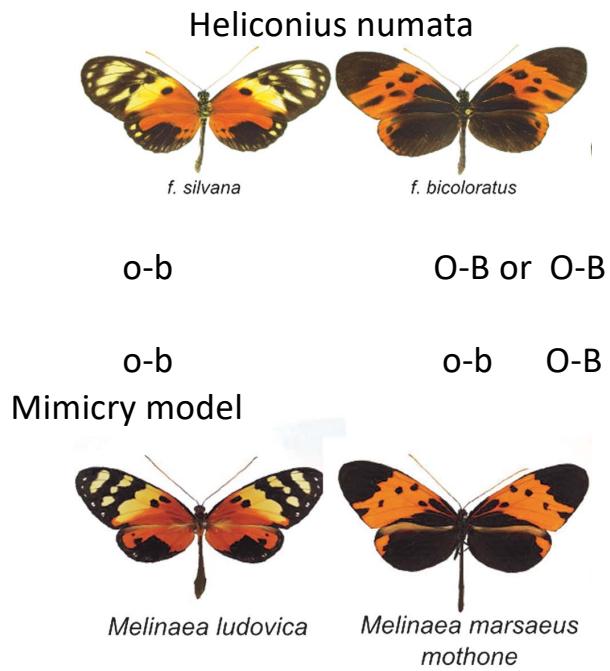


O = top-wing orange band, o=orange band absent
 B = bottom-wing black, b=bottom wing orange



M J Thompson^{1,2} and C D Jiggins¹

Inversions block recombination in heterozygotes

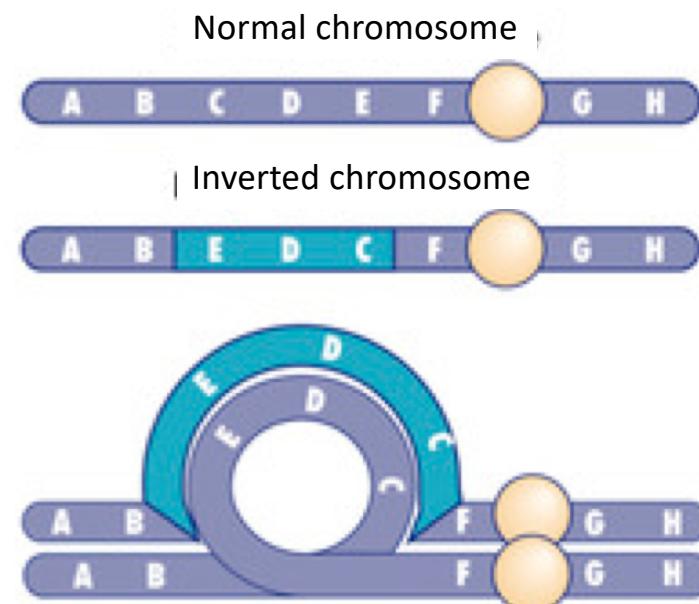
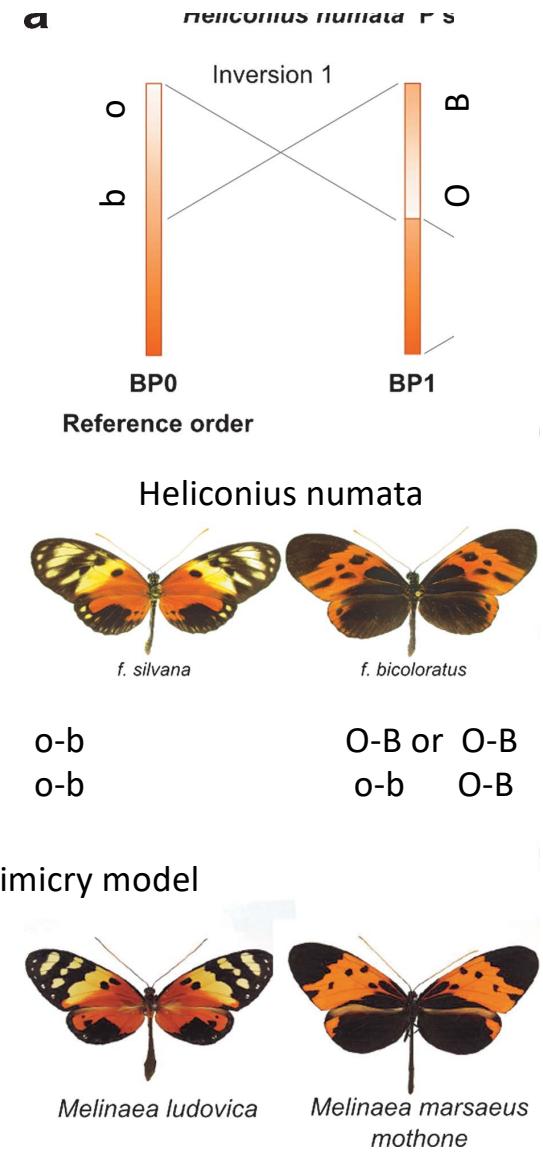


Figure 14.21 Principles of Genetics, 8/e
© 2008 John Wiley & Sons

Super genes

'coadapted combinations of several or many genes locked in inverted sections of chromosomes and therefore inherited as single units.'

(Dobzhansky, 1970).



Supergenes and their role in evolution

M J Thompson^{1,2} and C D Jiggins¹

Faeder-Independent inversion
4Mb

Structural genomic changes underlie alternative reproductive strategies in the ruff (*Philomachus pugnax*)

Sangeet Lamichhaney, Guangyi Fan, Fredrik Widemo, Ulrika Gunnarsson, Doreen Schwochow Thalmann, Marc P Hoeppner, Susanne Kerje, Ulla Gustafson, Chengcheng Shi, He Zhang, Wenbin Chen, Xinming Liang, Leihuan Huang, Jiahao Wang, Enjing Liang, Qiong Wu, Simon Ming-Yuen Lee, Xun Xu, Jacob Höglund, Xin Liu & Leif Andersson

A supergene determines highly divergent male reproductive morphs in the ruff

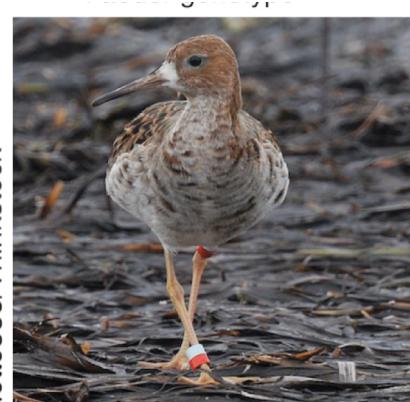
Clemens Küpper, Michael Stocks, Judith E Risse, Natalie dos Remedios, Lindsay L Farrell, Susan B McRae, Tawna C Morgan, Natalia Karlionova, Pavel Pinchuk, Yvonne I Verkuil, Alexander S Kitaysky, John C Wingfield, Theunis Piersma, Kai Zeng, Jon Slate, Mark Blaxter, David B Lank & Terry Burke



Fredrik Widemo



motto555/Thinkstock



Melissa Hafting

A

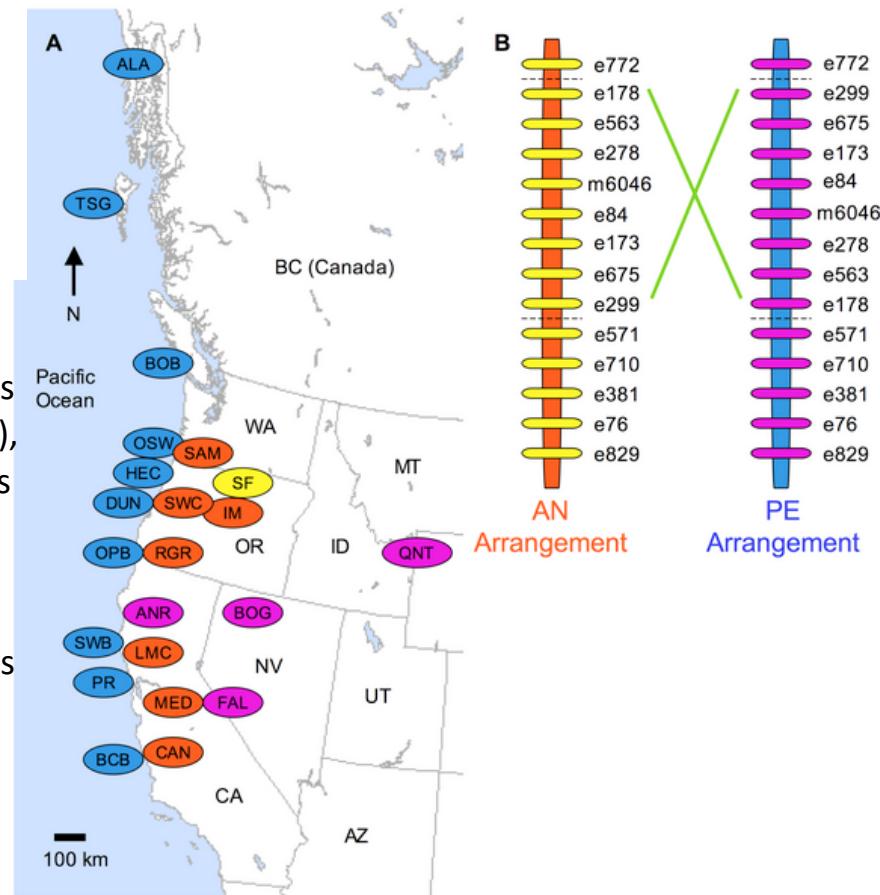


- coastal perennial and inland annual

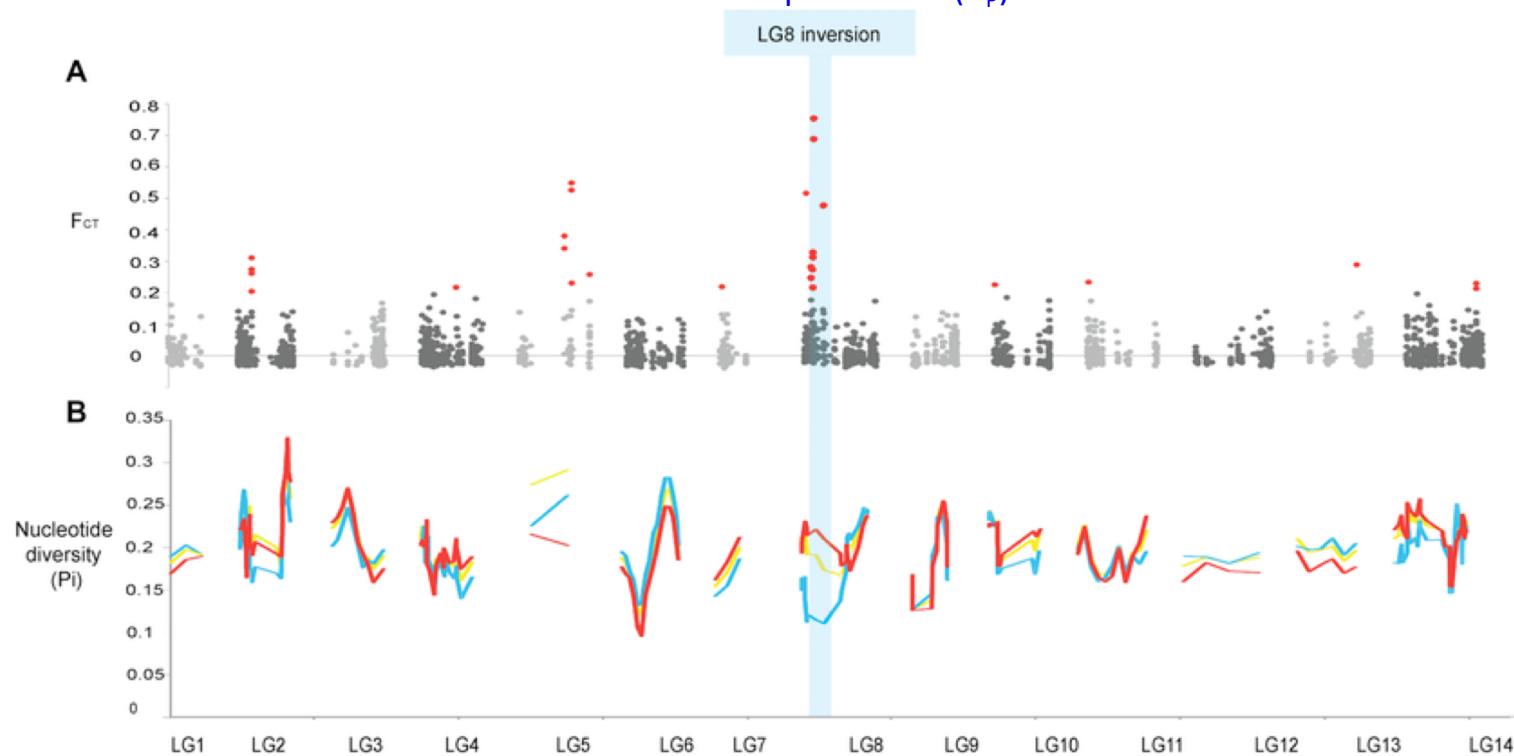
coastal perennials (blue), inland annuals (orange), and inland perennials (purple), as well as obligate self-fertilizing species *M. nasutus* (yellow)

Local adaptation mediated by inversions
Also seen in *Drosophila* & Mosquitos
And likely many other species

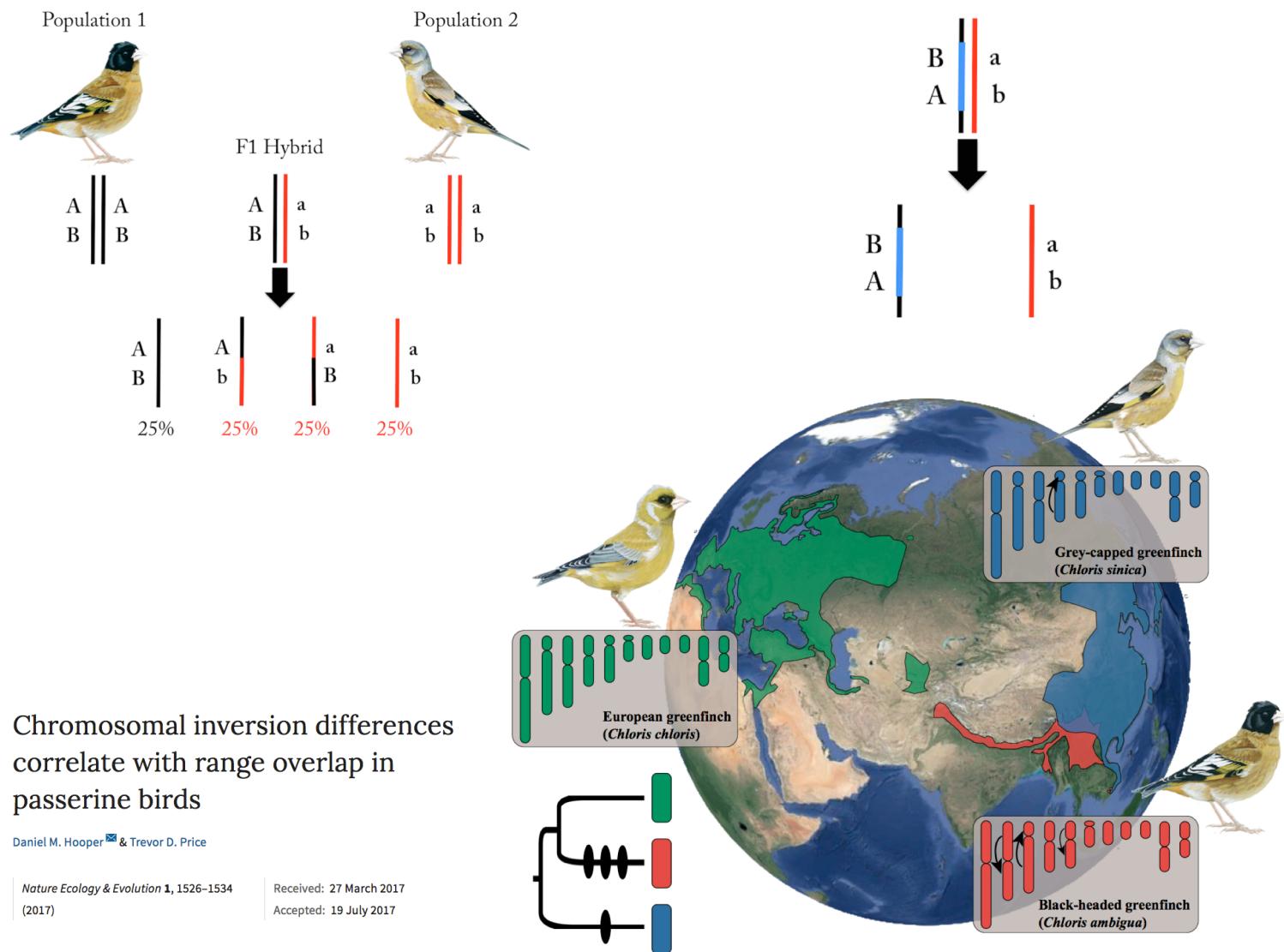
A Widespread Chromosomal Inversion Polymorphism Contributes to a Major Life-History Transition, Local Adaptation, and Reproductive Isolation. 2010 Lowry & Willis



Pairwise nucleotide divergence between ecotypes (D_{XY}) is shown in yellow, nucleotide diversity in annuals (π_A), perennials (π_p) in blue.

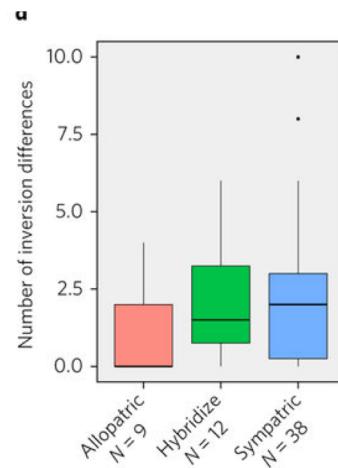
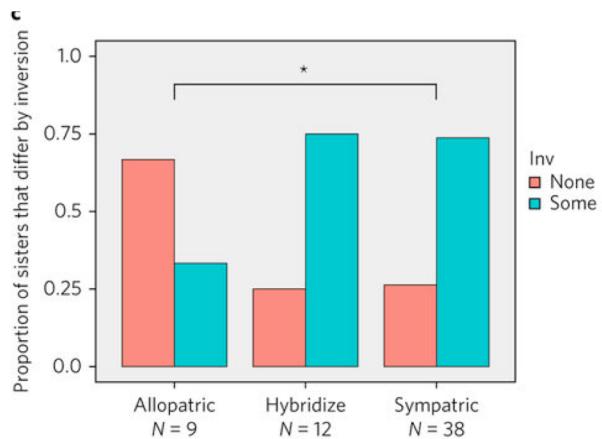
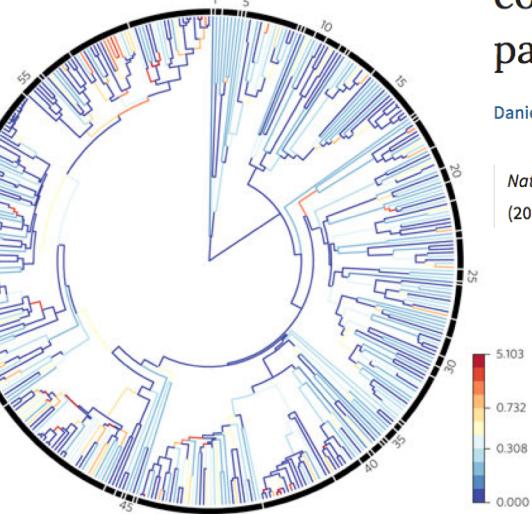


Twyford & Friedman. Adaptive divergence in the monkey flower *Mimulus guttatus* is maintained by a chromosomal inversion



Pericentric inversion fixation rate variation on the autosomes and Z chromosome combined across the Passeriformes.

Passerine families	
1 Eurylamidae (1, 1)	31 Pellorniidae (3, 3)
2 Furnariidae (2, 2)	32 Leiothrichidae (14, 28)
3 Thamnophilidae (4, 9)	33 Regulidae (1, 7)
4 Cotingidae (1, 3)	34 Bombycillidae (3, 0)
5 Tityridae (1, 2)	35 Sittidae (3, 6)
6 Tyrannidae (14, 34)	36 Certhiidae (1, 2)
7 Aegithinidae (1, 0)	37 Polioptilidae (1, 2)
8 Tephrodornithidae (1, 5)	38 Troglodytidae (3, 5)
9 Campephagidae (3, 9)	39 Cinclidae (1, 1)
10 Oriolidae (3, 2)	40 Mimidae (3, 6)
11 Vireonidae (4, 2)	41 Sturnidae (8, 7)
12 Dicruridae (2, 0)	42 Turdidae (20, 28)
13 Monarchidae (1, 1)	43 Muscicapidae (35, 77)
14 Laniidae (8, 13)	44 Nectariniidae (1, 2)
15 Corvidae (15, 21)	45 Chloropseidae (2, 2)
16 Picathartidae (1, 4)	46 Peucedramidae (1, 4)
17 Remizidae (1, 2)	47 Prunellidae (2, 0)
18 Paridae (8, 14)	48 Ploceidae (3, 0)
19 Alaudidae (6, 9)	49 Estrildidae (34, 83)
20 Locustellidae (4, 8)	50 Passeridae (7, 19)
21 Acrocephalidae (5, 10)	51 Motacillidae (8, 15)
22 Hirundinidae (8, 13)	52 Fringillidae (21, 40)
23 Cisticolidae (2, 5)	53 Cardinalidae (7, 5)
24 Pycnonotidae (8, 11)	54 Thraupidae (45, 52)
25 Aegithalidae (3, 8)	55 Parulidae (6, 2)
26 Cettidae (1, 1)	56 Icteridae (1, 3)
27 Phylloscopidae (9, 21)	57 Icteriidae (9, 8)
28 Sylviidae (5, 10)	58 Emberizidae (17, 55)
29 Zosteropidae (5, 3)	59 Passerellidae (22, 38)
30 Timaliidae (3, 2)	



Chromosomal inversion differences correlate with range overlap in passerine birds

Daniel M. Hooper & Trevor D. Price

Nature Ecology & Evolution 1, 1526–1534

(2017)

Received: 27 March 2017

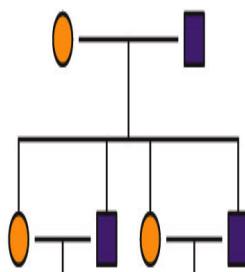
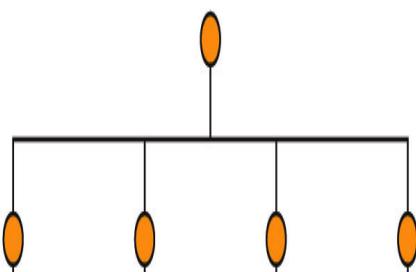
Accepted: 19 July 2017

The cost of sex.

Why risk breaking it up a winning genotype.

Finding and attracting a mate are costly and may be impossible, and mating is dangerous

The two fold cost of sex



Sexual organisms only contribute $\frac{1}{2}$ of their genome to their offspring. While asexual organisms contribute their entire genome. This is sometimes called the cost of males

Despite this sexual reproduction persists.

- Why have sex?

Vast majority of eukaryotic organisms reproduce sexually

Many species are not obligate sexuals and can reproduce clonally (i.e. asexually)

e.g. Vegetative growth in plants.

However, they will only do so for a few generations

Vertebrate asexual species can evolve



Unisexual Cnemidophorus



Unisexual *P. formosa* (left) sexually
parasitizes the sexual *P. latipinna* (right)

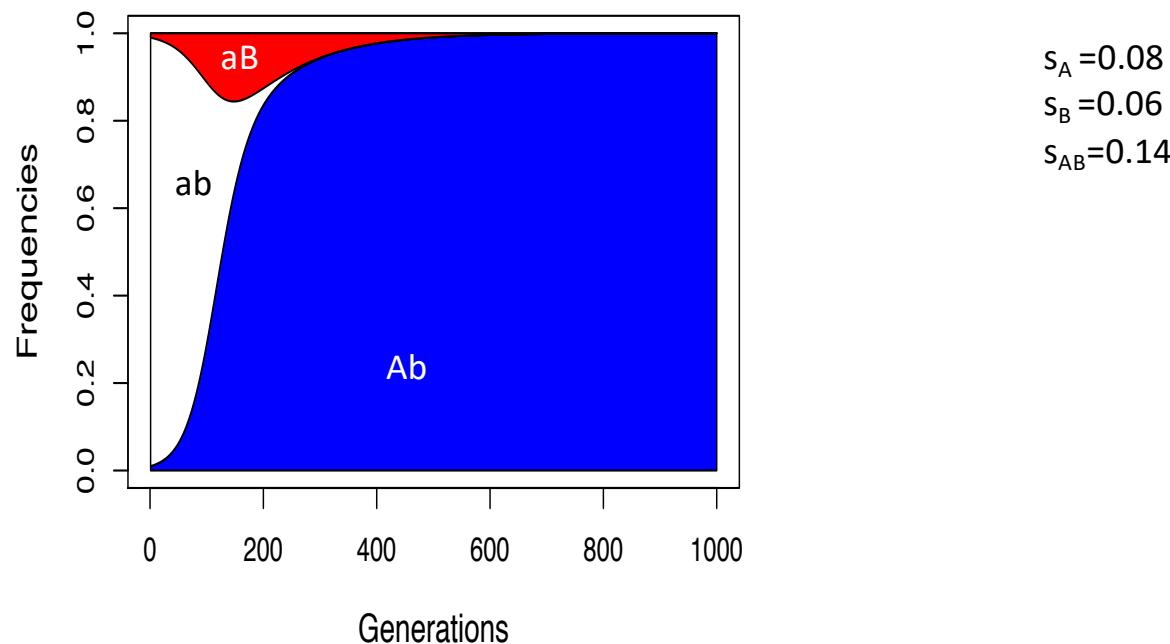
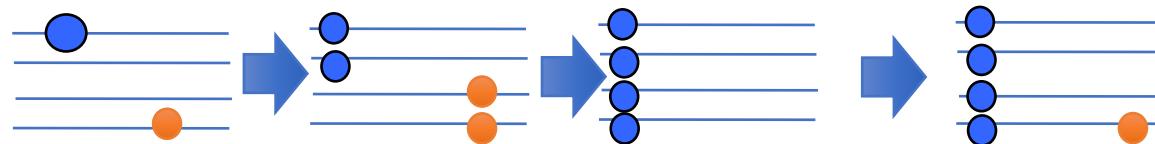
Despite this sexual reproduction persists.

Hypotheses for the evolutionary advantage and maintenance of sex

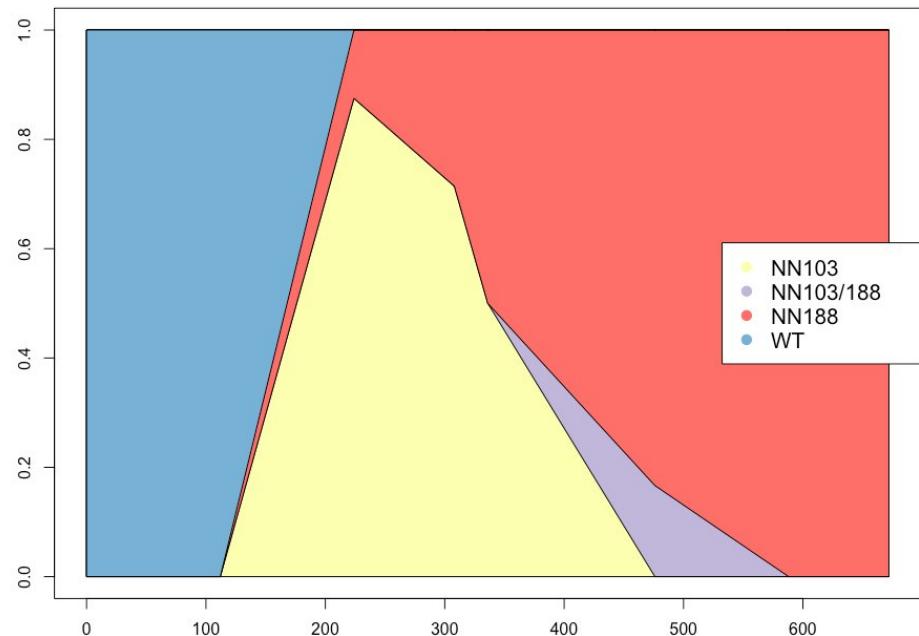
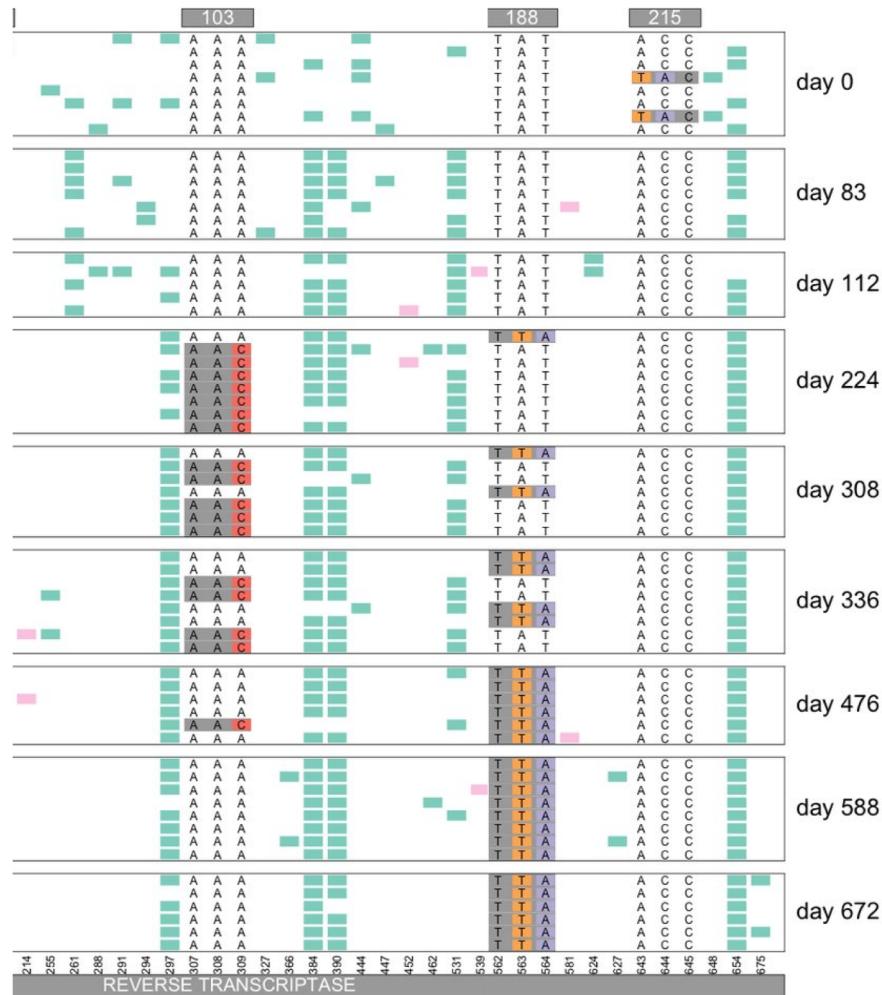
- Asexual species accumulate deleterious mutations
 - Hitchhiking of deleterious mutations
 - Due to Muller's Ratchet
- Asexual species adapt slower
 - forced to fix advantageous mutations sequentially (Clonal interference)
 - Creation of novel haplotypes in asexuals is mutation limited. Hard to keep pace with rapidly evolving pathogens (Red queen hypothesis)

Clonal interference hypothesis

Selected alleles must fix sequentially in absence of sex



Patient 084



Evidence of Clonal Interference

Pervasive genetic hitchhiking and clonal interference in forty evolving yeast populations

Gregory I. Lang^{1*†}, Daniel P. Rice^{2*}, Mark J. Hickman³, Erica Sodergren⁴, George M. Weinstock⁴, David Botstein¹ & Michael M. Desai²

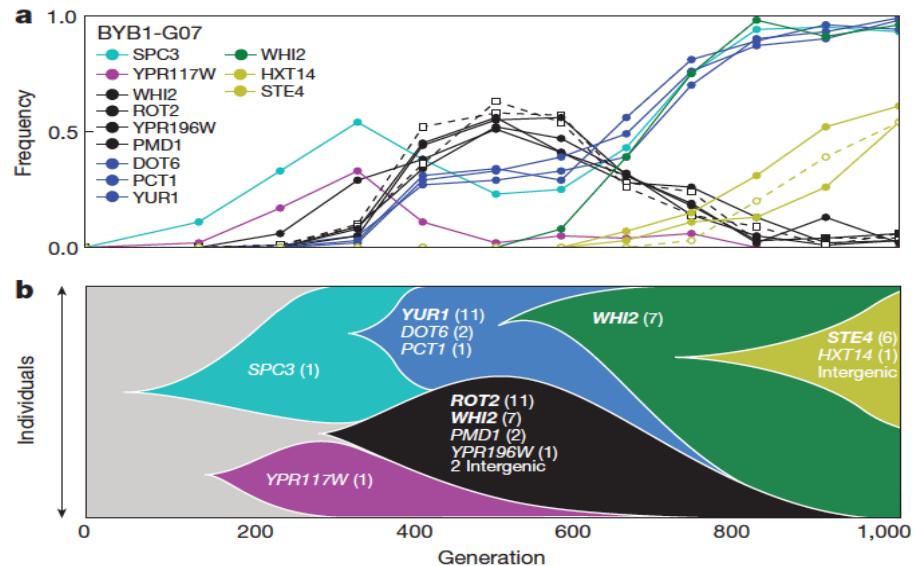
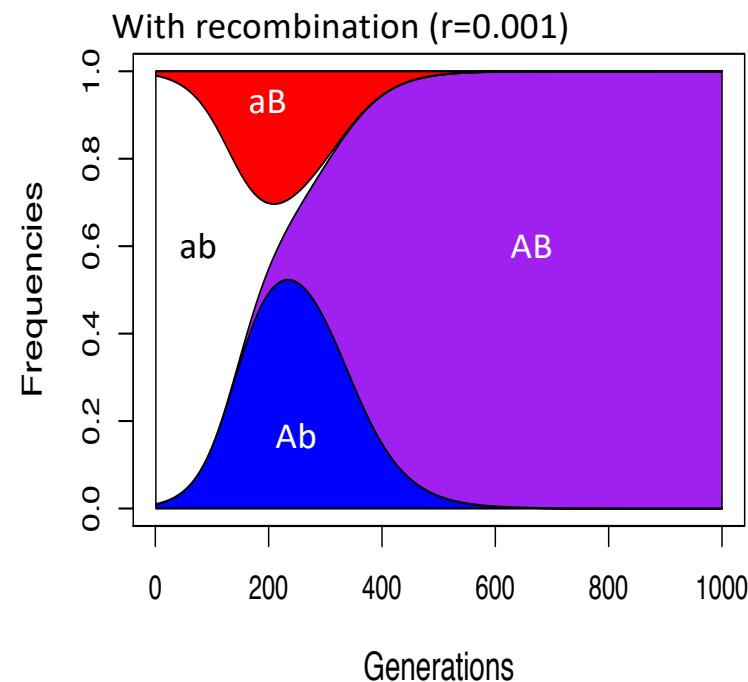
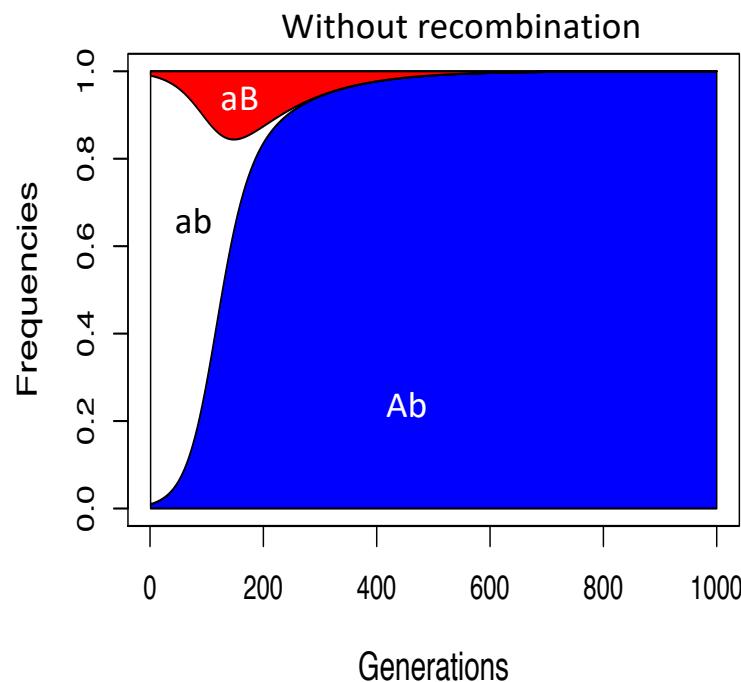
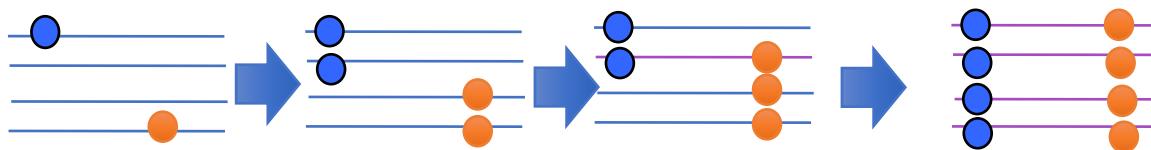


Figure 3 | The dynamics of sequence evolution in BYB1-G07. **a**, The trajectories of the 15 mutations that attain a frequency of at least 30%, hierarchically clustered into several distinct mutation ‘cohorts’, each of which is represented by a different colour (Methods). **b**, Muller diagram showing the

Clonal interference also plays a key role in thinking about evolution of drug resistance in pathogens.

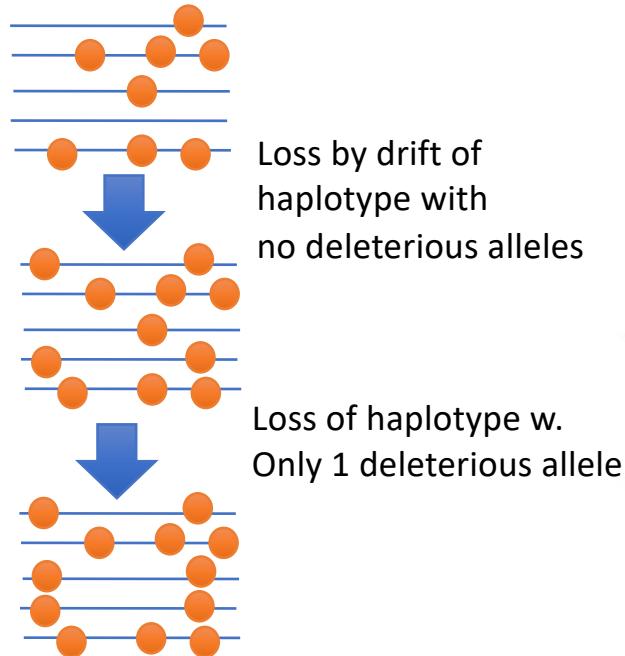
Clonal interference hypothesis

Selected alleles can fix simultaneously in presence of sex.

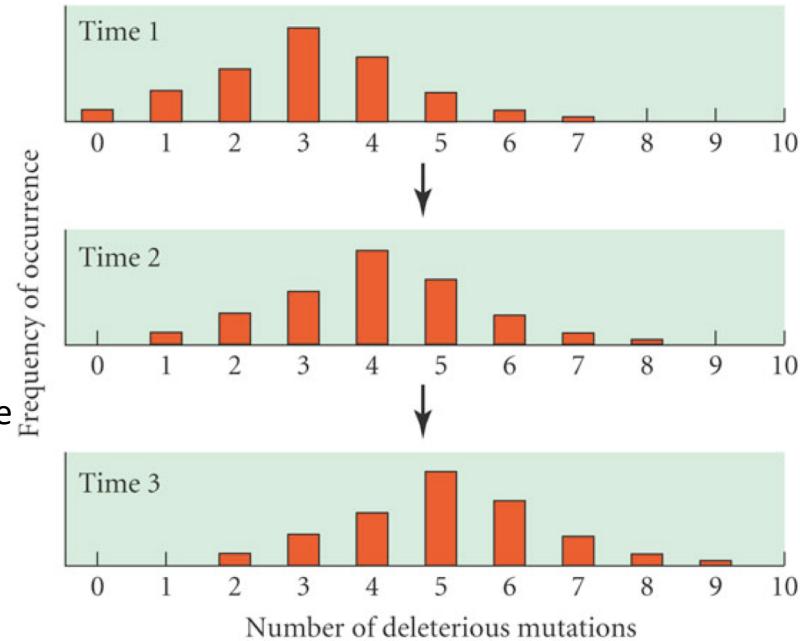
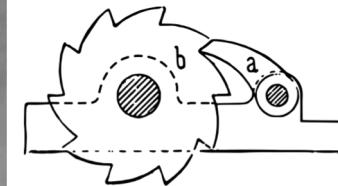


Muller's Ratchet in asexuals

● =Deleterious allele

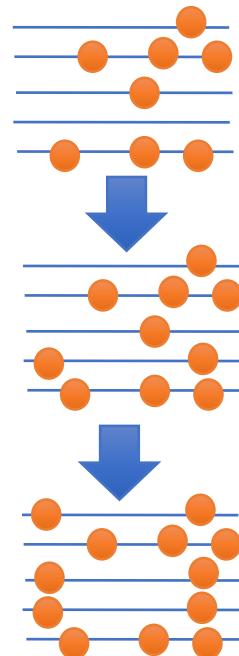


Hermann J. Muller

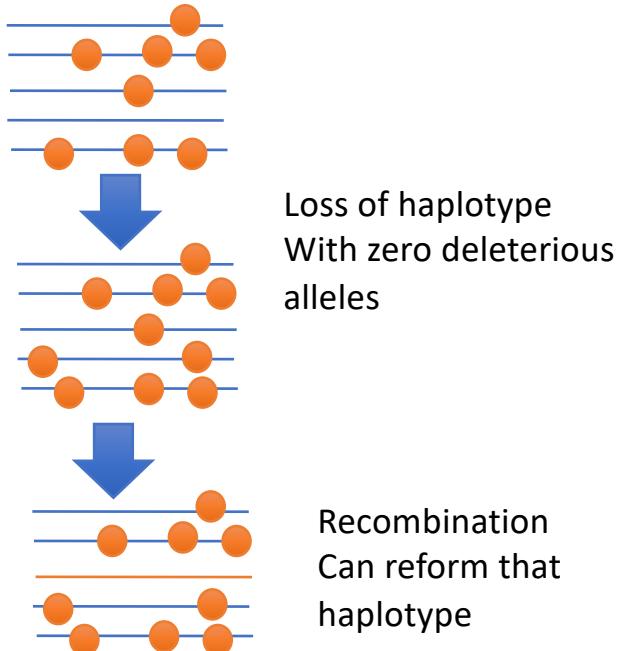


Muller's Ratchet

Ratchet in asexuals: Progressive loss by drift of haplotype with lowest number deleterious alleles. Lowers fitness of population.

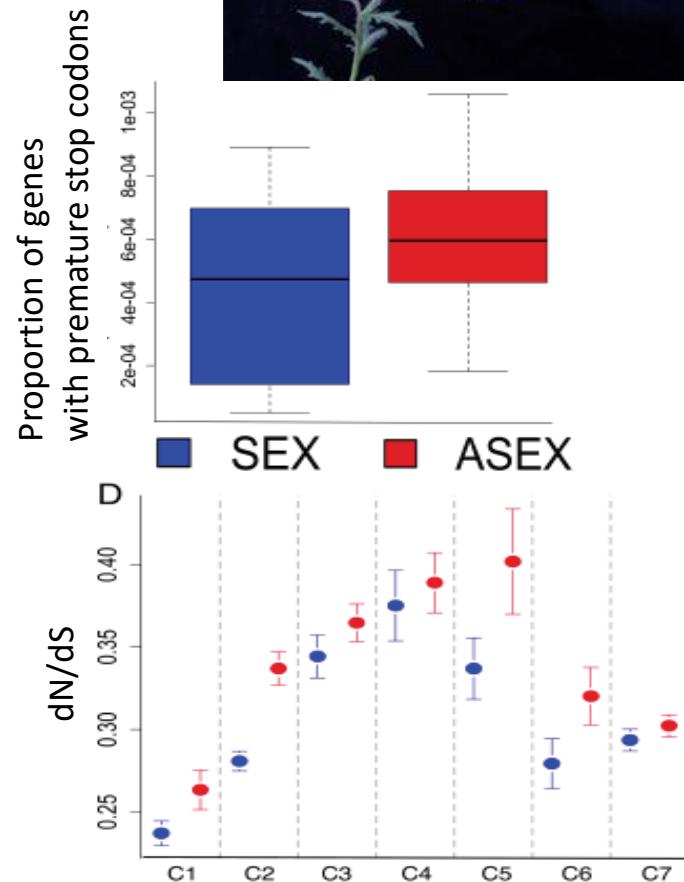
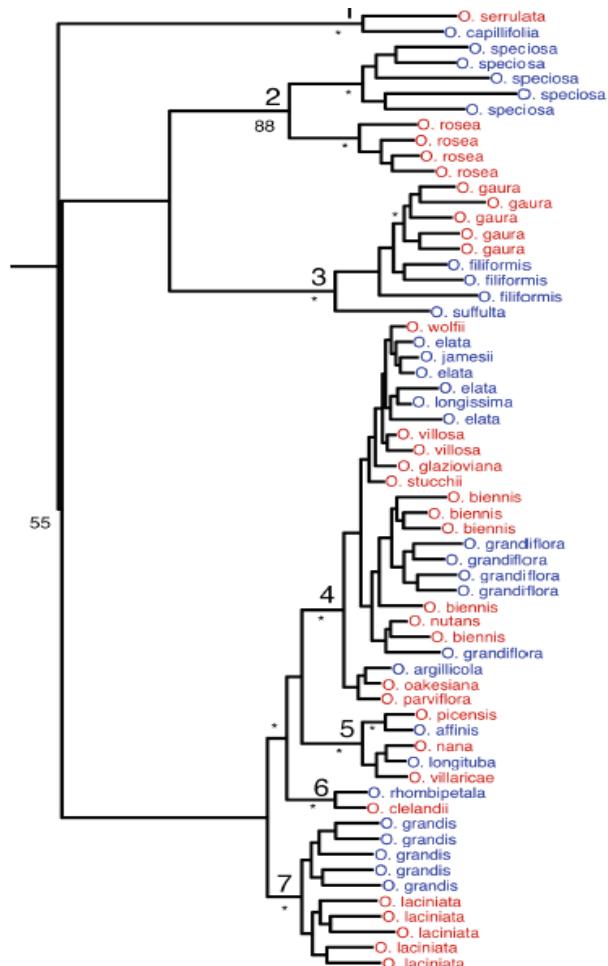


Sexual organisms avoid the effects Of Muller's ratchet.



Recurrent loss of sex is associated with accumulation of deleterious mutations in *Oenothera*

Jesse D. Hollister^{1,2,*}, Stephan Greiner³, Wei Wang¹, Jun Wang⁴, Yong Zhang⁴, Gane Ka-Shu Wong^{4,5,*}, Stephen I. Wright^{1,6}, Marc T. J. Johnson^{2,6}



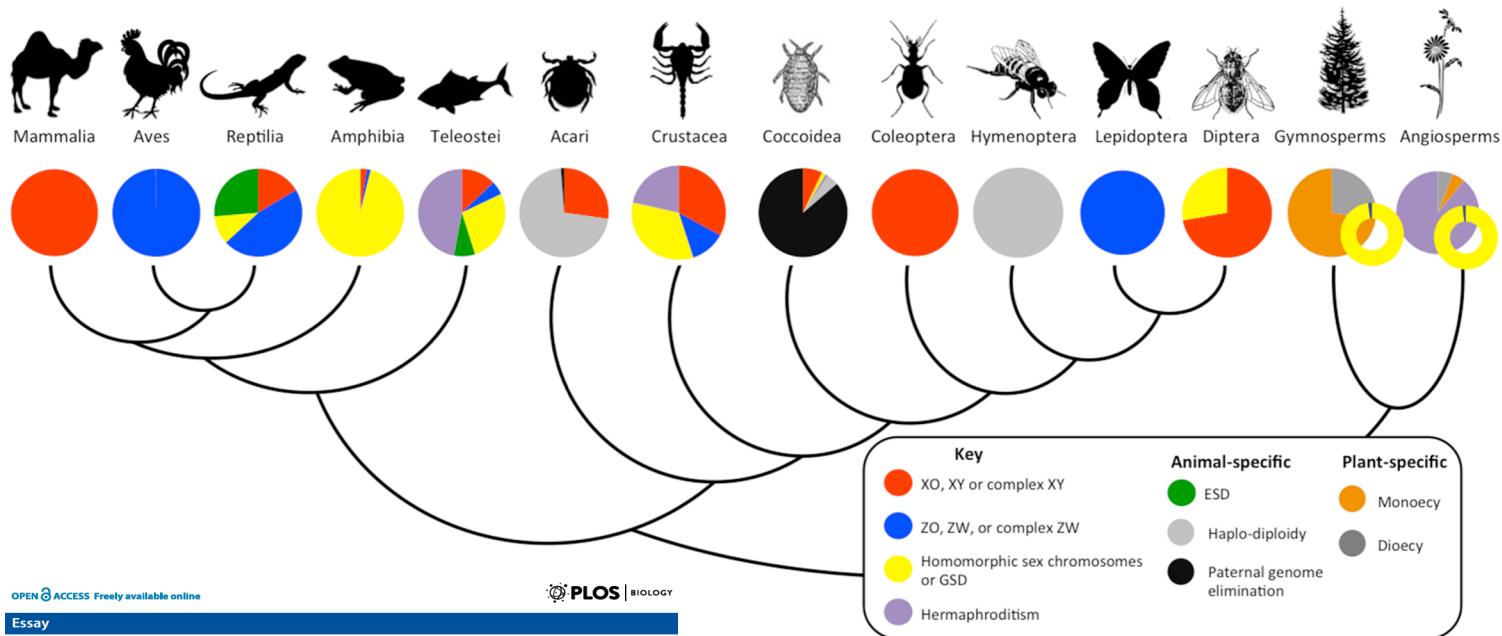
A species having sex is not the same as a species having different sexes

- The fundamental difference between male and female function is Anisogamy (Gametes differ in size)
- Male sexual function:
 - Small mobile gametes
- Female sexual function:
 - Larger less mobile gametes
 - Maternal provisions



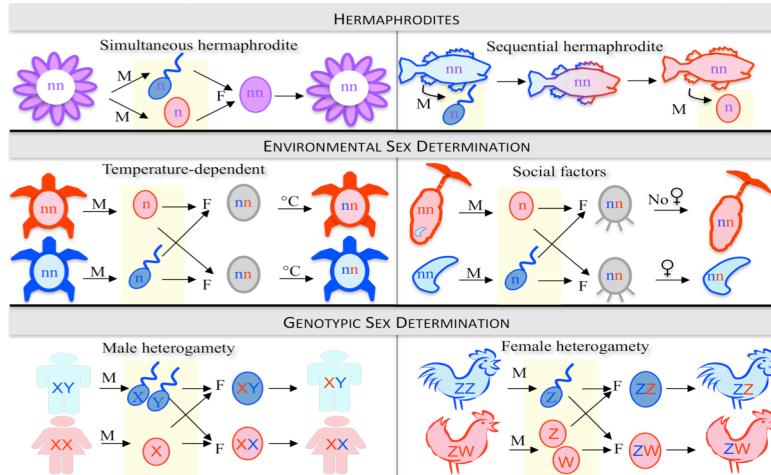
Zimmer book

Male and female functions do not necessarily mean sexes are separate individuals
But separate sexes have arisen many times
Perhaps because of:
Selection for specialization
or inbreeding avoidance.



Sex Determination: Why So Many Ways of Doing It?

Doris Bachtrog^{1*}, Judith E. Mank², Catherine L. Peichel³, Mark Kirkpatrick⁴, Sarah P. Otto⁵, Tia-Lynn Ashman⁶, Matthew W. Hahn⁷, Jun Kitano⁸, Itay Mayrose⁹, Ray Ming¹⁰, Nicolas Perrin¹¹, Laura Ross¹², Nicole Valenzuela¹³, Jana C. Vamosi¹⁴, The Tree of Sex Consortium¹

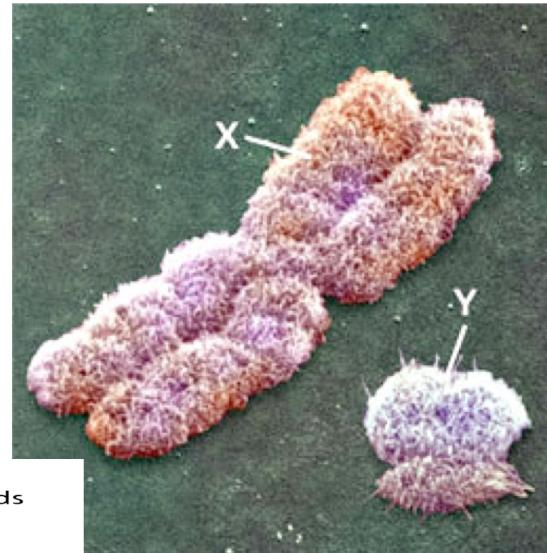
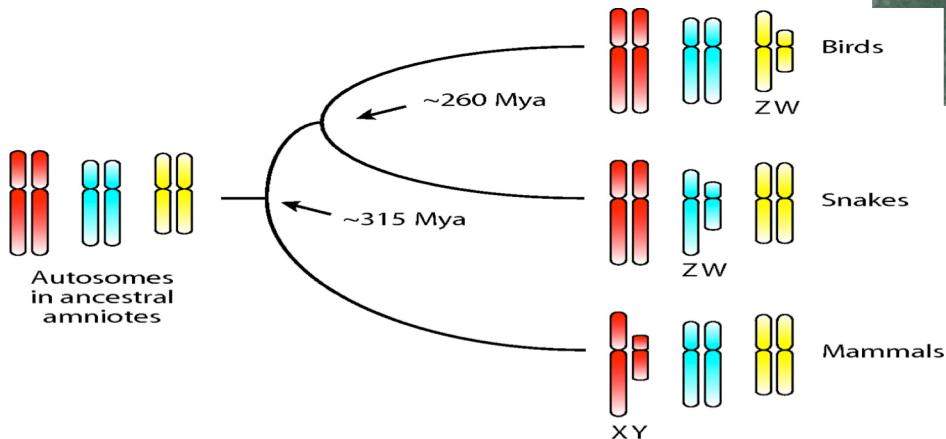


Evolution of sex chromosomes

In species with genetic sex determination
the chromosomes containing the sex determining factors
are often heteromorphic:
One is much reduced in
function and size.
And does not recombine.

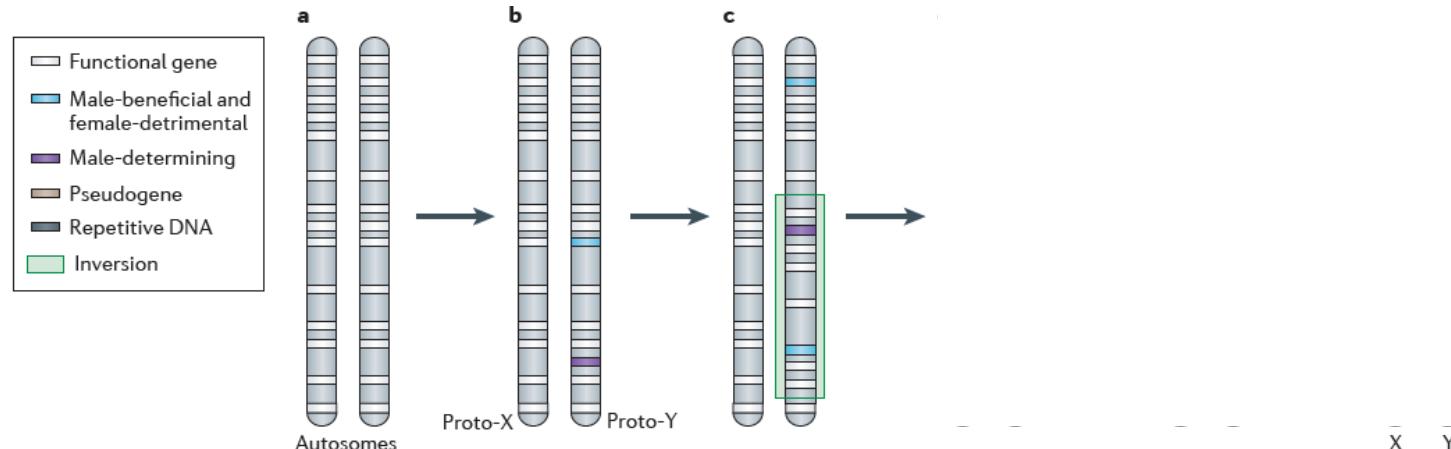
Human Y: 60 Mbp ~80 genes

Human X: 153 Mbp ~2000 genes



Heteromorphic sex chromosomes have evolved independently many times

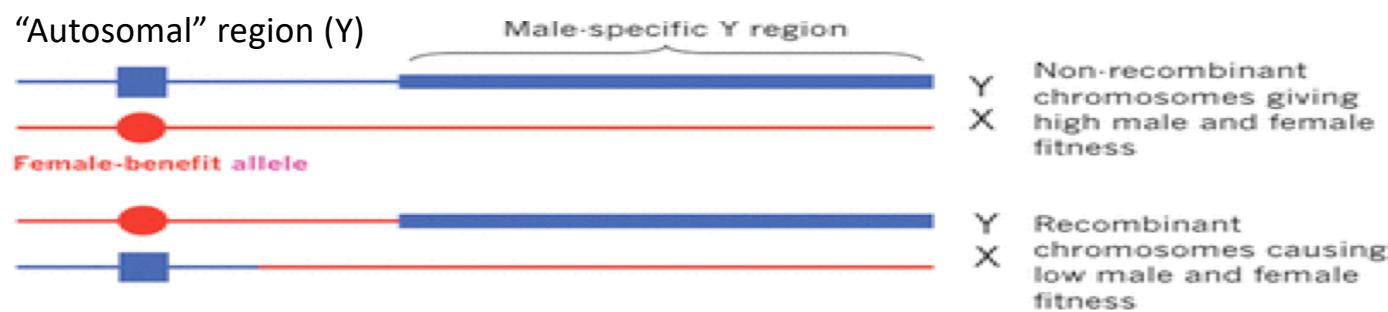
The evolution of sex chromosomes

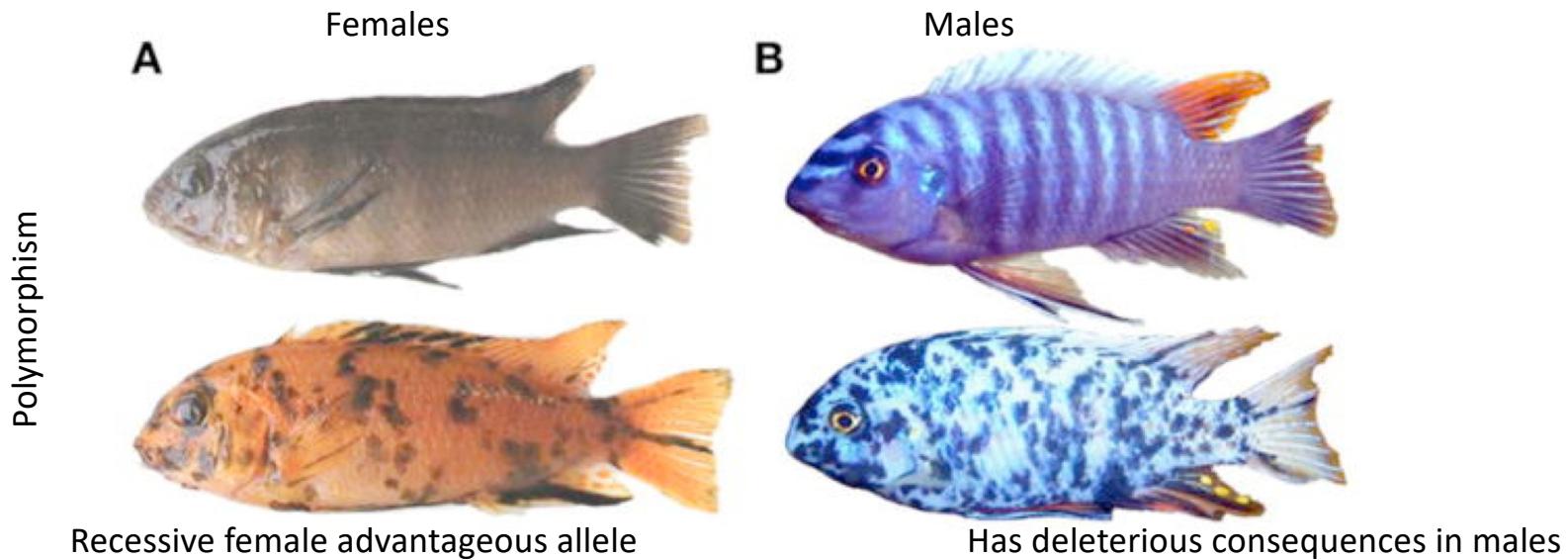


Sex determining allele arises (e.g. dominant male determining allele)

Recombination between sexually antagonistic allele and male-determining allele have lowers fitness.

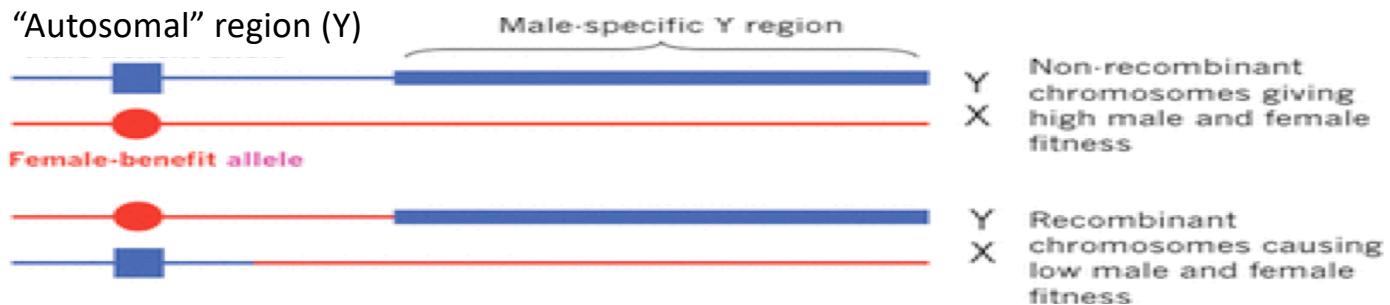
Recombination between these loci suppressed by inversion



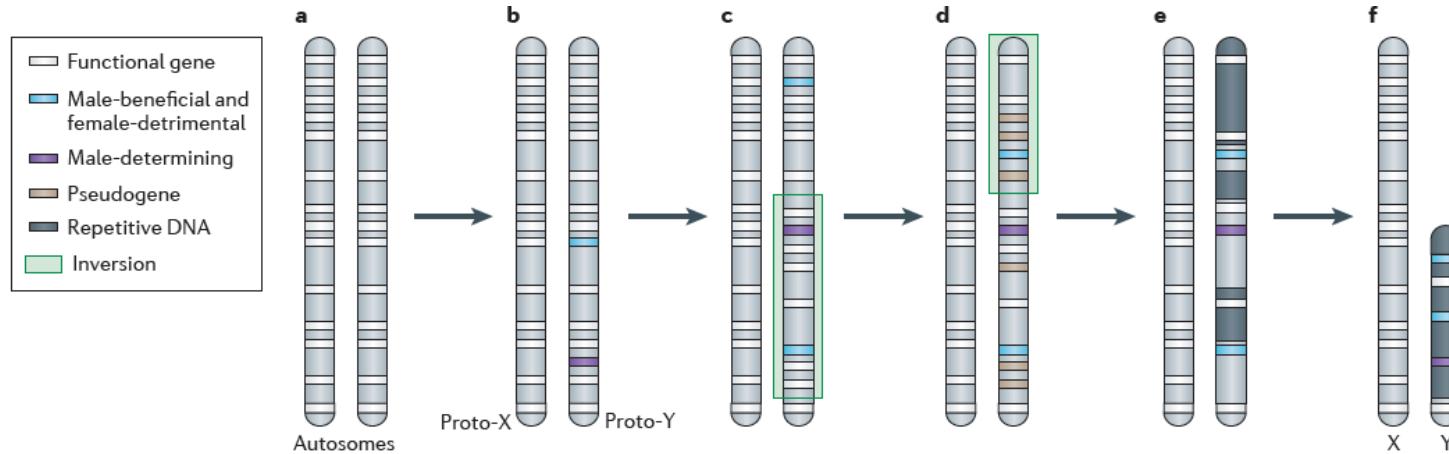


Sexual Conflict Resolved by Invasion of a Novel Sex Determiner in Lake Malawi Cichlid Fishes

Reade B. Roberts, Jennifer R. Ser, Thomas D. Kocher*



The evolution of sex chromosomes



Sex determining allele arises (e.g. dominant male determining allele)

Recombination between sexually antagonistic allele and male-determining allele have lowers fitness.

Recombination between these loci suppressed by inversion

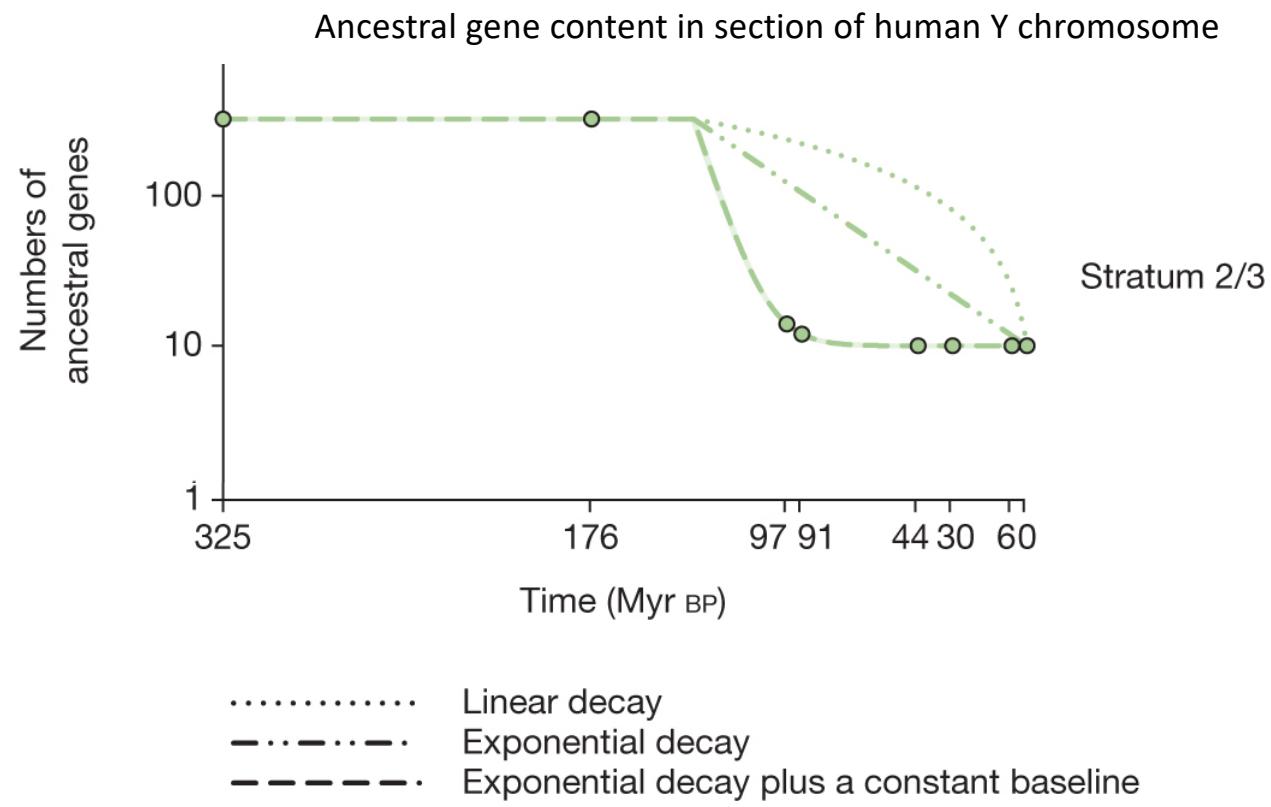
Shutting off recombination now means that this section of Proto-Y no long recombines (note that Proto-X can recombine with itself in females)

This in turn leads to degeneration of Y sex chromosome genes due to:

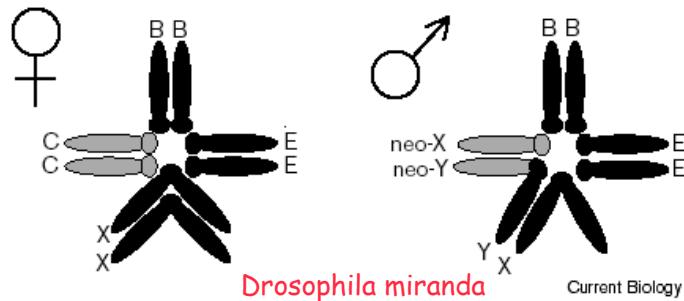
Muller's Ratchet

And the hitchhiking of deleterious alleles.

Accumulation of repeats and transposable elements.



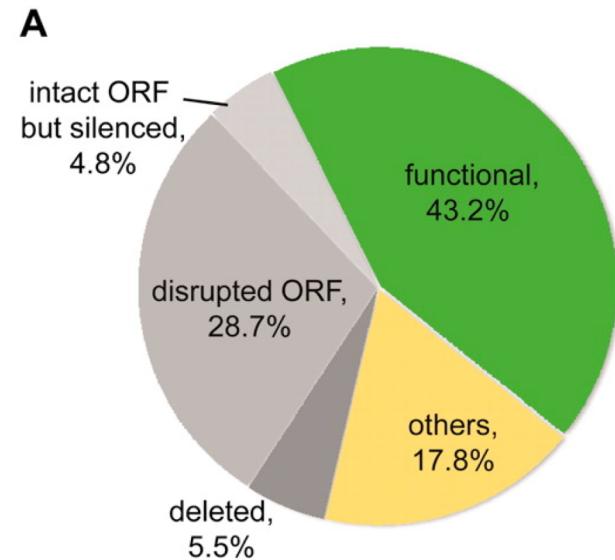
Bellot et al 2015, Nature



A neo-Y chromosome region was formed in *Drosophila miranda* 1.25 Myrs ago and has rapidly decayed

Majority of genes (open reading frames, ORFs)
In neo-Y region have become non-functional

degeneration of Y sex chromosome genes due to:
Muller's Ratchet
And the hitchhiking of deleterious alleles.
Accumulation of repeats and transposable elements.



The evolution of sex chromosomes

