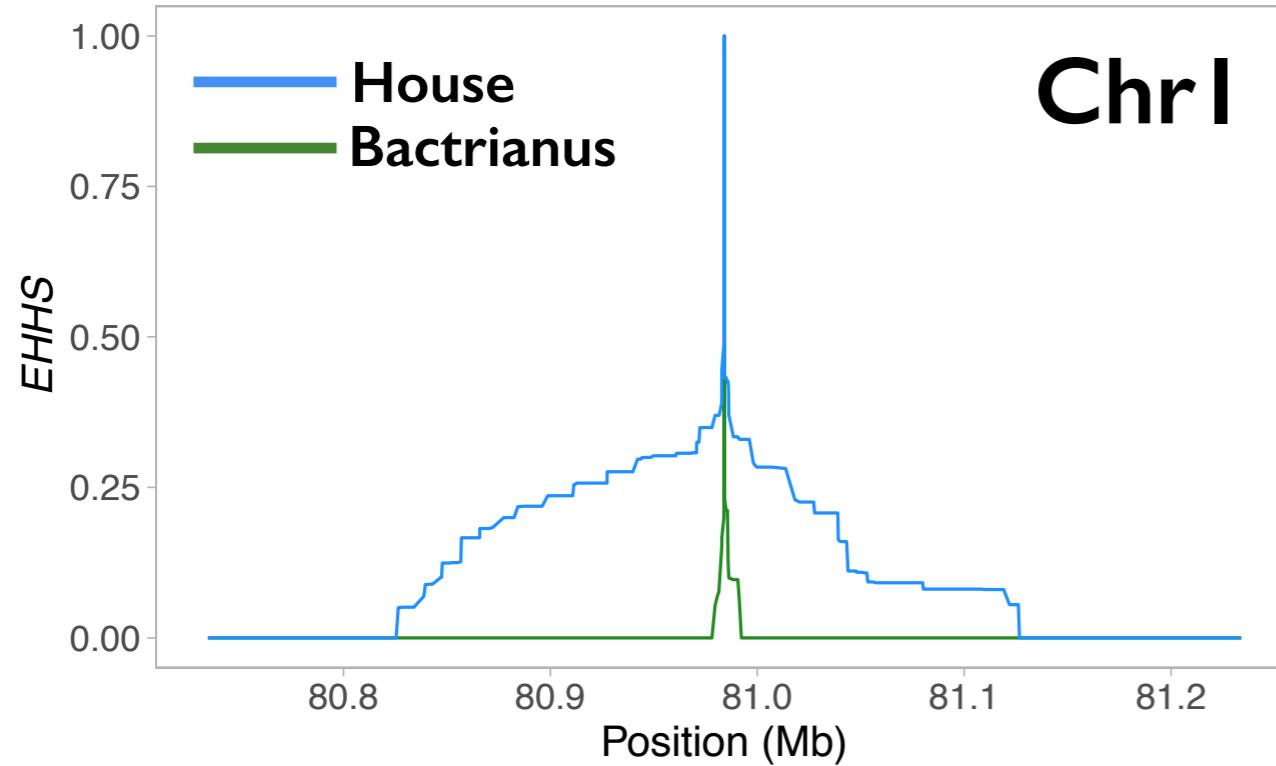
Strong selection limited to 4 chromosomes



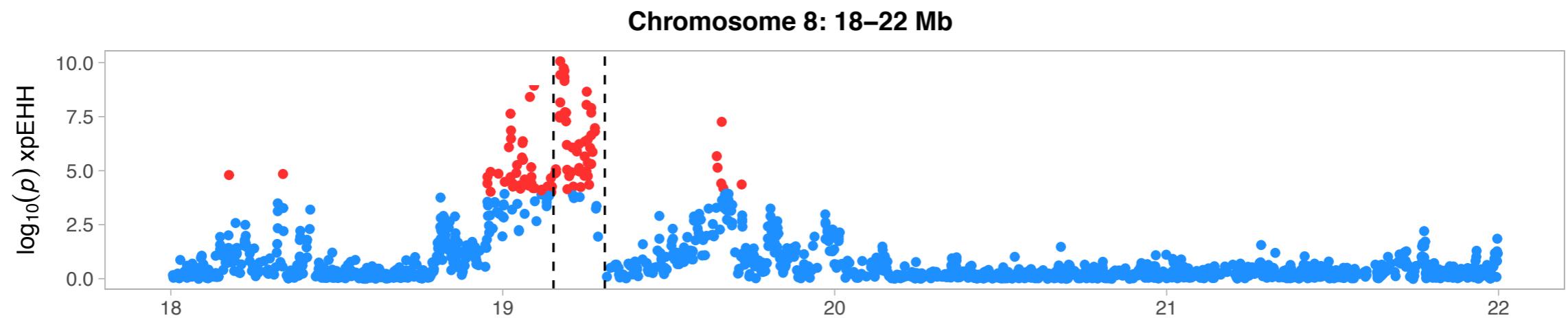
xp-EHH, 1.03 million SNPs

Ravinet et al. (2018) **Proc B**

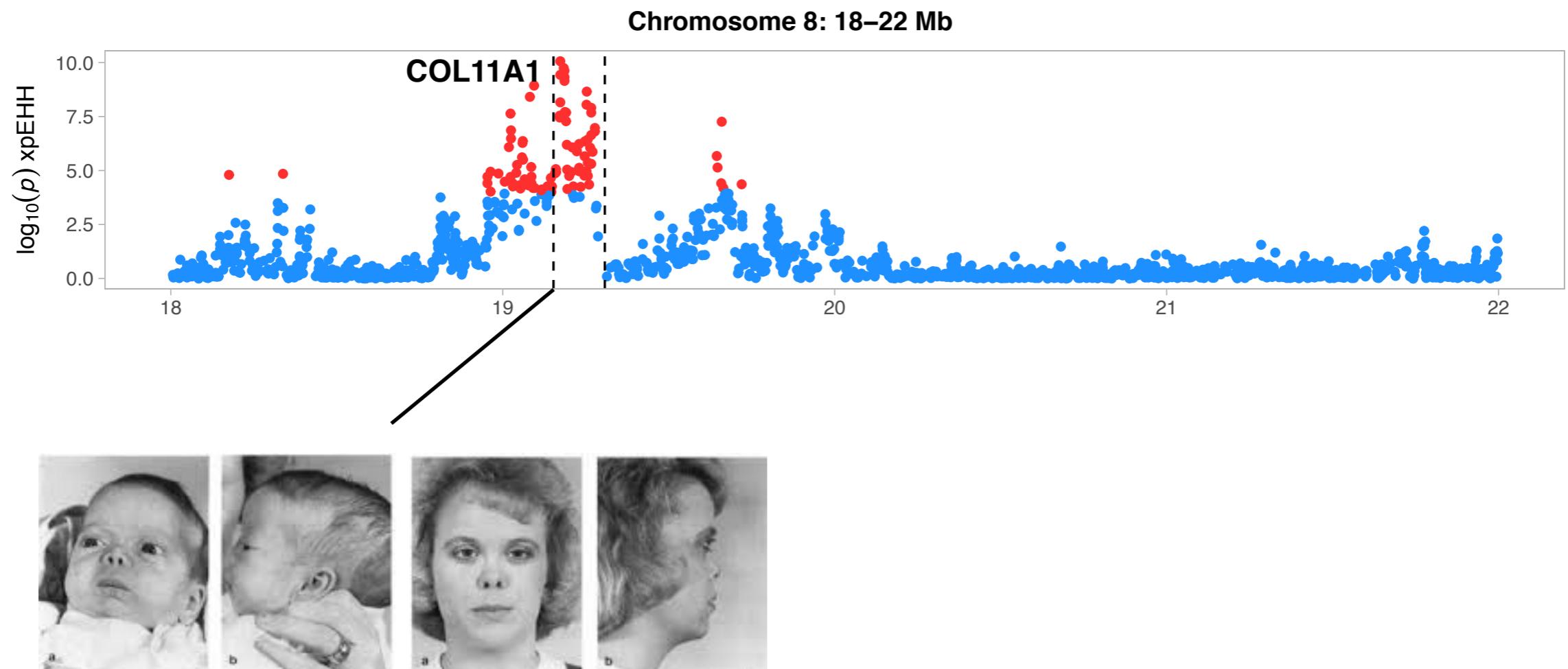
# Selective sweep signature in house only



# What genes lie beneath this peak?



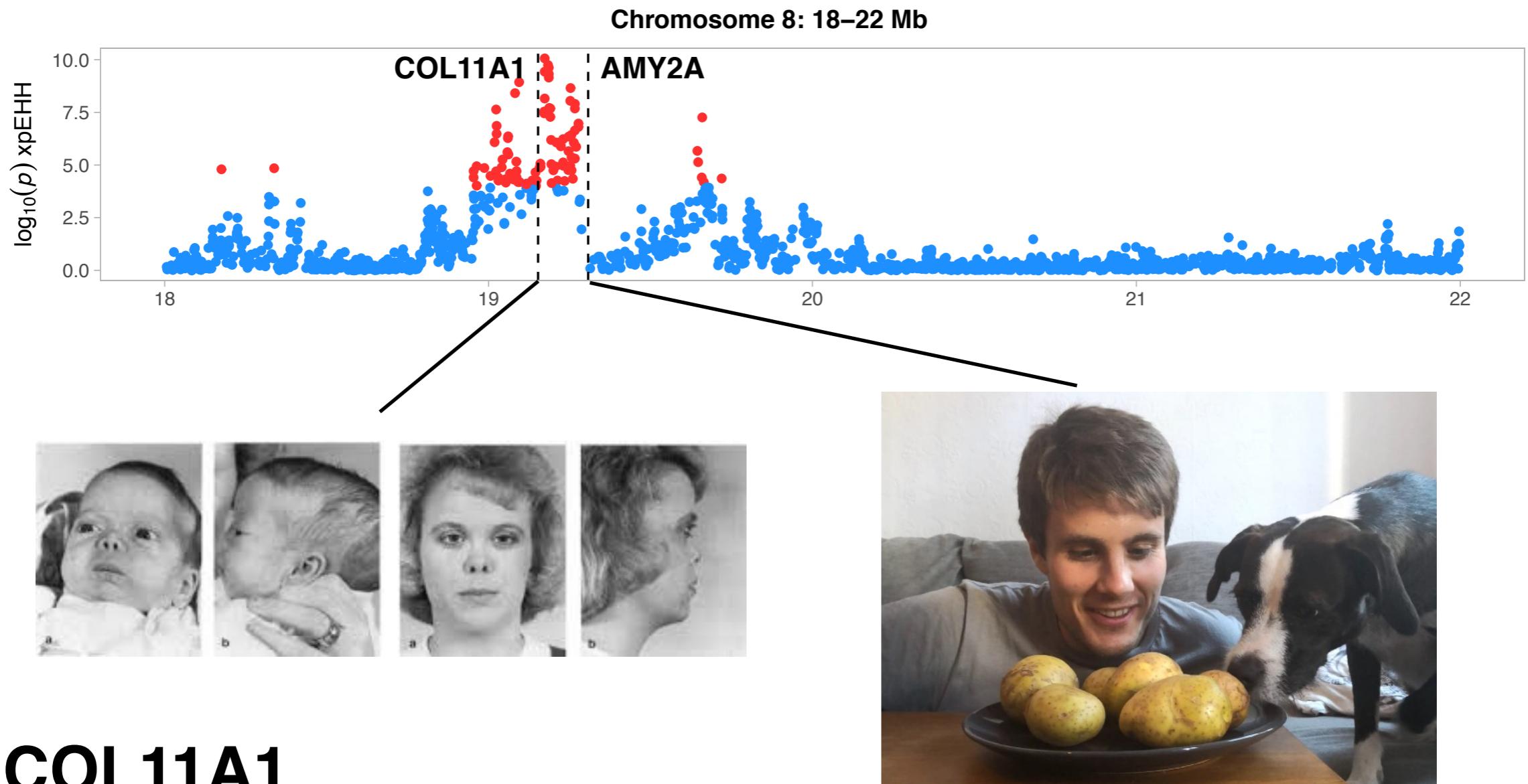
# What genes lie beneath this peak?



## COL11A1

mutations causes Marshall syndrome - a craniofacial disorder in humans

# What genes lie beneath this peak?



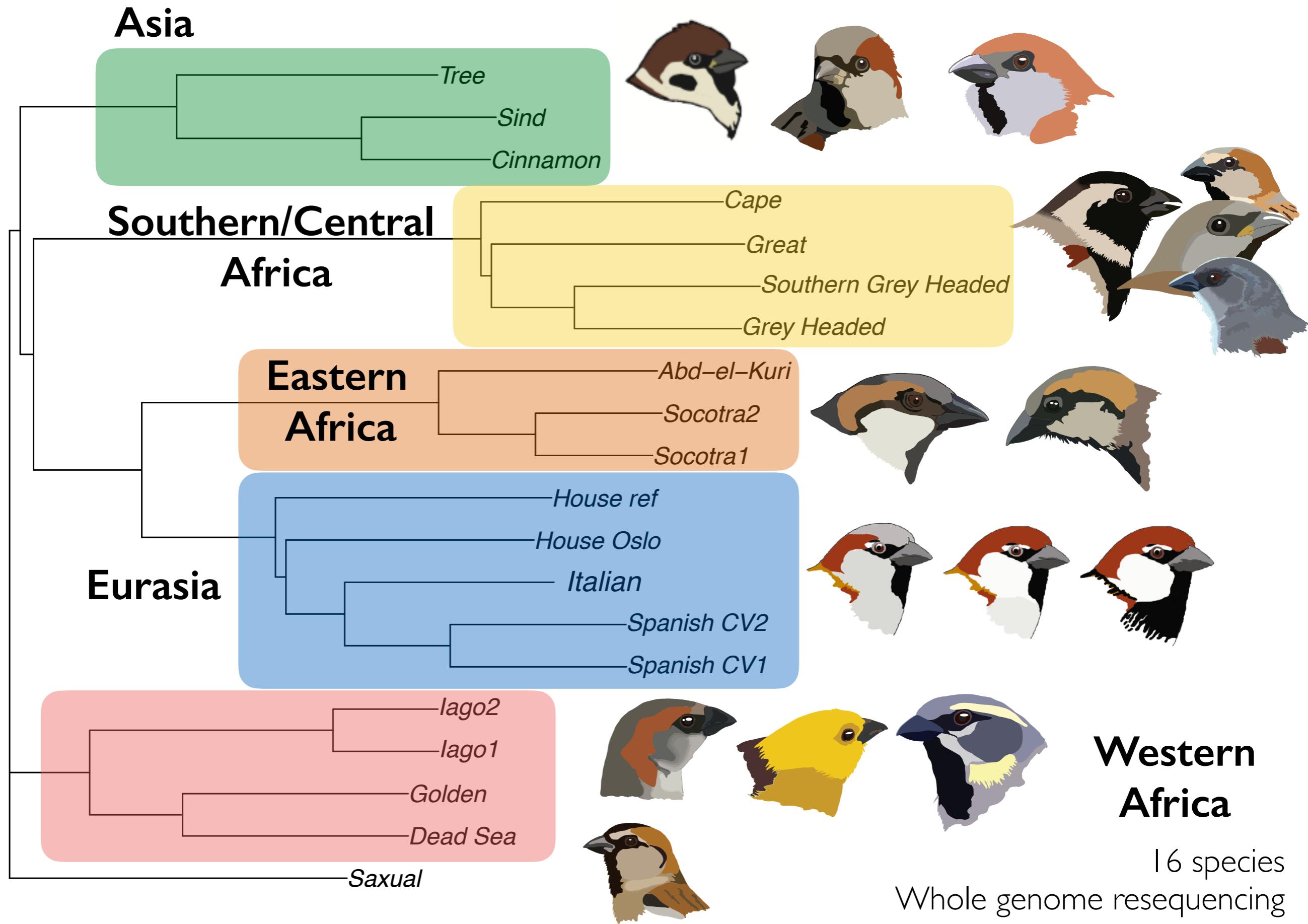
## COL11A1

mutations causes Marshall syndrome - a craniofacial disorder in humans

## AMY2A

copy number variation associated with starch digestion in humans and dogs

# Constructing a Passer phylogeny





# A confusing field - what is the way forward?



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**Inter-  
findin**

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Current Opinion in  
Genetics  
& Development

## Interpreting the genomic landscape of introgression

Simon H Martin and Chris D Jiggins



M. RAVINET\*† , R. FARIA‡§¶, R. K. BUTLIN¶\*\*, J. GALINDO††, N. BIEF  
M. RAFAJLOVIĆ§§ , M. A. F. NOOR¶¶ , B. MEHLIG§§ & A. M. WESTR

COMMENTARY

**Parallelism in genomic  
landscapes of differentiation,  
conserved genomic features  
and the role of linked selection**

EVIEWS

RESPONSE

**Land ahoy? Navigating the  
genomic landscape of  
speciation while avoiding  
shipwreck**

A. M. WESTRAM\*  & M. RAVINET† 

H. ELLEGREN

Making  
different



Open Access

Jochen B. W. Wolf<sup>1</sup>



Interpreting differentiation landscapes  
in

What is Speciation Genomics? The roles of ecology, gene  
flow, and genomic architecture in the formation of species

Reto<sup>1</sup>

C. RYAN CAMPBELL, J. W. POELSTRA and ANNE D. YODER\*

# What we hope to achieve

- Clarify an increasingly complex and difficult field
- Teach you the tools and approaches necessary to go from raw sequencing reads to finished analyses
- Teach best practices - learn from our mistakes!
- Generate discussion and interaction
- Create a resource you can refer back to throughout your analyses and research

**[speciationgenomics.github.io](https://speciationgenomics.github.io)**