

# Speciation and hybridisation

## Part 1: The quest for Isla de Muerta

Simon Martin

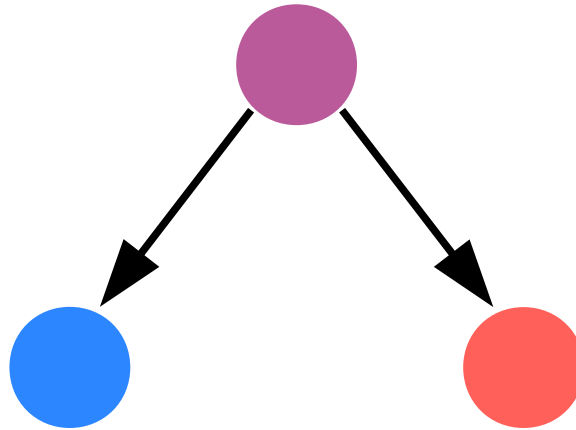
Institute of Evolutionary Biology  
University of Edinburgh

January 2020

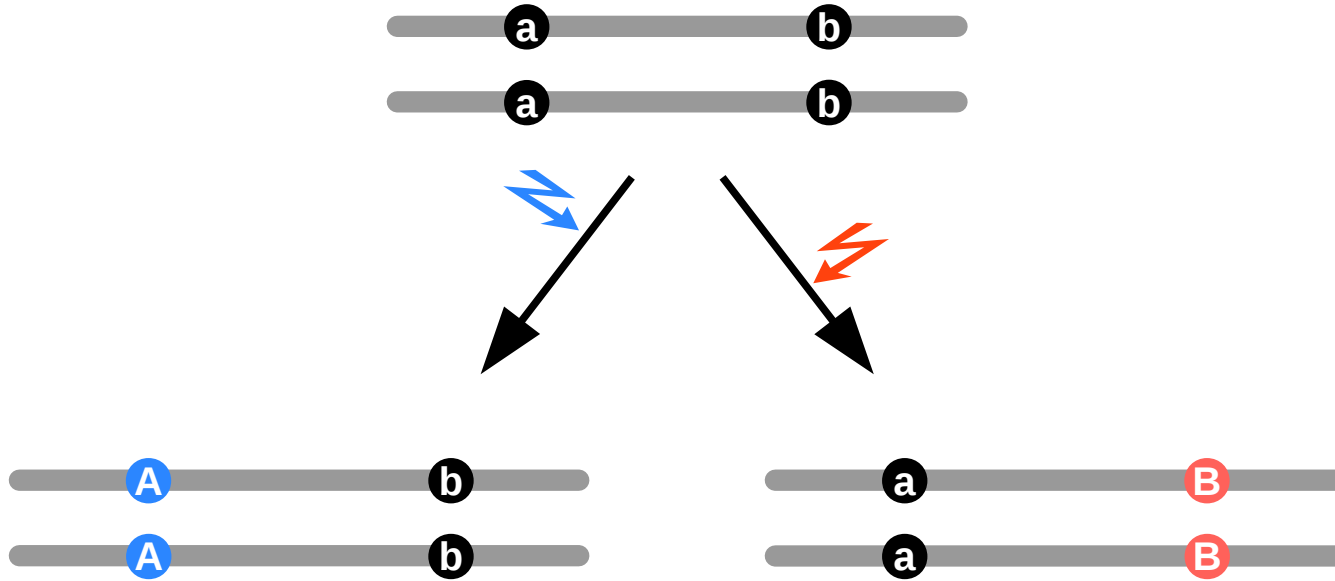
Using genomics to study reproductive isolation

**pattern** vs **process**

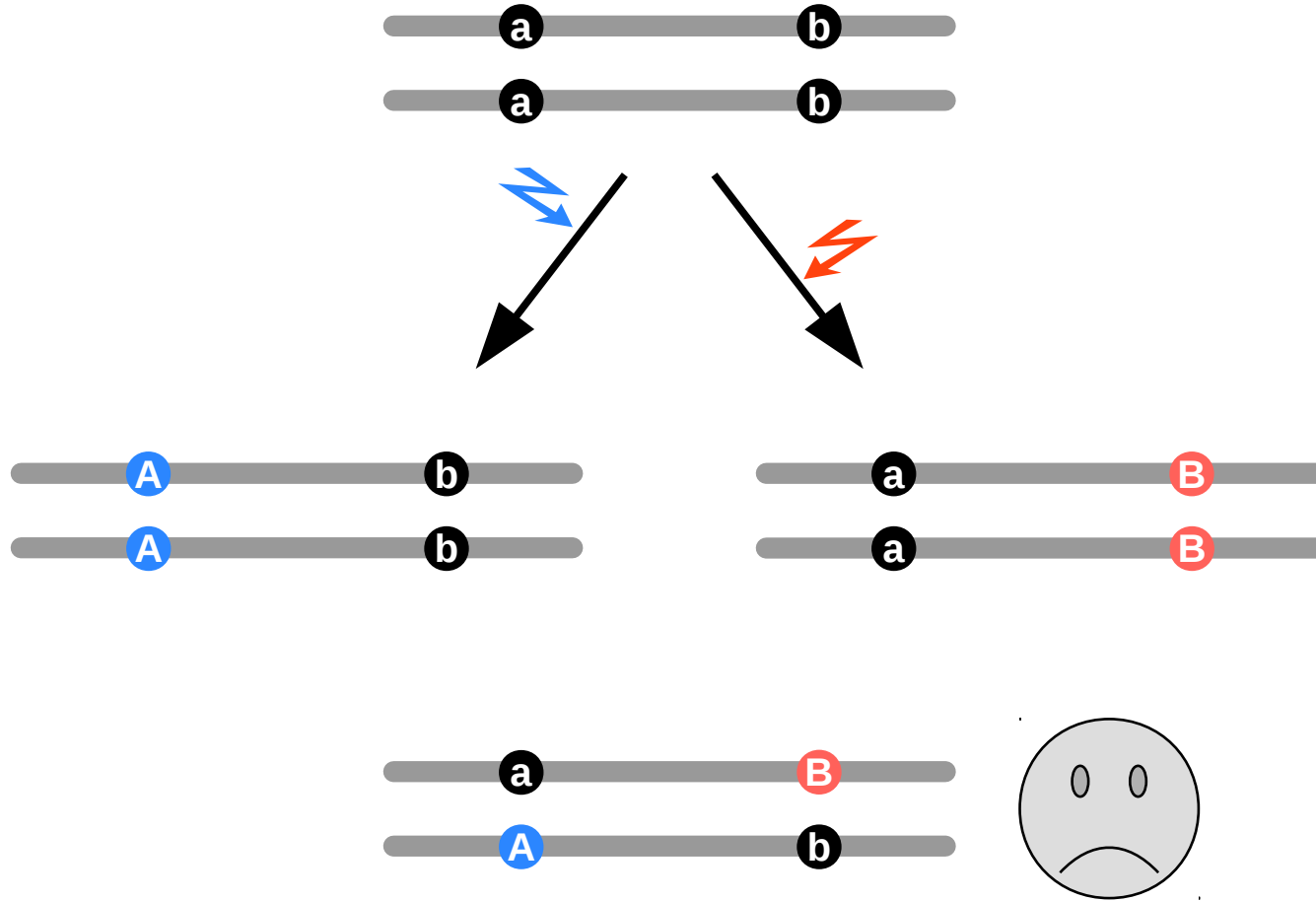
Some models of speciation  
through the evolution of reproductive isolation



“BDMIs”



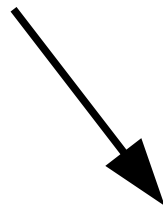
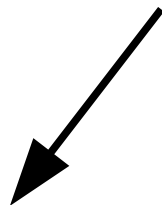
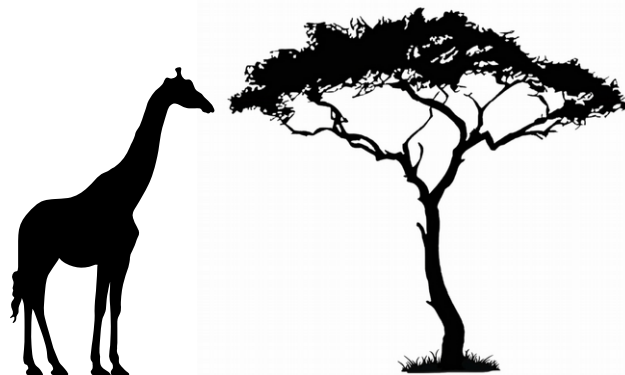
“BDMIs”



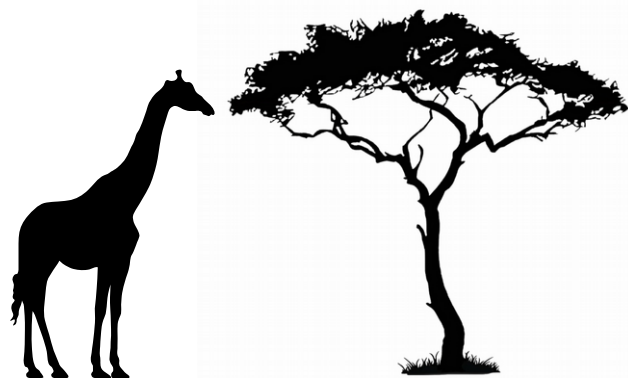
Bateson 1909, Dobzhansky 1937, Muller 1939, Orr 1996

# Indirect interaction models

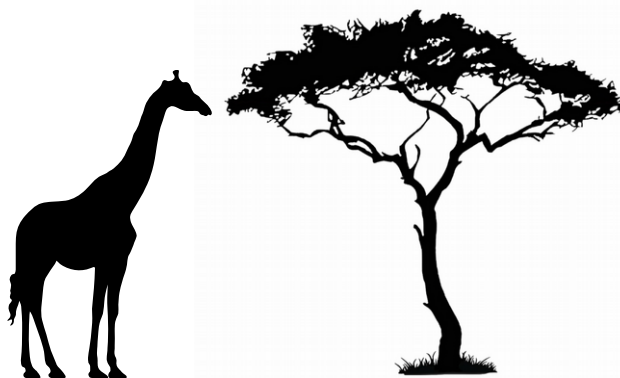
**a b c d e f g h i j ...**



+5 +15 -30 +10  
**A B c D e f G h i j ...**

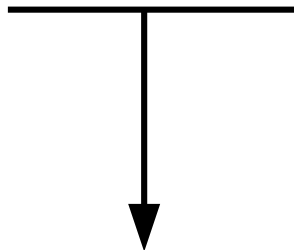


-20 +5 +15  
**a b C d e F g h I j ...**



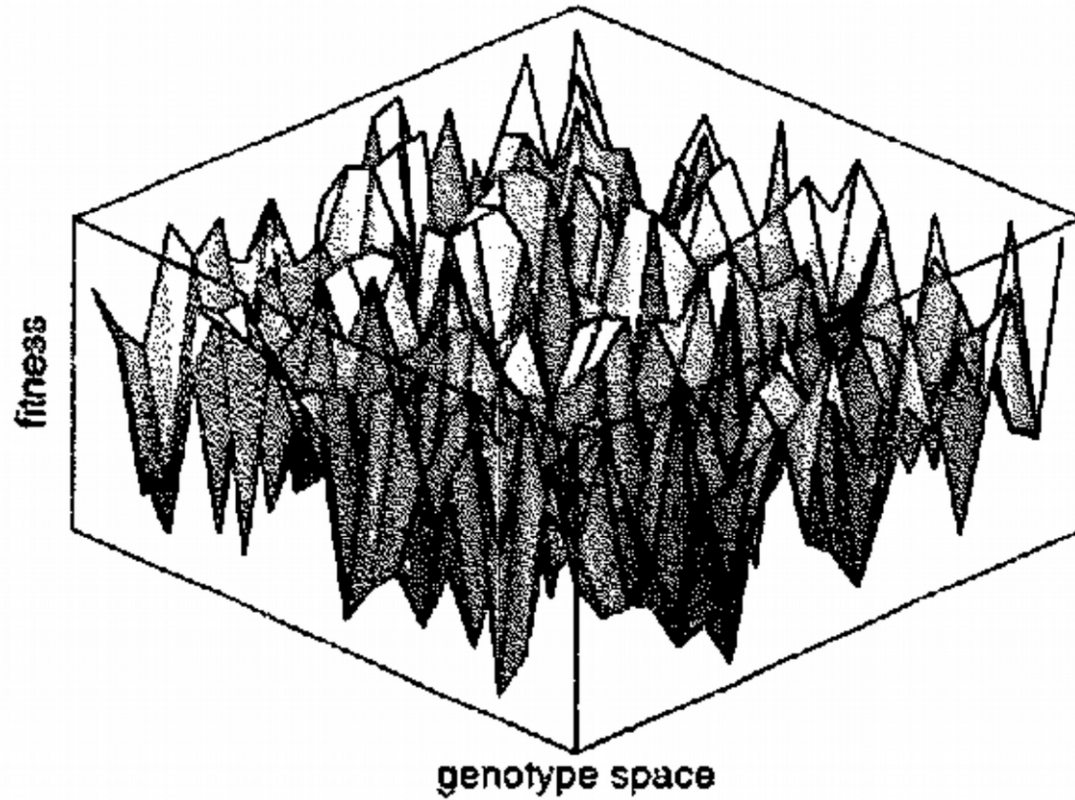
A black silhouette of a giraffe stands on the left, facing right. To its right is a black silhouette of an acacia tree with a thick, curved trunk and a dense, rounded canopy. The entire scene is set against a plain white background.

A black silhouette of a giraffe standing on the left, facing right, and a large, spreading acacia tree on the right. The giraffe's head is positioned near the lower branches of the tree. The entire scene is set against a plain white background.



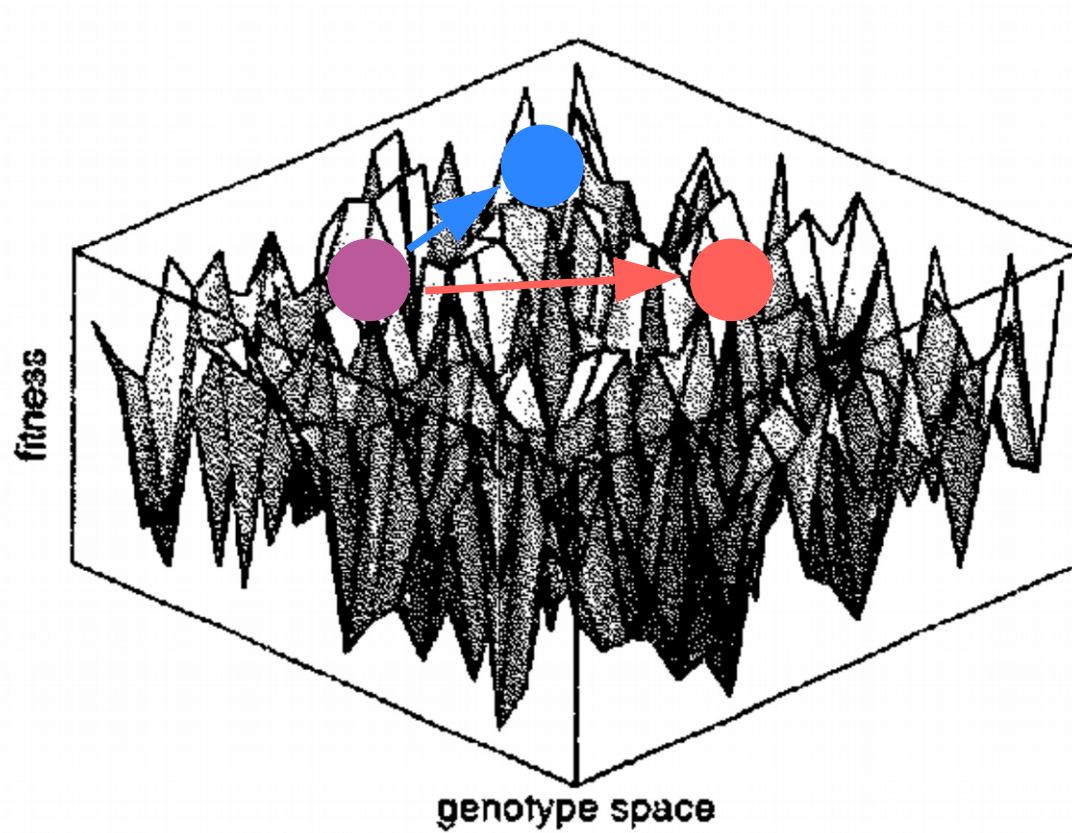
A black silhouette of a giraffe stands on the left, facing right. To its right is a black silhouette of an acacia tree with a thick, curved trunk and a wide, flat-topped canopy. The entire scene is set against a plain white background.

# The fitness landscape



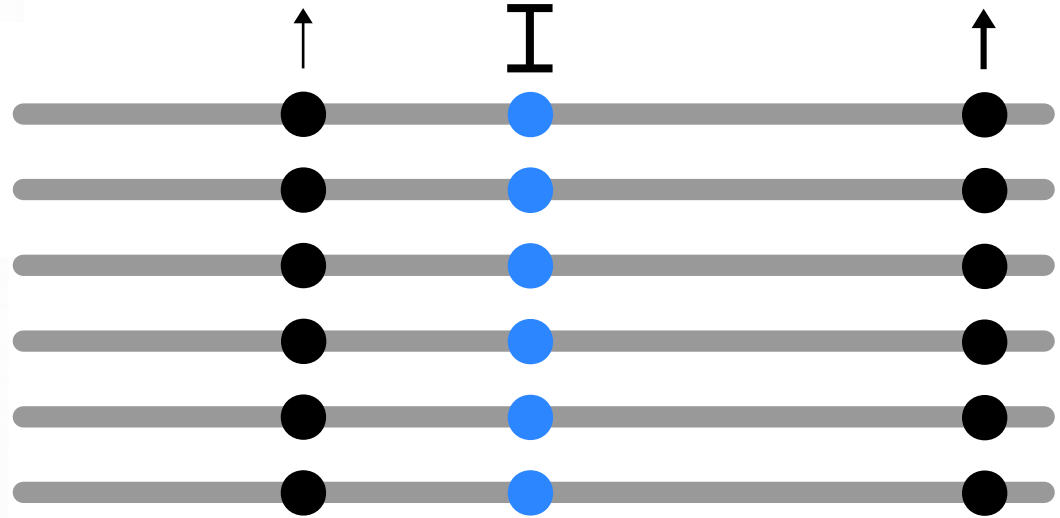
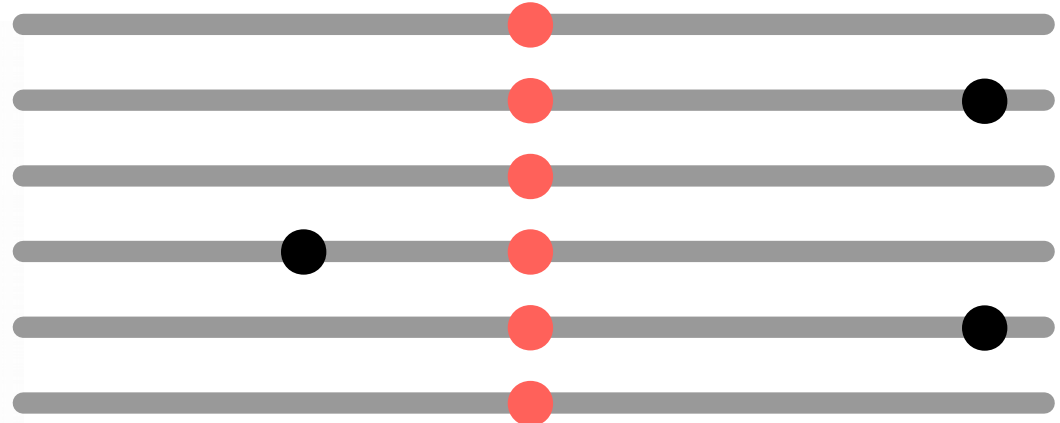
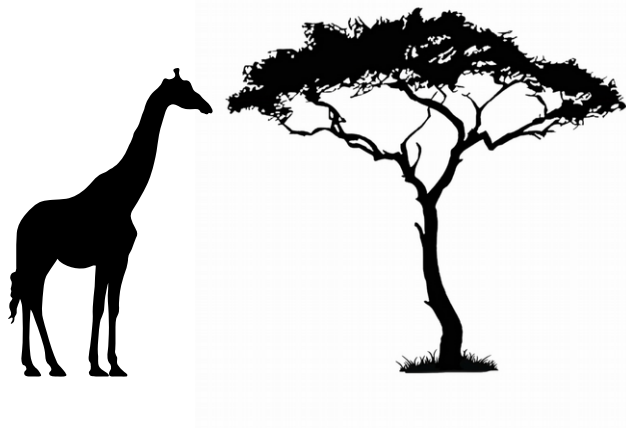
Gavrilets 1997, Wright 1935, Barton 1989, Fierst and Hansen 2010

Drift on the fitness landscape can lead to reproductive incompatibility

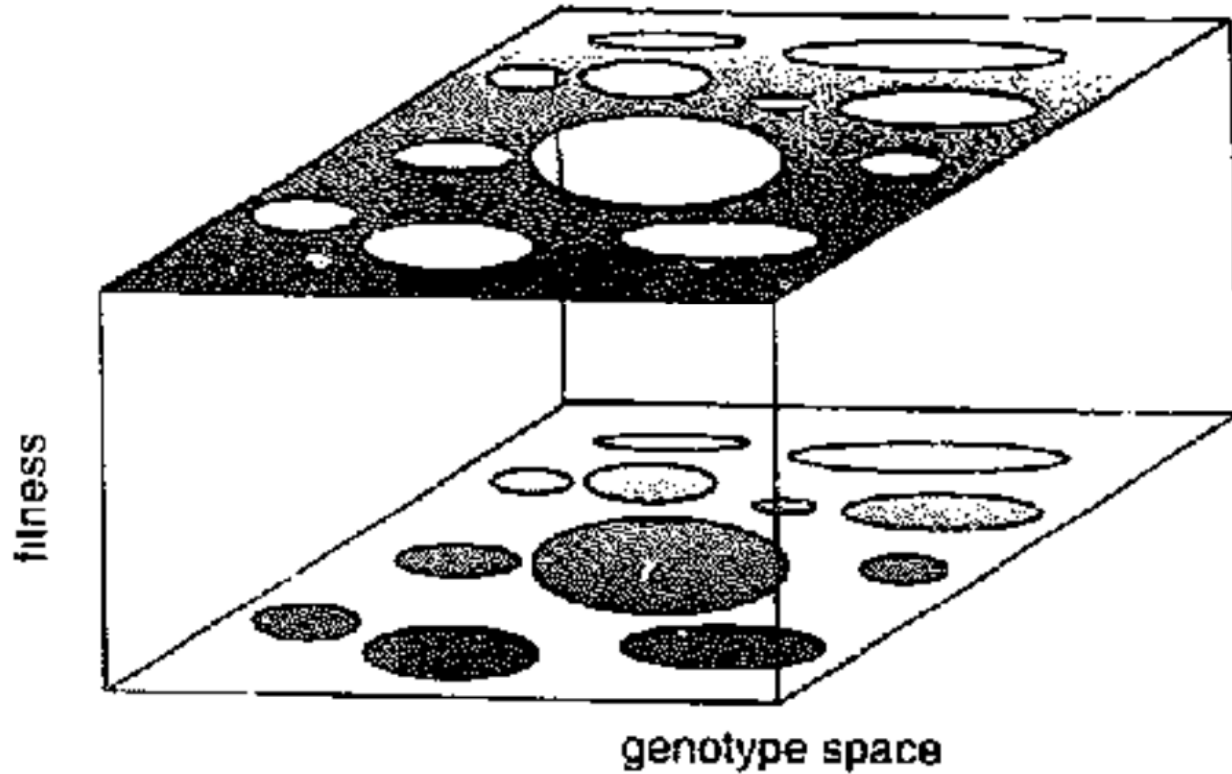


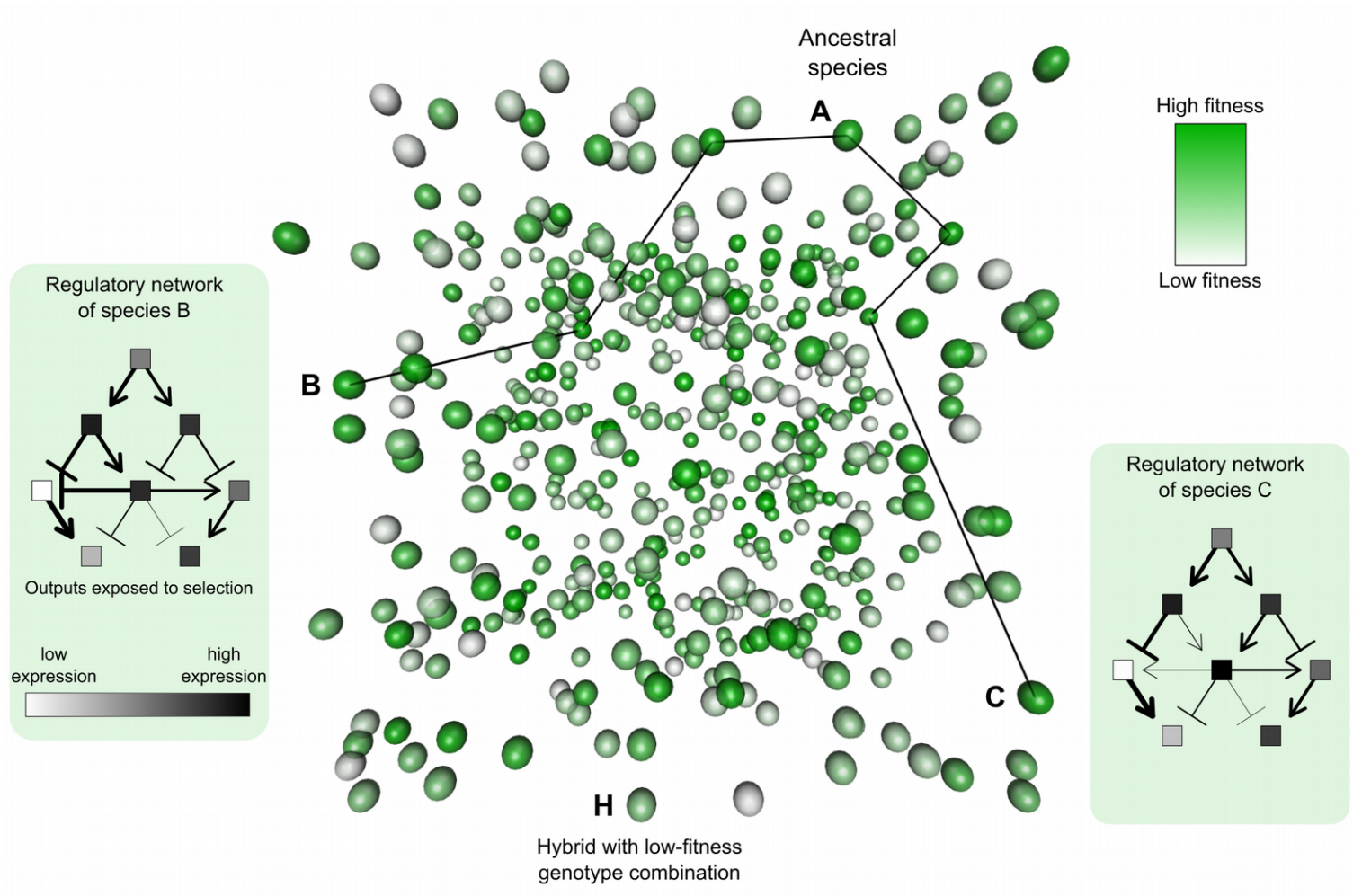
Gavrilets 1997, Wright 1935, Barton 1989, Fierst and Hansen 2010

# Local adaptation creates “barrier loci”

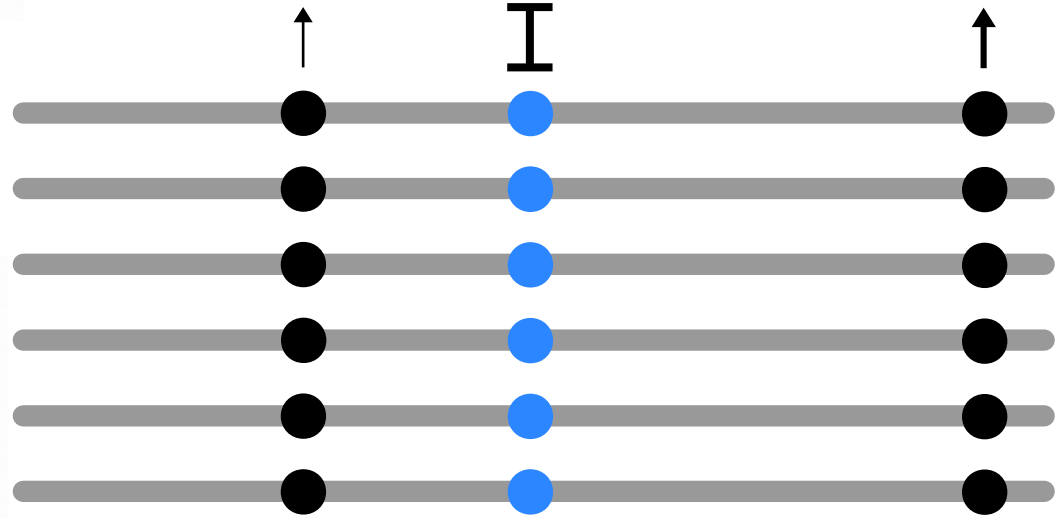
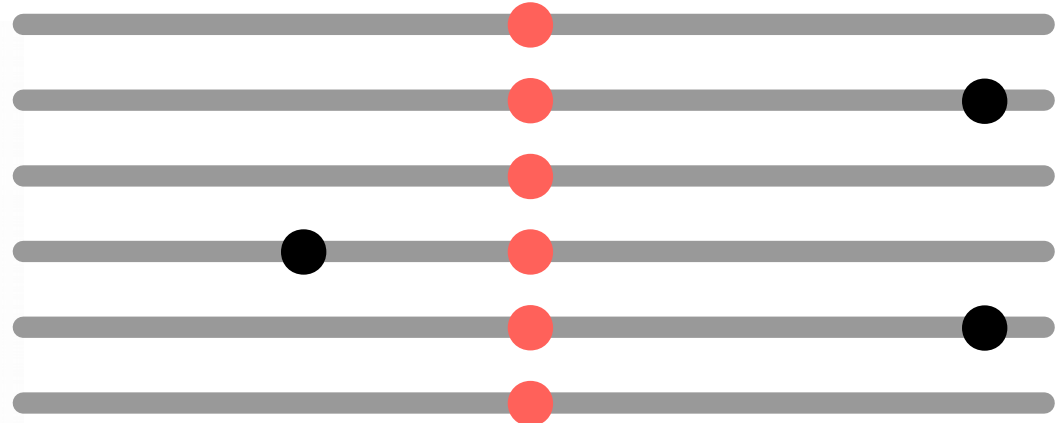
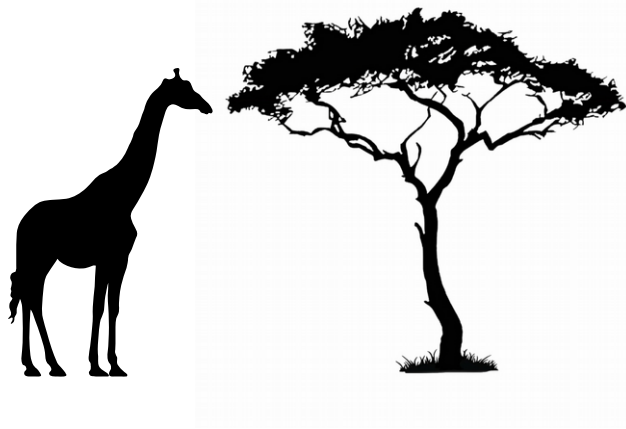


...and polygenic fitness landscapes could make drift very easy

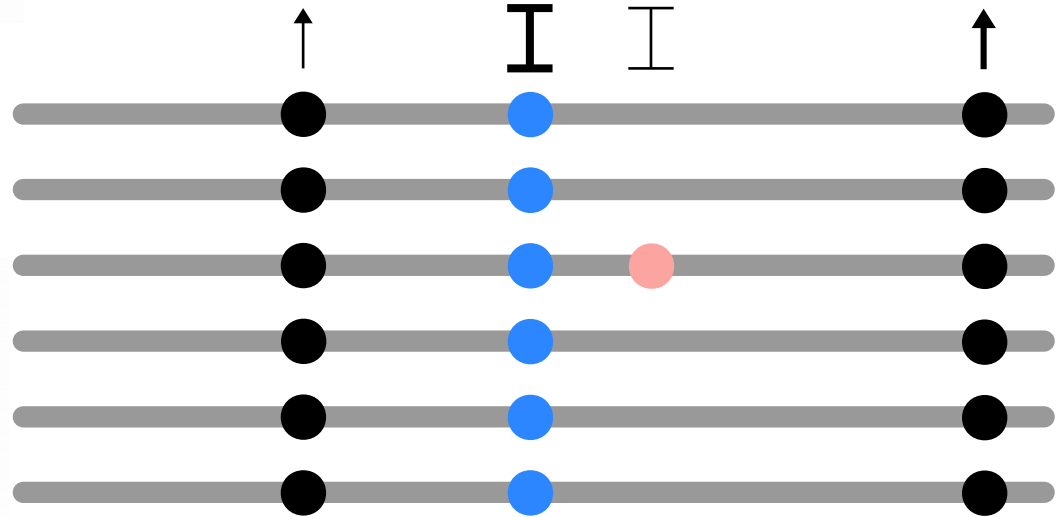
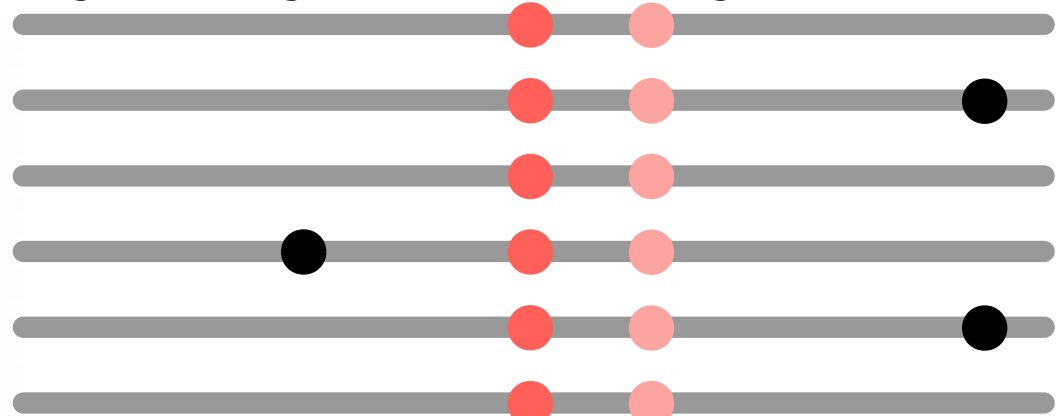
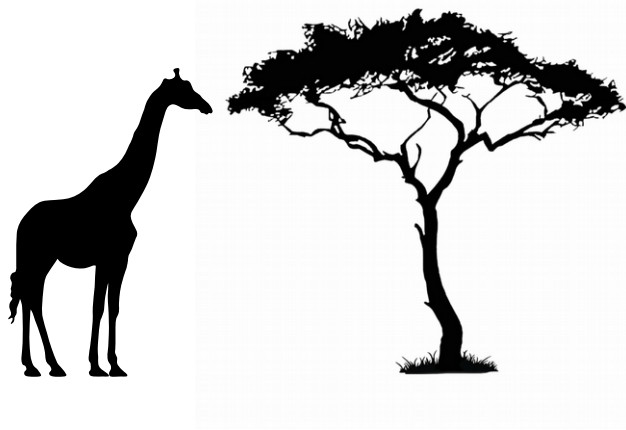




# Local adaptation creates “barrier loci”

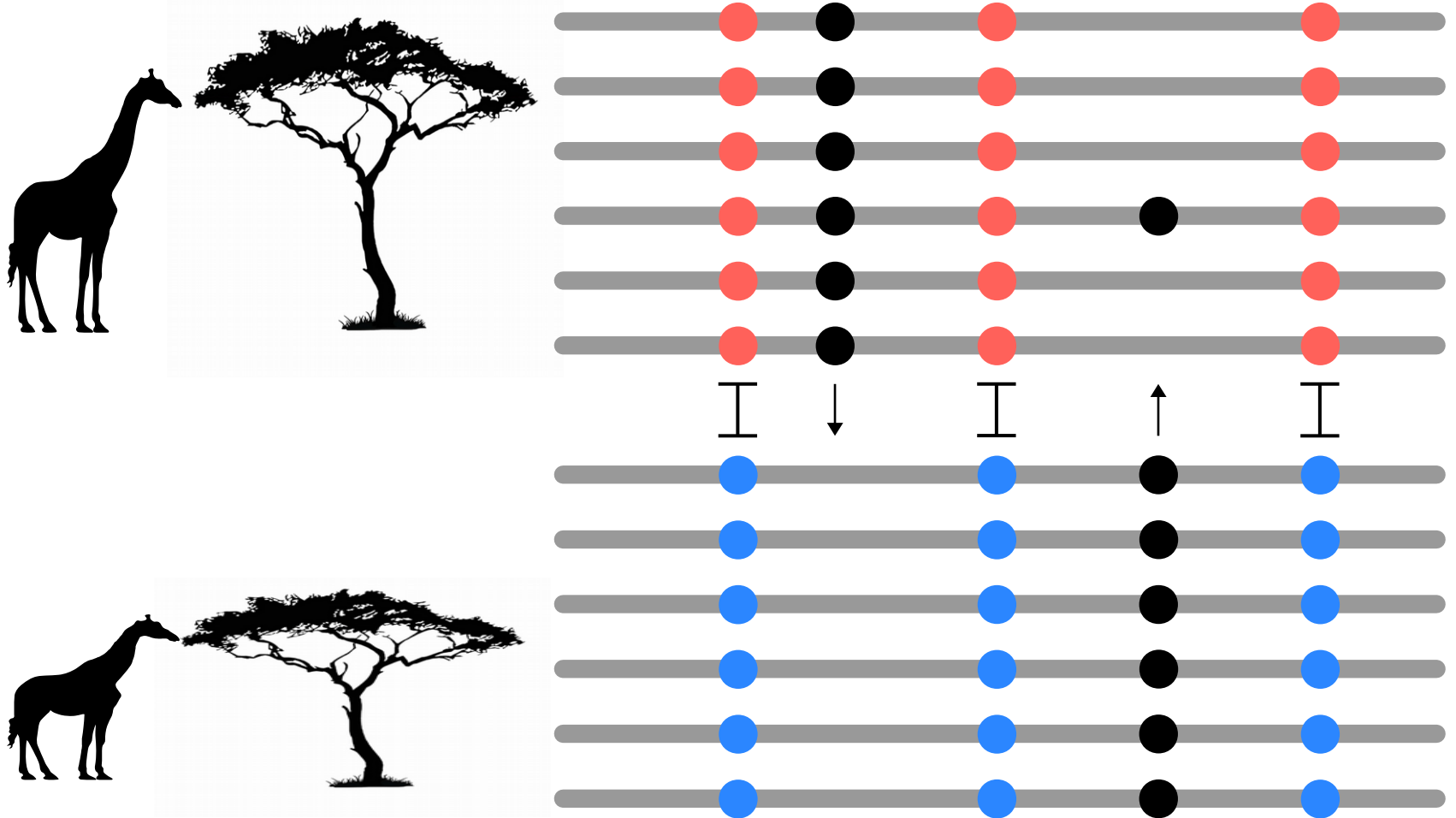


# Barrier loci could grow through divergence hitchhiking

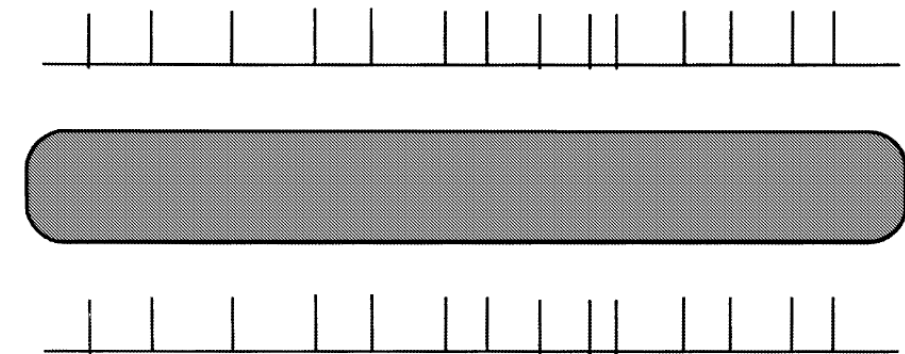
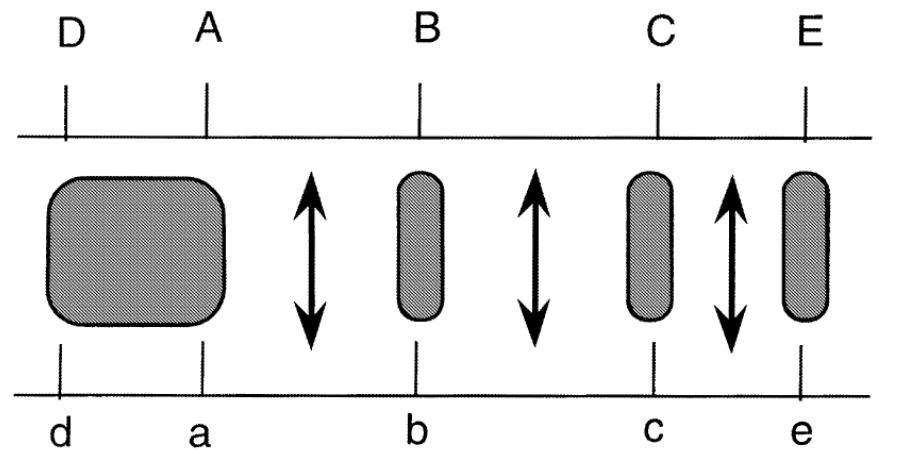
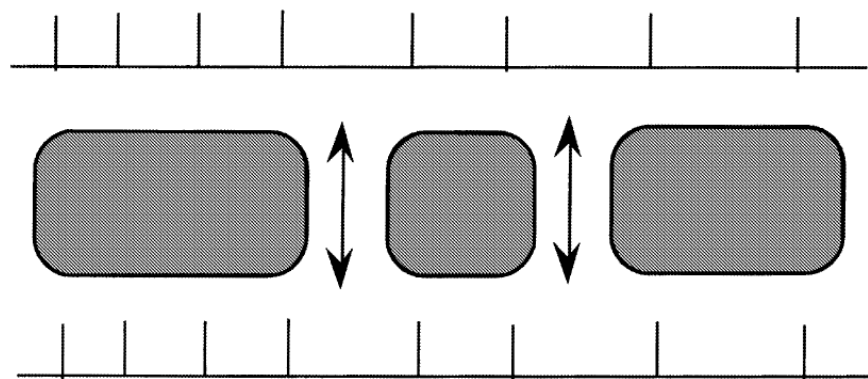
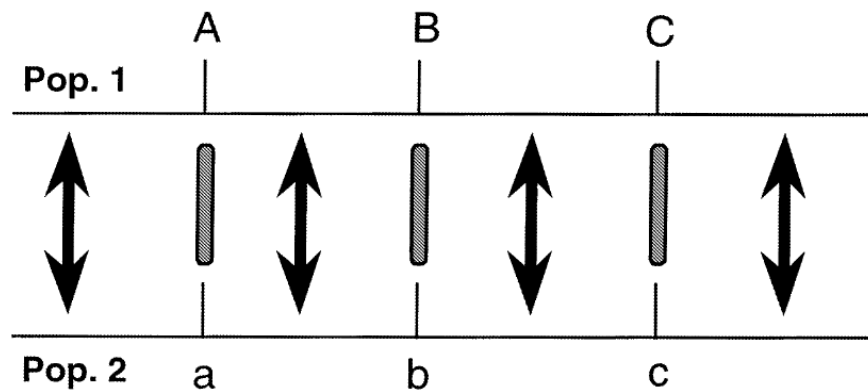


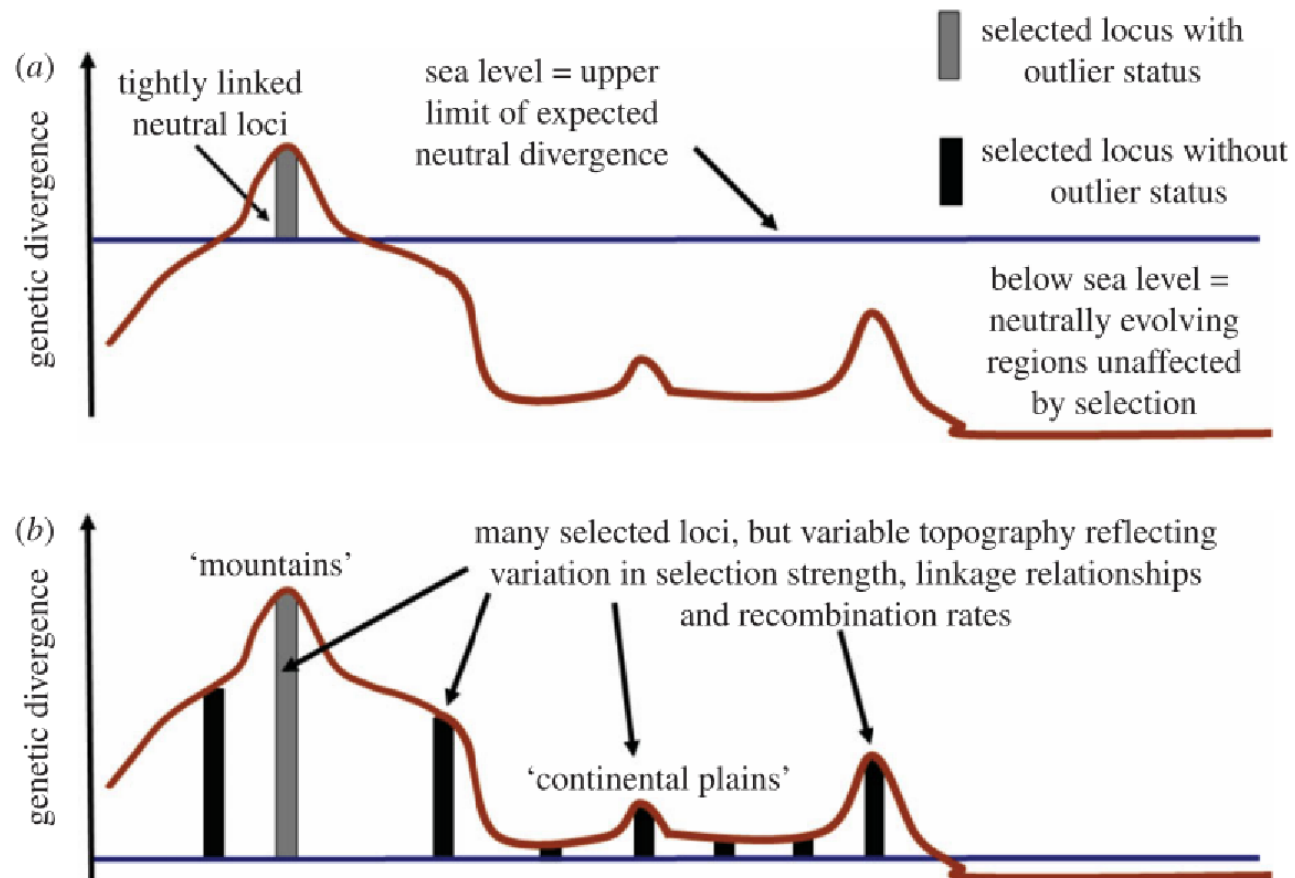
Navarro and Barton 2003, Yeaman & Whitlock 2011, Via et al. 2012, Feder et al. 2012  
Flaxman et al. 2013, Aeschbacher and Bürger 2014, Yeaman et al. 2016, Rafajlović et al. 2016

# Many barrier loci create a genome-wide barrier



Barton 1983, Barton & Bengtsson 1985, Baird 1995, Flaxman et al. 2014  
Tittes & Kane 2014, Nosil et al. 2017, Aeschbacher et al. 2018







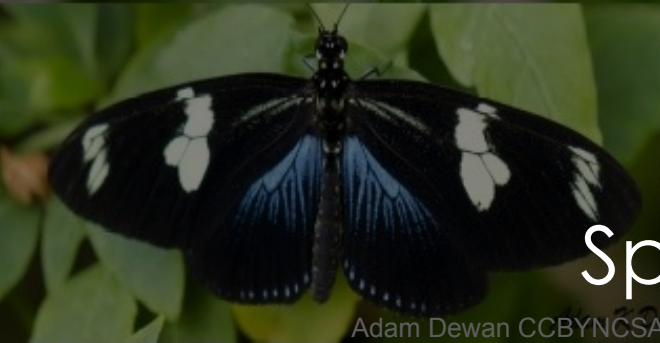
Roberto Monroy CCNC



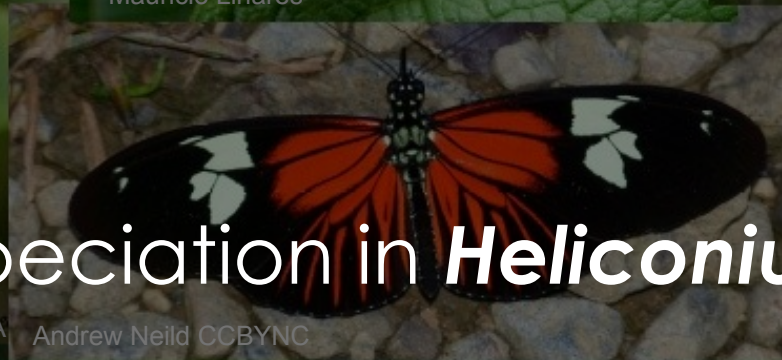
Mauricio Linares



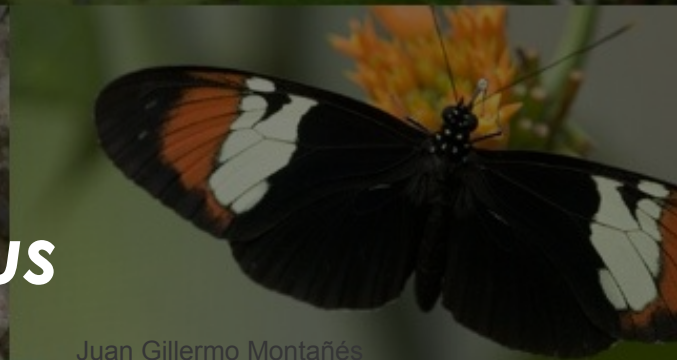
Mauricio Linares



Adam Dewan CCBYNCSA



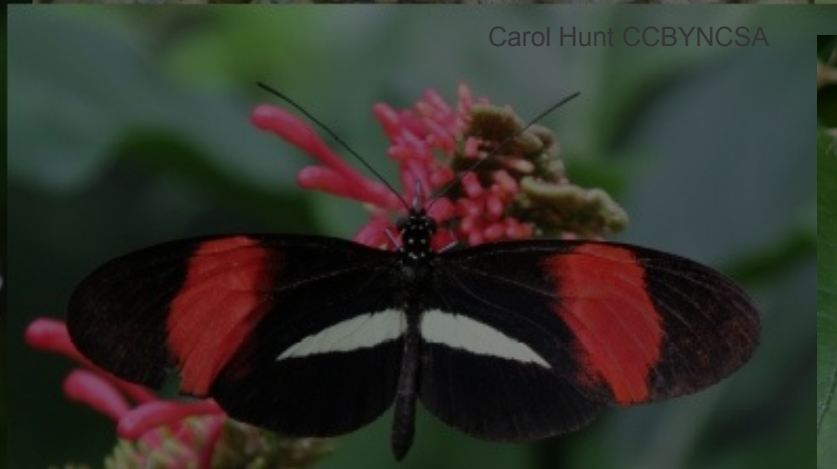
Andrew Neild CCBYNC



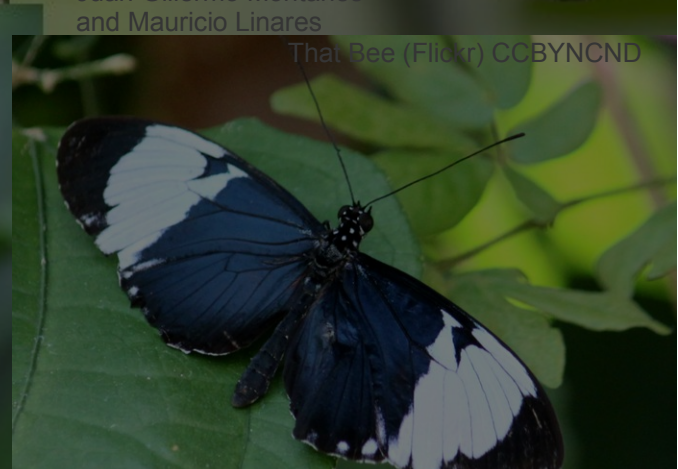
Juan Guillermo Montañés  
and Mauricio Linares



Pavel Kirillov CCBY



Carol Hunt CCBYNCSA



That Bee (Flirr) CCBYNCND

# Speciation in *Heliconius*



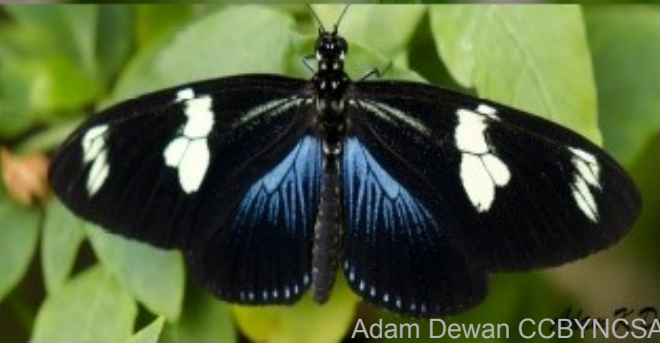
Roberto Monroy CCNC



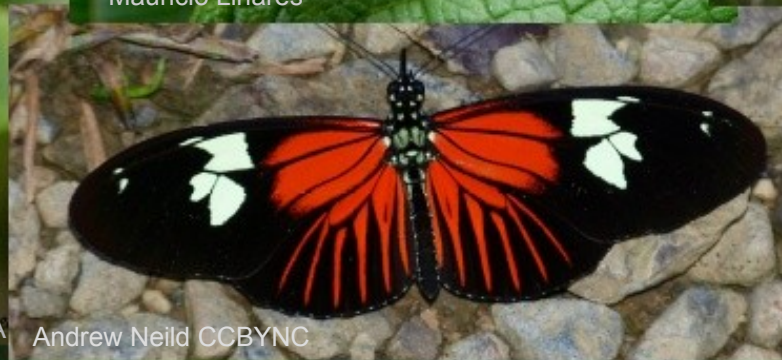
Mauricio Linares



Mauricio Linares



Adam Dewan CCBYNCSA



Andrew Neild CCBYNC



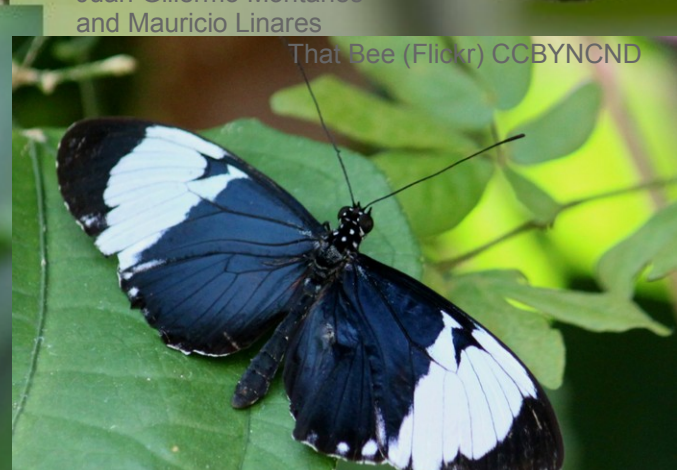
Juan Guillermo Montañés  
and Mauricio Linares



Pavel Kirillov CCBY



Carol Hunt CCBYNCSA



That Bee (Flickr) CCBYNCND

## *Heliconius* **Races**



Carol Hunt CCBYNCSA

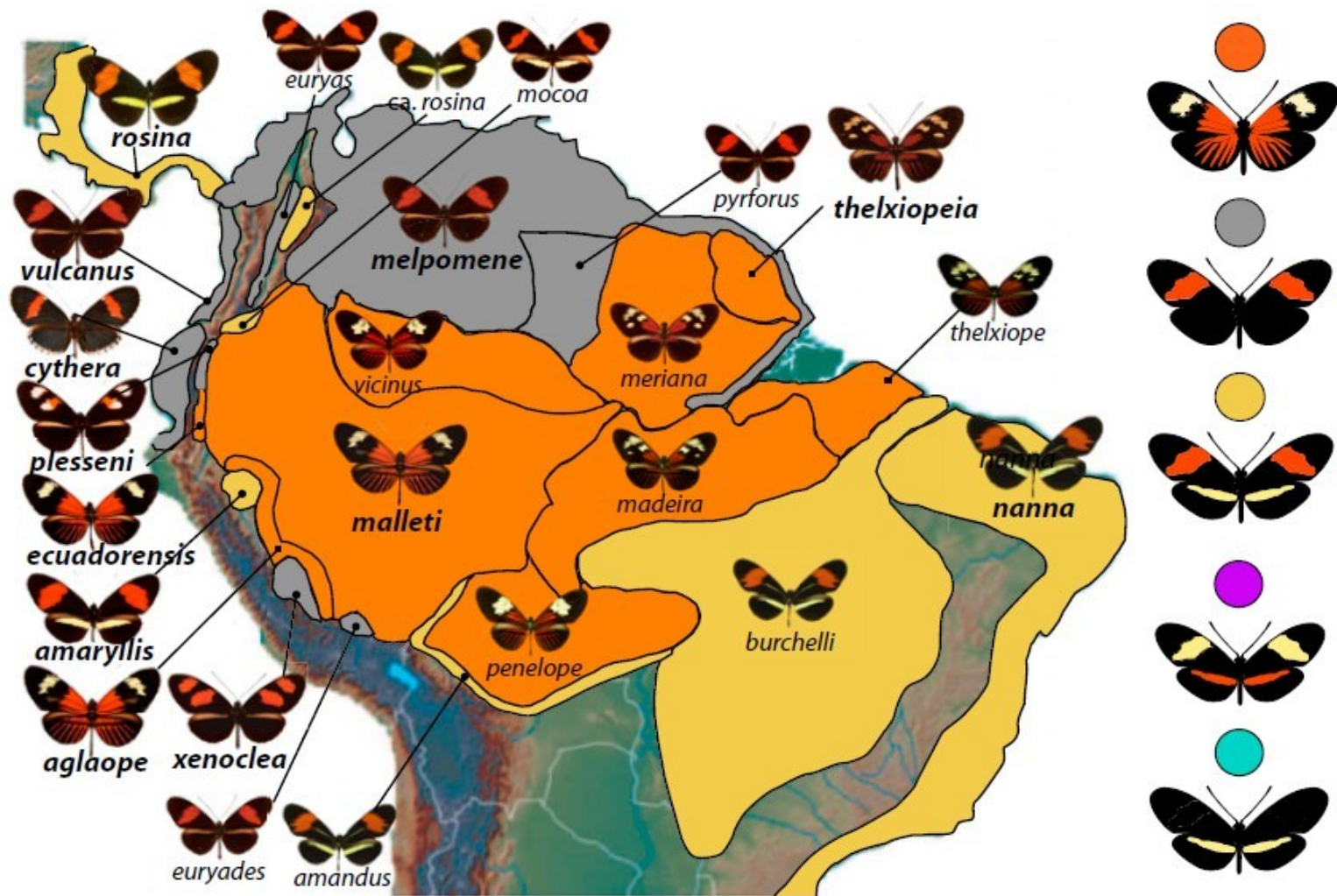
*H. melpomene rosina*

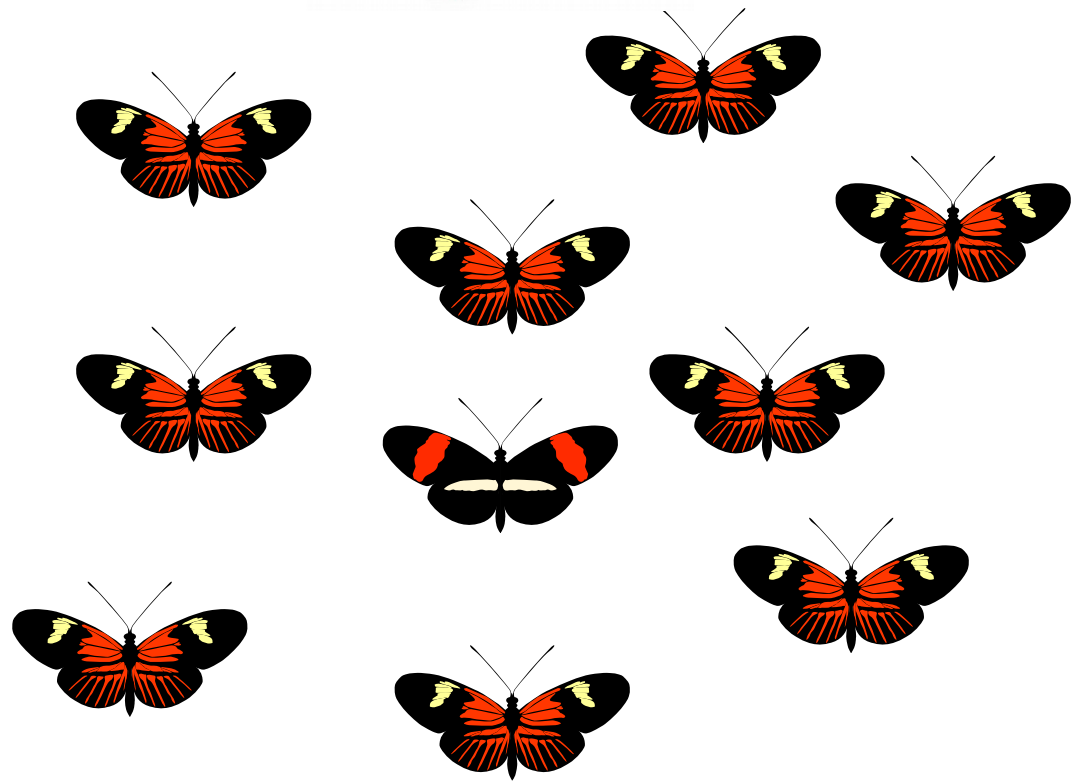
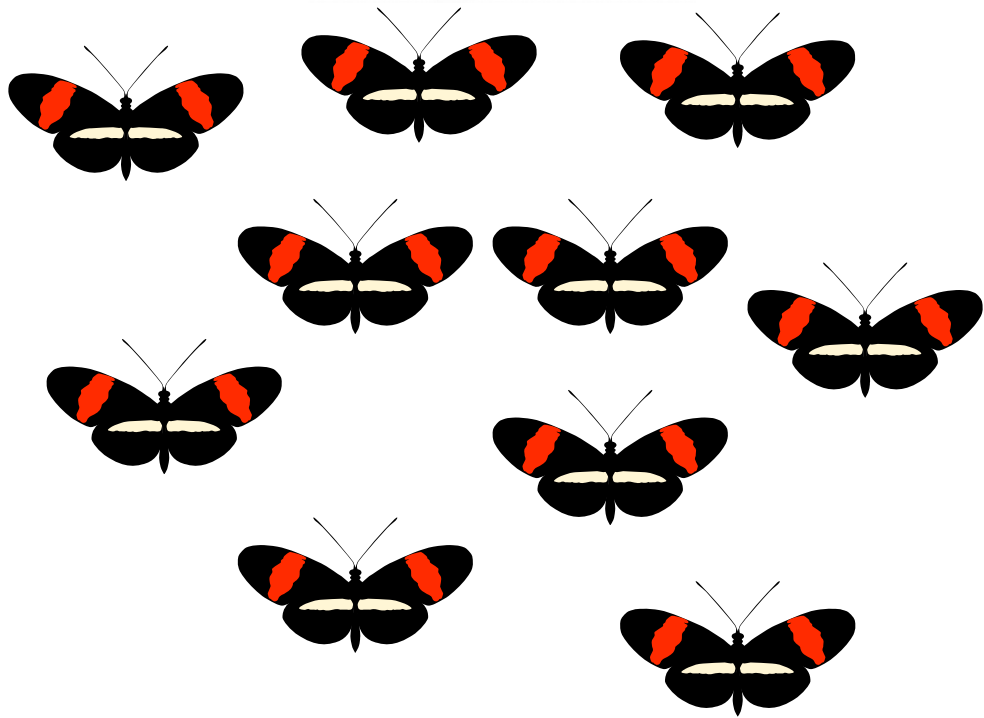


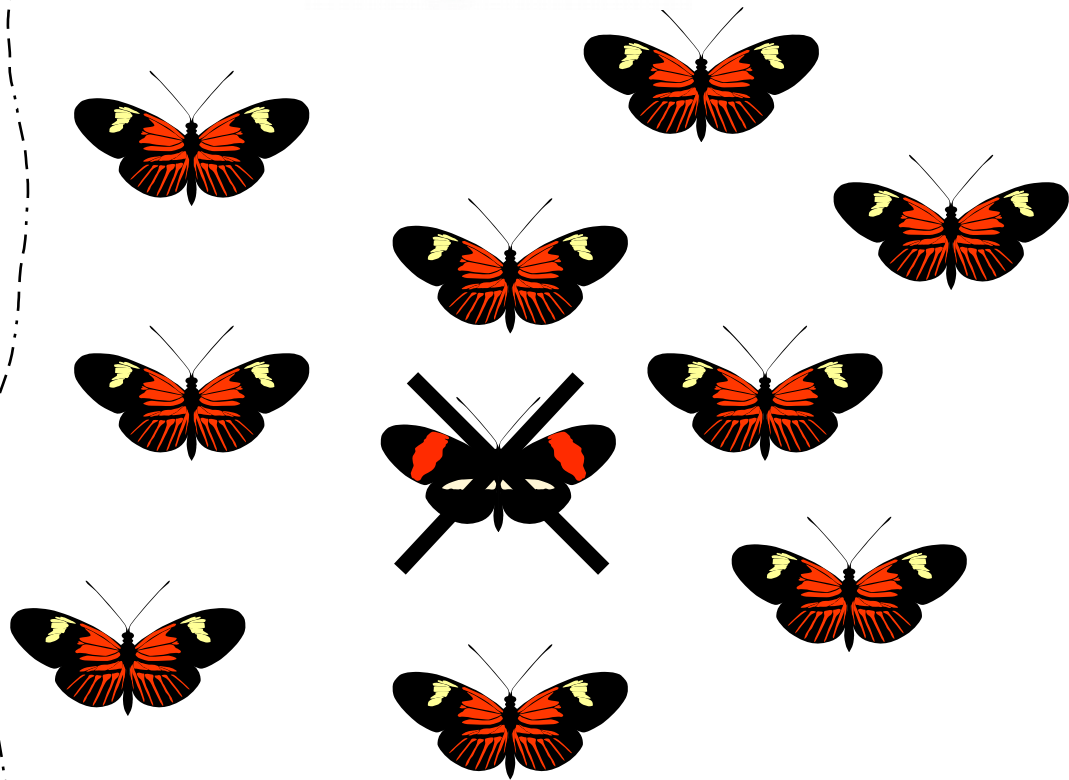
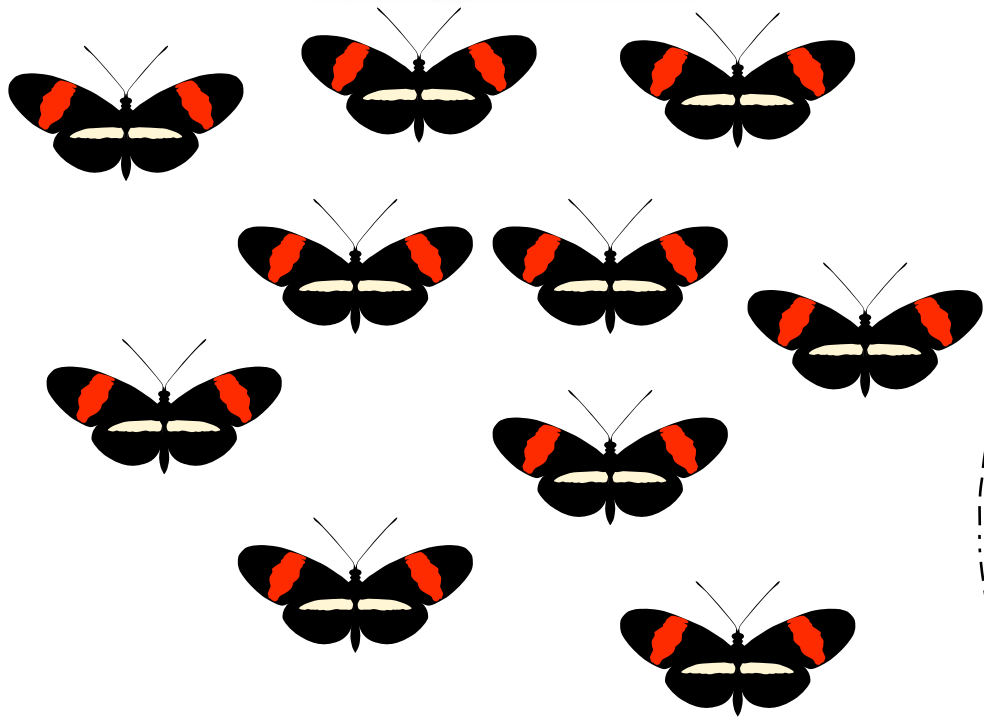
Mauricio Linares

*H. melpomene malleti*

# Races of *H. melpomene*







chromosome 18

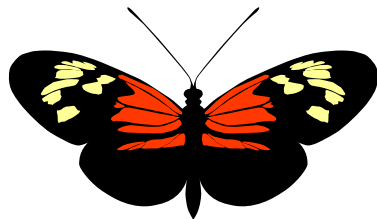
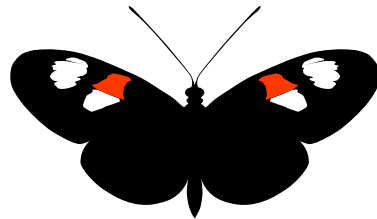
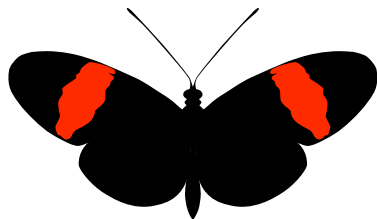
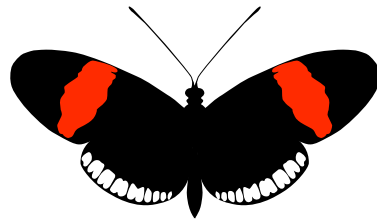
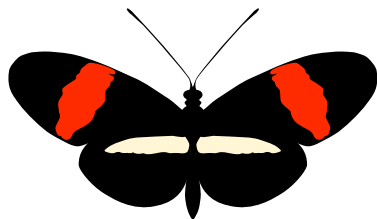
*optix*

chromosome 10

*wnt-A*

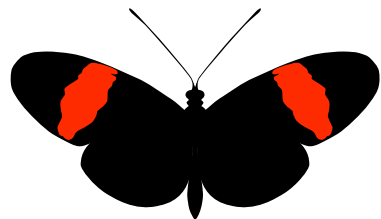
chromosome 15

*cortex*



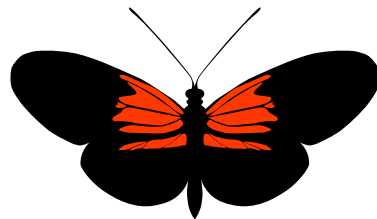
chromosome 18

*optix*



chromosome 10

*wnt-A*



chromosome 15

*cortex*



chromosome 18

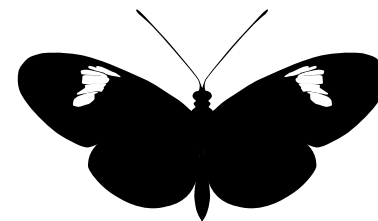
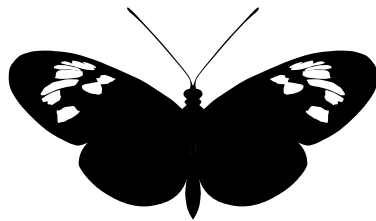
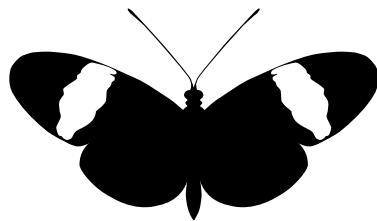
*optix*

chromosome 10

***wnt-A***

chromosome 15

*cortex*



chromosome 18

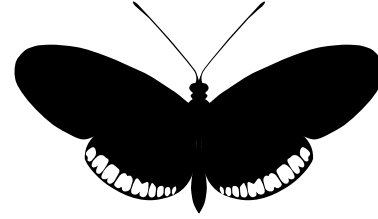
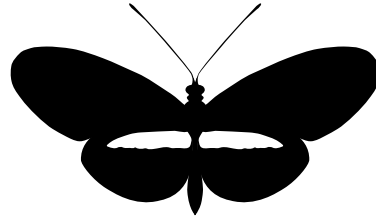
*optix*

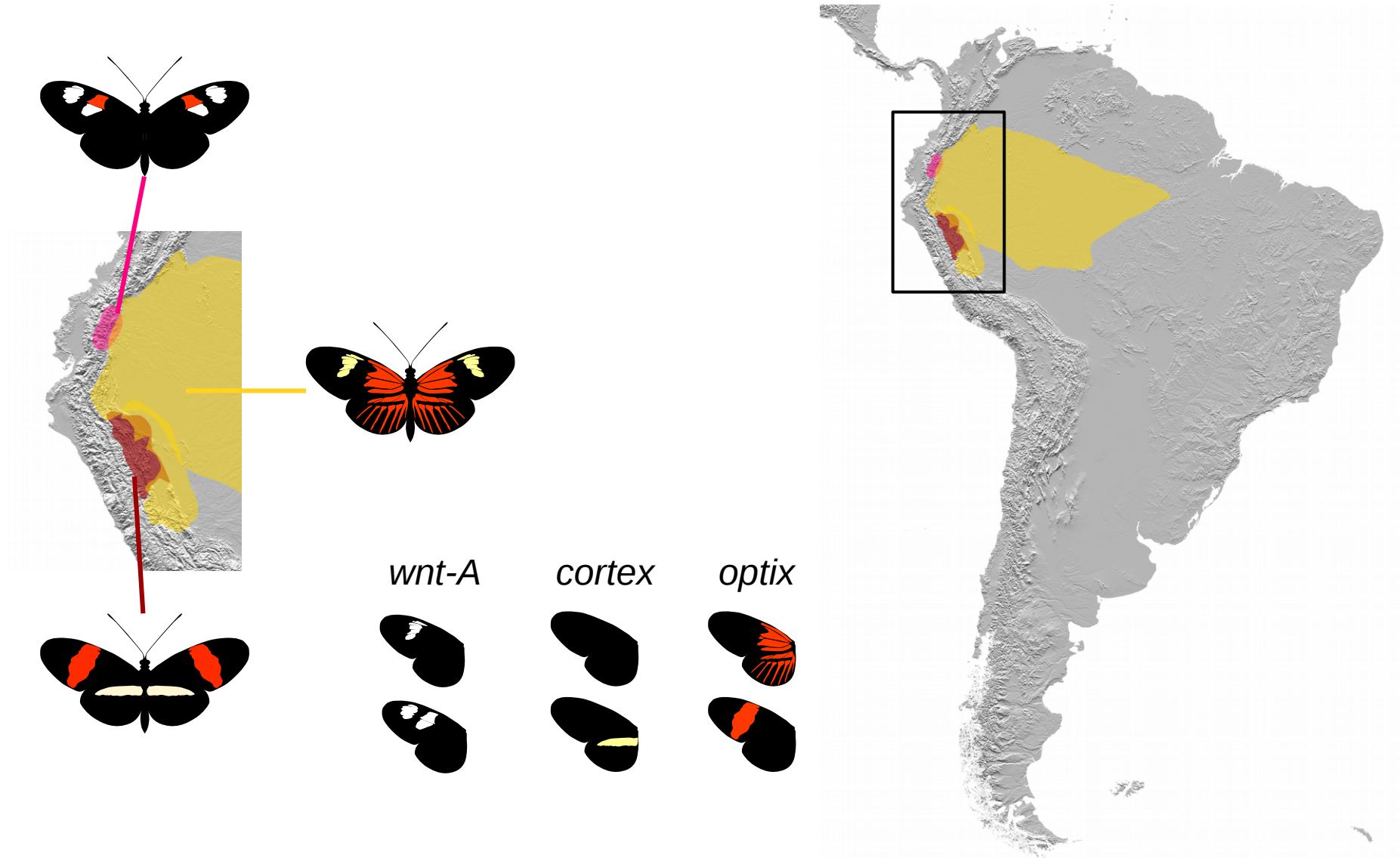
chromosome 10

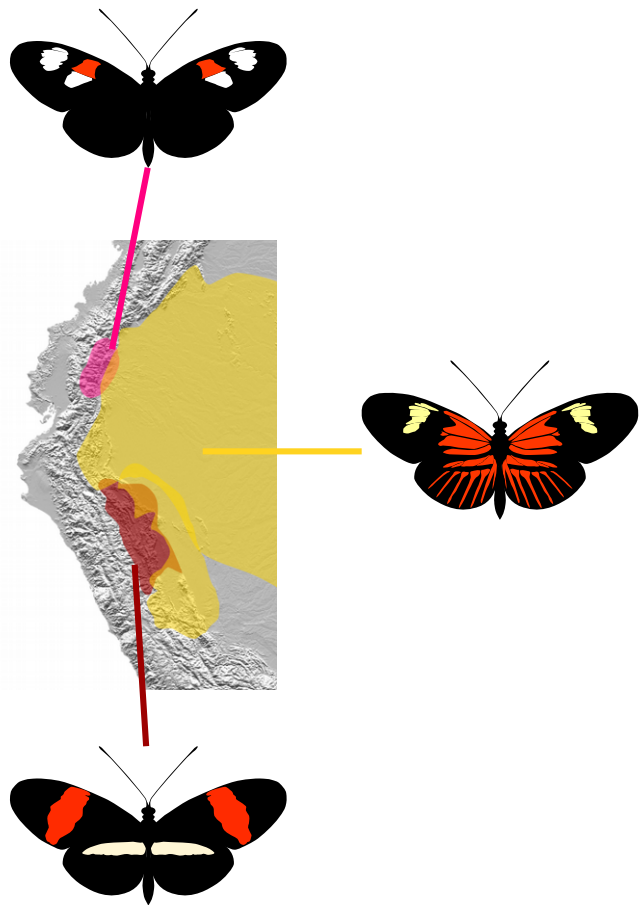
*wnt-A*

chromosome 15

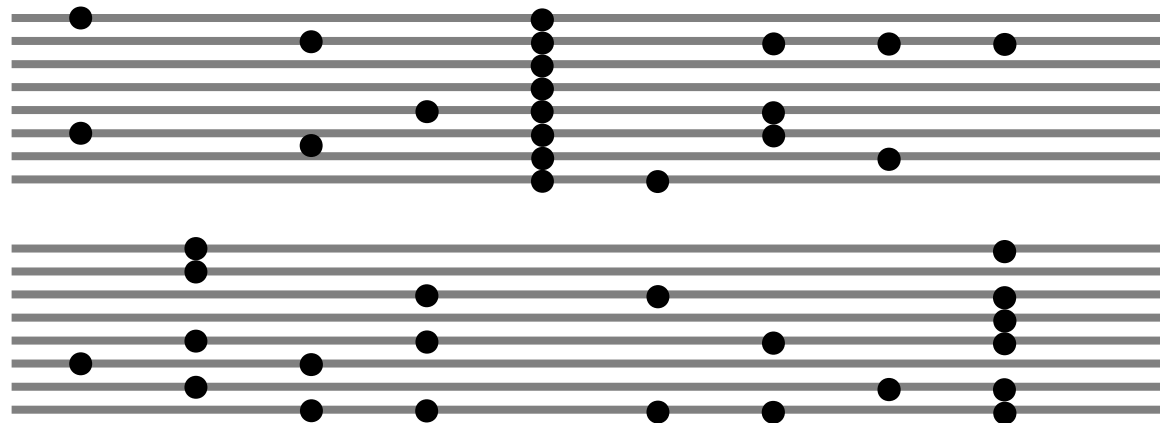
**cortex**



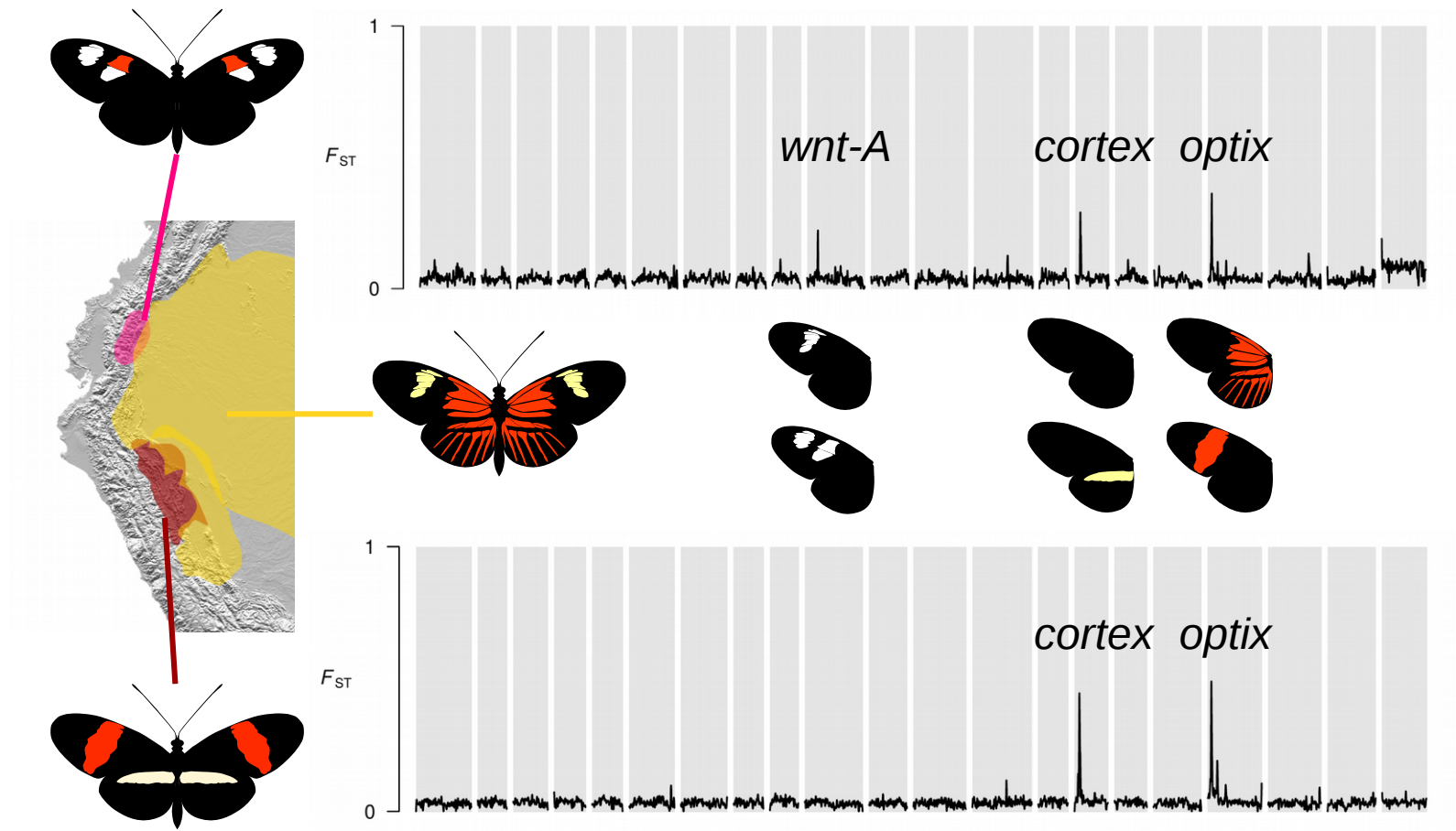




$$F_{ST} = \frac{\pi_{total} - \pi_{subpop}}{\pi_{total}} = 1 - \frac{\pi_{subpop}}{\pi_{total}}$$







## *Heliconius* **Species**



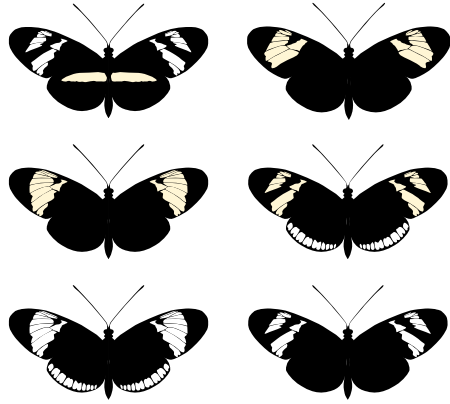
Henry T. McLin CCBYNCND

*H. cydno*

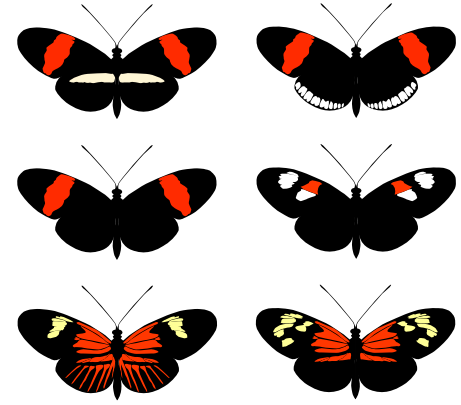
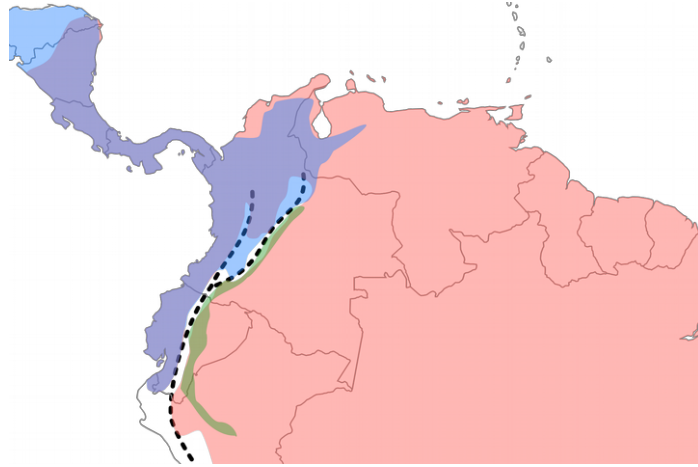


Carol Hunt CCBYNCNSA

*H. melpomene*



*H. cydno*



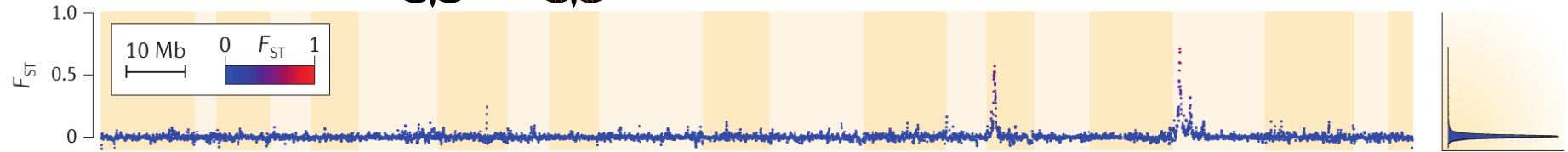
*H. melpomene*



- Habitat preference
- Host plant choice
- Assortative mating
- Hybrid female sterility (Haldane's Rule)



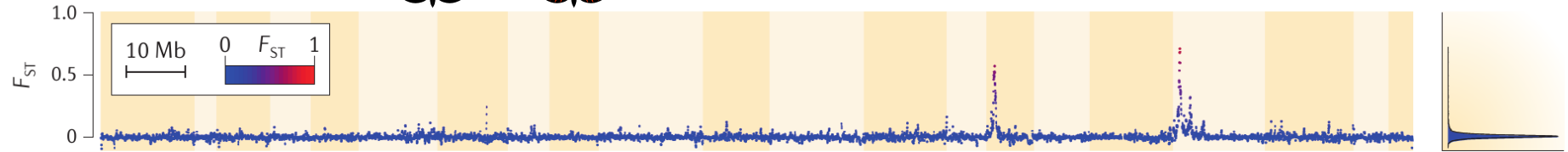
## Parapatric Races



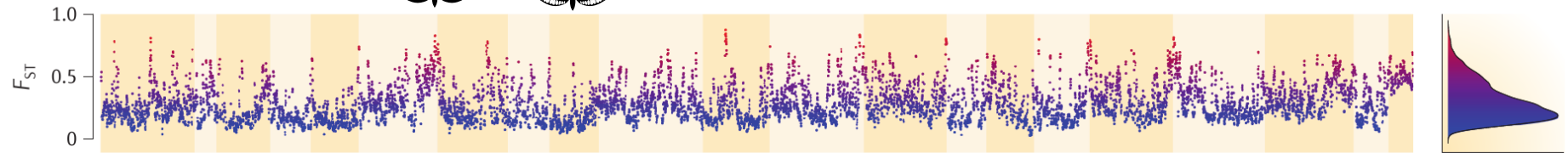
## Sympatric species

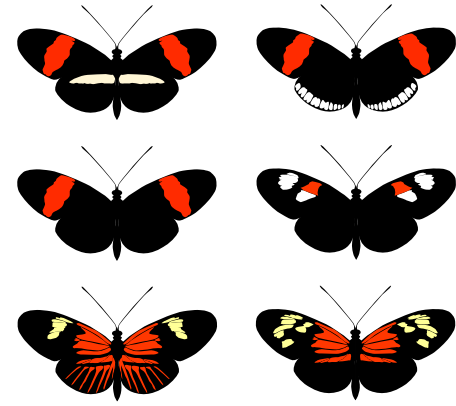


## Parapatric Races



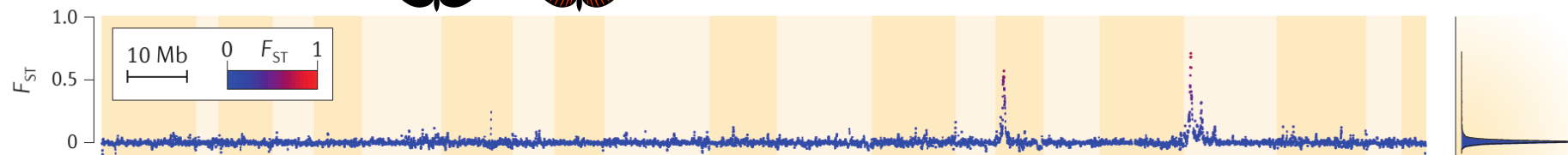
## Sympatric species



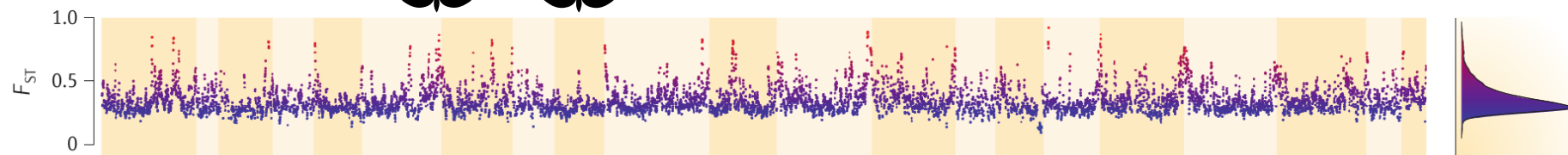


*H. melpomene*

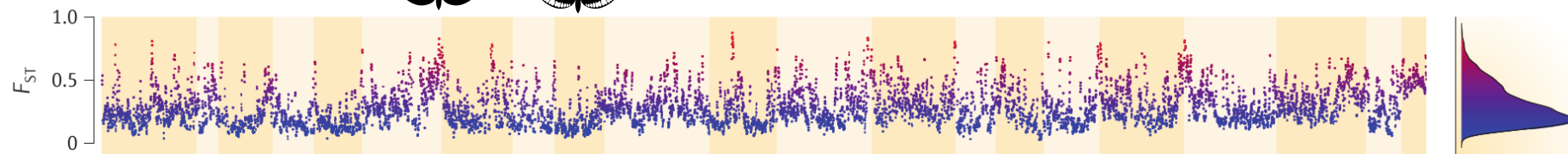
## Parapatric Races



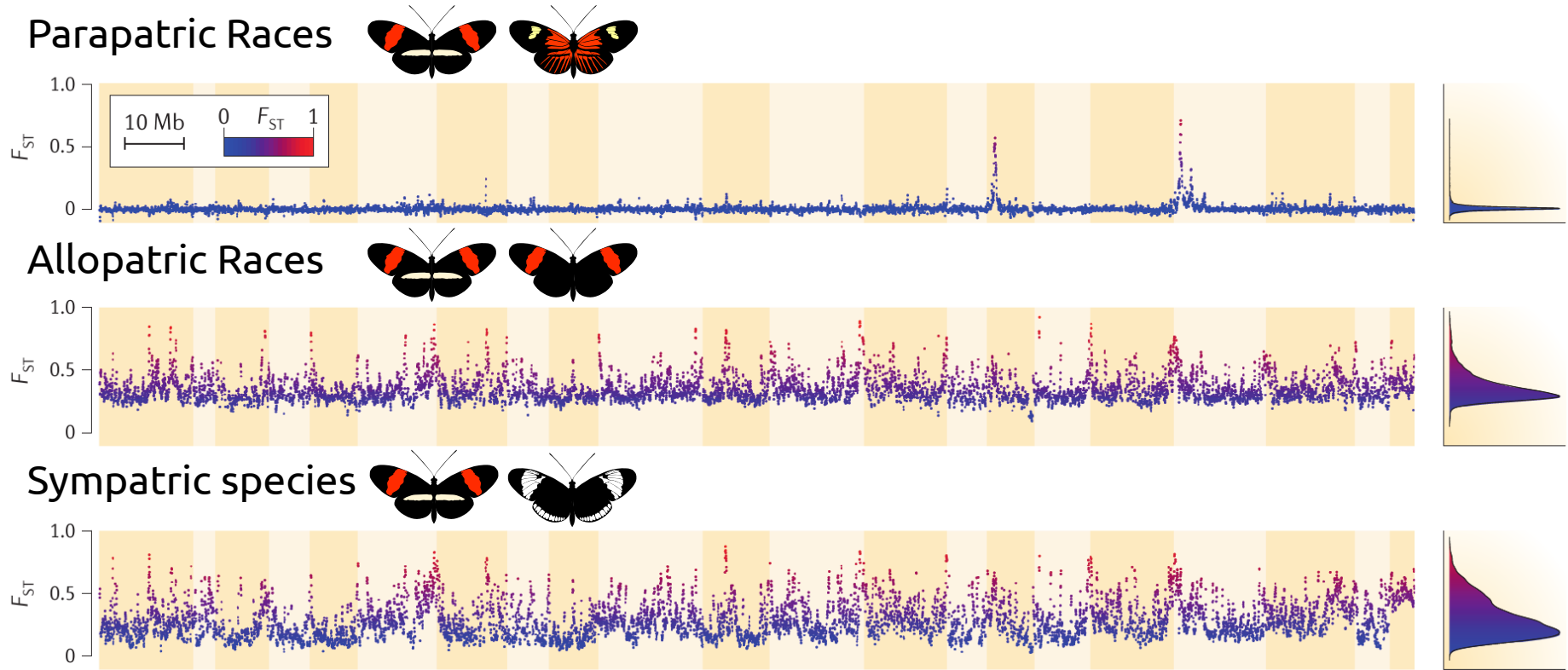
## Allopatric Races

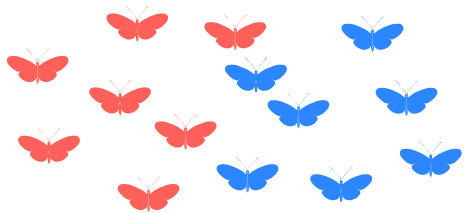


## Sympatric species



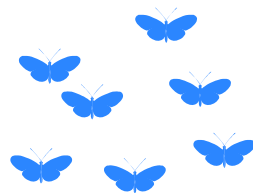
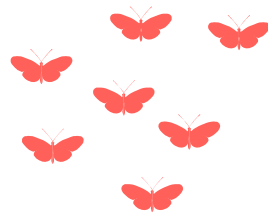
The problem is not FST, the problem is how we interpret it

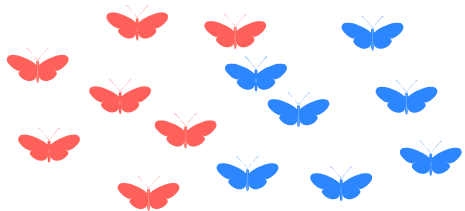




$$F_{ST} = 1 - \frac{\pi_{subpop}}{\pi_{total}}$$

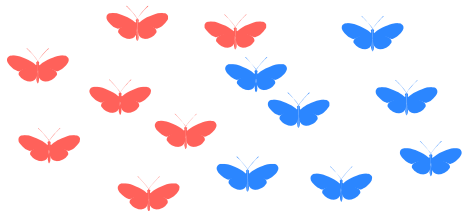
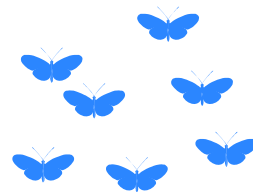
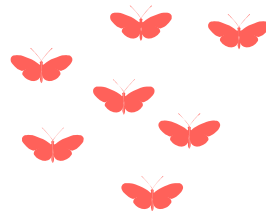
A red arrow points upwards from the  $\pi_{total}$  term in the denominator, indicating that as  $\pi_{total}$  increases, the value of  $F_{ST}$  decreases.





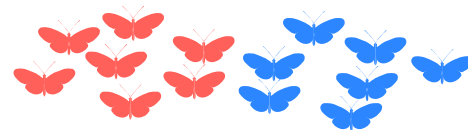
$$F_{ST} = 1 - \frac{\pi_{subpop}}{\pi_{total}}$$

↑



$$F_{ST} = 1 - \frac{\pi_{subpop}}{\pi_{total}}$$

↓



INVITED REVIEWS AND SYNTHESSES

# Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow

TAMI E. CRUICKSHANK\* and MATTHEW W. HAHN\*†

*\*Department of Biology, Indiana University, Bloomington, IN 47405, USA, †School of Informatics and Computing, Indiana University, Bloomington, IN 47405, USA*

INVITED REVIEWS AND SYNTHESSES

# Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow

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*\*Department of Biology, Indiana University, Bloomington, IN 47405, USA, †School of Informatics and Computing, Indiana University, Bloomington, IN 47405, USA*

## **Islands of Speciation or Mirages in the Desert? Examining the Role of Restricted Recombination in Maintaining Species\***

**Mohamed A. F. Noor<sup>1</sup> and Sarah M. Bennett<sup>1</sup>**

<sup>1</sup> Biology Department, Duke University, Durham, NC USA

# Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow

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## Islands of Speciation or Mirages in the Desert? Examining the Role of Restricted Recombination in Maintaining Species\*

**Mohamed A. F. Noor<sup>1</sup>** and **Sarah M. Bennett<sup>1</sup>**

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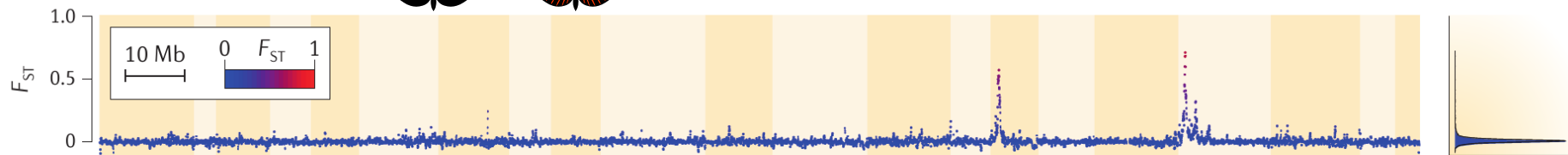
The effects of local selection, balanced polymorphism and background selection on equilibrium patterns of genetic diversity in subdivided populations

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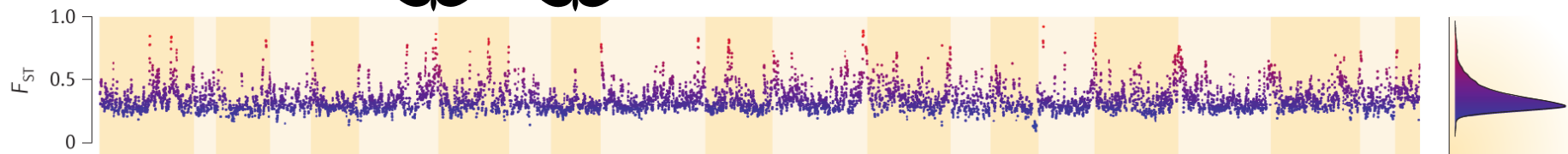
BRIAN CHARLESWORTH\*†, MAGNUS NORDBORG‡  
AND DEBORAH CHARLESWORTH†

*Department of Ecology and Evolution, University of Chicago, 1101 E 57th Street, Chicago, IL 60637, USA*

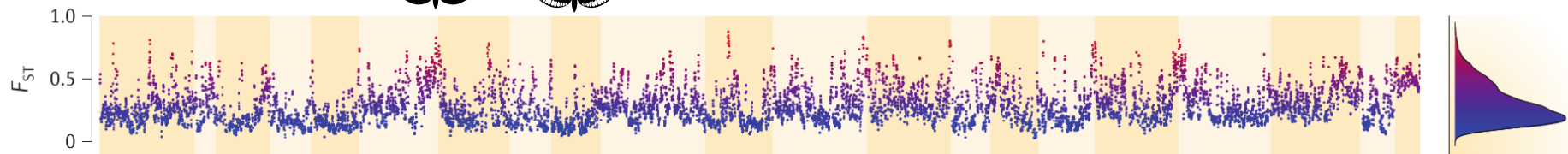
## Parapatric Races



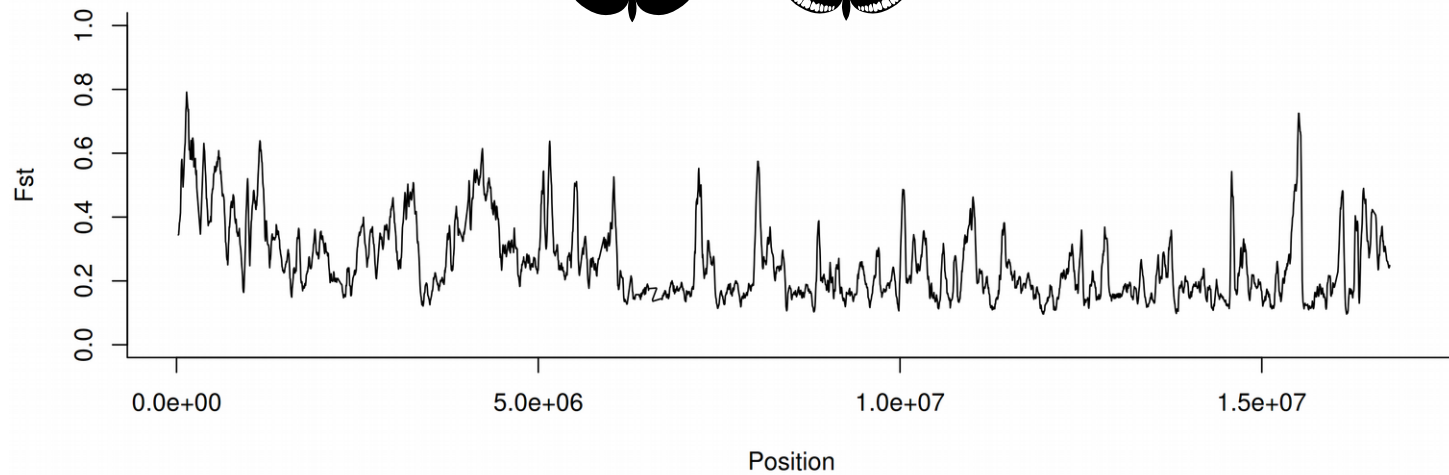
## Allopatric Races



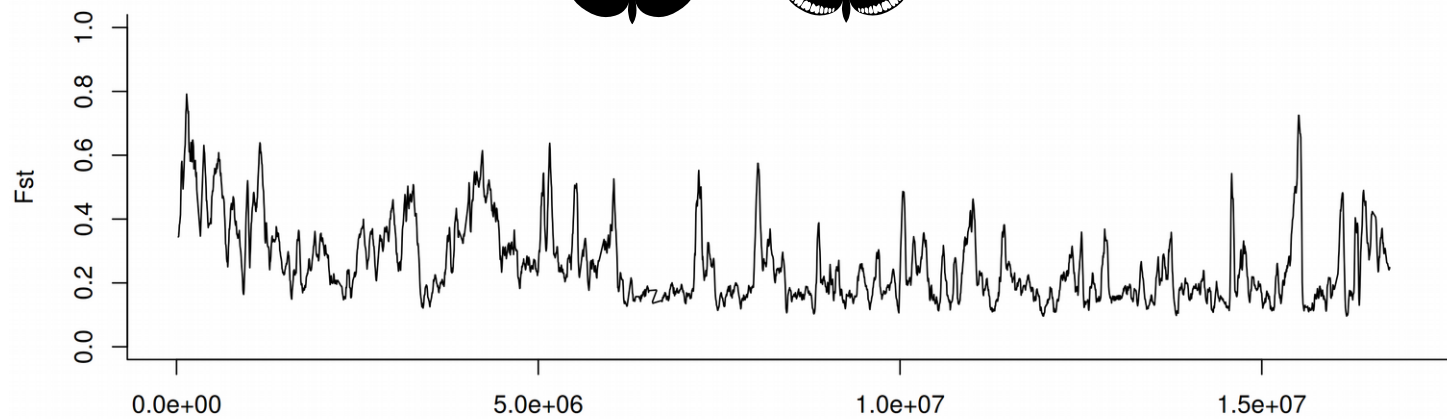
## Sympatric species



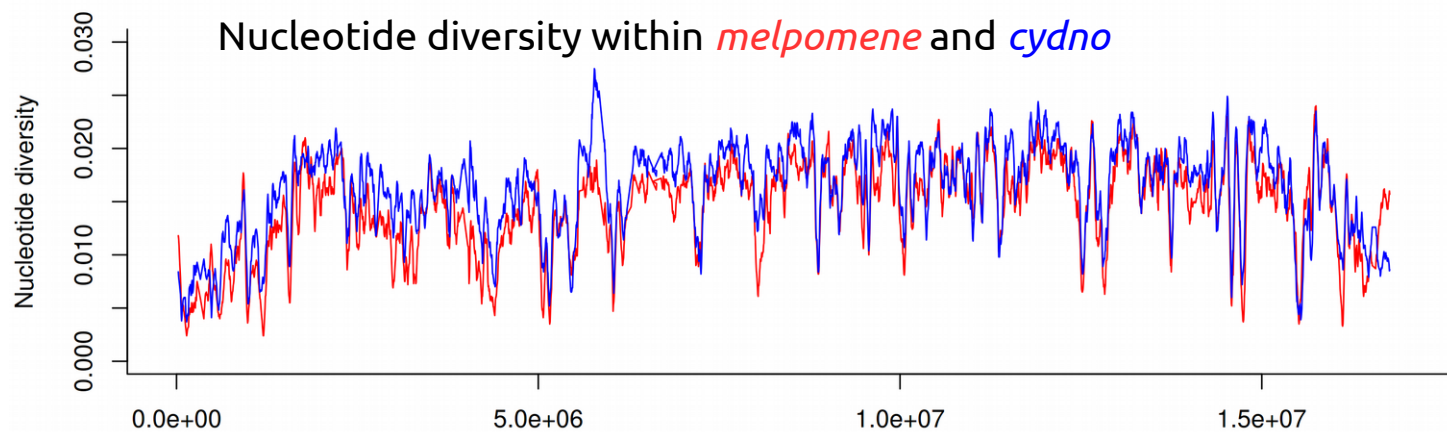
$F_{ST}$  between *melpomene* and *cydno*



$F_{ST}$  between *melpomene* and *cydno*

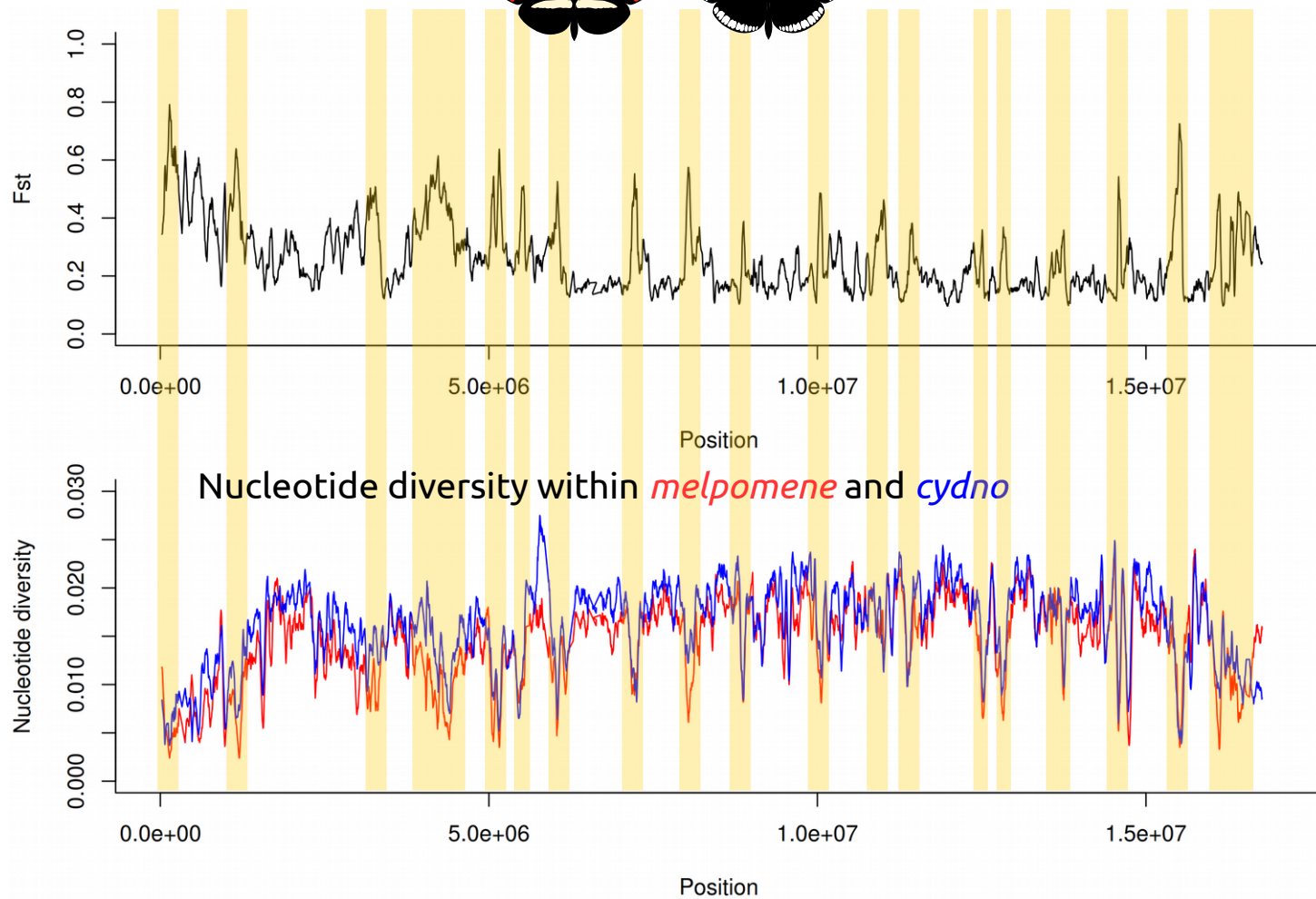


Position



Position

# $F_{ST}$ between *melpomene* and *cydno*



*"Surely you've heard the stories?"*

*The Black Pearl sails from the dreaded Isla de Mureta...*

*An island that cannot be found -- except by those who already know where it is."*

Pirates of the Caribbean, The curse of the Black Pearl, 2003

# Interpreting differentiation landscapes in the light of long-term linked selection

Reto Burri<sup>1,2</sup>

## NEWS AND VIEWS

Perspective

Linked selection, demography and the evolution of correlated genomic landscapes in birds and beyond

Reto Burri 

## TARGET REVIEW

**Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow**

M. RAVINET<sup>\*†</sup> , R. FARIA<sup>‡§¶</sup>, R. K. BUTLIN<sup>¶\*\*</sup>, J. GALINDO<sup>††</sup>, N. BIERNE<sup>‡‡</sup>,  
M. RAFAJLOVIĆ<sup>§§</sup> , M. A. F. NOOR<sup>¶¶</sup> , B. MEHLIG<sup>§§</sup> & A. M. WESTRAM<sup>¶</sup>

WILEY MOLECULAR ECOLOGY

COMMENTARY

**Dissecting differentiation landscapes: a linked selection's perspective**

R. BURRI 

*Department of Population Ecology, Institute of Ecology, Friedrich Schiller University Jena, Jena, Germany*

COMMENTARY

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

H. ELLEGREN<sup>\*</sup>  & J. B. W. WOLF<sup>\*†</sup>

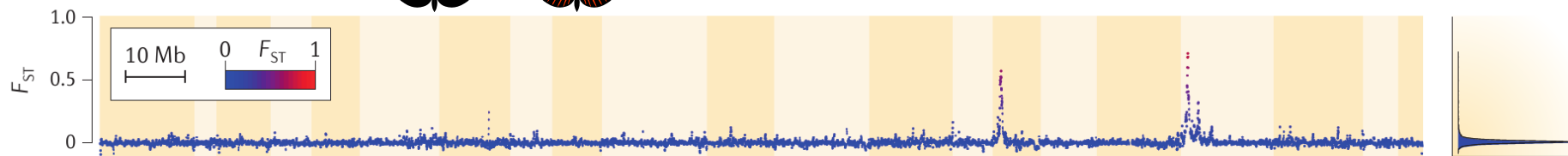
*\*Department of Evolutionary Biology, Uppsala University, Uppsala, Sweden*

*†Division of Evolutionary Biology, Faculty of Biology, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany*

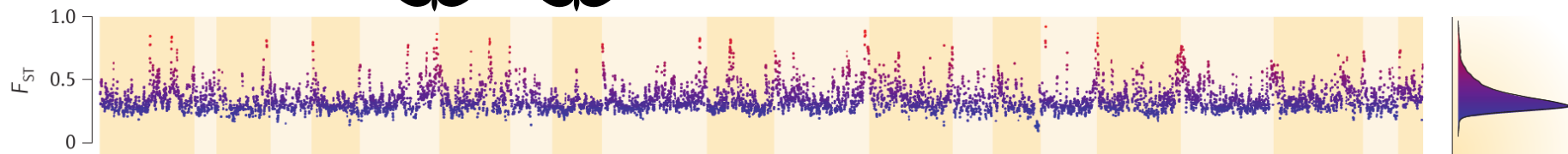
**Making sense of genomic islands of differentiation in light of speciation**

*Jochen B. W. Wolf<sup>1,2</sup> and Hans Ellegren<sup>1</sup>*

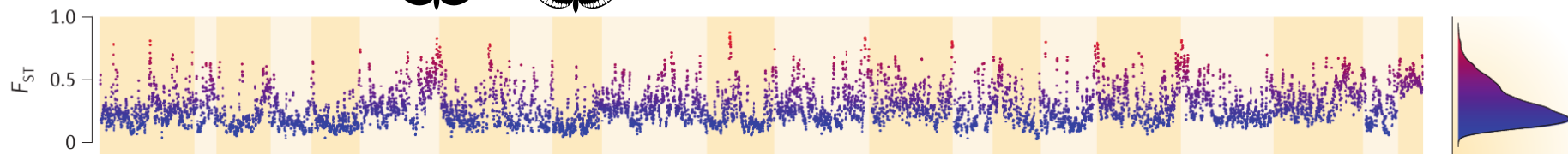
## Parapatric Races



## Allopatric Races

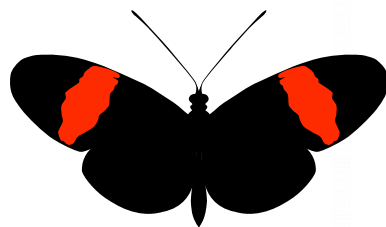
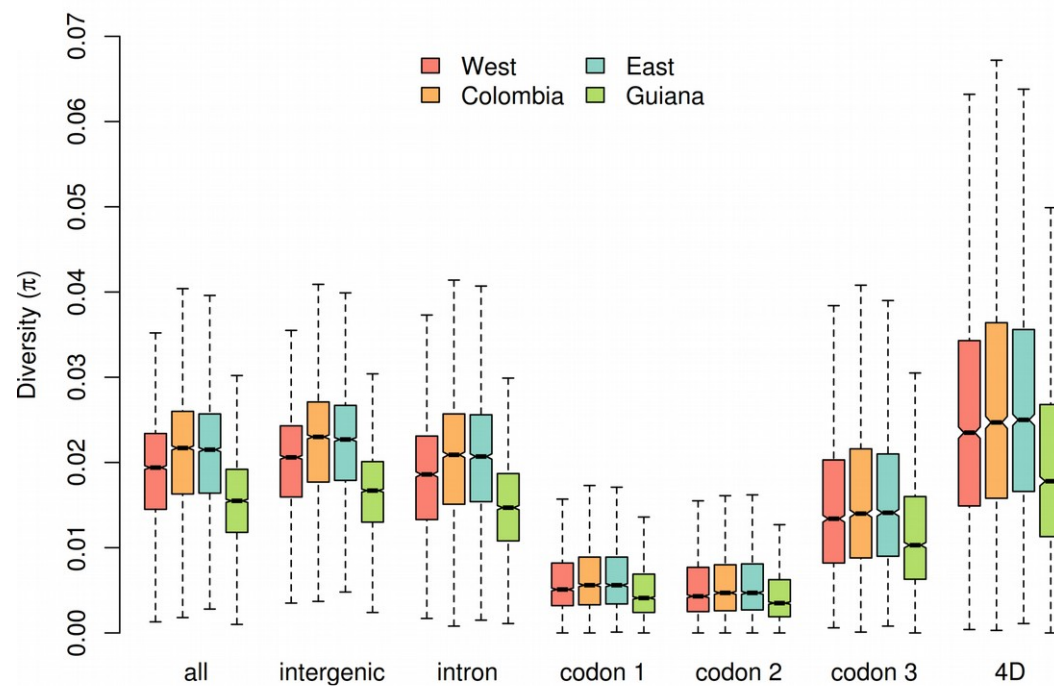


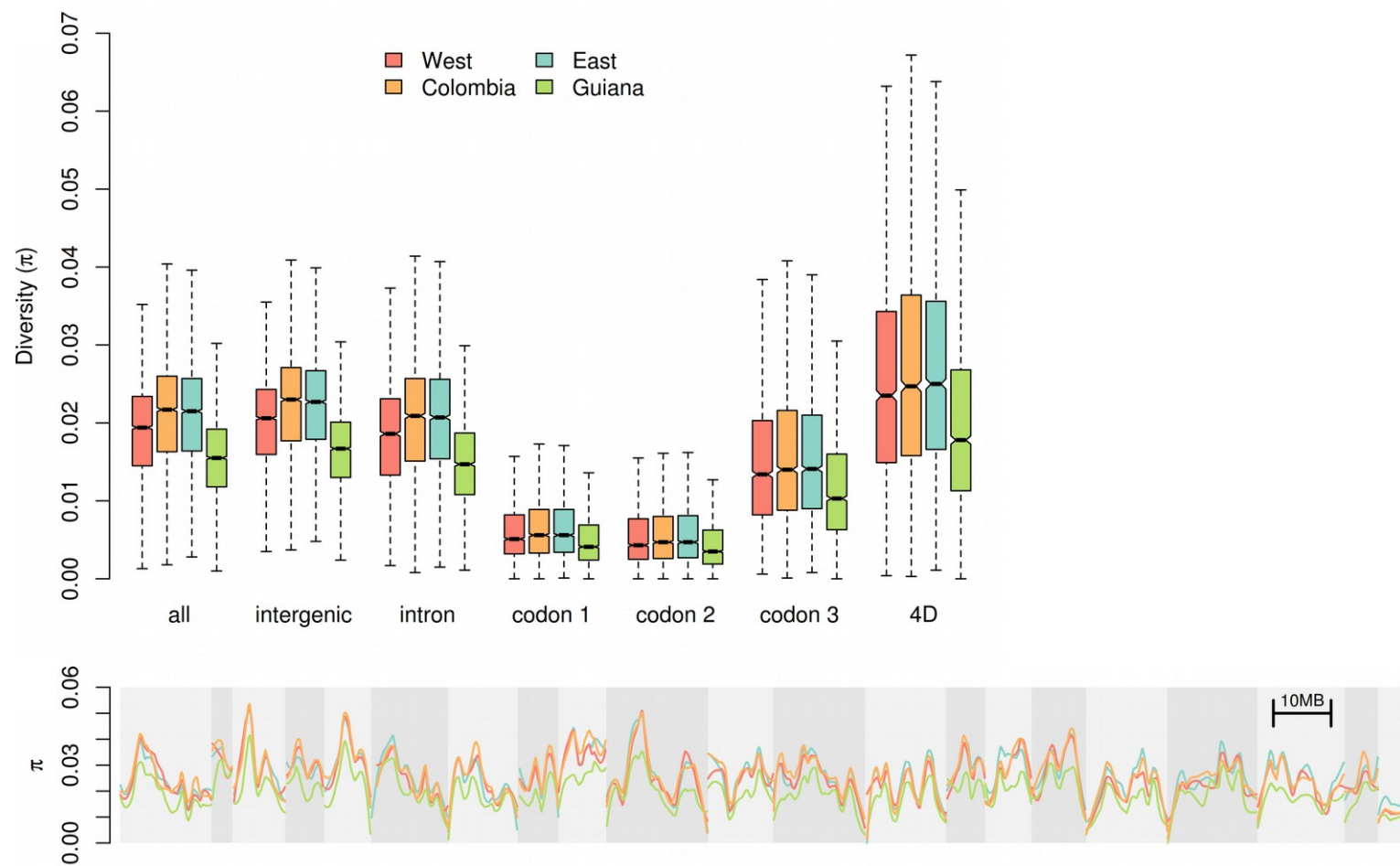
## Sympatric species



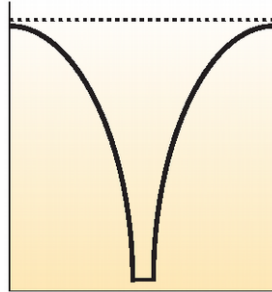
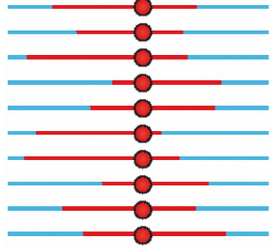
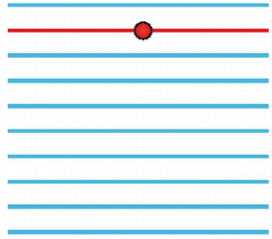
# Linked selection and recombination rate variation drive the evolution of the genomic landscape of differentiation across the speciation continuum of *Ficedula* flycatchers

Reto Burri,<sup>1</sup> Alexander Nater,<sup>1</sup> Takeshi Kawakami,<sup>1</sup> Carina F. Mugal,<sup>1</sup> Pall I. Olason,<sup>2</sup> Linnea Smeds,<sup>1</sup> Alexander Suh,<sup>1</sup> Ludovic Dutoit,<sup>1</sup> Stanislav Bureš,<sup>3</sup> Laszlo Z. Garamszegi,<sup>4</sup> Silje Hogner,<sup>5,6</sup> Juan Moreno,<sup>7</sup> Anna Qvarnström,<sup>8</sup> Milan Ružić,<sup>9</sup> Stein-Are Sæther,<sup>5,10</sup> Glenn-Peter Sætre,<sup>5</sup> Janos Török,<sup>11</sup> and Hans Ellegren<sup>1</sup>

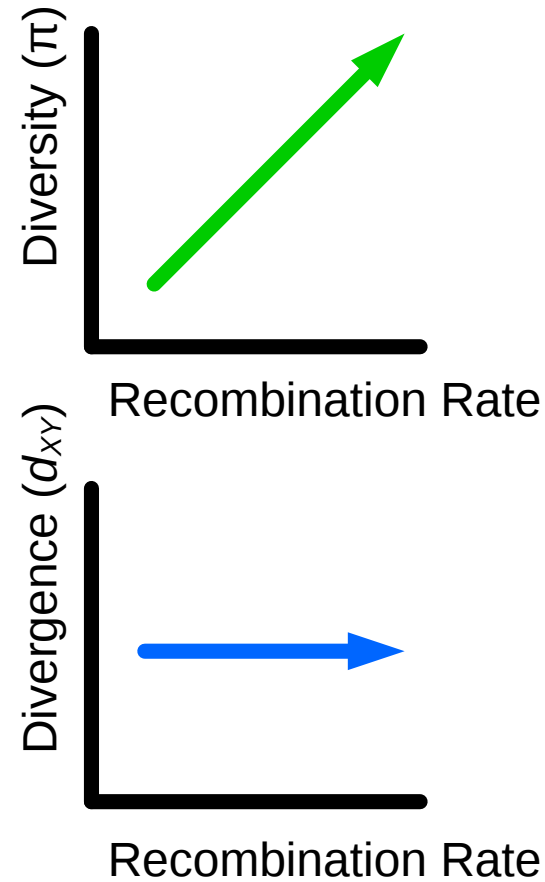
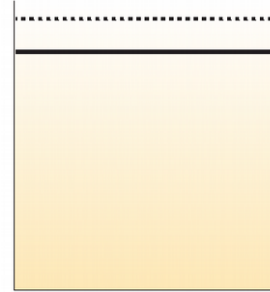
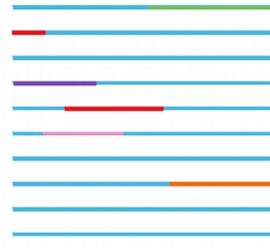




## Genetic Hitchhiking (Sweeps)



## Background Selection



# What explains variation in neutral diversity?

Synonymous  
substitution rate



Gene density



Recombination rate

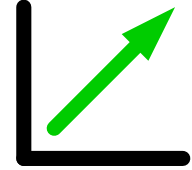


Non-synonymous  
substitutions

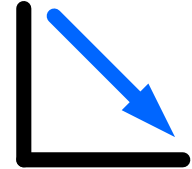


# What explains variation in neutral diversity?

Synonymous substitution rate



Gene density



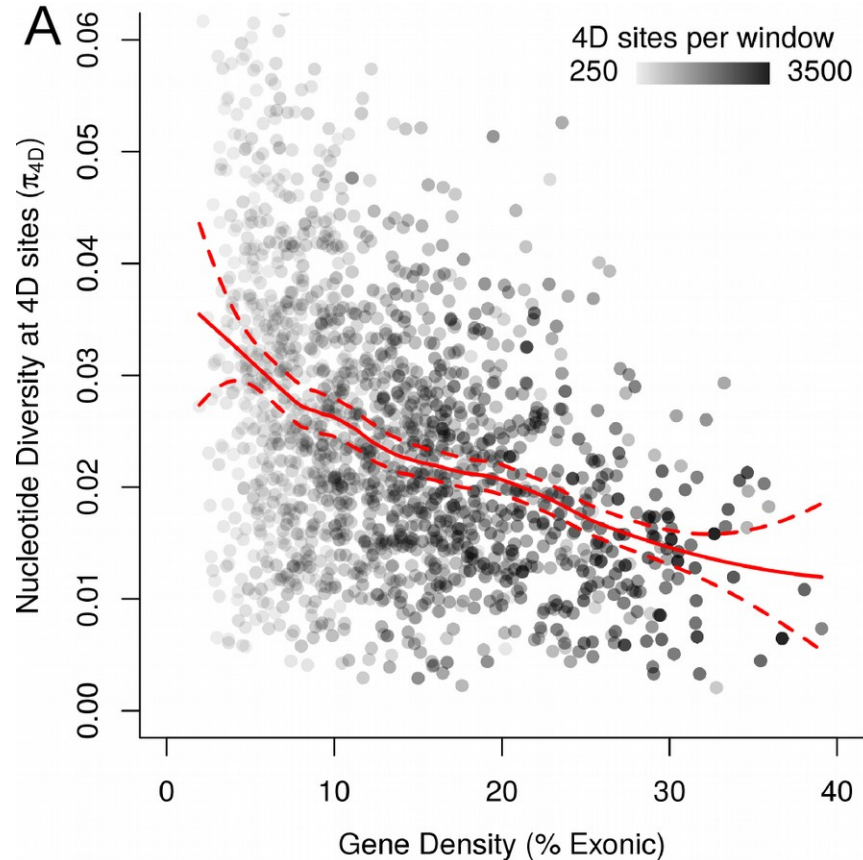
Recombination rate



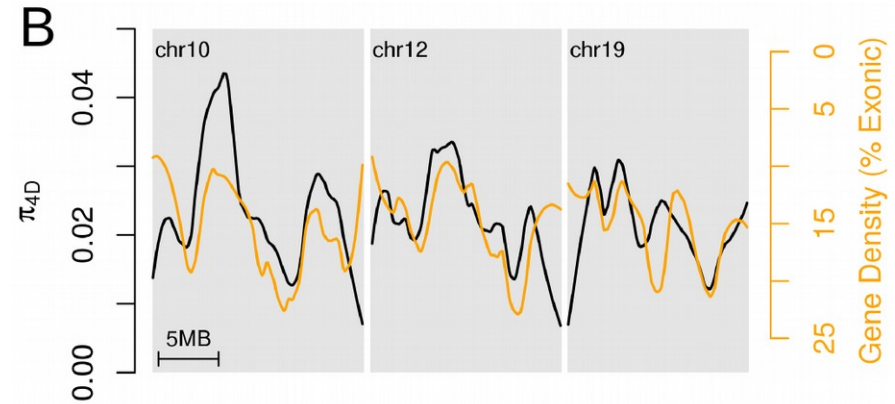
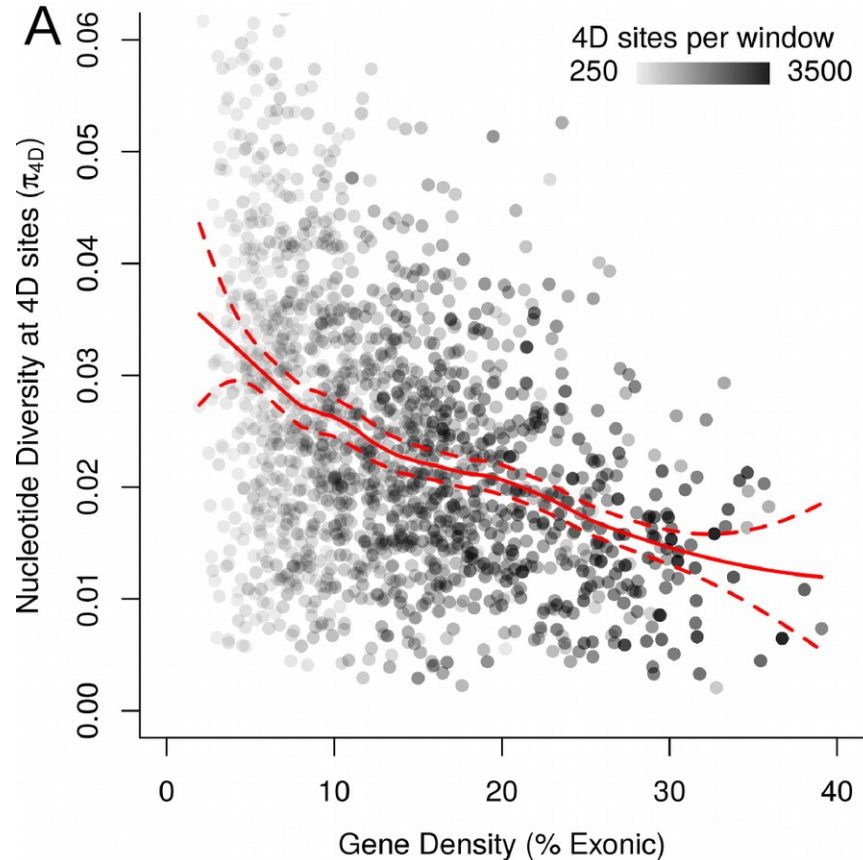
Non-synonymous substitutions



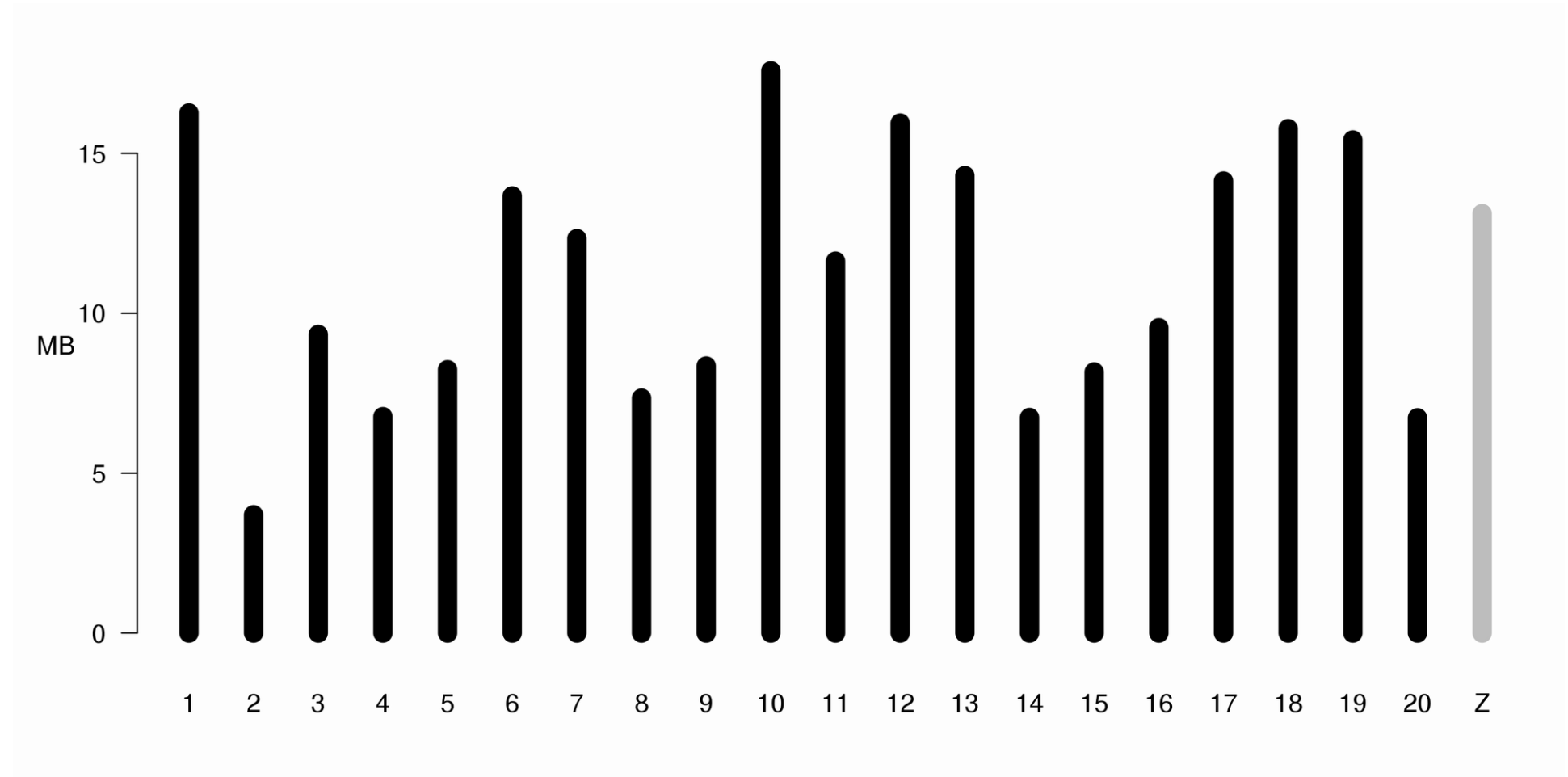
# Gene density is highly predictive of neutral diversity



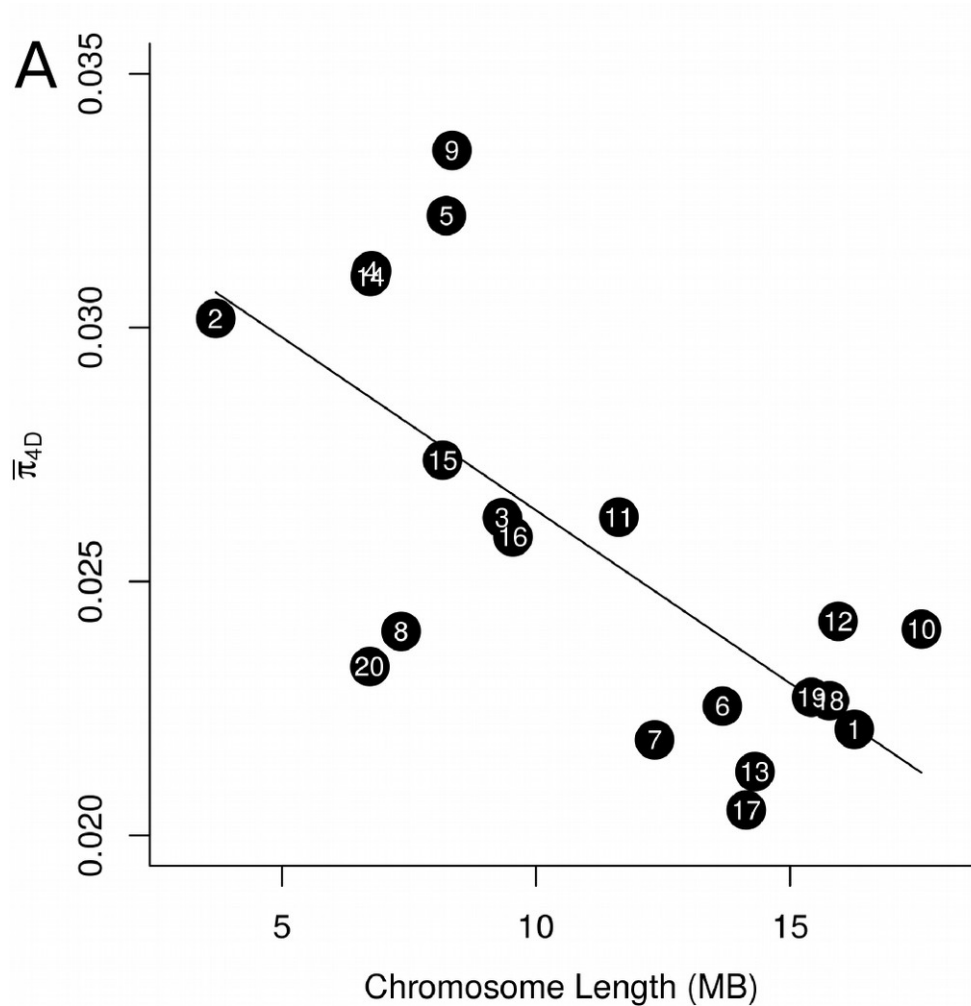
# Gene density is highly predictive of neutral diversity



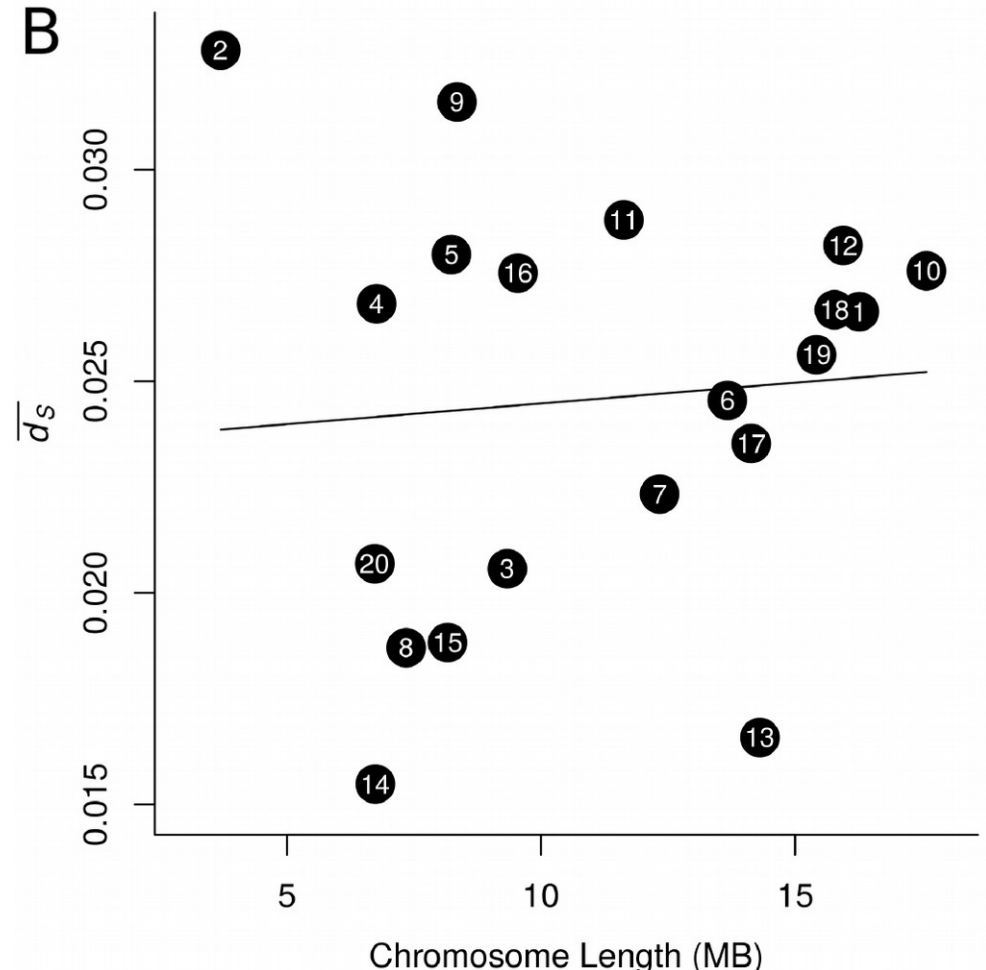
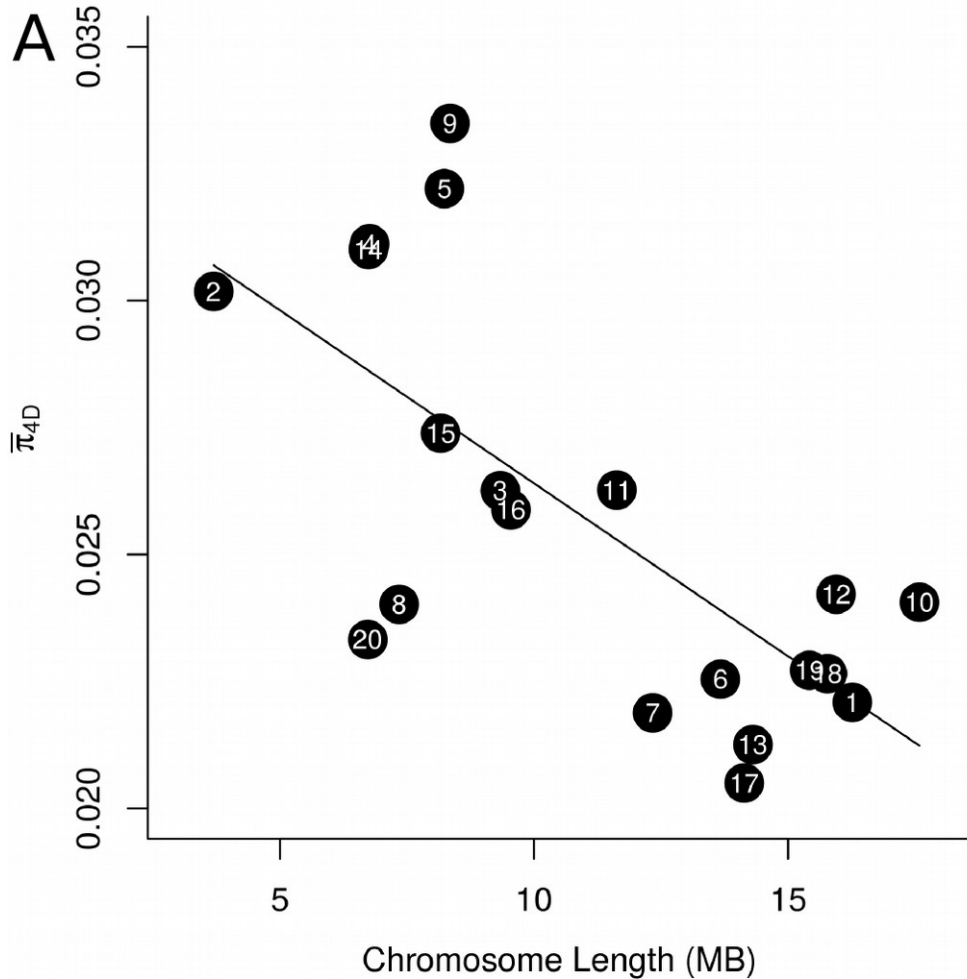
# Chromosome length is also predictive of diversity



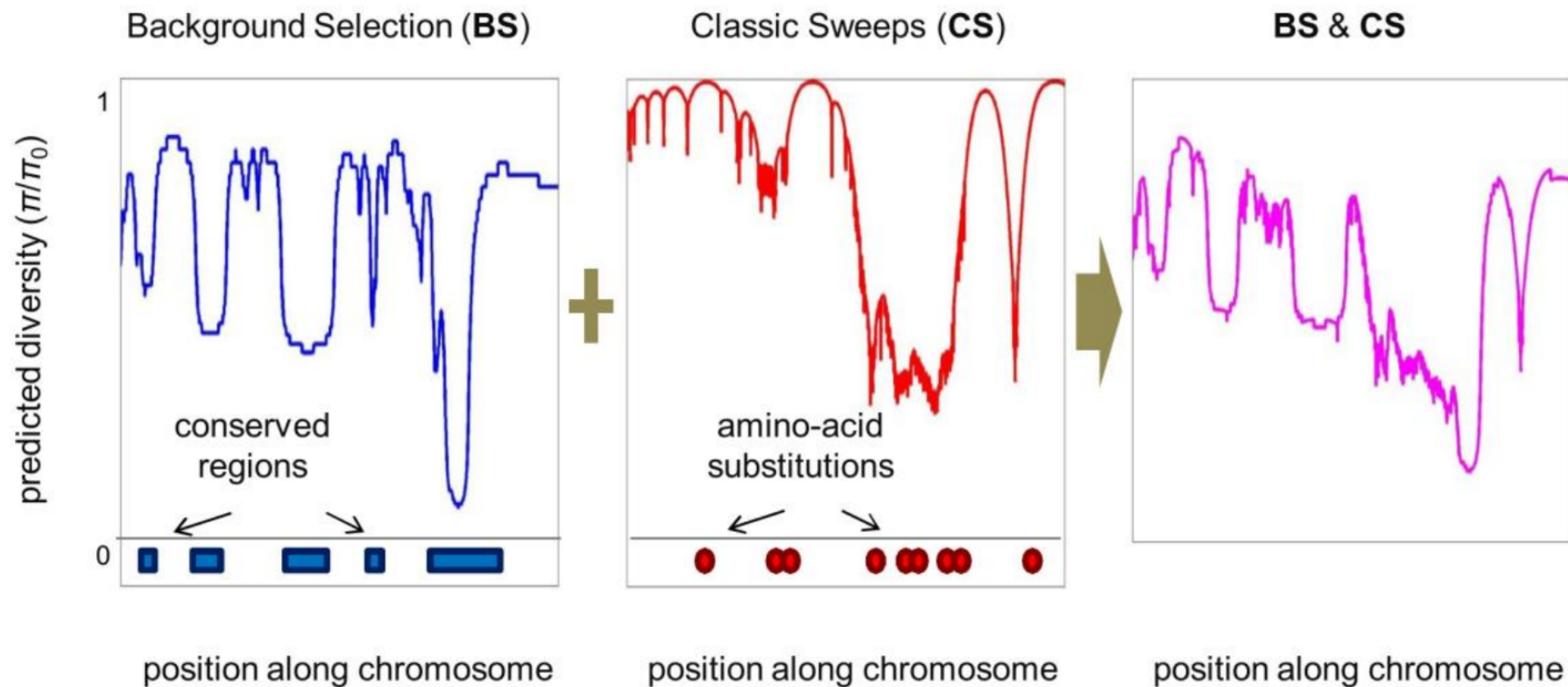
# Chromosome length is also predictive of diversity



# Chromosome length is also predictive of diversity



# Explicit models can predict genomic diversity



But how's this going to help us find speciation genes?

But how's this going to help us find speciation genes?

It isn't

But there ARE ways to better study species barriers using  
genomics