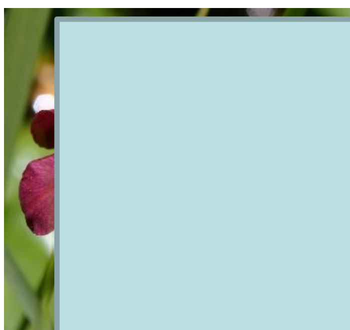
MODULARIZACE VÝUKY EVOLUČNÍ A EKOLOGICKÉ BIOLOGIE
CZ.1.07/2.2.00/15.0204

HYBRIDIZATION AND HYBRID ZONES



tok genů: Fst, Dxy
test Patterson s D = ABBA/BABA
ghost introgression: Zhang19 (mám PDF)

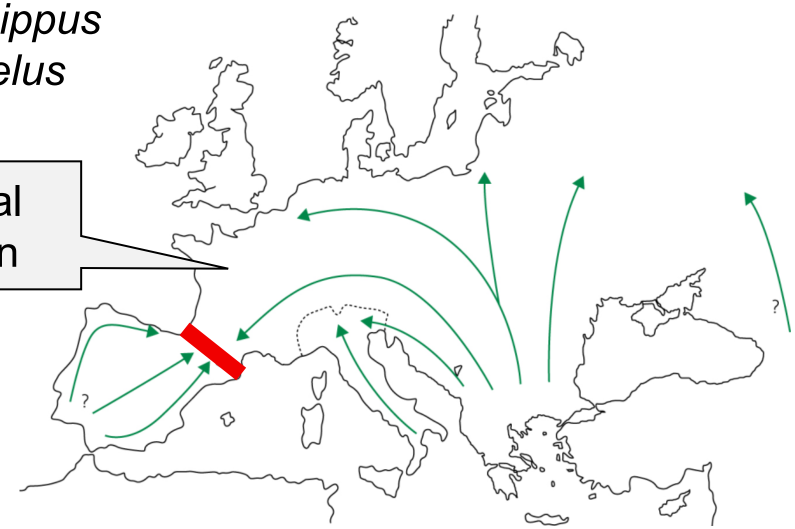
evropský sociální fond v ČR
EVROPSKÁ UNIE
MINISTERSTVO ŠKOLSTVÍ, MLÁDEŽE A TĚLOVÝCHOVY
OP Vzdělávání pro konkurenceschopnost
INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

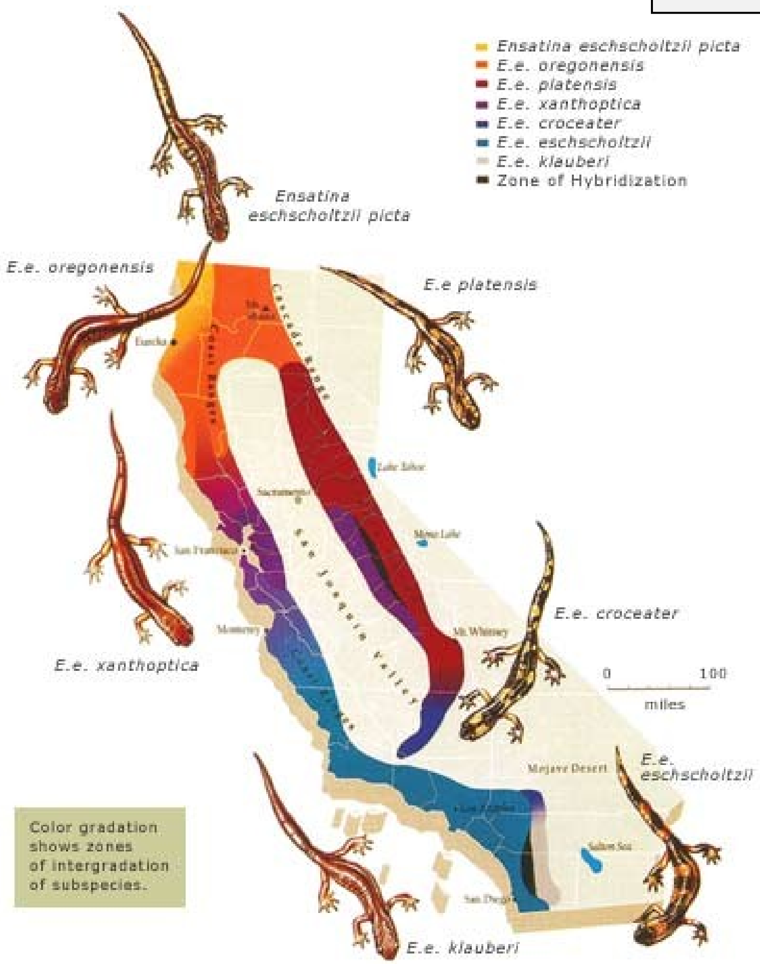
Secondary contact

ring species:

Chorthippus parallelus

postglacial expansion





Ensatina eschscholtzii - klauberi

greenish warbler (*Phylloscopus trochiloides*)

Larus argenteus/L. fuscus

Hybridization:

25% species of vascular plants

10% species of animals

probably underestimation (only conspicuous species: ducks, birds of paradise, butterflies)

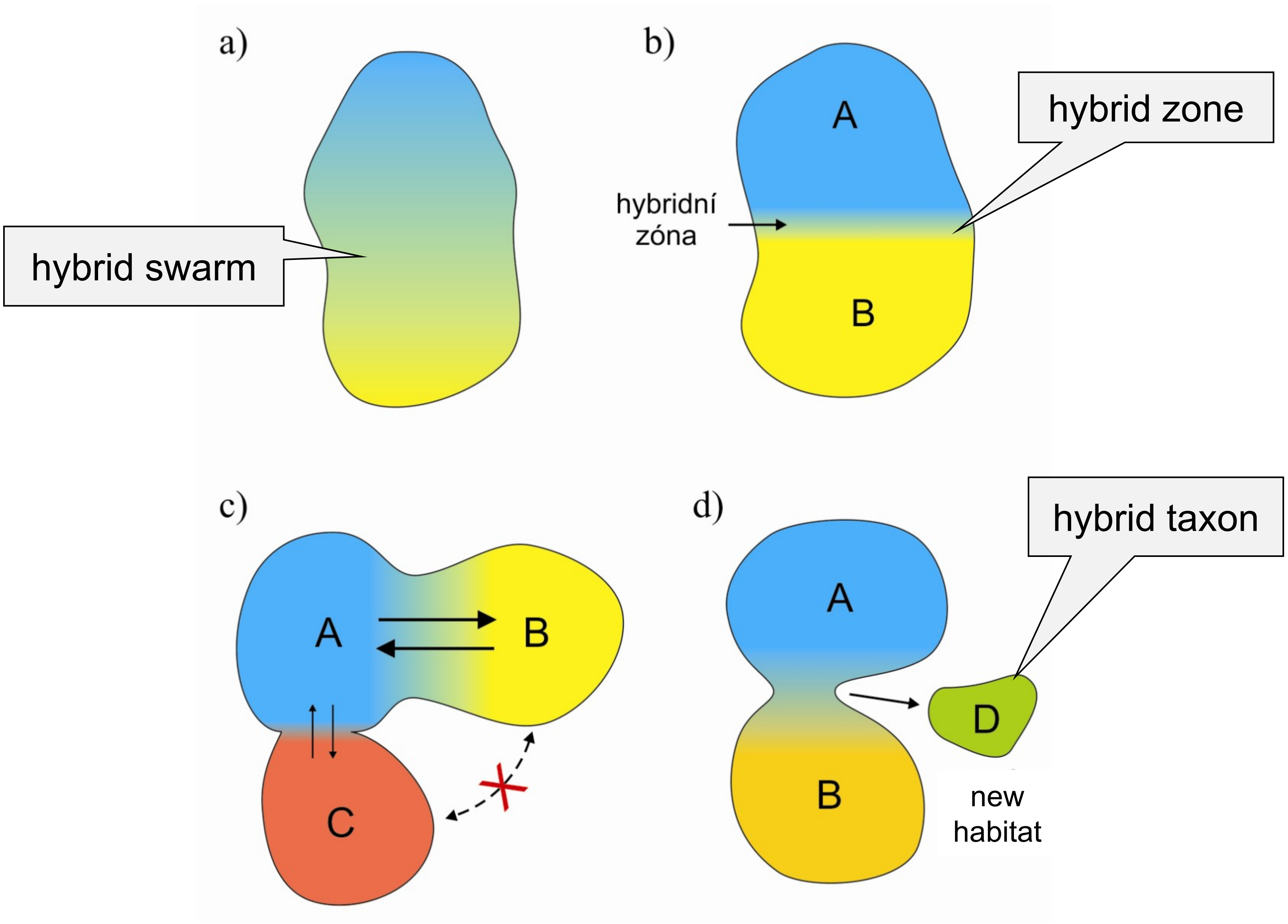
often result of environmental disturbance:
eg. „Darwin's finches“ *Geospiza fuliginosa*, *G. fortis* and *G. scandens* after El Niño event

Geospiza fuliginosa

G. fortis

G. scandens

Possible outcomes of hybridization



Program NewHybrids:

A Model-Based Method for Identifying Species Hybrids Using Multilocus Genetic Data

E. C. Anderson[1] and E. A. Thompson

Department of Statistics, University of Washington, Seattle, Washington 98195

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ABSTRACT

We present a statistical method for identifying species hybrids using data on multiple, unlinked markers. The method does not require that allele frequencies be known in the parental species nor that separate, pure samples of the parental species be available. The method is suitable for both markers with fixed allelic differences between the species and markers without fixed differences. The probability model used is one in which parentals and various classes of hybrids (F_1's, F_2's, and various backcrosses) form a mixture from which the sample is drawn. Using the framework of Bayesian model-based clustering allows us to compute, by Markov chain Monte Carlo, the posterior probability that each individual belongs to each of the distinct hybrid classes. We demonstrate the method on allozyme data from two species of hybridizing trout, as well as on two simulated data sets.

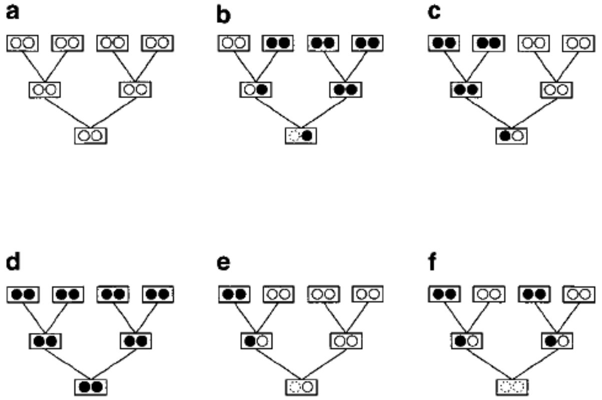
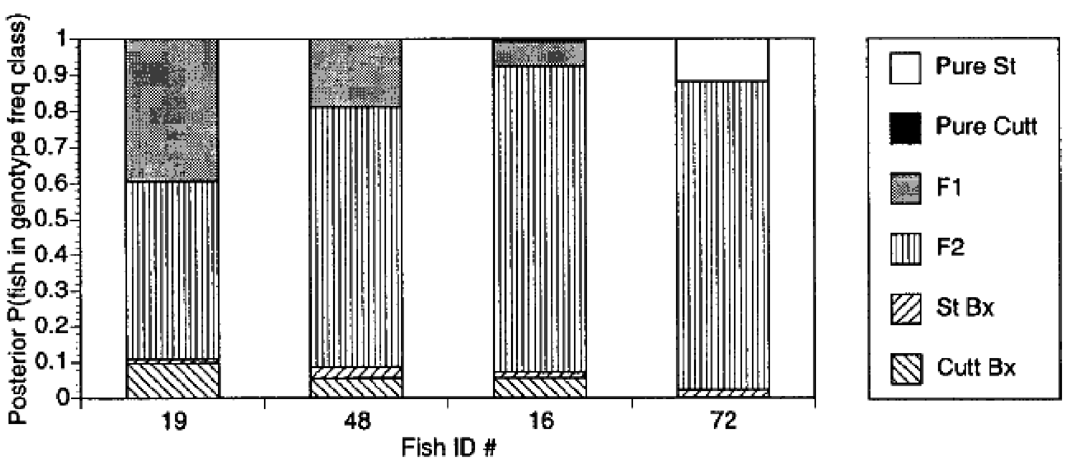
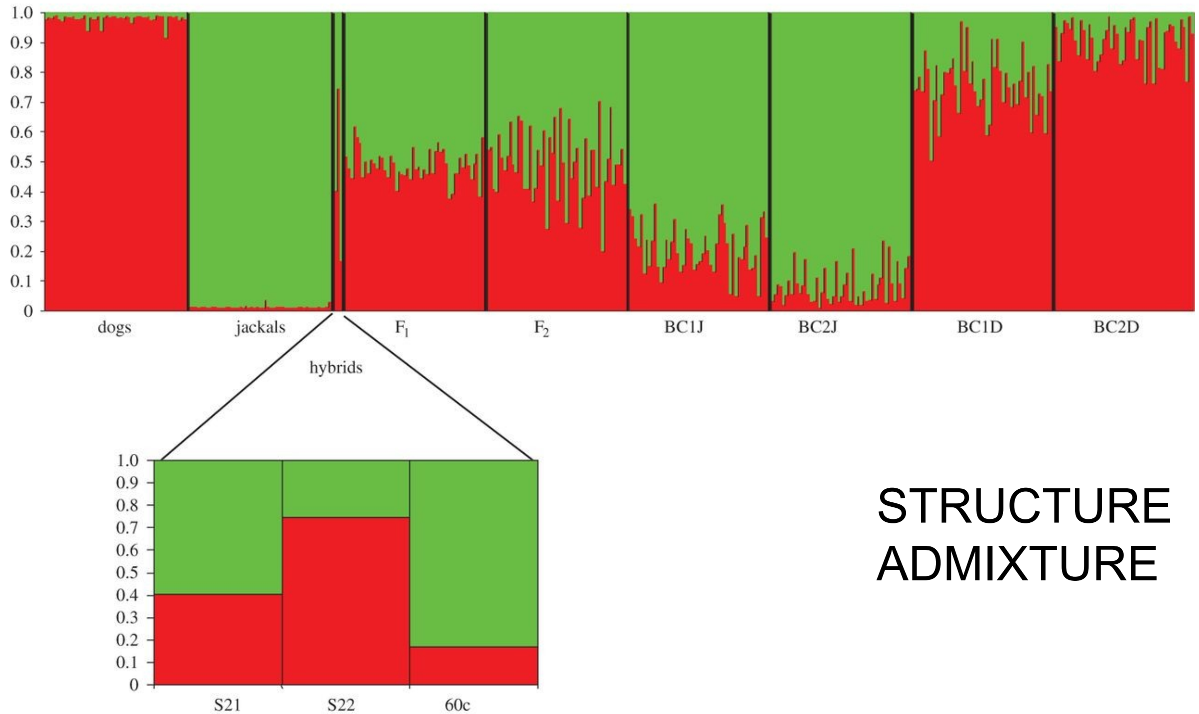
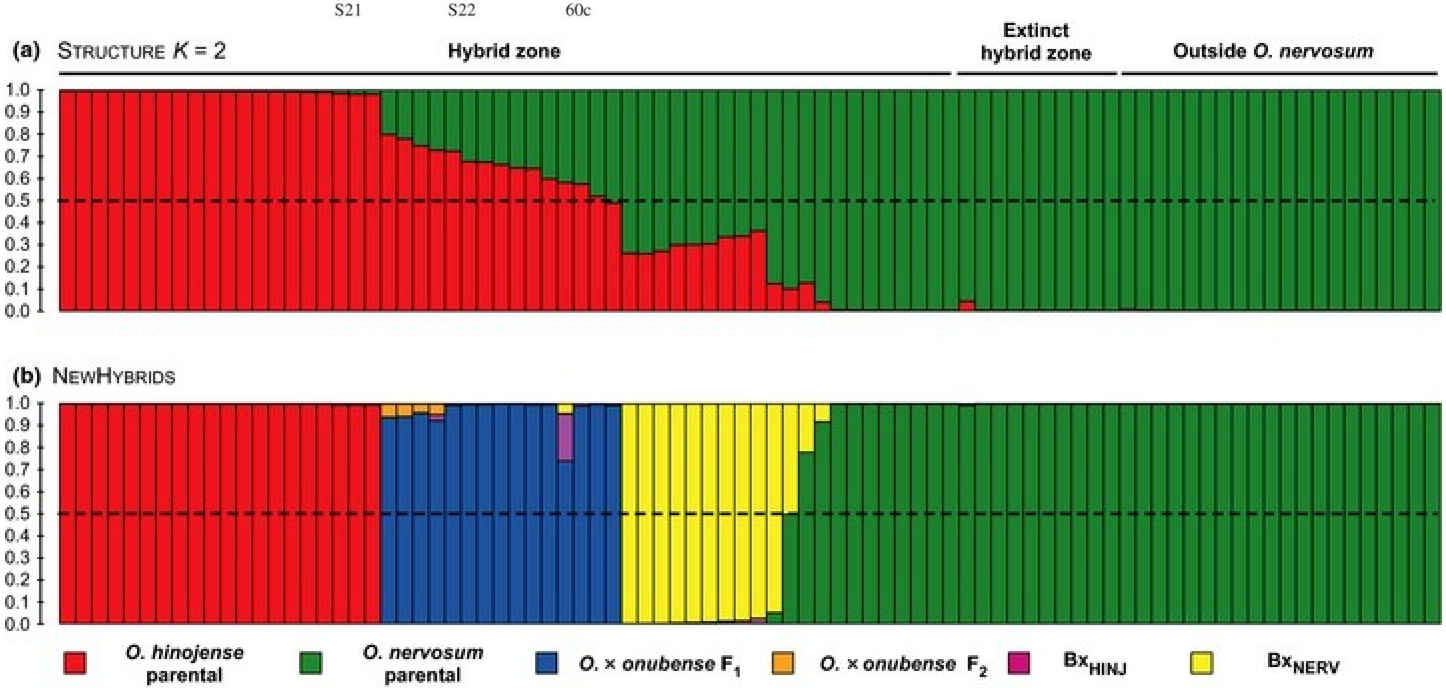


Figure 1.—Six arrangements of founders on a pedigree of $n = 2$ generations. Each box represents a locus. The circles within each box represent the two genes possessed by the diploid organism at the locus. The founders are the individuals in the top row of each pedigree. Black gene copies are those originating from the species *A* population, and the white genes are from species *B*. Genes that are not determined to be either black or white by the pedigree and the founders in it are denoted by broken circles. The individual at the bottom of each pedigree belongs to a different hybrid class, determined by the arrangement of species among the founders. a–f represent six distinct *genealogical classes*. a–f also represent six distinct *genotype frequency classes*. There are, however, only five distinct *gene frequency classes*; the individuals at the bottoms of pedigrees c and f are both in the same gene frequency class.





STRUCTURE
ADMIXTURE



Hybrid zone (Barton a Hewitt 1985)

= area, where genetically different populations meet, mate and give rise at least some hybrid offspring

Hybrid zones may be classified as:

primary

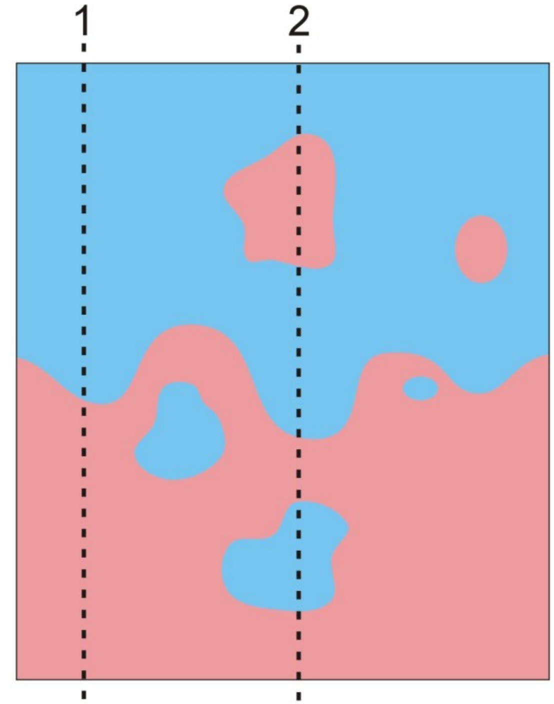
secondary

tension, mosaic, staggered, „mottled“ ...

extrinsic selection (external environment)

intrinsic selection (prezygotic or postzygotic barriers)

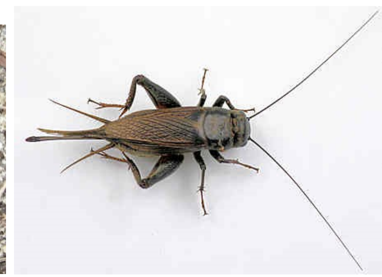
Mosaic hybrid zone:



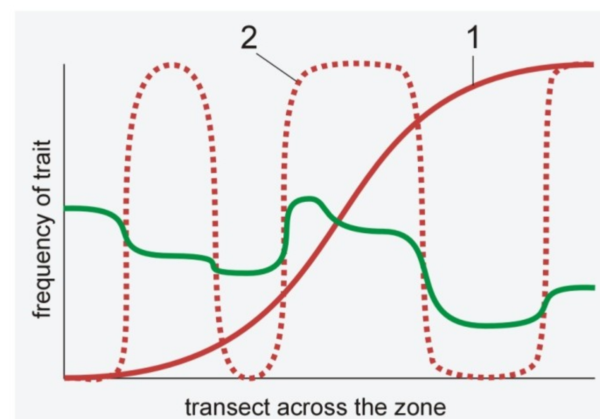
influence of environment

in fact a set of several hybrid zones

eg.: *Gryllus firmus* x *G. pennsylvanicus* (NE USA)
sandy x clayish soils

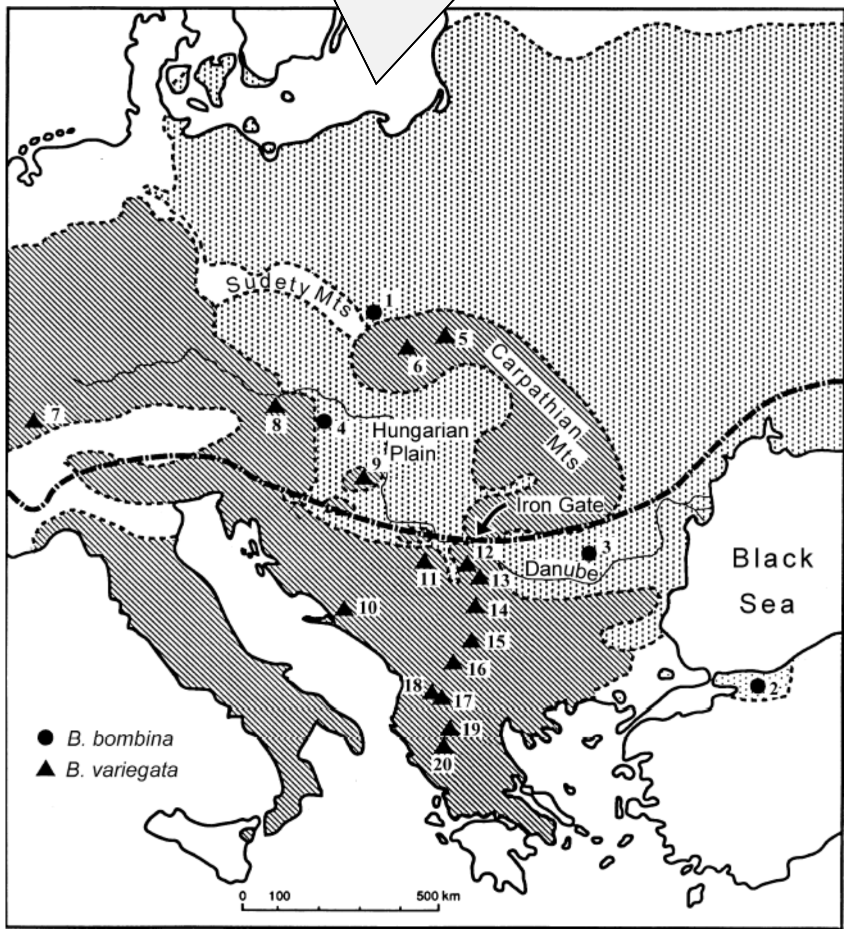


Iris fulva x *I. brevicaulis*:
I. fulva is limited to more forested sites



Bombina:

mosaic HZ in Croatia,
not in Poland



fire-bellied toad
B. bombina:

lowlands
mostly in water
larger water surfaces
thiner skin
territorial
530 Hz
longer development

yellow-bellied toad
B. variegata:

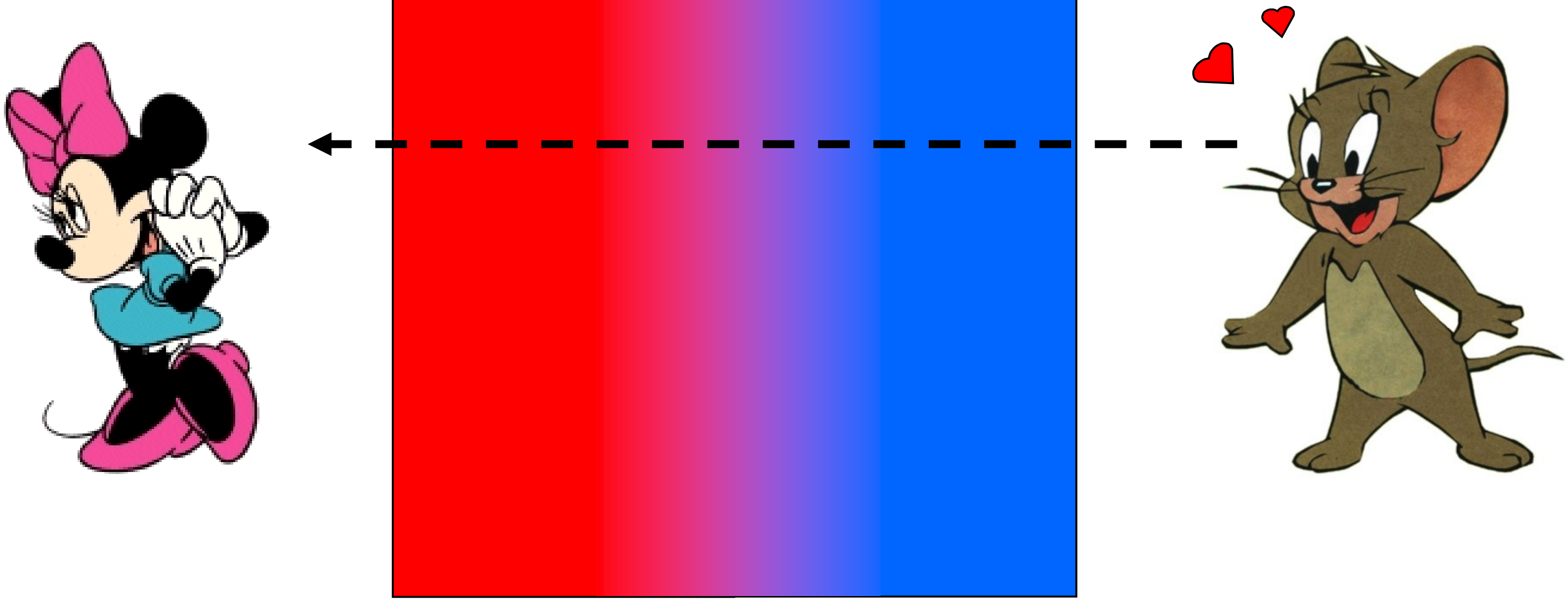
hills, highlands
terrestrial
mating in puddles
thick skin
nonterritorial
580 Hz
shorter development

Nick Barton

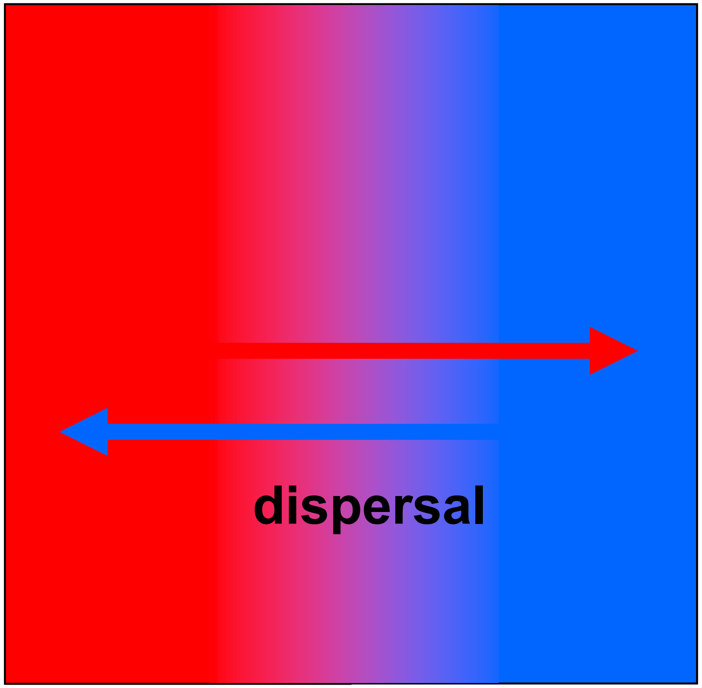
Most hybrid zones are
tension zones.

... i.e., they are maintained by balance between dispersal and selection (Barton & Hewitt, 1985)

Tension zone is when…

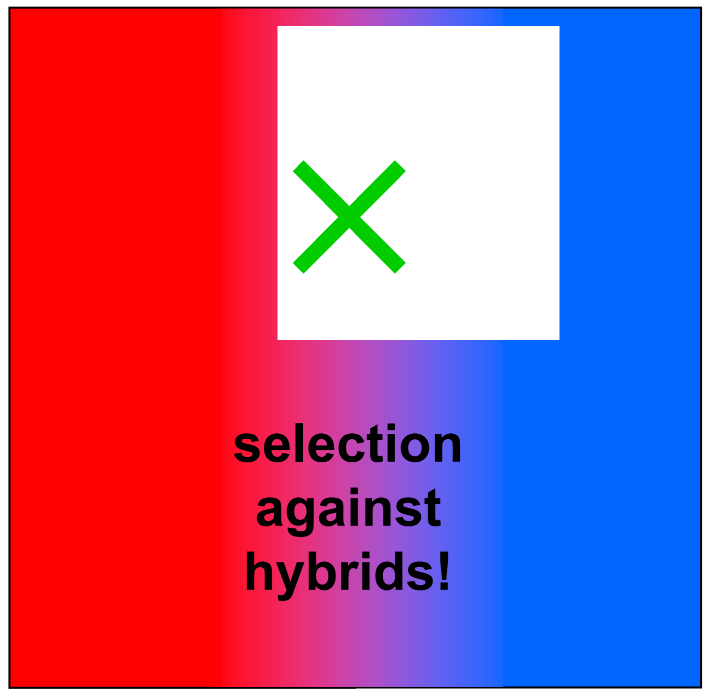


Tension zone is when…



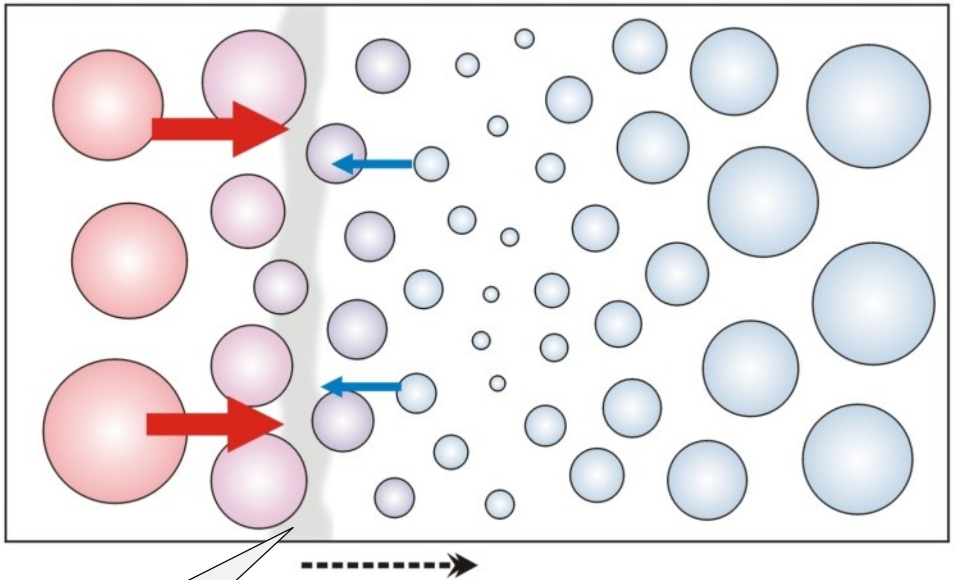
⇒ zone widening

Tension zone is when…



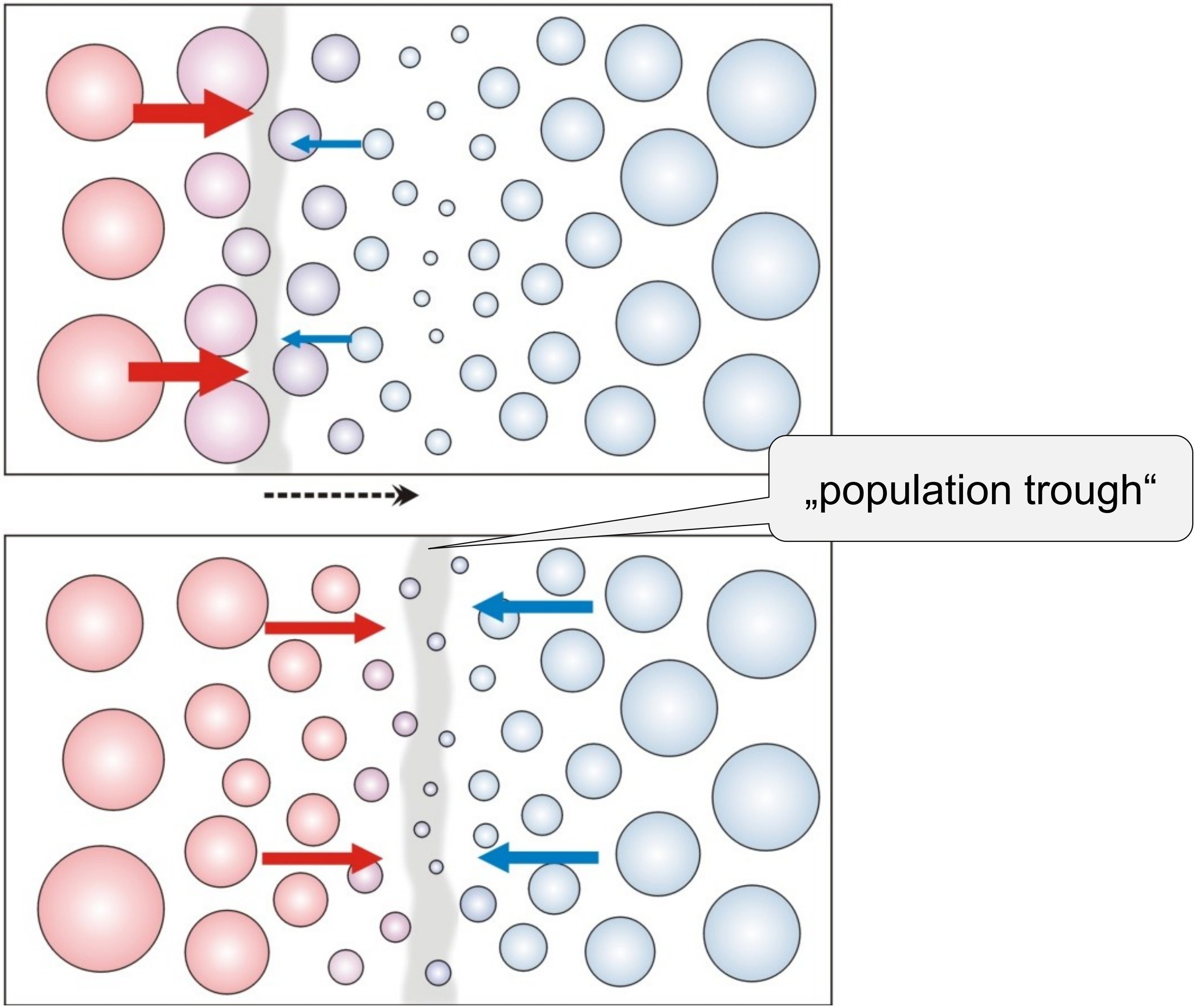
$\Rightarrow$ zone narrowing

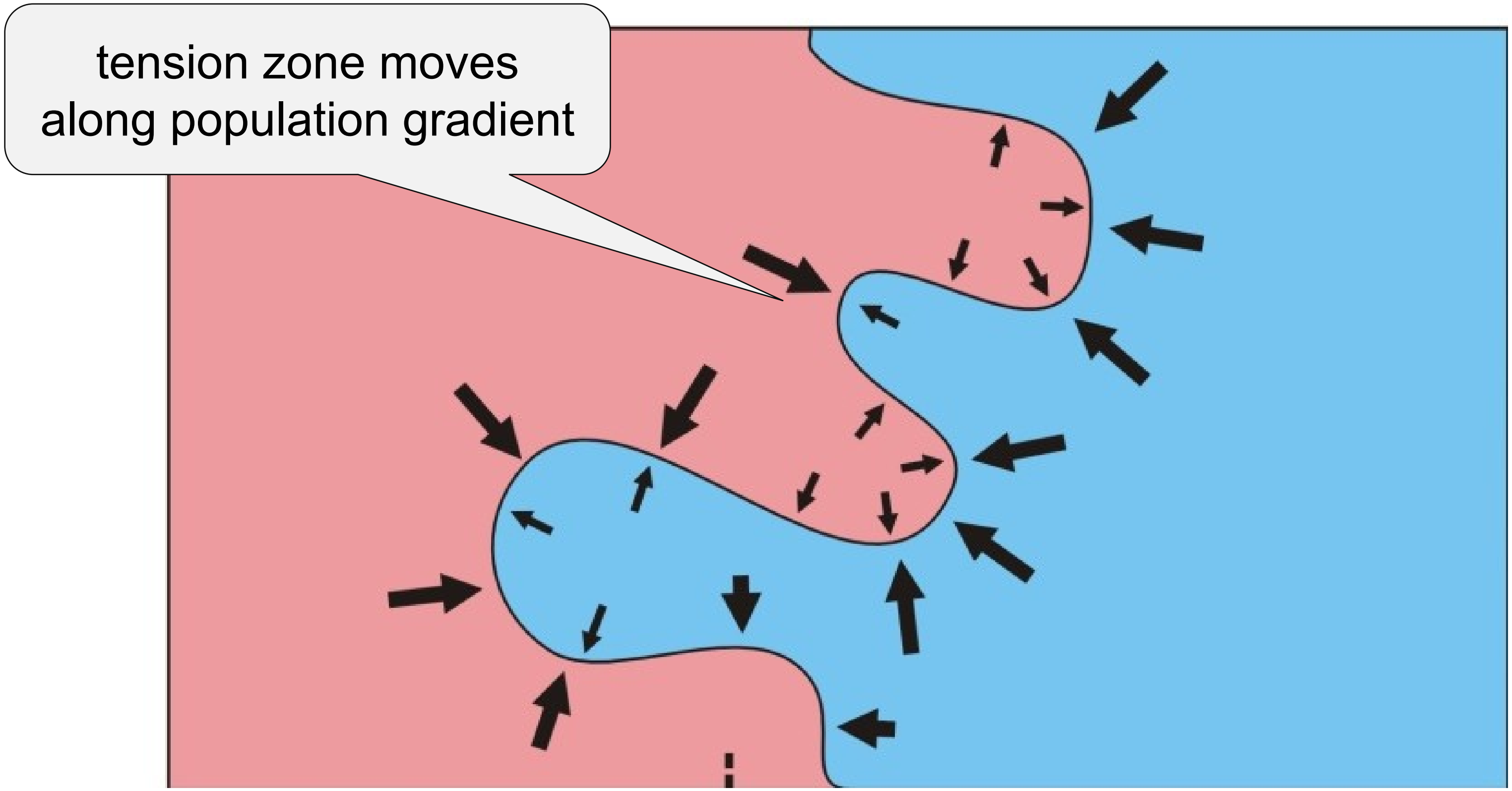
Tension zone is maintained by dynamic equilibrium between *dispersal* and *selection*

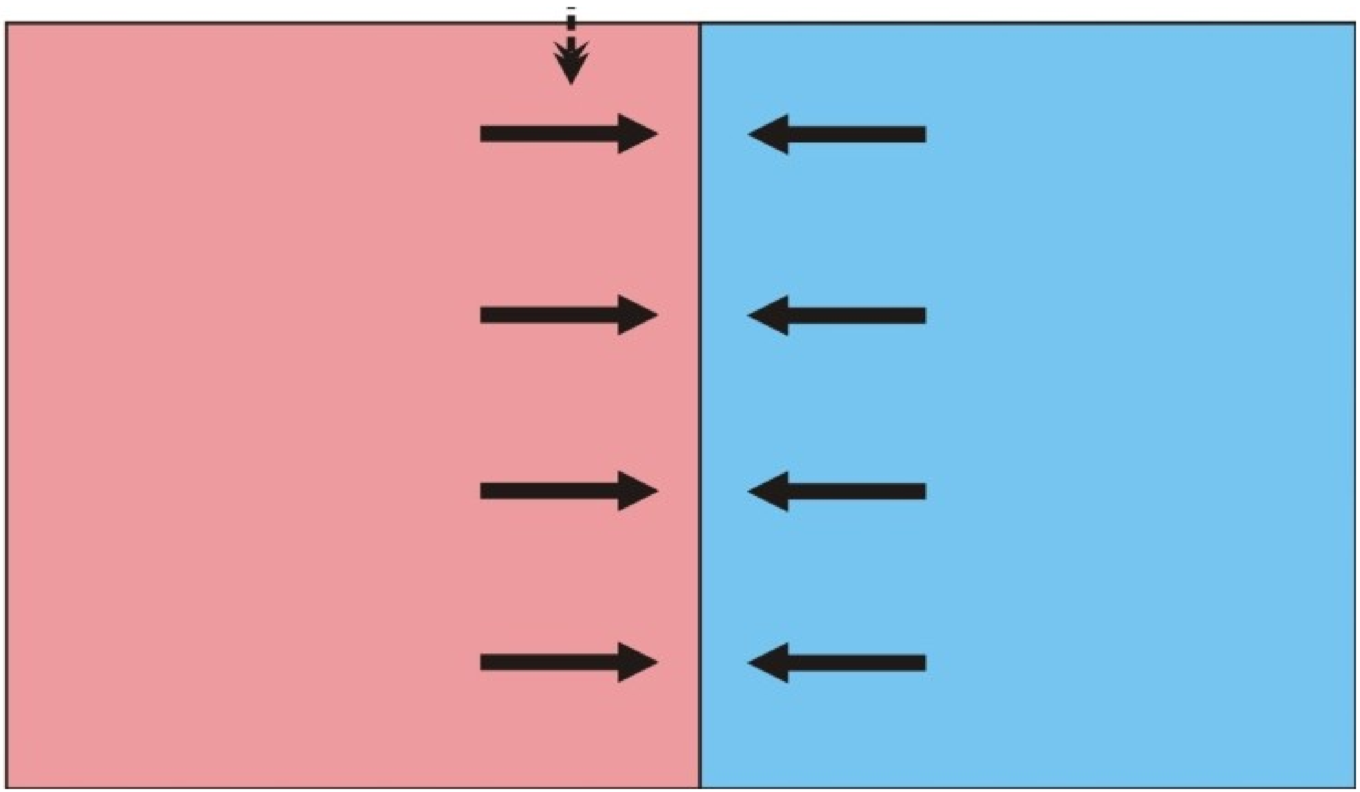


tension zone moves along the gradient of population density

Tension zone is independent of external conditions (*intrinsic selection*)
⇒ its movement ends at a geographical barrier or in the area of the lowest population density („*population/density trough*“)

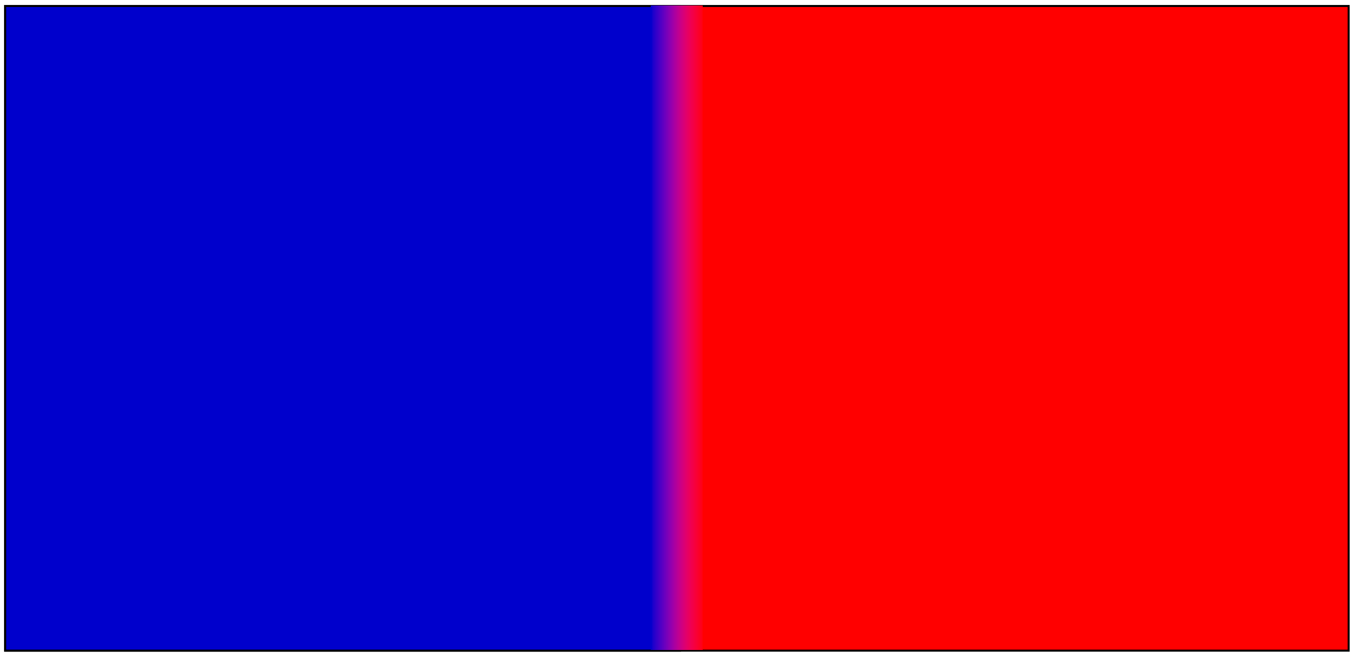

„population trough“


tension zone moves
along population gradient

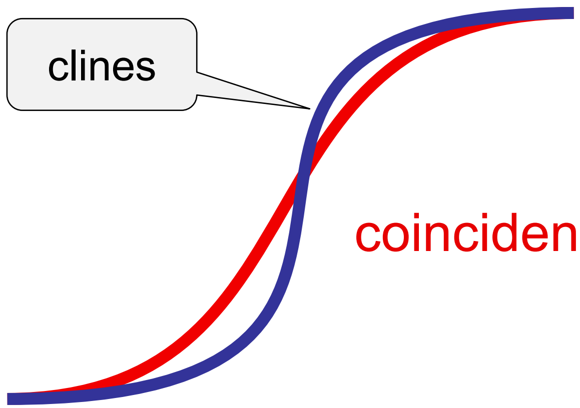


Theory of cline:

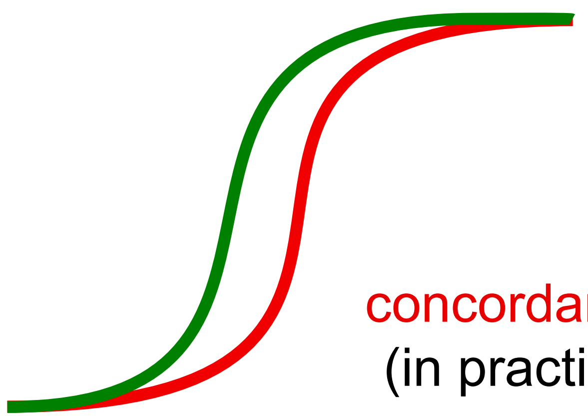
secondary contact: → coincident and concordant clines



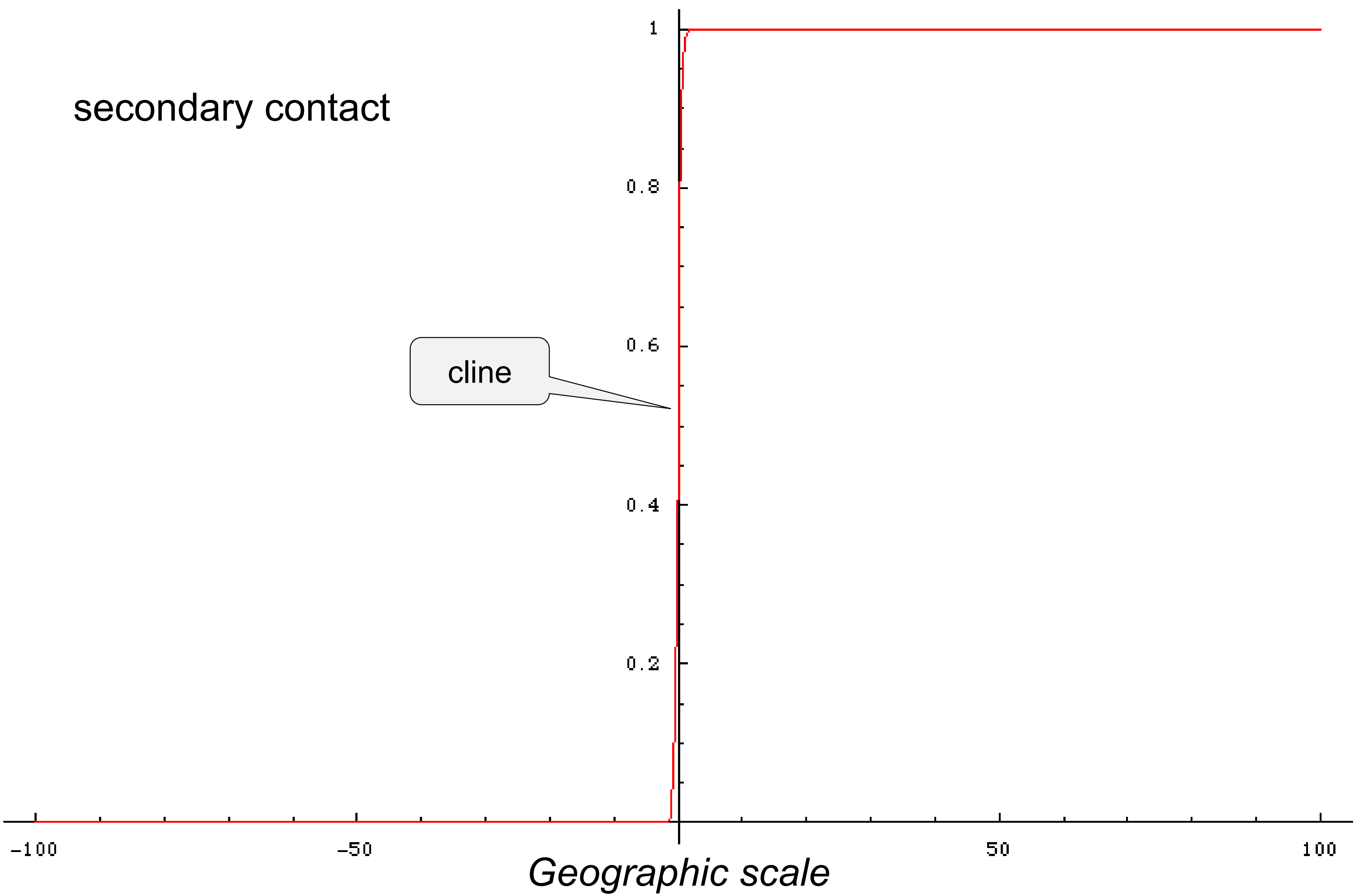
Cline = gradient of trait(s) (eg. allele frequency or mean of quantitative trait) across spatially continuous habitat



coincidence = same positions of zone centres



concordance = same cline shapes
(in practice usually same widths)

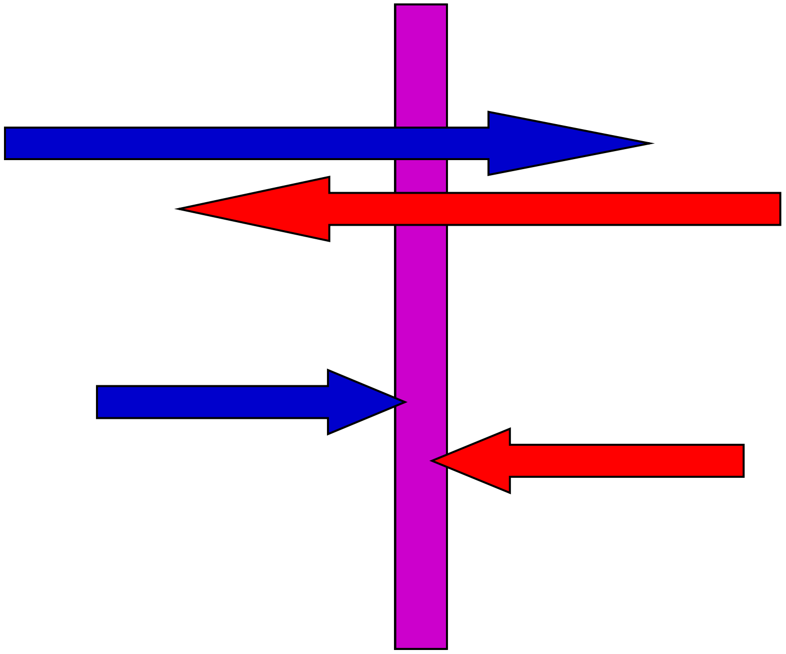

secondary contact
cline
1
0.8
0.6
0.4
0.2
-100
-50
50
100
Geographic scale

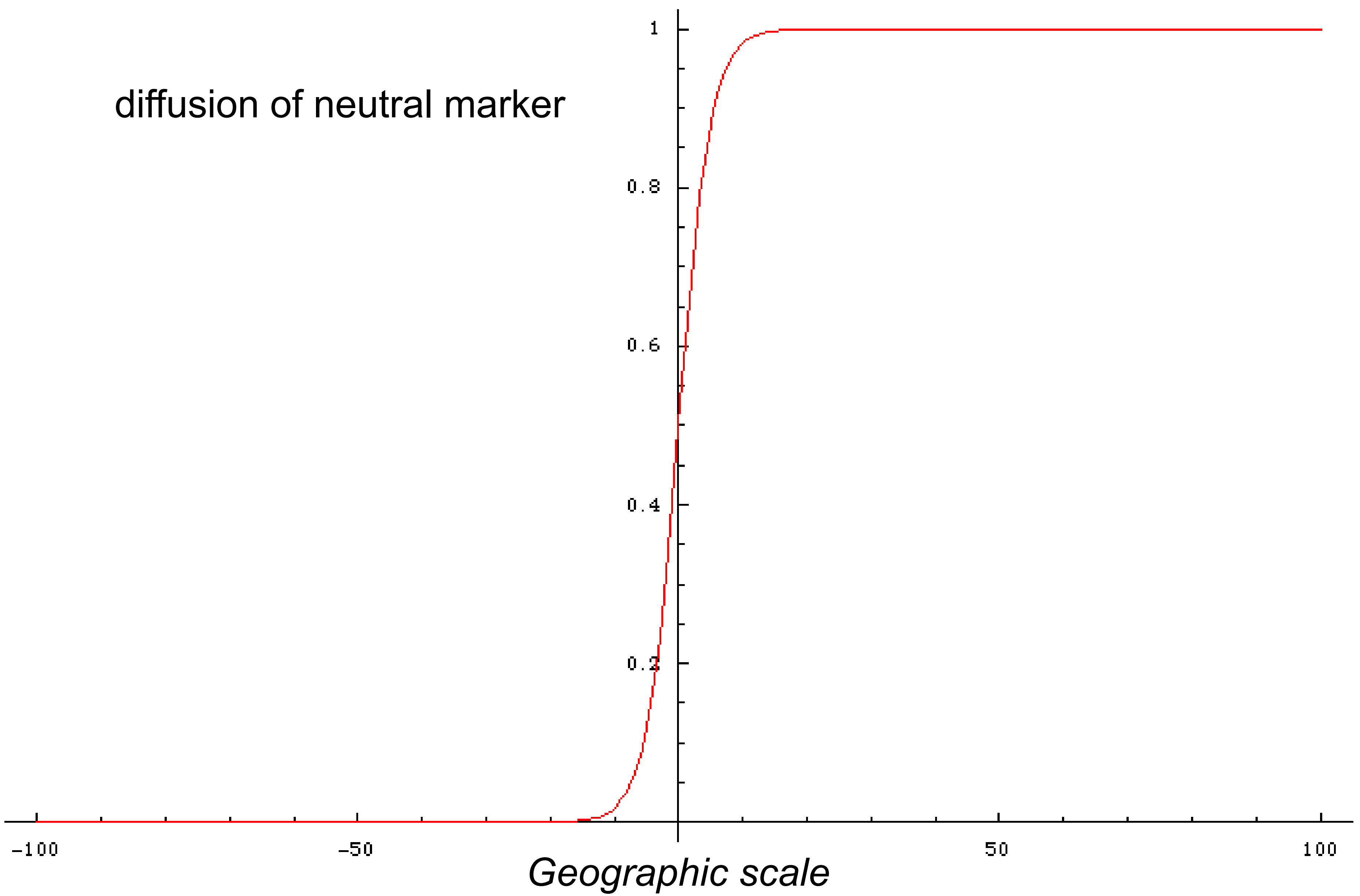
Theory of cline:

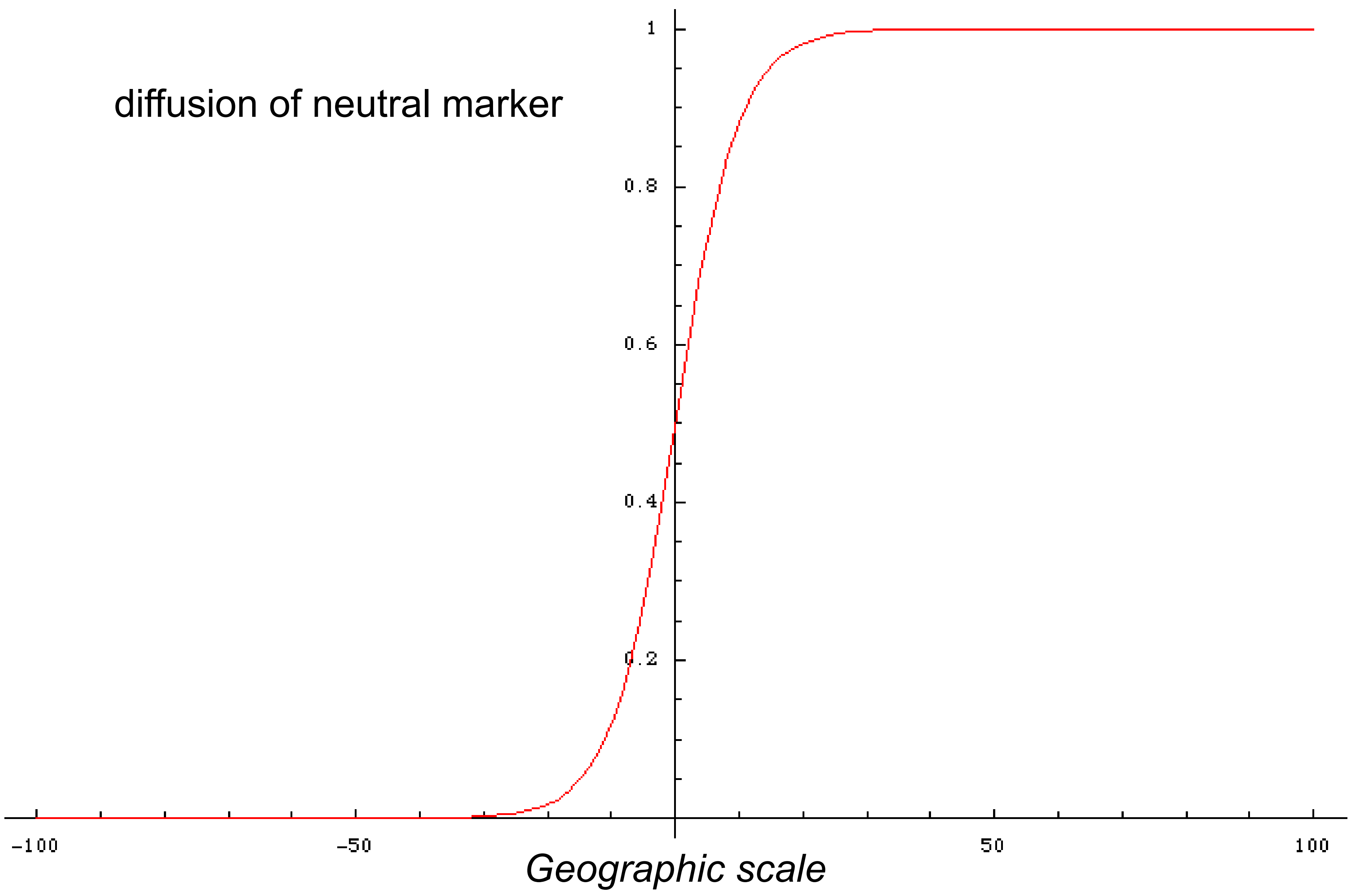
neutral vs. selected loci

neutral locus

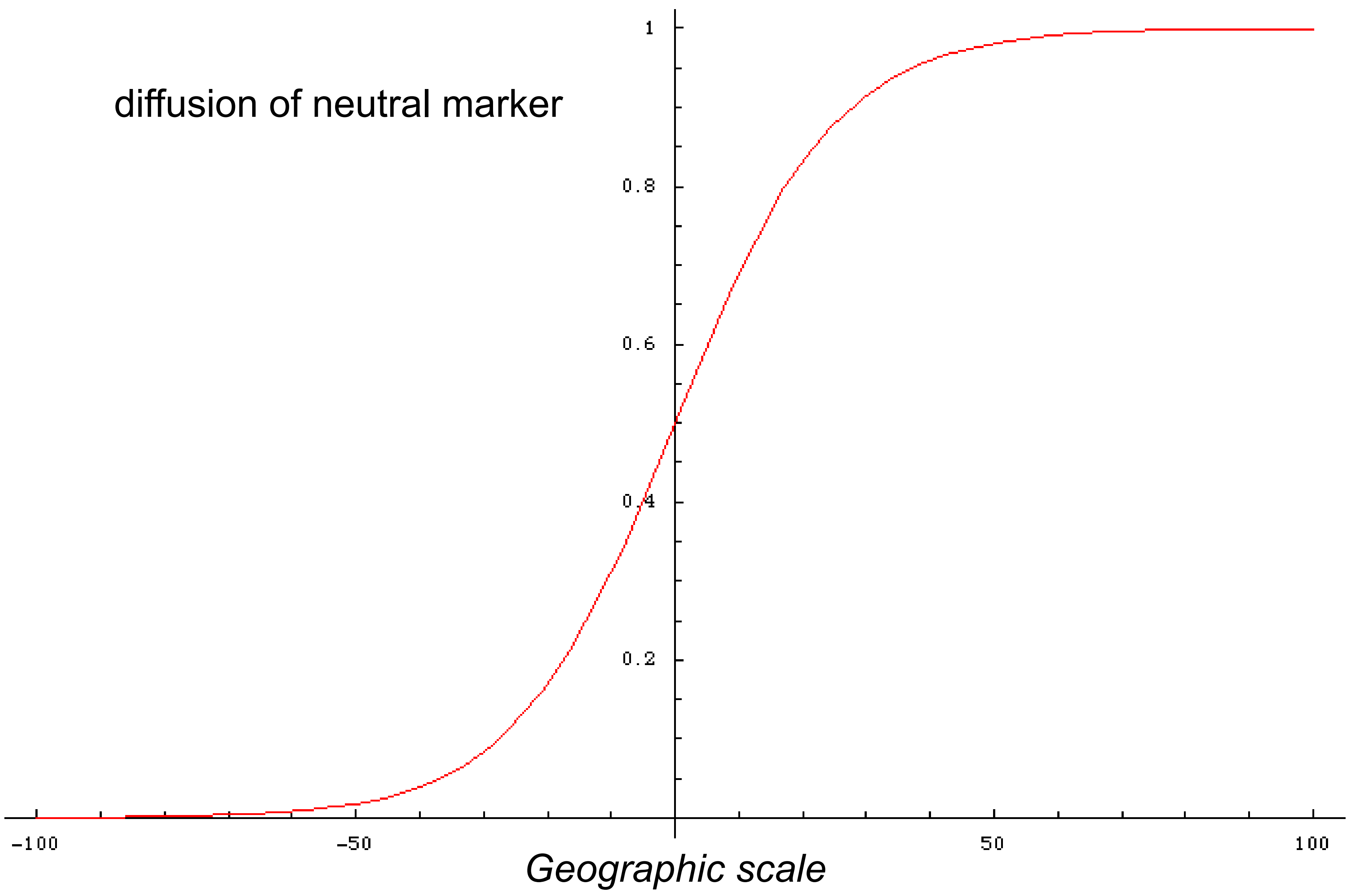
selection against hybrids



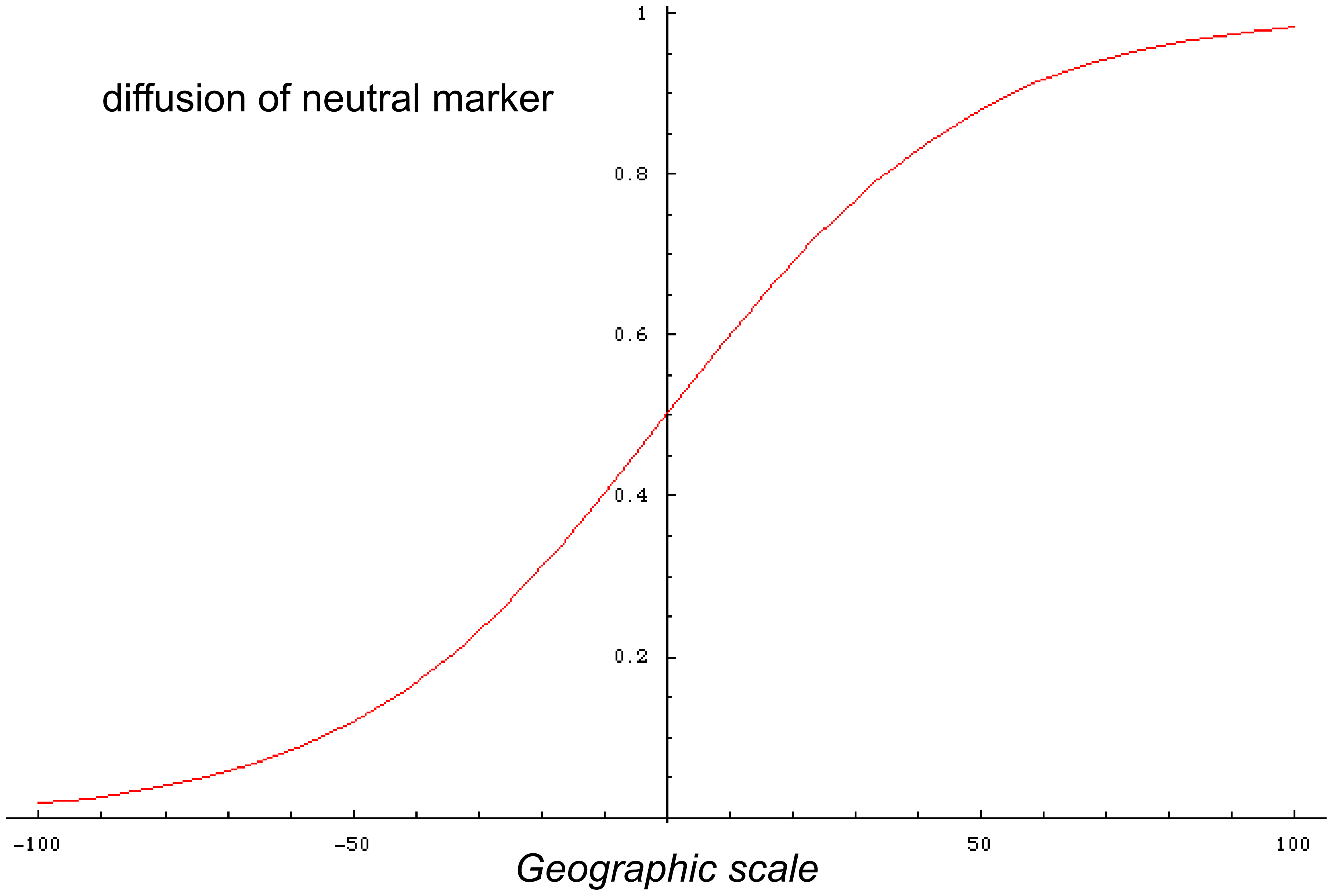

diffusion of neutral marker
1
0.8
0.6
0.4
0.2
-100
-50
50
100
Geographic scale



diffusion of neutral marker
1
0.8
0.6
0.4
0.2
-100
-50
50
100
Geographic scale

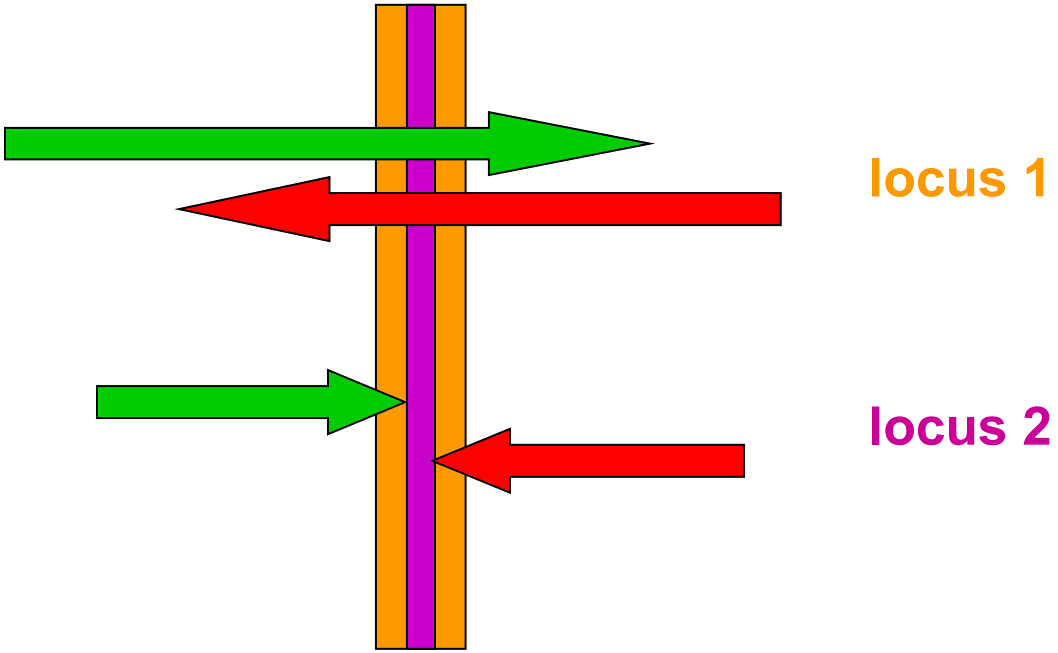


diffusion of neutral marker
1
0.8
0.6
0.4
0.2
-100
-50
50
100
Geographic scale


diffusion of neutral marker
1
0.8
0.6
0.4
0.2
-100
-50
50
100
Geographic scale

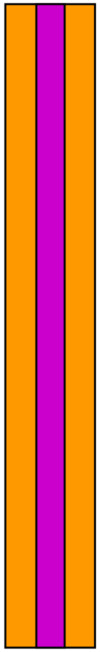
neutral vs. selected loci

with time, concordance is disappearing ...



... but (in tension zone) selection pushes clines for individual loci to each other
⇒ maintains coincidence

sometimes ...

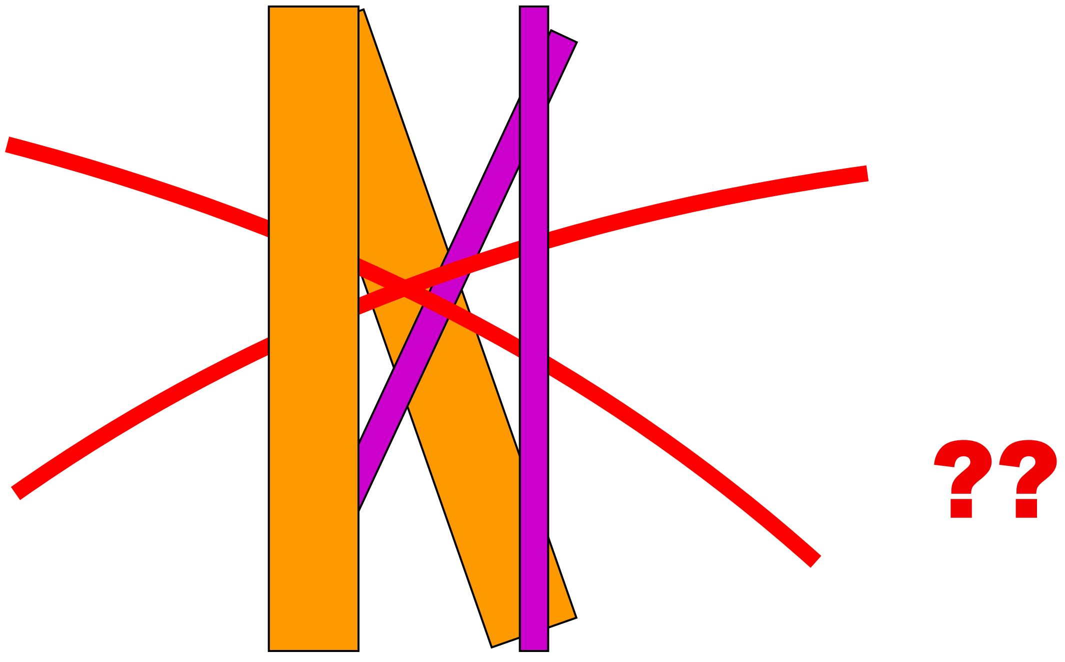


locus 1

locus 2

... but clines still parallel

cline models (diffusion approximation etc.), linkage disequilibrium, evolutionary parameters



problem, how to analyse

Hybrid zone study

1. Sampling along linear or 2D transect, geographic coordinates of localities
2. Genetic (morphological, behavioural etc.) analysis
   … problem of sample independence (F_{ST}, F_{IS} … effective No. alleles)
3. Geographic clines
4. Estimation of dispersal, selection, and other parametres
5. Alternative approaches:
   monotonic clines
   2D analysis
   genomic clines
   concordance analysis

Case study: house mouse hybrid zone


musculus
domesticus

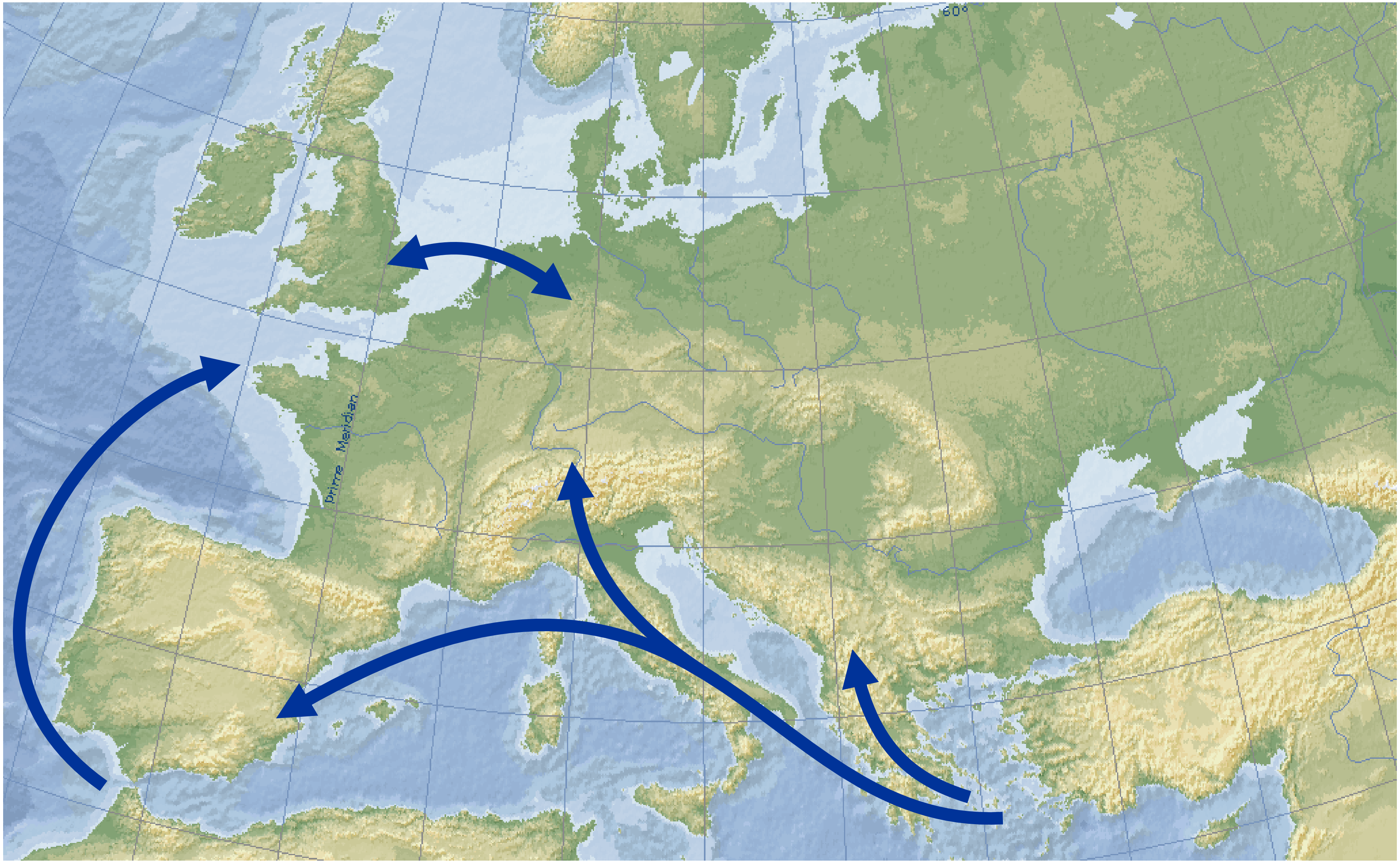
Mouse colonization of Europe

Neolithic

Cucchi et al. (2005)

Mouse colonization of Europe

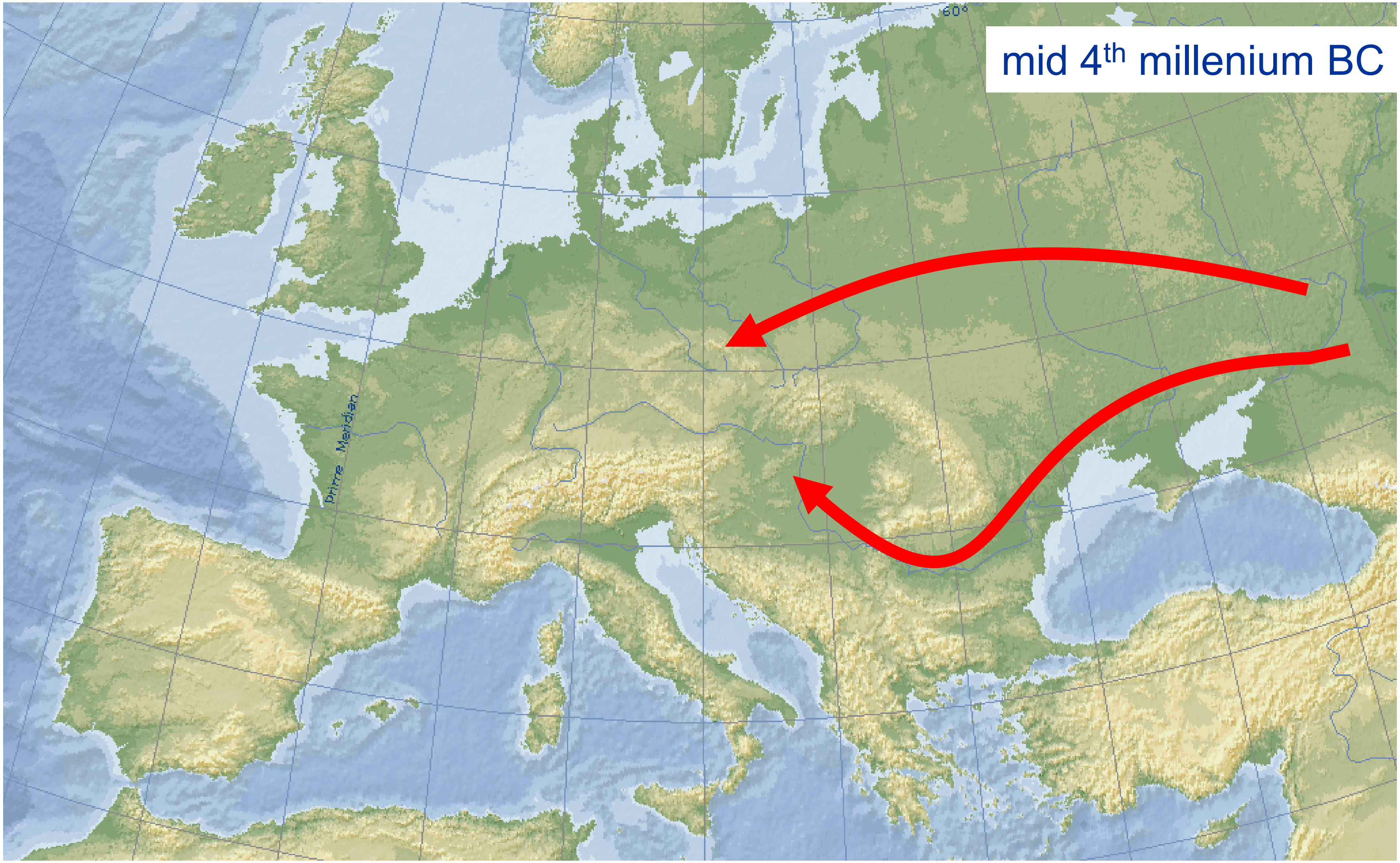
Bronze and Iron Age



Cucchi et al. (2005)

Mouse colonization of Europe

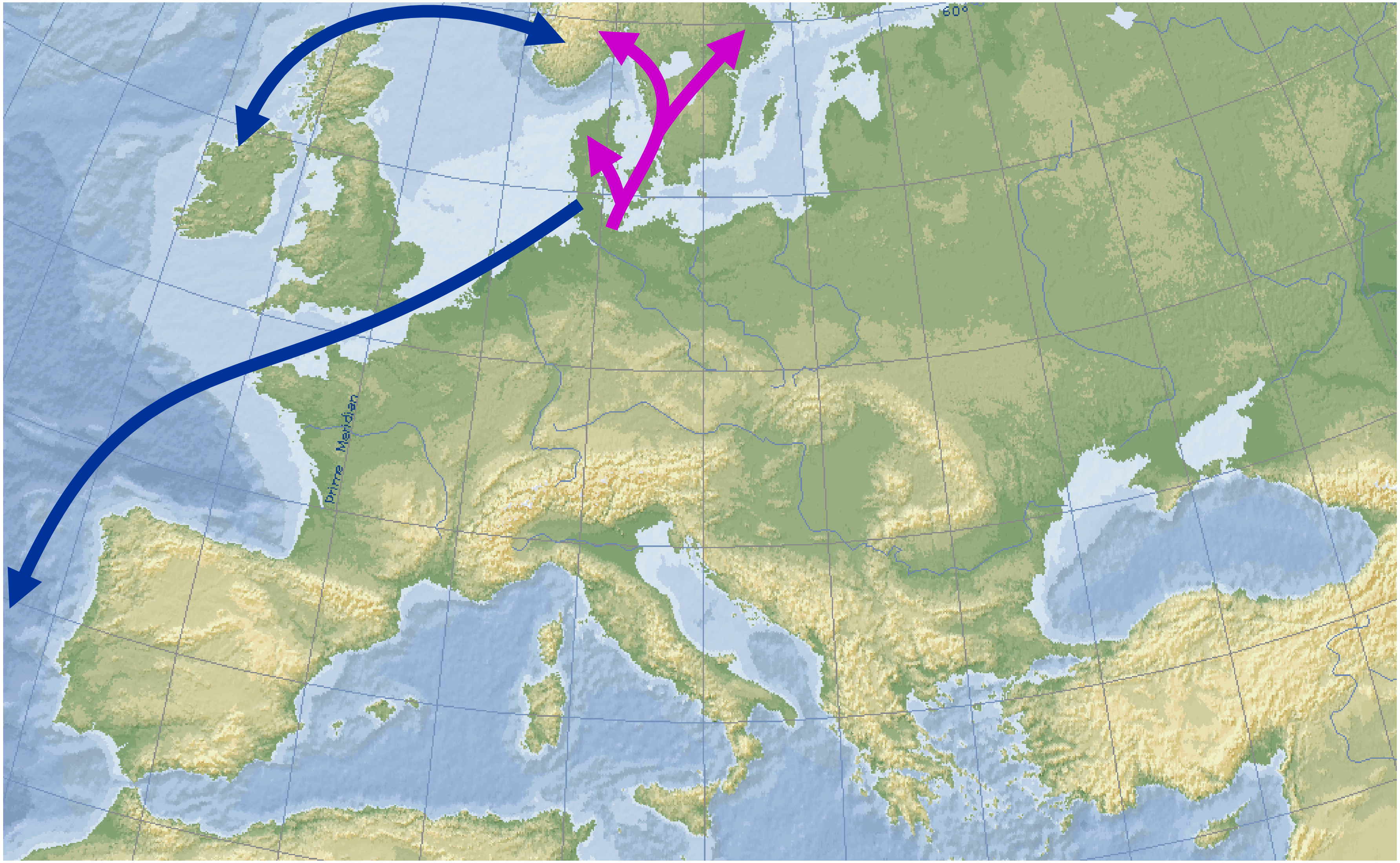
Late Neolitnic



Cucchi et al. (2011)

Mouse colonization of Europe

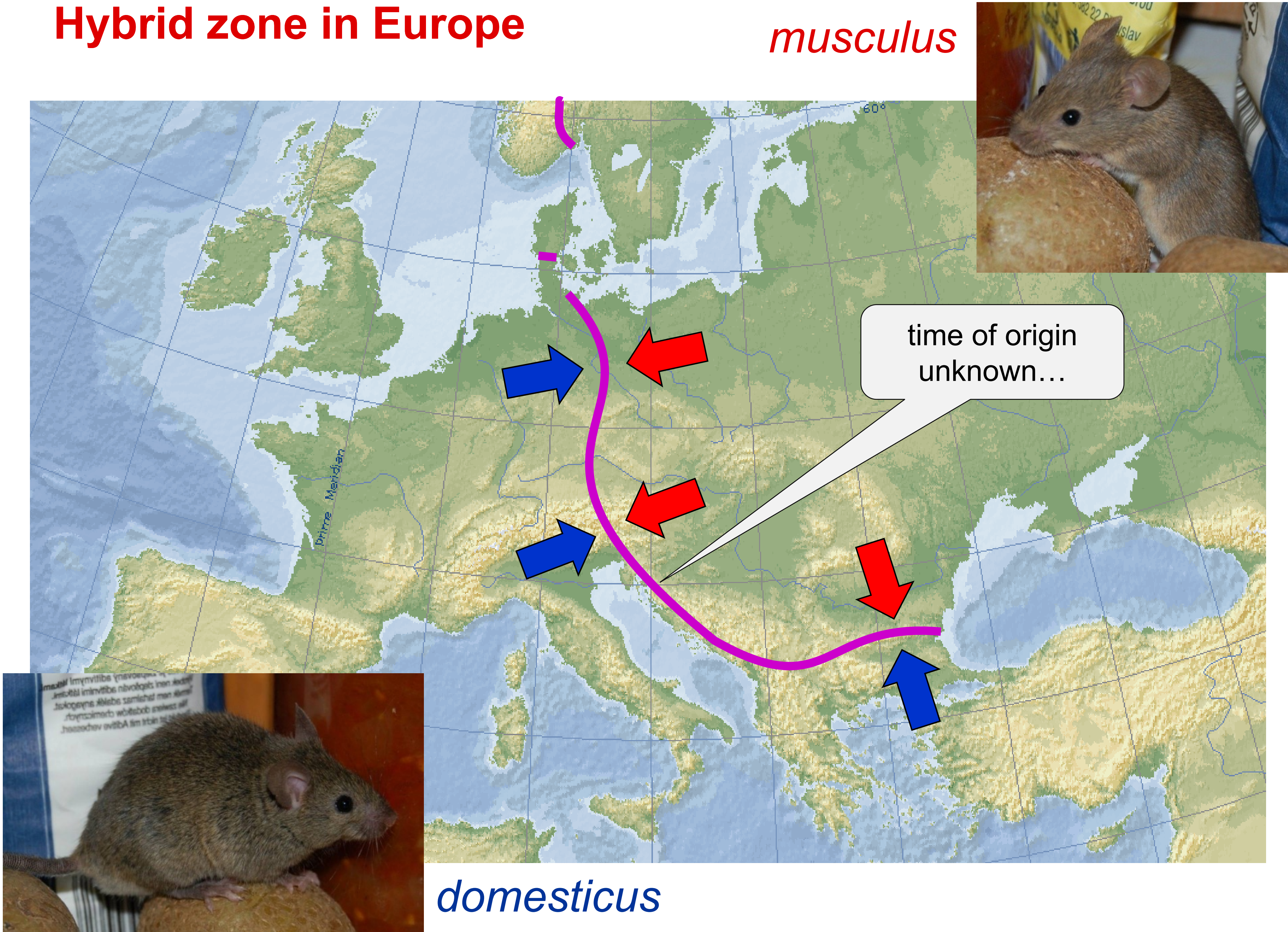
Vikings



Prager et al. (1993); Searle et al. (2009)

Hybrid zone in Europe

musculus

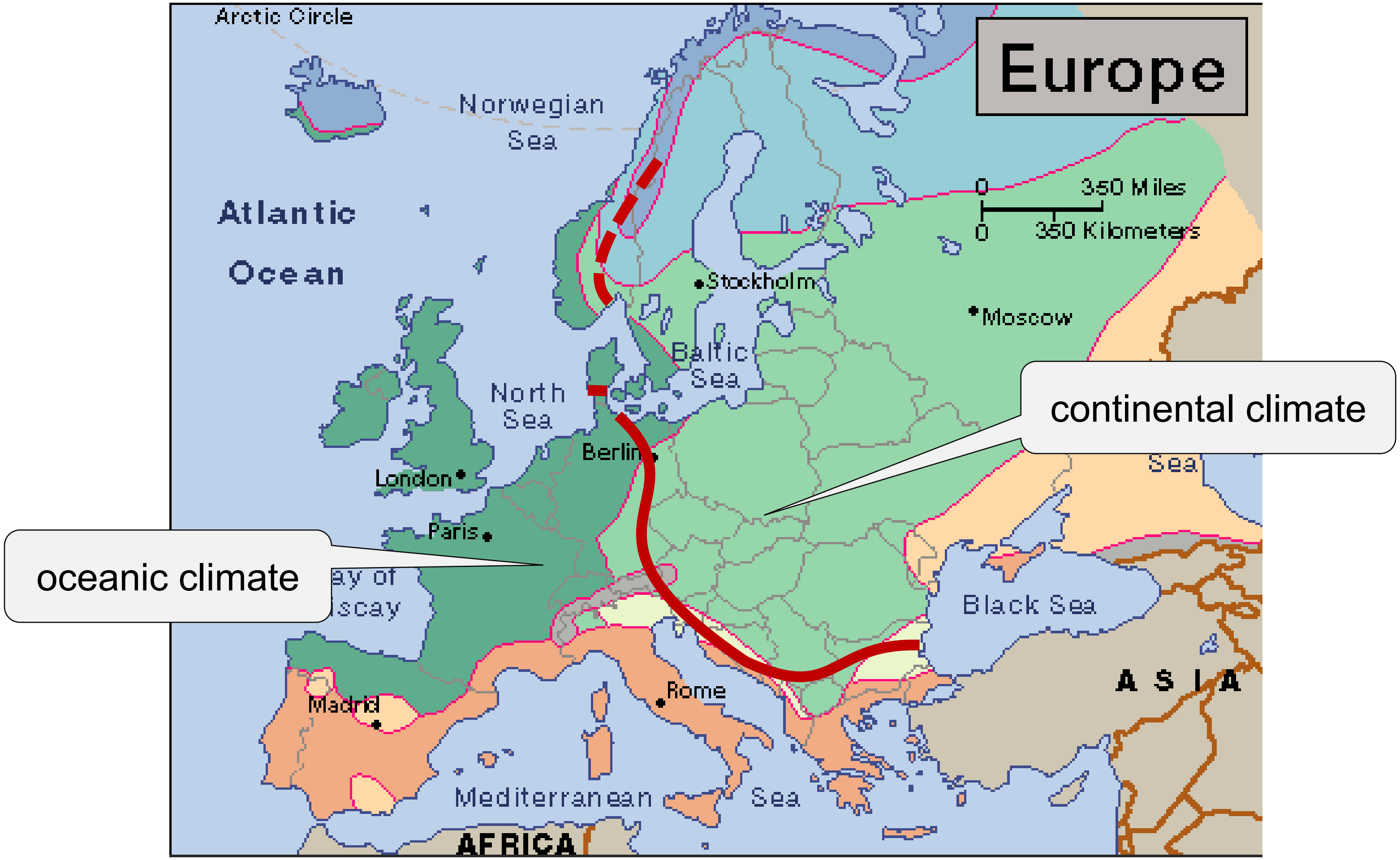


domesticus

Hybrid zone in Europe

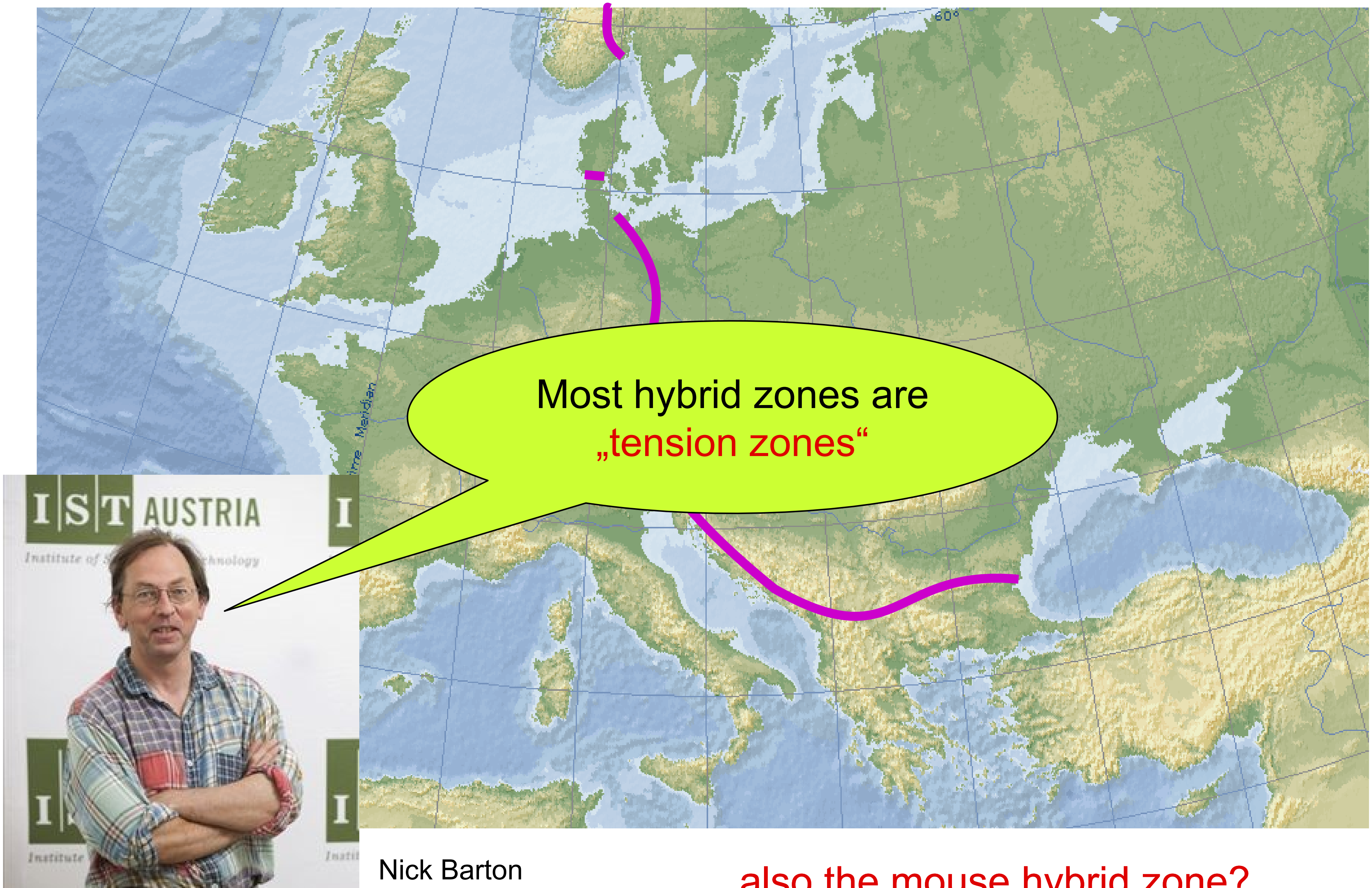
Co tuto zónu ovlivňuje?

Europe
Arctic Circle
Norwegian Sea
Atlantic Ocean
North Sea
Baltic Sea
Stockholm
Moscow
Berlin
London
Paris
Madrid
Rome
Black Sea
Mediterranean Sea
AFRICA
A S I A
0 350 Miles
0 350 Kilometers
continental climate
oceanic climate
Semiarid
Subtropical dry summer
Humid subtropical
Humid oceanic
Humid continental
Subarctic
Tundra
Highland



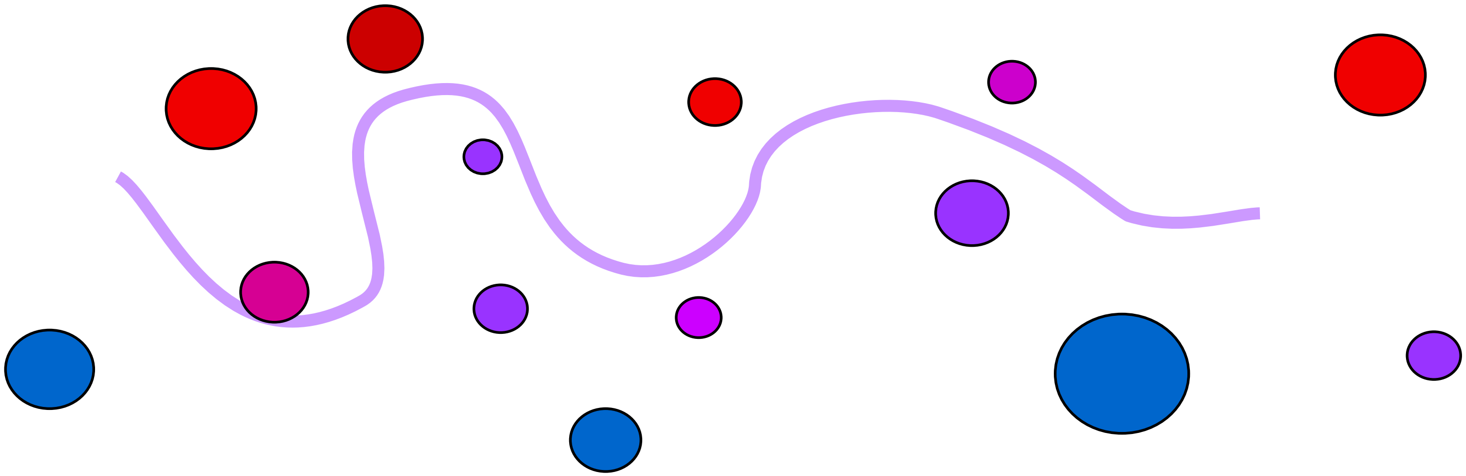
climatic factors don’t determine

Hybrid zone in Europe



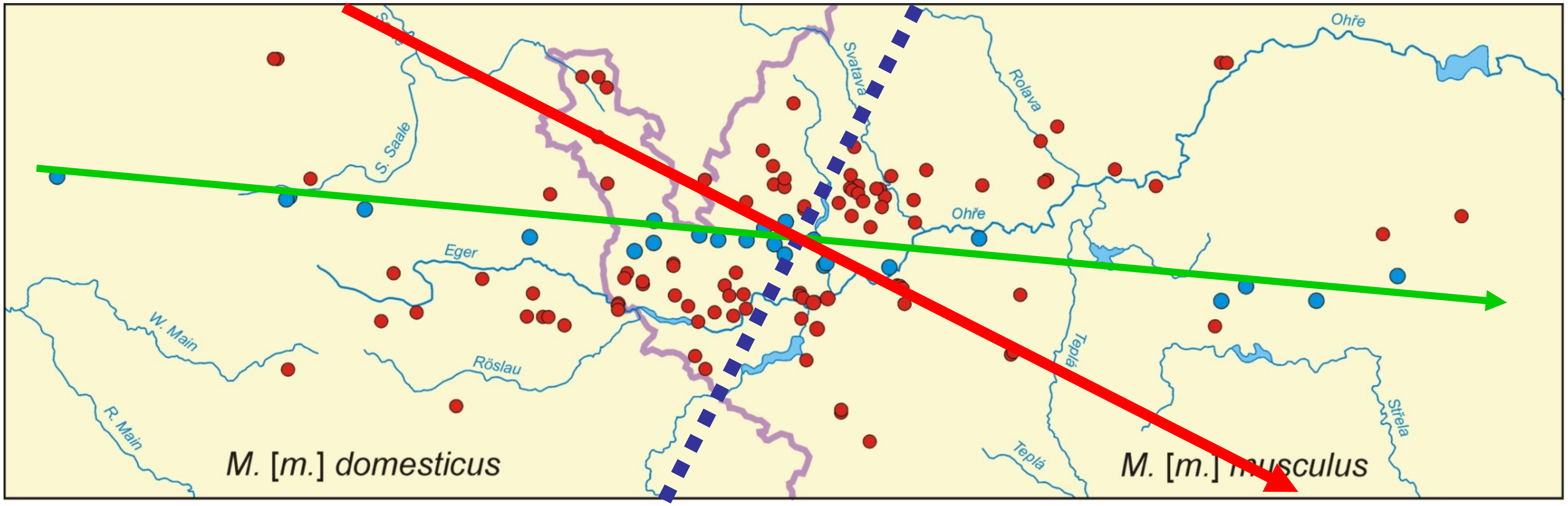
Nick Barton

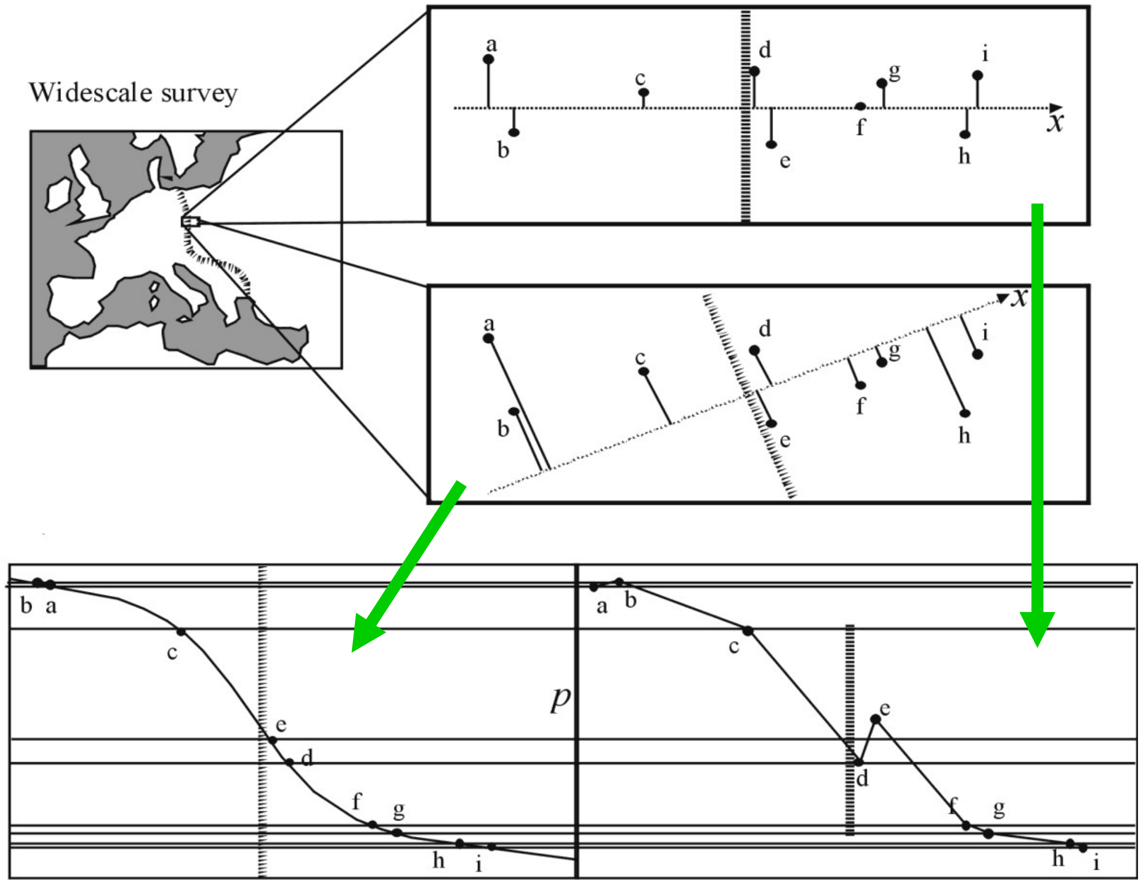
also the mouse hybrid zone?



hybrid zone course may be complex....

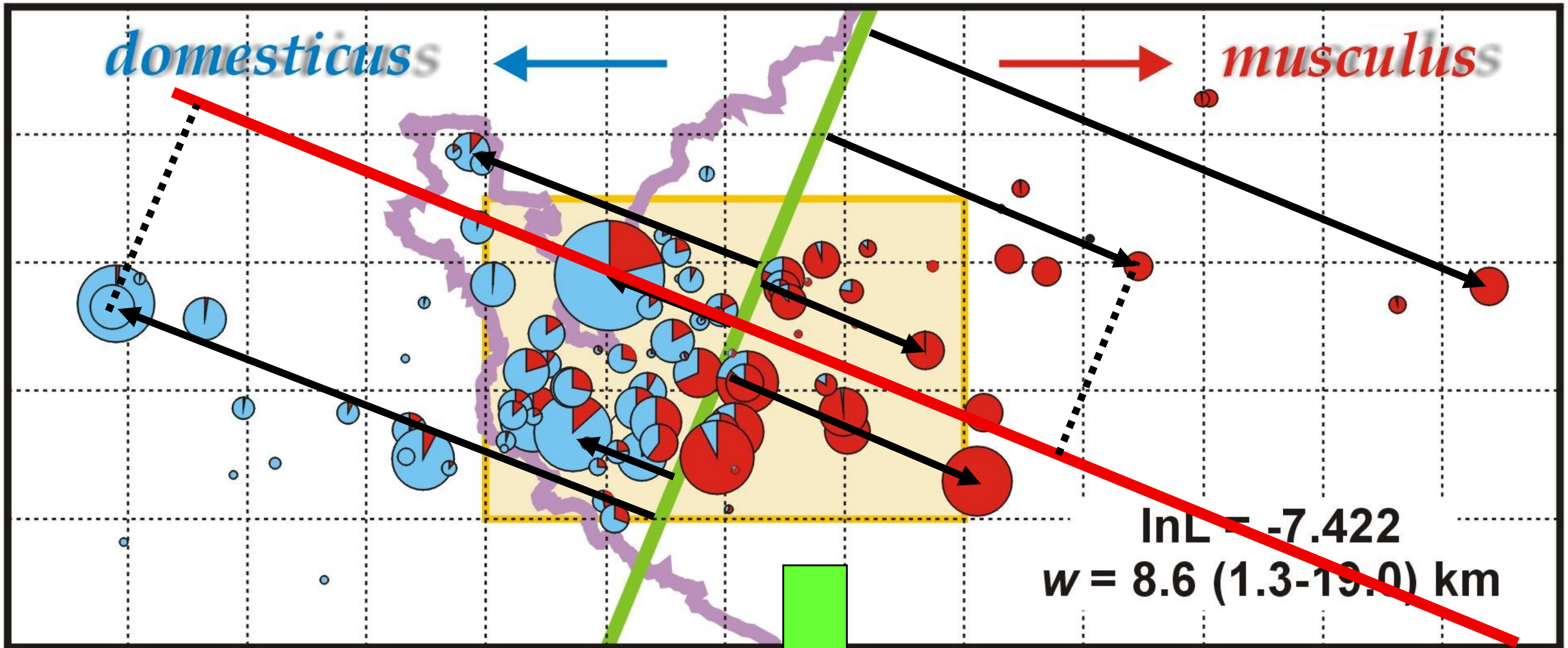
... moreover, usually we don’t know a priori, or we extrapolate from global direction

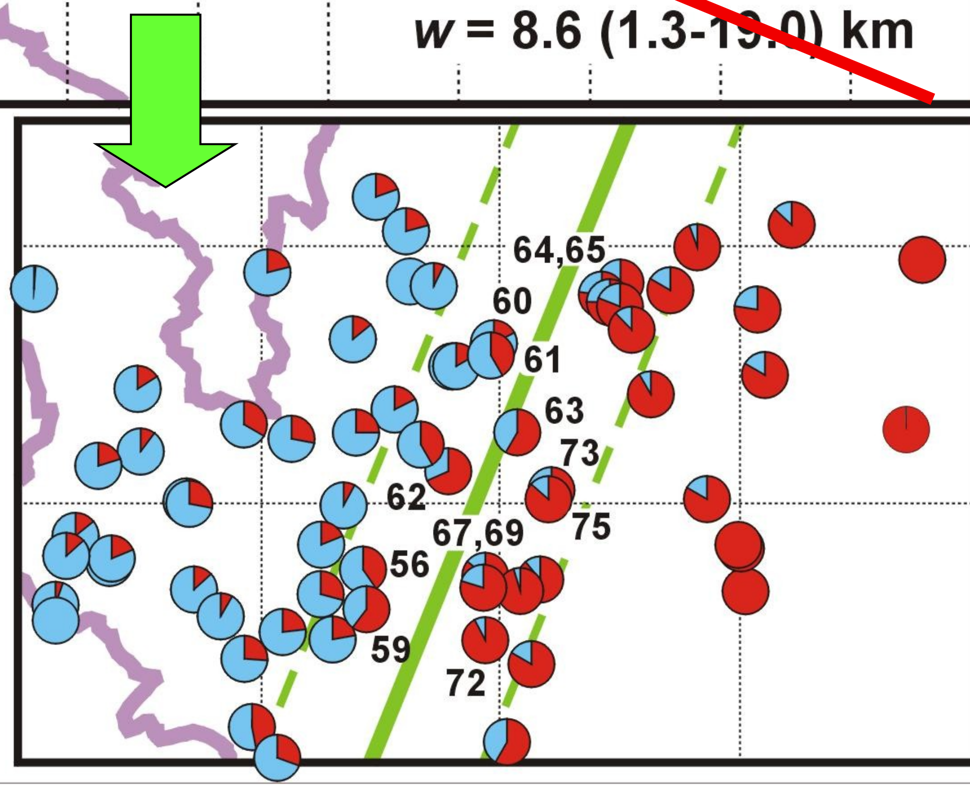




Real local cline

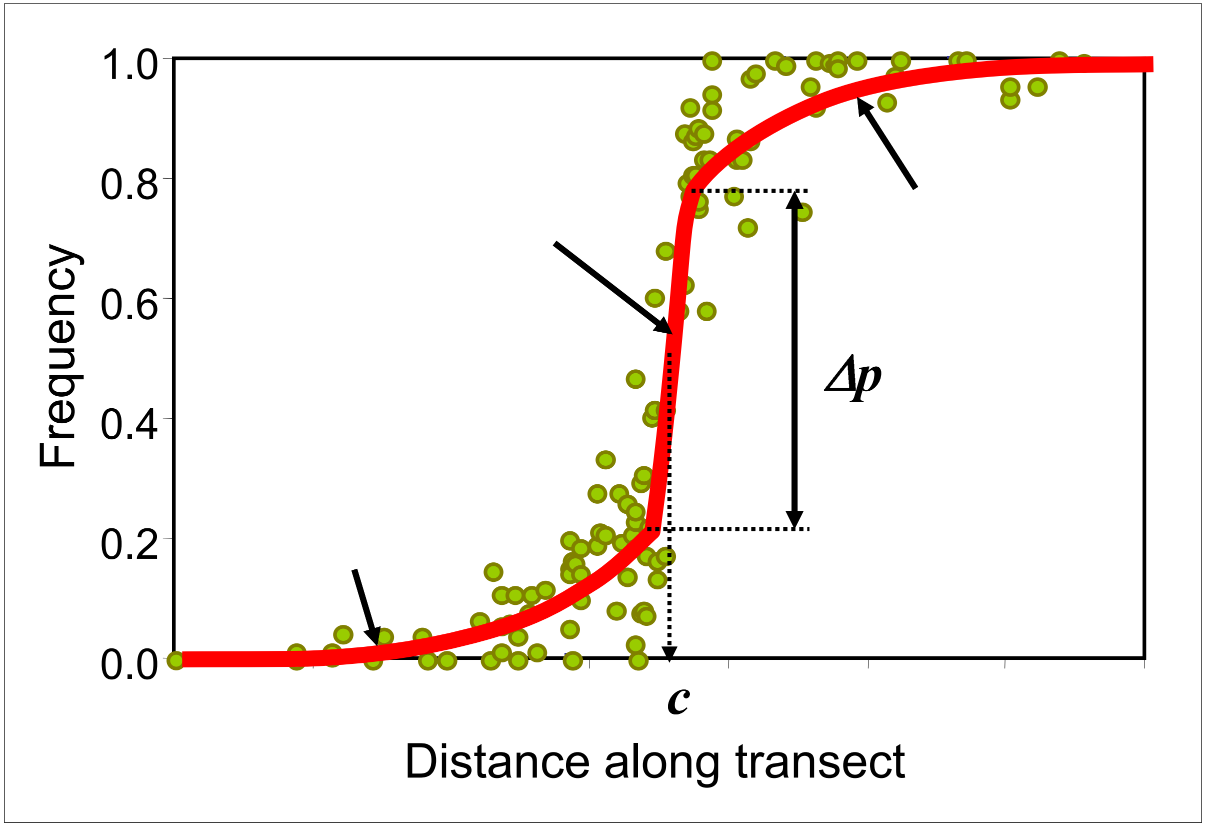
Cline interpolated from widescale survey


domesticus
musculus
lnL = -7.422
w = 8.6 (1.3-19.0) km


64,65
60
61
63
73
62
67,69
75
56
59
72

2D → 1D clines

Multiple genes:



„stepped“ model (symetrical, asymmetrical)

linkage disequilibrium resulting from influx of parental allele combinations ⇒ synergistic effect: strenghtening of selection in zone centre ⇒ central step

× introgression tails reflect selection at individual loci

We can estimate some other key evolutionary parametres from LD and cline parametres:

dispersal:

effective selection:

selection on marker loci:

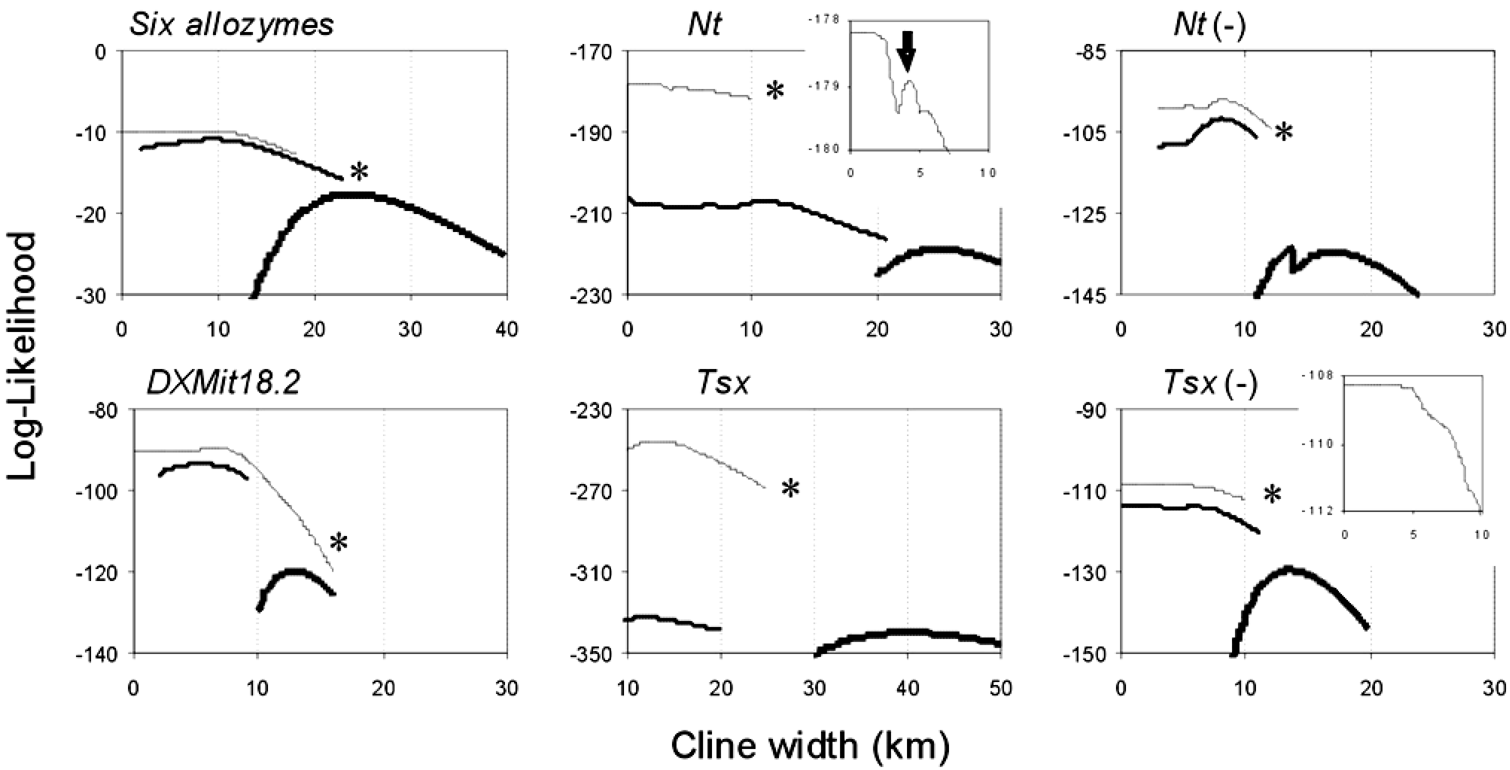
selection on selected loci:

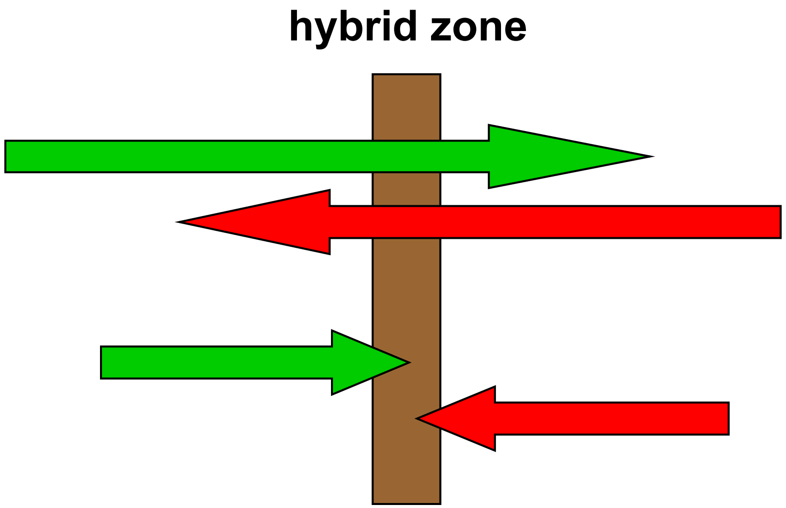
fitness of hybrids:

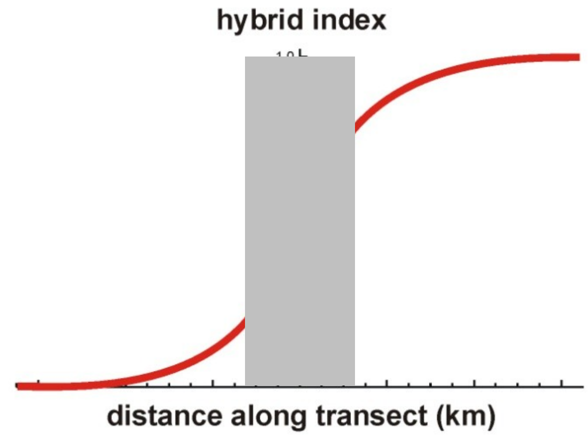
number of loci under selection:

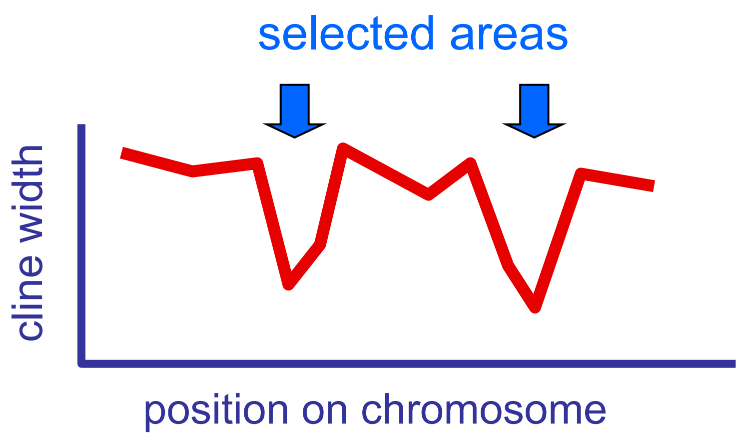
model comparison: LRT (they are nested); d.f. = difference in number of parametres

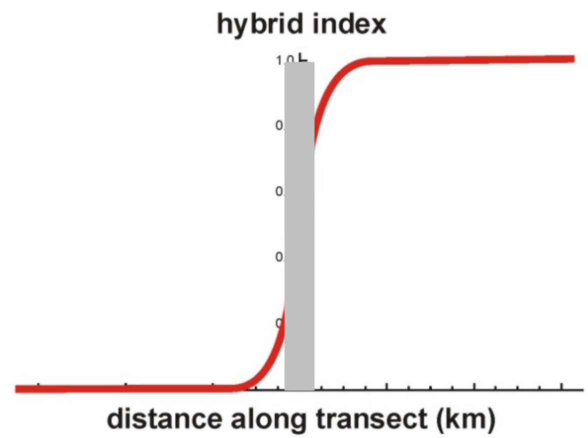
likelihood profiles:

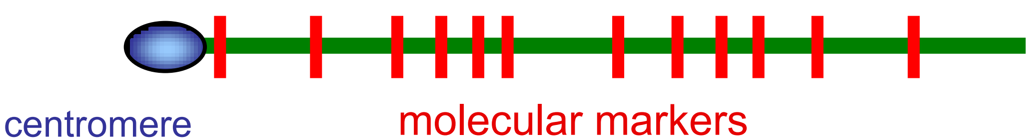



hybrid zone

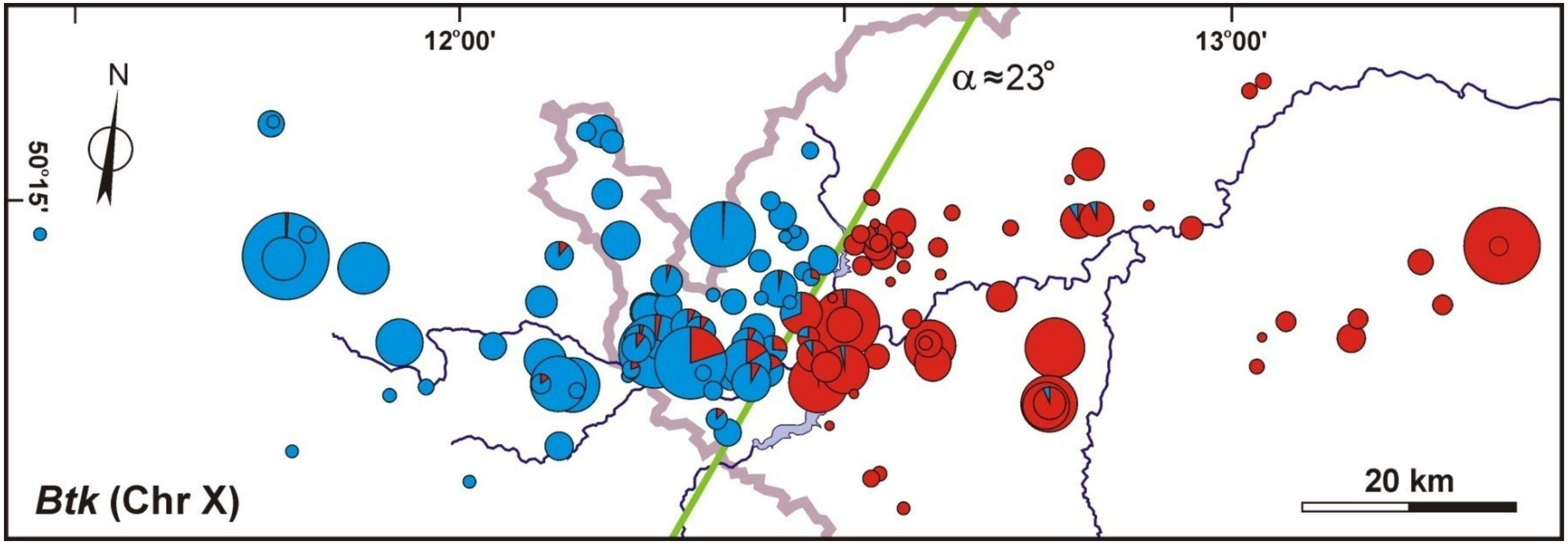

hybrid index
distance along transect (km)

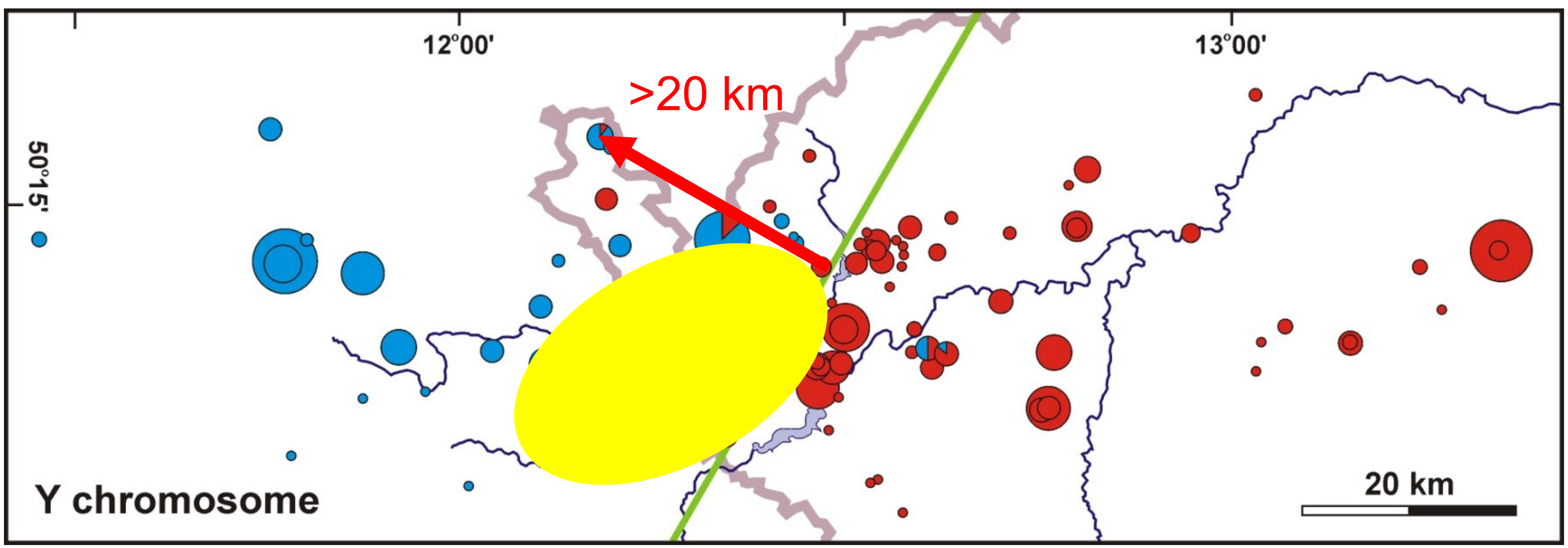

selected areas
cline width
position on chromosome


hybrid index
distance along transect (km)

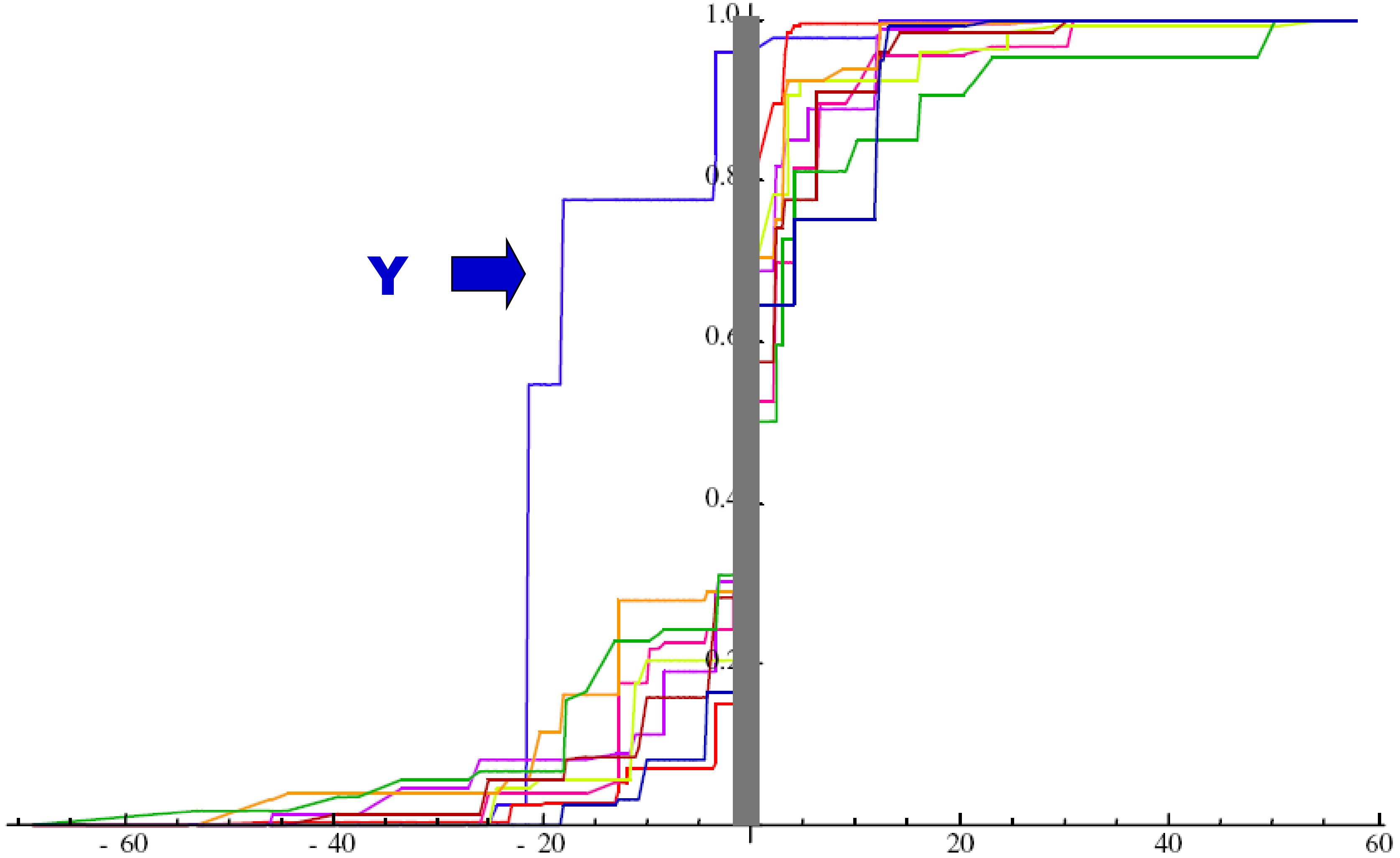

centromere
molecular markers

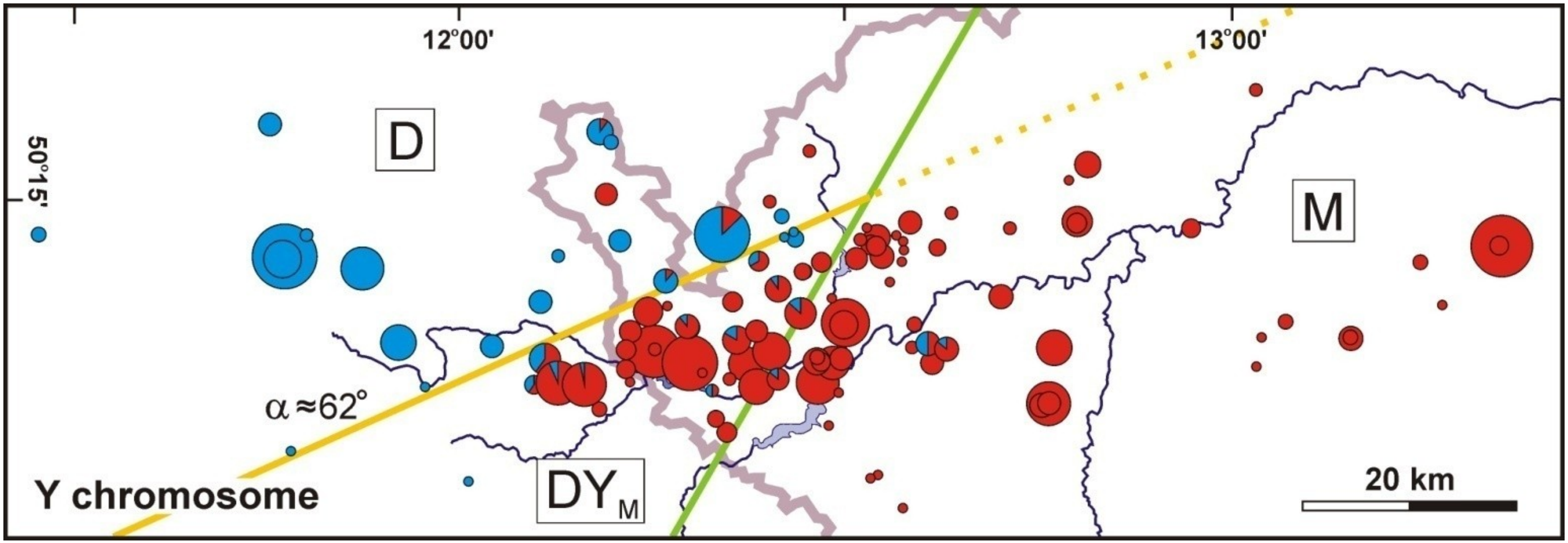
Problems – Y chromosome

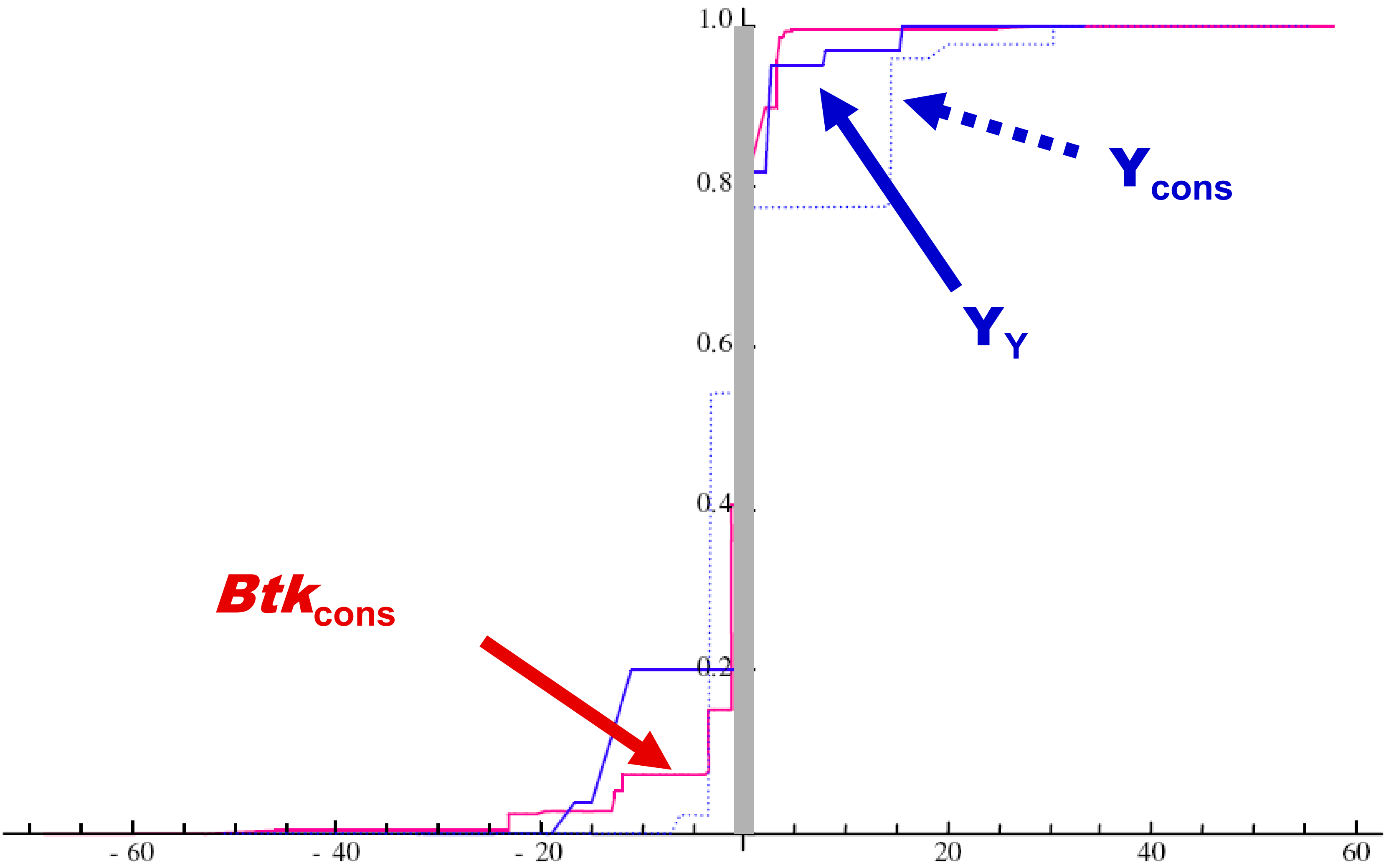




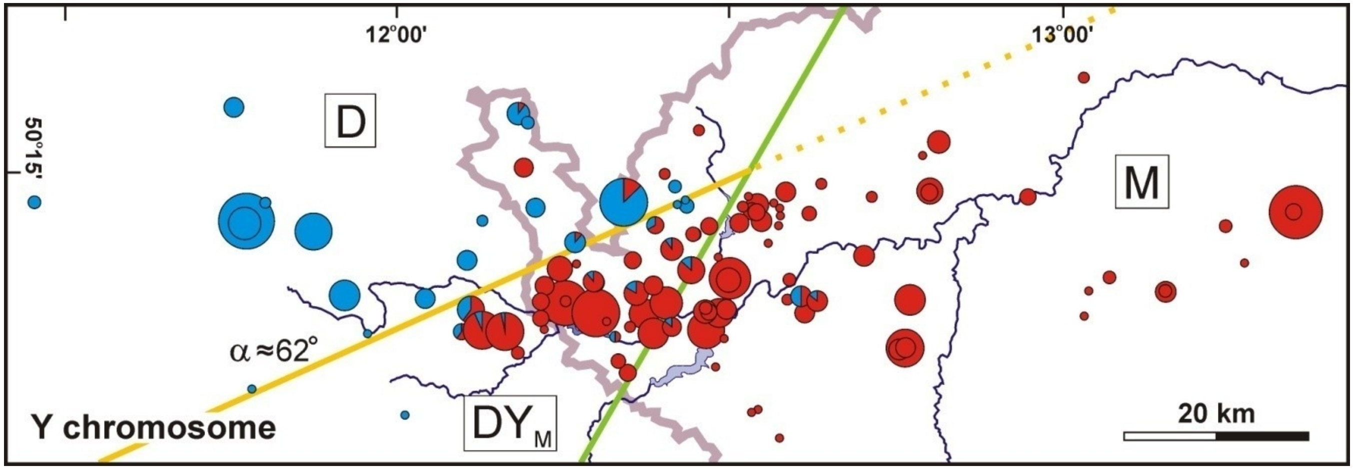
Monotonic clines – consensus orientation

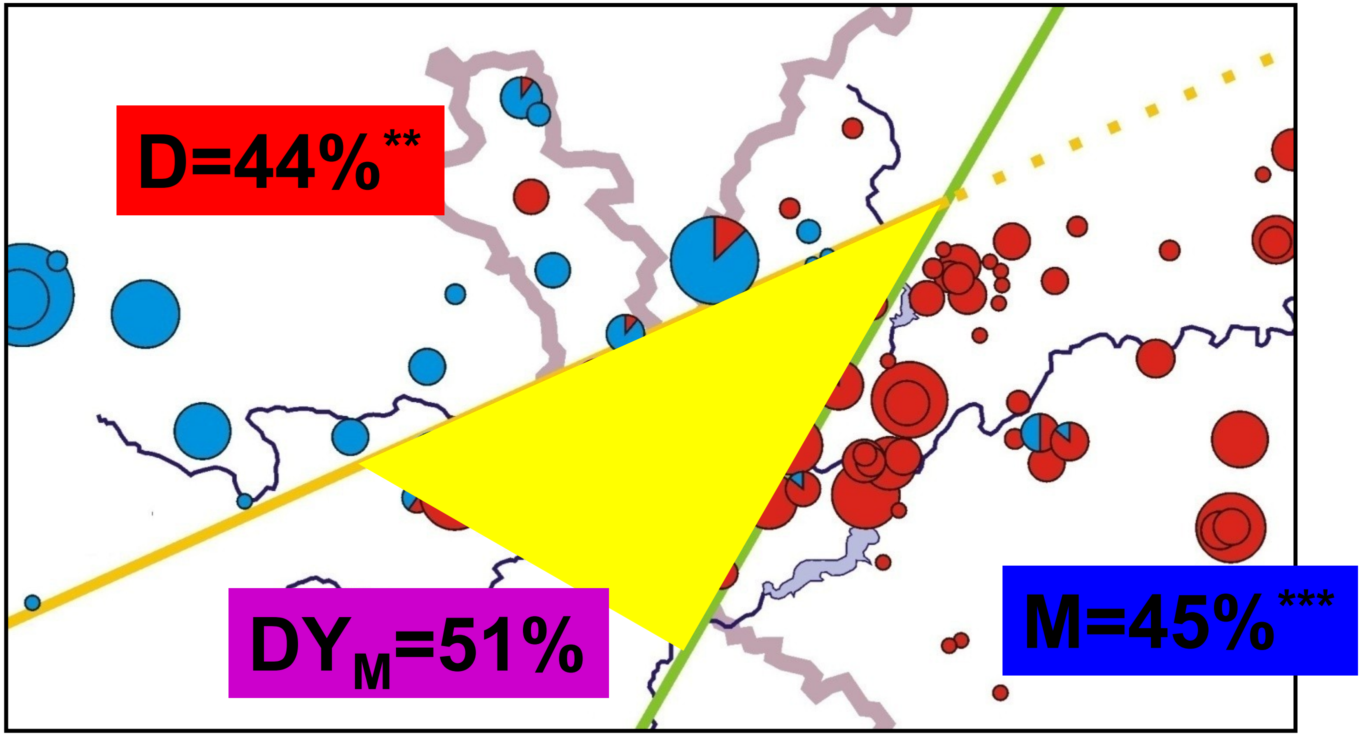



12°00'
13°00'
50°15'
D
M
DY_M
α ≈62°
Y chromosome
20 km



1.0
0.8
0.6
0.4
0.2
- 60
- 40
- 20
20
40
60
Y_{cons}
Y_Y
Btk_{cons}





salient/invagination ≈ 330 km^2

Weird behaviour of the Y in the hybrid zone – summary:

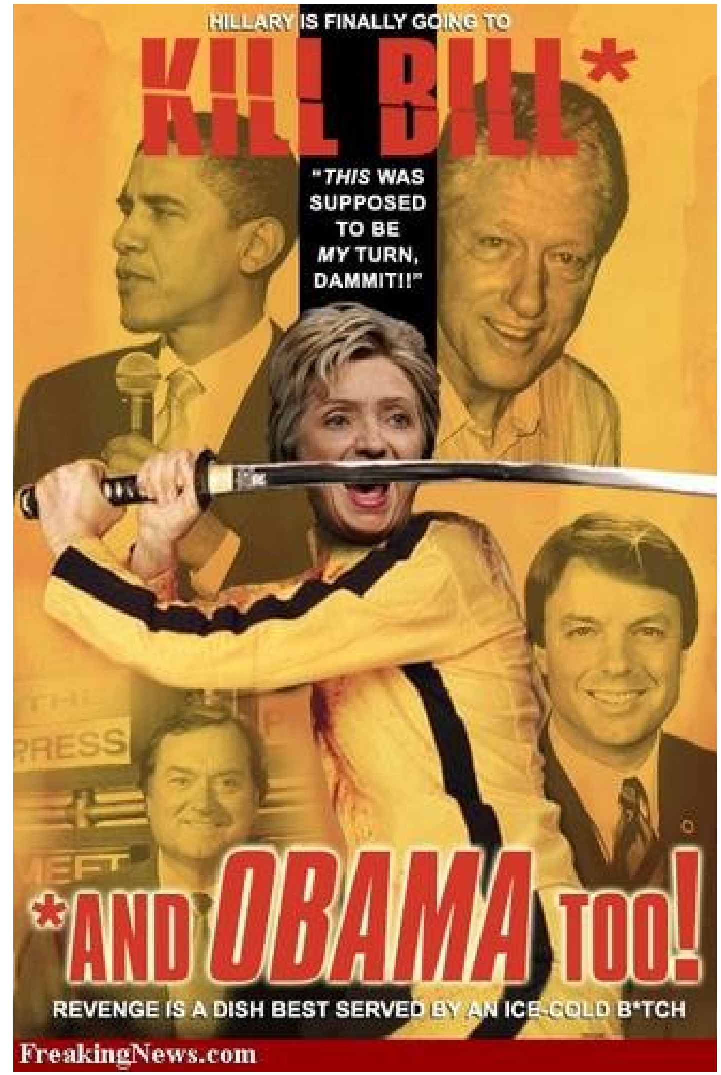
1. *musculus* Y more successful than *domesticus* Y on its own genetic background

2. higer proportion of males relative to other areas

Either coincidence, or ...

… or genetic conflict between X and Y

and probably some autosomal genes as well



segregation law

Gregor Mendel

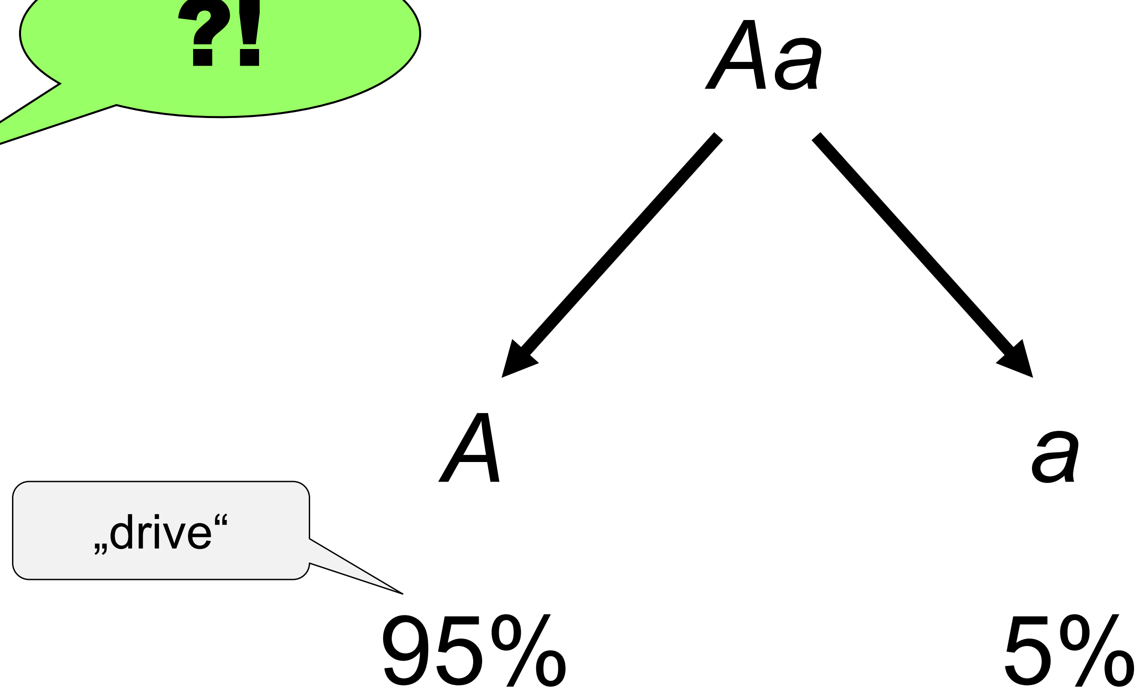
Aa

A 50%

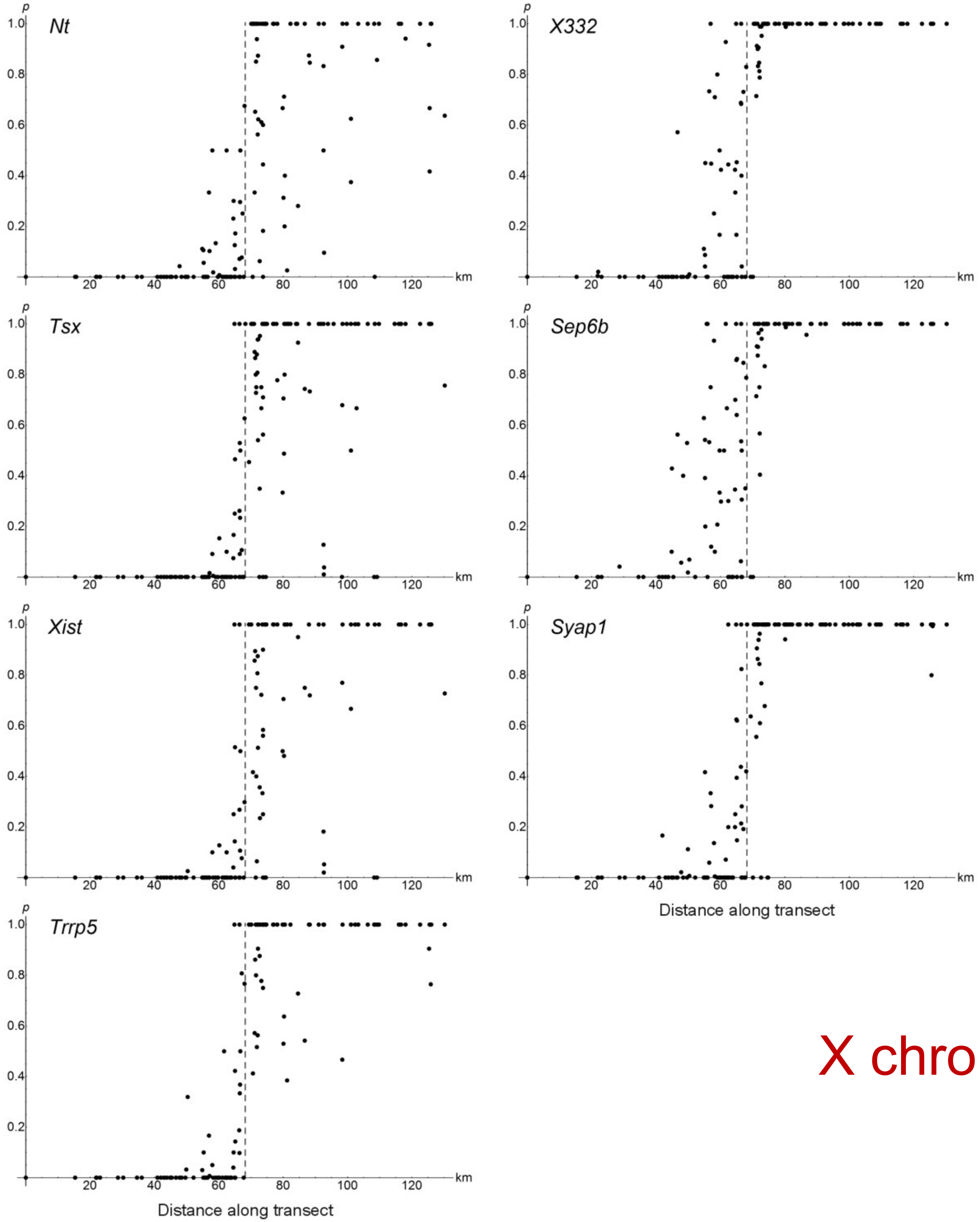
a 50%

Intragenomic conflict results in higher proportion of a genomic element in the next generation

Gregor Mendel

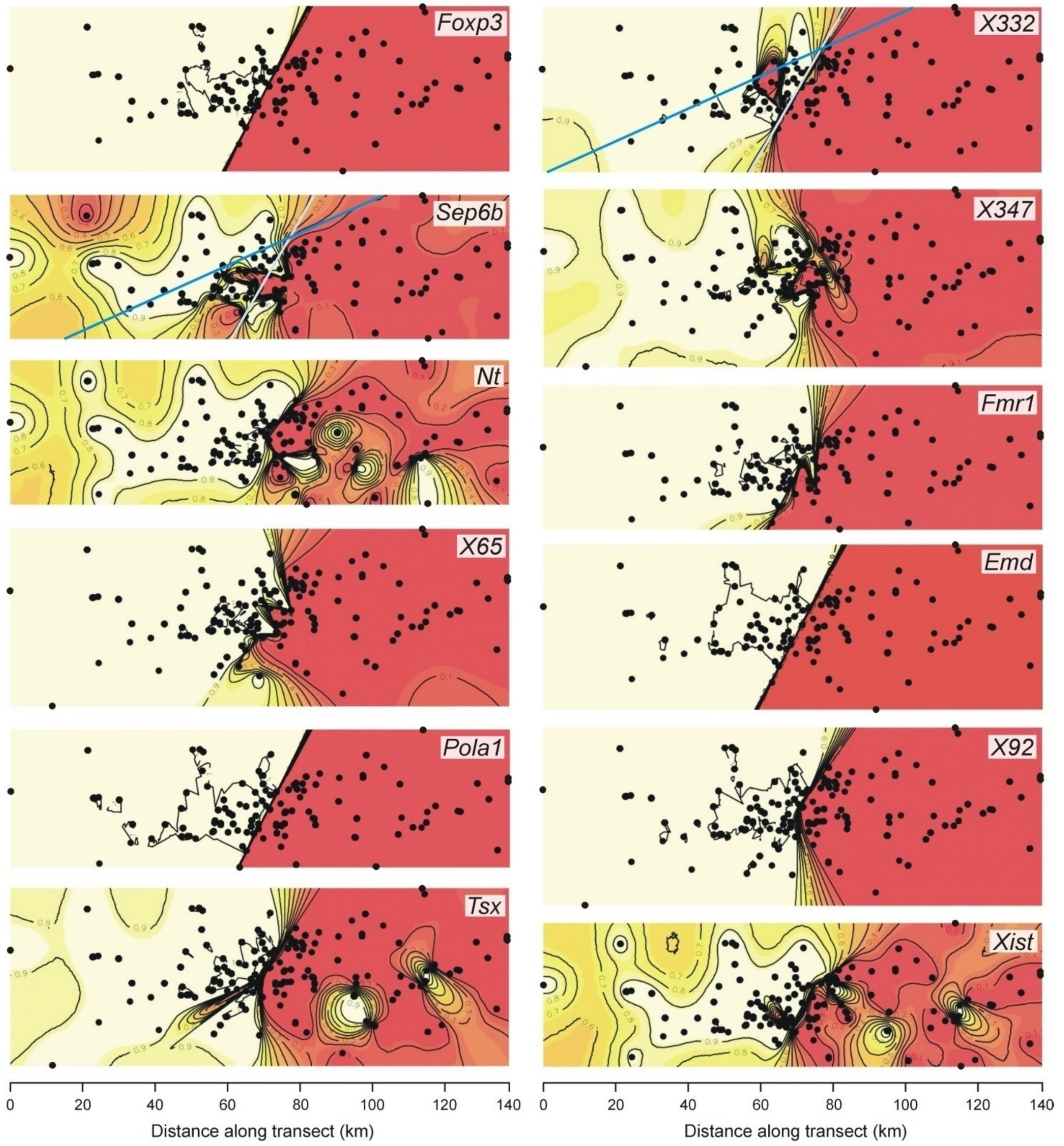


vychýlení segregačího (transmisního) poměru
= segregation distortion (SD)
= transmission ratio distortion (TRD)

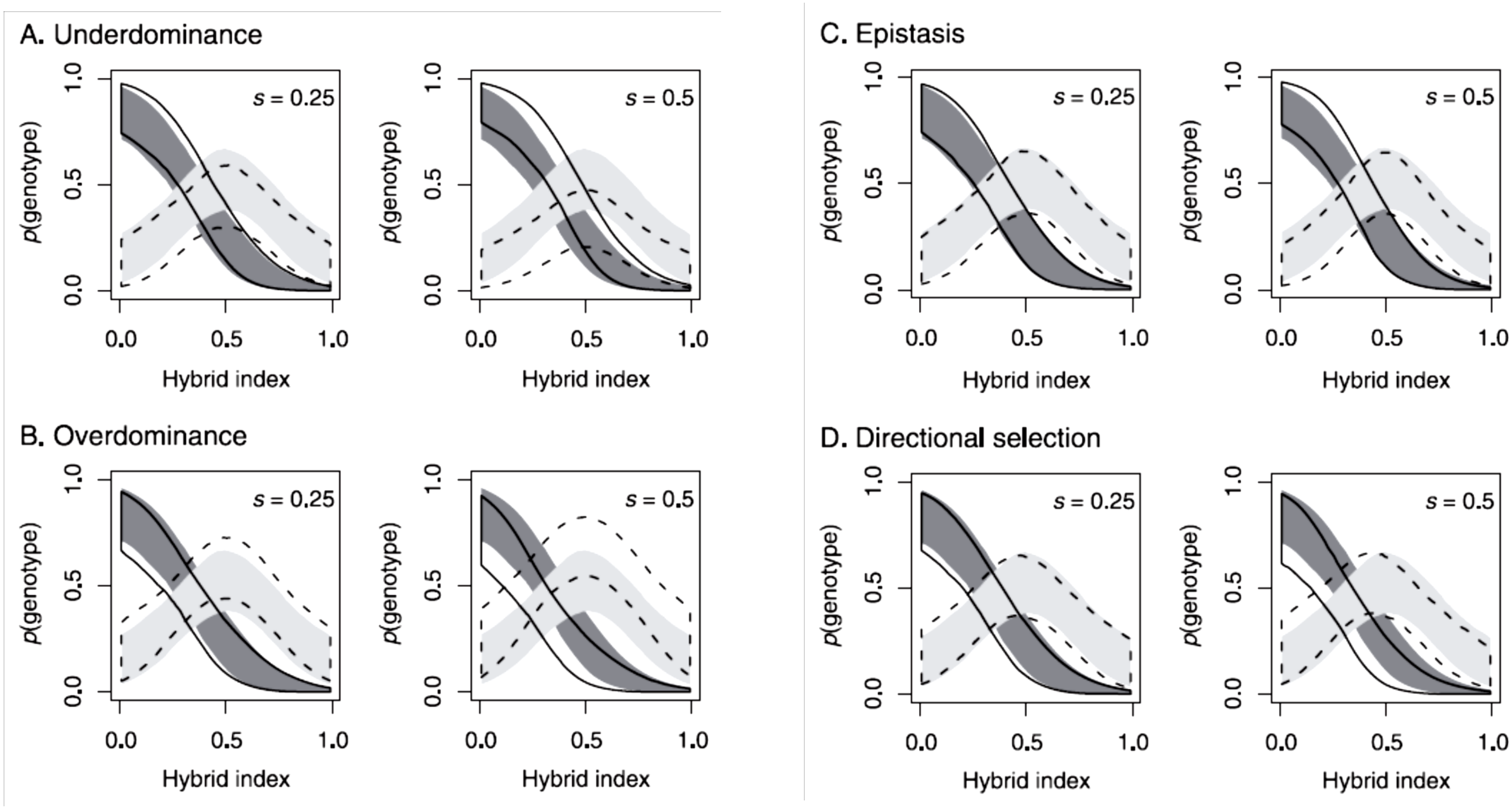


X chromosome

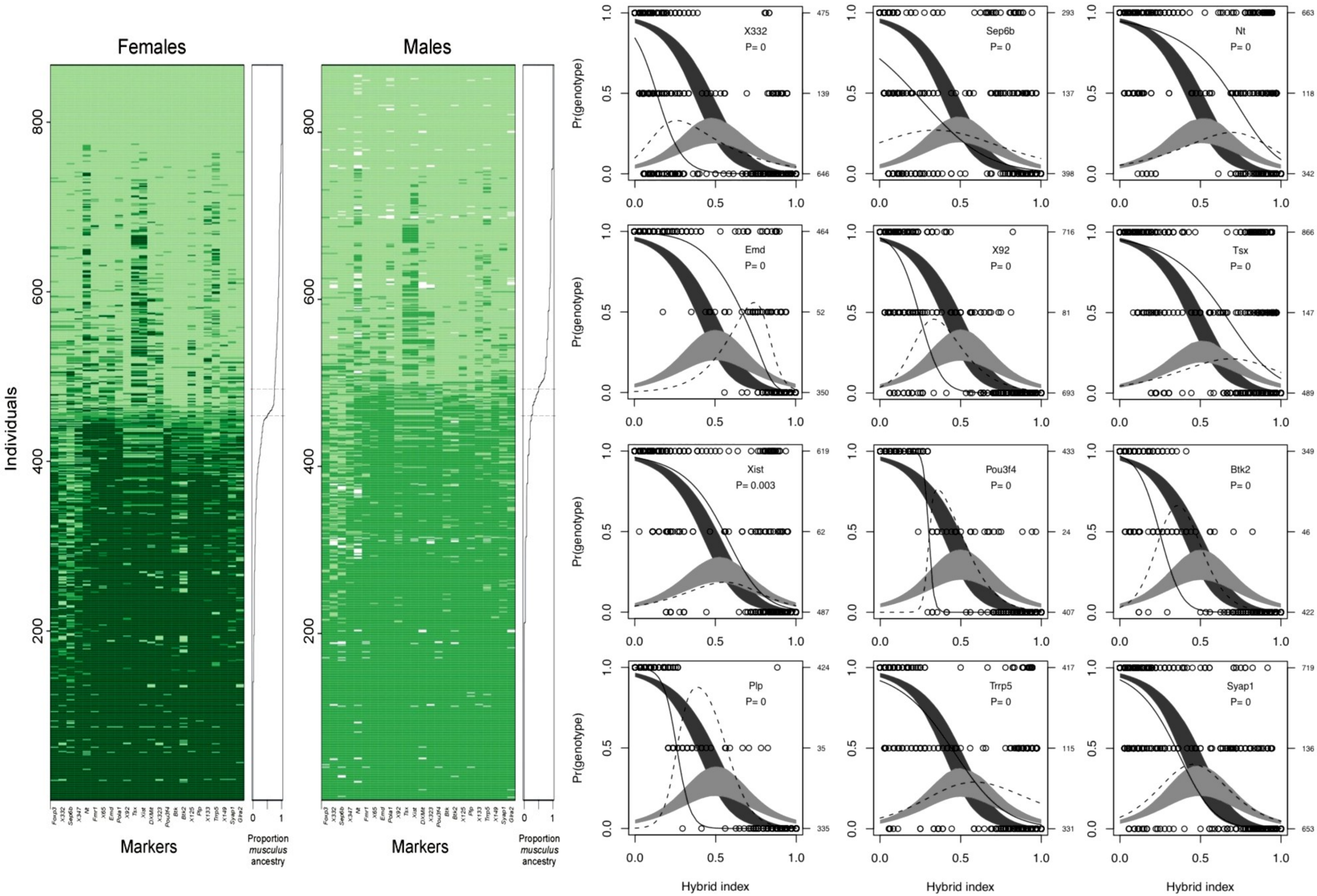
Chr. X - 2D analysis
Geneland



‘Genomic clines’

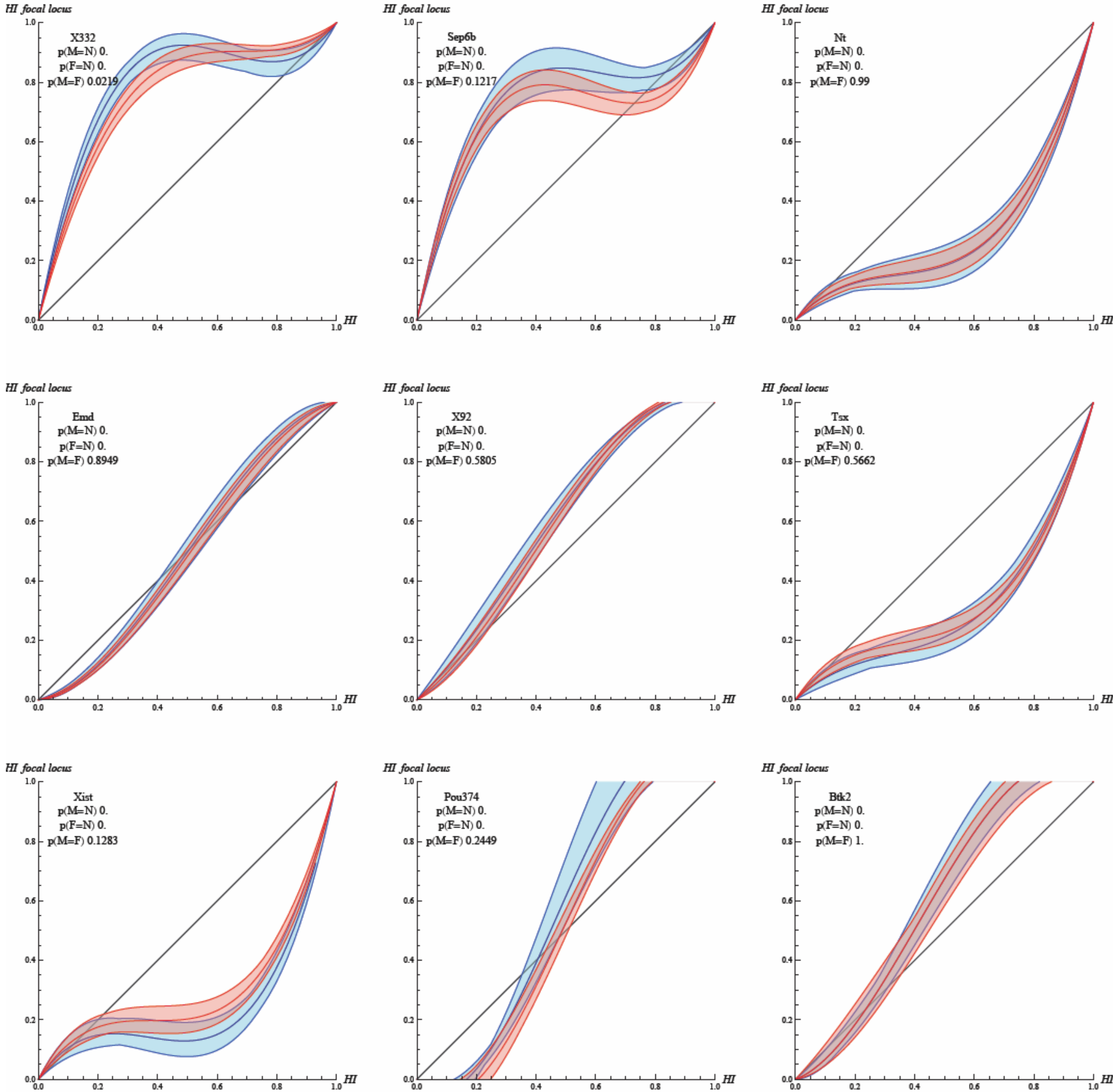


Z. Gompert & A. Buerkle



Females
Males
Individuals
Markers
Proportion musculus ancestry
Pr(genotype)
Hybrid index
X332
Sep6b
Nt
Emd
X92
Tsx
Xist
Pou3f4
Btk2
Plp
Trrp5
Syap1
P= 0
P= 0.003

Concordance analysis:



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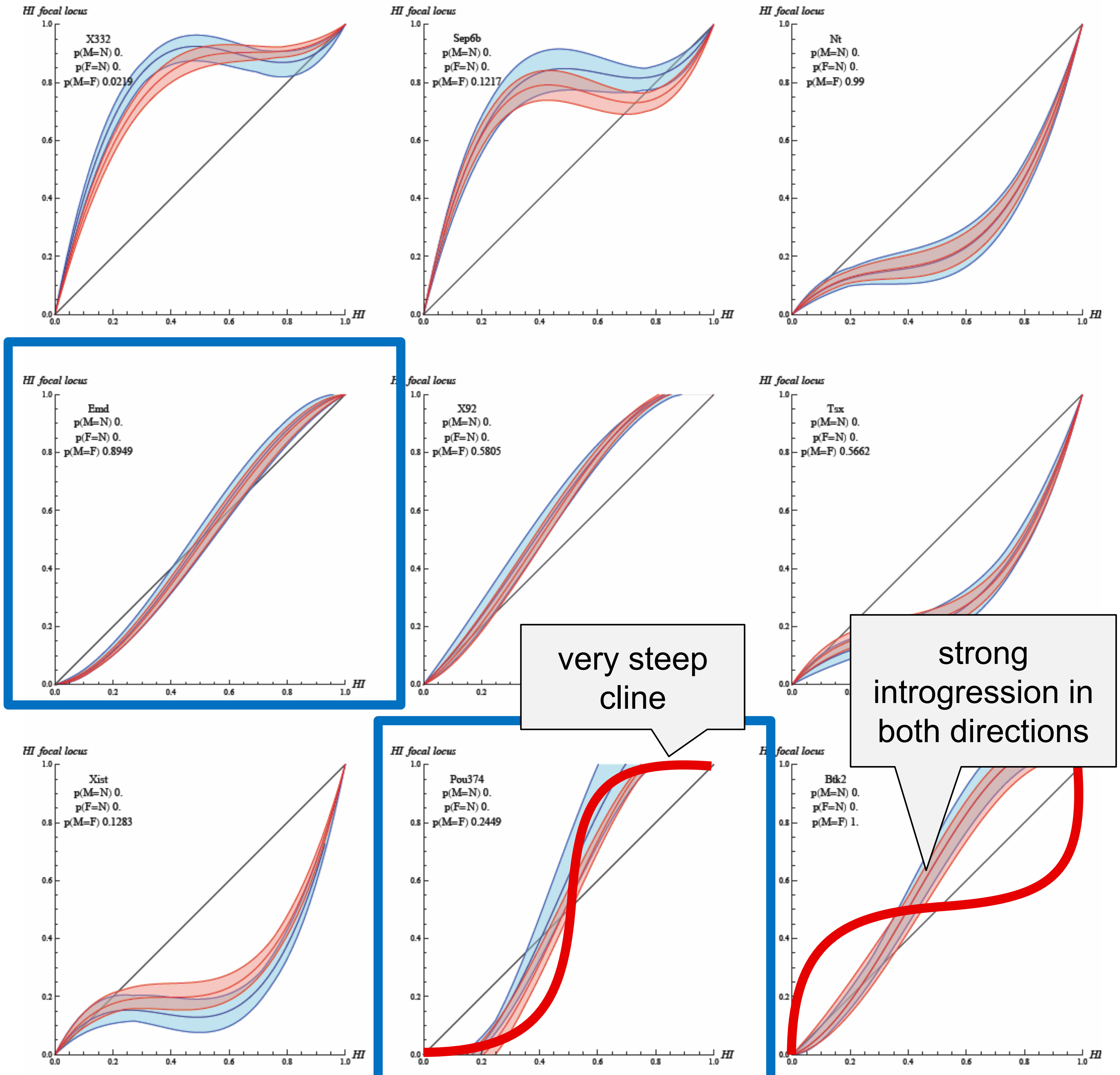
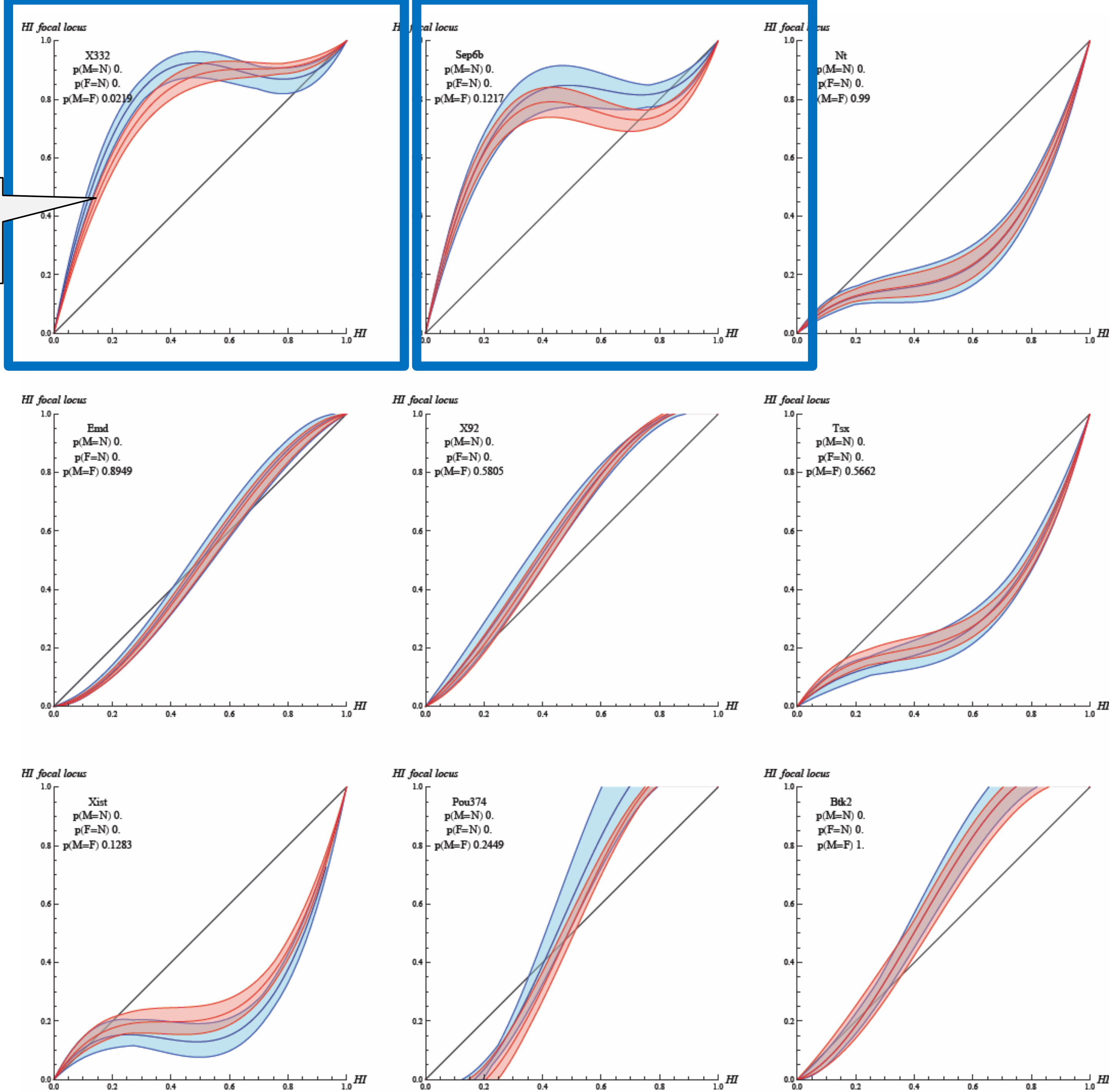


HI focal locus
HI
X332
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.0219
Sep6b
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.1217
Nt
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.99
Emd
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.8949
X92
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.5805
Tsx
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.5662
Xist
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.1283
Pou374
p(M=N) 0.
p(F=N) 0.
p(M=F) 0.2449
Btk2
p(M=N) 0.
p(F=N) 0.
p(M=F) 1.
very steep cline
strong introgression in both directions

S.J.E. Baird

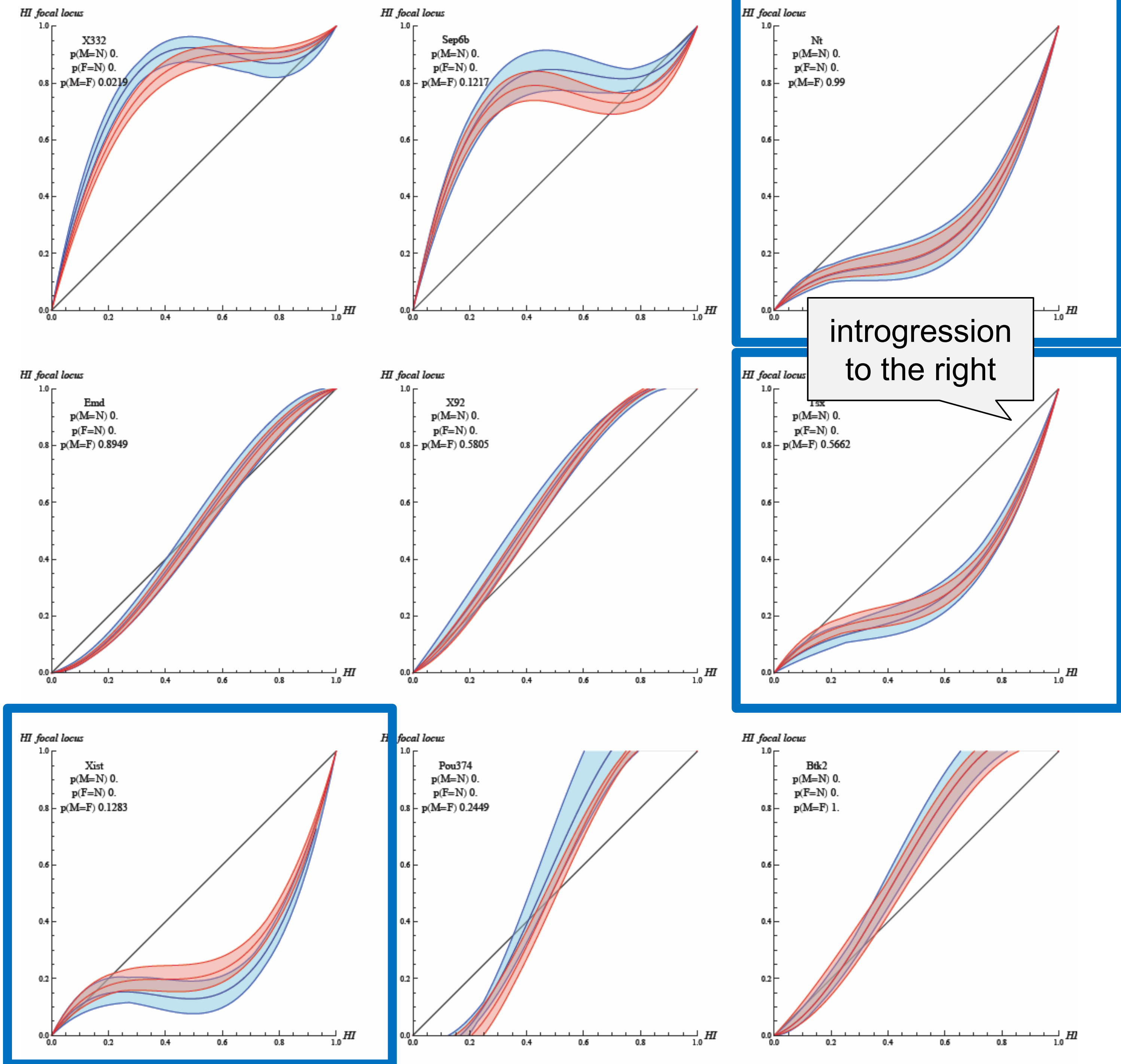
Concordance analysis:

introgression to the left



S.J.E. Baird

Concordance analysis:



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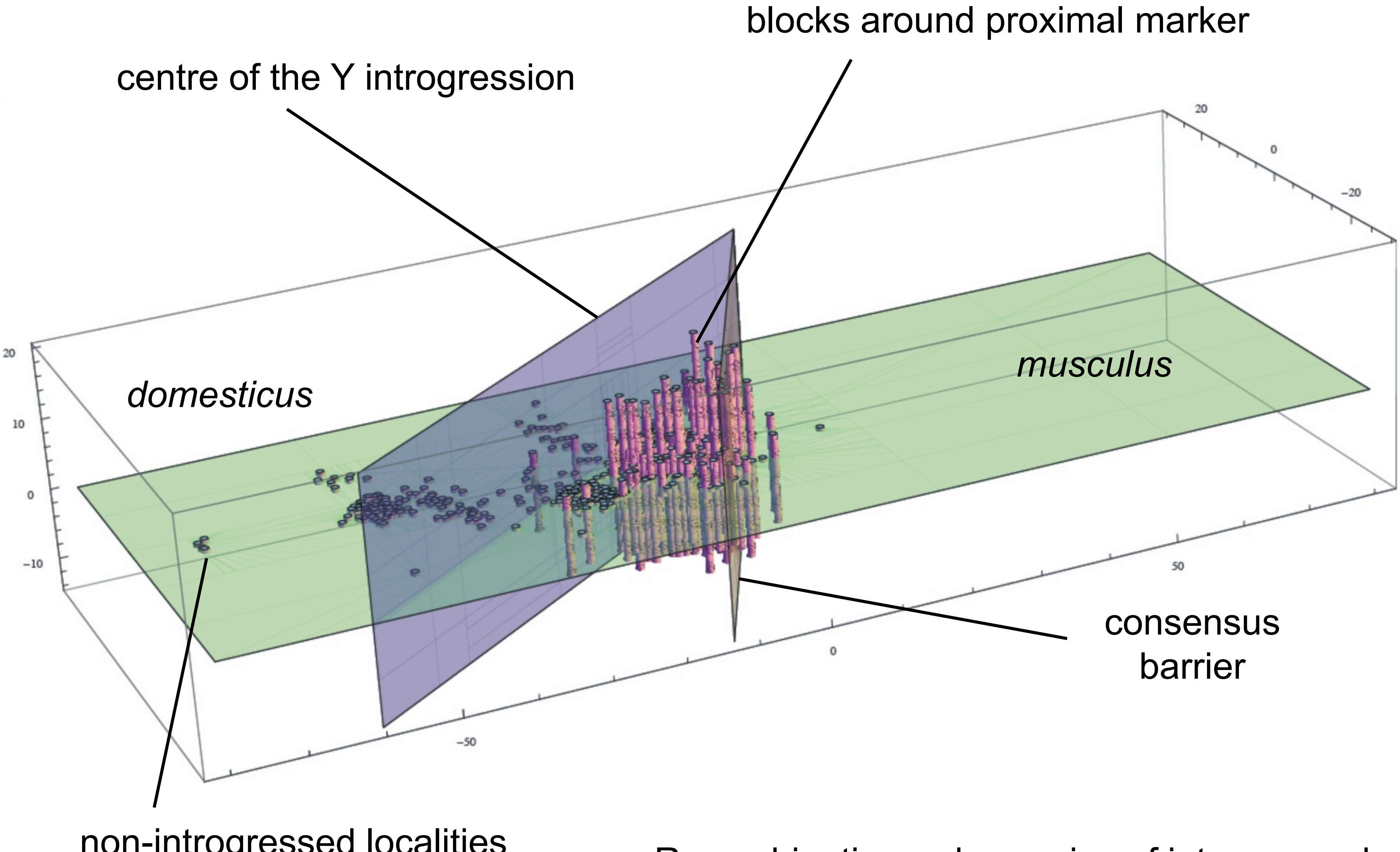
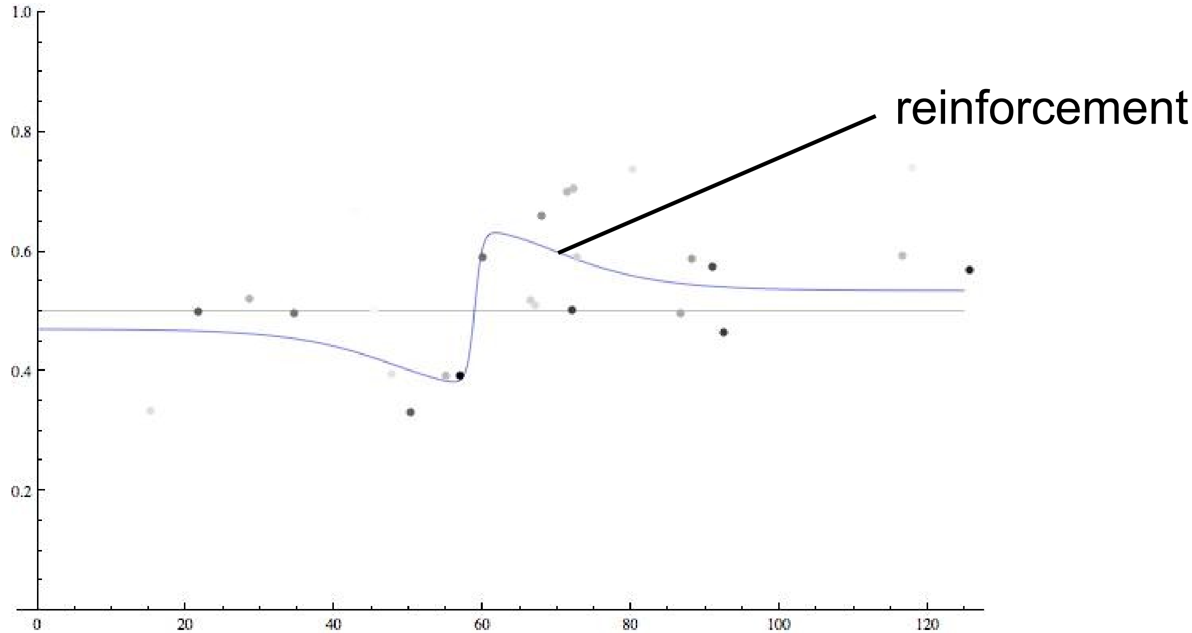
Proximal marker on the X

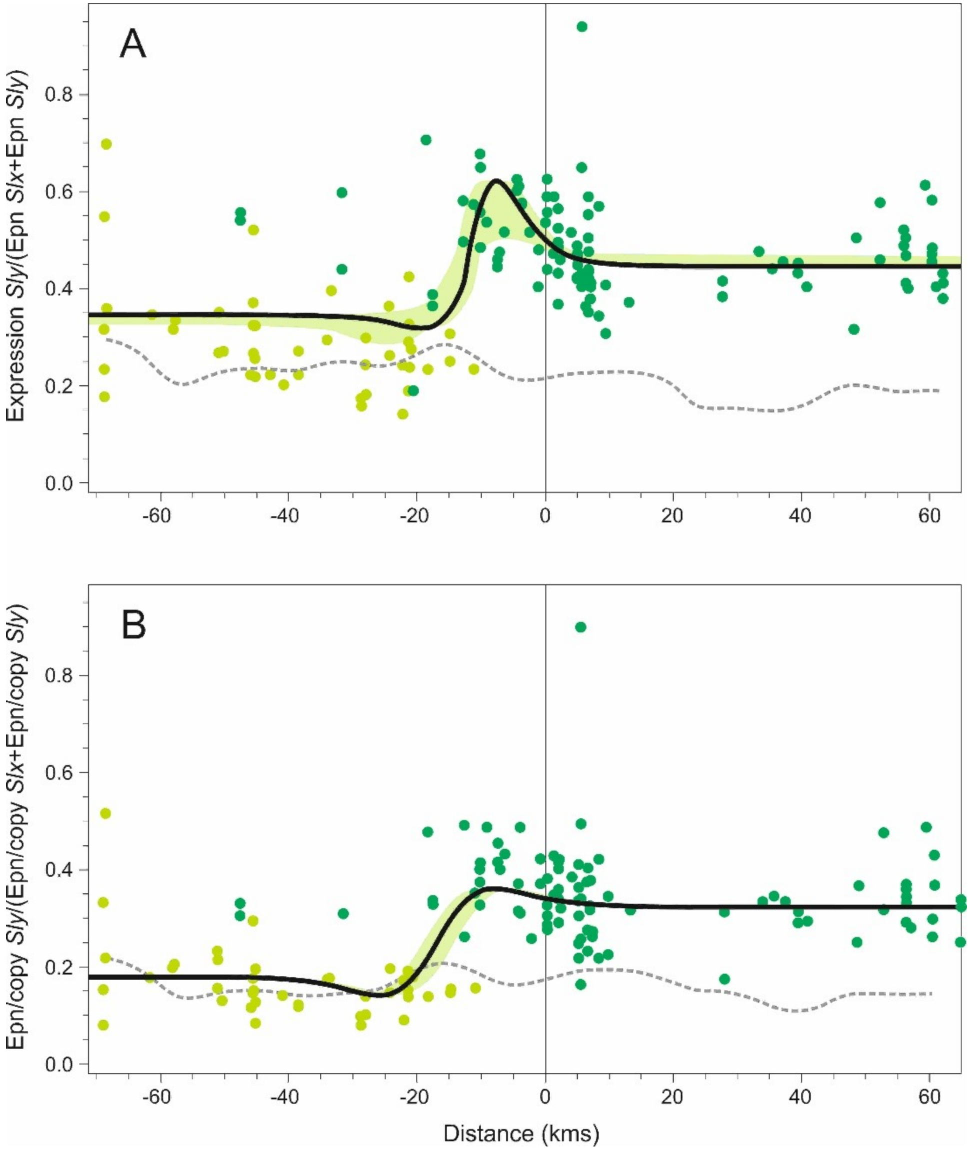


Recombination reduces size of introgressed block far of the zone centre

Using cline model for analysis of reinforcement – odour preference in the mouse hybrid zone



Using cline model for analysis of gene expression in the mouse hybrid zone – asymmetric model

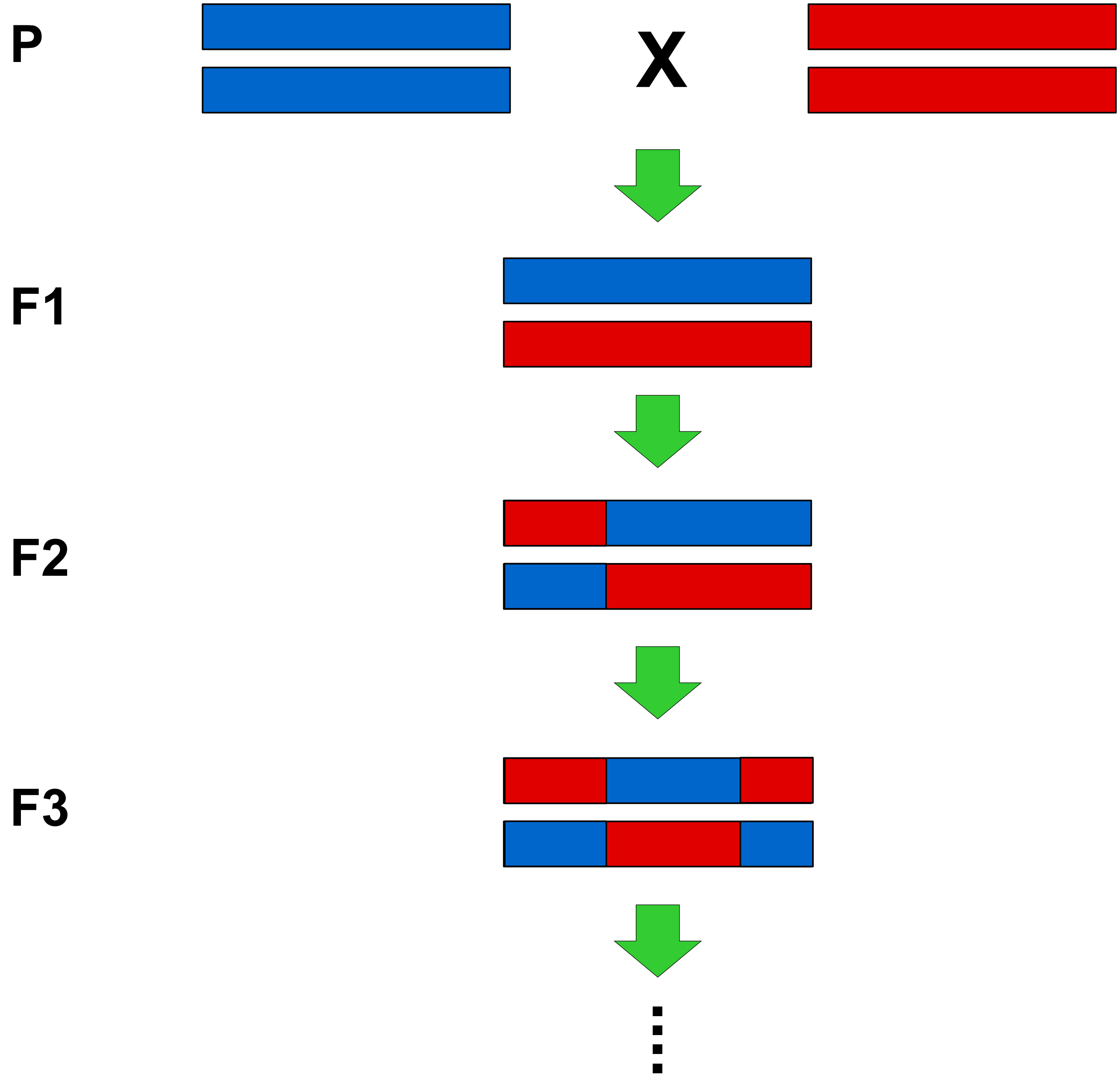


Neanderthal DNA specialist Svante Pääbo examines the
femur, found near Ust'-Ishim in western Siberia. Photogr

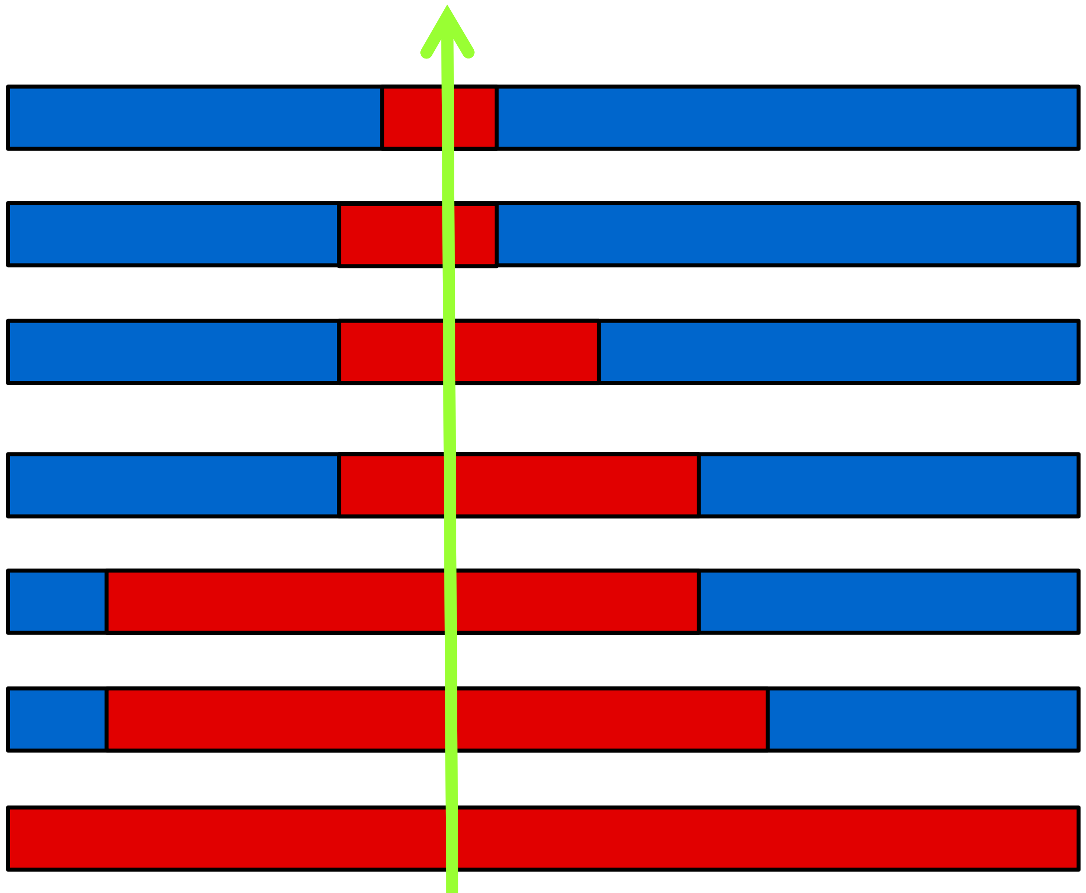
Blocks of Neanderthal DNA found in modern humans can act like a biological clock, because they are fragmented more and more with each generation since interbreeding happened. The **blocks** of Neanderthal DNA in the Siberian man were on average three times longer than those seen in people alive today. Working backwards, the scientists calculate that Neanderthals contributed to the man's genetic ancestry somewhere between 7,000 and 13,000 years before he lived.

The findings, published in the journal Nature, suggest that humans and Neanderthals had reproductive sex around 50,000 to 60,000 years ago…

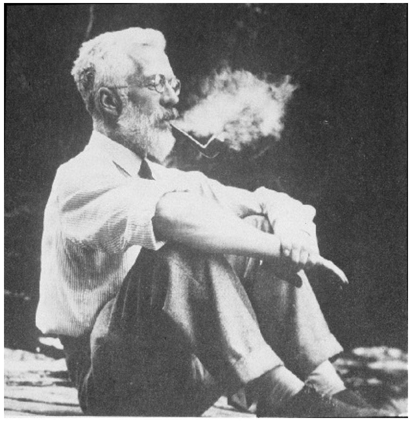
The Guardian Wednesday 22 October 2014


P
X
F1
F2
F3

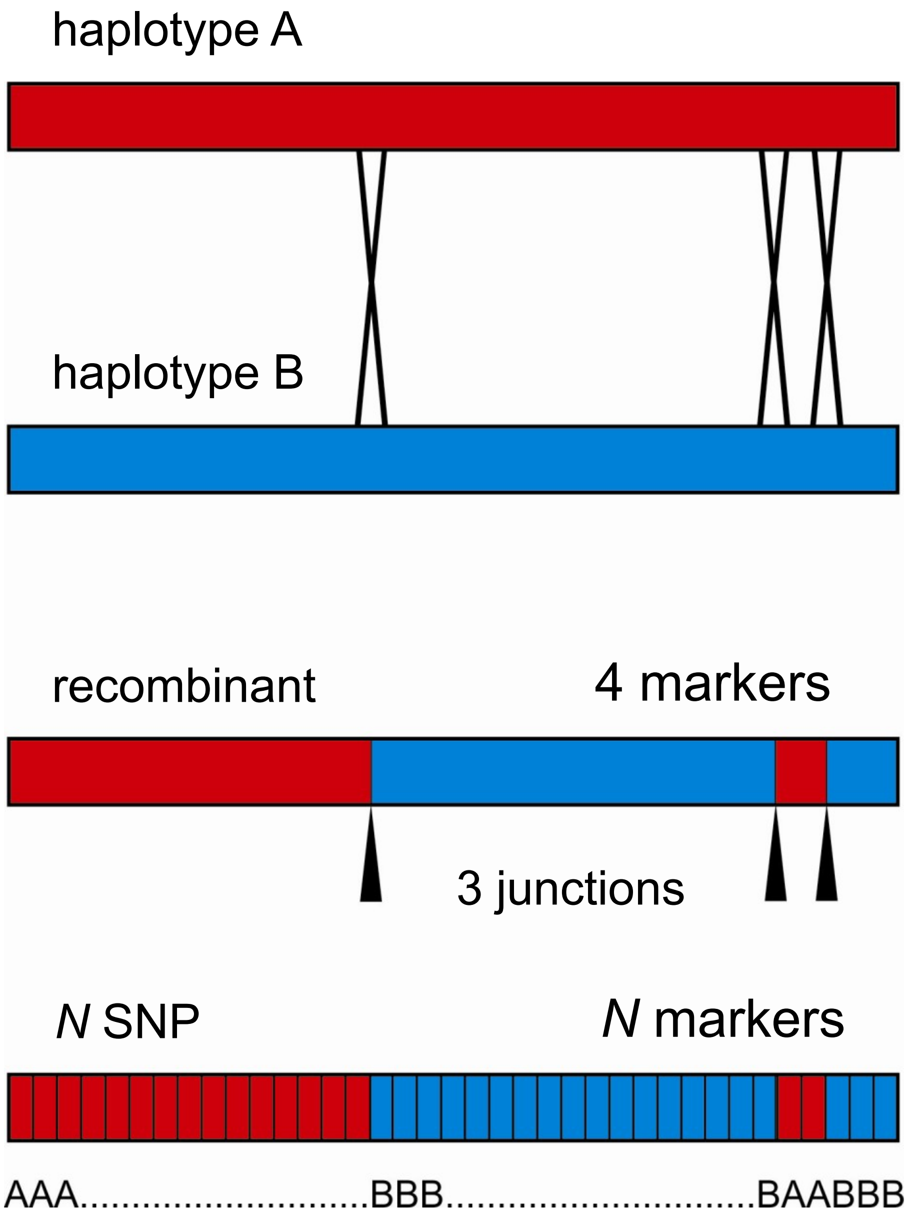
Hybridization makes a cascade of blocks



advancing introgression into ‘blue’ genome

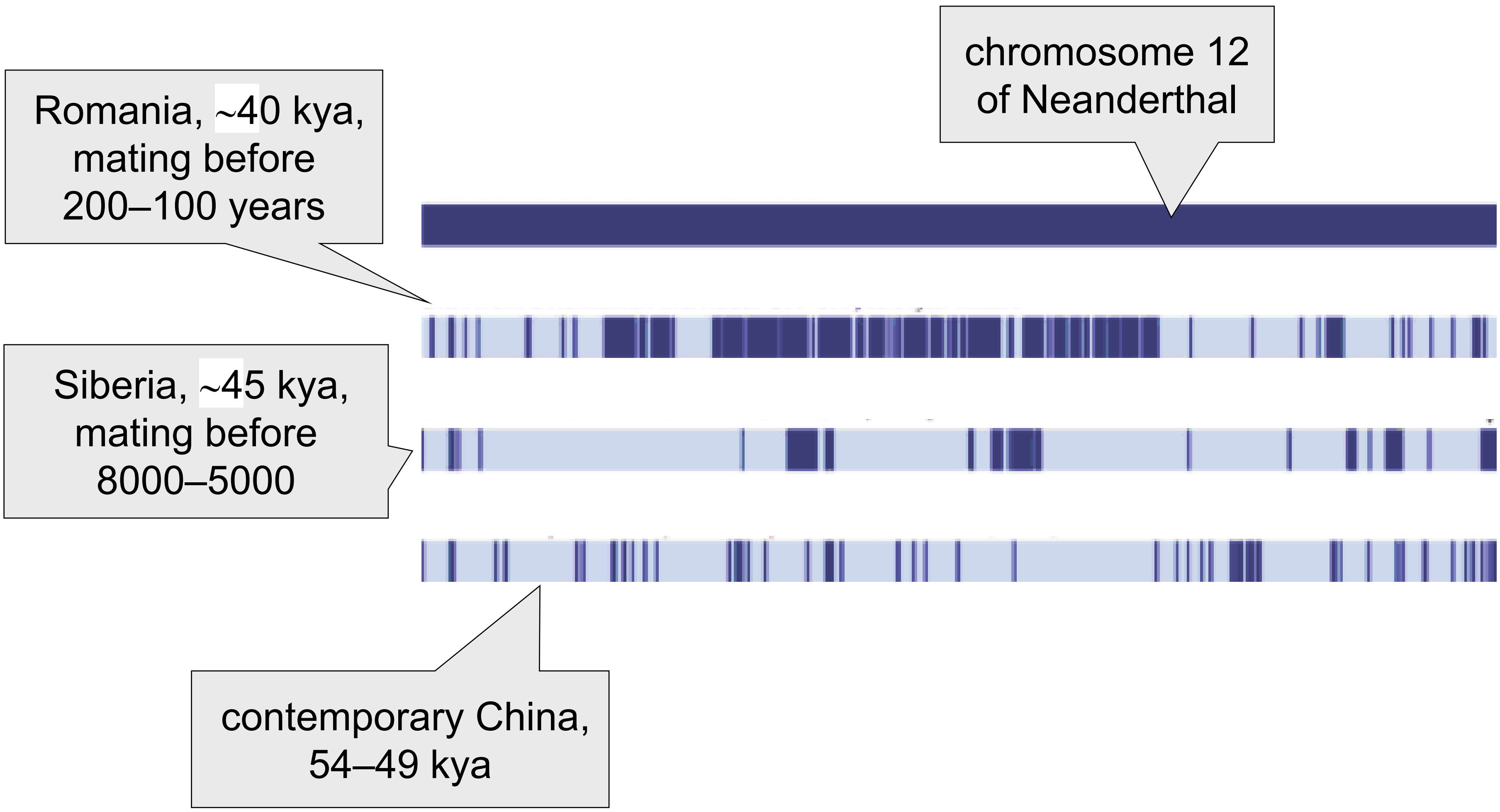


R. A. Fisher



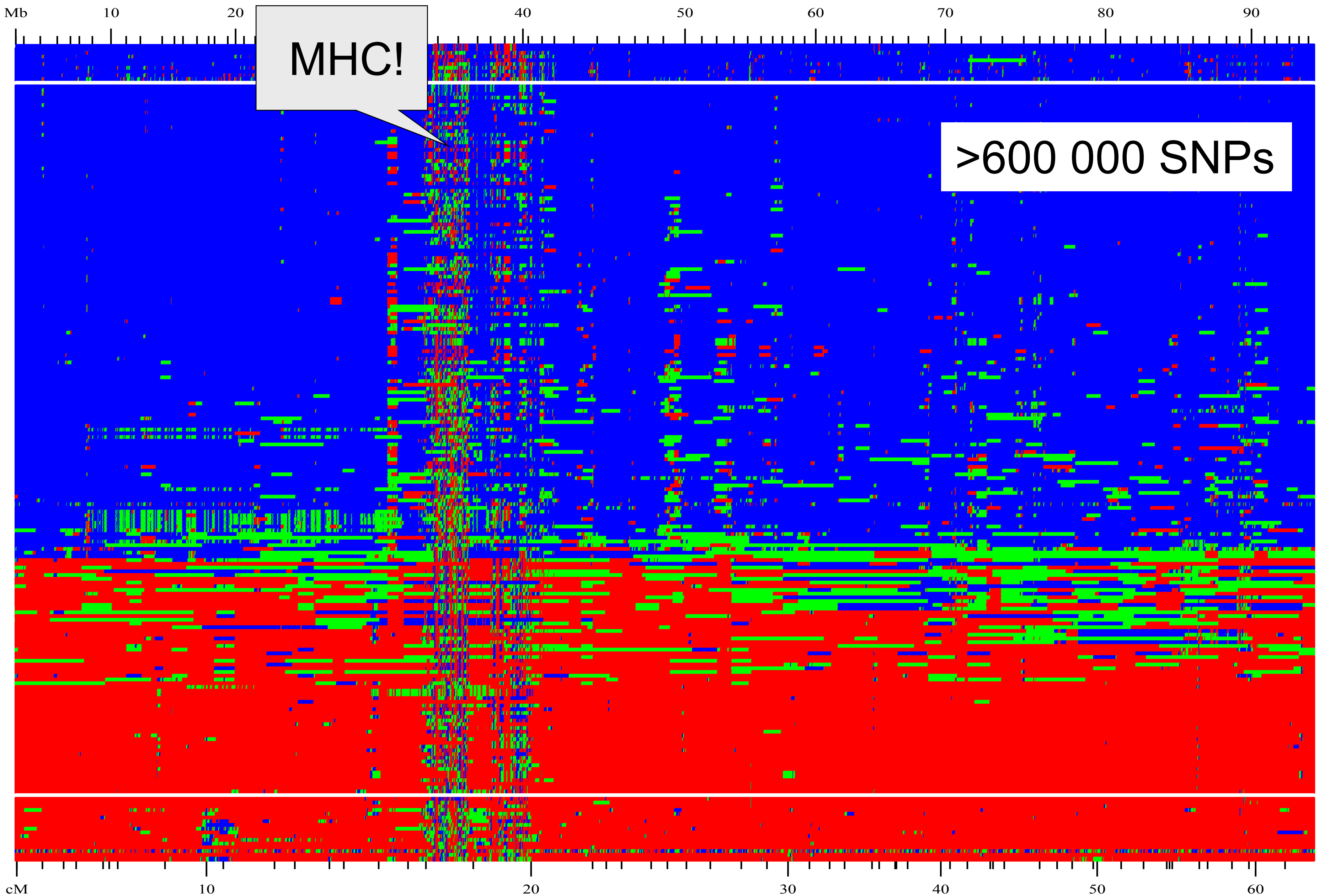
Recombination brings together DNA of different origin and makes *junctions* (*breakpoints*)

they divide genome into *blocks* (*chunks*, *tracts*, *segments*)

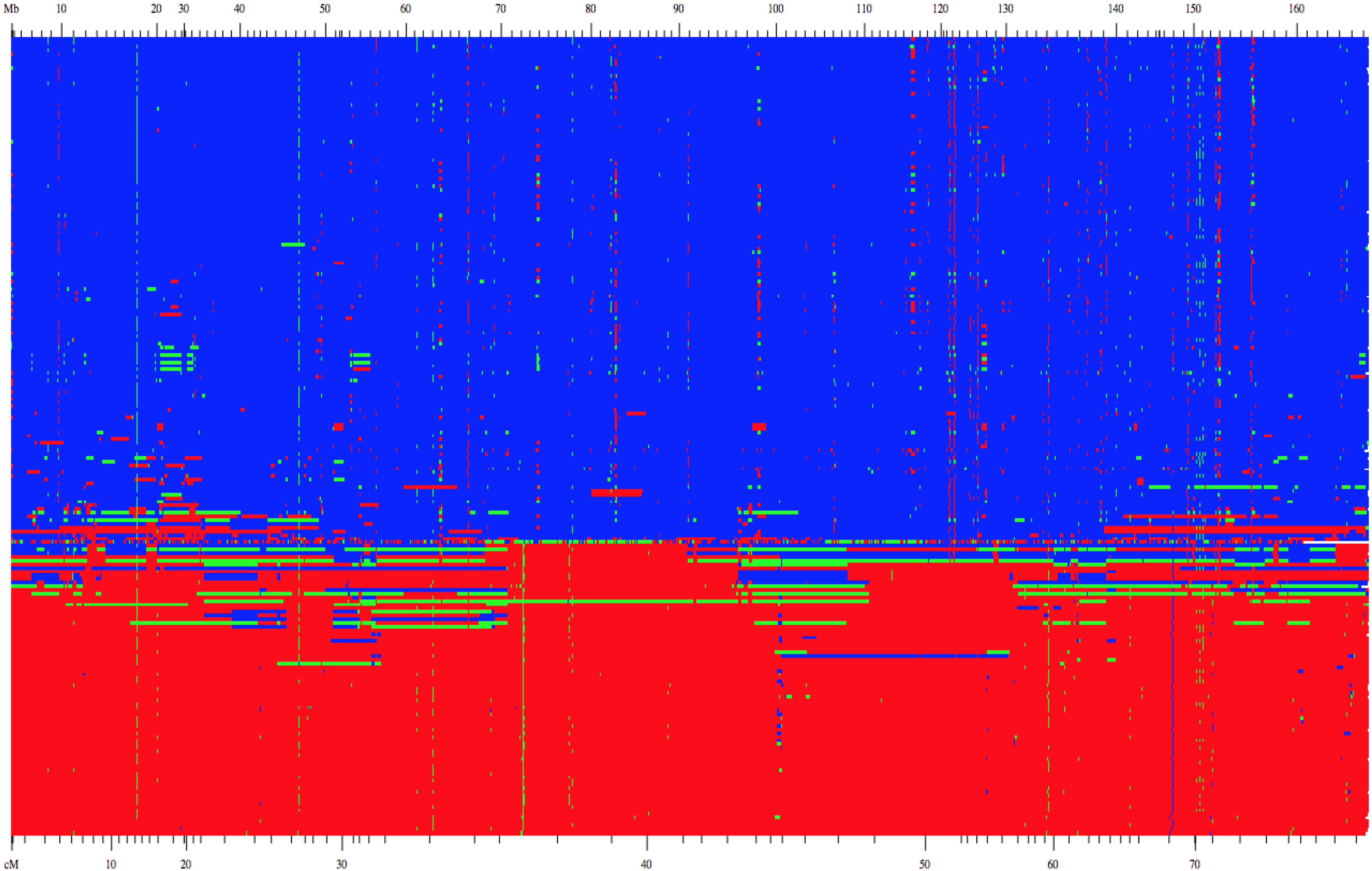


chromosome 12
of Neanderthal
Romania, ~40 kya,
mating before
200–100 years
Siberia, ~45 kya,
mating before
8000–5000
contemporary China,
54–49 kya

Chromosome 17



Chromozom X



Mb
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
cM
10
20
30
40
50
60
70

Why hybrid zones? Reproductive barriers and speciation!

Dobzhansky-Muller model

W. Bateson

T. Dobzhansky

H. Muller

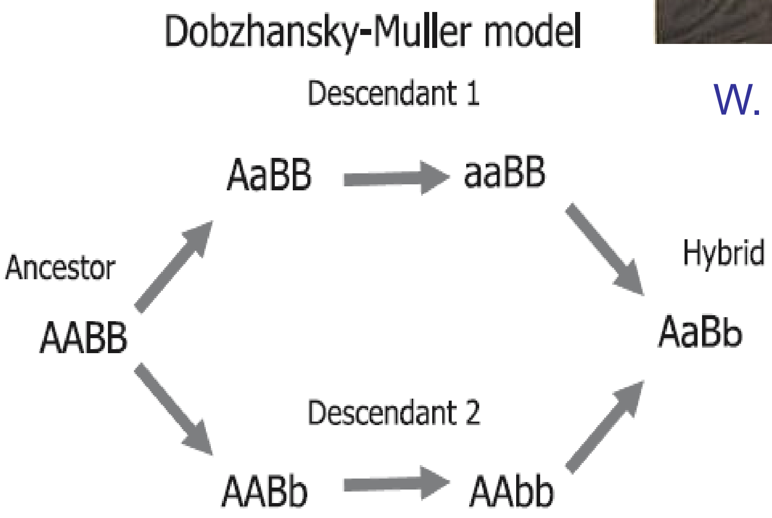
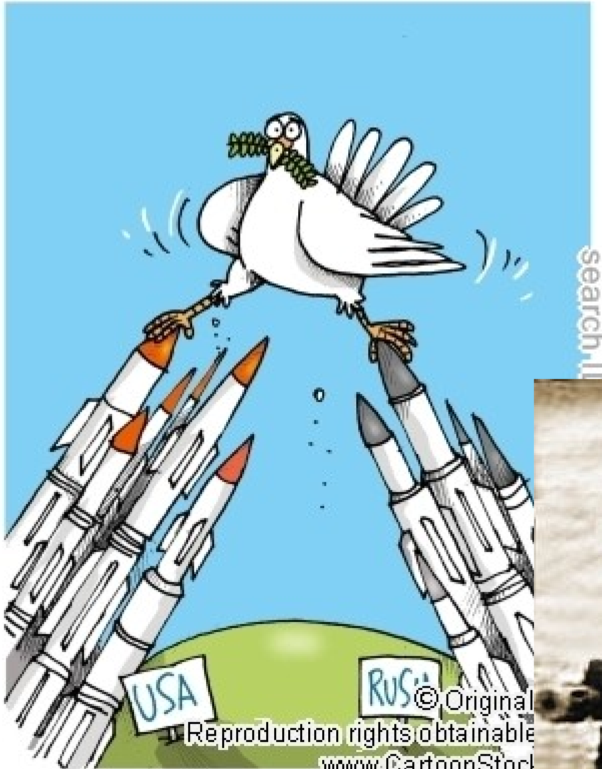
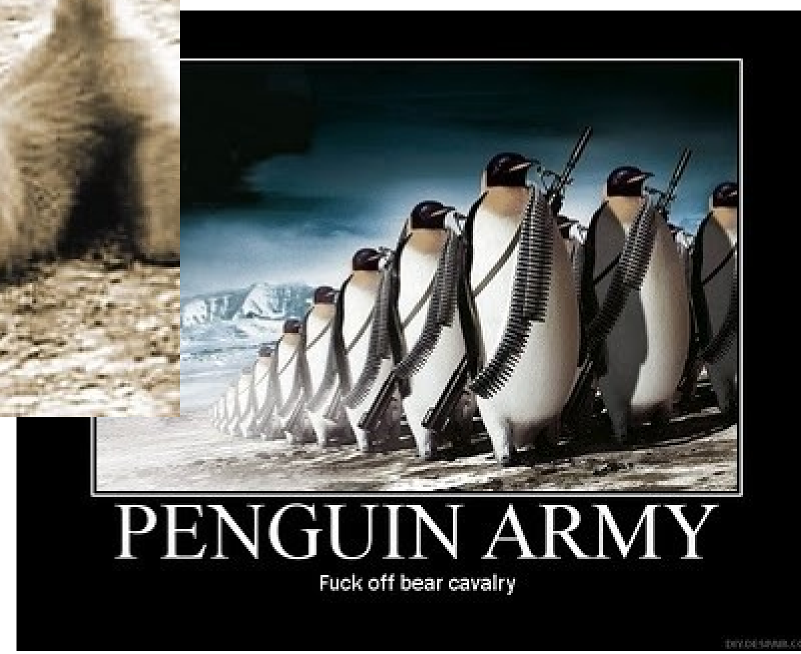


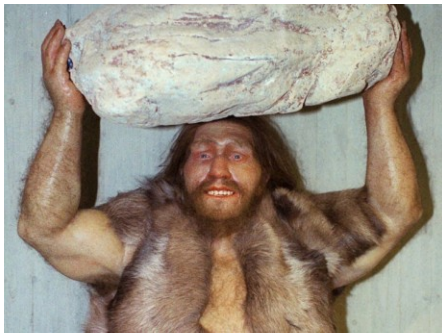
Fig. 1 The Dobzhansky–Muller model for postzygotic isolation

„Arms races“ and secondary contact





genetic conflict: “classical” scenario



subpop. 1

arms race
in ancestral
population

continuing
arms race

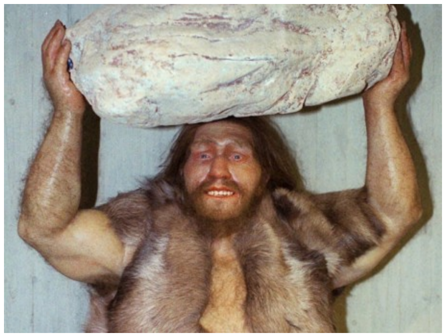
subpop. 2

incompatible!

secondary contact

MAD = *mutually assured destruction*

genetic conflict: alternative scenario

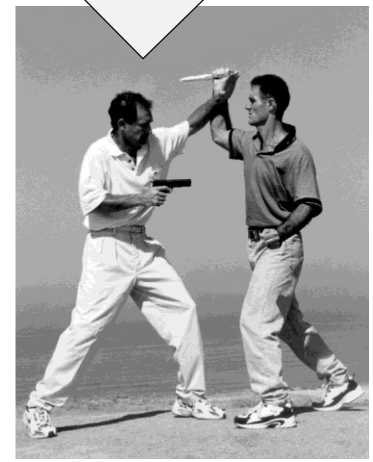


arms race
in ancestral
population

subpop. 1

continuing
arms race

subpop. 2



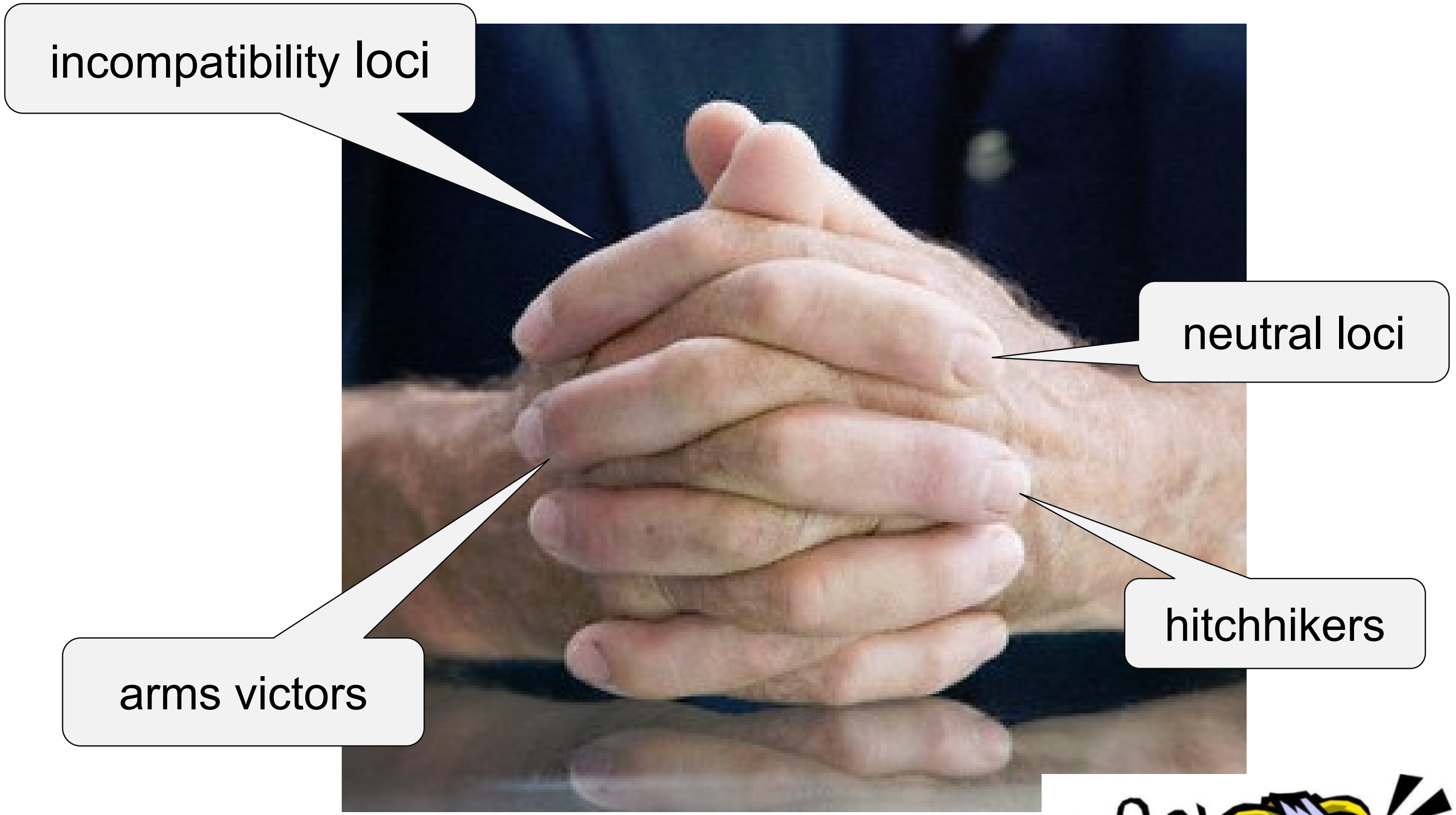
Never bring a knife to a gunfight!

secondary contact

the winner thrives on "naive" genetic background

"antispeciation genes"

Why we don't see this more often?



Ticking time-bomb...

Cytonuclear disequilibria

- = non/random associations of nuclear and cytoplasmic (mitochondrial) alleles
- 3 × 2 table

	nuclear genotype:			
mtDNA:	*AA*	*Aa*	*aa*	**total**
M	u_1	v_1	w_1	$\boldsymbol{x}$
m	u_2	v_2	w_2	$\boldsymbol{y}$
total	$\boldsymbol{u}$	$\boldsymbol{v}$	$\boldsymbol{w}$	**1**

No hybridization

	nuclear genotype:		
mtDNA:	*AA*	*Aa*	*aa*
M	+++	0	0
m	0	0	+++

Random mating, hybrid swarm

	nuclear genotype:		
mtDNA:	*AA*	*Aa*	*aa*
M	obs=exp	obs=exp	obs=exp
m	obs=exp	obs=exp	obs=exp

Hybridization without apparent introgression, crossing independent of sex

	nuclear genotype:		
mtDNA:	AA	Aa	aa
M	++	obs=exp	0
m	0	obs=exp	++

Hybridization without apparent introgression, crossing depends on sex

	nuclear genotype:		
mtDNA:	*AA*	*Aa*	*aa*
M	++	++	0
m	0	--	++

Hybrids mate more often with less discriminating species

mtDNA:	nuclear genotype: *AA*	*Aa*	*aa*
M	obs=exp	++	--
m	obs=exp	--	++

Symmetrical introgression

mtDNA:	nuclear genotype: *AA*	*Aa*	*aa*
M	++	obs=exp	--
m	--	obs=exp	++

Potential introgression, crossing dependent on sex

mtDNA:	nuclear genotype: AA	Aa	aa
M	++	++	--
m	0	0	++

Programs for hybrid zone analysis:

Analyse: Stuart J.E. Baird, Nick H. Barton (Mac)

ClineFit: Adam Porter (PC)

CFit: Thomas Lenormand (PC)

(Geneland)

S.J.E. Baird

N.H. Barton

A. Porter

T. Lenormand